THE ECOLOGY OF MACROMYCETES IN ROADSIDE VERGES PLANTED WITH TREES.

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II

Peter-Jan Keizer

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Proefschrift
ter verkrijging van de graad van doctor
in de landbouw- en milieuwetenschappen,
op gezag van de rector magnificus,
Dr. H.C. van der Plas,
in het openbaar te verdedigen
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Landbouwuniversiteit te Wageningen.

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"De hedendaagse architectuur, in stedebouw zowel als in de weg- en waterbouw, heeft de aansluiting op de menselijke maat en op de polsslag van culturele ontwikkelingen verlaten. Alles wat er nu gebeurt bestaat uit een meer dan honderdvoudige vergroting van een ontwerp op schaal. De ware grootte van de ontwerpen is onafzienbaar geworden. Niemand is in staat om deze megalomanie te beheersen, want al zou er een planoloog bestaan die zijn vak verstaat en die zijn verantwoordelijkheid beseft, dan mist hij nog de historische distantie die nodig is om deze buitenmaatse ontwikkelingen te overzien, laat staan te beoordelen. De ontwerpers volstaan met een verwijzing naar hun deskundigheid die uit een papieren bevoegdheid bestaat die lang geleden, ver weg van de werkelijkheid, op grond van een schoolwerkstuk verleend is."

Gerrit Noordzij, 1990. Woorden aan de dijk. In: Attila op de bulldozer - Rijkswaterstaat en het rivierengebied. G.A. van Oorschot, Amsterdam.

CIP-GEGEVENS KONINKLIJKE BIBLIOTHEEK, DEN HAAG

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ISBN 90-5485-131-7
Trefw.: paddestoelen; wegbermen.

onmogelijk.

Anoniem, 1984-1987. Verslag van het landelijk vitaliteitsonderzoek, Staatsbosbeheer.

6. Een kleiner aantal, geselecteerde taxonomische periodieken waarin het toegestaan is nieuwe taxa te publiceren, zal leiden tot een overzichtelijker situatie in de taxonomie.

7. Bij fungi die zeldzaam zijn en/of in discrete, ver van elkaar gelegen biotopen groeien, kan een beperkte verspreidingscapaciteit een probleem vormen voor het voortbestaan van de soort.

8. De begrippen r- en K-selecte strategie worden ten onrechte op ectomycorrhizafungi toegepast.

MacArthur, R.H. en Wilson, E.O., 1967. The theory of island biogeography. Princeton university press, Princeton, New Jersey.

Dighton, J. en Mason, P.A., 1985. Mycorrhizal dynamics during forest development. In: Moore, D. et al. (eds.) Developmental Biology of Higher Fungi. Brit. Mycol. Soc. Symp. 10: 117-139.

9. Niet alleen voor stadsuitbreidingen en wegenaanleg, maar ook ten behoeve van de stichting of uitbreiding van natuurreservaten zou onder bepaalde voorwaarden grond onteigend moeten kunnen worden.

Errata belonging to: Keizer, P.J., 1993. The ecology of macromycetes in roadside verges planted with trees. -> = to be replaced by

p. 14 l. 7 for an identification to be certain -> to ascertain an identification,
p. 14 l. 9 has had to be spend -> had to be spent
p. 15 l. 6 the numbers of mycorrhizas and eventually -> mycorrhizas and possibly
p. 15 l. 36 influencing -> causing
p. 26 l. 21 Biplot ... -> Ordination diagram in which the positions of environmental variables and of the plots are presented.
p. 29 l. 12 Idem.
p. 30 l. 2 ... of the specific epitheton. -> ... of the specific epitheton (explained in appendix 1, p. 279).
p. 35 l. 14 strong -> strongly
p. 35 l. 14 which are not always possible to remove ... -> which cannot always be removed
p. 37 l. 1 ... green plants. -> ... green plants occurring in roadside verges planted with Beech.
p. 37 l. 1 Westhoff & Van der Maarel. -> Westhoff & Van der Maarel (1973).
p. 54 l. 40 rised -> rose
p. 55 l. 8 canocical -> canonical
p. 58 l. 19 summerized -> summarized
p. 58 l. 39 erytrhinus -> erythrinus
p. 59 l. 8 mesopheum -> mesophaeum
p. 60 l. 7 Biplot ... -> Ordination diagram in which the positions of environmental variables and of the plots are presented.
p. 61 l. 6 both of them -> both
p. 61 l. 16 Idem
p. 62 l. 20 nitropilous -> nitrophilous
p. 65 l. 29 relative large -> relatively great
p. 65 l. 36 large -> high
p. 82 l. 2 (and following pages:) verge verges -> verges
p. 82 l. 37 If the certain ... -> If the ...
p. 83 l. 20 meteolrological -> meteorological
p. 91 l. 6 obligatory -> obligatorily
p. 102 l. 2 base -> basis
p. 103 l. 10 organical -> organic
p. 107 delete last two lines
p. 109 l. 3 due to a large quantity of -> due to much
p. 111 last line: or a relic of *Russula delica* ... -> or a relic of formerly forest types richer in macromycetes (hypothesis 4). Similar conclusions can be drawn from a comparison with mycocoenoses in the Hungarian Luzulo-Fagetum, investigated by Bohus & Babos (1960), where *Lactarius vellereus* and *Russula delica* ...
p. 114 l. 21 + 24 relative -> relatively
p. 117 l. 1 *sylvaticus* -> *sylvatica*
p. 142 l. 32 last et al. -> Last et al.
p. 142 l. 43 sqq. ± -> approx.

p. 155 after l. 7 add: Fungi growing on wood or on other accidentally present substrata (other fungi, insects, dung, feathers, burnt ground) were excluded from this study. The species that were excluded are listed in table 13.
p. 157 l. 6 relative -> relatively
p. 158 l. 2 some exceptions will be discussed above -> some exceptions have been mentioned above (section II 2, p. 155)
p. 159 l. 26 significant -> significantly
p. 162 l. 1 ectomycorrhizal -> saprotrophic
p. 164 l. 34 bach -> end
p. 165 l. 16, 17 unsignificant -> insignificant
p. 174 l. 14 add: Species were excluded from analysis in this study because of their occurrence on wood or substrata that were only accidentally present in the investigated habitat.
p. 176 l. 20 of the spores and Q indicates -> of the spores and Q indicates
p. 176 l. 22 natural size -> 0.8x natural size
p. 249 l. 10 replace by: Table 2. Numbers of differential and indifferent fungal species for Dutch forests dominated by Beech and Oak and for road-side verges with these trees.
p. 253 l. 21 eventual -> actual or potential
p. 254 (2nd) should be numbered 254a
p. 254a l. 1 factors particularly -> factors in the humus layer particularly
p. 256 l. 2 winterhoff -> Winterhoff; publishers -> Publishers
p. 259 after last line, add: Heij, G.J. & Schneider, T., 1991. Dutch programme on acidification. Eindrapport tweede fase Additioneel programma verzuringsonderzoek. Rapport no. 200-09. RIVM, Bilthoven, 250 pp.
p. 263 l. 13 71247-256 -> 71: 247-256
p. 267 l. 20 Weeda, E. 1983. -> Weeda, E. 1983. Over de plantengeografie van Nederland.
p. 279 l. 9 gras -> grasslands
p. 279 l. 10 add: %Fag and %Que refer to the percentage of *Fagus*- and *Quercus*-plots in which the species was found.
p. 288 after l. 25 Innovation phase: phase in which the information of the propagule bank is mobilized and maybe enriched. Succession series usually start with the innovation phase.

Stellingen

behorende bij het proefschrift
"The ecology of macromycetes in roadside verges planted with trees".

1. De mycoflora in met bomen beplante wegbermen op schrale bodem kan een indruk geven hoe de mycoflora in natuurlijke bossen met dezelfde boomsoort op eenzelfde bodemtype er vroeger uit gezien kan hebben.
Dit proefschrift.

2. Bij toenemende eutrophiëring van de bodem verdwijnen de aan één boomsoort gebonden ectomycorrhizasymbionten het eerst.
Arnolds, E. 1985. Veranderingen in de paddestoelenflora (mycoflora). Wet. meded. K.N.N.V. 167; Dit proefschrift.

3. Diverse soorten paddestoelen hebben hun laatste groeiplaatsen in Nederland in met bomen beplante wegbermen. Voor het behoud van deze soorten is bescherming en een juist beheer van deze plaatsen essentiëel.
Dit proefschrift.

4. Er wordt te weinig aandacht geschonken aan de relaties tussen de morfologie van ectomycorrhiza's en de oecologie van de betrokken schimmelsoorten.
Agerer, R., 1987-1991. Colour atlas of ectomycorrhizae. Einhorn verlag, Munich.
Ingleby, K., Mason, P.A., Last, F.T. en Fleming, L.V., 1990. Identification of ectomycorrhizas. ITE research publication no. 5.

10. Het is geen wonder dat veel Nederlanders hun vakantie liever in het buitenland dan in eigen land doorbrengen, gezien de verregaande landschappelijke onttakeling en het (mede daardoor) verdwijnen van regionale verschillen in het Nederlandse landschap.

11. Oude (half)natuurlijke ecosystemen met een grote biodiversiteit zijn evenmin na te maken als oude cultuurmonumenten of een oud, harmonieus landschap.

12. Invulling geven aan de "ecologische infrastructuur" zal leiden tot een leuk aangekleed landschap, nauwelijks tot een vergroting van biologische waarden in dat landschap.
Ministerie van Landbouw en Visserij, 1990. Natuurbeleidsplan.

13. De landelijke tafereeltjes afgebeeld op pakken vanillevla, aardbeienvla, enz., vormen een schril contrast met de milieuvijandige industriële vervaardiging van inhoud en verpakking en zijn daarom boerenbedrog.

14. Geplaatst tegen het huidige lawaainiveau in vele gebieden in Nederland is de fietsbel als veiligheidsvoorziening een anachronisme.

Voorwoord

De Landbouwuniversiteit Wageningen heeft dit onderzoek financieel mogelijk gemaakt.

Vele personen hebben bijgedragen aan de totstandkoming van dit proefschrift. Ik wil allen hiervoor hartelijk bedanken.

Allereerst en vooral wil ik Eef Arnolds bedanken voor zijn essentiële bijdragen aan dit onderzoek, als dagelijks begeleider, als geduldig en minutieus verbeteraar van mijn manuscripten, als copromotor, als vraagbaak en discussiepartner, en dat alles in een sfeer van warme vriendschap.

Prof. Dr. Jan J. Barkman zou mijn promotor zijn. Geen ander zou deze functie met meer recht hebben kunnen bekleden; hij heeft immers de fundamenten van de mycocoenologie in Nederland gelegd. Onverwachts echter overleed Jan Barkman in september 1990. Ik wil hem vanaf deze plaats bedanken voor zijn stimulansen en de nuttige discussies.

Gelukkig heb ik Prof. Dr. Ir. R.A.A. Oldeman bereid gevonden op te treden als promotor. Ook hem ben ik erkentelijk voor zijn inzet en de opbouwende kritiek die hij mij op de manuscripten gaf.

Aad Termorshuizen heeft veel tijd besteed aan het kritisch doorlezen van de manuscripten en deze voorzien van vele nuttige suggesties en aanvullingen. Heel veel dank hiervoor.

De studenten Arno de Bruin, Pina Dekker, Karla Everts en Marcel Reekers hebben belangrijke bijdragen aan het onderzoek geleverd. Arno en Karla hebben veel werk verricht bij het uitzoeken en tellen van beukenmycorrhiza's alsmede bij de interpretatie van de gegevens. Marcel heeft een vegetatiekundige analyse gemaakt van veel van de proefvlakken die bij dit onderzoek waren betrokken en een belangrijke evaluatie van de verschillen tussen eiken- en beukenbermen gepresenteerd. Pina heeft een studie gemaakt van de vitaliteit van de bomen in een groot aantal eiken- en beukenbermen, gebruik makend van vele vitaliteitsparameters. Zij heeft de vitaliteit van de bomen in verband gebracht met enkele physiologische boomkenmerken zoals de gehaltes van een aantal ionen in de bladeren. Hartelijk dank voor jullie inzet.

Aad Termorshuizen en André Schaffers wil ik bedanken voor hulp bij allerlei computerbewerkingen. Aad ook hartelijk dank voor de gastvrijheid tijdens het computerwerk in Wageningen.

Thom Kuyper wil ik bedanken voor zijn hulp, nuttige tips en uitgebreide discussies op het gebied van de taxonomie van de paddestoelen. Vaak heb ik gebruik mogen maken van zijn uitgebreide kennis van de Agaricales, speciaal van het geslacht *Inocybe*.

De heer Dr. E. Kits van Waveren ben ik erkentelijk voor zijn hulp bij de determinatie van enkele soorten van het geslacht *Psathyrella* en bij de beschrijving van een nieuwe soort in dit geslacht.

Dank ook aan de heer Norbert Arnold (Regensburg) voor zijn determinaties van en gedachtenwisseling over enige soorten van het geslacht *Cortinarius*.

Het personeel van de Provinciale Waterstaat van Drente wil ik gaarne danken voor het jaren achtereen uitvoeren van een aantal beheersvormen in de berm langs het Oranjekanaal te Odoornerveen ten behoeve van het veld-experimenteel onderzoek naar het effect van diverse beheersvormen.

Dank zij subsidies verstrekt door het Johanna Westerdijkfonds ben ik in staat geweest om het IV Internationaal Mycologisch Congres te Regensburg en het XI Europees Mycologisch Congres te Kew te bezoeken.

Marian Stevens en Gerda Weijenberg, ook jullie hartelijk dank voor het typen en verbeteren van de teksten.

I am greatful to Mr. Alex Weir (Cleveland) who suggested many linguistic improvements.

Mijn grote erkentelijkheid gaat uit naar het personeel van het Biologisch Station van de Landbouwuniversiteit te Wijster voor de gastvrijheid die aan mij is verleend, ook gedurende de periode dat mijn feitelijke aanstelling al voorbij was.

Last but not least wil ik graag mijn ouders, en ook Rosita, bedanken voor hun steun, begrip en stimulans voor iemand die jarenlang paddestoelen in wegbermen heeft bestudeerd.

Hieronder wil ik enkele woorden wijden aan persoonlijke indrukken die ik gedurende dit onderzoek kon opdoen.

Dit onderzoek was een nogal eenzame aangelegenheid. Gelukkig waren er geregeld studenten of andere belangstellenden die mee wilden. Ook waren buurtbewoners of toevallige passanten vaak heel belangstellend te vernemen wat iemand ertoe brengt jarenlang paddestoelen in wegbermen te zoeken. Dit, gevoegd bij de mooie omgeving van sommige proefvlakken en de mycologische verrassingen die er steeds weer te beleven waren, hield me op de been.

Duidelijke minpunten waren het verkeer dat in wisselende intensiteit langs raasde, zelfs over de zg. rustige wegen, en de verpletterende lelijkheid van het agrarische landschap in allerlei delen van Drente waar één of meer landinrichtingen hebben plaats gevonden. Helaas beslaat zulk landschap een groot deel van de provincie. Deze kale saaiheid in combinatie met het practisch altijd aanwezige lawaai van landbouwmachines en de eveneens vrijwel permanente stank van gier maakt dat het verblijf in een modern agrarisch landschap geen pretje is.

Peter-Jan Keizer

CONTENTS.

- aan mijn ouders -

1. GENERAL INTRODUCTION

The aims of this study were 1. to produce a qualitative and quantitative inventory of macromycetes in different types of roadside verges planted with trees and to assess the degree of similarity, or otherwise, of the macromycete flora of this habitat, through the identification of characteristic features, to other macromycete associations; 2. to investigate and identify the primary environmental variables controlling the observed patterns in macromycete species composition; 3. to compare the results observed with data from forest communities with the same dominant tree species; 4. to explain differences between the mycoflora of roadside verges and corresponding forest types in an ecological context and 5. to study the influence of different management practices on the mycoflora in the roadside verge habitat.

1.1 *Scope of this study*

This study forms part of the so-called mycocoenological research, carried out at the Biological Station, Wijster and founded in the Netherlands by Barkman (Barkman 1964), in which the macromycetes of various vegetation types in Drente were studied qualitatively (species composition) and quantitatively (numbers of carpophores). To date, studies have been made of the following habitat types: juniper shrubs (Barkman 1976), grasslands and heathlands (Arnolds, 1981, 1982), oakwoods (Jansen, 1984), beechwoods (Opdam, 1991), birchwoods (Jalink & Nauta, 1984), and alder and willow forests (Keizer, 1985, Keizer & Arnolds, 1990).

Some evidence was presented that in some roadside habitats a rich mycoflora can be present (Arnolds, 1968; Reijnders, 1968; 1974). These observations were restricted to roadside verges with a row of trees in the alluvial clay area near the Rhine and they indicated that some fungal species are predominantly found along roads, in particular ectomycorrhizal species. Only some incidental, unpublished observations, suggest the presence of macromycetes in roadside verges in the sand area.

Roadside verges are a common and important feature in the Netherlands. With the exception of the built-up areas roads occupy almost 1% of the land surface of the country and when roadside verges are included this figure is almost 2% (table 1). Because of their narrow ribbon-shape and their distribution in a more or less regular network all over the country, roads are a dominant element in the landscape.

In the Netherlands and especially in the diluvial sand plateau in the province of Drente many roadside verges are planted with trees. Common Oak (*Quercus robur* L.) is the most commonly planted species (approx. 70 % of the planted roadside verges; fig. 1), less frequently European Beech (*Fagus sylvatica* L.; approx. 20 %; fig. 2) and occasionally other tree species are used.

	Length of metalled + un-metalled roads (km)	Estimated surface of roadside verges (ha)	Length of canals (km)	Estimated surface of verges/slopes of canals (ha)
Netherlands	70000	35000	2500	2500
Drente	5000	2500	500	500

Table 1. Length and surface (rounded) of roads and canals and their verges in the Netherlands and Drente (after anonymus, 1992; pers. comm. C.B.S., 1991).

Fig. 1. Roadside verge planted with Common Oak (*Quercus robur*; plot Q 33; trees middle aged; situated in open landscape).

Roadside verges planted with trees form a special habitat because
1. they are strongly influenced by human activities, e.g. by significant disturbance of the soil profile during road (re)construction, by farming practice in the adjacent farmlands, by passing traffic on the road, and by management measures in the roadside verge vegetation itself (e.g. mowing);
2. the plant communities combine aspects of both forests (by the presence of ectomycorrhiza forming and litter producing trees) and grasslands (because of the grassy, often regularly mown vegetation);
3. they have a characteristic microclimate, different from both forests and open grasslands.

In a roadside verge with planted trees some ecological variables are simple and constant compared to forests: all trees in a roadside verge belong to a single species, they are of equal age and are planted at approximately equal distances from each other (fig. 3). Some variables are more complex. In almost all roadside verges a gradient occurs from a strongly influenced strip along the road to minor influence a few metres from the road. The variation between roadside verges is much larger than in oak forests in Drente, for

instance with regard to the exposure of the road (in open landscape or in forests), thus strongly influencing microclimate and litter accumulation, the type of management and the influence from the adjacent agricultural land. This variation can be regarded as a set of (uncontrolled and unintended) field experiments and can provide useful information

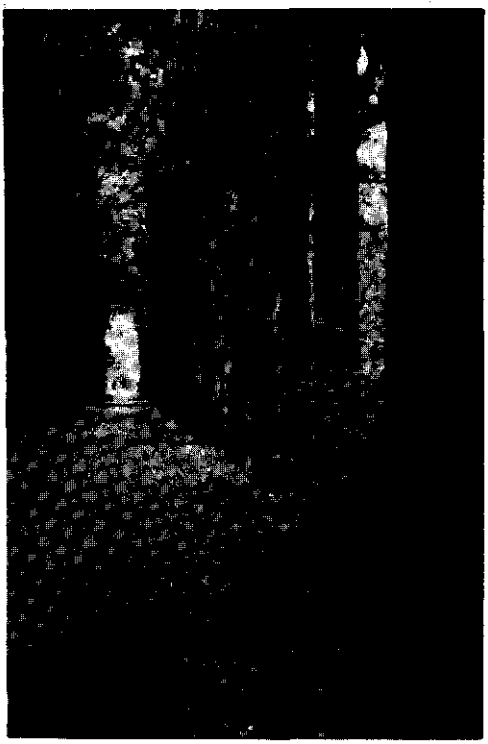


Fig. 2. Roadside verge planted with Beech (*Fagus sylvatica*; plot F32; old trees; situated in a forest).

on the relations between vegetation, mycoflora and environmental variables.

In this study an attempt was made to cover the variation of ecological variables outlined above in a set of mycocoenological plots. Plots were chosen in roadside verges planted with Beech (23 plots) and with Oaks (53 plots), all on sandy to loamy soil, but widely varying with regard to soil fertility, judged from the properties of the green plant

vegetation. Data on the management of the vegetation in the plots were brought together. Beech and Oak plots were chosen in open landscape (denoted as "open"; fig. 1) and inside forests ("shady"; fig. 2), and nine Oak plots were also established with forest on one side ("half shady"). The open plots were almost all along roads with a metalled surface, but the shady plots were along roads with either a metalled surface or an unmetalled surface. Among the Oak plots a wide variation was present in the age of the trees, ranging from approx. 15 to 140 years old.

1.2 *Mycocoenology*

The quantitative and qualitative study of the mycoflora in plots (mycocoenology)

differs profoundly from similar studies on green plants (phytocoenology). For an extensive survey of mycocoenological methods see Arnolds (1981).

1. Fungi are heterotrophic organisms and are therefore dependent on organic material. In the present study a distinction was made between ectomycorrhizal fungi on the one hand and saprotrophic and parasitic fungi on the other. The parasitic fungi (on trees, insects or other fungi) are of minor importance in the roadside verges. However, recent studies have indicated that the distinction of these functional groups may be not as sharp as often assumed, in view of the capability of some ectomycorrhizal fungi to reduce some organic substrates, mainly proteins (Read, 1991; Dighton et al, 1986). The non-mycorrhizal fungi may grow on different substrates: saprotrophs on humus, litter, wood, dung and sporocarps of other fungi, parasites on arthropods and fungal sporocarps, and associated in some way with bryophytes.

In addition to these general relationships with other organisms, some fungi may show more specific associations with plant taxa, e.g. a preference of a mycorrhizal fungus for a tree species or a preference of litter of certain plant species.

In most published mycological studies the macromycete species have been investigated in various phytocoenoses (e.g. Barkman (1976), Arnolds (1981), Jansen (1984), Bohus & Babos (1960, 1967), Haas (1932), Lisiewska (1963, 1965), Thoen (1970-71), and the mycocoenoses were considered as functional units within phyto- or, preferably, biocoenoses. A different approach was developed by Darimont (1973), who considered fungal communities as independent units and emphasized this view by proposing a special terminology for a hierarchic system of fungal communities.

In this study assemblages of green plants, mycorrhizal fungi and saprotrophic fungi in the plots were studied and classified independently and compared with each other in order to determine the degree of agreement between these three functional groups. A formal, independent classification of fungal assemblages was not considered to be useful.

2. Mycocoenology is dependent on observations of sporocarps. The vegetative part of the fungus, the mycelium, dwells in the substrate (soil, wood, dung, etc.), and is therefore hardly accessible to study. In addition, the mycelia of many fungi cannot (yet) be identified. It is not certain to what extent the number or production of sporocarps reflect the biological activity of the fungus in the ecosystem (Dahlberg, 1991). Further, some species produce only hypogeous sporocarps or no sporocarps at all. An example is the study of Vogt et al. (1981), who found that the above-ground sporocarp production was only 7% of the total sporocarp production in a mature stand of *Abies amabilis* (Dougl.)Forbes. However, in the Netherlands hypogeous species play probably a less important role.

Several abundance values to express the importance of the fungal species have been proposed. Many authors have used different scales for the estimation of sporocarps (for a review, see Arnolds, 1981, 1992), all more or less logarithmic and analogous to the scales of estimation of abundance and cover, widely used in phytocoenology. In this study the carpophores were counted during each visit, except for a few extremely abundant species with very small sporocarps which were estimated, e.g. *Mycena polyadelpha*. With regard to these figures the maximum number per visit was considered as an expression of the potential performance of the species in the study-period of three years. These values were recalculated to 1000 m^2 and for the analysis of the data the natural logarithm of these numbers was taken. Counting of carpophores also enables an estimation of the annual sporocarp production of each species by multiplying the average

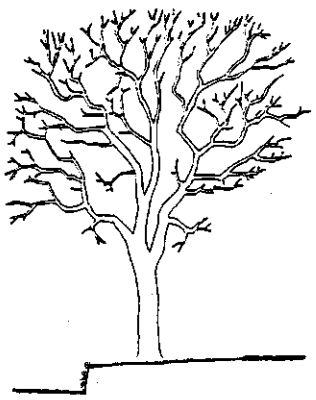


Fig. 3. Schematic sketch of the roadside verge habitat.

dry weight of a species by the average total number of carpophores per year during the period of the study.

3. Due to the generally short life time of sporocarps (mostly a few days to weeks) repeated counts in plots are necessary. The proportion of uncounted species depends on the frequency of plot inspections. In this study the plots were visited at 3 to 4 week intervals, so that the large majority of fleshy sporocarps (including almost all ectomycorrhizal species) will have been observed, but a considerable proportion of thin-fleshy, ephemeral sporocarps (mainly saprotrophs on litter) may have been missed. In addition, small sporocarps are more easilyoverlooked, especially among tall and dense herbs. This partly explains the fact that in this study many saprotrophic species were found less frequently than the mycorrhizal species.

4. Each species forms sporocarps in a certain period of the year, some being vernal, others early or late autumnal, and a few occurring in winter. The sporocarps of some species can be seen (almost) every year in the same locality but others appear irregularly with intervals of many years (Barkman, 1987). Their occasional appearence on exactly the same spot indicates that the mycelium has persisted during the years that sporocarps were absent. These features, together with the limited life span of sporocarps (2), make intensive examination of plots over a period of several years essential.

Mycocoenological studies carried out between five and seven years (Barkman, 1976, Arnolds, 1981) indicate that the total numbers of species observed are still increasing after 5 years, although the rate of increase levels off after three to five years. This increase may be caused by 1. the very irregular fruiting of some species permanently present in the investigated community; 2. the accidental establishment of species in the investigated community which may survive one or a few years and may disappear afterwards, either because the habitat for the species is suboptimal or the substrate is ephemeral (e.g. dung, burnt wood, etc.); 3. changes in the environment due to a relatively rapid succession in the vegetation in some habitats, e.g. grasslands, roadside verges, marshlands, dune-vegetation, young forest stands). Here the mycoflora changes

along with the changes in the vegetation.

The plots of the present study were visited at intervals of 3 to 4 weeks during the autumn (August to November) in a period of three successive years (1986, 1987, 1988).

5. In our region, the identification of green plants usually offers no substantial problems. Complete and up to date floras of vascular plants and bryophytes are available. However, the situation is completely different for macromycetes. It is often necessary to study microscopical characters for an identification to be certain and revisions and keys for different taxonomical groups are scattered in the mycological literature. For some groups modern revisions are lacking. Therefore, a large proportion of time has had to be spend during this research to collecting, describing, microscopical study and presentation of representative samples of the fungi in the plots.

In the roadside verges that were studied 439 species were found. They are listed in appendix 1. Genera which contain many critical species (e.g. *Cortinarius, Hebeloma, Inocybe, Psathyrella, Russula*) were well represented in the roadside verges. Many of the accepted species that were believed to be rare in the Netherlands or critical, were described in order to document the applied taxonomic concepts. In older mycocoenological studies a considerable part of the data has indeed become difficult to interpret, due to the lack of taxonomical accounts.

1.3 *Mycorrhizas*

The majority of plant species grow in a symbiotic association with fungi. The association is located in the root system of the plant. The permanent association of roots with hyphal fungi is called a mycorrhiza (Frank (1885) ex Harley & Smith, 1983). It has been demonstrated in many experiments that the plant-host receives water and mineral nutrients from the fungus and that the fungus obtains carbohydrates from the root. The association is therefore considered as a mutualistic symbiosis.

Several kinds of mycorrhizas can be distinguished (Harley & Smith, 1983): Vesicular-Arbuscular (VA-mycorrhiza), Ectomycorrhiza, Ectendomycorrhiza, Arbutoid, Monotropoid, Ericoid and Orchid mycorrhizas. The first two types of mycorrhizas are the most widespread. In VA-mycorrhizas the fungus penetrates host root cells, forming characteristic structures: vesicles and arbuscles; macroscopic fruitbodies are absent. In the temperate zone they predominate in herbaceous plants.

In ectomycorrhizas the fungal hyphae penetrate the root into the cortex but do not penetrate the cells. The root tips are surrounded by a mantle of fungal tissue. Most, but not all ectomycorrhiza forming fungi form macroscopic sporocarps. Under natural conditions, many important forest trees (e.g. *Quercus, Fagus, Pinus, Betula*) are always associated with ectomycorrhizal fungi and usually the large majority of the root tips are surrounded by fungal sheaths. Many fungal species (in the Netherlands approximately 800 species (Arnolds & de Vries, 1989)), especially of the Basidiomycetes, are capable of forming ectomycorrhizal symbioses. Several fungal species can be present on the roots of a single tree.

In the present study the ectomycorrhizas in some roadside verges planted with Beech trees and with Oaks were investigated. The chosen plots varied widely with regard to plant species composition and in numbers of sporocarps and species composition of ectomycorrhizal fungi, but were similar with regard to tree age and exposition. In the Oak plots various management treatments were applied. In the plots samples were taken in which the number, vitality and diversity of mycorrhizal root tips were determined. The aim was to detect whether the variation found in ectomycorrhizal sporocarp numbers

could be correlated with (explained by) these properties of the mycorrhizas. The results are presented in chapter 2 and 7.

Sporocarps of ectomycorrhizal fungi can only be produced if the underground mycelium and the mycorrhizas are present. Therefore presence of sporocarps of ectomycorrhizal fungi may offer an opportunity to obtain an approximate assessment of the numbers of the numbers of mycorrhizas and eventually their species composition. However, it should be borne in mind that:

1. several ectomycorrhizal fungi form hypogeous or inconspicuous sporocarps, which are easily missed, or no sporocarps at all;
2. the number of sporocarps or sporocarp biomass produced related to the number of mycorrhizal root tips may vary among different fungal species;
3. the conditions for development of sporocarps may differ from those for the development of mycorrhizas;
4. there is considerable fluctuation in numbers of sporocarps in different years, due to climatic variation.

Therefore, the numbers and species composition of carpophores do not necessarily reflect those of mycorrhizas. Termorshuizen (1990) and Taylor & Alexander (1989) found no significant correlation between mycorrhiza and sporocarp numbers in stands of Scots pine (*Pinus sylvestris* L.) and Sitka spruce (*Picea sitchensis* (Bong.)Carrière). On the other hand, Jansen & de Nie (1988) found significant positive correlations between numbers of sporocarps and mycorrhizas in Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands.

1.4 *Decline of ectomycorrhizal fungi.*

Recently a sharp decline in the numbers of ectomycorrhizal fungi in the Netherlands was reported (Arnolds, 1985, 1988b, 1992c). This decline is especially well-documented for some striking species such as *Cantharellus cibarius* and stipitate hydnaceous fungi (van Dobben & Jansen, 1987 and Arnolds 1989a respectively), but it has been demonstrated that many other species, which are in part less well-known, have undergone a similar decline, e.g. members of the genera *Cortinarius, Tricholoma, Boletus (s.l.), Russula* (cf. Arnolds, 1989b). Similar trends were found in some other European countries, e.g. Germany (Derbsch & Schmidt, 1987) and Czechoslovakia (Fellner, 1988). These studies on the decline of macromycetes resulted in national or regional "red data lists", each containing an enumeration of threatened macromycete species. A red data list for the Netherlands was published by Arnolds (1989b). It is suggested, for the Netherlands at least, that indirect effects of air pollution (acidification and N-deposition) are the most important factors influencing the decline of ectomycorrhizal fungi (Termorshuizen, 1990, Arnolds, 1985, Jansen & Dighton, 1990). In the Netherlands the annual deposition of nitrogen is 40-80 kg N ha^{-1} yr^{-1} (van Breemen & van Dijk, 1988; Houdijk & Roelofs, 1991), which is 8 to 16 times the natural background deposition of nitrogen in northern Europe (Emanuelsson et al. (1954), in Ellenberg, 1964). In some places extreme N-deposition values of more than 300 kg N ha^{-1} yr^{-1} have been measured (Jansen, 1989). From various experiments, it appeared that most ectomycorrhizal fungi decreased after application of N-fertilizer (review: Kuyper, 1989).

In the same period a decline of the vitality of several tree species was observed, e.g. Scots pine, Douglas fir, Oak, Beech (Staatsbosbeheer, 1987; Oosterbaan & Leffef, 1987). This decline of vitality is generally ascribed to effects of air pollution. The question arose (Smits, 1984) wether a causal relation existed between the forest die-back

and the decline of ectomycorrhizal fungi, expressed as numbers of mycorrhizas or as numbers of sporocarps. Some authors indeed found a relationship between reduced tree vitality and reduced fruiting of ectomycorrhizal fungi (e.g. Termorshuizen, 1991; Fellner, 1988).

In part of the plots of the present study a remarkably large proportion of the fungal species were ectomycorrhizal, among which many were considered as threatened according to the "red data list" for the Netherlands (Arnolds, 1989b). Many of these species have declined significantly in Oak or Beech forests but apparently have survived in some roadside verges planted with these trees (cf. chapter 5).

In order to detect a possible relationship between species numbers of ectomycorrhizal fungi, some environmental variables and tree vitality, an attempt has been made to determine tree vitality in part of our plots (chapter 2 and 3).

1.5 *Saprotrophic and parasitic fungi*

In the present study the saprotrophic and parasitic fungi were treated separately from the ectomycorrhizal fungi because they play a fundamentally different role in the ecosystem.

The saprotrophic fungi live on various organic substrates, e.g. wood, leaf litter (including small wood fragments and twigs), partly fermented humus, dung, burnt wood, old sporocarps of fungi, feathers. Also the fungi associated with bryophytes were included here, although there is evidence for some species that this association is a parasitic relation (Kost, 1984). Parasitic species include those growing on living plants (often trees, and causing damage to the host), living sporocarps of fungi and insects. The latter functional group was represented by only a few species, e.g. *Grifola frondosa* (Dicks.:Fr.)S.F.Gray, *Nyctalis asterophora* Fr., and *Cordyceps militaris* (L.)Link.

The saprophytes growing on litter and humus and moss-associated species were considered as proper to the studied communities. The other substrates are more or less accidental, often dependent on accidental human or animal activities, and so the fungi occurring on these substrates were considered as alien to the studied communities. In most analyses the alien fungal species were omitted, although their distribution over the plots was studied as well.

Compared to ectomycorrhizal species, relatively few saprotrophs are regarded as threatened in the Netherlands, viz. 47% of the mycorhizal fungi, 27% of the terrestrial saprotrophs and 12% of the lignicolous fungi. However, a large proportion of the fungi characteristic of dry, nutrient-poor grasslands is endangered, viz. 71-86%, depending on the grassland type (Arnolds, 1989c).

The causes of the decline and of the recent threatened status of many fungi characteristic of grasslands on nutrient-poor soils are mainly a result of more intensive agricultural methods where large quantities of fertilizer are applied, the loss of (old) grasslands to arable fields and in large areas "land-reallotments". Still existing nutrient-poor grassland reserves are seriously endangered by deposition of acidifying and fertilizing substances of agricultural and industrial origin and changes in ground water tables (Bakker, 1989).

In this study, many species characteristic of the grassland habitat were found in open situations where the vegetation is grassland-like. It appears that in some roadside verges on nutrient-poor soil a rich grassland mycoflora is present (chapter 2 and 3), with several threatened species. Consequently, this habitat is of high value for these species. A management system directed towards the maintenance or the development of the nutrient-

poor situation will support the species characteristic for this habitat (chapter 7).

1.6 *Succession of ectomycorrhizal fungi*

Recently, succession in communities of ectomycorrhizal fungi during tree growth and forest development has attracted much attention. Mason et al (1983) and Last & Fleming (1985) reported a clear shift in the fungi associated with young (1-6 years old) and older Birches (*Betula* L.). They designated the former as "early stage fungi" and the latter as "late stage fungi" and also reported some physiological differences between the two groups.

Last et al. (1987) presented a model in which it is suggested that the species diversity in stands of trees increases with the stand age until canopy closure is reached. After canopy closure this diversity decreases. This view is supported by the results of Hintikka (1988) and Termorshuizen (1990) in Scots pine-, and Jansen (1991) in Douglas fir plantations. These authors reported much lower species and sporocarp numbers in old stands than in young stands.

Along the roads in the study-area planted trees of various ages (from 15 to more than 100 years old) are present. This offers an opportunity to study the fungal communities under trees of different age classes under similar conditions with regard to the other environmental variables.

Therefore, plots were selected in three age classes ("young": up to 20, "medium": 21-50, and "old": more than 51 years old). The species composition and number of sporocarps were compared. The differences that were found between these age classes were considered as successional stages with increasing tree age. The successional pattern of communities of ectomycorrhizal fungi that was present in the roadside verges differed widely from the results of the authors cited above. An explanation in terms of environmental variables is proposed (chapter 6).

1.7 *Management of the vegetation*

The habitat of roadside verges planted with trees is a combination of environmental characteristics of both grasslands and forests: the herb layer is often dominated by grassland plants and managed like grassland, but at the same time ectomycorrhiza forming trees are present. The vegetation of the roadside verges is usually mown by local authorities, in most cases without subsequent removal of the hay, but sometimes the hay is removed. In many places the upper layer of the soil, including the vegetation, is removed at intervals of 5 to 10 years. Sometimes no management was carried out at all. Some roadside verges were strongly influenced by fertilizers which were applied to the adjacent farmland.

The influence of the management regime on the composition of plant communities has been studied on many occasions, see for instance the survey on grassland management by Bakker (1989). Such data on fungal communities are scarce.

In grasslands mowing or grazing is essential for the maintenance of these communities and this is also true for grassland fungi (Lange, 1982, Sadowska, 1973). The soil fertility, especially available nitrogen compounds, is a key factor determining the species composition of both green plants and fungi in grassland. It has been demonstrated that in unfertilized, old grasslands many characteristic species of macromycetes occur (e.g. Neuhoff, 1949, Arnolds, 1980, 1981). This situation is nowadays almost restricted to nature reserves and most fungal species of this habitat are rare and threatened (Arnolds, 1989b). Fertilizer application in originally nutrient-poor grasslands provokes a

drastic change in species composition and a general decline of many soil inhabiting species (Arnolds, 1989c). At present the remaining nutrient (nitrogen) -poor grasslands are seriously threatened by the effects of atmospheric pollution.

In some forests the influence of fertilization and liming on macrofungi has experimentally been investigated. Its purpose was to simulate the effects of atmospheric pollution (deposition of N-compounds) or to investigate methods to correct effects of (acidifying) pollution (Kuyper, 1989). The sporocarp numbers of only a few mycorrhizal fungi increased after N-fertilizing (e.g. *Paxillus involutus*), but the great majority showed a distinct decrease in numbers after application of either nitrate or ammonium. A similar effect was found after liming, due to an increased decomposition of litter leading to an enhanced release of nitrogen.

On the basis of these studies it was assumed that management practices have a profound influence on the vegetation and mycoflora of roadside verges. Therefore an experiment was set up in a homogeneous site in order to record the changes in the vegetation and mycoflora after various management measures and to compare the results with data on grassland and forest management (chapter 7).

1.8 *Outline of this book*

The communities of fungi and green plants in roadside verges planted with *Quercus robur* and *Fagus sylvatica* are studied in chapters 2 and 3 respectively.

The communities that are distinguished under *Q. robur* and *F. sylvatica* are compared in chapter 4.

The macromycete communities of the roadside verges are compared with those of forests that are dominated by *Quercus* spp. and *F. sylvatica* in and outside the Netherlands in chapter 5.

In chapter 6 the sequence of communities of ectomycorrhizal fungi in roadside verges with Oaks of different ages is studied.

A field experiment to determine the effects of various management treatments on the macromycetes in a roadside verge is described in chapter 7.

In chapter 8 taxonomical notes and illustrations of a number of rare and/or critical macromycete species encountered during the investigations of roadside verges are presented.

The significance of the roadside verge habitat for macromycetes is indicated in chapter 9; some recommandations for protection and maintainance of valuable sites are given. Suggestions for further research are presented.

MYCOCOENOLOGY OF ROADSIDE VERGES PLANTED WITH BEECH TREES (*FAGUS SYLVATICA* L.) IN DRENTE, THE NETHERLANDS.

P.J. Keizer

Summary.

The macromycetes occuring in 23 plots in roadside verges planted with Beech (*Fagus sylvatica* L.) were studied. The plots varied widely with regard to vegetation and exposition. The vegetation of vascular plants and of a number of environmental variables were studied as well. Samples of mycorrhizas were taken from a number of plots. Some different abundance values of the macromycetes were compared.

On the basis of the green plants three vegetation types could be recognized. Using the ectomycorrhizal fungi the plots were divided in a species-poor and two species-rich types. The former did not correspond with a recognized vegetation type but the latter two types corresponded to a limited extent with vegetation types. The two communities that were recognized among the saprotrophic fungi corresponded well with the vegetation types. The better correspondence of communities of vascular plants with those of saprotrophs than with those of ectomycorrhizal fungi indicates that plants and saprotrophs react in the same way on the environmental variables, differing from the ectomycorrhizal fungi. Environmental variables important for plants and saprotrophs are exposition of the plot, thickness of the organic layer, sodium concentration, Ellenberg N-indication values. Important for mycorrhizal fungi are higher nitrate, potassium and magnesium concentrations for the species-poor type and exposition, thickness of the organic layer and age of the trees for the other types.

The samples of plots of the type rich in ectomycorrhizal fungi had larger numbers of mycorrhizal root tips with a larger degree of ramification. There was a positive correlation between the number of mycorrhizal root tips and the species numbers. Logarithmized abundance values based on absolute maximum numbers of sporocarps, total numbers and dry weight production showed only minor differences.

Contents

1. Introduction.

This paper treats the coenology of macromycetes growing in roadside verges planted with Beech (*Fagus sylvatica* L.), in relation to environmental conditions. The studied area is situated in the province of Drente in the North of the Netherlands. The verges of roads in this area are often planted with trees, predominantly Oak (*Quercus robur* L.), less often Beech (approx. 20% of the roadside verges planted with trees) and exceptionally with other tree species. The mycoflora of various vegetation types in Drente is relatively well-known thanks to the work of Barkman (1976, n.p.; Juniper scrub, peat bogs), Arnolds (1981, 1982; grasslands), Jansen (1984; Oak woods), Jalink & Nauta (1984; Birch woods), Keizer (1985; marshy forests) and Jansen et al. (1993, in prep; Pine woods). The mycocoenology of beech forests has recently been studied by Opdam (1991) and Van Steenis (1991).

Very few accurate mycological data are available from roadside verges that are planted with trees, also in other countries. This is probably due to the artificial habitat, comprising planted trees of the same age, frequent disturbance by traffic and road works and management of the verges for instance by mowing. On the other hand, it has incidentally been observed that this habitat is sometimes inhabited by a rich mycoflora, in particular of ectomycorrhizal fungi and that this mycoflora differs in some respects from the mycoflora in forests of the same tree species (Derbsch, 1954; Kreisel, 1957; Jahn et al., 1967). At the same time, this habitat can be regarded as an experimental set-up, in which various environmental variables may vary in a known way.

The aims of this study are:

1. extending the mycocoenological knowledge to hitherto unexplored habitats;
2. establishing to what degree communities based on green plants correspond with those based on fungi;
3. studying the relations between fungal communities and several environmental variables;
4. a comparison of various abundance values of macromycetes.

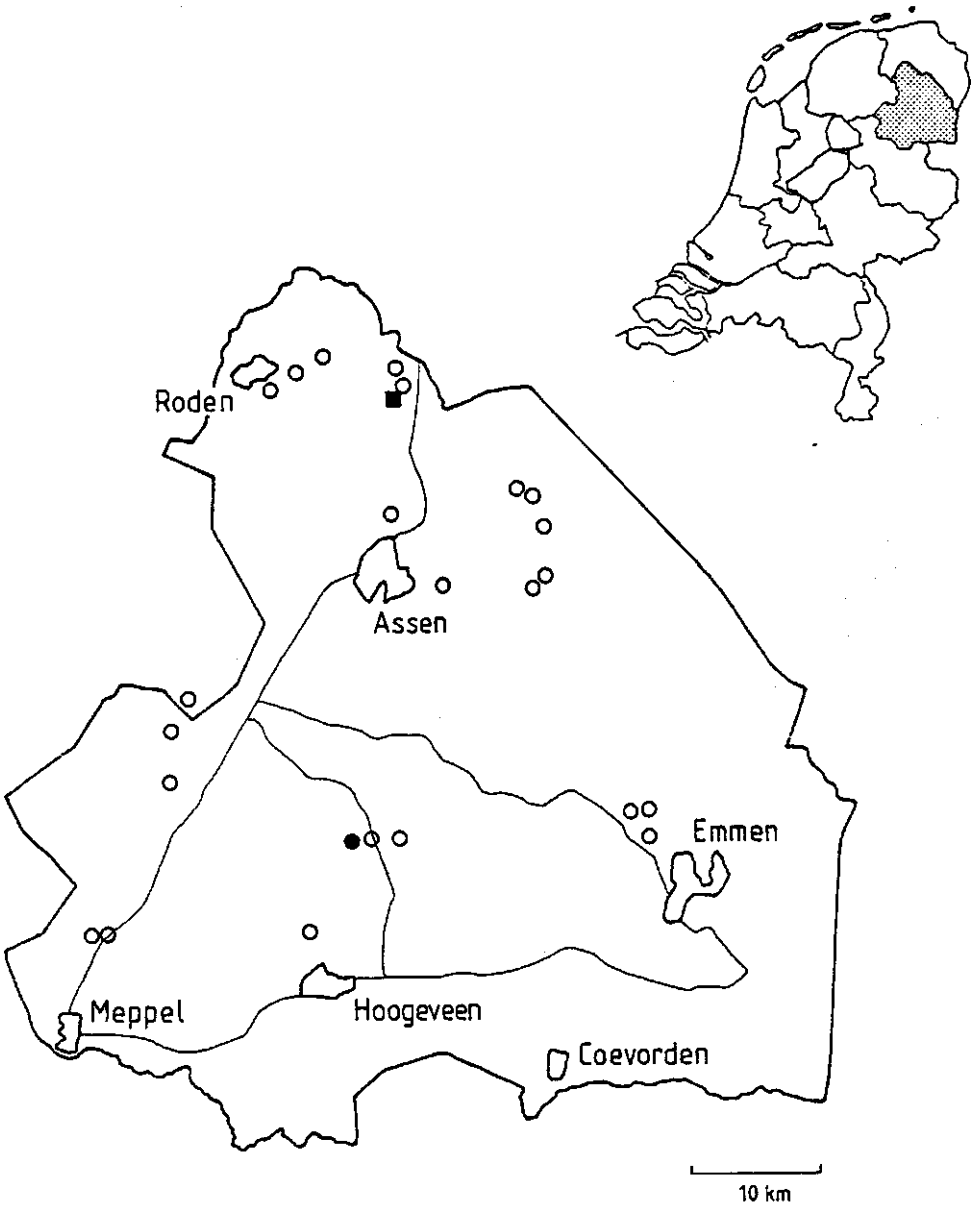
This paper forms part of a series on this subject. Others will deal with roadside verges planted with Oak, a field experiment to simulate various types of roadside management, a comparison of mycocoenoses of roadsides with mycocoenoses in Oak- and Beechwoods and a taxonomical survey of the macromycetes encountered during this study.

2. Material and methods.

2.1. Selection of plots.

Within the phytogeographical Drentian district (Weeda, 1983) 23 plots along roads were selected (fig. 1). This area is situated about 10-20 m above sea level and the soil consists of (originally) nutrient-poor cover-sands often with a layer of boulder-clay on a depth of 0-2 m. The climate is temperate-atlantic with an average annual precipitation of 781 mm, an average temperature in the coldest month (January) of 1.2°C and in the warmest months (July and August) of 15.9°C (KNMI, 1986, 1987, 1988).

Fig. 1. Location of the studied plots in the province of Drente, the Netherlands.
○ = Location of plots
● = Biological station Wijster
■ = Meteorological station Eelde



In July 1986, twenty three plots were selected in lengthwise homogeneous roadside verges with regard to the vegetation of vascular plants, but there was a zonation visible from the margin of the road towards the ditch. Twelve plots were selected in open landscapes, eleven plots were situated within forests including seven along roads with a metalled surface and four along sandy paths. All plots are provided with a single, uninterrupted row of mature beech trees between 37 and about 140 years old (in 1988). The length of the plots was 100 m, the width varied between 1.5 and 5 m, bordered by the road on one side, and usually a ditch on the other.

2.2. Recording of plants and fungi.

During the summer of 1986 vegetation relevés were made according to the Braun-Blanquet method (Braun-Blanquet, 1964). The coverage of all species was estimated in percentages and transformed into a 9-partite scale for data processing after Westhoff & Van der Maarel (1973). The margin of the ditch and the extreme margin along the road where trampling and riding are most intense, were neglected. The plots were visited once in a 3-4 week period from August until late November during the autumns of 1986-1988 in order to study the mycoflora. All sporocarps of macromycetes were counted and removed. Incidental visits in spring revealed that no noteworthy fructification occurred in that season.

The studied fungi comprise the larger part of the macrofungi, i.e. fungi with sporocarps greater than ca. 1 mm.
The following taxonomical groups were included:
Basidiomycetes: Agaricales; Russulales (after Bas, 1988); Aphyllophorales including pileate poroid fungi, hydnaceous fungi; Gasteromycetes (after Gams, 1979);
Ascomycetes: Pezizales and the genera *Cordyceps* (Fr.) Link, *Elaphomyces* Nees (Elaphomycetales), *Leotia* Pers. and *Geoglossum* Pers. (Helotiales) (after Hawksworth et al., 1983).
Deuteromycetes: *Paecilomyces* Bainier.

The macrofungi are treated separately for two ecologically (almost) independent functional groups, viz. the ectomycorrhizal and other fungi. The ectomycorrhizal fungi were those according to Trappe (1962) and Kreisel (1987) with a few exceptions: species belonging to the genera *Clavulina* Schroet. and *Leotia* Pers. and *Clitopilus prunulus* (Scop.:Fr.) Kumm. were considered as ectomycorrhizal on the basis of circumstantial indications (chapter 7). The ectomycorrhizal fungi are treated in § 3.3.

The second group consists mainly of saprotrophic fungi which are involved in the decomposition of dead organic matter, such as leaves, litter, humus, dung, wood and sporocarps of other fungi. This group is in § 3.4.

2.3. Soil description and analysis.

In 1987 in all plots the soil profiles were described up to a depth of 1.20 m. Colours, organic matter contents and texture of the various horizons were described. The profiles of all plots, except those along unpaved forest paths, were disturbed to a depth of 1 m or more, and made up by a mixture of podsol horizons. This could be concluded from the characteristic colours, still in patches visible. The thickness of the $A_0 + A_{00}$

layer varied considerably in the plots; the other soil profile characters have not been used in further analysis.

Five soil samples from the upper 0.1 m of the soil were taken, mixed to form one composite sample, dried at 40 °C and used for soil-chemical analysis. The analysis included the following: pH in 0.01 M $CaCl_2$, extractable Mg^{2+}, Na^+, K^+, PO_4^{3-}, NO_3^-, NH_4^+ in 0.01 m $CaCl_2$, total P, N and C, all according to standard methods described by Houba et al. (1988). As an indication for the availability of nitrogen to plants the C/N ratios were calculated. In addition the median Ellenberg values for nitrogen were calculated on the base of all phanerogams in the plot (Ellenberg, 1979).

2.4. Determination of other environmental variables.

Other parameters that were determined were the following:

-The number of trees in the plot, the surface of the plot and the number of trees per 1000 m^2.

-The intensity of the traffic on the roads along the plots. Data were obtained by interrogation of the local authorities and personal observations. Six classes were distinguished: I: < 625, II: 625-1250, III: 1250-2500, IV: 1250-2500, V: 5000-10000, VI: >10000 motorized vehicles per day.

-Tree vitality. The vitality of all trees in the plots was estimated using the method of the State Forestry Service (Staatsbosbeheer, 1985). Four vitality classes are distinguished, largely on the basis of canopy transparancy (being a measure for the amount of leaves and thus for the amount of photosynthesis). Class 1 indicates high vitality, class 4 low vitality. If "negative" characters (yellow leaves, early fall of leaves, small size of the leaves) were observed, the vitality class was augmented one unit. The tree vitality in a plot was the average of the vitality of the individual trees. The inventory and calculations with respect to tree vitality were carried out by P. Dekker (1988).

-The age of the trees was determined with the aid of an increment borer. The annual rings were counted in the pieces of wood obtained. It was assumed that in a plot all trees were of the same age.

-Management of the vegetation. Three different management types were recognized, which were applied by the local authorities: 1) mowing without removal of the hay; 2) mowing with subsequent removal of the hay; 3) no treatment. The information on the management was obtained by inquiring the local authorities and by personal observation.

-The potential maximum direct sunshine per day in October was estimated with aid of a horizontoscope (Barkman & Stoutjesdijk, 1987).

-Preliminary data on the moisture of the soil were obtained by collecting soil samples after a dry period of one week in June 1988. The samples were successively weighed, dried at 40° C and again weighed. The water content divided by the dry weight yields an expression of the soil moisture at the time of sampling.

The groundwater levels have not been determined directly. From the nearby ditches of 0.8-1.2 m depth it was clear that during summer and autumn the ground water was much deeper than 0.8-1.2 m below the soil surface. In late autumn, winter and early spring the level rises to 0.5-1.0 m below the soil surface. Between the plots, the groundwater tables showed little variation and have therefore not been used in further calculations.

2.5. Data processing.

After three years of sporocarp counts, for each species and for each plot figures were determined for:
1) the maximum abundance of sporocarps of all visits adjusted to 1000 m^2. This value approaches the potential maximum fructification of the mycelia. The actual fructification may vary considerably due to climatic variability (Barkman, 1976, 1987; Arnolds, 1981). The values were transformed using the formula $v=\ln(y+1)$ where v is the transformed value and y is the maximum abundance of sporocarps. This formula was applied in order to reduce extreme values in the dataset. The values of v were rounded to integers. This transformation was chosen because the successive values of v come close to the logarithmic scale for estimation of abundance of fungi as proposed by Arnolds (1981). Any number over 5000 sporocarps/1000 m^2 was given value 9.
2) The total production in three years, i.e. the total abundance of sporocarps multiplied by the "specific dry weight" of the respective species (Arnolds, 1981). For this purpose, of all species some representative air-dry sporocarps were carefully cleaned (removal of adhering soil particles, etc.) and weighed. In a few cases the specific dry weights were taken from Arnolds (1981).
3) The ln-transformed values of 2) as described under 1).

The vegetation relevés, mycological samples and the environmental data were analyzed using the computer programs TWINSPAN (Hill, 1979; Jongman et al., 1989) and CANOCO (Version 2.1, Ter Braak, 1987). From the latter program package the canonical correspondence analysis (CCA) was used. The results of the TWINSPAN analyses were modified "by hand" in order to obtain more lucid tables.

A number of different abundance measures were used in the computer analyses in order to evaluate the results obtained with these values (see section 4.2).

2.6. Sampling of mycorrhizas.

In June 1987 five root samples were taken from each of the plots F11, F12, F14, F15, F21, F22, F23 and F24, in order to detect a possible relation between the number of sporocarps of mycorrhizal fungi, the number of mycorrhizas and some environmental variables. These plots were selected because they cover a large variation in the quantity of sporocarps of mycorrhizal fungi and in vegetation types but were rather similar with respect to exposition, age of the trees and soil type. The samples were taken from 0-10 cm depth with aid of an empty tin 3.6 cm diameter and 10 cm length, i.e. approx. 100 cm^3. All samples were taken 1.5 m from the tree on the tree line parallel with the road. The samples were rinsed in order to remove sand and subsequently stored in glutaraldehyde buffer (Alexander & Bigg, 1981) awaiting further analysis. Before counting, larger soil particles, plant litter and roots of the plants other than trees were removed by hand. The tree root tips were counted and the total length of the fine roots (<2 mm diameter, cf. Vogt et al., 1983) was estimated using the line intercept method (Newman, 1966). The mycorrhizal root tips (always close to 100 % of all root tips) were divided in dead tips, defined by a dark brown colour, scurfy surface and an easily detachable mantle, and living tips, these being more vividly coloured, firm and without scurfy surface. The living tips were divided in a number of types on the basis of characters visible under a dissecting microscope with 6.4-40 x magnification. These types

could only incidentally be referred to fungal species and are therefore not separately treated, with the exception of the easily recognizable *Cenococcum geophilum* Fr.

2.7. Weather conditions during the study.

The weather during autumn has a large effect on the fruiting of fungi (Thoen, 1976; Dahlberg, 1991). The autumn of 1986 was rather unfavourable for fungi: the period July-November was relatively dry (84 mm less precipitation than average) and serious frost occurred early, during the nights of 11-12 and 16-17 October. The autumns of 1987 and 1988 were favourable with 27 and 90 mm rain more than average, respectively (KNMI, 1986-88). There were no noteworthy frosts until November. The climatic data are from Eelde (Meterological Station, fig. 1). Although some local variation may occur, it is assumed that the main climatic variables did not vary substantially within the studied area.

2.8. Nomenclature.

Nomenclature of vascular plants follows Heukels & Van der Meijden (1983); of Bryophytes Touw & Rubers (1989); of lichens Brand et al. (1988); of syntaxa Westhoff & Den Held (1969); of Basidiomycetes Kreisel (1987), except for the genera *Inocybe* (Kuyper, 1986) and *Psathyrella* (Kits van Waveren, 1985); of Ascomycetes Cannon et al. (1985).

3. Results.

3.1. Species diversity, numbers of sporocarps.

In the 23 plots 105 species of mycorrhizal fungi and 153 saprotrophic fungi were found. The number of species per plot varied from 3-49 in the former and from 6-45 in the latter group with averages of 21 and 23 species, respectively. The average number of green plant species varied between 3 and 42 with an average number of 26 and a total of 134 species. Thus, in the plots the number of macromycete species was about twice the number of green plant species. There was a positive correlation between the species number of mycorrhizal and saprotrophic species ($r=0.48$, $p<0.01$, $n=23$). There were no significant correlations between the green plant species numbers and the numbers of mycorrhizal or saprotrophic fungi, respectively.

3.2. Classification of plant communties.

The results of the TWINSPAN classification of the green plant species are presented in table 1 (tables at the end of this chapter). Two main vegetation types can be distinguished: the *Festuca rubra* type, characterized by a large number of differential species and the *Mnium hornum* type, mainly negatively characterized by the absence of these differential species and only with a few, weakly differential species. One plot (F44) is extremely poor in species and cannot be classified within one of these types. The *Festuca rubra* type comprises plots in open landscapes and contains mainly species

characteristic of the Plantaginetea majoris and Molinio-Arrhenatheretea. Two subtypes can be distinguished: the semiruderal *Elytrigia repens* subtype with affinity to the class Artemisietea vulgaris and the grassy *Festuca ovinia* subtype with affinity to the Koelerio-Corynephoretea. This subtype is also characterized by a relatively high cover of Bryophytes and a low cover of phanerogams. The *Mnium hornum* type contains shady plots, along paths and roads inside forests. It shows affinity with the Quercetea robori-petreae, on account of the occurrence of *Mnium hornum* and *Deschampsia flexuosa* although the last species also occurs in some of the open plots. Two weakly characterized subtypes can be distinguished: the *Poa trivialis* subtype and the *Dryopteris carthusiana* subtype. The former subtype is characterized by a relative high proportion of species which also occur in the *Festuca rubra* type and seems to represent a disturbed, ruderalized variant of the *Mnium hornum* type. The latter subtype lacks those species and may be considered more typically resembling the Quercetea robori-petraeae.

The results of CCA ordination are presented in fig. 2a and b. All plots of the *Festuca rubra* type are clustered left of the vertical axis, the plots of the *Mnium hornum* type to the right. The plots of the *Festuca rubra* type are relatively similar and the clusters of the *Elytrigia* and *Festuca ovina* subtypes show some overlap. The subtypes of the *Mnium hornum* type form separate, but very loose clusters, indicating a larger floristic variation. Plot F44 takes again a completely isolated position (fig. 2a). The differential species of the various types and subtypes show a similar pattern (fig. 2b).

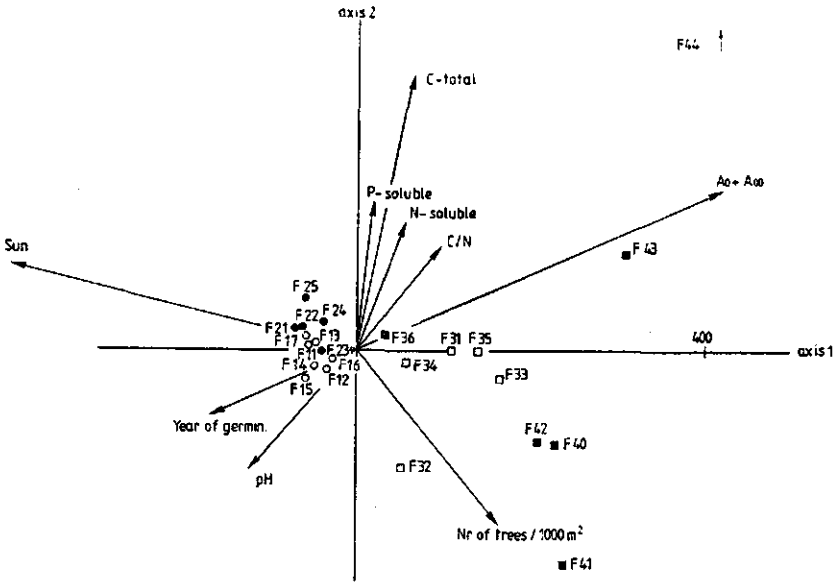


Fig. 2a. Biplot of environmental variables and plots of roadside verges planted with Beech on the basis of an ordination of the green plants.

○ = *Festuca rubra Fagus* type, subtype of *Elytrigia repens*

● = *Festuca rubra Fagus* type, subtype of *Festuca ovina*

■ = *Mnium hornum Fagus* type, subtype of *Poa trivialis*

□ = *Mnium hornum Fagus* type, subtype of *Dryopteris carthusiana*

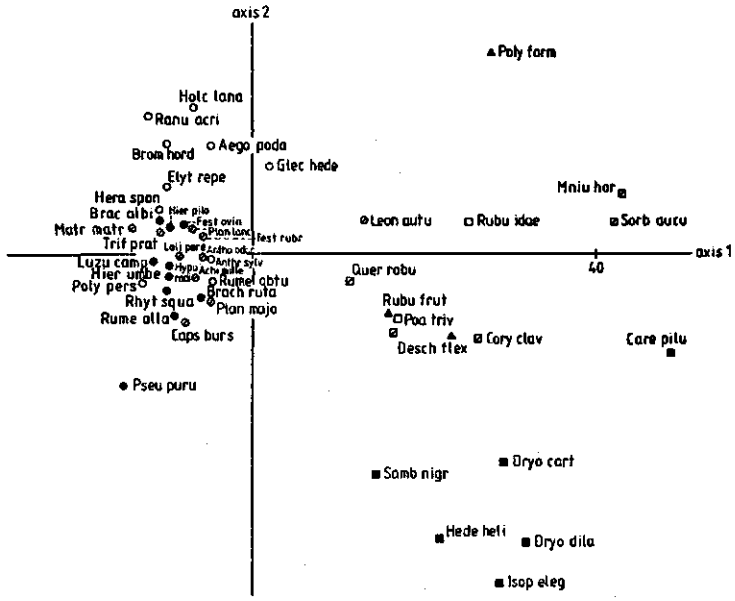


Fig. 2b. Positions of some differential plant species in the ordination of plots of roadside verges planted with Beech. The plant names are abbreviated to the first four letters of the generic name and of the specific epitheton.

⊘ = differential for the *Festuca rubra Fagus* type
○ = differential for the *Festuca rubra Fagus* type, subtype of *Elytrigia repens*
◔ = differential for the *Festuca rubra Fagus* type, subtype of *Festuca ovina*
⊠ = differential for the *Mnium hornum Fagus* type
□ = differential for the *Mnium hornum Fagus* type, subtype of *Poa trivialis*
■ = differential for the *Mnium hornum Fagus* type, subtype of *Dryopteris carthusiana*
▲ = differential for the *Festuca rubra Fagus* type, subtype of *Festuca ovina* + *Mnium hornum Fagus* type

3.3. Environmental variables.

The length and direction of the arrows in fig. 2a indicate the degree of importance and correlation of some environmental variables with the first two axes of the ordination. Most important environmental variables determining axis 1 are the thickness of the litter plus humus layer ("A_0+A_{00}") and the "openness" of the plots expressed as the potential amount of direct sunshine in October ("Sun"). Both variables are negatively correlated. The second axis is mainly determined by the total amount of organic matter ("C-total") and to a lesser extent the number of trees/1000 m². The plots are more scattered along the first axis than along the second and third axes (the latter is not shown here).

The average values and their standard deviations of some environmental variables for different (sub)types are presented in table 2. The two subtypes of the *Mnium hornum* type were not included separately, because they were only weakly characterized. The *Festuca rubra* type differed significantly (Mann-Whitney-test, $p<0.05$) from the *Mnium hornum* type by a larger "openness" of the plot (expressed as the amount of potential sunshine), a thinner organic layer, a higher sodium concentration and larger moisture of the soil, and by younger trees and more intense traffic. The average tree vitality in the *Festuca rubra* type was lower (=worse) than in the *M. hornum* type but this difference was not significant.

Within the *F. rubra* type, the *Festuca ovina* subtype had, compared with the *Elytrigia repens* subtype, significantly lower Ellenberg-nitrogen values and lower magnesium- and nitrate concentrations in the soil.

The open situation of plots of the *F. rubra* type explains the thin organic layer by blowing away of leaf-litter and the drier soil by a more intense sun irradiation and higher wind-speed, both causing a higher evaporation than in shady places. The high sodium-concentrations of the soil are connected with the on average higher traffic intensity in this type (all roads had a metalled surface) due to the application of more salt during the winter. The chloride ion of the salt in turn might cause a lower vitality of the Beech trees (van den Burg, 1981a, b).

The *Festuca ovina* subtype may be interpreted as open plots with a more or less nutrient-poor grassland aspect whereas the *Elytrigia* subtype represents plots with a somewhat ruderalized vegetation. In this case the (non-significant) worse vitality of the trees in the former subtype might be explained by lack of nutrients.

3.4. Ectomycorrhizal fungi.

The results of the TWINSPAN classification for the mycorrhizal fungi are presented in table 3. Two main types can be distinguished: the *Russula fellea* type, characterized by a large number of well-marked differential species, and a species-poor type without differential species (inops type). Within the *R. fellea* type two groups of plots can be distinguished: the *Boletus edulis* subtype and the *Inocybe napipes* subtype, both of them characterized by a number of differential species.

The inops type does not correspond with any (sub-)type of the plant communities. Of the communities based on green plants most (4) plots of the *Elytrigia* subtype are placed here but also 2 plots of the *Festuca ovina* subtype and one plot of the *Mnium hornum* type.

The *Russula fellea* type comprises plots, belonging to all four vegetation subtypes. However, the *Boletus edulis* subtype contains mainly plots of the *Festuca ovina* subtype and the *Inocybe napipes* subtype corresponds largely with the shady plots of the *Mnium hornum* type. Only plot F36 is placed in the inops type. It is interesting to note that this plot was assigned as transitional between the *Mnium hornum* and *Festuca rubra* type (Table 1). Within this group of plots no clear subdivision could be made on the basis of ectomycorrhizal fungi though the plots along paved roads (nrs. F31, 32, 33, 34 and 35) tend to be richer in species than those along sandy paths.

The deviating classification suggests that the environmental variables of primary importance to explain the variation in the mycorrhizal flora, are different from those for green plants.

The average values of the environmental variables in the *Russula fellea* type and the inops type are listed in table 2 (columns 5, 6). Compared with the *R. fellea* type, the plots of the inops type had significantly higher concentrations of nitrate, potassium, magnesium and also higher Ellenberg nitrogen values. In addition, the inops subtype showed non-significantly more potential sunshine, a thinner organic layer, a higher pH and a lower C/N ratio. Thus, the inops type seems to have higher mineral concentrations, including nitrate.

The CCA ordination (fig. 3a) reflects the results of the typology (table 3) and the corresponding environmental variables (table 2, col. 5, 6). The three (sub)types are recognizable in fig. 3a. Only the relatively species-poor (and therefore less representative)

plots F17 and F36 were placed in other groups than in the TWINSPAN classification. The first axis is mainly determined by the environmental variables sunshine ("openness"), age of trees, thickness of the organic layer, pH and traffic intensity (which are partly mutually dependent factors). In fig. 3b, it can be seen that the projection of the plots on the first ordination-axis shows fundamentally the same sequence as the sequence of the plots in the classification on the basis of the green plants. From the left to the right the groups are: sandy roads inside forest - forest roads with metalled surface - open plots with poor vegetation - open plots with a more or less ruderal vegetation. Although the result of this ordination appears to be meaningful, the first axis was not statistically significant ($p=0.10$; option in the CANOCO program package for a Monte Carlo permutation test; Ter Braak, 1988).

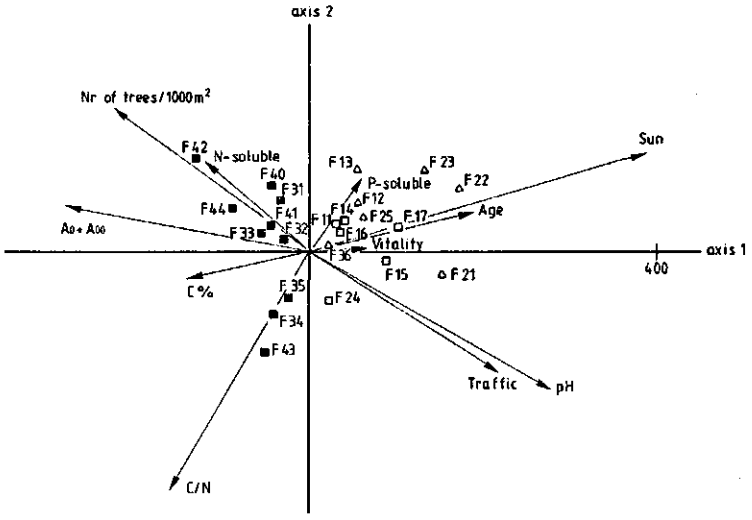


Fig. 3a. Biplot of environmental variables and plots of roadside verges planted with Beech on the basis of an ordination of the ectomycorrhizal fungi.
△ = inops type
□ = *Russula fellea Fagus* type, subtype of *Boletus edulis*
■ = *Russula fellea Fagus* type, subtype of *Inocybe napipes*

Despite some analogies of the two classifications, the classification on the basis of mycorrhizal fungi was different from the classification based on the green plants (compare table 1 and 3). Two factors may be responsible: 1. the flora of green plants contains species which are characteristic for all parts of the ordination gradient (i.e. the transition of the combined factors of the left end towards the right end of the first ordination axis of fig. 2a and b), but ectomycorrhizal fungi are absent on this part of the gradient; 2. some plots (F12, F13) seem phytocoenologically similar to mycologically rich plots, but nevertheless a rich mycoflora is absent for reasons that are not yet understood completely (see section 4.1).

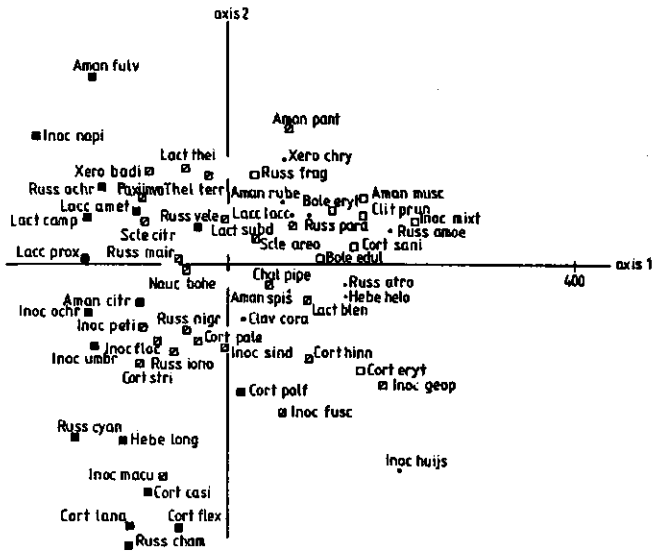


Fig. 3b. Positions of some ectomycorrhizal species in the ordination of plots of roadside verges planted with Beech. The fungal names are abbreviated to the first four letters of the generic name and of the specific epitheton.

☒ = differential for the inops type

☐ = differential for the *Russula fellea Fagus* type, subtype of *Boletus edulis*

■ = differential for the *Russula fellea Fagus* type, subtype of *Inocybe napipes*

● = differential for the inops type and the *Russula fellea Fagus* type, subtype of *Inocybe napipes*

The second axis is mainly determined by the C/N ratio and the third axis by the soluble phosphate concentration (not shown). The variation along the second axis is less than along the the first axis. This again indicates that the factors that strongly contribute to the first axis are the most important factors to explain the distribution of the species over the plots. An ordination with the other studied environmental variables showed that these (mainly soil chemical) factors were far less important than the factors that are shown in fig. 3a. This ordination is not presented.

3.5. Mycorrhizas.

The number of root tips and the total length of the roots per 100 cm^3 in the upper 0.1 m of the soil are indicated for all sampled plots in table 5. In the samples the rate of mycorrhiza formation was close to 100 %. Dead or dying mycorrhizas, comprised frequently about half of the sample. This may indicate a high turnover rate of the fine roots and is in concordance with other observations (Fogel, 1980; Vogt et al., 1983). The plots belonging to the *Boletus edulis* subtype (F11, 14, 15, 24; cf. table 3) showed significantly higher numbers of mycorrhizal root tips ($p<0.05$, t-test) and degree of ramification (i.e. the number of root tips divided by the root length; not shown) than the plots of the inops type (F21, 22, 23). The number of mycorrhizal root tips of the species-poor plot F12 is relatively high and comparable to those of the *Boletus edulis* subtype.

The proportion of *Cenococcum geophilum* on the roots was in most samples high, ranging from 31 to 91%, but was absent from one plot (F22; table 5). This fungus does not produce above-ground fruitbodies. However, the observed incidence of *C. geophilum* is probably higher than in reality because of the impossibility to recognize dead from living *C. geophilum* mycorrhizas and the slow decomposition rate (Meyer, 1962), and therefore long visibility, of the fungus. Meyer (1967) also mentions abundant occurrence of *C. geophilum* in (poor) podsol soils and ascribes this, among other things, to a relatively high resistance of this fungus to desiccation. In this study too, the plots on relatively dry and poor soil (the *Festuca ovina* subtype, plots F11, F12, F13, F14, cf. table 1) have higher proportions of *C. geophilum* than the other plots. The numbers of mycorrhizal root tips found in this study are comparable with numbers found in *Fagus* forests by Meyer & Göttsche (1971) in the upper 0.1 m of podsol soils.

The numbers of mycorrhizal root tips without *C. geophilum* were positively correlated with the species number ($r=0.64$, $n=8$, $p<0.05$), but not with the sporocarp production of mycorrhizal fungi. There was a non significant ($r=-0.43$) negative correlation between the number of mycorrhizal root tips and the average tree vitality in the studied plots.

3.6. Saprotrophic fungi.

The TWINSPAN analysis of the data on saprotrophic fungi is presented in table 4. Two main types of communities of saprotrophic fungi can clearly be distinguished, the *Mycena avenacea* type and the *Collybia butyracea* type, both characterized by a large number of differential species. These types correspond almost completely with the *Festuca rubra* and *Mnium hornum* type, respectively, as distinguished on the basis of green plants (table 1). The only exception is plot 23, combining a position in the *Collybia butyracea* type and *Festuca rubra* type. This plot was extremely poor in saprotrophic species, so that its position is doubtful anyhow. The *Mycena avenacea* type corresponds with open, grassy roadside verges and the *Collybia butyracea* type with shady roadside verges. It is very likely that the two types refer to differences in litter quality and quality. Because of the great similarity between the sets of plots arranged in saprotrophic communities and vegetation types, no averages for environmental variables in the former communities were calculated. The values in Table 2 for the phytocoena are also representative of these units.

The *Collybia butyracea* type can be subdivided into two, rather weakly characterized subtypes named after *Lepista nebularis* and *Psathyrella artemisiae*, respectively, and three plots without differential species. There is neither a relation with the subtypes of plant communities, nor with communities of mycorrhizal fungi. It is remarkable that the saprotrophic communities are not only characterized by soil-inhabiting fungi, but also by some wood-inhabiting fungi, although their occurrence would seem to be more or less accidental. The large number of wood-inhabiting fungi that occur in the *Collybia butyracea*-type and that are found only once, indicate that the substrate of these fungi is more often present in the shady plots, but that these fungi occur rather incidental.

The CCA ordination of the plots is presented in Fig. 4a. In this procedure, true wood inhabiting species and species of accidental habitats (animal droppings, arthropods etc.) were excluded. The plots of the *Mycena avenacea* type are readily recognizable as a

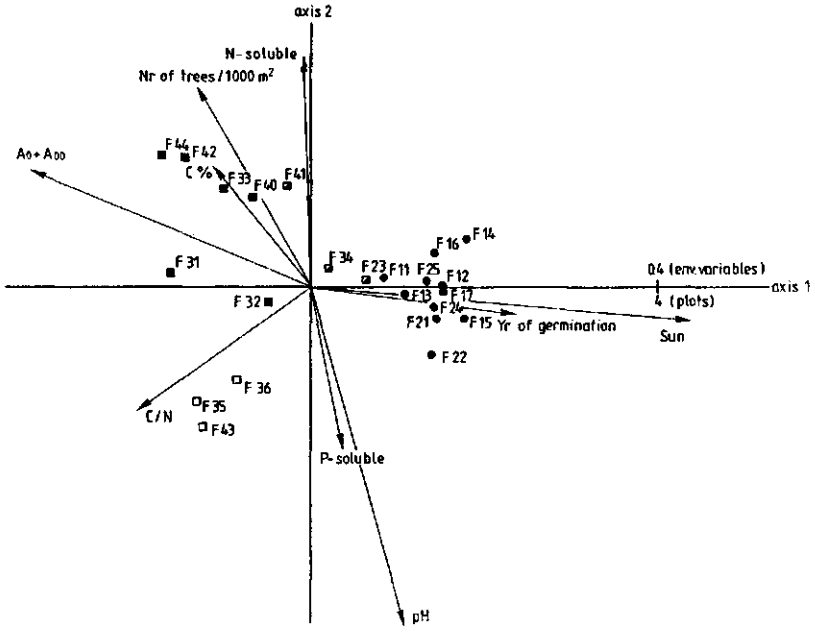


Fig. 4a. Biplot of environmental variables and plots of roadside verges planted with Beech on the basis of an ordination of the saprotrophic fungi.
● = *Mycena avenacea Fagus* type
□ = *Collybia butyracea Fagus* type, subtype of *Lepista nebularis*
■ = *Collybia butyracea Fagus* type, subtype of *Psathyrella artemisiae*
◪ = Three remaining plots of the *Collybia butyracea Fagus* type

rather compact cluster. The plots of the *Collybia butyracea* type are more dispersed. The *Psathyrella artemisiae* variant and the *Lepista nebularis* variant take the upper and lower part, respectively, of the *Collybia butyracea* type cluster. The plots F23, F34 and F41 have hardly sufficient differential species to warrant a separate variant; these plots form a transition between the *Mycena avenacea* type and the *Collybia butyracea* type. The first axis was mainly determined by the environmental variables sunshine, thickness of organic layer and age of the trees. The second axis was mainly determined by the variables pH and the concentrations of soluble N and P.

From this figure it can also be seen that plots of the *Lepista nebularis* variant correlate with a high C/N ratio and with a relatively high pH and soluble P concentration in the soil. The *Psathyrella artemisiae* subtype plots do not differ much from the *Lepista nebularis* subtype with regard to the thickness of the organic layer but generally have a higher pH, lower soluble P and higher soluble nitrogen concentrations of the soil. In fig. 4b the species are plotted. Along the first axis the division of the *Mycena avenacea* type (at the right side) and the *Collybia butyracea* type (left) is reflected in the order of the species. The species of the *Lepista*- and the *Psathyrella artemisiae* variant are scattered along the second axis (lower part and upper part respectively). Generally, it can be seen that in the shady plots the species along sandy paths concentrate in the upper part along the second axis. In the lower part most plots are situated along paved roads.

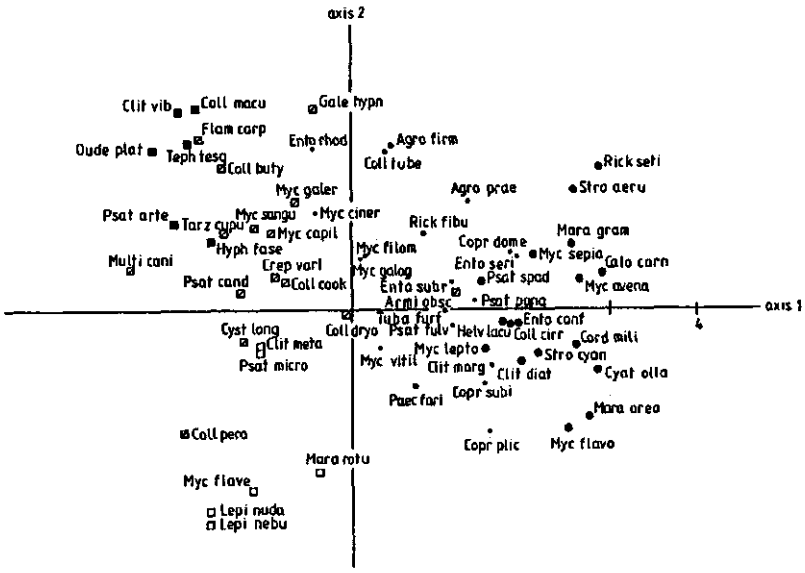


Fig. 4b. Positions of some saprotrophic species in the ordination of plots of roadside verges planted with Beech. The fungal names are abbreviated to the first four letters of the generic name and of the specific epitheton (see appendix 1 for the complete names).
● = differential for the *Mycena avenacea Fagus* type
▨ = differential for the *Collybia butyracea Fagus* type
□ = differential for the *Collybia butyracea Fagus* type, subtype of *Lepista nebularis*
■ = differential for the *Collybia butyracea Fagus* type, subtype of *Psathyrella artemisiae*
• = accompanying species

4. Discussion and conclusions.

4.1. Comparison of different classifications.

The division into shaded and open plots is the most fundamental classification for both green plants, saprotrophic and, to a lesser extent, mycorrhizal fungi. For green plants the quantity of light which reaches the soil, expressed in the variable sunshine (fig. 3a) appears to be the most important factor. For the fungi most probably the thickness and the quality of the organic layer together with the availability of nitrogen play a major role. The relation to the light factor is only indirect, but this factor is difficult to separate from the thickness of the organic layer (A_0 + A_{00}), because in open plots a large proportion of the leaves is blown away in the autumn and the decomposition of the litter is probably quicker due to higher soil temperatures (in an open plot the average soil temperature at 5 cm depth was 1.5 to 2.0 °C higher than in a shady plot; unpubl. measurements). The two types distinguished on the basis of the green plants can both be subdivided into a subtype with more eutraphent species and one with more oligotraphent species. This subdivision is not reflected in the data on saprotrophic fungi. For mycorrrhizal fungi not only the amount of sunshine and the thickness of the organic layer, but also the nitrogen availability seems to be important. An impression of the nitrogen

availability can be obtained by the Ellenberg N values (Ellenberg, 1979) or the C/N ratio of the soil. From a C.C.A. carried out with the environmental variables Ellenberg-N, NO_3^--concentration and C/N ratio (not presented here) it appeared that Ellenberg-N and C/N strongly correlated with the variables sunshine and thickness of the organic layer. The nitrate and phosphate concentrations did not correlate with sunshine and organic layer. The plots of the inops type (table 3), poor in mycorrhizal fungi, were grouped in the direction of higher concentrations of these ions. From table 2 it can be seen that the phosphate concentrations differed only slightly between the inops type and the *Russula fellea* type and it is therefore hypothesized that a recent and relatively high input of nitrogen may have caused a decline in (the fruiting of) the mycorrhizal fungi in the inops type plots (chapter 4), and that it is not (yet) reflected in the composition of the vegetation in all plots. Examples of such plots are F12 and F13, being poor in mycorrhizal species in spite of classification in the *Festuca ovina* subtype and seemingly favourable conditions. The shaded plot F36 is by exception classified with the open plots poor in mycorrhizal species, apparently due to the high nitrogen availability, expressed by the presence of nitrophilous plant species and consequently high Ellenberg N values.

Within the shady plots the rather weak distinction in a *Poa trivialis*- and a *Dryopteris carthusiana* subtype is not clearly reflected by the mycorrhizal fungi. The plots along paved roads (F31, 32, 34, 35, 43) appeared to be on the average richer in mycorrhizal species than the plots along unpaved paths, 35 and 20 species respectively. Apparently, the conditions for fructification are more favourable in these plots. Plot F33 is an exception because it belongs phytocoenologically and mycocoenologically to the footpaths in forests although it is paved with asphalt.

The classification on the basis of the mycorrhizal fungi offers valuable ecological information on the plots. The types and subtypes are clearly visible with many differential species. The provided information is partly different and supplementary to the information obtained by the study of green plants. In some cases, mainly in grassland types on poor soils, the characteristic saprotrophic fungi of that habitat add information to the community. In addition, places where many differential saprotrophic fungi are present but where differential mycorrhizal fungi and green plants are lacking, represent special ecological features.

Relatively few saprotrophic fungi are differential and many are accompanying, compared with the mycorrhizal symbionts. This is caused by two variables: 1. the occurrence of suitable substrate for saprotrophs is more accidental, more local than the widespread substrate for mycorrhizal fungi (tree roots), and partly dependent of for instance pruning of trees and presence of fallen branches. This might imply that the plots, being rather small, offer a relatively fragmentary view of the characteristic species composition of the saprotrophs. 2. The frequency of visits (once in 3-4 weeks) was low compared to the lifespan of the small sporocarps of some saprotrophic species. This implies a large chance that fruitbodies of such species are missed.

4.2. Evaluation of different abundance measures.

The abundance values of the plant species were used in this study according to the scale proposed by Westhoff & Van der Maarel (1973). This is a scale with more or less logarithmically increasing intervals of coverages, representing the importance of the species involved.

For each fungal species can be assessed: 1. the maximum numbers per visit found

during the study, 2. the logarithmic transformation of the maximum numbers, 3. the sporocarp production during the study or 4. the logarithmic transformation of the production. The first value expresses the best performance during the study (Barkman, 1967, 1987). The second value reduces extremely large numbers more than small ones. The production may express the biological activity during the studied period under assumption that above-ground sporocarps are positively correlated with under-ground metabolic activity. The fourth value again levels off the extremes in the production figures. From theoretical point of view, the untransformed production values are probably the best expression to estimate the biological activity of the species involved. Here it is assumed that for all species the sporocarp biomass reflect the fungal activity in the ecosystem to the same extent. Practically, it is difficult to obtain exact dry weights of all species: 1. the number of fruitbodies of rare species is usually low; this enlarges the risk of weighing non-representative individuals; 2. the weights of small species are relatively strong influenced by adhering soil particles, which are not always possible to remove completely; 3. it is not sure that sporocarps of a species have the same weights in different communities, but weighing all sporocarps is too laborious.

In table 6 a and b an example is given of the various values of abundance of sporocarps of plot F42. It appears that, although the plot was visited 12 times, the total number of sporocarps is only 1-2 times the maximum number of sporocarps. Among the mycorrhizal species, the maximum numbers of sporocarps varied a factor thousand, the total number a factor two thousand and the total production a factor thousand. The respective logarithmic transformations varied between 1-8, 1-9 and 1-7. The values of the logarithmic transformations of the total numbers of sporocarps and of the production were significantly positively correlated ($r=0.86$; $n=17$; $p< 0.05$). It may be concluded that there are only minor shifts in the various logarithmically transformed abundance values and that the relative abundance values of the species remain largely similar. In the saprotrophic species too, the maximal and total numbers of sporocarps were relatively similar with one noteworthy exception: the very numerous and very small *Mycena capillaris*. Because of the large differences in specific weight, the heaviest species of this plot weighing 161000 times more than the lightest, the pattern in the production figures differs considerably from the maximal and total numbers. For instance, one sporocarp of *Phallus impudicus* contributed more to the saprophyte production than 20000 sporocarps of *Mycena capillaris*. The values of the logarithmic transformations of the total numbers of sporocarps and of the production were therefore not significantly correlated ($r=0.17$). This is consistent with the results of Dahlberg (1991). It is concluded that the total production or the logarithmic transformation of the production represent best the biological importance of the saprotrophic fungi. However, using these values the limitations mentioned in section 4.2 should be kept in mind.

Nevertheless, usually sporocarps are counted, and often mycorrhizal and saprotrophic fungi are treated together in mycocoenological literature. Therefore the logarithmic transformations of the maximal numbers of sporocarps were used (Barkman, 1976, 1987) in the tables that were made with the aid of the program TWINSPAN for mycorrhizal and saprotrophic fungi. CCA ordinations with the aid of the program package CANOCO were carried out according to the following scheme.

1. Mycorrhizal fungi	Max. numbers	log-transformed (with and without rare species)
2. Mycorrhizal fungi	Production	log-transformed
3. Mycorrhizal fungi	Production	not transformed
4. Saprotrophic fungi	Max. numbers	log-transformed
5. Saprotrophic fungi	Production	log-transformed (with and without wood inhabiting species)
6. Saprotrophic fungi	Production	not transformed (with and without wood inhabiting species)

It appeared that the main results of the ordinations were hardly influenced by the various abundance values. Therefore only the first and the fifth combination of the above scheme are presented in figs. 3 and 4 respectively, according to the arguments pointed out above.

In conclusion, if one desires to present mycocoenological tables, the untransformed maximum numbers of sporocarps may provide the most lucid results, because it is the most direct representation of the situation in the field. Production figures may reflect the biological importance of the species involved, but by assessing the specific dry weights errors may be introduced, as mentioned above. Total production values of mycorrhizal or saprotrophic fungi per unit area are important parameters when fungal communities are compared. For the processing of data by computer programs log-transformed abundance values can be used. It seems that, because the variously transformed abundance values are largely similar, the final results of these procedures are largely similar as well (cf. table 6a and 6b).

Table 1. Vegetation table of the green plants. The abundance values are transformed after Westhoff & Van der Maarel.

Scheme of table 1.

Type Festuca rubra		**Type** Mnium hornum	
Subtype Elytrigia repens	**Subtype** Festuca ovina	**Subtype** Poa trivialis	**Subtype** Dryopteris carthusiana

Plot number	F21	F22	F23	F24	F25	F11	F12	F13	F14	F15	F16	F17	F31	F32	F34	F35	F36	F43	F40	F33	F41	F42	F44
Herb layer cover %	60	80	60	90	80	70	40	85	45	45	50	75	35	10	25	7	70	15	35	2	1	2	0
Moss layer cover %	0	0	0	15	2	3	0	<1	55	50	5	5	5	12	2	1	0	<1	30	<1	50	<1	<1
Number of species	28	30	38	39	37	32	24	32	41	32	35	42	21	32	18	19	35	19	17	9	7	3	6
I. Differental species for the Festuca rubra type.																							
Festuca rubra	5	7	1	5	7	5	5	8	7	7	7	5		1	1								
Plantago major	1	1	1	1		5	3	1	1	1	1	1		1	1	1							
Lolium perenne	5	5	5	5	7	5	5	5	5	5		5	1	3			1						
Polygonum aviculare	1	5	1	1		1	3		1	5	3	3		1		1	1						
Poa pratensis	5	1	5	5	5	5	1	3	1		5	5								1			
Achillea millefolium	1	1	1	1	1	1	1	1	1	1		1		1			1						
Matricaria matricarioides	5	5	1	1		1	1	1	1	3	1	1											
Anthoxanthum odoratum	1	1		3	1	5		1	5	1	3	1							1				
Plantago lanceolata		1	1	1	1	1		1	1	1	1	1					1						
Capsella bursa-pastoris	1	1	1	1	1	1		1			1						1						
Galeopsis tetrahit	1		1		1			1				1					1						
Trifolium pratense				1	1	1		1		1													
Trifolium repens	1			3		1			1	1							1						
Leontodon autumnalis	1	1				1	1	1			1	1											
II. Differential species for the Elytrigia repens subtype.																							
Rumex obtusifolius	1		1	1			3						1				1						
Elytrigia repens	3	5	5	7	5		1																
Polygonum persicaria	1	1	1				3																
Aegopodium podagraria				5	5	1																	
Heracleum sphondylium	1	1	1	1												1							
Ranunculus acris	1		1	1	3																		
Glechoma hederacea		1	1	1	1							1					5						
Holcus lanatus			1	1	5						1	1	1										
Anthriscus sylvestris		1	7	1	1			1									1						
Bromus hordeaceus spp. mollis		1	1	1	3							1											
III. Differential species for the Festuca ovina subtype.																							
Rumex acetosella							5	1	1		1	1			1								
Festuca ovina				1		1	1			3	3	7		1									
Hypochaeris radicata	1		1			1			1	1	1	1											
Spergula arvensis							1		1														
Chenopodium rubrum									1			1											
Chamaerion angustifolium									1	1			1										
Luzula campestris					1		1		1	1		1											
Hieracium pilosella						1		1	1			3											
Hieracium laevigatum		1				1	1	1	1	1	1	1	1	1	1								

Plot number	F21	F22	F23	F24	F25	F11	F12	F13	F14	F15	F16	F17	F31	F32	F34	F35	F36	F43	F40	F33	F41	F42	F44
Hieracium umbellatum						1		1	1														
Brachythecium rutabulum			3	1	2			7	1	1	1			1									
Rhytidiadelphus squarrosus				3	1		1	8	8	3	5			1									
Ceratodon purpureus			1		1	1			3		1	3			1								
Brachythecium albicans								1	1			3											
Pseudoscleropodium purum							1	1	5														
IV. Differential species for the Mnium hornum type.																							
Mnium hornum													5			1		5	5				
Sorbus aucuparia													1			1		1	1	1			
Prunus serotina										1			1		1				1				
Quercus robur (juv.)											1		1		1				1				
Ranunculus ficaria				3												1	1	1					
Corydalis claviculata																	1		1				
Digitalis purpurea															1				1				
Lonicera periclymenum																	1	1					
V. Differential species for the Poa trivialis subtype.																							
Poa trivialis				1										3		5	7						
Hedera helix														1		1							
Rubus idaeus													1			1							
Sambucus nigra														1			1						
Urticia dioica			3	1										1	1		3	1			1		
VI. Differential species for the Dryopteris carthusiana subtype.																							
Dryopteris carthusiana																				1	1	1	
Carex pilulifera																		1	3				
Dryopteris dilatata																			1		1		
Isopterygium elegans														3					7	8			
VII. Differential species for the deviating and species poor plot F44.																							
Calypogeia muelleriana																							1
Lepidozia reptans																							1
Leucobryum glaucum																							1
VIII. Differential species for the Festuca rubra type and Poa trivialis subtype.																							
Dactylis glomerata	5	1	5	1	3	5	3	5	3	3	1	1	1	1	1	1	3	1					
Taraxacum officinale	3	1	1	1	1	1	1	1	1	5	1	1	1	1		1	3	1					
Poa annua	3	1	3	1		5	3	5	3	1	1	1	5	1	5	3	5						
Rumex acetosa	1		1	1	3			1	1		1	1	3	1			1						
Ranunculus repens			1	1	1			1		1		1	1				5						
Stellaria media	1	1	1	1	1		3	3		1	1	1	1	1	1	1	1			1			
Cerastium fontanum					1	1				1				1			1						
Veronica chamaedrys		1		1	1										1		1						
Eurhynchium praelongum				3	1	1		1			1	1		1	3								
Hypnum cupressiforme									1	1	3	1	3	5	1								
IX. Differential species for the Festuca ovina subtype and the Mnium hornum type.																							
Deschampsia flexuosa							5		1		1		5	1	5	1		3	5	3	3	3	
Rubus fruticosus								1	1	1			3				1		3				
Polytrichum formosum									1		1		1					1	1				
X. Accompanying species.																							
Agrostis capillaris	5	7	3	5	5	5	5	5	5	5	5	5	3	5	5	1		5	7	3	1	1	
Holcus mollis	5	5	1	5	5	5	5	5	3	3	5	5	5			3	5	3		1	1		
Fagus sylvatica (juv.)	1		1	1								1					1		1				
Artemisia vulgaris			5											1			1						
Sisymbrium officinale			1					1									1						
Acer pseudoplatanus (juv.)																	1					1	
Alopecurus pratensis			5		1																		

Plot number	F21	F22	F23	F24	F25	F11	F12	F13	F14	F15	F16	F17	F31	F32	F34	F35	F36	F43	F40	F33	F41	F42	F44
Campanula rotundifolia		1													1								
Chenopodium album			1											1									
Cardamine hirsuta					1												1						
Dicranella heteromalla											5			5									
Equisetum arvense											1		2										
Lamium album			1														1						
Linaria vulgaris											1	1											
Matricaria maritima			1											1									
Populus canescens										1					1								
Ribes spec.																1		1					
Tanacetum vulgare					1												1						
Vicia cracca				1									1										

Species present in only one plot:
F21: Juncus bufonius 1, Senecio vulgaris 1; F22: Galinsoga parviflora 1, Geranium molle 1, Potentilla anserina 1, Viola arvensis 1; F23: Chaerophyllum temulum 1; F25: Bellis perennis 1, Polygonum amphibium 1; F11: Molinia caerulea 1, Salix repens 1; F12: Polygonum convolvulus 1; F13: Cytisus scoparius 1; F14: Arabidopsis thaliana 1, Calluna vulgaris 1, Cladonia chlorophaea 1, Erophila verna 1, Plagiothecium denticulatum 1, Polytrichum juniperinum 1, Polytrichum piliferum 1, Teesdalia nudicaulis 1; F15: Crataegus laevigata 1, Lupinus polyphyllus 1; F16: Pohlia nutans 1; F32 Sonchus oleraceus 1; F34: Solanum nigrum 1; F35: Impatiens parviflora 1; F36: Oxalis europaea 1, Veronica hederifolia 1; F43: Carex remota 1, Geum urbanum 1, Ilex aquifolium 1, Melandrium rubrum 1, Vicia sepium 1; F33: Senecio sylvaticus.

Table 2. Average values of environmental variables in groups of plots based on the composition of green plants (columns 1-4; cf. table 1) and mycorrhizal fungi (columns 5-6; cf. table 3). Bold figures are averages, the other are standard deviations. The average values of the subtypes of the Mnium hornum type are not given because these subtypes were weakly characterized. Significant differences between columns 1-2, 3-4 and 5-6 respectively are indicated with * ($p<0.05$) or ** ($p<0.01$); Mann-Whitney test.

	Types based on green plants				Types based on mycorrhizal fungi (table 3)	
	Festuca rubra type	Mnium hornum type	Festuca ovina subtype	Elytrigia repens subtype	inops type	Russula fellea type
Nr of plots	12	11	7	5	7	16
Nr. of trees/1000m²	**46**	**61**	**54**	**34**	**41**	**59**
	18	26	16	16	19	23
Traffic intensity class (I-VI)	**2.7***	**1.4**	**2.4**	**3.0**	**2.9**	**2.0**
	1.8	0.8	1.8	1.9	1.7	1.2
Vitality class (I-IV)	**2.8**	**2.2**	**3.1**	**2.3**	**2.3**	**2.6**
	0.7	0.3	0.5	0.8	0.7	0.6
Age of trees (1988)	**54***	**73**	**52**	**58**	**56**	**67**
	12	26	14	10	16	23
Potential sunshine	**5.9****	**0.3**	**6.0**	**5.7**	**5.8**	**2.1**
(hrs/day (Oct.))	1.3	1.1	1.5	1.8	2.8	2.6
A_0+A_{00} (cm)	**0.2****	**3.9**	**0.3**	**0**	**0.3**	**2.7**
	0.9	1.2	0.8	0	0.8	3.5
Ellenberg value (Nitrogen)	**5.8**	**4.6**	**5.3***	**6.6**	**6.4***	**4.7**
	0.9	2.2	0.8	0.6	0.5	1.8
pH-$CaCl_2$	**4.2**	**3.8**	**4.0**	**4.4**	**4.4**	**3.8**
	0.4	0.6	0.3	0.4	0.5	0.4
Mg^{2+} (mg kg^{-1} soil)	**26.7**	**22.9**	**18.0***	**38.8**	**34.7***	**12.2**
	13.4	13.9	5.7	11.5	20.6	11.9
Na^+ (mg kg^{-1} soil)	**38.7****	**17.8**	**39.0**	**38.2**	**38.1**	**24.6**
	18.3	10.7	17.3	21.8	24.7	13.6
K^+ (mg kg^{-1} soil)	**42.3**	**37.2**	**37.1**	**49.4**	**51.1***	**34.9**
	12.1	22.0	10.9	10.6	20.54	14.4
NO_3^- (mg kg^{-1} soil)	**2.1**	**0.9**	**1.0***	**3.6**	**3.7****	**0.6**
	4.0	2.4	1.8	5.9	4.8	2.0
NH_4^+ (mg kg^{-1}) soil)	**6.8**	**7.5**	**7.1**	**6.4**	**6.3**	**7.5**
	4.3	3.3	4.0	5.2	4.5	3.6
N-soluble (mg kg^{-1} soil)	**14.6**	**15.5**	**15.4**	**13.4**	**14.3**	**15.3**
	5.2	5.6	6.1	3.9	4.2	5.8
N-total (% N)	**0.17**	**0.16**	**0.16**	**0.19**	**0.18**	**0.16**
	0.04	0.06	0.04	0.34	0.04	0.06
C-total (% C)	**2.9**	**3.3**	**2.8**	**3.0**	**2.9**	**3.2**
	1.0	1.8	1.2	0.8	1.2	1.6
C/N	**17.1**	**21.0**	**18.1**	**15.8**	**16.1**	**20.3**
	4.9	6.8	6.0	3.0	6.1	5.8
P-soluble (mg kg^{-1} soil)	**0.5**	**0.4**	**0.1**	**1.0**	**0.6**	**0.4**
	0.7	0.7	0.4	0.7	0.8	0.6
P-total (mg kg^{-1} soil)	**275**	**213**	**224**	**346**	**297**	**223**
	118	92	87	128	126	96
Moisture (% of dry weigt)	**10.2****	**17.8**	**8.9**	**12.0**	**11.9**	**14.7**
	2.7	9.0	2.7	1.4	2.6	8.8

Table 3. Table of mycological relevé's of ectomycorrhizal fungi. The values are the ln(y+1) transformed maximal numbers of sporocarps per visit during three years, adjusted to 1000 m^2.

Scheme of table 3.

Type inops	Type Russula fellea	
	Subtype Boletus edulis	Subtype Inocybe napipes

Plot number	F23	13	22	25	36	12	21	11	17	14	15	16	24	31	32	34	35	43	40	33	19	41	42	44
Number of species	3	4	8	7	11	12	17	33	20	19	23	22	28	24	28	39	34	49	10	19	44	17	11	
Differential species for the Russula fellea type.																								
Paxillus involutus						1	1	2	1			2		3	5	2	1	4	2		1	4	3	
Laccaria amethystea								6				7	3	5	4	5	4	3		5	7	8		
Cortinarius striaepilus							2					4			4	3	4		5	7				
Inocybe petiginosa										2			5		3	6		5		3		3		
Scleroderma citrinum							1		1	2	2	4		4	4	3	3	3		4	5	4	2	
Russula fellea						1		3	1	4	3	3	6	5	2	5	4	4		3	6	3	2	
Cortinarius paleaceus								3	2				3			6	2	2			7			
Russula nigricans								3				4			1	3	3	3			4			
Xerocomus badius						1		1		2		1		3	2			1	1		3			2
Russula mairei								5		5	3	2	6	5		5	5	2		3	5	4	1	
Lactarius theiogalus					2					5	3	5		2			2	1				7	5	
Thelephora terrestris								4		4				5	3	2								
Lactarius subdulcis								5			3	1	4		5				2		5	1		
Lactarius blennius			1				4	5	3	5	6	5	7	1		5	3	4		3	6			
Tricholoma ustale						2		2		4	3	4		1			1	2			2			
Scleroderma areolatum								1	1	4			1			1		1			2			
Chalciporus piperatus								2			2					1					1			
Amanita pantherina						2		4		1				2	2									
Inocybe fuscidula							1						3				2				1			
Inocybe geophylla							4				4	4						5						
Cortinarius hinnuleus												2	1				1							
Inocybe sindonia					3							4	1					4			3			
Inocybe flocculosa													2			2					4			
Russula ionochlora								1							1			2						
Inocybe maculata													2		3			5						
Differential species for the Boletus edulis subtype.																								
Boletus edulis								3	2	4	4	1	2			1	2				2			
Inocybe mixtilis	4							2	3				3					2						
Cortinarius saniosus								3	4	4	4		4		2					1				
Clitopilus prunulus				1				3	3	3	3						2							
Russula fragilis								3				3									2			
Amanita muscaria						1		2	2		3										2			
Boletus erythropus								2	2		3										3			
Cortinarius erythrinus								3	2		5		6			2	1							
Differential species for the Inocybe napipes subtype.																								
Amanita citrina														3	3	1	3							
Inocybe umbrina														1		3		1		3				
Lactarius camphoratus														2		3						1		
Laccaria proxima								2					4	2	5	5		3	3	2	5	2	2	
Russula ochroleuca		1						3					1	2	4		3	2	4	4	4	3	2	

Plot number	F23	13	22	25	36	12	21	11	17	14	15	16	24	31	32	34	35	43	40	33	41	42	44
Russula lutea																	2	1					
Russula cyanoxantha																		2			1		
Cortinarius casimiri																2	1						
Inocybe ochroalba																	1				1		
Inocybe napipes															3			2	3	3	6	3	
Hebeloma longicaudum																3		3	3				
Russula velenovskyi						2								1		1	2	1				1	
Cortinarius lanatus																3		2					
Amanita fulva														1					1		1		
Cortinarius flexipes													2			3	3	3					
Cortinarius paleiferus									1							1	1	1					
Differential species for the inops type and Inocybe napipes subtype.																							
Clavulina coralloides			1	3			2								5	4		7			4		
Russula atropurpurea						4	4								4		2	1					
Naucoria bohemica				2	2										3			2			2		
Accompanying species:																							
Amanita rubescens			1	2	1	2	2	3	5	2	4	4		2	3	3	1	2	2	2	2	1	2
Laccaria laccata	5		3	7	5	4	6	4	3		1	4	5	6	7	6	4	4	6	4	8		1
Russula parazurea		2	3	3	2	3	5	2	1		5	4		4	3	3	1	2	4	3	4		
Xerocomus chrysenteron		4	2	1	2			2	1	1				2	1		1			2	2		1
Hebeloma helodes					2		4			5	4	5	5				1	1			3		
Russula amoenolens		1	2				3	3			3	3		1			1			2			
Amanita spissa						1	1	1							2	1		1					
Hebeloma mesophaeum					4		1	2					2							3	7		
Inocybe lacera	1													2							1		
Inocybe huijsmanni							1						1								1		
Cantharellus cibarius											5					8							
Cortinarius obtusus									3							4							
Cortinarius violilamellatus													4			1							
Lactarius serifluus											2				4								
Russula grisea											2							1					

Species present in only one plot:
F22: Inocybe lanuginella 3; F36: Russula solaris 1; F21: Clavulina rugosa 4; Laccaria bicolor 2; F17: Inocbye praetervisa 1; F14: Lactarius rufus 1; F16: Russula odorata 3; F24: Cortinarius causticus 3; Inocybe amethystina 2; F32: Hebeloma spoliatum 3; F33 Cortinarius parvannulatus 2; F42: Hydnotria tulasnei 1; Russula brunneoviolacea 2; Russula emetica 2; F44: Cortinarius anomalus 1; F35: Hebeloma anthracophilum 1; Elaphomyces muricatus 2; Hebeloma crustuliniforme 3; Hebeloma latifolium 1; Laccaria tortilis 3; Xerocomus subtomentosus 1; F34: Cortinarius velenovskyi 3; Inocybe cookei 3; Inocybe xantholeuca 1; Tricholoma saponaceum 1; F43: Inocybe asterospora 1; I. grammata 1; I. hirtella 5; I. rimosa 1; Leotia lubrica 5; Otidea bufon 3; Russula vesca 1;

Table 4. Table of mycological relevés of saprotrophic fungi. The values are the ln(y + 1) transformed maximal numbers of sporocarps per visit during three years, adjusted to 1000 m^2. A 9 was given in any case where the max. number of sporocarps exceeded 5000.

Scheme of table 4.

Type Mycena avenacea	Type Collybia butyracea	
	Subtype Lepista nebularis	Subtype Psathyrella artemisiae.

Plot nr.	F16	15	17	11	25	13	14	21	12	22	24	35	36	43	32	22	31	40	42	44	23	34	41
Number of species	28	16	17	12	22	11	21	11	7	30	29	21	30	45	24	14	26	26	24	13	6	19	30
Differential species for the Mycena avenacea type.																							
Helvella lacunosa		3								1	4												2
Mycena leptocephala	3	3	3	4	2	3	3	3	2	4	5		2		3	1						1	3
Collybia cirrhata		4	1				2	2	2													2	3
Psathyrella spadiceogrisea	2				2	3				2	3								2				
Marasmius graminum					3						2												
Stropharia aeruginosa	2						1																
Mycena sepia			3	2			4		4		2				2								
Cordyceps militaris			2					2			1												
Mycena avenacea		2	4	1	5		4	2		4													
Mycena flavoalba						3	3	3		5													
Clitocybe diatreta					2	3	1			4								2					
Marasmius oreades		4			1					1													
Cyathus olla								2	2	2													
Calocybe carnea		2			1		2																
Rickenella setipes			1				3			1													
Entoloma conferendum		2									3												
Stropharia cyanea	1									1	2												
Differential species for the Collybia butyracea type.																							
Collybia butyracea	2			3	3							4	3	6	1	4	2	5	2				4
Collybia dryophila					2	2	2						5	3				3	1		3	1	4
Crepidotus variabilis	3					2						2		2	6	4	4	3					3
Mycena galericulata		1	2								2		2			2	3	4	3	1		1	3
Mycena sanguinolenta	2			1									1				3	1	2			1	1
Mycena capillaris												5	5		9	9							
Armillaria obscura											2	2		2	2	6	3	4		3		4	2
Mutinus caninus														2			4		2				
Flammulaster carpophiloides													1	3	2			3					
Collybia cookei														2				4				4	
Galerina hypnorum	1											1					1	1		2			9
Collybia peronata												3		5	4		3			1			
Psathyrella candolleana											1	5		2				2				4	
Tarzetta cupularis													2	2									3
Cystoderma longisporum														3									3

Plot nr.	F16	15	17	11	25	13	14	21	12	22	24	35	36	43	32	22	31	40	42	44	23	34	41
Differential species of the Lepista variant.																							
Lepista nebularis												1	4										
Lepista nuda													3	2									
Pluteus phlebophorus													1	1									
Psathyrella microrhiza												1	4	2					4				
Clitocybe metachroa												2	3						3				
Mycena flavescens						1					4		7	5									
Marasmius rotula											6	5		5									
Species of the Psathyrella artemisiae variant.																							
Hypholoma fasciculare																	6	4					
Clitocybe vibecina																		4	2	4			
Psathyrella artemisiae															2	1	3	2	3				4
Tephrocybe tesquorum																		3		3			
Oudemansiella platyphylla															1	2		2					
Collybia maculata																1			1				
Phallus impudicus																			1	1			
Entoloma rhodocylix																		2				3	5
Entoloma sordidulum																					3	1	2
Accompanying species.																							
Tubaria furfuracea	6	6	5	3	4	5	4	4	1	4	3	1	3	4	4	1	2	1	2	2	1	3	6
Mycena galopus	3	4	4	3	2		1	1		1	4	2	2	2	6	3	3	3	3	2	2	3	6
Mycena vitilis	1	2		1	3			4		1	1	2	4	3	3	2	2	1	2			2	3
Mycena filopes var. filopes	1	4	3			2	2	1		1		2		1	1	1	1	2				1	
Psathyrella fulvescens var. brevicystis	6	3			3	1				3			4	2	1	2		1		1			1
Rickenella fibula		4			1		1				1	3		2	1			3				1	
Mycena cinerella	3			1	2		3							3		3	3	6	1				
Mycena filopes var. metata				1					3	3	1						2	5					
Agrocybe praecox	3						2						1										2
Clitocybe marginella	2									4								1	1				
Coprinus subimpatiens								3		2				1	3								
Paecilomyces farinosus					1	1						1										1	
Psathyrella panaeoloides	1		1																	1	1		
Agrocybe firma											1									2	3		
Collybia tuberosa	3																					1	3
Coprinus domesticus							2			1			1										
Coprinus plicatilis s.l.	1								3							1							
Entoloma sericeum var. sericeum	4										2				1								
Pluteus atricapillus	2																2						1
Polyporus brumalis		2															3					1	
Coprinus micaceus	7														8								
Delicatula integrella											2												8
Lepista inversa										1			3										
Marasmius vaillantii											4			3									
Melanoleuca polioleuca										1			1										
Oudemansiella radicata														2			1						
Pluteus podospileus											1		1										
Psathyrella frustulenta									1					1									
Psilocybe inquilina							1												4				
Trametes versicolor	1													2									

Species present in only one plot:
F16: Sphaerobolus stellatus 7, Psathyrella seymii 4, Psathyrella lutensis 3, Entoloma turbidum 2; F15: Galerina vittaeformis ssp. atkinsoniana 2; F17: Ramariopsis helveola 2, Ramariopsis laeticolor 1;F11: Pleurotus ostreatus 2; F25: Clitocybe agrestis 1, Conocybe kuehneriana 1, Stropharia inuncta 1; F14: Polyporus badius 2, Agaricus arvensis 1, Mycena aetites 1; F22: Mycena avenacea var.roseofusca 2, Clitocybe candicans 1, Clitocybe odora 1, Conocybe siliginea 1, Stropharia coronilla 1; F24: Psathyrella prona 4, Psathyrella pygmaea 4, Stropharia albonitens 2, Clavaria acuta 1, Coprinus comatus 1; F35: Panaeolus sphinctrinus 2, Tremella mesenterica 1; F36: Clitocybe clavipes 3, Helvella villosa 3, Marasmius recubans 2, Lycoperdon perlatum 2, Ripartites tricholoma 2, Mycena polyadelpha 8, Mycena mucor 5; F43: Crepidotus luteolus 3, Ramaria stricta 3, Panellus stipticus 3, Lyophyllum decastes 3, Helvella crispa 2, Coprinus stercoreus 2, Marasmius epiphyllus 2, Clitocybe costata 2, Crepidotus sphaerosporus 2, Conocybe mairei 1, Helvella corium 1, Lepiota cristata 1, Lepiota ventriosospora 1, Mycena adcendens 1, Polyporus varius 1, Stropharia semiglobata 1; F32: Resupinatus trichotus 3, Mycena oortiana 3, Coprinus sclerocystidiosus 1, Mycena polygramma var. pumila 1, Psathyrella spec. 1; F31: Psilocybe crobulus 2, Hypholoma sublateritium 1, Tyromyces subcaesius 1; F40: Mycena polygramma var. polygramma 3, Marasmius androsaceus 1; F42: Leucoscypha leucotricha 5, Pholiota lenta 2, Antrodia semisupina 2, Gymnopilus penetrans 2; F44: Calocera cornea 4, Mycena haematopoda 2; F23: Panaeolus fimicola 1; F34: Crucibulum laeve 2; F41: Pulvinula constellatio 8, Pustularia catinus 6, Pleurotellus herbarum 5, Cordyceps ophioglossoides 3.

Table 5. The average numbers and standard deviations of mycorrhizal root tips and the length of the fine roots (< 2 mm ϕ), and the frequency of *Cenococcum geophilum* fine roots in the top soil in selected plots in roadside verges with *Fagus sylvatica* L..

Plot	number of mycorrhizal root tips per 100 cm^3	% *C. geophilum*	length of fine roots (m per 100 cm^3)
Plots of the *Boletus edulus* subtype			
F11	1842 ± 1966	63	2.9 ± 2.6
F14	13621 ± 7365	91	17.1 ± 9.2
F15	1940 ± 1870	50	2.5 ± 2.1
F24	1942 ± 332	31	8.8 ± 2.6
Plots of the inops type			
F12	2569 ± 2484	70	2.9 ± 2.8
F21	350 ± 2484	55	0.6 ± 0.4
F22	107 ± 101	0	1.6 ± 0.9
F23	173 ± 264	61	0.3 ± 0.3

Table 6a. Various abundance values of the ectomycorrhizal fungi in plot F42 over 3 years. For explanation of the logarithmic transformation see text.

Mycorrhizal fungi Plot F42 (300 m²)	max. in plot	total in plot	max. /1000m²	total /1000m²	ln(y+1) max. /1000m²	ln(y+1) total /1000m²	prod.tot. g/1000m²	ln(y+1) prod.
Paxillus involutus	40	78	133	260	5	6	259	6
Laccaria amethystea	987	1843	3290	6143	8	9	1106	7
Russula ochroleuca	6	11	20	37	3	4	45	4
Lactarius subdulcis	1	2	3	7	1	2	5	2
Inocybe napipes	10	23	33	77	4	4	21	3
Hydnotria tulasnei	1	1	3	3	1	1	2	1
Scleroderma citrinum	25	71	83	237	4	5	1176	7
Lactarius tabidus	70	101	233	337	5	6	122	5
Amanita rubescens	1	1	3	3	1	1	11	2
Inocybe petiginosa	9	18	30	60	3	4	1	1
Russula mairei	18	29	60	97	4	5	97	5
Russula fellea	9	17	30	57	3	4	154	5
Russula brunneoviolacea	2	2	7	7	2	2	6	2
Russula velenovskyi	1	1	3	3	1	1	3	1
Laccaria proxima	3	3	10	10	2	2	2	1
Russula emetica	3	5	10	17	2	3	10	2
Lactarius camphoratus	1	1	3	3	1	1	1	1

Table 6b. Various abundance values of the saprotrophic fungi of plot F42 over 3 years.

Plot F42 (300 m²) Saprotrophic fungi	max. in plot	total in plot	max. /1000m²	total /1000m²	ln(y+1) max. /1000m²	ln(y+1) total /1000m²	prod.tot. mg/1000m²	ln(y+1) prod.
Mycena galericulata	8	12	27	40	3	4	6613	9
Mycena vitilis	3	7	10	23	2	3	467	6
Collybia butyracea	4	8	13	27	3	3	3333	8
Mycena capillaris	10000*	20000*	33333	66667	9	9	2000	8
Mycena galopus	7	12	23	40	3	4	347	6
Psathyrella microrhiza	16	26	53	87	4	4	2658	8
Psathyrella fulvescens v.br.	4	12	13	40	3	4	3940	8
Clitocybe marginella	1	1	3	3	1	1	323	6
Clitocybe metachroa	11	16	37	53	4	4	4382	8
Clitocybe vibecina	3	5	10	17	2	3	1262	7
Mycena cinerella	1	1	3	3	1	1	37	4
Flammulaster carpophiloides	13	14	43	47	4	4	187	5
Mutinus caninus	5	5	17	17	3	3	1750	7
Megacollybia platyphylla	4	9	13	30	3	3	16620	10
Leucoscypha leucotricha	50	50	167	167	5	5	500	6
Psathyrella candolleana	5	5	17	17	3	3	6417	9
Psathyrella artemisiae	7	10	23	33	3	4	2833	8
Collybia maculata	1	1	3	3	1	1	3753	8
Pholiota lenta	4	6	13	20	3	3	5400	9
Tubaria furfuracea	5	6	17	20	3	3	1733	7
Mycena sanguinolenta	2	2	7	7	2	2	28	3
Phallus impudicus	1	1	3	3	1	1	16100	10
Antrodiella semisupina	3	3	10	10	2	2	2790	8
Collybia dryophila	1	1	3	3	1	1	493	6
Psathyrella spadiceogrisea	5	5	17	17	3	3	2021	8
Gymnopilus penetrans	2	2	7	7	2	2	333	6

* estimation

MYCOCOENOLOGY OF ROADSIDE VERGES PLANTED WITH COMMON OAKS (*QUERCUS ROBUR* L.) IN DRENTE, THE NETHERLANDS.

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Summary.

In the northern part of the Netherlands the vegetation, the macromycetes and a number of environmental variables were studied in 53 plots in roadside verges planted with Common Oak (*Quercus robur* L.). The plots varied widely regarding exposition, nutrient content of the soil and age of the trees.

Three main vegetation types were distinguished, the *Mnium hornum* type of forest roads, the semiruderal *Anthriscus sylvestris* type of open to shady plots and the *Hypochaeris radicata* type of open, rather nutrient poor plots. For the ectomycorrhizal fungi, four types were recognized: the *Xerocomus rubellus*-, the *Russula ochroleuca*-, the *Cortinarius erythrinus*- and the *Hebeloma mesophaeum* type, characteristic for shady plots, semiruderal open to shady plots, open nutrient poor plots and open plots with young trees respectively. In the ordination, the environmental factors tree age, exposition of the plot and Ellenberg N indication values were most important. In the plots of the *R. ochroleuca* type a thicker organic layer and larger amounts of soluble and total nitrogen were present. Based on the saprotrophic fungi, three communities were distinguished: the *Psathyrella fulvescens*-, the *Mycena avenacea*- and the *Collybia cookei* type. The latter is a small, weakly characterized type. The *P. fulvescens* type comprises shady to open plots with several vegetation types, the *M. avenacea* type open plots with a short, grassy vegetation. Most important environmental factors for the distinction of the types were exposition, tree age, Ellenberg N-indication values and thickness of the organic layer. The communities of saprotrophic fungi corresponded better with the vegetation types than the communities of mycorrhizal fungi.

Contents.

1. Introduction.

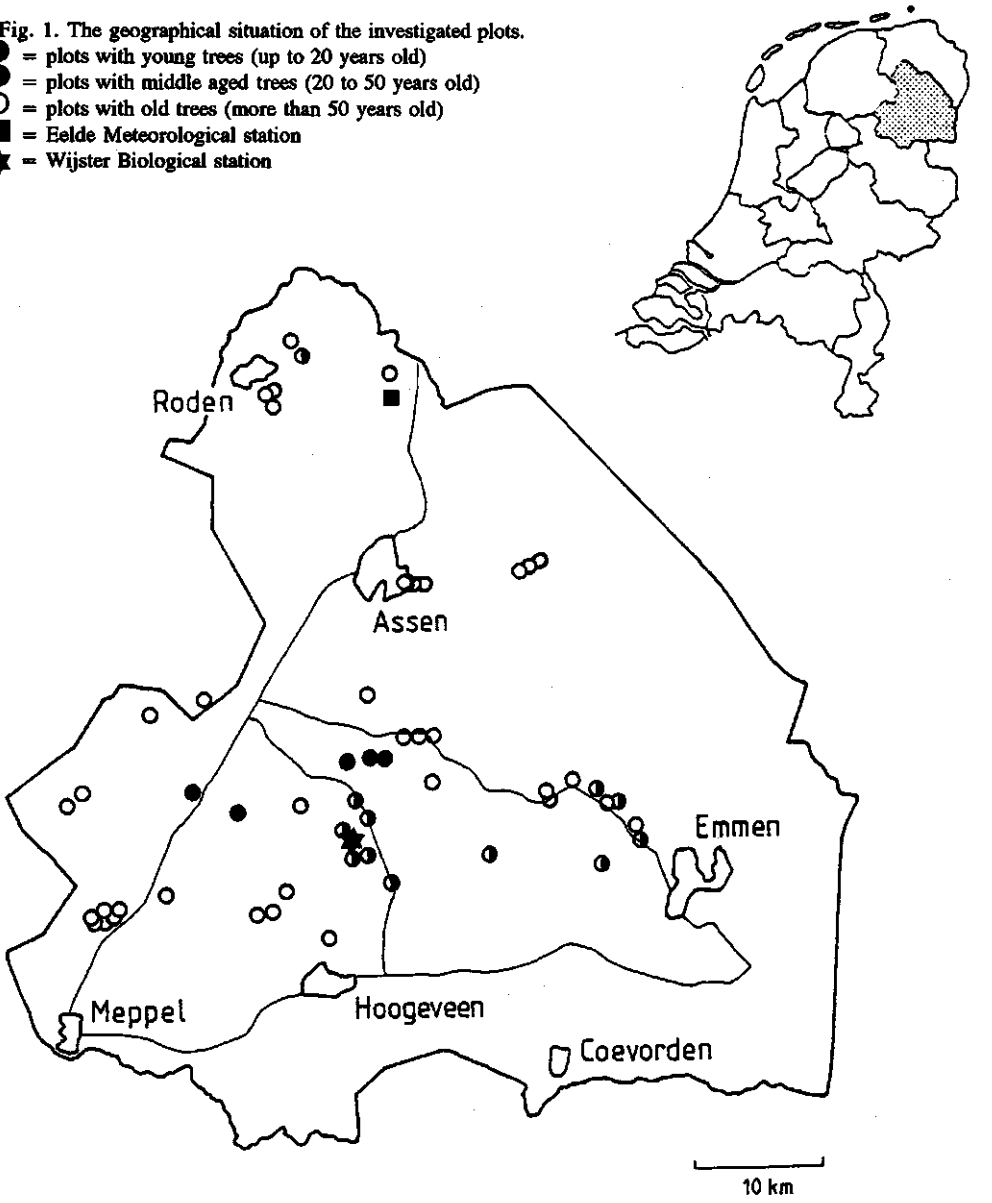
This paper treats the ecology of macromycetes occurring in roadside verges that are planted with the Common Oak (*Quercus robur* L.), in the province of Drente, the Netherlands. In this area many roads are bordered with trees, in most cases Common Oak, less often Beech (*Fagus sylvatica* L.). In Drenthe the mycoflora is relatively well-known, by mycocoenological studies in, among others, Oak forests (Jansen, 1984), Beech forests (Opdam, 1991 and Van Steenis, 1991), Birch forests (Jalink & Nauta, 1984), Juniper scrub (Barkman, 1976) and grasslands (Arnolds, 1981, 1982).

Although incidental observations have indicated that roadside verges planted with trees can be rich in macromycetes, including some characteristic species, very few accurate data are available on this subject. Some authors have drawn attention to the deviating mycoflora that occurs along forest paths and roads (Derbsch, 1954; Kreisel, 1957; Jahn et al., 1967), but they only made some general remarks. Arnolds (1968) and Reijnders (1967) mentioned the rich mycoflora (especially Boletoid fungi) which was present along some alleys in old estates on alluvial clay. Runge (1989a) drew attention to roadside verges as a habitat for endangered grassland fungi and proposed some recommendations for roadside management that protect these inhabiting fungi. Kreisel (l.c.) even advised not to investigate this habitat because of the deviating mycoflora and abiotic factors. Darimont (1973) discussed the differences between the mycoflora of a roadside verge in an Oak forest (Fago-Quercetum) and the Oak forest itself in the Belgian Ardennes on the basis of mycocoenological relevés. The relatively poor knowledge on this habitat may be caused by its artificial character, comprising of a row of planted trees, of the same species and age, often with a regularly mown undergrowth and with a frequently disturbed soil by traffic and road works as well as by its unattractiveness. However, the study of roadside verges planted with trees, which shows a wide variation in fungal species diversity and composition as well as in environmental variables, offers an opportunity evaluate the importance of this habitat as an environment of rare and endangered fungi. The aims of this study are:

1. To present mycocoenological descriptions of a hitherto unexplored habitat, enabling an interpretation of possible changes in future.
2. To compare between mycocoenoses in roadside verges with those of (Oak) forest and grassland communities.
3. To compare between communities based on green plants, mycorrhizal fungi and saprotrophic fungi.
4. To disentangle the roles of various environmental variables acting on these communities.

This paper forms part of a series of mycocoenological studies in roadside verges planted with trees. Others will deal with Beech alleys; a field experiment to assess the effects of various types of management in a particular roadside with all trees and a taxonomical survey of the macromycetes encountered during these studies. Special papers will treat the differences between mycocoenoses in roadside verges with trees and forests of the same tree species, and succession of mycocoenoses in roadside verges with Oak.

Fig. 1. The geographical situation of the investigated plots.
● = plots with young trees (up to 20 years old)
◑ = plots with middle aged trees (20 to 50 years old)
○ = plots with old trees (more than 50 years old)
■ = Eelde Meteorological station
★ = Wijster Biological station



2. **Material and Methods.**

2.1. *Selection of the plots.*

Fiftythree plots were selected within the Drentian phytogeographical district (Weeda in Heukels & Van der Meijden, 1983) in roadside verges with Oak (Fig. 1). The area is situated in the N.E. part of the Netherlands, about 10-20 m above sea level. The soil consists of nutrient-poor cover sands, often with a underlying layer of boulder-clay, incidentally with some remains of peat on a depth of 0-2 m.

Most plots were selected in July 1986, in homogeneous stands with regard to the phanerogam vegetation. Nine plots were selected in 1987. Variable factors were (1) exposition, (2) age of trees and (3) composition of herb layer as a reflection of soil conditions. The length of the plots was 100 m, the width varied between 1.5 and 6.5 m, bordered by the road on one side and usually a ditch on the other. The number of trees per plot varied between 9 and 35 (mean 15 ± 5) and the number of trees per 1000 m^2 varied from 16 to 93 (mean 47 ± 17).

Most plots were provided with a single, uninterrupted row of trees. Three plots had a double row of trees and in a few cases the plot was interrupted because there was a gap in the row of the trees. The plots were selected with regard to exposition and road metalling according the following scheme (fig. 2). "Open plots" were situated along roads in open landscapes, bordered by meadows and arable fields. The plots along roads through forests, are indicated as "shady plots". Plots that were bordered at one side by forest and at the other side by open land were called "half-open" or "half shady" plots; those with forest at the southern side "North-exposed" and those with forest at the northern side "South-exposed" (4 plots).

Exposition	Road surface		Total
	metalled	sand	
Open	32	2	34
N-exposition	5	0	5
S-exposition	4	0	4
Shady	7	3	10

Fig. 2. Number of studied plots according to their exposition and surface of the road.

In all shady and half-open plots the trees were old, here defined as more than 50 years old. The 34 open plots comprised 5 plots with young trees (i.e. less than 20 years old), 12 with medium-aged trees (20-50 years old) and 17 with old trees (50 to 140 years old).

The plots varied widely with regard to soil fertility, judged from the variation in composition of the herb layer.

2.2. *Recording of plants and fungi.*

Vegetation relevés were made during summer 1986 according to the Braun-Blanquet method (e.g. Westhoff & Van der Maarel, 1973). The plots Q3, 5, 6, 36, 37, 38, 39, 46 and 54 were added and studied in 1987. In the phytocoenological study of the plots the extreme margins along the roads, where trampling or riding are most intense, and the margins of the ditches were excluded. The cover of all species was estimated in percentages and later transformed into weighed values after Westhoff & Van der Maarel (l.c.) for data processing. For mycocoenological purposes, the plots were visited during the autumns of 1986-1988 once in a 3-4 week period from August until the first severe frosts, usually in November. Mycocoenological methods as proposed by Arnolds (1981) and Barkman (1976, 1987) were used. The plots that were added in 1987 have been studied only in 1987 and 1988. All carpophores of macromycetes were counted and removed in order to prevent double countings. Incidental visits in spring revealed that no noteworthy fructification occurred in that season.

After three years (two years for the plots that started in 1987) the following figures were assessed for each species in each plot:

1) the maximum abundance of carpophores during a visit, adjusted to 1000 m^2. The values were transformed for data processing using the formula $V=\ln(y+1)$ where V is the transformed value and y is the maximum abundance of carpophores. The values of V were rounded to integers. This transformation was chosen because it was meaningful to reduce extreme values in the calculations and because the successive values of V come close to the logarithmic scale for estimation of abundance of fungi by Arnolds (1981). Any number over 5000 carpophores/1000m^2 was given value 9;
2) the total dry weight production in three (two) years. This is the total abundance of carpophores multiplied by the specific weight of a species, i.e. the average dry weight of a number of representative carpophores of that species (Arnolds, 1981). The specific weights were assessed by weighing a number of air-dry specimens. For some of the saprotrophic species, which were not collected, the dry weights as given by Arnolds (1989) were adopted;
3) the transformed values of 2) as described under 1).

It is assumed that the maximum abundance of the carpophores during the study represents the potential performance of the species (Haas, 1932; Barkman, 1976, 1987; Arnolds, 1981), i.e. the number of carpophores produced under the most favourable weather conditions during these three years.

2.3. *Soil description and analysis.*

In 1987, in all plots soil profiles were described in one or two spots from 0-1.20 m depth. Colour, organic matter content and texture of the various horizons were recorded. The profiles in all plots, except those along unpaved forest paths, appeared to be disturbed to a depth of 0.5 m or more, and consisted mostly of a mixture of former podsol horizons. This could be concluded from the characteristic colours, still visible in patches. In most profiles the upper 5-10 cm were darker brown than the deeper layer, due to a higher organic matter content. The thickness of the A_0 and A_{00} layer varied considerably in the plots. The other soil profile characters have not been used in further data processing.

In each plot five soil samples were taken from the upper 0.1 m of the soil with the aid

of an auger, 15 mm diameter, mixed into one composite sample, dried at 40 °C and used for soil chemical analysis. This analysis included the following factors: pH-CaCl2, extractable Mg2+, Na+, K+, $PO4^{3-}$, NO_3^-, NH_4^+ (all in 0.01 mol/l $CaCl_2$), total P, N and C, all according to standard methods described by Houba et al. (1988). As indication for availability of nitrogen to plants the C/N ratios were calculated. In addition, the median Ellenberg values for nitrogen were calculated on the basis of all phanerogams in the plot (Ellenberg, 1979).

2.4. *Determination of other environmental variables.*

Other variables that have been determined include:
-the number of trees in the plot, adjusted to 1000 m^2;
-the intensity of traffic on the road. An estimation of this quantity was obtained by inquiry of the local authorities and own observations. Six classes were distinguished: class I: <625, II: 625-1250, III: 1250-2500, IV: 2500-5000, V: 5000-10000, VI: >10000 motorized vehicles per day.
-tree vitality. The vitality of the old trees in the plots was estimated using the method of the State Forestry Service (1985, 1987). The determination of the vitality of young and middle-aged trees with this method is problematic because the results would probably not be comparable with the vitalities of the old trees. Crown transparancy, being the most important character of tree-vitality, is in young trees always larger than in old trees. Therefore, only the vitality of old trees was determined. Four vitality classes were distinguished based on the canopy transparancy: the more transparant (i.e. less or smaller leaves), the less vital, the higher the vitality class. If additional "unhealthy" characters (yellow leaves, presence of dead twigs and branches, leaves mainly in clusters along the main branches) were seen, the vitality value was augmented one unit. The plot tree vitality was calculated by averaging the vitalities of the individual trees. The inventory and calculations were carried out by Dekker (1988).
-the age of the trees was assessed with the aid of a hollow increment bore. The number of annual rings of the obtained piece of wood represents the age of the tree.
-management of the vegetation. Three different management types were applied by the local authorities: 1. mowing without removal of the hay, 2-4 times a year; 2. mowing with subsequent removal of the hay, 1-2 times a year; 3. no treatment or incidental mowing with long intervals of several years.
-the potential quantity of direct sunshine per day in October was estimated with the aid of a horizontoscope (Barkman & Stoutjesdijk, 1987). This figure indicates the "openness" of a plot and is used as an indication of the microclimate in the fruiting season of macrofungi. In open plots the microclimate is drier and warmer than in shady plots.
-moisture of the soil. The fluctuations in groundwater level have not been determined directly. From the nearby ditches of 0.8-1.2 m depth it was clear that during summer and autumn the groundwater was deeper than 0.8-1.2 m, often considerably so. In late autumn, winter and early spring the level rised to 0.5-1.0 m depth. The plots along canals (Q1, 32, 42, 52) had a more constant water supply, the water level in the canal being 0.5-1.0 m below the soil surface. Generally, the groundwater tables showed little variation between plots. In addition, the median Ellenberg values for moisture were calculated on the base of all phanerogams in the plots. It appeared that all plots scored the value 5, indicating moderate humidity. Consequently, these data were not included in further analyses. Preliminary data on the actual moisture of the soil were obtained by

collecting soil samples after a dry period of one week in June 1988. The samples were successively weighed, dried at 40 °C and again weighed. The difference between the two weights divided by the dry weight is the soil moisture at the sampling time.

2.5. *Data processing.*

The vegetation relevés, mycocoenological relevés and the environmental data were analysed using the computer programs TWINSPAN (Hill, 1979; Jongman et al., 1989) and CANOCO (version 2.1 (1987); Ter Braak, 1988; Jongman et al., 1989). Of the latter program the canocical correspondence analyses (CCA) was used.

The program TWINSPAN rearranges plots and species in such a manner that plots with similar species composition and species with similar distribution in the plots are grouped together, in analogy to the methods by Braun-Blanquet (e.g. Westhoff & Van der Maarel, 1973; Mueller-Dombois & Ellenberg, 1974). The results of the TWINSPAN analysis were modified "by hand" in order to obtain more lucid tables.

The CCA performs an ordination of the data so that the plots are arranged along axes according to the variation between plots in species composition. Subsequently, the data of environmental factors were correlated with the ordination. These calculations were carried-out separately for phanerogams, saprotrophic and ectomycorrhizal fungi because they play different roles in the ecosystem. For each of the saprotrophic species and in each plot, the logarithmic transformation (natural logarithm) of the production of carpophores in the studied period was used in the computations. Of the mycorrhizal fungi the logarithmic transformation of the maximal numbers of carpophores was used (chapter 2). The production and maximal numbers were both adjusted to 1000 m^2. No species were excluded.

Fungi were considered to be ectomycorrhizal if listed as such by Trappe (1962) or Kreisel (1987). Exceptions are *Clavulina* Schroet. (not included in Trappe (l.c.) and reported as saprotrophic by Kreisel (l.c.)), *Clitopilus prunulus* (possibly ectomycorrhizal after Trappe (l.c.); saprotrophic after Kreisel, l.c.) and *Leotia lubrica* (not mentioned by Trappe and Kreisel, l.c.), which were included in the group of ectomycorrhizal species on the basis of circumstantial indications (cf. chapter 7).

2.6. Weather conditions during the study.

The weather during the fruiting period has a large effect on the appearance of carpophores (Zeuner, 1923; Thoen, 1976; Agerer, 1985, Dahlberg, 1991). The autumn of 1986 was rather unfavourable for fungi: the period July - November was relatively dry (84 mm precipitation less than average) and serious frost occurred early in the season. The autumns of 1987 and 1988 were favourable with 27 and 90 mm rain more than average, respectively (K.N.M.I., 1986-88). There were no noteworthy frosts until November. These data are from the meteorological station of Eelde in the north of the research area (Fig. 1). Although some local variation may have occurred, it is assumed that the main climatic variables did not differ substantially within the studied area. No special attention was paid to relations between weather conditions and fluctuations of fruiting. However, it can be concluded that weather conditions in the period of this study were sufficiently representative to obtain meaningful results concerning the macromycetes.

2.7. *Nomenclature.*

The fungi studied comprise the larger part of the macromycetes as defined by Arnolds (1981), i.e. fungi with carpophores larger than ca. 1 mm. The following taxonomical groups were included:
Basidiomycetes: Agaricales, Russulales (After Bas, 1988). Aphyllophorales: pileate poroid and hydnaceous fungi (after Gams, 1979).
Gasteromycetes.
Ascomycetes: Pezizales and the genera *Cordyceps* (Fr.) Link, *Elaphomyces* Nees, *Leotia* Pers. and *Geoglossum* Pers. (after Hawksworth et al., 1983).
Deuteromycetes: *Paecilomyces* Bainier.
Nomenclature of vascular plants is according to Heukels & Van der Meijden (1983); of Bryophytes after Touw & Rubers (1989); of Lichens after Brand et al. (1988); of syntaxa after Westhoff & Den Held (1969); of Basidiomycetes after Kreisel (1987), except for the genera *Inocybe* (after Kuyper, 1986) and *Psathyrella* (after Kits van Waveren, 1985); of Ascomycetes after Cannon et al. (1985).

3. **Results.**

3.1. *Plant communities.*

In table 1 (tables at the end of this paper) the result of the TWINSPAN analysis of the data on green plants is presented. Three main types of plant communities are distinguished, each characterized by a number of differential species.
1. The *Hypochaeris radicata* type, 26 plots (Q5 - Q42), characterized by a large number of differential species. In this type two subtypes can be distinguished: the *Hieracium pilosella* and the *Lotus corniculatus* subtype (plots Q5 - Q32 and Q36 - Q42 respectively).
2. The *Anthriscus sylvestris* type, comprising 23 plots: Q34 - Q87. Of this type, six plots (Q34 - Q84) lack a number of species that are present in most other plots of the type. These six plots form an impoverished variant (inops) of the *A. sylvestris* type.
3. The *Mnium hornum* type, a small group of 4 plots: Q88 - Q94.

The *Mnium hornum* type contains only shady plots; three out of four are along sandy paths inside forests. In syntaxonomic respect it shows affinity to the Quercion roboripetraeae. The *Anthriscus sylvestris* type comprises open north- and south-exposed as well as shady plots with a grassy, more or less ruderal vegetation, with affinity to the Artemisietea vulgaris. The inops variant of this type lacks a number of eutraphent species (e.g. *Poa trivialis, Lamium album*) and may be considered as transitional to the *Hypochaeris radiata* type. The *Hypohaeris radicata* type consists of open plots combining some characters of the Koelerio-Corynephoretea, Plantaginetea majoris and Molinio-Arrhenatheretea. This variation, even within single plots, is caused by the gradient of traffic influence perpendicular on the road into the roadside verge. The *Hieracium pilosella* subtype shows affinity with the Koelerio-Corynephoretea, the *Lotus corniculatus* subtype contains more species of the Molinio-Arrhenatheretea.

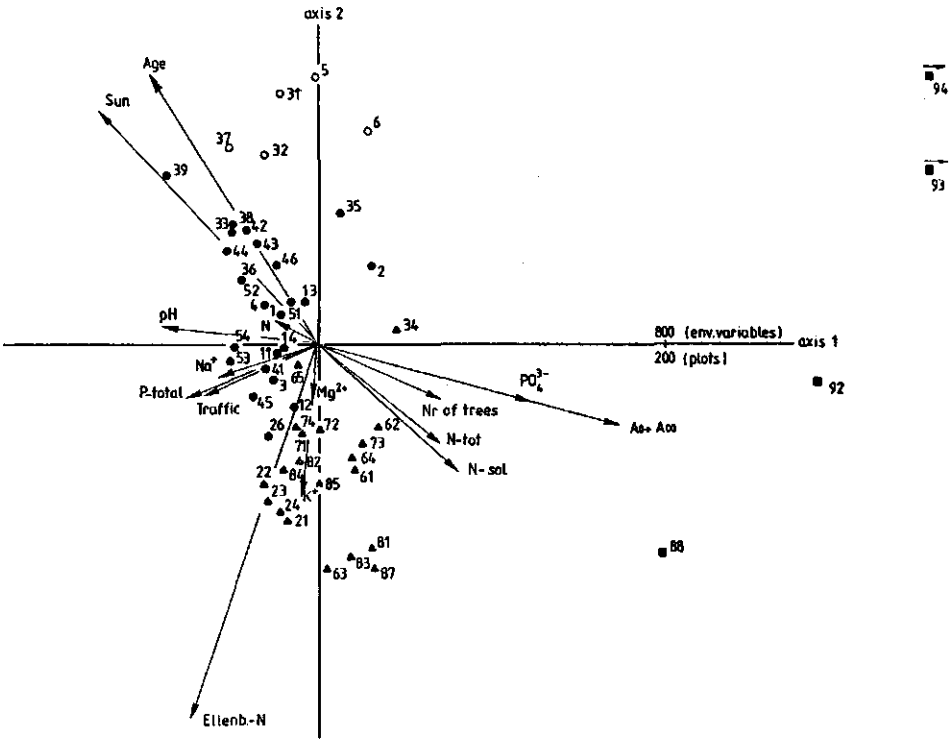


Fig. 3. Biplot of environmental variables and plots of roadside verges planted with Common Oak on the basis of an ordination of the green plants.
○ = *Hypochaeris radicata Quercus* type, subtype of *Hieracium pilosella*
● = *Hypochaeris radicata Quercus* type, subtype of *Lotus corniculatus*
▲ = *Anthriscus sylvestris* type
■ = *Mnium hornum* type

3.1.1. Environmental factors.

The result of the ordination with the computer program CANOCO is presented in fig. 3. This result is in good accordance with the classification presented above. The (sub)types that were distinguished appear as clusters in the biplot. The *Mnium hornum* type is placed at the far right side of the first ordination axis. This axis correlates most obviously in a positive way with the environmental factor Ao + Aoo, i.e. the thickness of the organic layer. There is a weaker, negative correlation with the amount of potential sunshine ("openness") of the plot and with the pH of the soil. The second ordination axis correlates strongly with the Ellenberg values for nitrogen, the age of the trees and the openness of the plots. The last two factors are mutually strongly related and not independent: young trees hardly shade the plot. Apparently, most of the young plots have

a vegetation with low average Ellenberg-N value (see also table 2b). Plot Q39 takes in both fig. 3 and in table 1 an intermediate position between the *Hieracium pilosella* and the *Lotus corniculatus* subtypes.

The average values of the environmental factors for the distinguished plant communities are presented in table 2a. No significant differences between the *Hieracium pilosella*- and the *Lotus corniculatus* subtypes could be detected in any of the studied environmental factors. It appeared that the Ellenberg-N values of the *Anthriscus sylvestris* type were significantly higher than in each of the other (sub)types. In this type the trees were significantly older than in the *Hypochaeris radicata* type. The potential amount of sunshine was significantly lower than in the *Hypochaeris* type but higher than in the *Mnium hornum* type. The *Mnium hornum* type differed significantly from both other types with respect to potential amount of sunshine (lower), Ellenberg-N (lower), thickness of the organic layer (thicker), pH of the soil (lower) and the total N- and PO_4^{3-} concentration (higher). The moisture of the soil was higher than in the *Hypochaeris radicata* type but not higher than in the *Anthriscus sylvestris* type. Some correlations are the logical consequence of the strong causal relations that exist between some environmental variables, e.g. the amount of sunshine (low), thickness of the organic layer (large), pH (low) and moisture of the soil, see table 3.

The environmental differences between the types can be summerized as follows: the *Mnium hornum* type represents a typical forest habitat along sandy forest paths (except for plot Q88 which is along a paved road) which are not mown or otherwise managed. The *Anthriscus sylvestris* type plots are open to shady (but than along paved roads) with old trees and a nitrophilous vegetation. The *Hypochaeris radicata* type comprises plots with trees of all ages, with a grassland vegetation that is poorer in nutrients than plots of the *Anthriscus sylvestris* type. Within this type, the plots with the least productive vegetation are united in the *Hieracium pilosella* subtype. The majority of the plots were managed: 40 plots were mown 2 - 4 times a year without removal of the hay, 7 plots were mown with subsequent removal of the hay and in 6 plots no management was carried out during the study period. Of the *H. radicata* type 4 plots were mown with removal of the hay (Q4, Q11, Q14, Q35) and one plot got no treatment (Q43). The plots Q65, Q84 and Q21 of the *A. sylvestris* type were mown with removal of the hay and plot Q81 was not treated. All plots of the *M. hornum* type remained untreated.

3.2. *Ectomycorrhizal fungi.*

The results of the TWINSPAN classification for the ectomycorrhizal fungi are presented in table 4. Four types are recognized. The type richest in species is the *Cortinarius erythrinus* type, which can be subdivided in two subtypes, the *Laccaria amethystea* and the *Boletus edulis* subtype, both characterized by a large number of species. The *Russula ochroleuca* type has only two differential species and in addition many species in common with the *C. erytrhinus* type. However, differential species of the two subtypes are rare. The third type, the *Xerocomus rubellus* type is characterized by a few differential species. It is divided into a *X. rubellus* and an inops variant. The former has three differential species and many species in common with the *C. erythrinus* and the *R. ochroleuca* types. The latter variant lacks differential species but shares two species (*Russula parazurea*, *Xerocomus chrysenteron*) with the other types mentioned so far. The last type, the *Hebeloma mesophaeum* type is characterized by three differential species. It

can also be split up in a typical variant and an inops variant. The typical variant comprises only three plots (Q26, Q38, Q39) with three differential species and the inops variant lacks any differential species. However, the *H. mesophaeum* type has four differential species in common with the *C. erythrinus* type. The inops variants of the *X. rubellus* and the *H. mesophaeum* types differ mainly in the much lower presence in the latter variant of *Russula parazurea* and *Xerocomus chrysenteron* and the occurrence - although rather sparse- of some common differential species of the *C. erythrinus* type and the *H. mesopheum* type. The *X. rubellus* variant of the *X. rubellus* type, the *R. ochroleuca* type and the *C. erythrinus* type may be considered as related, owing to the large number of common differential species. Clearly there is increasing species richness in the order *X. rubellus* inops variant, *X. rubellus* typical variant, *R. ochroleuca* type, *C. erythrinus* type (see section 4.4). In plot Q54 (young trees, dominant herb plant species: *Elytrigia repens*) no mycorrhizal species were found at all. Consequently, this plot could not be classified. However, because of the lack of species it is assumed that the plot is mycologically related to the other species poor plots with young trees, i.e. the *H. mesophaeum* type. It is striking that the number of accompanying species is relatively small in comparison with the classification based on green plants (Table 1).

3.2.1. Environmental factors.

The CANOCO biplot for the plots and some environmental variables (fig. 4) is largely in accordance with the results of the TWINSPAN classification. The distinguished types appear more or less clustered in the figure. The first axis is mainly determined by the factors tree age and potential amount of sunshine (which are logically strongly correlated) and to a lesser extend the factors Ellenberg-N, Na^+-concentration and traffic intensity (the last two factors are also mutually correlated: roads with more traffic are more salted in winter). The second axis is built up mainly by the factors pH, N-soluble, thickness of the organic layer and the phosphate concentration.

The average values of the measured environmental variables are presented in table 2b. The plots of the *X. rubellus* type are characterized by a combination of old trees and relatively high nitrogen availability, expressed in the highest Ellenberg-N value and significantly higher nitrate concentrations. They vary from open to shady. The *R. ochroleuca* type has a significantly thicker organic layer and larger amounts of soluble and total nitrogen in the soil compared with the *C. erythrinus* type. The plots of the *R. ochroleuca* type are open to shady, along paved roads, have frequently a well developed organic layer and a vegetation which is less nitrophilous than in the *X. rubellus* type. The plots along sandy paths in forests are also included in this type (plots Q92, Q93, Q94). The *C. erythrinus* type consists of open to shady plots with a grassy vegetation, lacking an organic layer and relatively poor in nutrients (esp. P, N-soluble and N-total). The *Laccaria amethystea* subtype of this type unites the plots with old trees whereas the trees of the *Boletus edulis* subtype are middle-aged. The *H. mesophaeum* type has significantly more sunshine, a higher pH and a lower moisture than the *R. ochroleuca* type and the trees are younger than in all other plots (exception: plot Q26 which is old) and the plots are consequently hardly shadowed. The soil was often recently disturbed by road works, before the trees were planted.

The majority of the plots were managed by mowing without removal of the hay (40 plots of the 53). Four plots of the *C. erythrinus* type were mown with removal of the hay and of the *X. rubellus* and *R. ochroleuca* type two plots and one plot respectively. In 4

plots of the *R. ochroleuca* type no management was carried out; these were the plots along sandy paths inside forests. From the analyses, carried out with several combinations of environmental characters, it appeared that the concentrations of Mg^{2+}, Na^{+}, K^{+}, the C/N ratio, the number of trees per plot, the traffic intensity and the tree vitality contributed very little to the total amount of variation. Thus these factors were of little importance compared with the other environmental factors.

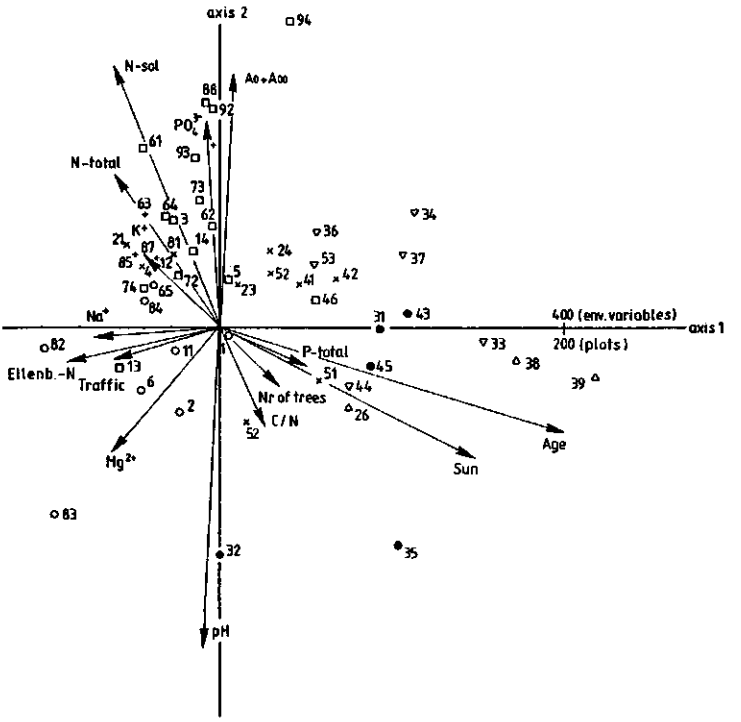


Fig. 4. Biplot of environmental variables and plots of roadside verges planted with Common Oak on the basis of an ordination of the ectomycorrhizal fungi.
✕ = *Xerocomus rubellus* type - inops variant
+ = *Xerocomus rubellus* type - typical variant
□ = *Russula ochroleuca* type
○ = *Cortinarius erythrinus* type, subtype of *Laccaria amethystea*
● = *Cortinarius erythrinus* type, subtype of *Boletus edulis*
△ = *Hebeloma mesophaeum* type, inops variant
▽ = *Hebeloma mesophaeum* type, typical variant

3.3. *Saprotrophic fungi.*

The group of saprotrophic fungi is ecologically less homogeneous than the group of mycorrhizal symbionts. Most saprotrophs in this investigation are proper terrestrial fungi, i.e. fungi growing on litter and humus of organisms living within the investigated

community (Arnolds, 1981), others are wood-inhabiting saprotrophs (marked with * in table 6). The distinction between these two groups is not clear-cut in species which grow on litter as well as on small pieces of wood (e.g. *Tubaria furfuracea*). These species were included in the analuses. A small number of species are associated with bryophytes, growing on dung, decaying fungi, or on other fungi or insects as parasites.

The two most important types are the *Psathyrella fulvescens* type and the *Mycena avenacea* type, both of them characterized by a large number of differential species. They also have many common differential species with regard to the third type, named after *Collybia cookei*. This type comprises 7 plots and 3 differential species. It is striking by its much lower number of species. Two species are in common with the *M. avenacea* type (*Rickenella fibula*, *R. setipes*), indicating that the *Collybia cookei* type is an impoverished variant of the former type. Plots Q36, Q37 and Q52 are somewhat intermediate. The *P. fulvescens* type can be subdivided into two subtypes on the basis of a large number of rather weakly differential species.

3.3.1. Environmental factors.

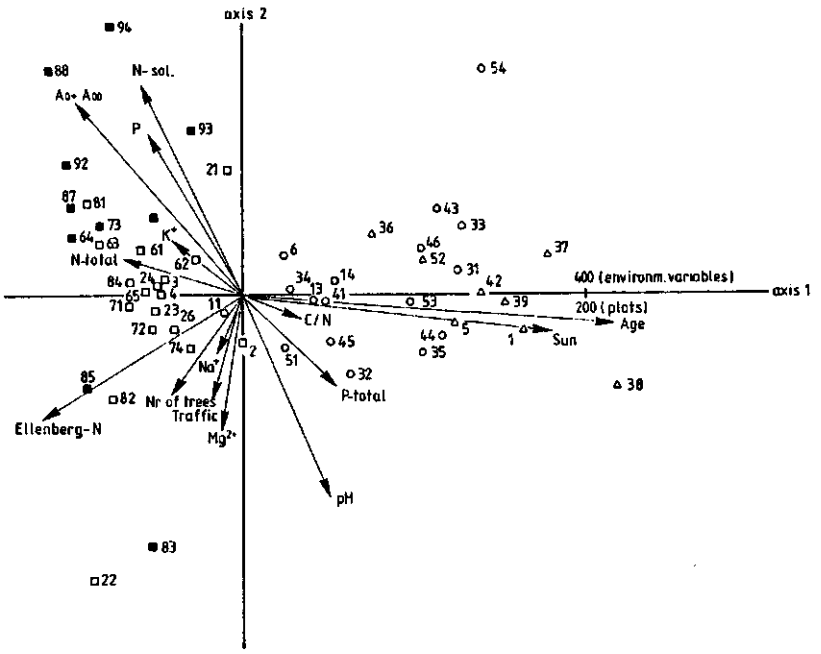


Fig. 5. Biplot of environmental variables and plots of roadside verges planted with Common Oak on the basis of an ordination of the saprotrophic fungi.
■ = *Psathyrella fulvescens Quercus* type, subtype of *Clitocybe vibecina*
□ = *Psathyrella fulvescens Quercus* type, subtype of *Lycoperdon foetidum*
○ = *Mycena avenacea* type
△ = *Collybia cookei* type

Fig. 5 illustrates the C.C.A. ordination based on the saprotrophic fungi. Generally, the arrangement of the plots coincides with the TWINSPAN typology. The species-poor plots Q52 and Q36 lie somewhat outside the cluster of the *Collybia cookei* type, indicating the intermediate position of these plots.

The first ordination axis correlates best with "age" and "sunshine" and to a lesser extent with the Ellenberg-N value and A_0+A_{00} (the thickness of the organic layer). The second axis correlates best with the concentration of soluble nitrogen and phosphate, the pH ($CaCl_2$) of the soil and the thickness of the organic layer. The cluster of the *P. fulvescens* type is widespread over the diagram along the second axis, indicating large variation in the environmental variables that correlate with that axis. Interestingly, the half-open plots, which were partly north- and partly south-exposed (plots Q61 - Q65 and Q71 - Q74 respectively), did not differentiate in the direction of the environmental factor "sunshine", as might be expected. This indicates that other factors influence more strongly the species composition in these plots.

The mean values of the environmental variables for the three types are presented in table 2c. The plots of the *P. fulvescens* type have a significantly higher Ellenberg-N value, thicker organic layer, moister upper soil layer with lower pH ($CaCl_2$) and older trees than all other plots. The plots of this type were shady with a well-developed organic layer (the *Clitocybe vibecina* subtype) or half open to open with a grassy, rather nitropilous vegetation (the *Lycoperdon foetidum* subtype). The environmental factors of the *M. avenacea* type showed no significant differences with the *Collybia cookei* type, although there is a tendency that the trees of the latter type are younger than in the other types and the soil nitrate content higher. The plots of the *M. avenacea* type are in open habitats with predominantly middle-aged trees and a grassland vegetation indicating a poorer soil than in the *P. fulvescens* type. Finally, the *C. cookei* type is characterized by a majority of plots with young trees, a rather oligotraphent (except for NO_3^-) vegetation, and occurrence on relatively recently disturbed soils.

The present management regimes in the plots of the *P. fulvescens* type and of the *M. avenacea* type do not differ much: respectively 4 and 3 plots were mown with removal of the hay. In the plots of the *P. fulvescens* type this management has started only recently. Four other plots of this type (plots along sandy forest paths) were not managed at all. This indicated that plots of the *M. avenacea* type are more intensively managed with more often removal of the hay.

4. **Conclusions and discussion.**

4.1. *General.*

In 53 plots 144 taxa of mycorrhizal fungi and 214 saprotrophs were found. The numbers of species per plot varied strongly, the extremes being plot Q54 (with young trees and eutraphent vegetation), with no ctomycorrhizal fungi and plot Q2 (with old trees and an oligotraphent vegetation) 68 ectomycorrhizal species were present. The number of saprotrophic species per plot varied between 6 and 45. Again, the plots with young trees were poorest in species. Richest in species were shady plots with old trees along paved roads.

4.2. *Discussion on applied methods.*

This investigation was basically carried out according to the methods proposed by Barkman (1976, 1987) and Arnolds (1981). Some adaptations were necessary, for practical reasons, owing to the habitat:

1. The plots are not of equal size, which might cause a bias in the data on species numbers, the expectation being that larger plots will contain more species. However, in this study there was no (significant) correlation between plot size and species numbers (e.g. for mycorrhizal fungi a correlation coefficient 0.07; n=53). In addition, plots with a larger or smaller size were neither grouped together in the phytocoenological nor in the mycocoenological types. It is therefore concluded that the sizes of the plots were sufficiently similar to enable meaningful conclusions.
2. Barkman (1976), Jansen (1984), Senn-Irlet (1986) and Winterhoff (1987) showed a clear relationship between the duration of the study and the number of species found. In this study, some plots were visited only two years, viz. 1987 and 1988. From the data of the other plots, it appeared that both years were mycologically richer than 1986, owing to less favourable climatic conditions in 1986. It is therefore assumed that the shorter period of the research in these plots has not essentially influenced the final results of this study, which are based on maximum numbers of carpophores and on total production.

4.3. *Comparison of communities based on plants, saprotrophic and mycorrhizal fungi.*

An abstraction of fungal communities (mycocoenoses) is called a mycocoenon (Arnolds, 1981). In an analogous way the terms ectomycocoenon and sapromycocoenon are introduced here to denote in a short way a fungal community of ectomycorrhizal symbionts and a fungal community of saprotrophs respectively. By using these terms, which may have some mnemonic value, one can avoid repeated circumscriptions of the communities.

The relationships between the distinguished community types based on green plants, saprotrophic and mycorrhizal fungi are expressed with the aid of the Sørensen Index of Similarity. The number of plots common to these communities served to determine the degree of similarity (table 7). There is a reasonable accordance between the phytocoena and the mycocoena. Apparently the three groups of organisms are to some degree determined by similar environmental conditions. However, some differences are present as well. Concerning the ectomycocoena, the *Xerocomus rubellus* type corresponds mainly with the *Anthriscus sylvestris* type, also with the *Lotus corniculatus* type. The *Russula ochroleuca* type is scattered over all plant communities, but with preference for the *A. sylvestris* type and *Mnium hornum* type. The *Cortinarius erythrinus* and *Hebeloma mesophaeum* type also occur in various plant communities, but are lacking in the *M. hornum* type.

The correlations are more clear in the sapromycocoena. The *Psathyrella fulvescens* type is mainly found in plots of the *A. sylvestris* phytocoenon and is also the only sapromycocoenon present in the *M. hornum* type. The *Mycena avenacea* and *Collybia cookei* types correlate with the *Hieracium pilosella* and *L. corniculatus* type.

The correlations between the sapro- and the ectomycocoena are less clear. The plots of the *P. fulvescens* type are mainly present in the *X. rubellus*- and *R. ochroleuca* types. The *M. avenacea*-type plots are more represented in the *C. erythrinus*- and *H. mesophaeum*

types and the *C. cookei* type has most resemblance with the *H. mesophaeum* type.

From this, it can be seen that the ecological results as shown in section 3.2 and 3.3 are largely confirmed. In contrast with the green plants, both saprotrophic and mycorrhizal fungi seem to be influenced by the tree age. This may also indicate the soil age because in many places tree-planting (often together with road reconstructing works) was probably the last main soil disturbance.

It is remarkable that the *H. pilosella* subtype, indicative for poor soil conditions, is not clearly represented in the fungal communities. Also remarkable is the observation that the grassland plots of the *L. corniculatus* phytocoenon have similar affinity with three different ectomycocoena.

In general, from table 7 it can be seen that the phytocoena and the sapromycocoena show a better mutual accordance than the ectomycocoena with each of these two coena. Apparently, green plants and saprotrophic fungi react in a more similar way on the present environmental variables than the mycorrhizal fungi. This can be understood by the fact that the latter are largely dependent on the phytobiont (the trees). For instance, a succession of ectomycorrhizal fungi has been described with increasing tree age (e.g. Dighton & Mason (1985); see also chapter 6).

4.4. *Evaluation of some environmental factors.*

The main environmental factors that determine the classification of plants and fungi are partly different (figs. 1, 2, 3 and table 2a-c). For the green plants, the presence of a well-developed organic layer (and mutually correlated environmental factors: P soluble, total N, number of trees) forms the main contribution to the first ordination axis and the Ellenberg-N values contribute most to the second axis. For both the ectomycorrhizal and saprotrophic fungi, the age of the trees and the strongly correlated potential amount of sunshine form largely the first axis and the organic layer, pH and related factors form the second axis. The Ellenberg-N values are a factor of less importance for the fungi. It is striking that the concentrations of most minerals (Mg^{2+}, Na^{+}, K^{+}) contribute hardly to the explanation of the distribution of plants and fungi in the plots. Phosphate (and to a lesser extent soluble nitrogen) seems to have more importance. However, the amount of phospate is positively correlated with thickness of the organic layer and therefore difficult to separate from it. It is also striking that none of the measured forms of nitrogen correlates with the Ellenberg-N values, which only correlated significantly with the K^{+}- and P-total concentration. A possible explanation is that during the period of soil sampling the greatest part of the N-compounds were present in the vegetation (Ellenberg, 1964). This is in concordance with the very low concentrations of especially NO_3 that were frequently found in this study.

The traffic intensity and tree vitality were originally supposed to constitute important factors influencing the fungi. However, from the ordinations it appeared that both factors play only minor roles (figs. 1-3). There was a significant negative correlation between the traffic intensity and thickness of organic matter layer. Along forest paths usually a well-developed organic layer is present, but along paved roads the traffic causes strong air currents that blow away part of the leaves. The thinner organic layer along roads (also inside forests) may be the most important reason for the deviating and often remarkably richer mycoflora in the roadside verges compared with the adjacent forest (personal observations; chapter 6).

The positive correlation between traffic intensity and the Na^{+} concentration in the soil

is probably due to salting of the roads in winter. Generally, roads with more traffic are more intensely salted. The Cl^- concentration in the soil (not determined in this study), enhanced by this measure, might reach toxic levels for trees, especially Beech (van der Burg, (1981); Dekker, 1988), but in Oaks no injury ascribable to Cl^- intoxication was found.

The tree vitality of stands of forest trees was repeatedly found to correlate positively with species numbers and carpophore numbers of ectomycorrhizal fungi, e.g. for stands of *Pinus sylvestris* (Termorshuizen & Schaffers, 1987) and *Pseudotsuga menziesii* (Jansen, 1991). This relation was not found in this study. There was a non-significant negative correlation between tree vitality and mycorrhizal species numbers ($p=-0.25$; $n=29$) and a non-significant positive correlation with Ellenberg-N values ($p=0.28$, $n=29$). This suggests that in roadsides, where the trees receive more light, the crown density as main vitality character is not usable in the same way as in forests, and that the relation tree vitality-species richness in roadsides might act differently.

In addition, in comparison with the above-mentioned investigations in forests, in the roadsides there is a wide variation in soil fertility and little variation in air pollution. In the poorest soils, the roadside trees have a reasonably high vitality thanks to the ectomycorrhizal symbionts and in the fertile soil plots the trees don't "need" an abundant ectomycorrhizal symbiosis / root development to reach sufficient nutrients.

From table 4 it is obvious that (except the *H. mesophaeum* type) the (sub)types of communities of mycorrhizal fungi constitute a series with increasing numbers of specis from the *X. rubellus* inops variant (left) to the *C. erythrinus* type (right). In table 5 the changes of some environmental factors along this series are presented. It appears that the most important change in these factors is towards lower NO_3^- and NH_4^+ concentrations, somewhat lower Ellenberg-N values and a thinner organic layer. This indicates that in plots with the highest nitrogen availability many species are lacking that are present in the other plots, but that very few species are favoured by or are characteristic for the higher nitrogen concentrations. On the other hand, among the green plants many nitrophilous species exist. This explains the relative large importance of the Ellenberg-N values in the ordination based on the green plants, compared with that on mycorrhizal fungi. The saprotrophs occupy an intermediate position.

It is repeatedly reported that negative correlations exist between the abundance of herbs in forests and fungi (Haas, 1952: 41, 69; Leischner-Siska, 1937; Runge, 1963; Barkman, 1976; Jahn, 1986). However, other data do not support this hypothesis: some forests lacking herbs are poor in (mycorrhizal) fungi and some young plantations with a large grass cover can be relatively rich in fungi (Jansen & De Vries, 1988).

In fig. 6a the relation between the coverage degree of the phanerogams and the number of ectomycorrhizal species is plotted. There is a significantly negative correlation ($r=-0.43^{**}$, $p<0.001$, $n=53$) between plant cover and number of ectomycorhizal species. However, the correlation between the coverage degree of the phanerogams and the number of saprotrophic species is not significant ($r=0.19$, $n=53$); see fig. 6b. Therefore, the above-mentioned hypothesis is supported by the present data regarding ectomycorrhizal species, not for saprotrophic fungi. On the other hand, in a dense vegetation a rich mycoflora can be present, e.g. plot Q32 with a coverage of 95% and 30 ectomycorrhizal species. In the field often carpophores of fungi were observed penetrating dense tufts of grasses. It is therefore concluded that a well-developed grass cover alone does not necessarily hamper the occurrence of a rich mycorrhizal mycoflora. Under some circumstances, a high cover by herbs and a low number of mycorrhizal fungi are caused

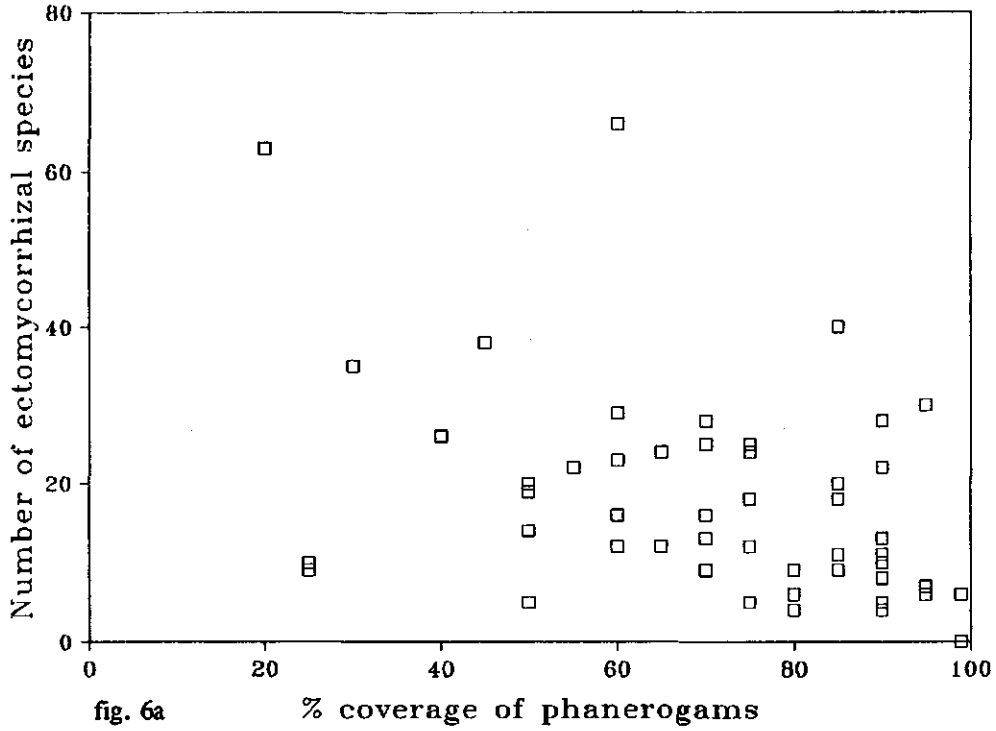

Number of ectomycorrhizal species
0
20
40
60
80
0
20
40
60
80
100
% coverage of phanerogams

fig. 6a

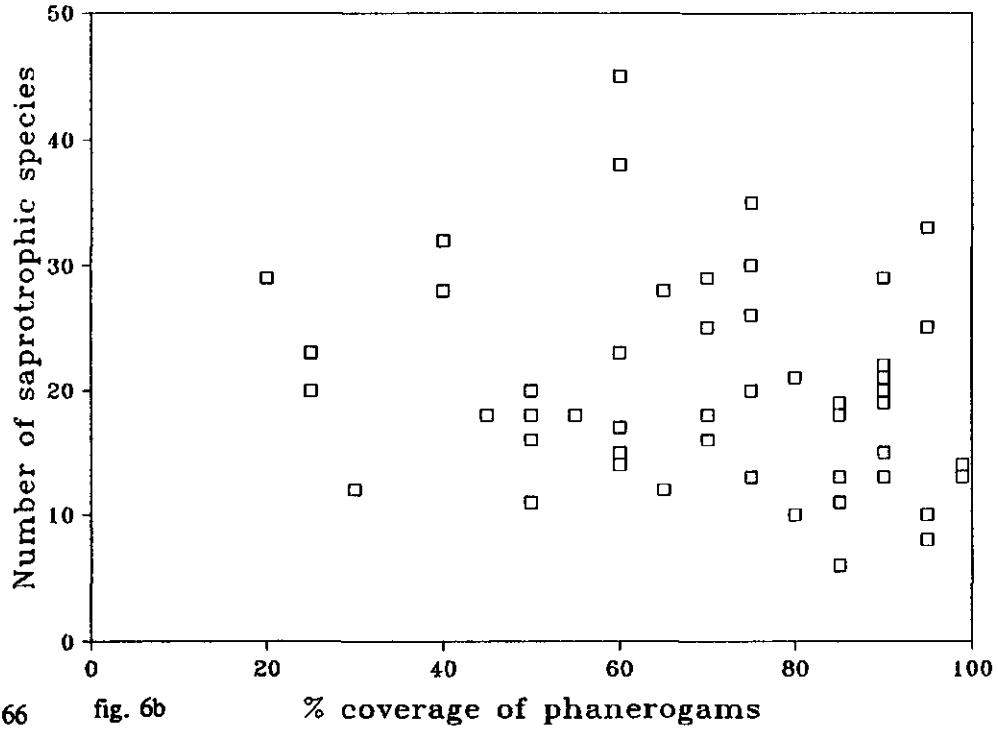

Number of saprotrophic species
0
10
20
30
40
50
0
20
40
60
80
100
% coverage of phanerogams

fig. 6b

Fig. 6a. Relation between the number of ectomycorrhizal species and the coverage of phanerogams in roadside verges plantes with Oak.
Fig. 6b. Relation between the number of saprotrophic species and the coverage of phanerogams in roadside verges plantes with Oak.

by the same event, e.g. eutrophication. However, it is still possible that some plant species release substances harmful to (some) mycorrhizal fungi.

In roadside verges the numbers of some mycorrhizal fungi decrease after termination of mowing when dead grass material begins to accumulate (cf chapter 7). This may indicate that the presence of a thick layer of grass litter is an unfavourable factor for the fructification of mycorrhizal fungi. The data of table 5 confirm this, the species-rich *Cortinarius erythrinus* type having a thinner $A_0 + A_{00}$ layer than the species-poor *Xerocomus rubellus*- and *Russula ochroleuca* type. However, the thicker litter and humus layer originated partly from the trees and not from the herbs. For the saprotrophic fungi no relation was found between the phanerogam coverage and the species richness. In plots with old trees the plots rich in species (more than 30 species) had an average coverage of 69% and the plots poor in species (less than 15 species) with old trees had an average coverage of 67%.

Table 1. Vegetation table of plots in roadside verges planted with Oaks. The values are cover estimations transformed after Westhoff & van der Maarel (1973).

Scheme of table 1.

Type Hypochaeris radicata		**Type** Anthriscus sylvestris		**Type** Mnium hornum
Subtype Hieracium pilosella	**Subtype** Lotus corniculatus			
		Variant inops		

```
Plot             3 333345    1113344445534316778222225667788668888999
nr.             576126944123413438135612524252441234631213253413782 34

cover           576699899829877678578969497659738778999689479566722 45
herb layer (%)  055050559500505000055005050050000050900050550055005 00

cover           52 23321  6 . 1  1 1   13  .   .           . .      11
moss layer (%)  005550035501055200005000311000100000000001010000050 0

number          332343352453243243322324433214322332322332333133212 21
of species      759024687841919847489969526173408302844916948337691 52
```

Differential species of the Hypochaeris radicata type (26 plots)

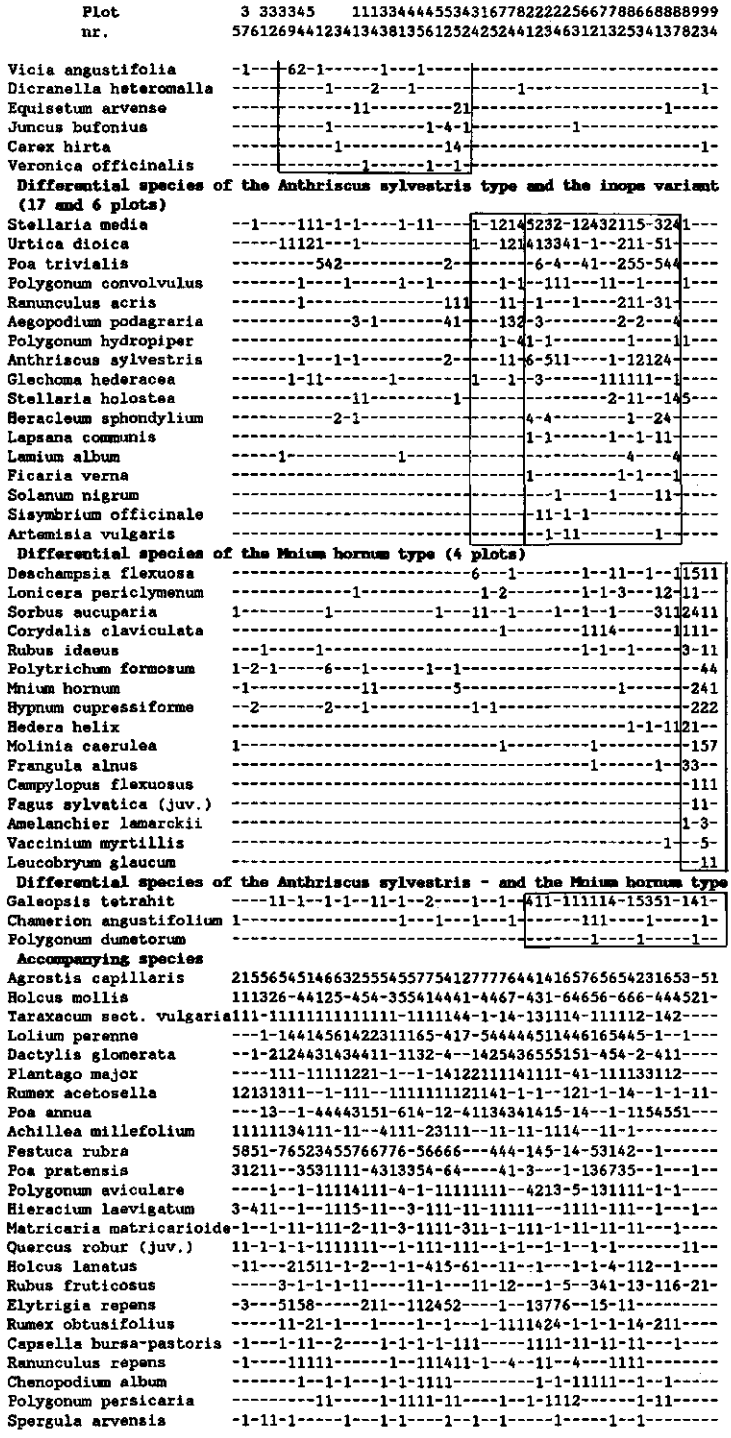
```
Plantago lanceolata      11111124-111111-1211111134---11---1-11-11----------
Trifolium repens         11--14521211-11-1211111114---11-------1-11-1---------
Anthoxanthum odoratum    -1315--3-24-112516-5-1-516-1-14--------1-11--1-------
Rumex acetosa            11---1-111111-1-11---1-11----1-111-----11---1-------
Brachythecium rutabulum  4---1114441---111214--15111---------1----------------
Leontodon autumnalis     1--11-434---11--1111-111-1-1-----1--16---------------
Ceratodon purpureus      652521111---11-11-11-4--3-1-----------------1--------
Festuca ovina            6477813--85662-2-5-------1-241-5--------------------
Hypochaeris radicata     -111-442-1--11--11-111111-----------2---------------
Rhytidiadelphus squarros13--64---331----14-6-2-513-------------1-------------
Pseudoscleropodium purum12--21-4--11--2-1--4-1--411-------------------------
Luzula campestris        4-4-3----11--12-1--1-1-31----1-----------------------
Phleum pratense          ----311-111---11-1--1-----------1-1----1--------
Trifolium pratense       1-1----2--1---111---11-4-41--1-----------------------
Cerastium fontanum       12---111------1-11---1141-------------------------
Vicia cracca             --1----1-11--11-1-------1-------1--------------------
Trifolium dubium         11---151--------11-----1--------------------------
Genista scoparia         -2-1--1--111-------------1-------------------------
Stellaria graminis       1------1--------1----2---1----------------1---------
Hieracium umbellatum     --1--------11-1-1--------------------------------
Phragmites australis     --1-1----1-------------1-1-------------------------
Ornithopus perpusillus   ---1--1----------2-----1---------------------------
Salix aurita             1-1---1-----------------1--------------------------
Veronica arvensis        -1-----11--------------------------------------
Hypericum perforatum     1---------1-------1-------------------------------
Campanula rotundifolia   -------1----2-----1-------------------------------
```

Differential species of the Hieracium pilosella subtype (5 plots)

```
Hieracium pilosella      4-211--1--1-------1--1-11-----------------------------
Brachythecium albicans   65-144----------5-1-------1---------------------------
Arabidopsis thaliana     1--11--1-----------------------------------------------
Polytrichum piliferum    21-51-------------------------------------------------
Aira praecox             ---31--------1-----------------------------------------
Plagiomnium affine       --1-1-------------------1-----------------------------
Polytrichum juniperinum  --421-------------------------------------------------
```

Differential species of the Lotus corniculatus subtype (21 plots)

```
Eurhynchium praelongum   ----11----1--134-3-4----21--1-1-----------1----------
Lotus corniculatus       -1----1--1--11-1--1-1---1-------------------------
Atrichum undulatum       -----14------111-1-2-1----1---1-----------1----------
```


Plot nr.
3 333345 111334444553431677822222566778668888999
576126944123413438135612524252441234631213253413782 34
Vicia angustifolia
Dicranella heteromalla
Equisetum arvense
Juncus bufonius
Carex hirta
Veronica officinalis
Differential species of the Anthriscus sylvestris type and the inops variant (17 and 6 plots)
Stellaria media
Urtica dioica
Poa trivialis
Polygonum convolvulus
Ranunculus acris
Aegopodium podagraria
Polygonum hydropiper
Anthriscus sylvestris
Glechoma hederacea
Stellaria holostea
Heracleum sphondylium
Lapsana communis
Lamium album
Ficaria verna
Solanum nigrum
Sisymbrium officinale
Artemisia vulgaris
Differential species of the Mnium hornum type (4 plots)
Deschampsia flexuosa
Lonicera periclymenum
Sorbus aucuparia
Corydalis claviculata
Rubus idaeus
Polytrichum formosum
Mnium hornum
Hypnum cupressiforme
Hedera helix
Molinia caerulea
Frangula alnus
Campylopus flexuosus
Fagus sylvatica (juv.)
Amelanchier lamarckii
Vaccinium myrtillis
Leucobryum glaucum
Differential species of the Anthriscus sylvestris - and the Mnium hornum type
Galeopsis tetrahit
Chamerion angustifolium
Polygonum dumetorum
Accompanying species
Agrostis capillaris
Holcus mollis
Taraxacum sect. vulgaria
Lolium perenne
Dactylis glomerata
Plantago major
Rumex acetosella
Poa annua
Achillea millefolium
Festuca rubra
Poa pratensis
Polygonum aviculare
Hieracium laevigatum
Matricaria matricarioide
Quercus robur (juv.)
Holcus lanatus
Rubus fruticosus
Elytrigia repens
Rumex obtusifolius
Capsella bursa-pastoris
Ranunculus repens
Chenopodium album
Polygonum persicaria
Spergula arvensis

```
Plot            3 333345    1113344445534316778222225667788668888999
nr.            576126944123413438135612524252441234631213253413782334

Lysimachia vulgaris     ---------1---1---------111-1--1-------1-1-1----------
Prunus serotinus        1------1--111-------------11-------------1----2---1--
Bromus hordeaceus ssp.
 mollis                 ----2--11-------1------1--1------1---2--1------------
Senecio sylvatica       -1---1------1-------------1-4--3-------1-------1-----
Viola arvensis          -2-----11-------1-1-----------------1---------------
Tanacetum officinale    ----1-------1---1-2-------------1--2----------------
Senecio vulgaris        -------1--------1----------1-----1--11---------------
Galium aparine          -------1--------1---1----------1--------------1-----
Crataegis laevigata     -------1----------------1---------1----------1-------
Gnaphalium uliginosum   -------------1---------1----------------------11-----
Myosotis arvensis       -------11-----------------------1------1------------
Veronica arvensis       ---------1----1---------------1----------------1-----
Silene dioica           --------------1--------1------2----------------1-----
Betula sp.              ----------1---------------1--2-----------------------
Cladonia chlorophaea    1-----------------------1-1-------------------------
Melampyrum pratense     --1-------------------------------------1--------1--
Populus canescens       -------------------------3-------------------11-----
Carex pilulifera        ----------1---------------1-----------------------1-
```

Species occurring in less than three plots

Q5: Erica tetralix 1, Trifolium hybridum 1; Q37: Anthoxanthum puelli 2; Q6: Dicranum scoparium 1; Q31: Aphanea arvensis 1, Erophila verna, Jasione montana 1, Teesdalia nudicaulis 1; Q32: Calluna vulgaris 1, Chrysanthemum leucanthemum 1, Ranunculus bulbosus 1, Vicia spec. 1, Bryum bicolor 1; Q36: Cirsium arvense 1; Q39: Crepis capillaris 2, Vicia hirsuta 4, Polytrichum commune 5, Geranium molle; Q44: Crepis capillaris 2, Vicia hirsuta 1, Cerastium arvense 4, Fumaria officinalis, Prunus spinosa 1; Q1: Juncus effusus 1, Lupinus polyphyllus 1, Bidens tripartitus, Potentilla anserina, Angelica sylvestris 1, Carex nigra 4, Sedum reflexum 1; Q2: Luzula multiflora 1, Galium saxatile 1, Calluna vulgaris 1, Erica tetralix 1, Acer pseudoplatanus (juv.) 1, Apera spica-venti 1, Campylopus pyriformis 1; Q3: Galium saxatile 1; Q11: Sedum telephium 3, Calamagrostis canescens 1; Q13: Sedum telephium 1, Lysimachia nummularia 1; Q14: Cirsium arvense 1; Q33: Linaria vulgaris 1, Viola canina 1; Q41: Thlaspi arvense 1, Bryum argenteum 1; Q45: Sonchus oleraceus 1; Q51: Lupinus polyphyllus 4; Q52: Juncus effusus 1, Rumex crispus 1, Symphytum officinale 1; Q35: Pohlia nutans 4, Bryum caespiticium 1, Cladonia coniocraea 1; Q42: Galeopsis speciosa 1; Q34: Linaria vulgaris 1, Campanula rapunculoides 1; Q65: Spergularia rubra 3; Q72: Bidens tripartitus 1, Calamagrostis canescens 2, Phalaris arundinacea 1, Succisa pratensis 1; Q74: Dryopteris dilatata 1, Bellis perennis 1, Rubus caesius 1; Q84: Gnaphalium sylvaticum 1; Q22: Thlaspi arvense 1, Calamagrostis epigeios 1; Q26: Geranium molle 1, Potentilla anserina 1, Silene pratense 1; Q53: Rumex crispus 1, Avena sativa 1; Q62: Agrostis gigantea 1; Q71: Apera spica-venti 1; Q82: Acer pseudoplatanus (juv.) 1, Oxalis acetosella 1; Q63: Phalaris arundinacea 1, Calamagrostis epigeios 2, Dryopteris carthusiana 1, Festuca pratensis 1, Geum urbanum 1, Valeriana officinalis 1; Q64: Polygonatum multiflorum 1, Populus tremula 1; Q81: Prunus padus 1; Q83: Sonchus oleraceus 1, Dryopteris dilatata 1, Corylus avellana 1, Galinsoga parviflora 1, Luzula pilosa 1, Milium effusum 1, Stachys sylvatica 1; Q87: Sambucus nigra 1, Q88: Polypodium vulgare 1; Q92: Campylopus pyriformis 1; Q93: Luzula multiflora 1, Digitalis purpurea 1, Plagiothecium undulatum 1; Q94: Dicranum scoparium 1, Pohlia nutans 1.

Table 2a. Average values and standard deviations of environmental variables of plot types based on the composition of green plants. For explanation of the environmental factors, see text.
a: difference significant (Kruskal-Wallist test, $p<0,05$) between columns 1 and 3; b: idem for columns 2 and 3; c: idem for columns 3 and 4; d: idem for columns 1 and 4; e: idem for columns 2 and 4.

Phytocoenon	1. Hieracium pilosella-subtype (n=5)		2. Lotus corniculatus-type (n=23)		3. Anthriscus sylvestris-type (n=23)		4. Mnium hornum-type (n=4)	
Environmental variable	mean	std.	mean	std.	mean	std.	mean	std.
trees (nr.1000 m^{-2})	41	18	43	14	50	22	65	3
traffic (classes I-VI)	1.6	1.3	2.0	2.1	2.3	1.3	1.0	0.0
Ellenberg-N	3.8	0.8	5.4	0.7	6.7^{abc}	0.6	4.0	2.0
Vitality (classes I-IV)	x	x	2.1	0.7	1.8	0.2	1.8	0.5
A_0+A_{00} (cm)	0.0	0.0	0.2	0.5	1.1	1.3	$5.5^{d,e}$	4.4
Age (years, in 1988)	54	29	55	39	102^{ab}	30	116	19
Potential sunshine *	6.9	1.2	6.8	1.7	3.1^{b}	3.2	$0^{d,e}$	
pH($CaCl_2$)	4.2	0.4	4.2	0.4	4.0	1.0	3.3^{d}	0.4
Mg^{2+} ($mg.kg^{-1}$)	27.2	29.0	35.1	21.4	33.0	18.9	36.0	14.4
Na^{+} ($mg.kg^{-1}$)	26.0	15.1	22.2	11.2	27.8	20.0	12.5	2.4
K^{+} ($mg.kg^{-1}$)	31.0	10.3	48.6	24.0	51.8	24.6	46.8	7.7
NO_3^{-} ($mg.kg^{-1}$)	0.8	1.8	1.0	2.3	1.1	1.0	0.8	0.5
NH_4^{+} ($mg.kg^{-1}$)	6.2	2.3	9.7	6.5	9.1	5.0	12.3^{d}	1.3
N soluble ($mg.kg^{-1}$)	13.2	1.1	16.5	6.4	17.8	5.8	26.3^{d}	3.4
N total (% N)	0.14	0.03	0.17	0.06	0.19	0.06	$0.24^{c,d,e}$	0.08
PO_4^{3-} ($mg.kg^{-1}$)	0	0	0.5	1.0	0.4	0.6	$3.0^{c,d,e}$	2.0
P total ($mg.kg^{-1}$)	213	79	281	160	275	135	146	43
C (%C)	2.4	0.9	3.2	1.0	2.8	0.8	3.7	1.5
C/N	17.9	4.7	19.2	6.4	16.7	7.1	16.5	8.6
soil moisture	11.9	5.2	10.6	4.4	18.5	10.3	35.2^{e}	9.4

x = not observed.
* = hours potential sunshine per day in October.

Table 2b. Average values and standard deviations of environmental variables of plot types based on the composition of mycorrhizal symbionts. For explanation of the environmental variables, see text.
a: difference significant (Kruskal-Wallis test, $p<0.05$) between columns 1 and 3; b: idem for columns 2 and 3; c: idem for columns 4 and 3; d: idem for columns 1 and 4; e: idem for columns 2 and 4.

Ectomycocoenon	1. Xerocomus rubellus type (n=16)		2. Russula ochroleuca type (n=15)		3. Cortinarius erythrinus type (n=13)		4. Hebeloma mesophaeum type (n=9)	
Environmental variable	mean	std.	mean	std.	mean	std.	mean	std.
Trees (nr-1000m²)	45	24	52	15	46	17	43	8
Traffic (classes I-VI)	2.3	1.2	1.4	1.1	2.2	2.3	2.1	1.4
Ellenberg-N	6.4	1.0	5.3	1.7	5.3	1.3	5.4	0.5
Vitality (classes I-IV)	1.9	0.3	1.8	0.3	2.6	0.6		
A_0+A_{00} (cm)	1.0	1.4	2.2[b]	3.3	0.1	0.3	0.3	0.5
Age (years in 1988)	97	40	98	27	80	31	20[c,d,e]	8
Potential sunshine *	4.7	3.2	3.1	3.2	4.7	3.5	7.3[e]	1.1
pH ($CaCl_2$)	4.2	0.4	3.5[e]	1.1	4.4	0.7	4.3	0.4
Mg^{2+} ($mg.kg^{-1}$)	39.6	21.2	35.2	19.5	28.6	21.2	25.8	15.5
Na^{+} ($mg.kg^{-1}$)	23.4	13.0	20.6	17.8	31.8	18.4	21.0	11.5
K^{+} ($mg.kg^{-1}$)	54.3	28.3	49.0	15.9	38.6	9.1	50.0	34.4
NO_3^{-} ($mg.kg^{-1}$)	1.44[a]	0.89	.93	1.22	0.84	2.76	0.62	0.74
NH_4^{+} ($mg.kg^{-1}$)	10.13	6.82	10.20	4.33	6.54	2.44	10.38	6.65
N soluble ($mg.kg^{-1}$)	17.43	5.68	20.93[b]	6.67	13.69	3.73	17.25	7.05
N total (% N)	0.18	0.06	.21[b]	0.07	0.14	0.04	0.19	0.07
PO_4^{3-} ($mg.kg^{-1}$)	0.31	0.60	1.13	1.60	0.15	0.38	0.63	1.41
P total ($mg.kg^{-1}$)	278	124	216	101	262	184	313	147
C (% C)	3.3	0.9	3.1	1.3	2.7	0.7	2.7	0.9
C/N	21.0	9.4	14.9	4.7	18.7	3.4	14.8	3.5
Soil moisture	13.6	6.7	21.6[e]	10.9	16.8	13.2	9.9	3.4

* = hours potential sunshine per day in October.

Table 2c. Average values and standard deviations of environmental variables of plots of types based on the saprotrophic fungi. For explanation of the environmental variable see text.
a: difference significant (Kruskal-Wallis test, $p<0.05$) between columns 1 and 3; b: idem for columns 2 and 3; c: idem for columns 1 and 2.

Sapromycocoenon	1. Psathyrella fulvescens type (n=28)		2. Mycena avenacea type (n=17)		3. Entoloma sericeum type (n=8)	
	mean	std.	mean	std.	mean	std.
Trees (nr-1000m²)	49	20	47	18	40	16
Traffic (classes I-VI)	2.0	1.3	1.8	1.2	2.3	1.3
Ellenberg-N	$6.2^{a,c}$	1.3	5.3	1.1	4.9	0.8
Vitality (classes I-IV)	1.8	0.2	1.9	1.1	3.3	0.0
A_0+A_{00} (cm)	1.7^{a}	2.5	0.4	0.6	0.0	0.0
Age (years in 1988)	$111^{a,c}$	19	52	31	33	31
Potential sunshine*	$2.7^{a,c}$	3.1	6.8	1.5	6.8	2.0
pH ($CaCl_2$)	3.9^{c}	1.0	4.3	0.4	4.2	0.3
Mg^{2+} (mg.kg-1)	33.3	17.8	36.6	22.7	26.6	23.4
Na^{+}(mg.kg^{-1})	24.5	19.5	26.0	12.2	19.6	5.6
K^{+} (mg.kg^{-1})	51.0	21.7	48.2	26.9	36.9	14.0
NO_3^{-} (mg.kg^{-1})	0.96	1.90	0.59	0.71	2.29	3.73
NH_4^{+} (mg.kg^{-1})	9.4	4.69	9.47	6.47	9.86	5.84
N soluble (mg.kg^{-1})	18.50	6.34	16.41	6.69	16.00	4.51
N total (% N)	0.19	0.06	0.18	0.07	0.16	0.02
P (mg.kg^{-1})	0.68	1.28	0.53	1.07	0.14	0.38
P total (mg.kg^{-1})	234	110	311	185	252	87
C (% C)	3.1	1.0	2.8	1.0	3.0	1.0
C/N	18.1	7.9	16.9	5.5	18.1	3.4
Soil moisture	$21.1^{a,c}$	11.4	10.2	3.6	10.7	4.4

* = hours potential sunshine per day in October.

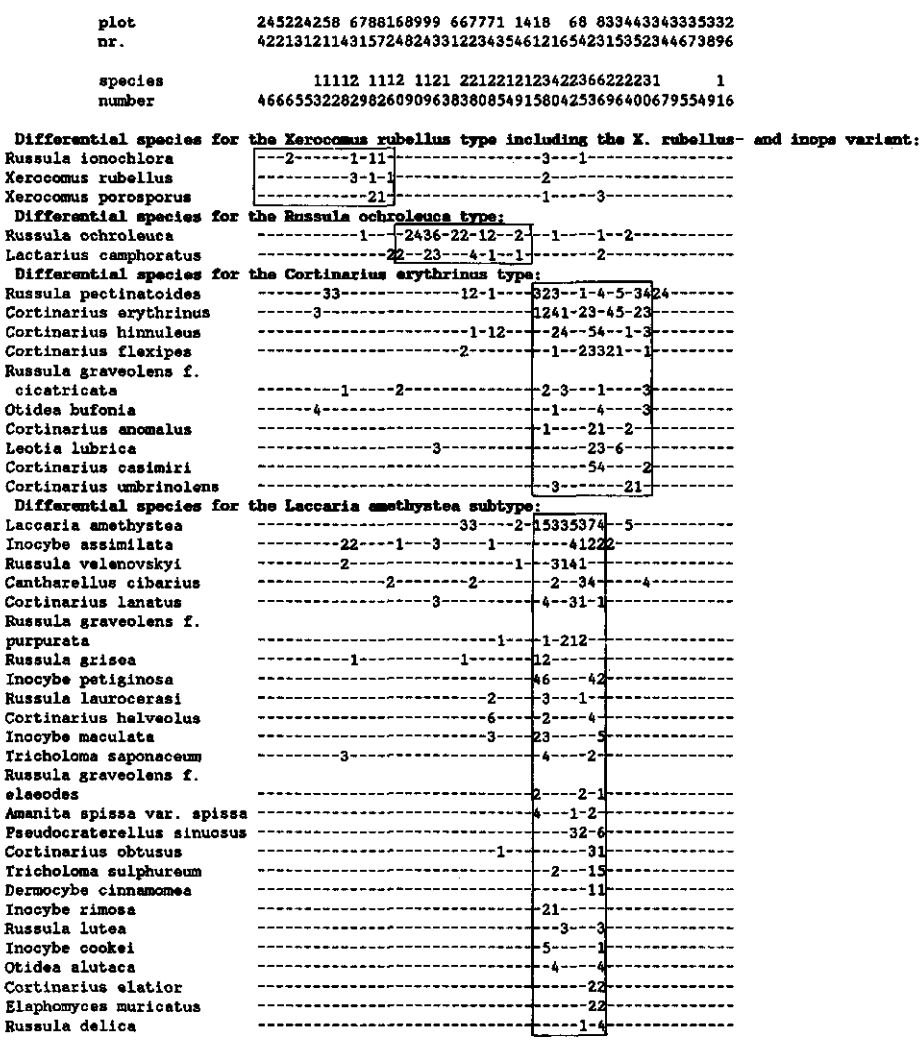
Table 3. Correlations between some environmental factors and the number of mycorrhizal species (Nsp-mr), * = significant at level $p<0.05$, ** = idem, $p<0.01$.

	Organic layer A_0+A_{00} (cm)	N total	Soil moisture	Number of ecto-mycorrhizal species
Traffic	-0.24*	0.10	0.09	0.06
Ellenberg-N	-0.14	0.13	-0.04	-0.05
A_0+A_{00} (cm)	1.00	0.18	0.30*	-0.11
Age (years in 1988)	0.23	0.02	0.46**	0.28*
Sun (hours/day^{-1})	-0.38*	-0.04	0.72**	-0.26*
pH ($CaCl_2$)	-0.40**	-0.00	-0.19	0.21
Mg^+ (mg.kg^{-1})	0.10	0.42*	-0.06	0.12
Na^+ (mg.kg^{-1})	-0.28	0.04	0.12	0.13
K^+ (mg.kg^{-1})	0.09	0.60**	0.01	-0.16
NO_{3-} (mg.kg^{-1})	0.02	0.10	-0.00	-0.40**
NH_4^+ (mg.kg^{-1})	0.04	0.38**	-0.02	-0.28*
N-soluble (mg.kg^{-1})	0.16	0.59**	0.27*	-0.15
N-total (% N)	0.17	1.00	0.24*	-0.19
PO_4^{3-} (mg.kg^{-1})	0.38**	0.54**	0.33**	-0.14
P total (mg.kg^{-1})	-0.18	0.24*	-0.21	-0.12
C (% C)	0.19	0.44**	0.0	0.00
C/N	-0.01	0.55**	0.12	0.12
Moist (fraction of dry weight)	0.30*	0.24*	1.00	0.20

Table 4. Mycocoenological table of ectomycorrhizal fungi in roadside verges planted with Common Oak. The values are the ln(y+1) transformed maximal numbers of carpophores per visit during three years, adjusted to 1000 m^2.

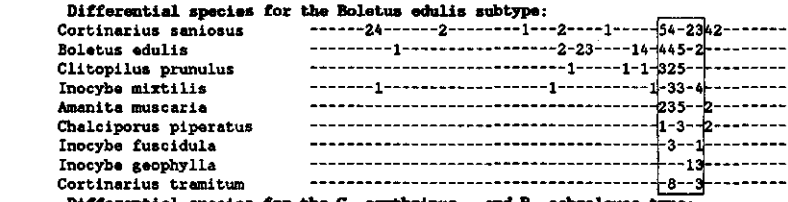
Scheme of table 4.

Type Xerocomus rubellus		Type Russula ochroleuca	Type Cortinarius erythrinus		Type Hebeloma mesophaeum	
			Subtype Laccaria amethystea	**Subtype** Boletus edulis		
Variant inops					**Variant** inops	

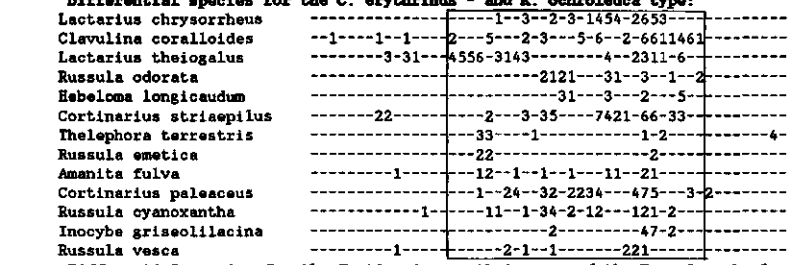


plot 245224258 6788168999 667771 1418 68 833443343335332
nr. 42213121143157248243312234354612165423153523446738 96

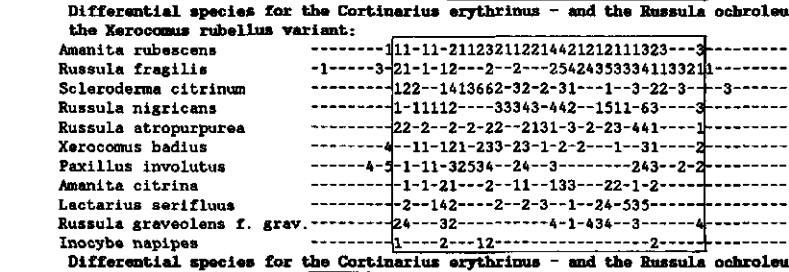
Differential species for the Boletus edulis subtype:



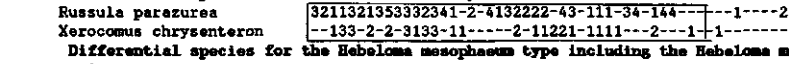
Differential species for the C. erythrinus - and R. ochroleuca type:



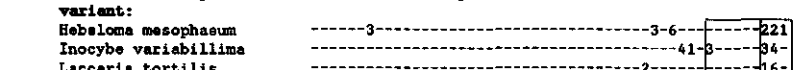
Differential species for the Cortinarius erythrinus - and the Russula ochroleuca type and the Xerocomus rubellus variant:



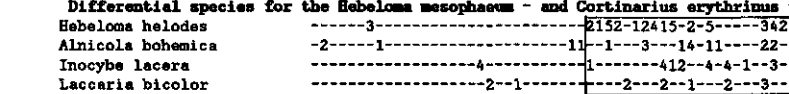
Differential species for the Cortinarius erythrinus - and the Russula ochroleuca and the X. rubellus type:



Differential species for the Hebeloma mesophaeum type including the Hebeloma mesophaeum- and inops variant:



Differential species for the Hebeloma mesophaeum - and Cortinarius erythrinus type:



Accompanying species:

Laccaria laccata 7451324331714325224 53-55243-3366627655646617434245 1-
Lactarius quietus 1322-24422423445454522331534351532127455842 4-21-3--1
Russula amoenolens 2--22214333-2111----2-43132551351312425445243 2-11--2
Sclerodema areolatum -21-2233--1-11--------12-3------2--22424-31411121231
Laccaria proxima ----------3-2----245--33-32-3-3-42333-4-32-3-324-55-
Inocybe albomarginata ------1-2----------4--2--------3----------

Species ocurring in less than three plots:

Q63: Inocybe pseudoasterospora var. microsperma 1; Q94: Cortinarius hemitrichus 1, Hydnotria tulasnei 2, Dermocybe cinnabarina 3; Q93: Inocybe pseudoasterospora var microsperma 3, Hebeloma anthracophilum 2; Q61: Lactarius vellereus 1; Q72: Alnicola escharoides 2, Xerocomus subtomentosus 1; Q74: Cortinarius comptulus 1; Q13: Amanita pantherina 1, Russula decipiens 5; Q14: Lactarius vellereus 3, Tricholoma scalpturatum 3; Q46: Inocybe calospora 1; Q11: Amanita pantherina 3; Cortinarius velenovskyi 1, Russula chloroides 2, Gyroporus castaneus 2, Boletus erythropus 3; Q1: Laccaria purpureobadia 4, Inocybe lanuginosa 1, Tylopilus felleus 1; Q6: Leccinum quercinum 1; Q65: Inocybe xanthomelas 2; Q2: Cortinarius parvannulatus 4, Hebeloma truncatum 3, Cortinarius privignus 2, Cortinarius hemitrichus 3, Hebeloma pallidoluctuosum 2, Alnicola escharoides 2, Phellodon confluens 1, Leccinum oxydabile 1, Boletopsis leucomelaena 1, Cortinarius balteatoalbus 1, Hebeloma spoliatum 2, Cortinarius causticus 2, Cortinarius tabularis 2, Hydnum repandum 4, Inocybe splendens 4, Hydnellum concrescens 4; Q83: Inocybe flocculosa 3, Russula densifolia 1, Hydnellum spongiosipes 1, Cortinarius torvus 1, Octavianina asterosperma 1, Inocybe cryptocystis 2, Inocybe grammata 2, Hymenogaster tener 2, Clavulina rugosa 3, Inocybe phaeocomis 3, Inocybe hirtella 4; Q31: Cortinarius paleiferus 1, Inocybe praetervisa 2; Q35: Cortinarius subbalaustinus 4; Q45: Inocybe spec. (see chapter 8) 1, Inocybe flocculosa 1; Q32: Inocybe sindonia 1, Hebeloma truncatum 4, Cortinarius privignus 5; Q44: Inocybe lanuginosa 4; Q34: Lactarius necator 1; Q39: Hebeloma pallidoluctuosum 3.

Table 5. Values of selected environmental variables in different subsets of plots which form a series of increasing richness in ectomycorrhizal species as a percentage of the average of the respective environmental factors of all plots except those of the *Hebeloma mesophaeum* type. For explanation of the communities see table 4.

	Cortinarius erythrinus	Cortinarius erythrinus and Russula ochroleuca type	Xerocomus rubellus variant, Russula ochroleuca and Cortinarius erythrinus type	Xerocomus rubellus and Russula ochroleuca type	Xerocomus rubellus type	Xerocomus rubellus inops variant
nr. of plots	13	28	33	30	15	10
nr. of species/plot	34	26	24	15	11	8.7
NO_3^- ($mg.kg^{-1}$)	10	64	82	139	167	155
NH_4^+ ($mg.kg^{-1}$)	72	93	90	112	113	134
Ellenberg-N	93	94	97	103	110	108
PO_4^{3-} ($mg.kg^{-1}$)	27	120	114	130	59	54
pH ($CaCl_2$)	110	98	98	89	105	100
Soil moisture	97	111	110	101	78	67
A_0+A_{00} (cm)	7	103	104	141	95	86

Table 6. Mycocoenological table of saprotrophic fungi in roadside verges planted with Common Oak. The values are the ln(y+1) transformed maximal numbers of carpophores per visit during three years, adjusted to 1000 m^2. Any maximal number of carpophores > 5000 have been given the value 9. * = wood inhabiting species.

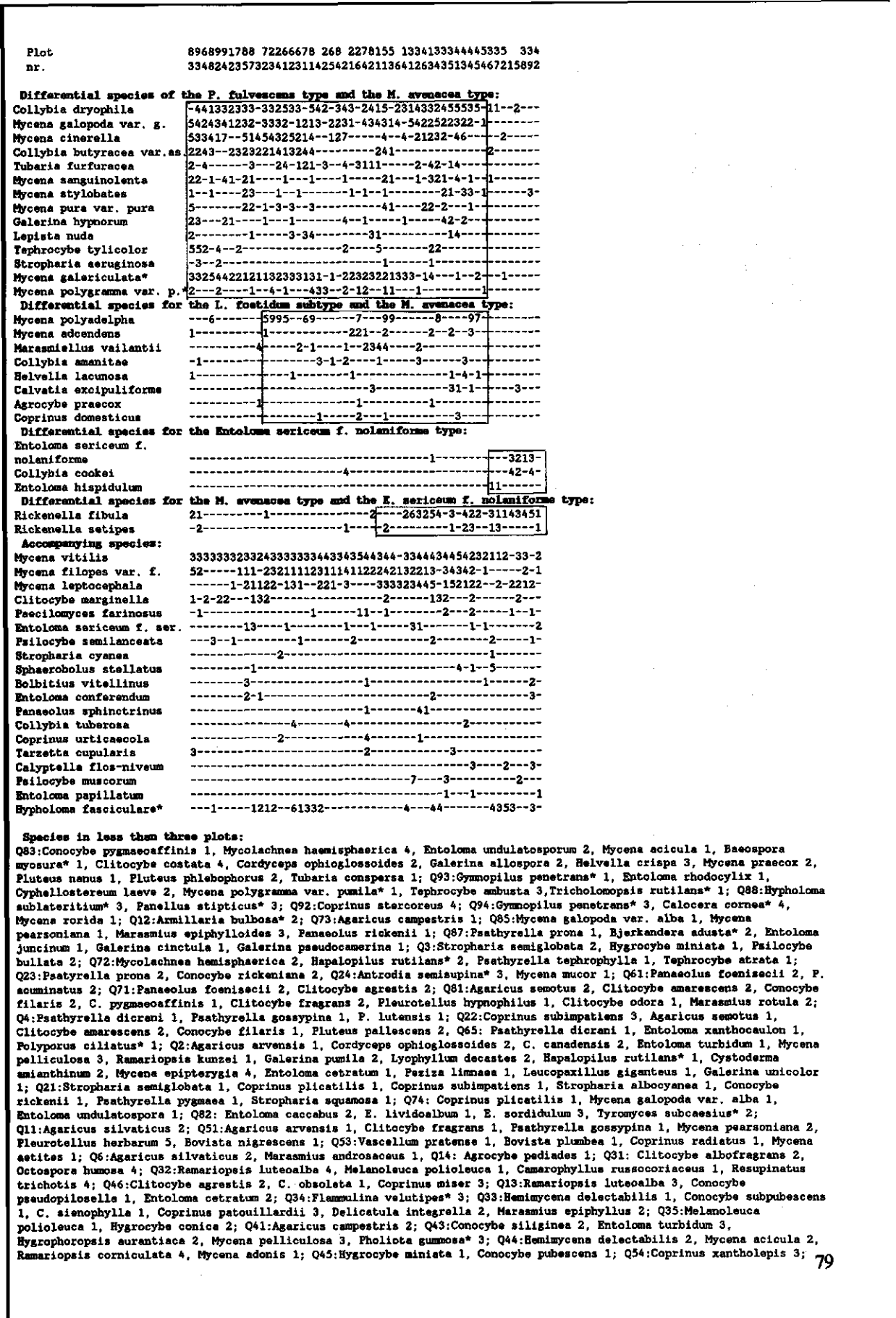
Scheme of table 6.

Type Psathyrella fulvescens		**Type** mycena avenacea	**Type** Collybia cookei
Subtype Clitocybe vibecina	**Subtype** Lycoperdon foetidum		

```
Plot                8968991788 72266678 268 2278155 1334133344445335  334
nr.                 33482423573234123114254216421136412634351345467215892

Species             43122111332222122121111221211321112231222231111  1111
number              52830643552901932689882914588802755106980633353661010

 Differential species of the Psathyrella fulvescens type:
Psathyrella fulv. var. br 22-33-133156653324534312411 2-------11---------------
Clitocybe metachroa      1113332122221221215 2---3-------12--------1---1-------
Clitocybe diatreta       --2-2---12---1----2----22---+2---1-------------------
Mycena flavescens        9----------5------4----2--45+1----1-------------------
Nyctalis asterophora     2-------1-23---------224----+--------3---------------
Psathyrella frustulenta  -1--2---2---2---3----11----+-----------------------
Marasmius graminum       --------3--------------1-2--+----------------1-------
Lepista nebularis        -------23------2---------1--+-----------------------
Clitocybe candicans      ----2----3--------2----------+----------1-------------
Panaeolus fimicola       ------1-----------------11--+-----------------------
Psathyrella gracilis     --------1---------4-1-------+-----------------------
Clitocybe ditopa         ----1---------1----1----1---+-----------------------
Psathyrella artemisiae   -33-32----3----11-3--211----+-----------------------
Trametes versicolor*     ---------3-------------1--41+-----------------------
Cyathus striatus         ---------4------5------1----+-----------------------
 Differential species of the Clitocybe vibecina subtype:
Clitocybe vibecina       --1433--43+------------2------------------1----------
Megacollybia platyphylla 21-3-------1--------1-----------------------------------
Mutinus caninus          1-33--------------------------------------------------
Psilocybe crobula        2-1---------+------------1-----------------------------
Lepista flaccida         --------12--+--------3-----------------------------------
Macrolepiota procera     -------21---+-----------------------------------------
Phallus impudicus        ----1----2--+-----------------------------------------
Collybia peronata        ----4-----4-+-----------------------------------------
Clitocybe gibba          --------23---+------2---------------------------------
Clitocybe clavipes       --2------2---+------2---------------------------------
Armillaria obscura*      -14-3-3121---+--1----64-4--------21-------------------
Mycena haematopus *      34---3-----+-------------1---------------------------
Panellus serotinus *     ----32------+-----------------------------------------
 Differential species of the Lycoperdon foetidum subtype:
Crepidotus variabilis    ---3--------+355--2--3----3----+1-------4--------------
Lycoperdon foetidum      ---------1--+2---3--3-------1--+-----------------------
Psathyrella spadiceogrisea---2-------+------3---1---1---+-----------------------
Anthurus archeri         ----------32+----------1------+-----------------------
Psathyrella microrhiza   ----------+--------2-3--1-----+-----------------------
Lycoperdon perlatum      ----------+-------22--2-------+-----------------------
Psathyrella piluliformis* 2---------+2----4132-433-----+--------------2---------
Psathyrella candolleana* ----------+---3---1-32--------2-----------------------
Pluteus atricapillus*    ----------+---1---111---------+-----------------------
Coprinus micaceus*       ----------+----------4-4---2--+-----------------------
Mycena cortiana*         ----------+---2--1-2---------+-----------------------
 Differential species of the Mycena avenacea type:
Mycena avenacea var. a.  ----------------1-----1----+223151413433311---+--3----2
Marasmius oreades        ----------1----3---11---2----+4334--2--234-4-------+----3---
Mycena vitrea            ----------------1-------1--1-1-2-44-33311-1---+1----2--
Cordyceps militaris      3-------------------1-------+-2-1-112--2-1---+1---4--
Galerina atkinsoniana    -2--------------------3-----+------22-45-3---+2------
Calocybe carnea          ----------------------------+1---------2-1---+--------
Ripartites tricholoma    1-------1-----------------+2-----------22---+--------
Clitopilus scyphoides    ----------------------------+-----------222--+--------
Coprinus friesii         ----------------------------+4----------2-2--+--------
Mycena filopes var. metata12-------12-2-------2--2----+1--1---5-414222-11------
Mycena speirea           -1---1---------1-----------+3-----2--1-4-2---+--------
Mycena flavoalba         2---------------------------+33--12---225-4---+--------
Melanotus philipsii      ----------3----------------+1-----4-----1--2--2-----
Conocybe semiglobata     ----------------------------+-------1-1-----1+--------
Camarophyllus niveus     ----------------------------+------1----5--1-+--------
Polyporus brumalis*      ---1------1-2-------1--1----+22-1--12--132----+----3---
```


Plot 8968991788 72266678 268 2278155 1334133344445335 334
nr. 33482423573234123114254216421136412634351345467215892
Differential species of the P. fulvescens type and the M. avenacea type:
Collybia dryophila -441332333-332533-542-343-2415-2314332455535-11--2---
Mycena galopoda var. g. 5424341232-3332-1213-2231-434314-5422522322-1-------
Mycena cinerella 533417--51454325214--127-----4--4-21232-46-----2-----
Collybia butyracea var.as 2243--2323221413244---------241-------------2-------
Tubaria furfuracea 2-4------3---24-121-3--4-3111-----2-42-14----------
Mycena sanguinolenta 22-1-41-21----1---1----1-----21---1-321-4-1-1-1-------
Mycena stylobates 1--1----23---1--1-------1-1--1--------21-33-1------3-
Mycena pura var. pura 5-------22-1-3-3--3----------41----22-2---1---------
Galerina hypnorum 23---21----1---1-------4--1-----1-----42-2---------
Lepista nuda 2--------1-----3-34---------31----------14----------
Tephrocybe tylicolor 552-4--2---------------2----5-------22----------
Stropharia aeruginosa -3--2-----------------------1------1----------
Mycena galericulata* 33254422121132333131-1-22323221333-14---1--2---1-----
Mycena polygramma var. p.* 2---2----1--4-1---433--2-12--11---1---------1-------
Differential species for the L. foetidum subtype and the M. avenacea type:
Mycena polyadelpha ---6------5995--69------7---99------8----97---------
Mycena adcendens 1----------1-----------221--2------2--2--3----------
Marasmiellus vailantii ----------4-----2-1----1--2344----2----------
Collybia amanitae -1---------------3-1-2----1-----3------3----------
Helvella lacunosa 1----------1--------1-------------1-4-1----------
Calvatia excipuliforme ----------3----------31-1-----3---
Agrocybe praecox ----------1----------1----------1----------
Coprinus domesticus ----------1-----2---1----------3----------
Differential species for the Entoloma sericeum f. nolaniforme type:
Entoloma sericeum f. nolaniforme ----------1---------3213-
Collybia cookei ----------4----------42-4-
Entoloma hispidulum ----------11------
Differential species for the M. avenacea type and the E. sericeum f. nolaniforme type:
Rickenella fibula 21---------1----------2----263254-3-422-31143451
Rickenella setipes -2----------1----2---------1-23--13-----1
Accompanying species:
Mycena vitilis 333333323324333333443343544344-3344434454232112-33-2
Mycena filopes var. f. 52-----111-232111123111411222423213 3-34342-1-----2-1
Mycena leptocephala ------1-21122-131--221-3----333323445-152122--2-2212-
Clitocybe marginella 1-2-22---132----------2------132---2------2---
Paecilomyces farinosus -1----------1------11--1--------2---2-----1--1-
Entoloma sericeum f. ser. --------13----1--------1---1-----31-------1-1-------2
Psilocybe semilanceata ---3--1---------1-------2----------2--------2-----1-
Stropharia cyanea ----------2----------1-------
Sphaerobolus stellatus --------1----------4-1--5------
Bolbitius vitellinus --------3----------1----------1------2-
Entoloma conferendum --------2-1----------2----------3-
Panaeolus sphinctrinus ----------1-------41----------
Collybia tuberosa ----------4-------4----------2----------
Coprinus urticaecola ----------2----------4-------1----------
Tarzetta cupularis 3----------2----------3----------
Calyptella flos-niveum ----------3----2---3-
Psilocybe muscorum ----------7----3----------2---
Entoloma papillatum ----------1---1---------1
Hypholoma fasciculare* ---1-----1212--61332----------4---44-------4353--3-
Species in less than three plots:
Q83:Conocybe pygmaeoaffinis 1, Mycolachnea haemisphaerica 4, Entoloma undulatosporum 2, Mycena acicula 1, Baeospora myosura* 1, Clitocybe costata 4, Cordyceps ophioglossoides 2, Galerina allospora 2, Helvella crispa 3, Mycena praecox 2, Pluteus nanus 1, Pluteus phlebophorus 2, Tubaria conspersa 1; Q93:Gymnopilus penetrans* 1, Entoloma rhodocylix 1, Cyphellostereum laeve 2, Mycena polygramma var. pumila* 1, Tephrocybe ambusta 3,Tricholomopsis rutilans* 1; Q88:Hypholoma sublateritium* 3, Panellus stipticus* 3; Q92:Coprinus stercoreus 4; Q94:Gymnopilus penetrans* 3, Calocera cornea* 4, Mycena rorida 1; Q12:Armillaria bulbosa* 2; Q73:Agaricus campestris 1; Q85:Mycena galopoda var. alba 1, Mycena pearsoniana 1, Marasmius epiphylloides 3, Panaeolus rickenii 1; Q87:Psathyrella prona 1, Bjerkandera adusta* 2, Entoloma juncinum 1, Galerina cinctula 1, Galerina pseudocamerina 1; Q3:Stropharia semiglobata 2, Hygrocybe miniata 1, Psilocybe bullata 2; Q72:Mycolachnea hemisphaerica 2, Hapalopilus rutilans* 2, Psathyrella tephrophylla 1, Tephrocybe atrata 1; Q23:Psatyrella prona 2, Conocybe rickeniana 2, Q24:Antrodia semisupina* 3, Mycena mucor 1; Q61:Panaeolus foenisecii 2, P. acuminatus 2; Q71:Panaeolus foenisecii 2, Clitocybe agrestis 2; Q81:Agaricus semotus 2, Clitocybe amarescens 2, Conocybe filaris 2, C. pygmaeoaffinis 1, Clitocybe fragrans 2, Pleurotellus hypnophilus 1, Clitocybe odora 1, Marasmius rotula 2; Q4:Psathyrella dicrani 1, Psathyrella gossypina 1, P. lutensis 1; Q22:Coprinus subimpatiens 3, Agaricus semotus 1, Clitocybe amarescens 2, Conocybe filaris 1, Pluteus pallescens 2, Q65: Psathyrella dicrani 1, Entoloma xanthocaulon 1, Polyporus ciliatus* 1; Q2:Agaricus arvensis 1, Cordyceps ophioglossoides 2, C. canadensis 2, Entoloma turbidum 1, Mycena pelliculosa 3, Ramariopsis kunzei 1, Galerina pumila 2, Lyophyllum decastes 2, Hapalopilus rutilans* 1, Cystoderma amianthinum 2, Mycena epipterygia 4, Entoloma cetratum 1, Peziza limnaea 1, Leucopaxillus giganteus 1, Galerina unicolor 1; Q21:Stropharia semiglobata 1, Coprinus plicatilis 1, Coprinus subimpatiens 1, Stropharia albocyanea 1, Conocybe rickenii 1, Psathyrella pygmaea 1, Stropharia squamosa 1; Q74: Coprinus plicatilis 1, Mycena galopoda var. alba 1, Entoloma undulatospora 1; Q82: Entoloma caccabus 2, E. lividoalbum 1, E. sordidulum 3, Tyromyces subcaesius* 2; Q11:Agaricus silvaticus 2; Q51:Agaricus arvensis 1, Clitocybe fragrans 1, Psathyrella gossypina 1, Mycena pearsoniana 2, Pleurotellus herbarum 5, Bovista nigrescens 1; Q53:Vascellum pratense 1, Bovista plumbea 1, Coprinus radiatus 1, Mycena aetites 1; Q6:Agaricus silvaticus 2, Marasmius androsaceus 1, Q14: Agrocybe pediades 1; Q31: Clitocybe albofragrans 2, Octospora humosa 4; Q32:Ramariopsis luteoalba 4, Melanoleuca polioleuca 1, Camarophyllus russocoriaceus 1, Resupinatus trichotis 4; Q46:Clitocybe agrestis 2, C. obsoleta 1, Coprinus miser 3; Q13:Ramariopsis luteoalba 3, Conocybe pseudopilosella 1, Entoloma cetratum 2; Q34:Flammulina velutipes* 3; Q33:Hemimycena delectabilis 1, Conocybe subpubescens 1, C. sienophylla 1, Coprinus patouillardii 3, Delicatula integrella 2, Marasmius epiphyllus 2; Q35:Melanoleuca polioleuca 1, Hygrocybe conica 2; Q41:Agaricus campestris 2; Q43:Conocybe siliginea 2, Entoloma turbidum 3, Hygrophoropsis aurantiaca 2, Mycena pelliculosa 3, Pholiota gummosa* 3; Q44:Hemimycena delectabilis 2, Mycena acicula 2, Ramariopsis corniculata 4, Mycena adonis 1; Q45:Hygrocybe miniata 1, Conocybe pubescens 1; Q54:Coprinus xantholepis 3;

Q36:Stropharia albocyanea 1; Q37:Entoloma cephalotrichum 1, Lepista sordida 2, Psathyrella cotonea* 1; Q38:Bovista plumbea 2, Mycena avenacea var. roseofusca 1, Ramariopsis kunzei 3; Q42:Ramariopsis laeticolor 4, Vascellum pratense 1, Ramariopsis helvecla 1.

Table 7. Sørensen indices of similarity* between the phytocoena, ectomycocoena and sapromycocoena.

Phyto- or mycocoena (types and subtypes)	Hieracium pilosella	Lotus corniculatus	Anthriscus sylvestris	Mnium hornum	Psathyrella fulvescens	Mycena avenacea	Collybia cookei
H. pilosella					0	27	31
L. corniculatus					12	63	41
A. sylvestris					82	10	0
M. hornum					25	0	0
X. rubellus	0	36	53	0	51	13	17
R. ochroleuca	10	22	32	38	51	19	9
C. erythrinus	33	35	22	0	24	40	10
H. mesophaeum	13	39	18	0	5	37	44

* Sørensen index of similarity (S):

$$S = \frac{2c}{A+B} \times 100$$

where c = number of plots common to two communities;
A = total number of plots in community A;
B = total number of plots in community B.

A COMPARISON OF THE MACROMYCETES OCCURRING IN ROADSIDE VERGES PLANTED WITH COMMON OAK (*QUERCUS ROBUR* L.) AND WITH BEECH (*FAGUS SYLVATICA* L.).

P.J. Keizer

Abstract.

The plant- and macromycete communities in plots in roadside verges planted with Common Oak (*Quercus robur* L.) and with Beech (*Fagus sylvatica* L.) are compared. The phytocoena distinguished in plots with oaks and beech trees are largely analogous. The communities of saprotrophic fungi are primarily based on Ellenberg nitrogen values, thickness of the organic layer, exposition of the plot, and the interdependent cover degrees of the herb layer and bryophyte layer. The distribution of the ectomycorrhizal fungi, however, depends in the first place on the tree species. The communities of ectomycorrhizal fungi in all plots together (with oak and with beech) are more or less similar to the communities distinguished in oak- and beech plots separately. Non-host specific ectomycorrhizal species dominate the plots on nutrient rich soil, causing a large resemblance between oak- and beech plots on such soils.

Contents

1. Introduction.

In this paper the macromycete communities occurring in roadside verge verges that are planted with Common Oak (*Quercus robur* L.) and with Beech (*Fagus sylvatica* L.) are compared. Sites were situated in the province of Drenthe, in the Northeast of the Netherlands. In this area many of the roads are bordered with trees, in most cases common Oak, less often Beech. The habitat "roadside verge verges planted with trees" has not received much attention in the mycological literature, although some incidental observations have indicated that a rich macromycete flora can be present along alleys. Darimont (1973) described the differences in mycoflora between a grassy verge of a road through an Ardennean Oak forest (Fago-Quercetum) and the forest itself. In the Netherlands, Reijnders (1968) and Arnolds (1968) mentioned the presence of a rich mycoflora along some alleys in old estates on alluvial clay. The macromycetes occurring in roadside verges on pleistocene sandy soils never were studied systematically.

Roadside verges planted with trees form a highly artificial habitat, deviating in many respects from forests. Due to these artificial properties, comprising the origin and arrangement of the trees, many environmental variables are constant or vary in a known way, which usually vary in forests, e.g. microclimate, structure and texture of the soil, concentration of minerals in the soil, tree species composition, age of the trees, treatment of the undergrowth, etc.. Therefore, roadside verge verges with trees offer a good opportunity of ecological studies on macromycetes.

This paper is one of a series of studies of macromycetes in roadside verge verges planted with trees. Other studies include the coenology and the ecology of the macromycetes that occur in roadside verge verges planted with Oaks or Beech trees (chapter 2 and 3). The fungal communities of roadside verges with Oaks and with Beech trees are compared with fungal communities in forests dominated by the same tree species in the Netherlands and other countries (chapter 5). The succession of fungal communities was studied in roadside verge verges with Oaks of various ages (chapter 6). In addition a field experiment was carried out to investigate the influence of different management treatments in a roadside verge with old Oaks (chapter 7).

The aims of this paper are:
1. to evaluate the differences between the mycoflora in roadside verge verges planted with Oak or Beech respectively;
2. to analyse the differences in ecology of some functional-ecological groups of fungi, i.c. ectomycorrhizal symbionts and saprotrophic fungi;
3. to investigate to what extent similarities in mycoflora between plots are determined either by tree species or by environmental conditions.

If the certain environmental variables or their combination are most important for the mycological composition of the plots, Beech and Oak plots belong to one ecological class of plots; if the dependence on the tree species is the most important determining factor for the fungal species composition, the plots are to be classified according to the host tree species.

2. Material and methods.

2.1. *Selection of the plots.*

Seventy six plots were selected within the Drentian phytogeographical district (Weeda in Heukels & Van der Meijden, 1983) in roadside verge verges with Oak (*Quercus*-plots) or Beech trees (*Fagus*-plots; Fig. 1). The area is situated in the northeastern part of the Netherlands, about 10 to 20 m above sea level. The soil consists of acidic pleistocene cover sands, often with a underlying layer of boulder-clay, incidentally with some remains of peat on a depth of 0 to 2 m. The original soil profile in the studied sites was usually disturbed due to road construction works.

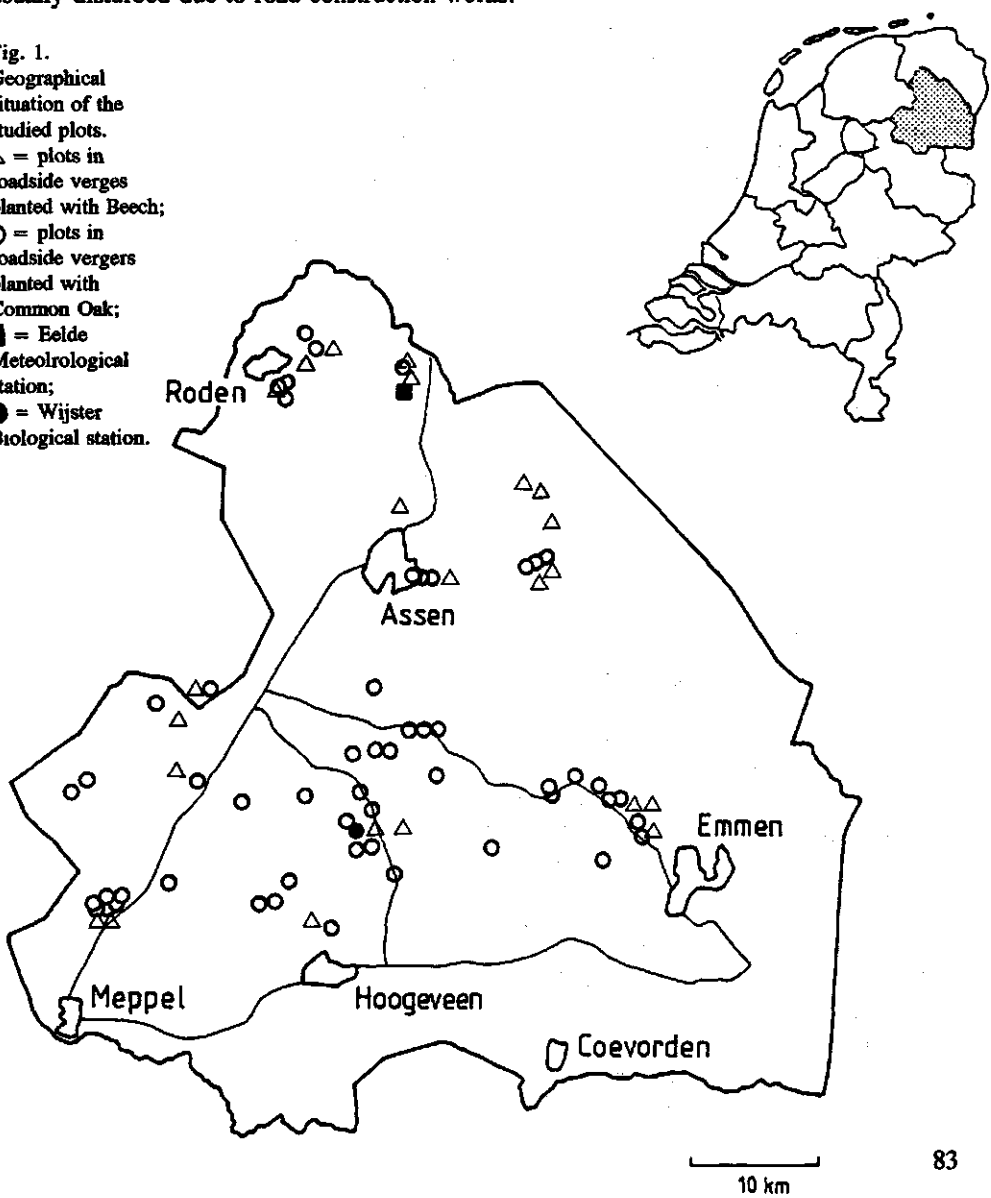


Fig. 1.
Geographical situation of the studied plots.
△ = plots in roadside verges planted with Beech;
○ = plots in roadside vergers planted with Common Oak;
■ = Eelde Meteolrological station;
● = Wijster Biological station.

Most of the plots were selected in July 1986, in homogeneous stands with regard to the phanerogamous vegetation. A few additional plots were selected in 1987. Variables are (1) exposition, (2) age of trees and (3) composition of herb layer as a reflection of soil conditions. The length of the plots was 100 m, the width varied between 1.5 and 6.5 m, bordered by the road on one side and usually a ditch on the other. In the phytocoenological study of the plots the extreme margins along the roads, where trampling or riding are most intense, as well as the margins and the sides of the ditches were excluded. The cover of all species was estimated in percentages and later transformed into weighed values (Westhoff & Van der Maarel, l.c.) for data processing. The number of trees per plot varied between 9 and 35 (mean 15 ± 5) and the number of trees per 1000 m^2 varied from 16 to 95 (mean 49 ± 19). Most plots were provided with a single, uninterrupted row of trees. Four plots had a double row of trees and in a few cases the the row of the trees in the plot was interrupted.

The 76 plots were arranged with regard to exposition and road metalling according to the scheme in fig. 2.

	Open	Half shady	Shady and metalled	Shady un-metalled	Total
Beech	12	0	6	5	23
Oak	34	9	7	3	53

Fig. 2. Arrangement of the plots according to exposition and to road metalling. "Open" = plot situated in open landscape; "Half shady" = plot bordered at one side by forest; "Shady" = plot situated inside forest.

Of the 76 plots 23 were planted with Beech trees and 53 with Oaks. Half shady plots with forest at the southern side were called "North-exposed" (5 plots); those with forest at the northern side "South-exposed" (4 plots).

In the *Fagus*-plots the age of the trees in 1988 ranged from 37 to 82 years old (in one plot up to 140 years old). In further analyses no distinction in age classes was made. In the plots with Oaks, three age classes were distinguished: "young", with trees < 20 years old; "medium aged", 20 - 50 years old and "old", with trees 50 - 140 years old. All shady and half-shady plots contained old trees. The 34 open plots comprised 5 plots with young trees, 12 with medium-aged trees and 17 with old trees. The age of the trees was determined with the aid of an increment borer.

The plots varied widely with regard to soil fertility, judged from the variation in species composition and cover degree of the herb layer.

2.2. *Recording plants and fungi.*

Vegetation relevés were made during the summer of 1986 and in some additional plots in 1987, according to the Braun-Blanquet method (e.g. Westhoff & Van der Maarel, 1973). For mycocoenological purposes the plots were visited during the autumns of 1986-1988 once in a 3 to 4 week period from August until the first severe frosts, usually in November. The mycocoenological methods proposed by Arnolds (1981) and Barkman

(1976, 1987) were applied. Some plots were added in 1987 and have been studied only in 1987 and 1988. All sporocarps of macromycetes were counted and removed in order to prevent double countings. Incidental visits in spring revealed that no noteworthy fructification occurred in that season.

After three years (two years of the plots that started in 1987), the maximum abundance of sporocarps during a visit was determined for each species in each plot, and adjusted to 1000 m^2. For data processing the values were transformed using the formula $V=\ln(y+1)$ in which V is the transformed value and y is the maximum abundance of sporocarps. The values of V were rounded to integers. This transformation was chosen 1. in order to reduce extreme values, in analogy to weighted abundance-coverage values in phytocoenology (Westhoff & van der Maarel, 1973) and 2. because the successive values of V come close to the logarithmic scale of estimation of abundance of fungi by Arnolds (1981). This facilitates eventual comparisons with other data. Any number over 5000 sporocarps/1000m^2 was given a value of 9. This occurred in few species with very small sporocarps, e.g. *Mycena polyadelpha, M. capillaris.*

It is assumed that the maximum abundance of the sporocarps during the study represents the potential performance of the species during these three years (Haas, 1932; Barkman, 1976, 1987; Arnolds, 1981), i.e. the number of sporocarps produced under the most favourable weather conditions.

Descriptions of the soil profiles, analyses of the upper 0.1 m of the soil and measurements of some environmental variables (traffic intensity, tree vitality, tree age, management of the undergrowth, amount of potential direct sunshine in the plot, soil moisture, soil pH($CaCl_2$), concentrations of Mg^{2+}, Na^+, K^+, NO_3^-, NH_4^+, N-soluble, N-total, P-soluble, P-total (all in 0.1 M $CaCl_2$), C content and C/N ratio) were made. The soil-chemical analyses were carried-out according to the methods described by Houba et al. (1988); see also chapter 3.

2.3. *Data processing.*

The vegetation relevés, mycocoenological relevés and the environmental data were analyzed using the computer program TWINSPAN (Hill, 1979; Jongman et al., 1989).

The program TWINSPAN rearranges plots and species in such a manner that plots with similar species composition and species with similar distribution in the plots are grouped together in analogy to the methods by Braun-Blanquet (e.g. Westhoff & van der Maarel, 1973; Mueller-Dombois & Ellenberg, 1974). Groups of plots with similar properties can be distinguished. The results of the TWINSPAN analysis were modified "by hand" in order to obtain more lucid tables. These procedures were carried-out separately for phanerogams, saprotrophic and mycorrhizal fungi because they play different roles in the ecosystem (Agerer, 1985, Arnolds, 1988) and react differently to environmental variables. Saprotrophic fungi growing on wood, dung, insects and (other) fungi were excluded so that only true terrestrial and litter inhabiting species were used in the analyses.

Species were classified in one of these functional groups on the base of various literature accounts (e.g. Trappe (1962), Arnolds (1984) or Kreisel (1987) and in some cases on the base of personal observations. For instance, *Clitopilus prunulus, Clavulina coralloides* and *Leotia lubrica* were treated here as ectomycorrhizal fungi on the base of circumstantial evidence (see chapter 7). The distinction between "true terrestrial and litter

inhabiting species" and other saprotrophic fungi (on wood, dung, etc.) was made after Arnolds (1984) or according to personal observation. Information on the weather conditions during the research period is presented in chapter 3.

Nomenclature of phanerogams is after Heukels & van der Meijden (1983), that of bryophytes after Margadant & During (1982), and that of fungi mainly after Kreisel (1987). A complete list of fungi encountered in the present study is presented in chapter 2, 3 and apendix 1. Taxonomic and nomenclatural notes on critical and rare species were published in chapter 8. The names of vegetation types in roadside verge verges are according to Keizer (chapter 2, 3) and are only preliminary, and lack an official syntaxonomic status.

3. **Results.**

3.1. *Vegetation*

The results of the vegetation analysis of the plots with Oaks or with Beech trees, as described in chapter 2 and 3, are summarized in table 1; tables are at the back of this chapter. In the *Fagus*-plots the *Festuca rubra* type comprises plots in open landscapes with a grassy vegetation. The *Elytrigia repens* subtype of this type contains plots with a more or less ruderal vegetation, indicating soils rich in nutrients, whereas the *Festuca ovina* subtype represents a vegetation indicating soils poor in nutrients. The shady plots are united in the *Mnium hornum* type with two subtypes, the *Poa trivialis* subtype, with a rather ruderal vegetation and a subtype with a less ruderal forest vegetation, the *Dryopteris carthusiana* subtype.

Table 1. Brief representation of the vegetation classification of the plots in roadside verge verges planted with Oak or with Beech. Of each (sub)type, three common differential and characteristic species are given (after chapter 2 and 3).

Roadside verges with Beech trees:

	Festuca rubra type	
Diff. sp.	*Festuca rubra*	
	Poa pratensis	
	Plantago lanceolata	
	Elytrigia repens subtype	**Festuca ovina subtype**
Diff. sp.	*Elytrigia repens*	*Festuca ovina*
	Rumex obtusifolius	*Hypochaeris radicata*
	Anthriscus sylvestris	*Rhytidiadelphus squarrosus*
	Mnium hornum type	
Diff. sp.	*Mnium hornum*	
	Sorbus aucuparia	
	Prunus serotina	
	Poa trivialis subtype	**Dryopteris carthusiana subtype**
Diff. sp.	*Poa trivialis*	*Dryopteris carthusiana*
	Hedera helix	*Carex pilulifera*
	Urtica dioica	*Dryopteris dilatata*

Roadside verges with Oaks:

Hypochaeris radicata type

Diff. sp. *Hypochaeris radicata*
Plantago lanceolata
Anthoxanthum odoratum

Hieracium pilosella subtype

Diff. sp. *Hieracium pilosella*
Brachythecium albicans
Polytrichum piliferum

Lotus corniculatus subtype

Lotus corniculatus
Vicia angustifolium
Eurhynchium praelongum

Anthriscus sylvestris type

Diff. sp. *Anthriscus sylvestris*
Stellaria media
Urtica dioica

Mnium hornum type

Diff. sp. *Mnium hornum*
Deschampsia flexuosa
Hypnum cupressiforme

In the classification of the *Quercus*-plots, the plots of the *Hypochaeris radicata* type are situated in open landscapes and have a grassy vegetation. The *Hieracium pilosella* subtype of this type comprises the nutrient-poor plots and the *Lotus corniculatus* subtype represents a vegetation type on soils richer in nutrients. The semiruderal half shady to shady plots are united in the *Anthriscus sylvestris* type. The shady plots belong to the *Mnium hornum* type.

The classification of the vegetation of the plots with Oaks is more or less analogous to that of the *Fagus*-plots. The *Festuca rubra* type of the latter corresponds with the *Hypochaeris radicata* type of the former; the *Festuca ovina*- and *Elytrigia repens* subtypes of the *F. rubra* type correspond with the *Hieracium pilosella*- and the *Lotus corniculatus* subtypes of the *Hypochaeris radicata* type, respectively. The *Poa trivialis* and *Dryopteris carthusiana* subtypes of the *Mnium hornum* type in the *Fagus*-plots can be considered as analogous to the *Anthriscus sylvestris* type and the *Mnium hornum* type in the *Quercus*-plots, respectively.

Due to the larger number of plots with oaks in open and half shady landscape, the classification of the *Quercus*-plots is more detailed than the classification of the *Fagus*-plots.

3.2. *Saprotrophic fungi*

In the TWINSPAN analysis of the data of the saprotrophic fungi in *Fagus*- and *Quercus* plots, three groups can be recognized (table 2). Each group is characterized by a number of differential species, which are arbitrarily defined as species with a presence-degree which is at least twice the presence-degree in another group of plots and which occur in three or more plots.

The first division is between group A and the remainder of the plots. In the second division groups B and C are distinguished, but a further splitting does not give

ecologically relevant results. The groups are named after a common differential species with a high degree of fidelity.

The average values of some environmental biotic and abiotic variables of the plots of the three groups have been calculated and are presented in table 3.

Group A (*Rickenella fibula* group). 20 plots; 5 *Fagus*- and 15 *Quercus*-plots; 5 differential species. The most common are: *Rickenella fibula, R. setipes* and *Galerina atkinsoniana*.

This group is not only characterized by the presence of the differential species listed in table 2, but also by the absence of a fairly large number of species, which are present in the other plots and which are therefore differential for groups B and C. In addition, a large number of rare species are present that are often characteristic of poor, unfertilized grasslands with a well-developed bryophyte layer e.g. *Camarophyllus russocoriaceus, Hygrocybe conica, Mycena pelliculosa, Ramariopsis luteoalba*. Owing to the criteria for differential species, mentioned above, these species do not contribute to the characterization of the groups and were therefore left out in table 2 (but see chapter 3).

This group comprises open plots with a poor grassland vegetation (low Ellenberg N-values, i.e. a measure of nitrogen availability in the soil) on dry soil and a relatively large coverage of bryophytes. Plots with young trees (only with Oak) are often included in this group.

In the *Rickenella fibula* group a relatively large proportion of the species are fungi that are associated with bryophytes. The well developed bryophyte layer in these plots explains their occurrence.

Group B (*Mycena flavoalba* group). 22 plots; 5 *Fagus*- and 17 *Quercus*-plots; 12 differential species, among others: *Mycena flavoalba, Mycena adcendens, Marasmius graminum*.

This group includes open plots with a grassland vegetation on moderately nutrient-rich (Ellenberg N-values higher than in group A) and dry soil with a low coverage of bryophytes.

Group C (*Psathyrella artemisiae* group). 34 plots; 10 *Fagus*- and 24 *Quercus*-plots; 27 differential species. Common differential species are: *Mycena cinerella, Collybia butyracea, Clitocybe metachroa*.

This group is also characterized by:

1. a number of species (with low frequencies) indicative of nutrient rich places or accumulated leaf litter (e.g. *Bolbitius vitellinus, Clitocybe amarescens, Coprinus comatus* and *Marasmius recubans, Mycena mucor, Psathyrella tephrophylla* respectively);
2. the large number of (but partly infrequently occurring) wood inhabiting species that were found in plots of this group e.g. *Ramaria stricta, Mycena oortiana, Oudemansiella radicata, Panellus stypticus*. Their occurrence can be explained by the presence of many branches and other woody remains.

This group consists mostly of half shady and shady plots with a vegetation varying from semiruderal grassland to forest vegetation, illustrated by the rather high Ellenberg N-values, with a large standard deviation. The shady environment in this group causes a lower coverage degree of phanerogams. In these circumstances, the soil is less subject to desiccation and therefore had a larger moisture. The bryophyte layer is poorly developed.

Comparing the three groups, it appears that the contents of the minerals in the groups A, B and C are rather similar except for the concentration of soluble P, which is in group A lower than in the other groups, although the difference is not significant. The trees in group B are on average older than in group A, but not than in group B. The magnesium and sodium concentrations in this group are significantly higher than in the other groups. The concentrations of potassium, nitrate and ammonium are also higher, but the differences with the other groups are not significant.
The organic layer in group C is significantly thicker than in the plots of groups A and B. The trees are older than in groups A and B. The pH ($CaCl_2$) and the total P concentration are lower than in the other groups.

3.3 *Ectomycorrhizal fungi.*

By TWINSPAN analysis of the data on the ectomycorrhizal fungi five groups are recognized (table 4).

In the first division two main groups are distinguished:
1. a group of 19 plots of which 17 are plots with Beech trees and two plots with Oaks (the "*Fagus* group");
2. a group of 56 plots of which six were planted with beech and 50 with oak trees (the "*Quercus* group").

One plot was excluded because of the complete absence of ectomycorrhizal fungi (plot Q54).

Differential species of the first group are among others: *Russula fellea, Lactarius subdulcis*, known as obligate symbionts of *Fagus* (e.g. Arnolds, 1984), but otherwise with a broad ecological range. Other species that are associated with *Fagus* are differential of one of the types that can be distinguished within this main group. The non-obligate *Fagus* symbionts, among others *Amanita muscaria, Boletus edulis, B. erythropus, Chalciporus piperatus, Clitopilus prunulus, Inocybe sindonia* and *Laccaria amethystea* occur mainly in the *Fagus* group. Differential or preferential species of the second (*Quercus*) group are: *Laccaria bicolor, Lactarius chrysorrheus, L. quietus, L. serifluus, Russula amoenolens, R. atropurpurea, R. cyanoxantha, R. fragilis, R. graveolens formae, R. odorata, R. vesca, Xerocomus porosporus, X. rubellus*, and some more. Many of them are known as obligate or preferent *Quercus* symbionts.

The subgroups within these two main groups coincide largely with the groups recognized in the separate classifications of the plots with Beech or Oak (chapter 2, 3). In short, this classification is as follows.

The beech group can be divided in two groups:
1. the *Russula mairei* group, a species-rich type, mainly occurring in open plots on nutrient-poor soil. This group corresponds with the *Russula fellea* type (chapter 2)
2. the *Inocybe napipes* group, a less species-rich type mainly in shady plots. This group is analogous to the *Inocybe napipes* type.

These groups are indicated as groups D and E, respectively (table 4). Some *Fagus*-plots with only few ectomycorrizal fungi (the inops type, i.e. an impoverished variant), appeared to be more related to some of the *Quercus*-plots in the present classification, and are therefore placed in the *Quercus* group.

The Oak group is divided here in three groups, each characterized by a number of differential species (table 4):

1. The *Lactarius chrysorrheus* group, a species-rich type on nutrient-poor soil, analogous to the *Cortinarius erythrinus* type (chapter 3), here indicated as group F;
2. the *Xerocomus rubellus* group, a moderately species-poor type on nutrient-rich, open to shady roadside verges, analogous to the *Russula ochroleuca* type and part of the *Xerocomus rubellus* type, including some *Fagus* plots of the species-poor *inops* type of the *Fagus*-plots. This type is indicated as group G;
3. the *Inocybe lanuginella* group, a species-poor type on open, rather nutrient-rich roadside verges with young or middle aged (< 50 years old) trees, analogous to the *Hebeloma mesophaeum* type and part of the *Xerocomus rubellus* type, in table 4 indicated as group H.
The G and H groups are characterized by only few, weakly differential species.

It is obvious that many ectomycorrhizal fungi show either an association with Oak or Beech, or do not show a clear preference for one of these trees. Differential species of group D and E are *Fagus* symbionts; differential species of groups F, G and H are *Quercus* symbionts. The majority of the ectomycorrhizal species have a preference for Oak or Beech. More species show a preference for Beech than for Oak, in spite of the larger number of Oak plots. The preferences of species for *Fagus* or *Quercus* are presented in table 6. For a more extensive discussion on these preferences, see chapter 5.

Interestingly, there is a fairly large group of species that are differential for the combined groups D and F, comprising the plots on nutrient poor, open roadside verges with either *Fagus* or *Quercus*. This distribution fits in with these species, being favoured only by these environmental circumstances, irrespective of the tree species. They constitute an ecological contrast with the "accompanying species", which also grow in both *Fagus*- and *Quercus*- plots. The former are rare and confined to these habitats whereas the latter are common ubiquists (Arnolds, 1984, 1989b).

4. Conclusions and discussion.

The distribution of the distinguished fungal communities over the vegetation types is presented in table 5. The vegetation types as distinguished for *Fagus* and *Quercus* plots are merged to three combined types. This table gives an indication of the degree of correspondence between the fungal and the phanerogam communities. The communities of saprotrophs and of mycorrhizal fungi correspond to the phanerogam vegetation to a limited extent. The communities of ectomycorrhizal fungi agree better with the phytocoena than the communities of saprotrophic fungi. This is indicated by the larger average standard deviation of the similarities of phytocoena with ectomycorrhizal communities (SD = 36), compared with saprotrophic communities (SD = 26). A standard deviation close to 0 would indicate an absence of correspondence of fungal and phanerogam communities because in that case, the plots of fungal communities are evenly distributed over the phytocoena.

The *Rickenella fibula* group corresponds well with the *Hypochaeris radicata* type + *Festuca ovina* subtype. The *Mycena flavoalba* group is about as strongly related to the *Hypochaeris radicata* type + *Festuca ovina* subtype as to the *Anthriscus sylvestris* + *Poa trivialis* type + *Elytrigia repens* subtype. The *Psathyrella artemisiae* group plots are distributed over the *Anthriscus sylvestris* + *Poa trivialis* type + *Elytrigia repens* subtype and the *Mnium hornum* type + *Dryopteris carthusiana* subtype.

The communities of ectomycorrhizal fungi are somewhat more evenly spread over the phanerogam types (table 5). This indicates that the factors responsible for species composition of the communities are more similar for phanerogams and saprotrophs than for phanerogams and ectomycorrhizal fungi.

It is clear that in the classification of the plots on the basis of the ectomycorrhizal fungi the symbionts that are (obligatory or preferentially) associated with either *Fagus* or *Quercus* are the most important differential species. In other words, the presence of Oak or Beech trees determines in the first place the species composition of the ectomycorrhizal fungi. Within the *Fagus* or *Quercus* plots, groups can be distinguished with other ecological features.

However, six *Fagus* plots were classified in the TWINSPAN analysis in the group of *Quercus*-plots of the ectomycorrhizal fungi. These plots belong to the inops type according to the classification of *Fagus* plots (cf. chapter 2), which is a type poor in species, mainly found in roadside verges with a semiruderal vegetation. Apparently, under such circumstances non-specialist symbionts dominate among the rather few species present and the plots become more related with *Quercus* plots poor in species than with species rich *Fagus* plots. In the same way a shady *Quercus* plot, rather poor in species is placed among the shady *Fagus* plots, also rather poor in species. In these impoverished situations the obligate and preferent symbionts are almost absent; the non-host-specific symbionts (the common species, listed as "accompanying species" in table 4, remain present. This indicates physiological differences between the host-specific and non-host-specific ectomycorrhizal fungi.

The above-mentioned pattern is consistent with the stronger decrease that was observed over the last decades in the Netherlands among host-specific ectomycorrhizal fungi than among non-specific symbionts, a fact presumably caused by pollution with Nitrogen containing compounds (Arnolds, 1988; Termorshuizen, 1990).

Among the saprotrophic fungi, however, environmental variables that are not directly dependent of the tree species determine the main groups. Only a small number of saprotrophs live exclusively or preferently on litter of either Beech (e.g. *Marasmius recubans, Flammulaster carpophiloides, Mycena capillaris*) or Oak (e.g. *Mycena polyadelpha*). These species occur rather infrequently in the plots and have therefore a rather weak indication value in the analysis.

The Ellenberg N values, exposition (expressed as potential amount of direct sunshine), thickness of the organic layer and the pH ($CaCl_2$) are the most important environmental variables determining the flora of the terrestrial saprophytes (table 3; chapter 2, 3). The low herb layer coverage of the shady plots of the *Psathyrella artemisiae* group is doubtlessly caused by the low light intensity in these plots and it does not influence the macrofungi directly. The presence of a litter layer probably prevents the development of an extensive moss layer (Barkman, 1974). The relatively high coverage degree of the bryophytes in plots of the *Rickenella fibula* group can be explained by the absence of litter in combination with a low nutrient (nitrogen; cf. low Ellenberg N-values) status of these plots. This is partly caused by the originally nutrient poor soil, which is maintained by the presence of the trees. The tree roots absorb nutrients from the upper soil layers and the leaves are blown away in the autumn, especially where a short, mown vegetation is present (personal observation). The nutrients therefore are not recycled into the soil. In this situation, where competition for nutrients in the upper soil layer is

particularly intense, bryophytes can better compete with herbs. The fungi that are associated with bryophytes are concentrated in this vegetation type. The absence of a well-developed organic layer causes the absence of species characteristic of raw litter (e.g. *Collybia* species). Likewise, the presence of grassland vegetation on nutrient-poor soil enables the presence of characteristic grassland fungi (e.g. *Entoloma*-species) of which many live on organic material that is incorporated in the soil (Arnolds, 1992).

It is remarkable that, although the vegetation on the verges of shady forest roads differs widely from the semiruderal vegetation in half shady plots, this difference is only weakly expressed in the saprotrophic mycoflora. The *Psathyrella artemisiae* group includes plots of both vegetation types. Also subgroups within this group, plots of forest roads and of half shady (and some open) roads do not appear as separate units. Apparently, the resemblance in saprotrophs between shady and half shady plots is larger than between these and the open plots. A possible explanation is that species of this group are unspecific regarding the nature of the organic substrate which makes them relatively independent of the vegetation. Some other species appear late in the autumn, a season in which microclimatic factors converge temporarily after treeleaf shedding in both plot types, e.g. *Mycena cinerella, Collybia butyracea, Lepista spp.*.

At the bottom of table 2 the wood-inhabiting species are listed. It is striking that most wood-inhabiting species occur in group C (*Psathyrella artemisiae* group). It seems that the plots of group C are also more similar to forests by the presence of more dead wood and/or the wood present forms a more favourable substrate for these fungi in shady plots, compared with the open and half shady plots. No exact counts of the amount of dead wood were made in the plots, but in general more fallen branches and tree trunks can be seen in verges of forest roads, which explains the presence of the wood inhabiting species. Some species however, e.g. *Trametes versicolor* and especially *Polyporus brumalis* prefer dry wood in open places (cf. Runge, 1988).

Table 2. Synoptic table of saprotrophic fungi.
Only species occurring in three or more plots were included. Species were considered as differential of a community if the presence degree in that community was two or more times the presence degree in the other communities and differing more than one class unit. Frequency classes of the species: I= in 1-10%, II= in 11-20%, ..., X= in 91-100% of the plots.
A= *Rickenella fibula* group
B= *Mycena flavoalba* group
C= *Psathyrella artemisiae* group
For further explanation of the fungal communities, see text.

Fungal community	A	B	C
Number of plots	20	22	34
Differential species of the *Rickenella fibula* group:			
Rickenella fibula	X	III	III
Rickenella setipes	IV	II	I
Galerina atkinsoniana	III	I	I
Differential species of the *Mycena flavoalba* group:			
Mycena flavoalba	II	IV	I
Mycena adcendens	I	III	I
Marasmius graminum		III	I
Coprinus friesii		II	
Conocybe semiglobata		II	
Differential species of the *Psathyrella artemisiae* group:			
Mycena cinerella	III	III	VIII
Collybia butyracea	I	III	VIII
Clitocybe metachroa	II	II	VII
Galerina hypnorum	II	I	IV
Tephrocybe tesquorum	I	I	III
Psathyrella artemisiae			V
Crepidotus variabilis			V
Psathyrella frustulenta		I	III
Psathyrella candolleana		I	III
Clitocybe vibecina		I	III
Collybia peronata			III
Psilocybe crobula			II
Phallus impudicus			II
Mycena capillaris			II
Mutinus caninus			II
Lycoperdon perlatum			II
Flammulaster carpophiloides			II
Clitocybe clavipes			II
Differential species of the *Rickenella fibula* group and the *Mycena flavoalba* group:			
Mycena avenacea	VI	VI	I
Mycena sepia	V	IV	I
Marasmius oreades	III	V	I
Helvella lacunosa	II	II	I

Differential species of the *Mycena flavoalba* group and the *Psathyrella artemisiae* group:			
Psathyrella fulvescens	I	V	IX
Mycena sanguinolenta	II	IV	V
Mycena pura var. pura	I	IV	III
Mycena stylobates	I	III	III
Mycena polyadelpha	I	III	III
Clitocybe marginella	I	III	III
Clitocybe diatreta	I	III	III
Marasmiellus vaillantii	I	III	II
Lepista nuda	I	II	III
Psathyrella spadiceogrisea		III	II
Psathyrella microrhiza		III	II
Mycena flavescens		III	II
Some common accompanying species:			
Mycena vitilis	VIII	IX	X
Mycena galopoda var. galopoda	V	IX	X
Mycena leptocephala	IX	VIII	V
Mycena filopes var. filopes	VI	IX	VII
Collybia dryophila	VI	VII	VIII
Tubaria furfuracea	IV	IV	VI
Mycena filopes var. metata	IV	V	III
Entoloma sericeum f. sericeum	II	II	II
Wood inhabiting species:			
Mycena haematopoda	II		
Coprinus micaceus	II	I	
Oudemansiella platyphylla	III		
Pluteus atricapillus	III		
Psathyrella pilulifera	I	I	IV
Armillaria obscura	I	II	VI
Trametes versicolor	I	II	I
Coprinus domesticus	I	II	I
Agrocybe firma	I	I	
Mycena polygramma var. polygramma	I	III	III
Hypholoma fasciculare	III	I	IV
Polyporus brumalis	III	IV	II
Mycena galericulata	IV	VI	IX

Table 3. Average values and standard deviations of some environmental variables of groups of plots characterized on the basis of a TWINSPAN analysis of the saprotrophic fungi.
For further explanation of the fungal communities, see text.

Environmental variable	*Rickenella fibula* group	*Mycena flavoalba* group	*Psathyrella artemisiae* group
Coverage herb layer (%)	70*± 22 a	72± 19 a	51± 31 b
Coverage moss layer (%)	17± 18 a	5± 14 b	4± 10 b
Average Ellenberg N values	5.1± 1.0 a	6.0± 1.1 b	5.6± 1.8 a,b
Organic layer (cm)	0.2± 0.5 a	0.3± 0.6 a	2.6± 3.1 b
Tree age (years in 1988)	46± 27 a	70± 34 b	96± 32 c
Potential daily amount of direct sunshine in the plot in Oct. (hours)	6.4± 2.2 a	6.0± 2.0 a	1.8± 2.8 b
pH (CaCl2)	4.2± 0.4 a	4.3± 0.3 a	3.8± 0.9 b
Mg^{2+} (mg.kg-1)	29± 25 a,b	38± 16 a	27± 15 b
Na+ (mg.kg-1)	27± 16 a,b	31± 16 a	21± 17 b
K+ (mg.kg-1)	42± 19	50± 23	44± 22.6
NO3- (mg.kg-1)	1.1± 2.4	1.6± 3.0	1.0± 1.6
NH4+ (mg.kg-1)	8.3± 4.9	9.2± 6.7	8.5± 3.8
N-soluble (mg.kg-1)	15.0± 5.6	17.0± 6.1	17.5± 6.2
N-total (% N)	0.16± 0.05	0.18± 0.06	0.18± 0.16
P-soluble (mg.kg-1 of PO43-)	0.21± 0.54	0.59± 0.96	0.65± 1.2
P-total (mg.kg-1)	291± 163 a	292± 112 a,b	215± 111 c
C (% C)	2.9± 1.1	3.1± 0.8	3.1± 1.3
C/N ratio	17.5± 4.3	18.4± 7.3	18.2± 7.1
Moisture (fraction of dry weight of the soil sample)	10.4± 4.3	11.6± 3.4	20.7± 11.5

* Different letter appearing in different columns indicate a significant difference ($P<0.05$). Absence of letters indicate no sinificance.

Table 4. Synoptic table of mycorrhizal fungi. Only species occurring in more than three plots were included. Species were differential of a community if the frequency in that community was two or more times the frequency in the other communities and differing more than one class unit. Frequency classes of the species: I= in 1-10%, II= in 11-20%, ... , X= in 91-100% o the plots.
D= *Russula mairei* group
E= *Inocybe napipes* group
F= *Lactarius chrysorrheus* group
G= *Xerocomus rubellus* group
H= *Inocybe lanuginella* group
For further explanation of the fungal communities, see text.

Fungal community:	D	E	F	G	H
Number of plots:	11	8	13	27	16
Differential species of the *Inocybe lanuginella* group:					
Inocybe lanuginella	I		I		II
Laccaria tortilis	I		I		II
Differential species of the *Xerocomus chrysenteron* group:					
Xerocomus rubellus			I	II	
Inocybe albomarginata	I		I	II	I
Differential species of the *Lactarius chrysorrheus* group:					
Russula fragilis	IV		X	V	II
Russula pectinatoides	II		VII	II	II
Lactarius chrysorrheus	I		VII	II	
Russula odorata	I		V	II	
Russula graveolens f. gr.			V	II	
Russula vesca	I		IV	II	
Cortinarius lanatus	II		IV	I	
Cantharellus cibarius	II		IV	I	
Cortinarius anomalus	I	II	III		
Russula graveolens f. cicatricata			IV	I	
Otidea bufonia	I		III		I
Leotia lubrica	I		III	I	
Inocybe griseolilacina			IV		
Russula graveolens f. purpurata			IV		
Differential species of the *Lactarius chrysorrheus* group and the *Xerocomus chrysenteron* group:					
Lactarius serifluus	II	III	IV	III	
Differential species of the *Lactarius chrysorrheus* group, the *Xerocomus chrysenteron* group and the *Inocybe lanuginella* group:					
Lactarius quietus	II	II	X	IX	VI
Laccaria bicolor			III	II	II
Differential species of the *Russula mairei* group:					
Boletus edulis	X		V	II	
Russula mairei	X	V			
Lactarius blennius	X	III		I	
Tricholoma ustale	VII	III			
Amanita muscaria	V	II	II		I
Chalciporus piperatus	V		I	I	I
Cortinarius paleiferus	IV		I		
Boletus erythropus	IV		I		

Fungal community:	D	E	F	G	H
Differential species of the *Inocybe napipes* group:					
Inocybe napipes	II	VII	I		
Amanita pantherina	II	IV	II		
Russula emetica		III	I	I	
Differential species of the *Russula mairei* group and the *Inocybe napipes* group:					
Russula fellea	X	VIII			
Lactarius subdulcis	IV	IV			
Differential species of the *Russula mairei* group and the *Lactarius chrysorrheus* group:					
Cortinarius striaepilus	VII	II	VII	III	
Cortinarius paleaceus	VII	II	VI	II	I
Cortinarius erythrinus	VI	I	VIII	I	
Clitopilus prunulus	VI		IV	I	
Inocybe mixtilis	V	I	IV	I	I
Cortinarius flexipes	IV		VI	I	
Cortinarius hinnuleus	IV		V	I	
Inocybe geophylla	III		II	I	
Inocybe fuscidula	III		II	I	
Cortinarius casimiri	III		III		
Cortinarius obtusus	II		III		
Russula grisea	II		II	I	
Inocybe flocculosa	III		II		
Cortinarius violilamellatus	II		II		
Russula lutea	II		II		
Differential species of the *Russula mairei* group, the *Lactarius chrysorrheus* group and the *Xerocomus chrysenteron* group:					
Clavulina coralloides	V	II	VII	IV	I
Russula cyanoxantha	II		VI	III	
Russula nigricans	VI	II	VII	V	
Differential species of the *Russula mairei* group, the *Inocybe napipes* group and the *Lactarius chrysorrheus* group:					
Laccaria amethystea	VIII	IV	VII	II	
Russula velenovskyi	III	IV	IV	I	
Inocybe petiginosa	V	IV	IV		
Thelephora terrestris	III	IV	II	I	I
Amanita spissa	III	III	III	I	
Accompanying species:					
Laccaria laccata	X	IX	X	IX	X
Amanita rubescens	IX	X	IX	VIII	I
Russula parazurea	VIII	VII	VII	X	V
Russula amoenolens	V	III	X	VIII	VI
Laccaria proxima	VI	IX	VII	III	IV
Scleroderma citrinum	IX	VIII	IV	VI	I
Paxillus involutus	VIII	IX	IV	V	I
Xerocomus chrysenteron	V	V	VI	VI	IV
Scleroderma areolatum	VII		VII	III	IX
Xerocomus badius	V	VIII	IV	V	
Russula ochroleuca	VI	IX	II	V	
Lactarius theiogalus	VII	IV	IV	IV	I
Hebeloma helodes	VIII		VIII	I	IV
Russula atropurpurea	II	III	VII	V	
Cortinarius saniosus	V	III	IV	II	II
Naucoria bohemica	III	II	III	II	IV
Amanita citrina	II	III	IV	IV	
Hebeloma mesophaeum	III	II	II	I	IV

Fungal community:	D	E	F	G	H
Inocybe lacera	II	III	III		IV
Amanita fulva	I	IV	IV	III	
Inocybe assimilata	II	III	IV	II	
Lactarius camphoratus	I	IV	I	III	
Hebeloma longicaudum	III	II	II	I	
Inocybe maculata	II	II	III	I	
Russula ionochlora	II	II	II	II	
Xerocomus porosporus			II	I	
Tricholoma saponaceum	I		II	I	

Table 5. Percentages of plots of communities of saprotrophic and ectomycorrhizal fungi in three main vegetation types.
A= *Rickenella fibula* group
B= *Mycena flavoalba* group
C= *Psathyrella artemisiae* group
D= *Russula mairei* group
E= *Inocybe napipes* group
F= *Lactarius chrysorrheus* group
G= *Xerocomus rubellus* group
H= *Inocybe lanuginella* group
For further explanation of the fungal communities, see text.

			Hypochaeris radicata type + *Festuca ovina* subtype	*Anthriscus sylvestris* + *Poa trivialis* type + *Elytrigia repens* subtype	*Mnium hornum* type + *Dryopteris carthusiana* subtype	
		Fungal communities	32 plots	34 plots	10 plots	Standard deviation
Saprotrophic fungi		A 20 plots	95	5	0	53
		B 22 plots	45	55	0	29
		C 34 plots	9	62	29	26
Ecomycorrhizal fungi	"Fagus" group	D 11 plots	45	36	18	14
		E 8 plots	13	25	63	26
	"Quercus" group	F 13 plots	69	31	0	35
		G 27 plots	26	63	11	27
		H 16 plots	56	44	0	29

Table 6. List of species with preference for *Quercus* or *Fagus*. The numbers are precence-degrees in %. Species ocurring less than three times were excuded.

Plot planted with:	*Fagus*	*Quercus*
Number of plots	23	53
Species with preference for *Fagus*:		
Amanita spissa	26	6
Amanita muscaria	22	8
Amanita pantherina	22	4
Boletus edulis	39	19
Boletus erythropus	17	2
Chalciporus piperatus	17	6
Clitopilus prunulus	26	11
Cortinarius paleiferus	14	2
Hebeloma mesophaeum	26	11
Inocybe flocculosa	13	4
Inocybe sindonia	22	2
Inocybe petiginosa	30	8
Inocybe huysmani	13	-
Inocybe geophylla	17	4
Inocybe napipes	26	11
Inocybe fuscidula	17	4
Laccaria amethystea	48	23
Lactarius blennius	61	-
Lactarius camphoratus	13	1
Lactarius subdulcis	35	-
Russula fellea	70	-
Russula ochroleuca	52	26
Russula mairei	57	-
Russula lutea	9	4
Russula velenovskyi	26	11
Thelephora terrestris	22	11
Tricholoma ustale	39	-
Species with preference for *Quercus*:		
Cortinarius umbrinolens (incl. *C. glandicolor*)	-	6
Cortinarius anomalus	4	8
Inocybe albomarginata	4	9
Inocybe griseolilacina	-	8
Laccaria bicolor	4	13
Lactarius quietus	4	89
Lactarius chrysorrheus	4	23
Lactarius serifluus	9	25
Russula graveolens f. purpurata	-	9
Russula cyanoxantha	9	25
Russula graveolens f. cicatricata	-	11
Russula graveolens f. graveolens	-	21
Russula fragilis	13	40
Russula odorata	4	17
Russula amoenolens	39	77
Russula pectinatoides	-	28
Russula vesca	4	13
Xerocomus porosporus	-	8
Xerocomus rubellus	-	8
Species without preference:		
Amanita rubescens	87	57
Amanita citrina	17	26
Amanita fulva	13	21
Cantharellus cibarius	9	11
Clavulina coralloides	35	32
Cortinarius lanatus	9	9
Cortinarius casimiri (incl. *C. decipiens* s. Henry)	9	6
Cortinarius obtusus	9	6
Cortinarius paleaceus	30	26
Cortinarius saniosus	30	23
Cortinarius hinnuleus	13	17
Cortinarius striaepilus	30	28
Cortinarius flexipes	17	17
Cortinarius erythrinus	26	21
Hebeloma helodes	39	28
Hebeloma longicaudum	13	9
Inocybe mixtilis (incl. *I. xanthomelas*)	22	13
Inocybe lacera	13	17
Inocybe maculata	13	8
Inocybe umbrina	17	19
Laccaria laccata	87	92
Lactarius proxima	48	47
Lactarius theiogalus	39	32
Naucoria bohemica	22	23
Paxillus involutus	61	34
Russula emetica	4	6
Russula nigricans	30	40
Russula parazurea	78	68
Russula ionochlora	13	11
Russula grisea	9	8
Russula atropurpurea	22	36
Scleroderma areolatum	30	57
Scleroderma citrinum	61	40
Xerocomus badius	43	34
Xerocomus chrysenteron	57	45

THE MACROMYCETE FLORA IN ROADSIDE VERGES PLANTED WITH TREES IN COMPARISON WITH RELATED FOREST TYPES

P.J. Keizer & E. Arnolds[1]

Abstract.

The results of mycocoenological research in different types of roadside verges with planted *Quercus robur* and *Fagus sylvaticus* in Drenthe, northeastern Netherlands, are compared with studies in forest types of the same tree species in the same area. The roadside verges were investigated in the years 1986-1988. Three types of roadside verges with *Quercus* and two with *Fagus* were distinguished on the basis of their communities of green plants. Three types of oak forests were studied in the period 1972-1979 by Jansen and IJpelaar. Two types of beech forest were studied by Van Steenis and Opdam. Forests and roadside verges are situated on sandy soils. A comparison is made between the presence-degrees of macromycete species in these types. The differences between roadside verges with trees and forest communities are described and discussed, emphasizing the different patterns for ectomycorrhizal and saprotrophic fungi. Differences between *Quercus* and *Fagus* plots are outlined and discussed. In addition, the data are compared with results of mycocoenological research in other parts of Europe. Effords are made to explain the occurrence of many characteristic ectomycorrhizal species in roadside verges. The significance of different types of roadside verges and forests for threatened macrofungi is evaluated.

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1. Introduction.

Comparative mycocoenological studies were carried out by Keizer in the years 1986-1988 in roadside verges planted with Common Oak (Quercus robur L.) or Beech (Fagus sylvatica L.). All plots were situated on sandy soils in Drenthe in the north-eastern part of the Netherlands. Detailed results of these studies have been published elsewhere (chapter 2, 3, 4) including classifications of mycocoenoses and phytocoenoses, and their relation to various environmental variables.

The main aim of this research was to determine the characteristics of mycocoenoses of roadside verges planted with trees as compared with those of forests with the same tree species. Factors which may reduce the mycoflora in roadside verges are: 1. their openness, making them subject to increased drought stress and 2. pollution and soil compaction, as caused by traffic. On the other hand, factors which may increase the mycoflora are: 1. the heterogeneity of the habitat caused by a gradient perpendicular to the road and 2. the annual mowing regime with eventual removal of the herb layer.

In this paper, a quantitative comparison is made with mycocoenological studies previously carried out by different researchers in *Quercus* and *Fagus* forests in Drenthe. It is tried to assess if species are characteristic for the habitats under consideration.

In addition, more qualitative comparisons are made with some mycocoenological studies from other areas in Europe.

Roadside verges planted with trees are a very important habitat for rare and decreasing macromycetes (section 4.7; chapter 3). This importance is evaluated with the aid of the Red Data List for macrofungi in the Netherlands (Arnolds, 1989b), also in comparison with data on related forest types.

After the observation that the mycoflora of roadside verges differs widely from forests, five hypotheses were formulated in order to explain the striking differences in mycorrhizal flora between these two habitats, in particular the occurrence of so many characteristic species in a man-made habitat:

(1) The differences in mycoflora are mainly caused by differences in microclimate, exposed roadside verges being warmer and drier than forests.

(2) The differential species of roadside verges do not occur optimally in the forest types with which a comparison was made, but are more frequent in different, sympatric forest communities, for instance on richer and/or disturbed soils.

(3) The differential species of roadside verges are indigenous in forest types, which do not occur in the region.

(4) The differential species of roadside verges are relics, which have disappeared from comparable forest types in recent years.

(5) Roadside verges are a man-made habitat with unique ecological characteristics, so that some ectomycorrhizal fungi are regularly found in roadside verges which are very rare in more natural forest types.

The above-mentioned explanatory hypotheses are discussed on the base of research, carried out in the Netherlands. Additional support will be given, using data from other countries.

2. Material and methods.

2.1. *Selection of plots.*

A total of 76 plots were selected in Drente in the northeastern Netherlands in 1986. The area is situated about 10-20 metres above sea-level and has a cool-temperate climate (average precipitation 781 mm./year, mean temperature in January 1.2 °C and in July 15.9 °C. All plots were situated on more or less acid, pleistocene sands with a variable organic matter content. The organical soil profiles were disturbed due to road (re)construction. Fifty-three plots, planted with *Quercus robur* and 23 with *Fagus sylvatica* were selected. In addition, plots were selected based on: (1) exposition (a. exposed roads in open landscapes; b. roads along forest margins and c. roads inside forests), (2) composition of the herb layer, ranging from oligotraphent to eutraphent as an expression of soil conditions and (3) the age of the trees (only for *Quercus*), in three age-classes: young: <20 years; middle-aged: 21-50 years and old: >51 years old.

Within the plots with mature oak trees a subset of 9 plots was selected in order to investigate the influence of the microclimate by selecting roadside verges with different exposure. Four plots were selected along roads bordering the southern edges of forest stands ("south-exposed plots"), five plots the northern or northwestern edges ("north-exposed plots"). The structure of the herb layer and soil fertility were comparable in the two groups.

All plots were 100 metres long and the width varied between 1.5 and 6.5 metres with a number of trees per plot between 9 and 35. All sporocarps of macromycetes were counted and identified with intervals of 3 to 4 weeks in the period August-November during the years 1986-1988. Soil profiles and soil-chemical characteristics were determined in all plots and published in chapter 2 and 3. In addition, the communities of green plants were described and classified according to the Braun-Blanquet method (e.g. Westhoff & Van der Maarel, 1973).

On the basis of vegetation relevés, phytocoenological classifications were carried out, for the roadside verges with *Fagus* and *Quercus* separately, using the computer program TWINSPAN (Hill, 1979). The roadside verges with *Fagus* were divided into two types and each of them into two subtypes. The roadside verges with *Quercus* were divided into three types and two of them were subdivided. A summary of the most important phytocoenological and environmental characteristics of these types is presented in Table 1.

In addition, a mycocoenological classification was made on the basis of the mycological data. This classification in some respects gives different results, that are treated and discussed in chapters 2, 3 and 4. In this publication we will compare mycological characteristics on the basis of the phytocoenological types because (1) these types are based on primary producers and therefore are more relevant for a biocoenological classification; (2) they are more generally used in ecological studies than mycocoenological classifications; (3) they are more easily recognized in the field, and (4) the comparable data on forests in principle are also based on phytocoenological classifications. In spite of some discrepancies, the phytocoenological typology of roadside verge communities has a high predictive value concerning composition and development of the macromycete flora (chapter 2, 3).

2.2. *Forests of Quercus and Fagus.*

The mycocoenological data on roadside verges are compared with data on *Quercus* and *Fagus* forests on acidic sandy soils in Drente. These forests were studied in homogeneous rectangular plots of 30x35 m² (c. 1000 m²), visited with intervals of 3 to 4 weeks, consequently about 3 to 4 times during the main fruiting season (September-November).

Three types of native forests dominated by *Quercus robur* were investigated by Jansen (1984) in the period 1976-1979: (1) the Dicrano-Quercetum (3 plots) on very nutrient-poor windblown sand dunes without developed soil profile and with thin litter layer, the undergrowth with very few herbs but rich in bryophytes such as *Dicranum scoparium* Hedw. and *Leucobryum glaucum*, (2) the Querco-Betuletum (8 plots) on poor, in general podzolic soils, with a understorey of e.g. *Vaccinium myrtillus* and *Melampyrum pratense* and (3) the Violo-Quercetum (18 plots) on slightly richer soils with a thick litter layer and herbs such as *Maianthemum bifolium* and *Oxalis acetosella*. The data published by Jansen on the Dicrano-Quercetum comprised also data on 11 plots, studied by P. IJpelaar, in the years 1972 and 1973.

In forests of *Fagus sylvatica* 19 plots were studied in 1989 and 1990 by Van Steenis (1990) and Opdam (1990). All of them are situated in planted stands since *Fagus* occurs only as scattered trees in hypothetical climax forest communities in Drente. A phytocoenological classification of *Fagus* stands was not well possible due to the very poor development of a herb and moss layer. The authors divided their plots therefore on the basis of the macromycete flora into two main types: the *Laccaria amethystea* type on nutrient-poor soils with a thin litter layer, corresponding with Dicrano-Quercetum and part of Querco-Betuletum, and the *Rickenella fibula* type on somewhat richer soils with a thicker litter layer, corresponding with the Fago-Quercetum and part of the Querco-Betuletum. Some important phytocoenological and environmental parameters of these forest types are included in Table 1.

2.3. *Comparison between roadside verges and forests.*

In this paper the frequency of macromycete species in roadsides and forest types is compared on the basis of their presence-degree: the percentage of plots of a certain type in which a species has been found during the investigation (Tables 2, 3). A species is considered as differential when its presence-degree in a certain type is at least twice as high as in other types. Data on the abundance of sporocarps were omitted since they are more sensitive for differences in methodology (Arnolds, 1981), e.g. different abundance values, different visit frequencies. In addition, the numbers of species of different niche-substrate groups (groups of species which inhabit a common microhabitat and substrate and which have a similar way of habitat exploitation; Arnolds, 1988a) in these types are compared (Table 5).

For sake of surveyability the data on roadsides are only divided into two groups, those with *Quercus* and with *Fagus*, respectively. In fact nine types of roadside verge communities have been distinguished (chapter 2, 3; Table 1). A synoptic table of macrofungi in these types has been published elsewhere (chapter 4). The data presented here allow the distinction of differential species for the entire variety of roadside habitats with regard to various forest communities and vice versa. However, some species may be differential for a certain type of roadside verges with regard to one certain forest type only. These data may also elucidate ecological differences in the mycoflora between roadside verges and forests. Therefore, tables 2 and 3 also indicate the types of roadside verges where a species has its highest presence-

degree.

On the base of these tables we have expressed the value for nature conservation of the roadside verges and the comparable forest types, using the Red Data List of macrofungi in the Netherlands (Arnolds, 1989b). In this list five categories of threatened macrofungi are distinguished, ranging from (probably) extinct to potentially threatened (see also Table 5). For each category two figures are calculated: (1) the total number of threatened species found in a type, (2) the average number of threatened species per plot.

2.4. *Nomenclature.*

Nomenclature of phanerogams is after Heukels & Van der Meijden (1983), of bryophytes after Margadant & During (1982), of fungi mainly after Kreisel (1987). Taxonomic notes on critical and rare species are published in chapter 8. The names of Oak forests are after Westhoff & Den Held (1969). The other phyto- and mycocoena are indicated with -type or -subtype in order to stress their preliminary and inofficial status.

3. **Results.**

The numbers of species belonging to various "niche-substrate groups" in roadside verges, oak forests and beech forests are presented in table 5. From this table it appears that the number of ectomycorrhizal species found in roadside verges is higher than in any of the forest communities. In contrast with roadside verges, forests are extremely poor in saprotrophic grassland-fungi. The numbers of species associated with bryophytes and with other substrates (dung, burnt wood, feathers, sporocarps of fungi, insects) are similar in all studied communities.

The macromycetes in roadside verges and forests are divided into two main groups on the basis of their functional relationship with green plants, the ectomycorrhizal fungi and the saprotrophic and parasitic fungi. This classification is based on various sources (Trappe, 1962; Arnolds, 1984; Kreisel, 1987) including our own field-experience. However, of a few species no functional group can be established with certainty (see discussion).

3.1. *Ectomycorrhizal species.*

The presence-degrees of the more important ectomycorrhizal macromycetes in roadside verges with *Quercus* and *Fagus* and in corresponding forest types in Drente are presented in Table 2. Only species with a presence-degree of >8 % in at least one of the types are included. The species are divided into three differential groups on the basis of their preference for either roadside verges (group I), forest communities (group II) or the lack of preference (group III). For some frequent species a slightly less-pronounced difference in present-degree is allowed when they show also a large difference in abundance of sporocarps (data not presented here, see chapter 2, 3). Within these groups subgroups are distinguished on the basis of preference for *Fagus* (B), *Quercus* (C) or the lack of preference (A).

Among the 99 treated species, 44 are differential for roadside verges, 39 for related forests and only 15 are indifferent to these habitats. Twenty-one species prefer roadsides and/or forests with *Fagus*, 37 are differential for vegetation types with *Quercus* and 41 do

not show a distinct preference for the tree species.

3.2. *Saprotrophic and parasitic species.*

The presence-degrees of the more important saprotrophic and parasitic macromycetes in roadside verges and corresponding forest types are presented in table 3. They are divided into groups and subgroups using the same criteria as for the mycorrhizal fungi (see above). This group is much more heterogeneous as to its microhabitats and substrates. Therefore a subdivision is made within each subgroup into species mainly occurring on (a) litter and humus of grassland plants, (b) litter and humus of forest plants, (c) dead wood and (d) sporocarps of other macromycetes.

A total of 107 species are included in Table 3. Only 21 of them (20%) have a preference for roadside verges, 62 (58%) occur mainly in forests and the remaining 24 species (22%) are indifferent in this respect. Seventeen species (16%) have a preference for *Fagus* vegetation, 17 other species (16%) for *Quercus* vegetation whereas the remaining 73 species (68%) are indifferent.

3.3. *Threatened macromycete species.*

The total and average numbers of threatened species in the studied vegetation types are presented in Table 4, also differentiated for ectomycorrhizal and saprotrophic macromycetes. The species are classified according to the preliminary red data list of threatened species by Arnolds (1989b) into 5 classes:

- class 0: species, (probably) extinct in the Netherlands, i.e. not recorded since 1970 (not present in the studied plots);
- class 1: species threatened with extinction, i.e. very rare species restricted to strongly threatened habitats;
- class 2: strongly threatened species, i.e. rare species, restricted to threatened habitats, or species with strong decline;
- class 3: uncommon species, mainly found in threatened habitats or distinctly declining;
- class 4: potentially threatened species: rare and very rare species without tendency to decrease.

The average number of threatened species per plot varies in forests from 0.4 in the *Rickenella-Fagus* type to 10.8 in the Dicrano-Quercetum, in roadside verges between 0.6 in the *Elytrigia* subtype of the *Festuca-Fagus* type and 3.6 in the *Lotus* subtype of the *Hypochaeris-Quercus* type.

4. Discussion.

4.1. *Differential ectomycorrhizal species for the studied vegetation types.*

44% of all species appear to be differential for roadside verges with regard to forests (Table 2, group I). This group comprises both widespread species with a distinct preference for this habitat, such as *Russula nigricans*, *R. parazurea* and *Xerocomus chrysenteron*, and less common species which are restricted to roadside verges, e.g. *Tricholoma ustale*,

Lactarius serifluus and *Cortinarius erythrinus*. The latter group includes also many rare species, which were observed in one or two plots only, but which are also (almost) exclusively found in roadsides in other areas, e.g. *Cortinarius subbalaustinus*, *C. valgus*, *C. velenovskyi*, *Inocybe amethystina*, *Lactarius vellereus*, *Russula brunneoviolacea*, *R. chloroides* and *R. decipiens*.

Within the roadside verges most species have their highest presence-degree in the nutrient-poor, exposed types (*Fagus* plots: *Festuca ovina* subtype of the *Festuca rubra* type (FFf): 11 species; *Quercus* plots: *Hieracium pilosella* subtype of the *Hypochaeris* type (HQh): 11 species), or in the slightly richer and more shady *Mnium hornum* - *Fagus* type, subtype of *Poa trivialis* (11 species). Environmental conditions in these types show the most pronounced differences with the forest communities under comparison concerning both microclimate and soil-factors (Table 1).

On the other hand, only five species of group I have their highest frequency in shady forest roads with *Fagus* (*Dryopteris* subtype of the *Mnium hornum* type): 2 species) and/or *Quercus* (*Deschampsia flexuosa* (DfQ) type: 3 species). These types show the largest resemblance to corresponding forest types, in particular with respect to the shady, relatively cool microclimate and the accumulation of litter. Considering the forest communities, the mycorrhizal floras of the Dicrano-Quercetum and the *Laccaria* - *Fagus* type have the largest affinity to roadsides in general. The essential ecological variables in common seem to be the thin litter layer, at least in places, and the strongly oligotrophic soil conditions.

Thirty-nine species are more frequent in (part of) the studied forest types than in roadside verges. Only seven species are exclusively found in forests, all of them being characteristic species of the Dicrano-Quercetum on very nutrient-poor sand dunes, e.g. *Tricholoma portentosum*, *T. columbetta*, *Inocybe sambucina* and *Cortinarius alboviolaceus*.

However, the data on the Dicrano-Quercetum were mainly collected in the period 1972-1973. It has been demonstrated that the mycorrhizal flora in this association has become strongly impoverished during the last twenty years (Arnolds, 1991) and almost all characteristic species have nowadays disappeared completely, even a species such as *Cantharellus cibarius*, which was found in the early seventies in all plots in great abundance. A number of these species were probably equally widespread in the poorest types of *Fagus* forests and of roadside verges (FFf and HQh), but have now also become very rare in these habitats. In fact, the few remaining localities of former characteristic species of the Dicrano-Quercetum are now mainly situated in roadsides planted with *Quercus*. Consequently, it is questionable whether exclusive species for forest communities do really exist or do not.

It is striking that among the differential species of forests, only few species within roadside verges have their optimum in open, exposed types (1 species in *Festuca ovina* subtype of the *Festuca rubra-Fagus* type, 1 species in HQh). Highest presence-degree values are most often reached along shady forest roads with litter accumulation (*Fagus* plots: the *Poa trivialis* subtype (MFp) and the *Dryopteris* subtype (MFd) of the *Mnium hornum* type: 7 and 6 times respectively; *Quercus* plots: DfQ: 7 times). This habitat type comes closest to the forest communities. Their frequency in these types is often comparable to that in forests. Only 16 species do not show a distinct preference for either roadside verges or forests. None of them has an optimum in one of the roadside verge types.

4.2. *Preference of ectomycorrhizal species for Quercus or Fagus.*

The majority of the studied species (58 species, 59%) have a distinct preference for either

4.2. *Preference of ectomycorrhizal species for Quercus or Fagus.*

The majority of the studied species (58 species, 59%) have a distinct preference for either *Fagus* or *Quercus*. This preference is the same in both roadside verges and forests, with the following exceptions:

1. *Russula pectinatoides* in roadsides was only found with *Quercus*, but in one *Fagus* forest plot;
2. *Laccaria bicolor* had a weak preference for roadside verges with *Quercus*, but was only reported from *Fagus* forests. However, both species occur only in one or a few plots. *L. bicolor* may have been included in *L. proxima* in the study of *Quercus* forests (Jansen, 1984) and is known to occur with many tree species, also coniferous trees (Kreisel, 1987; Jansen, 1991).
3. *Lactarius camphoratus* was found in rather few roadside verges with both *Quercus* and *Fagus*, but in forests it was restricted to *Quercus*. It is usually regarded as an aspecific symbiont of these tree species as well as coniferous trees (Neuhoff, 1956; Kreisel, 1987).
4. *Boletus erythropus* had in the investigated roadsides a preference for *Fagus*, in forests for *Quercus*. It is reported as a mycorrhizal symbiont of both trees in literature (e.g. Kreisel, 1987) and has been observed by us in roadside verges with *Quercus* outside the plots.

Mycorrhizal fungi show different host ranges which may vary from broad, intermediate or narrow (Molina & Trappe, 1982). Examples from this study are *Russula ochroleuca* and *R. parazurea* and *Laccaria proxima* with a broad, and *Lactarius quietus* and *L. chrysorrheus* with a narrow host range (with *Quercus*). Host ranges are caused by physiological interactions involving recognition and/or defence mechanisms. The exact mechanisms of such host specific relations are largely unknown, but depend possibly on the excretion of substances (elicitors) by the host, which prevent a successful symbiosis in incompatible combinations, but are masked or not produced in compatible combinations (Duddridge, 1987).

More indirectly, the host preference may be influenced by environmental variables such as climate or soil properties (fertility, pH, etc.), or properties of the host itself such as vitality or age (Mason, 1989; Termorshuizen, 1990). Environmental variables may either affect the predisposition of the host to infection, or determine the suitability for the mycorrhizal fungus to establish and survive in the soil.

Thus, physiological interactions may play a role in the exclusive occurrence of *Lactarius quietus* and *L. chrysorrheus* with *Quercus* and *Russula fellea, R. mairei* and *Tricholoma ustale* with *Fagus*. Environmental variables may "explain" the preference of *Inocybe* spp. for the *Fagus* group IB and of *Cantharellus cibarius* for the *Quercus* group IIc. The occurrence of *Hebeloma mesophaeum* in group IIIB may be connected with the age of the host.

However, many species showing a preference in this study for either *Fagus* or *Quercus* are reported in literature having a broader host range (Arnolds, 1984, Kreisel, 1987). In addition, differences between the studies concerning the years of observations may influence the observed preferences. The oak forests were studied in the period 1972-1979, beech forests in 1989-1991. The lower presence degree of, for instance, *Cantharellus cibarius* in *Fagus* forests compared to *Quercus* forests, is probably mainly caused by the strong impoverishment of the mycoflora that started in the sixties (Arnolds, 1988b, 1991). This species has probably been equally common in *Fagus* forests of the *Laccaria amethystea* type.

4.3. *Differences in ectomycorrhizal fungi between roadside verges and forests.*

No arguments to support the microclimate-hypothesis (1) can be found. The microclimate was supposed to be relatively warm and dry in the south-exposed plots due to a large quantity of direct solar radiation, and relatively cool and wet in the north-exposed plots (Barkman & Stoutjesdijk, 1987). On the basis of the above hypothesis, it should be expected that differential species of roadside verges were more frequent in south-exposed plots. However, there was no significant difference: the average number of such species were 24 and 36 in north- and south-exposed plots respectively. Moreover, all plots of this subset were classified on the basis of their mycorrhizal fungi in a single type, the *Russula ochroleuca* type (chapter 3), another indication that microclimatological factors play a minor role for the explanation of differences in the mycorrhizal flora, in comparison with other environmental variables. In addition, there is no indication that the observed differential species of roadside verges have a more southern or continental distribution in Europe, which would be expected for thermo- or xerophilous species. Microclimatological conditions on the mycorrhizal fungi along roads on clay or calcareous soils may possibly be more important (Reijnders, 1968).

Hypothesis 2 ("roadside-species" are more common in different indigenous forest types) is supported by data for a few species, such as *Amanita muscaria*, which is more often found in forests dominated by *Betula* in Drente (Jalink & Nauta, 1984). *Clavulina coralloides*, *Inocybe geophylla* and *Scleroderma areolatum* are regularly found in mixed deciduous forests on weakly acid soils, rather rich in nutrients, for instance in the Alno-Padion on loamy soil in Drente (Arnolds, unpublished mycocoenological data). These species are not characteristic for road sides. Their occurrence in roadside verges can be explained by the higher pH and higher nutrient contents in this habitat than the compared forest communities. However, the vast majority of species of group I (Table 2) are also characteristic of roadsides in other parts of the Netherlands and only rarely found in forests (unpubl. data Netherlands Mycological Society).

Hypothesis 3 is probably valid for the majority of differential species of roadside verges, viz. that these species are characteristic of forest types, not indigenous in the Netherlands at the moment. In this connection we think for instance of open, natural woodlands, grazed by large herbivores, with a herb-rich understorey or the anthropogenic equivalent: so-called "tree-meadows", i.e. very open cattle-grazed "forests" with a grassland undergrowth (Ryman & Holmåsen, 1984:23), or old, small-scaled agricultural landscapes consisting of a mosaic of small, extensively grazed woodlands and grasslands (Jahn & Jahn, 1986). In the Netherlands, many differential species of roadside verges indeed are also found in meadows with scattered trees on old estates. Some species might have their optimal, natural habitat in foreign forest communities on steep slopes, with a permanent natural removal of litter and nutrients (Jahn, 1986). Additional support is found in some data from forests in other countries (see section 4.4.). Examples of this group are *Lactarius serifluus*, *Russula odorata*, *Clitopilus prunulus* and *Lactarius vellereus*.

Hypothesis 4, postulating that roadside verge fungi may be relics, which were once widespread in forests, is probable for part of the species. It was noticed before that presently many former characteristic species of the Dicrano-Quercetum are confined to roadside verges on poor soils (mainly the *Hieracium pilosella* subtype of the *Hypochaeris* type, also the typical variant of the *Anthriscus-Quercus* type). The resemblance of the environmental conditions is striking: in the two vegetation types the herb layer is open, the moss layer is well-developed, the soil is acid, dry, very poor in nutrients, the soil profile is poorly developed and little litter accumulation occurs (Table 1). Probably, the roadside verges of

the *Festuca rubra-Fagus* type (mainly *Festuca ovina* subtype) have a similar relationship to *Fagus* forests on very poor soils, but unfortunately accurate old data on the mycoflora in these forests are lacking. Examples of this group are *Boletus erythropus*, *Cantharellus cibarius* and *Lactarius blennius*, which are nowadays more frequent in roadside verges than in forests on poor sand.

Hypothesis 5 seems to apply to a fairly large group of species, which in most areas are mainly known from roadside verges with trees and only rarely are found in natural forest communities, for instance *Russula amoenolens*, *R. pectinatoides*, *Inocybe maculata* and several other *Inocybe* species. The unique combination of environmental conditions along roads - disturbance of the soil profile, removal of litter, mowing of grass, irregular water supply, local soil compaction and local soil enrichment is very rare and localized in forest communities, but may have been selective for some ectomycorrhizal species, which could extend their distribution area after the appearance of man-made roadside verges with trees. Naturally, there is a connection with the human-influenced landscapes described above.

At present it is not possible to determine per species which is the most probable hypothesis to explain its preference for road sides because reliable data on the frequency of such species in many other forest communities are still lacking.

4.4. *Mycorrhizal fungi in forests built by Quercus species outside the Netherlands.*

Mycocoenological studies in European oak forests have been carried out, by Wilkins et al. (1937) in England, Bohus & Babos (1960, 1967) in Hungary and Darimont (1973) in Belgium.

The oak forests studied by Wilkins et al. comprised 26 plots, distributed over three types; on rather dry, weakly loamy sand soil (comparable to Violo-Quercetum), moist loamy soil (comparable to Querco-Carpinetum) and on wet clay (comparable to Alno-Quercetum). None of the communities showed much resemblance concerning its mycoflora to roadsides and/or oak forests in the Netherlands, presumably owing to considerable differences in soil conditions. Constant species in all types, such as *Amanita phalloides* and *Hydnum repandum* were hardly or not found at all in our plots. Some species, characteristic of roadsides in the Netherlands, were mentioned from forests in England, for instance *Clitopilus prunulus*, *Cortinarius hinnuleus*, *Lactarius serifluus*, *L. vellereus* (in 17 out of 20 plots!), *Russula atropurpurea*, *R. lutea*.

Several grassland species were reported from oak forests by Wilkins et al. (l.c.), e.g. *Hygrocybe coccinea* and *Camarophyllus niveus* (as *Hygrophorus virgineus*), which might suggest an open structure of the canopy and possibly grazing by cattle. Unfortunately no details on management of the stands are presented by the authors. These data support the validity of hypothesis 4, postulated in the previous section.

Bohus & Babos (1960) studied several forest associations dominated by *Quercus* in the Hungarian mountains. Only the community called "Luzulo-Quercetum subcarpaticum, *Dicranum* facies" shows considerable similarities with oak forests in Drente, in particular the Dicrano-Quercetum, and with the roadside verges with Oak on very poor soils (*Hypochaeris-Quercus* type). The environmental conditions are also comparable: on slopes with acid soils without well-developed profile, at most a micropodzol. Some species reported by Bohus & Babos (1960) from forests have an optimum in roadside verges in Drente, e.g. *Amanita pantherina*, *Lactarius serifluus*, *Russula chamaeleontina* (as *R. lutea*), *R. nigricans* and *R. graveolens* (as *R. xerampelina*).

Darimont (1973) investigated in the period 1940-1945 four communities in Belgium where *Quercus* was dominant, three of them on neutral to basic, calcareous soils and consequently with a mycoflora strongly different from the oak communities in Drente. The "Quercetum sessiliflorae medioeuropaeum" occurs on weakly acid brown earth and is more or less comparable with the Violo-Quercetum in the Netherlands. However, the Belgian community is much richer in mycorrhizal species, which may indicate that the stands in the Netherlands are strongly impoverished in this respect. A repeated inventory of Darimont's plots might throw light on this question.

Interestingly, several species which are nowadays regarded as differential of roadside verges were found by Darimont in acid oak forests, e.g. *Amanita spissa*, *Chalciporus piperatus*, *Clitopilus prunulus*, *Helvella lacunosa* (in this study arranged among the saprotrophs), *Inocybe petiginosa*, *Lactarius vellereus*, *Russula atropurpurea*, *R. nigricans* and *R. graveolens* (as *R. xerampelina*).

Darimont (1973) was one of the very few mycocoenologists who paid attention to verges of forest roads and main roads, considered by him as two microcommunities ("synmycies") inside the Quercetum sessiliflorae. He was among the first researchers who noticed that the mycoflora along roads with trees is a combination of grassland- and forest elements. The microcommunity along main roads was characterized by a great variety of 14 *Inocybe* species, including *I. maculata*, *I. griseolilacina* and *I. flocculosa*, which are regarded as differential for roadside verges in Drente as well. Differences in methodology prevent a more accurate, quantitative comparison, because Darimont counted groups of sporocarps which he supposed to represent mycelia.

In conclusion, the data by Bohus & Babos (1960) and Darimont (1973) support hypotheses 3 and 5 for a number of species.

4.5. *Mycorrhizal fungi in forests of Fagus outside the Netherlands.*

Mycocoenological studies of *Fagus* dominated forests were carried out by Jahn (1986) and Jahn et al. (1967), Haas (1932) and Runge (1989) in Germany, Wilkins et al. (1937, 1938) in England, Smarda (1972) in Czechoslovakia, Guminska (1962) and Lisiewska (1963, 1974) in Poland and Darimont (1973) in Belgium. Data on roadsides with planted *Fagus* are lacking. Most of the studies concern beech forests on rich, loamy and/or calcareous soils, for instance belonging to the associations Carici-Fagetum and Melico-Fagetum. The communities of green plants and fungi are widely different from the acidophytic communities in Drente and are not further considered here.

Wilkins et al. (1957) mentioned six fungi with highest frequency in *Fagus* forests on acid (pH 4.0-4.5) sand or clay with raw humus in England: (*Amanita citrina*, *Boletus edulis*, *Cortinarius elatior*, *Russula fellea*, *Russula rosea* Pers. (as *R. lepida*) and *Xerocomus chrysenteron*. Most of them have been found in both forests and roadside verges in the Netherlands, except *R. rosea*, which was not recorded at all.

Jahn & Nespiak (1967) studied the mycoflora in plots in various beech communities in the Weser mountains. The stands of the Luzulo-Fagetum on acid, loamy soil show most affinity to the roadsides with *Fagus* of the *Festuca rubra* type and the *Laccaria-Fagus* forest in Drente. Typical roadside species, such as *Inocybe petiginosa*, *Lactarius blennius*, *Russula lutea*, *R. nigricans*, *Tricholoma ustale* were observed with rather high presence degrees in Luzulo-Fagetum forests, mainly in the subassociation Leucobryetosum on very poor soils. This confirms the hypotheses in which the mycorrhizal flora in roadside verges is considered to be a fragment of a community not present in the Netherlands (hypothesis 3) or a relic of

Russula delica were the most abundant macrofungi. In the Netherlands they are almost confined to roadside verges, at least at present. Likewise, characteristic roadside fungi, such as *Amanita spissa*, *Cortinarius elatior*, *Inocybe umbrina*, *Lactarius blennius* and *Xerocomus chrysenteron* were reported by Darimont (1973) from acidophytic beech forests in the Belgian Ardennes.

However, several differential species of roadsides were not or only rarely reported during mycocoenological studies in forests elsewhere in Europe, for instance *Naucoria bohemica*, *Russula amoenolens*, *R. pectinatoides*, *R. odorata* and various *Inocybe* species. These species probably belong to the group of truly characteristic roadside verge fungi, which are rare in natural forest communities (hypothesis 5).

4.6. *Differential saprotrophic species.*

The communities of saprotrophic fungi in roadside verges and corresponding forests are much more different from each other than those of ectomycorrhizal fungi: Only 24 species (22 %) occur with comparable frequencies in the two groups of habitats (Table 3, group III). Most of them are very common saprotrophs on leaf litter and humus without distinct preference for a certain kind of substrate (ubiquists, group II A1). It should be noticed that the abundance of sporocarps is often considerably larger in forests than in road sides. *Rickenella fibula* and *R. setipes* are associated with living bryophytes, which are growing in both roadside verges and forests. Only seven wood-inhabiting species are equally common in roadside verges and forests. They are able to grow on small wood remains, such as twigs and wood chips, a substrate widespread in the two habitat types.

The number of saprotrophic species, differential for roadside verges, is considerably smaller than the number of differential ectomycorrhizal species (Table 3, group I). Among the twenty differential species nine are characteristic for litter or humus in grassland communities (Arnolds, 1981, 1984). Eight of them are equally common in roadside verges with *Quercus* and *Fagus*, but *Psathyrella panaeoloides* has an unexplained preference for *Fagus*.

The remaining species of differential group I are more heterogeneous in ecological respect. *Entoloma subradiatum*, which has a preference for *Fagus*, is a terrestrial forest species (Noordeloos, 1988:103) and may possibly be a mycorrhizal symbiont. The nutritional status of many *Entoloma* species is still unclear.

Nyctalis asterophora is a saprophyte on dead sporocarps of *Russula nigricans* (Kreisel, 1987). This ectomycorrhizal species occurs in large quantities only in some roadsides with old *Quercus* trees and is much rarer in forest communities (Table 2 group Ia). It is striking that *Nyctalis* is almost confined to areas with high densities of sporocarps of *Russula nigricans*.

Agrocybe praecox, *Helvella lacunosa*, *Mycena flavescens* and *Tarzetta cupularis* are mainly found outside roadside verges on leaf litter and humus in nutrient-enriched, disturbed places in forests, for instance along foot paths and forest edges among *Urtica dioica* L.. Such microhabitats were excluded from the plots in *Fagus* and *Quercus* forests, which explains their absence from these forests.

Mycena polyadelpha is a very small agaric on intact, dead leaves of *Quercus* and may be either overlooked in the study of *Quercus* forests or characteristic of forests on richer soils.

Coprinus subimpatiens, *Marasmius rotula*, *Mycena adscendens*, and *Tubaria furfuracea*, inhabit small twigs and wood chips and have their optima in forests on richer soils, such as

the Alno-Padion (Arnolds, unpublished data). Within the plots, *Mycena adscendens* has a preference for *Quercus*, the other species of *Fagus* twigs.

The occurrence of many indicator species of nutrient-rich soils in roadside verges can be explained by eutrophication by traffic, blown-in fertilizers, deposition of waste, wood chips and excrements (dogs, horses). In addition, decomposition rates may be higher in some roadside verges than in forests.

The list of differential saprotrophic species for forests (Table 3, group II) is considerably longer, which is likely the result of the much larger quantities of available substrates, mainly leaf litter and wood. In exposed roadside verges most of the leaf litter is blown away in the course of the autumn (chapter 9). Fallen boughs and branches are always removed and most wood remains in roadside verges are small twigs and occasionally stumps of died trees. Exceptions to this rule are the verges of forest paths, where normal litter accumulation occurs and dead wood is often allowed. Such roadside verges mainly belong to the *Mnium hornum-Fagus* type (F3, F4) and the *Deschampsia flexuosa-Quercus* type (Q5) (chapter 2, 3). Many species of group II in Table 3 are within the roadside verges differential for these types, where they often have a presence degree comparable to the corresponding forest types.

4.7. *Mycological evaluation of roadside verges and forests with Fagus and Quercus in the scope of nature conservation.*

The numbers of threatened species per vegetation type are presented in Table 4. The highest number of threatened species (45) is found in the *Lotus* subtype of the *Hypochaeris-Quercus* roadside verges, but the highest average number per plot is found in forests of the Dicrano-Quercetum. The categories of severely threatened species (classes 1 and 2) are also best represented in this type. However, these figures are not well comparable with the other data in Table 4 since the Dicrano-Quercetum was mainly investigated in the period 1972-1973 (only 3 plots also in 1976-1979) and it has been demonstrated that a strong decline of mycorrhizal fungi has taken place since 1960-70 (Arnolds, 1989b; 1991). The entire fungal community of the Dicrano-Quercetum has become practically extinct in the Netherlands, partially due to natural succession of the community, but mainly caused by atmospheric deposition of nitrogen compounds (Arnolds, l.c.), and the mycological value is nowadays comparable to the levels of the Querco-Betuletum and the *Laccaria amethystea-Fagus* type. The occurrence of threatened fungi in the most widespread, more eutrophic forest types of *Rickenella-Fagus* and the Violo-Quercetum is very limited.

A considerable number of threatened fungi occur in roadside verges planted with trees. In the investigated plots a total of 69 species, reported in the "Red List" of threatened macromycetes in the Netherlands (Arnolds, 1989b), were recorded, including six species which are considered to be threatened with extinction, viz. *Boletopsis leucomelaena*, *Cortinarius causticus*, *Dermocybe cinnabarina*, *Leucopaxillus giganteus*, *Lyophyllum semitale*, and *Phellodon confluens*. In addition, twelve strongly threatened species were found, viz. *Amanita porphyria*, *Cortinarius fusisporus*, *C. subbalaustinus*, *C. torvus*, *Entoloma solstitiale*, *Inocybe calospora*, *Hydnellum concrescens*, *H. spongiosipes* and *Pseudocraterellus sinuosus*, *Tricholoma saponaceum*, *T. scalpturatum*, *Tylopilus felleus*.

The average numbers of threatened species are highest in the *Festuca ovina* subtype of the *Festuca rubra-Fagus* community, the two subtypes of the *Hypochaeris-Quercus* community and the inops subtype of the *Anthriscus-Quercus* community. These numbers (approx. 3 species per plot) are much lower than in the former Dicrano-Quercetum, but, on

the other hand, they are higher than in the actual relics of this forest type (Arnolds, 1991) and the *Laccaria-Fagus* type. The roadside verges contain more different threatended species than the forests, for instance, in the 11 plots of the Dicrano-Quercetum a total of 32 Red List species have been found with an average number of 10.8 species per plot; in the 21 plots of the *Lotus* subtype of the *Hypochaeris-Quercus* type, 45 species with an average of 3.6 species per plot. Consequently, roadside verges offer a potential habitat to a large number of threatened fungi, which enhance their value from a nature conservation point of view.

All four types of roadsides being rich in threatened fungi, have a number of environmental characteristics in common (Table 1): they are situated in open landscapes, the organic layers (A_0+ A_{00}) are relatively thin, a moss layer is usually well-developed (with exception of the inops variant of the Anthriscus-Quercus type, the AQi), the herb layer is usually short and the soluble phosphor content and nitrogen availability (expressed as Ellenberg N-value) are low (except Ellenberg N-value in AQi). These ecological conditions in the forest types studied are most similar to the situation in the Dicrano-Quercetum and the *Laccaria-Fagus* forest type, in particular concerning the occurrence of a thin litter layer. In these forest types a patchy pattern occurs of places where litter is blown away and where it accumulates. The places with a thin litter layer have a high moss cover and here concentrations of threatened and rare mycorrhizal species are found (Jansen, 1984). Important differences are the higher pH and lower C/N ratio in roadside verges.

The majority of threatened species in the investigated types of roadside verges and forests belong to the ectomycorrhizal fungi. The relative high number of threatened saprotrophic and parasitic fungi in the Dicrano-Quercetum is mainly caused by the high frequency of two *Cordyceps* species, growing as parasites on ectomycorrhizal *Elaphomyces* species, consequently in fact caused by ectomycorrhizal fungi in an indirect way. The relative high numbers of threatened saprotrophs in some types of roadside verges (FFf, HQh, HQl) are mainly caused by the occurrence of decreasing species of poor, unfertilized grasslands.

The occurrence of severely threatened ectomycorrhizal species (classes 1 and 2) is usually correlated with the occurrence of a large number of less threatened species (classes 3 and 4). High numbers of threatened species are concentrated in only very few plots, viz. plot Q2 (23 threatened species), Q83 (16), Q32 (8) and F43 (4). Plots Q2, Q83 and Q32 are roadside verges with old *Quercus* trees on nutrient-poor soil. Roadside verges with Beech are less rich in threatened fungi, the richest being plot F43 with 4 Red List species. These localities certainly deserve special attention concerning planological protection and management (chapter 3, 9).

The knowledge on the ecology of mycologically rich roadside verges can be used in favour of nature management measures which can be carried out in forests that are mycologically impoverished. In forests where a thick organic layer has accumulated, sod removal can cause a regeneration of the mycoflora. In other forests, repeated litter collection may create the absence of a litter layer, together with a decrease of the nutrient content of the soil, which are necessary for a rich mycoflora. These measures are most promising in areas with an originally nutrient-poor soil. In view of the experiences in roadside verges, most success is to be expected in ectomycorrhizal fungi.

Grazing with large grazers (horses, cattle) in combination with the development of an open forest structure will develop in the long run a landscape type approaching the "tree-

meadows", the old agricultural land use where a rich mycoflora can be present (see section 4.3).

There are some promising examples of these nature management types in the Netherlands (Baar & Kuyper, 1993; Keizer, 1993; chapter 7).

5. Conclusions.

In this paper we analyzed and discussed the differences between mycocoenoses in roadsides with planted *Quercus* and *Fagus* on the one hand and forests on sandy, acid soils dominated by these trees on the other. Both are strongly different, for ectomycorrhizal as well as saprotrophic fungi. In both groups only a minority of species are equally frequent in roadsides and forests.

The differential saprotrophic fungi of roadside verges are in part characteristic for grasslands, which is understandable since the herb layer in open, exposed roadsides (*Hypochaeris-Quercus* type, *Festuca rubra-Fagus* type) is comparable with some grassland communities and is treated in the same way; i.e. it is usually mown once or twice a year. Some differential species of roadside verges are characteristic of forest types on richer soils which were not considered in this study. Their occurrence is determined by local enrichment of roadside verges. Differential fungi of forests are many saprotrophs on leaf litter and wood-remains, in particular those on larger branches, trunks and stumps. This can be explained by the much larger frequency of these substrates in forest stands. Shady roadside verges, situated in forests (*Mnium-Hornum-Fagus* type, *Deschampsia flexuosa-Quercus* type), are in these respects intermediate: differential grassland species are lacking and forest saprophytes are much more frequent than in other types of road sides, but less frequent than in forests.

The explanation of the differences in ectomycorrhizal fungi is more complicated. Many species have their optimum in roadside verges with planted trees and most of them occur mainly in open, exposed roadside types. The mycocoenoses in such roadside verges mostly resemble forest types on very poor, acid, sandy soils without distinct soil profile development and a thin litter layer, i.e. in the Netherlands the Dicrano-Quercetum and *Laccaria amethystea-Fagus* community. The differential species of roadside verges may in part be considered as species which have disappeared from these forest communities in recent years (Arnolds, 1988b, 1991). This phenomenon is ascribed to natural forest succession in combination with high nitrogen deposition. It is beyond the scope of this paper to treat this subject in detail.

The characteristic ectomycorrhizal flora along roads is made up of four elements:
(1) species which have become rare or extinct in forests on poor, sandy soils;
(2) species which have their optimum in indigenous forest associations on richer soils;
(3) species which have their optimum in forest associations, not or hardly occurring in the Netherlands, e.g. the Luzulo-Fagetum;
(4) species which occur sporadically in natural forest communities, and are stimulated by the prevalent environmental conditions in roadside verges.

On the other hand, a number of mycorrhizal species have their optimum in forest communities. Many of them are known as differential species for the Dicrano-Quercetum, but all of these species have strongly decreased in the forests themselves since the early seventies, when this forest association was studied. At present their frequency in such forests is very low and many of them have become differential for roadside verges, be it with a

lower presence-degree than in formerly well-developed stands of the Dicrano-Quercetum, for instance *Cantharellus cibarius*. The corresponding *Fagus* forests on very poor soils, belonging to the *Laccaria-Fagus* community, were only recently studied and therefore no long list of differential species is available with respect to roadside verges with beech. Part of the differential species of forests are found with comparable frequency along shady forest roads.

At present, roadside verges with trees are extremely valuable as habitat for rare and threatened macrofungi, in particular ectomycorrhizal species, but also for some grassland fungi. The richest plots, rating urgent protection, are all exposed roadside verges with medium-old to old trees on very poor, acid soil with a low, grassy or moss-rich understorey, usually mown with regular intervals. They contain the last localities of some species in the Netherlands, which can be regarded as relics which have become extinct in forest communities. It should be emphasized that the valuable roadside verges make up a very small proportion (less than approx. 1%) of all roadsides planted with trees. Therefore their protection, adequate management and extension of their area is necessary. Most roadside verges are situated on primarily nutrient-rich soils, often supplied from elsewhere, or strongly influenced by fertilizers and dung from adjacent agricultural land. Such roadside verges have a poorly developed mycoflora.

We consider as key factors for a well-developed mycorrhizal flora with rare species an extremely low availability of nitrogen (and phosphorus?), absence of litter accumulation and a short, low productive herb layer. These conditions were fulfilled in the past in many forest stands, but the increased acidification and atmospheric deposition of nitrogen have disturbed these ecosystems (Termorshuizen, 1990) and have lead to a virtual extinction of the communities of Dicrano-Quercetum and Cladonio-Pinetum in the Netherlands, with the exception of some relics along the coast (Arnolds, 1991; Van der Werf, 1991). Although nitrogen deposition is at least equally high in roadside verges with trees, the influence on the soil conditions is considerably less in well-managed, exposed roadsides due to the transport of nitrogen from the system by the removal of litter by the wind and the removal of part of the sward by mowing practices (chapter 7).

Management measures in forests, directed towards a reduction of the organic matter and nutrient content of the soil, combined with an open forest structure (wind influence) can regenerate a rich ectomycorrhizal mycoflora.

TABLE 1. Characteristics of vegetation types in roadside verges planted with *Fagus sylvaticus* or *Quercus robur* in Drente, the Netherlands, compared with characteristics in forests of these tree species in the same area.

Landscape type	Roadside verges									Forests				
Vegetation type	FFe	FFf	MFp	MFd	HQh	HQl	AQi	AQt	DfQ	LF	RF	DQ	QB	VQ
Dominant tree			Fagus sylvaticus					Quercus robur		F. sylvaticus			Q. robur	
Number of plots	5	7	5	6	5	21	6	17	4	10	9	11	8	18
Nr. trees/1000 m²	34	55	58	64	41	43	38	50	65	-[7]	-	-	-	-
Av. age of trees (yr in 1988)	58	52	77	69	54	55	95	106	116	-	-	-	-	-
Av. vitality (class I-IV)[1]	2.3	3.1	2.0	2.4	-	2.1	1.8	1.9	1.8	-	-	-	-	-
Av. cover herb layer (%)	74	59	29	9	69	76	63	75	35	2	1	4[6]	60	33
Av. cover moss layer (%)	3	17	4	13	26	11	0	0	6	2	6	27	3	1
Av. traffic intensity (class I-VI)[2]	3.0	2.4	1.8	1.0	1.6	2.0	2.3	2.2.	1.0	-	-	-	-	-
Av. potential sun (hr/day Oct.)[3]	5.7	6.0	0.7	0	6.9	6.8	3.6	2.7	0	0	0	0	0	0
Av. Ellenberg N value[4]	6.6	5.3	6.0	3.3.	3.8	5.4	6.2	6.9	4.0	4.6	6.2	2.7	3.3	4.1
Av. thickness organic layer (mm)	0	30	24	52	0	20	7	12	55	47	60	50	70	60
Av. pH-$CaCl_2$	4.4	4.0	4.2	3.5	4.2	3.9	4.0	3.3	3.0	3.1	-	-	-	-
Av. pH-H_2O	-	-	-	-	-	-	-	-	-	-	-	3.9[6]	3.8	3.8
Av. NO_3^- (mg.kg^{-1} soil)	3.6	1.0	0.4	1.3	0.8	1.0	0.17	1.5	0.8	0.9	4.8	-	-	-
Av. NH_4^+ (mg.kg^{-1} soil)	6.4	7.1	5.2	9.3	6.2	9.7	8.8	9.1	12.3	7.3	10.4	-	-	-
Av. N total (%)	.19	.16	.13	.17	.14	.17	.17	.19	.24	.37	.43	-	-	-
Av. C total (%)	3.0	2.8	2.6	3.9	2.4	3.2	3.3	2.8	3.7	12.2	10.7	-	-	-
Av. C/N ratio	16	18	20	22	18	19	20	17	16	33	25	24	23	22
Av. P soluble (mg.kg.$^{-1}$ soil)	1.0	0.1	0	0.7	0	0.5	0.2	0.4	3.0	1.0	4.2	-	-	-
Av. P total (mg.kg.$^{-1}$ soil)	346	224	254	179	213	281	200	296	146	183	368	-	-	-

Explanation table 1:

1) Vitality classes: I = vital; IV = not vital.
2) Traffic intensity classes: 1: <625, 2: 625-1250, 3: 1250-2500, 4: 2500-5000, 5: 5000-10000, 6: >10000 motorized vehicles day^{-1}.
3) Potential sunshine hours/day in October: determined with a horizontoscope (Barkman & Stoutjesdijk, 1987).
4) Ellenberg values: 1: characteristic for habitats poorest in Nitrogen, 9: characterisitc for habitats extemely rich in nitrogen (polluted). (Ellenberg, 1979).
5) Soil chemical analyses: standard methods in 0.01 N $CaCl_2$, according to Houba et al. (1988).
6) Average values based on 3 plots, only studied by Jansen (1984).
7) - = not determined

The following vegetation types are distinguished:
Roadside verges:
FFe: *Elytrigia* subtype of *Festuca rubra-Fagus* type,
FFf: Idem, *Festuca ovina* subtype,
MFp: *Poa trivialis* subtype of *Mnium hornum-Fagus* type,
MFd: Idem, *Dryopteris* subtype.
HQh: *Hieracium pilosella* subtype of *Hypochaeris-Quercus* type,
HQl: Idem, *Lotus corniculatus* subtype,
AQi: Inops variant of *Anthriscus-Quercus* type,
AQt: Idem, typical variant,
DFQ: *Deschampsia flexuosa-Quercus* type.
Forests:
LF: *Laccaria amethystea-Fagus* type,
RF: *Rickenella fibula-Fagus* type (after Opdam, 1991),
DQ: Dicrano-Quercetum,
QB: Querco-Betuletum,
VQ: Violo-Quercetum (after Jansen, 1984).

ABLE 2. Synoptic table of ectomycorrhizal macromycetes in roadside verges planted with *Fagus sylvaticus* or *Quercus robur* in Drente, Netherlands, compared with forests of *Fagus* and *Quercus* in the same area.
e figures are presence-degrees in %.
followed by a number indicates the threatened status of a species according to the "Red List" (Arnolds, 1989b): 1= threatened with tinction; 2= strongly threatened; 3= threatened; 4= potentially threatened.

breviations of the forest types:
= *Laccaria amethystea* - *Fagus* forest (after Opdam, 1991),
= *Rickenella fibula* - *Fagus* forest (after Opdam, 1991),
Q = Dicrano-Quercetum (after Jansen, 1984),
B = Querco-Betuletum (after Jansen, 1984),
Q = Violo-Quercetum (after Jansen, 1984).

the last column vegetation types of roadside verges are mentioned for which a species is differential within roadside verge communities cording to the following abbreviations (the figures are presence-degrees in %):
Fe: *Festuca-rubra-Fagus* type, subtype of *Elytrigia repens*.
Ff: *Festuca-rubra-Fagus* type, subtype of *Festuca ovina*.
Fp: *Mnium hornum-Fagus* type, subtype of *Poa trivialis*.
Fd: *Mnium hornum-Fagus* type, subtype of *Dryopteris carthusiana*.
Qh: *Hypochaeris-Quercus* type, subtype of *Hieracium pilosella*.
Ql: *Hypochaeris-Quercus* type, subtype of *Lotus corniculatus*.
Qi: *Anthriscus-Quercus* type, inops variant.
Qt: *Anthriscus-Quercus* type, typical variant.
FQ: *Deschampsia flexuosa-Quercus* type.

bitat type	ROADSIDE VERGES		FORESTS					
minant type	Fag.	Que.	Fagus		Quercus			
getation type			LF	RF	DQ	QB	VQ	presence degrees in vegetation types in roadside verges
mber of plots	23	53	10	9	11	8	18	
Differential species for roadsides with trees:								
) **For roadsides with *Fagus* and *Quercus***								
ssula parazurea	78	68	30	44	-	-	17	MFp:100, AQt:94
rocomus chrysenteron	57	45	-	33	-	25	22	MFp:80, AQt:76
leroderma areolatum	30	57	10	-	-	6	11	FFf:42, AQi:67
ssula nigricans	30	40	-	22	9	12	6	MFp:60, DfQ:75
beloma helodes	39	28	-	-	-	-	-	FFf:42, HQ:40
avulina coralloides	35	32	-	-	-	-	-	FFe:60, HQh:60
ssula atropurpurea	22	36	-	-	9	-	17	DfQ:100
rtinarius striaepilus	30	28	10	-	-	-	-	MFp:40, AQi:50
rtinarius saniosus	30	23	-	-	-	-	-	FFf:57, HQh:60
rtinarius erythrinus	26	21	-	-	-	-	-	FFf:42, HQh:60
ucoria bohemica	22	23	-	11	-	-	-	HQl:60
itopilus prunulus *3	26	11	-	-	-	-	-	FFf:57, HQh:60
ocybe umbrina	17	19	-	-	-	-	-	MFp:40, AQi:50
rtinarius flexipes	17	17	-	-	-	-	-	MFP:40, HQh:40
ssula ionochlora	13	11	-	-	-	-	-	AQi;29
ocybe maculata	13	8	-	-	-	-	-	FFe:20, MFp:20
rtinarius lanatus	9	9	-	-	-	-	-	MFp:20, AQi:33
ssula grisea	9	8	-	-	-	-	-	MFd:20, AQt:18
ssula chamaeleontina	9	4	-	-	-	-	-	MFp:20, HQh:20
ocybe albomarginata	4	9	-	-	-	-	-	AQt:18

Habitat type	ROADSIDE VERGES		FORESTS					
Dominant type	Fag.	Que.	Fagus		Quercus			
Vegetation type			LF	RF	DQ	QB	VQ	presence degrees in vegetation types
(B) For roadsides with *Fagus*:								
Lactarius blennius	61	-	20	-	-	-	-	FFf:71
Tricholoma ustale *3	39	-	-	-	-	-	-	FFf:71
Inocybe petiginosa	30	8	-	-	-	-	-	MFp:40, MFd:50
Russula velenovskyi	26	11	-	11	-	-	-	MFp:60
Amanita spissa	26	6	-	-	-	-	-	MFp:40
Amanita muscaria	22	8	10	-	-	-	-	FFf:57
Amanita pantherina	22	4	-	-	-	-	-	FFf:42
Inocybe sindonia	22	2	10	11	-	-	-	MFd:33
Inocybe fuscidula	17	4	-	-	-	-	-	FFe:40
Inocybe geophylla	17	4	-	-	-	-	-	FFf:29
Chalciporus piperatus	17	6	-	-	-	-	-	FFf:29, HQH:20
Inocybe flocculosa	13	4	-	-	-	-	-	FFe:20
Inocybe huysmanii	13	-	-	-	-	-	-	FFe:40
Inocybe ochroalba	9	-	-	-	-	-	-	MFp:20
(C) For roadsides with *Quercus*:								
Russula amoenolens	39	77	-	-	9	-	6	HQh:100, AQi:100
Lactarius serifluus	9	25	-	-	-	-	-	DfQ:50
Russula pectinatoides	-	28	-	11	-	-	-	AQi:50
Russula odorata *3	4	17	-	-	-	-	-	HQh:60
Russula graveolens f. graveolens	-	21	-	-	-	-	-	AQi:33
Russula graveolens f. cicatricata	-	11	-	-	-	-	-	HQh:40
Russula graveolens f. purpurata	-	9	-	-	-	-	-	AQi:33
Xerocomus rubellus	-	8	-	-	-	-	-	AQt:18
Xerocomus porosporus	-	8	-	-	-	-	-	AQt;24
Inocybe griseolilacina	-	8	-	-	-	-	-	HQl:15
II. Differential species for forests:								
(A) For forests of *Fagus* and *Quercus*:								
Russula ochroleuca	52	26	100	89	55	87	72	MFd:100, DfQ:100
Lactarius theiogalus	39	32	90	78	82	87	89	MFp:60, DfQ;75
Laccaria amethystea	48	23	100	-	100	50	11	MFp:80, Aqi:50
Xerocomus badius	43	34	80	-	73	50	22	MFd:67, AQi:50
Cortinarius paleaceus	30	26	70	-	82	-12	-	MFp:40, HQl: 35
Inocybe napipes	26	11	80	44	55	37	17	MFd:83, DfQ:50
Amanita fulva	13	21	80	-	100	25	-	MFd:33, DfQ:50
Thelephora terrestris	22	11	30	-	55	-	-	MFp:60, DfQ:50
Russula emetica	4	6	80	-	73	50	33	DfQ:50
Xerocomus subtomentosus *3	4	2	40	-	-	25	11	
Cortinarius elatior *3	-	4	20	-	36	25	-	
(B) For forests of *Fagus*:								
Cortinarius paleiferus	14	2	40	-	-?	-?	-?	MFp:40
Laccaria bicolor	4	13	60	22	-?	-?	-?	AQi:33
Lactarius necator	-	2	70	-	27	-	17	
(C) For forests of *Quercus*:								
Lactarius proxima	48	47	40	-	100	75	50	MFd:100, AQi:83
Russula fragilis	13	40	20	-	100	25	-	HqH:60
Lactarius camphoratus *3	13	15	-	-	64	62	11	MFp:40, AQi:50
Lactarius chrysorrheus *3	4	23	-	-	73	25	-	HQh:40
Hebeloma longicaudum	13	9	-	-	36	25	-	MFd:33
Cantharellus cibarius *3	9	11	20	-	100	-	-	AQi:50

Habitat type	ROADSIDE VERGES		FORESTS					
Dominant type	Fag.	Que.	Fagus		Quercus			
Vegetation type			LF	RF	DQ	QB	VQ	presence degrees in vegetation types
Boletus erythropus *3	17	2	10	-	55	-	-	FFf:42
Russula vesca	4	13	-	11	36	12	-	AQi:50
Cortinarius casimiri (incl. *C. decipiens* s. Henry)	9	6	10	-	36	62	22	MFp:40
Cortinarius obtusus	9	6	-	-	62	-	-	DfQ:25
Leotia lubrica *3	4	8	10	-	64	-	-	
Cortinarius umbrinolens (incl. *C. glandicolor*)	-	6	10	-	45	-	-	
Dermocybe cinnamomea s. lat.	-	4	10	-	62	12	-	
Cortinarius fusisporus *2	4	-	10	-	62	12	-	
Tylopilus felleus *2	-	2	10	-	9	25	6	
Hydnellum concrescens *2	-	2	-	-	36	-	-	
Hydnellum spongiosipes *2	-	2	-	-	27	-	-	
Tricholoma columbetta *2	-	-	-	-	27	-	-	
Tricholoma virgatum *1	-	-	-	-	27	-	-	
Tricholoma portentosum *2	-	-	10	-	36	-	-	
Sarcodon scabrosus *2	-	-	-	-	27	-	-	
Russula adusta	-	-	-	-	36	-	-	
Inocybe sambucina *2	-	-	-	-	36	-	-	
Hebeloma pumilum	-	-	-	-	27	12	-	
Cortinarius bolaris *2	-	-	-	-	36	-	-	
Cortinarius alboviolaceus *2	-	-	-	-	27	-	-	
III. Indifferent species for roadsides and forests:								
(A) For *Fagus* and *Quercus*:								
Laccaria laccata	87	92	70	56	9	37	28	5types:100
Amanita rubescens	87	57	90	33	82	75	50	MF:100, DfQ:100
Scleroderma citrinum	61	40	50	22	100	100	56	MFd:83, DfQ:50
Paxillus involutus	61	34	80	56	100	100	100	MFd:83, AQi:83
Boletus edulis	39	19	-	-	36	-	-	FFf:71, HQh:60
Amanita citrina	17	26	30	-	27	37	11	MFp:80
Inocybe mixtilis (incl. *I. xanthomelas*)	22	13	20	-	27	12	-	FFe:40
Inocybe lacera	13	17	20	-	-	-	-	HQh:40
Cortinarius hinnuleus *3	13	17	-	-	9	-	-	HQh:40
Cortinarius anomalus	4	8	10	11	-	-	-	AQt:12
(B) For *Fagus*:								
Russula fellea	70	-	70	44	-	-	-	FFf:86
Russula mairei	57	-	70	-	9	-	-	MFd:83
Lactarius subdulcis	35	-	50	22	-	-	-	MFd:50
Hebeloma mesophaeum	26	11	-	33	-	-	-	FFe:40
(C) For *Quercus*:								
Lactarius quietus	4	89	-	-	100	100	100	AQi:100, DfQ:100
Russula cyanoxantha	9	25	-	-	36	12	-	AQi:50

Table 3. Synoptic table of saprotrophic and parasitic macromycetes in roadside verges planted with *Fagus sylvaticus* or *Quercus robu* in Drente, the Netherlands, compared with forests of *Fagus* and *Quercus* in the same area.
The figures are presence-degrees in %.
* followed by a number indicates the threatened status of a species according to the "Red List" (Arnolds, 1989b): 1= threatened wit extinction; 2= strongly threatened; 3= threatened; 4= potentially threatened.

Abbreviations of the forest types:
LF = *Laccaria amethystea-Fagus* forest (after Opdam, 1991).
RF = *Rickenella fibula - Fagus* forest (after Opdam, 1991).
DQ = Dicrano-Quercetum (after Jansen, 1984).
QB = Querco-Betuletum (after Jansen, 1984).
VQ = Viololo-Quercetum (after Jansen, 1984).

In the last column types of roadside verges are mentioned for which a species is differential within roadside verge communities accordin to the following abbreviations (the figures are presence-degrees in %):
FFe: *Festuca rubra-Fagus* type, subtype of *Elytrigia repens*.
FFf: Idem, subtype of *Festuca ovina*.
MFp: *Mnium hornum-Fagus* type, subtype of *Poa trivialis*.
MFd: Idem, subtype of *Dryopteris*.
HQh: *Hypochaeris-Quercus* type, subtype of *Hieracium pilosella*.
HQl: Idem, subtype of *Lotus corniculatus*.
AQi = *Anthriscus-Quercus* type, inops variant.
AQt = Idem, typical variant.
DfQ = *Deschampsia flexuosa-Quercus* type.

Habitat type	ROADSIDE VERGES		FORESTS					
Dominant type	Fag	Que	Fagus		Quercus			
Vegetation type			LF	RF	DQ	QB	VQ	presence degrees in vegetation types in roadside verges
Number of plots	23	53	10	9	11	8	18	
I. DIFFERENTIAL SPECIES FOR ROADSIDE VERGES								
IA. Without preference for *Fagus* and *Quercus*.								
IA1. Saprotrophic species on litter or humus of grassland plants.								
Mycena avenacea	30	36	-	-	-	-	-	FFe:60, FFf:57, HQh:60, HQl:62
Mycena sepia	26	30	-	-	-	-	-	FFf:57, HQl:51
Marasmius oreades	13	28	-	-	-	-	-	FFe:40, HQh:40, HQl:43
Mycena flavoalba	17	17	-	-	-	-	-	FFe:40, HQh:40
Entoloma sericeum f. sericeum	13	19	-	-	-	-	-	FQh:40
Psilocybe semilanceata	9	11	-	-	-	-	-	
Marasmius graminum	9	11	-	-	-	-	-	
Calocybe carnea	13	6	-	-	-	-	-	FFe:20, FFf:29
IA2. Saprotrophic species on litter or humus of forest plants.								
Mycena flavescens	17	17	-	-	-	-	-	
Helvella lacunosa	17	11	-	-	-	-	-	FFe:40
Tarzetta cupularis	13	6	-	-	-	-	-	
IB. With preference for *Fagus*.								
IB1. Saprotrophic species on litter or humus of grassland plants.								
Psathyrella panaeoloides	17	2	-	-	-	-	-	
IB2. Saprotrophic species on litter or humus of forest plants.								
Agrocybe praecox	17	6	-	-	-	-	-	
Entoloma subradiatum	17	2	-	-	-	-	-	FFe:40

Habitat type	ROADSIDE VERGES		FORESTS					
Dominant type	Fag	Que	Fagus		Quercus			
Vegetation type			LF	RF	DQ	QB	VQ	presence degrees in vegetation types
IB3. Saprotrophic species on wood.								
Tubaria furfuracea	100	36	30	44	-	12	17	
Psathyrella microrhiza	17	6	-	-	-	-	-	MFp:40, MFd:33
Coprinus subimpatiens	17	4	-	-	-	-	-	FFe:40
Marasmius rotula	13	2	-	-	-	-	-	
IC. With preference for *Quercus*.								
IC2. Saprotrophic species on litter of forest plants.								
Mycena polyadelpha	4	26	-	-	-	-	6	
IC3. Saprotrophic species on wood.								
Mycena adscendens	4	17	-	-	-	-	-	
IC4. Saprotrophic species on sporocarps of other macromycetes.								
Nyctalis asterophora Fr. *3	-	15	-	-	-	-	-	AQi:50
II. DIFFERENTIAL SPECIES FOR FORESTS.								
IIA. For forests of *Fagus* and *Quercus*.								
IIA1. Soil-inhabiting fungi on litter, humus and bryophytes.								
Mycena sanguinolenta	35	40	100	67	64	100	89	MFp:60, MFd:50, DfQ:75
Clitocybe metachroa	17	49	70	78	18	100	78	MFp:40, DfQ:100
Galerina hypnorum	26	23	100	89	64	100	89	MFp:40, MFd:50
Stropharia aeruginosa s. lato	22	15	10	33	-	25	50	FFe:40, FFf:43, DfQ:50
Clitocybe vibecina	13	17	70	22	82	100	83	MFd:50, DfQ:75
Collybia peronata	22	4	20	33	9	37	72	MFp:60, DfQ:25
Mutinus caninus	13	6	10	22	-	25	33	MFd:33, DfQ:25
Entoloma rhodocylix	13	4	40	22	36	25	6	MFd:33, DfQ:25
Phallus impudicus	9	4	40	11	9	50	94	MFd:33, DfQ:25
Cystoderma amianthinum s. lato	9	4	50	-	100	62	33	
Clitocybe clavipes	4	6	30	33	55	25	6	
Marasmius androsaceus	4	4	50	-	82	50	22	
Entoloma turbidum *3	4	4	40	-	36	-	-	
Mycena epipterygia	-	2	80	22	-	50	33	
Galerina luteofulva	0	2	60	11	27	50	44	
IIA2. Wood-inhabiting fungi (selection).								
Armillaria obscura	43	25	60	89	45	87	67	MFp:80, MFd:83,DfQ:50
Psathyrella artemisiae	26	20	90	67	36	100	78	MFd:67, DfQ:95
Polyporus brumalis	13	28	50	22	9	91	50	MFp:40, HQh:60
Hypholoma fasciculare	9	32	100	89	82	100	94	
Psathyrella piluliformis	13	20	50	44	27	62	44	AQi:50
Pluteus atricapillus	13	8	50	89	45	100	94	
Oudemansiella platyphylla	13	9	80	89	36	100	100	MFd:33, DfQ:50
Trametes versicolor	9	8	50	56	36	87	39	
Mycena haematopus	4	8	50	44	-	62	50	DfQ:50
Gymnopilus penetrans	4	4	100	56	64	87	44	DfQ:50
Hypholoma sublateritium	4	2	60	44	36	62	61	
Calocera cornea	4	2	70	44	64	75	94	
Bjerkandera adusta	0	2	50	33	9	62	56	
Kuehneromyces mutabilis	-	-	50	11	-	25	28	
IIA3. Species growing on sporocarps of other macromycetes.								
Collybia cirrhata	30	15	80	11	36	62	28	FFf:57
Collybia cookei	13	6	80	44	18	87	50	

Habitat type	ROADSIDE VERGES		FOREST					
Dominant type	Fag	Que	Fagus		Quercus			
Vegetation type			LF	RF	DQ	QB	VQ	presence degrees in vegetation types
IIB. For forests with *Fagus*.								
IIB1. Soil-inhabiting fungi on litter and humus.								
Mycena capillaris	17	-	40	44	-	25	6	MFp:60
Flammulaster subincarnatus	17	-	70	67	-	-	-	MFd:50
Collybia maculata	9	-	40	33	18	-	6	MFd:33
Hygrophoropsis aurantiaca	-	4	50	-	-	-	-	
Collybia konradiana	-	-	70	22	-	-	-	
IIb2. Wood-inhabiting fungi.								
Oudemansiella radicata	9	-	30	44	-	-	-	
Mycena oortiana	4	6	50	22	-	-	6	MFp:20, MFd:17
Pholiota lenta	4	-	-	44	-	-	-	
IIC. For forests with *Quercus*.								
IIC1. Soil-inhabiting fungi on litter, humus and bryophytes.								
Tephrocybe tesquorum	9	19	10	-	27	87	56	MFd:33, DfQ:50
Mycena stylobates	-	20	-	11	-	75	56	
Galerina atkinsoniana	4	15	10	-	55	62	17	
Clitocybe candicans	-	9	10	-	27	75	22	
Psathyrella dicrani	-	4	-	-	36	-	-	
Tephrocybe ambusta	-	2	-	-	27	37	28	
Mycena rorida	-	2	10	-	27	100	50	
Galerina cinctula	-	2	-	-	9	37	50	
Galerina calyptrata	-	-	30	-	73	50	6	
Galerina ampullaceocystis	-	-	10	-	18	25	56	
Clitocybe phyllophila	-	-	-	11	9	37	22	
IIC2. Wood-inhabiting fungi with preference for *Quercus* (selection).								
Psilocybe crobula	4	6	10	-	-	-25	44	
Panellus stypticus	4	2	20	-	18	50	22	MFd:17, DfQ:25
Panellus serotinus	-	4	20	-11	18	50	56	DfQ:50
Hapalopilus rutilans	-	4	-	-	-	50	33	
Tyromyces chioneus	-	-	-	-	-	62	33	
Pluteus salicinus	-	-	-	-	-	36	39	
Mycena inclinata	-	-	-	-	-	12	56	
Marasmiellus ramealis	-	-	-	-	-	50	39	
Hohenbuehelia atrocaerulea	-	-	-	-	-	25	28	
IIC3. Species growing on sporocarps of other macromycetes.								
Cordyceps ophioglossoides *3	4	4	10	-	100	12	-	
Cordyceps canadensis *3	-	2	10	-	73	12	-	
III. SPECIES WITHOUT PREFERENCE FOR ROADSIDE VERGES OR FORESTS.								
IIIA. Without preference for *Quercus* or *Fagus*.								
IIIA1. Soil-inhabiting fungi on litter, humus and bryophytes.								
Mycena galopus	95	75	100	89	100	100	100	
Mycena filopes (Bull.:Fr.) Kumm. var. *filopes*)	56	77	70	56	9?	50?	78?	
Mycena leptocephala	69	62	20	44	?	?	?	
Collybia dryophila	43	77	80	56	100	100	61	
Psathyrella fulvescens	56	55	50	44	36	75	72	
Mycena cinerella	39	57	100	89	64	87	50	
Collybia butyracea	52	40	80	44	45	87	67	MFp:80, MFd:83,AQf:76
Rickenella fibula	43	43	40	56	-	37	28	

Habitat type	ROADSIDE VERGES		FORESTS					
Dominant type	Fag	Que	Fagus		Quercus			
Vegetation type			LF	RF	DQ	QB	VQ	presence degrees in vegetation types
Mycena filopes (Bull.:Fr.) Kumm. var. *metata*	26	36	20	44	-?	-?	-?	
Mycena pura	21	25	30	44	-	50	22	
Psathyrella spadiceogrisea	26	6	-	-	9	12	22	
Rickenella setipes	13	17	10	22	-	12	-	
Lepista nuda	9	19	-	-	9	12	28	
Marasmiellus vaillantii	9	17	-	11	-	20	6	
Lycoperdon foetidum	-	11	10	-	36	12	17	
IIIA2. Wood-inhabiting fungi.								
Mycena vitilis	74	96	100	89	36	100	100	
Mycena galericulata	48	72	100	100	100	100	100	
Psathyrella frustulenta	9	13	-	11	-	-	17	
IIIA3. Species growing on sporocarps of other macromycetes or on puppae of insects.								
Collybia tuberosa *3	13	8	10	-	18	12	-	
Cordyceps militaris	13	20	-	-	-	12	-	
IIIB. With preference for *Fagus*.								
IIIB1. Wood-inhabiting fungi.								
Crepidotus variabilis	43	17	80	78	9	25	22	
Psathyrella candolleana	22	11	-	22	-	-	-	
IIIC. With preference for *Quercus*.								
IIIC1. Wood-inhabiting fungi.								
Mycena polygramma	4	26	30	33	55	87	61	
Mycena speirea	-	15	-	-	18	25	22	

TABLE 4. Numbers of threatened species of macrofungi in different types of roadsides planted with trees in Drente, the Netherlands.
Vegetation types distinguished according to Keizer (1992a, b; see also Table 1).
The following categories of threatened species are distinguished (after Arnolds, 1989b):
1: threatened with extinction, 2: strongly threatened, 3: threatened, 4: potentially threatened.
The following vegetation types are distinguished:

Roadside verges:
FFe: *Festuca rubra-Fagus* type, *Elytrigia* subtype
FFf: *Festuca rubra-Fagus* type, *Festuca ovina* subtype
MFp: *Mnium hornum-Fagus* type, *Poa trivialis* subtype
MFd: *Mnium hornum-Fagus* type, *Dryopteris* subtype
HQh: *Hypochaeris-Quercus* type, *Hieracium pilosella* subtype
HQl: *Lotus corniculatus* subtype, *Hieracium pilosella* subtype
AQi: *Anthriscus-Quercus* type, inops variant
AQt: *Anthriscus-Quercus* type, typical variant
DFQ: *Deschampsia flexuosa-Quercus* type

Forests:
LF: *Laccaria amethystea-Fagus* type
RF: *Rickenella fibula-Fagus* type (after Opdam, 1991)
DQ: Dicrano-Quercetum
QB: Querco-Betuletum
VQ: Violo-Quercetum (after Jansen, 1984)

Functional group of fungi:			Ectomycorrhizal				Saprotrophs				Total				
Category of threat:			1	2	3	4	1	2	3	4	1	2	3	4	1-4
Vegetation types, number of plots															
A. TOTAL NUMBER OF SPECIES PER TYPE															
FFe 5			1	-	2	-	-	-	-	-	1	-	2	-	3
FFf 7		FAGUS			6				4	1	-	-	10	1	11
MFp 5	ROAD			1	8	1			1		-	1	9	1	11
MFd 6	SIDE			6				1		-	-	7	-	7	
	VERGES														
HQh 5					7	1			4		-	-	11	1	12
HQl 21		QUERCUS	3	7	18	2	1		14		4	7	32	2	45
AQi 6				1	7				1		-	1	8	-	9
AQt 17				4	12	1			3	3	-	4	15	4	23
DfQ 4			1		4						1	-	4	-	5

Table 4 (continued).

Functional group of fungi:			Ectomycorrhizal				Saprotrophs					Total			
Category of threat:			1	2	3	4	1	2	3	4	1-4	1	2	3	4	
LF 10		FAGUS	-	3	7	-	-	-	3	1		-	3	10	1	14
RF 9			-	1	-	-	-	-	2	1		-	1	2	1	4
	FORESTS															
DQ 11			5	12	10	-	-	-	5	-		5	12	15	-	32
QB 8		QUERCUS	-	3	8	-	-	-	-	-		-	3	8	-	11
VQ 18			1	-	2	-	-	-	2	-		1	-	4	-	5
B. AVERAGE NUMBER OF SPECIES PER PLOT																
Vegetation type																
FFe 5			.2	-	.4	-	-	-	-	-		.2	-	.4	-	.6
FFf 7			-	-	2.1	-	-	-	.7	.1		-	-	2.8	.1	2.9
MFp 5		FAGUS	-	.2	1.6	.2	-	-	.2	-		-	.2	1.8	.2	2.2
MFd 6			-	-	1.5	-	-	-	.3	-		-	-	1.8	-	1.8
	ROAD															
HQh 5	SIDE		-	-	2.0	.2	-	-	.8	-		-	-	2.8	.2	3.0
HQl 21	VERGES		.2	.4	1.8	.1	.1	-	1.0	-		.3	.4	2.8	.1	3.6
AQi 6		QUERCUS	-	.3	2.3	-	-	-	.3	-		-	.3	2.6	-	2.9
AQl 17			-	.2	.7	.1	-	-	.2	.1		-	.2	.9	.2	1.3
DfQ 4			.2	-	1.5	-	-	-	-	-		.2	-	1.5	-	1.7
LF 10		FAGUS	-	.3	1.2	-	-	-	.6	.3		-	.3	1.8	.3	2.4
RF 9			-	.1	-	-	-	-	.2	.1		-	.1	.2	.1	1.4
	FORESTS															
DQ 11			.6	2.5	5.0	-	-	-	2.7	-		.6	2.5	7.7	-	10.8
QB 8		QUERCUS	-	.4	1.7	-	-	-	-	-		-	.4	1.7	-	2.1
VQ 18			.1	-	.2	-	-	-	.2	-		.1	-	.4	-	.5

Table 5. Comparison of species numbers of saprotrophic and ectomycorrhizal fungi in roadside verges and forests with Oaks and B trees. For the species the same selection criteria were used as for tables 2 and 3.

	Roadside verges			Forests		
	Fagus (23 plots)	Quercus (53 plots)	Total	Fagus (19 plots)	Quercus (37 plots)	Total
Ectomycorrhizal fungi	78 (47%)	81 (47%)	91	47 (39%)	56 (43%)	68
Saprotrophic fungi	89 (53%)	91 (53%)	96	73 (61%)	73 (57%)	88

SUCCESSION OF ECTOMYCORRHIZAL FUNGI IN ROADSIDE VERGES PLANTED WITH COMMON OAK (*QUERCUS ROBUR* L.) IN DRENTHE, THE NETHERLANDS.

P.J. Keizer & E. Arnolds[1]

Abstract.

In the period 1986-1988 sporocarps of ectomycorrhizal fungi were counted in 53 plots in roadside verges planted with Common Oak in Drenthe, the Netherlands, belonging to three vegetation types. Twenty five plots belong to the *Hypochaeris radicata-Quercus* community, comprising roadside verges in open landscapes on dry, acid, sandy soils, poor in nutrients. In each plot the trees are even-aged, but they vary between the ages of 10 and 140 years. Relations between tree age and numbers of ectomycorrhizal species and sporocarps are studied. The species composition of roadside verges is compared between young trees (10-20 years), medium-old trees (20-50 years) and old trees (50-140 years). The species composition in roadside verges in open landscape with old trees is also compared with the ectomycorrhizal fungi in two different types of roadside verges with old oak trees, viz. the *Anthriscus-Quercus* type, comprising open to half-open plots on soils richer in nutrients, and the *Mnium hornum-Quercus* type, comprising shady plots surrounded by forest. The data reveal a distinct succession of ectomycorrhizal fungi with increasing tree age. The results are compared with data on succession of ectomycorrhizal fungi in forest stands. It is concluded that the succession cannot be simply modeled as suggested by some authors. Instead, changes in species composition and diversity show much variation in relation to different environmental conditions. The factors relevant to the course of ectomycorrhizal succession are discussed. The concepts of early-and late-stage fungi are critically considered. It is concluded that this classification is not appropriate for the description of the ectomycorrhizal succession during stand development. A new, provisional classification of ectomycorrhizal fungi concerning their appearance during forest succession is proposed.

Contents.

[1]Comm.no. 466 of the Biological Station, Wijster

1. Introduction.

In the present paper, the temporal sequence of fungal communities in roadside verges is studied. According to Clements (1928), succession is the sequence of developmental stages of a (phytocoenological) formation, comparable with the life-history of an individual plant. This concept was mainly based on the development of phytocoena from pioneer to climax stages, under natural circumstances. In this study, the concept of succession is applied to the sequence of fungal communities in a highly artificial habitat, where the natural climax vegetation never will develop. Therefore, in this paper succession is regarded as "the non-seasonal, directional and continuous pattern of colonization and extinction on a site by species populations" (Begon, et al., 1986).

Thus, the main aim is to describe the different fungal communities observed in roadside verges with trees of different ages, but similar in other respects. The study is restricted to ectomycorrhizal fungi, which are associated with the roots of the trees. In fact, a part of the community is studied, because only the fungi were considered whereas the ageing trees remained the same. In this way, succession as conceived here may differ from other approaches, where usually complete phytocoenoses are studied. But clearly a succession of fungi is present in the sense of the above-mentioned definition as fungal populations colonize and disappear from the studied sites according to general rules.

Information on the succession of ectomycorrhizal fungi during forest development was mainly derived from experimental stands of *Betula pendula* Roth with trees up to 15 years old (e.g. Last et al., 1987). The ectomycorrhizal flora changed continuously over the years as convincingly shown by both the appearance of sporocarps and the occurrence of different types of ectomycorrhizas (Gibson & Deacon, 1988). The mycelia of early colonizers expanded from the tree stem with the growing root system at a rate of approx. 0.1 to 0.2 m yr^{-1} (Last et al., 1984). After some years ectomycorrhizal fungi tend to occur in circles around trees, the early colonizers near the margin of the root system, the late colonizers near the trunk (Mason et al., 1982).

In order to explain this sequence, experiments were carried out with different species in various conditions. It appeared that fungi appearing early and late in the succession were both able to form mycorrhizas on seedlings in axenic laboratory conditions. However, only one group, termed "early-stage fungi", were able to colonize seedlings from basidiospores in unsterile conditions (e.g. Deacon et al., 1983; Mason et al., 1984). Early-stage fungi are considered as *r*-strategists, combining in general a relatively low carbon demand, a rapid mycelial growth, the production of relatively small sporocarps and occurrence in soils with nutrients mainly in the anorganic pool (Dighton & Mason, 1985). Early-stage fungi are the only ectomycorrhizal species in very young, even-aged stands, e.g. on afforested arable land and in silvicultures by clear-cutting system. The first sporocarps in stands of *Betula* appeared two years after planting of seedlings (Mason et al., 1987). The early-stage fungi comprise relatively few species, mainly of the genera *Laccaria*, *Hebeloma*, *Inocybe* and *Thelephora*. Some species are considered to be restricted exclusively to young trees (e.g. *Laccaria tortilis*, *Hebeloma crustuliniforme*, *Thelephora terrestris*), whereas others are also observed in older stands (Dighton & Mason, 1985).

"Late-stage fungi", on the other hand, are considered as *K*-strategists, having in general a higher carbohydrate demand, a slower mycelial growth, the formation of hyphal strands, on the average larger sporocarps and they grow in environments where nutrients

are mainly in the organic pool (Dighton & Mason, 1985). They are not able to colonize roots of seedlings from basidiospores under unsterile conditions, but at least some species are able to colonize young trees vegetatively from ectomycorrhizal roots of neighbouring mature trees (Fleming, 1984). In stands of *Betula pendula*, sporocarps of the first late-stage fungi appear already four years after planting and they are dominant on roots of trees of 10 years and older (Last et al., 1987). The great majority of ectomycorrhizal fungi belongs to this category, for instance *Paxillus involutus* and all species of *Boletus* and allies, *Russula*, *Lactarius*, *Cortinarius* and *Amanita*.

Comparative mycocoenological studies were carried out by Keizer in the period 1986-1988 in roadside verges planted with Common oak (*Quercus robur* L.) and Beech (*Fagus sylvaticus* L.), further referred to as *Quercus* and *Fagus* respectively. The aims of this research were (1) to describe the variation in macromycete communities in this habitat, (2) to compare a classification of macromycete communities with that of communities of green plants, (3) to determine the main factors which contribute to differences in composition of mycocoenoses and (4) to compare the macromycete communities in roadside verges with trees with those of related forest communities.

From studies on succession of ectomycorrhizal fungi it has become evident that one of the main factors, determining the composition of the ectomycorrhizal flora, is the age of the associated host trees (e.g. Dighton & Mason, 1985; Mason et al., 1987).

Therefore, tree age was chosen as one of the variables studied in roadside verges. The age of the trees in these plots ranged from 10 to 140 years (in 1988). The selection of plots with trees of different age classes was restricted to roadside verges in open landscapes ("open" plots) with oak on relatively poor soils, belonging to the *Hypochaeris radicata-Quercus* type (chapter 3).

Naturally, the investigation of succession phenomena by this method is only indirect, because spatially separate units do not necessarily represent instant pictures from one and the same time series. The data should therefore be interpreted with care. On the other hand, direct observations on succession series of this duration are practically impossible (Oldeman, 1990). Moreover, in roadside verges the course of the process may be strongly influenced by changing environmental factors, among other things the deposition of pollutants (Fellner, 1988; Arnolds, 1991) or changed use of these verges. We have tried to meet most objections connected with indirect observations by the selection of plots with relatively homogeneous soil conditions, in one vegetation type and in a small area (approx. 1800 km^2). Oak trees are planted along roads from nurseries when they are approximately 10 years old. A methodological advantage of roadside verges (and most other tree plantations) above natural forest stands is that trees along a road are even-aged.

All plots with *Quercus*, belonging to other vegetation types and those with *Fagus*, had only mature trees over 50 years old. Detailed results of these studies have been published elsewhere, including classification of the mycocoenoses in roadside verges with *Quercus* and *Fagus* (chapter 3 and 2), correlations between mycocoenological characteristics and environmental factors, and a comparative study with related forest communities (chapter 5).

2. Material and methods.

In 1986, a total of 53 plots in roadside verges planted with *Quercus robur* were

selected in Drente, in the northeastern Netherlands. The area lies about 10 to 20 metres above sea-level and has a cool-temperate climate (average precipitation 781 mm.yr^{-1}, mean temperature in January 1.2 °C, in July 15.9 °C). All plots were situated on acidic, pleistocene sands with a variable organic matter content and a more or less disturbed soil profile due to road construction. The trees were of local provenance.

The plots were 100 metres long and the width varied between 1.5 and 6.5 m with 9 to 35 trees per plot. All sporocarps of macromycetes were counted by species with intervals of 3 to 4 weeks in the period August-November during the years 1986-1988. In most plots the position of all sporocarps of ectomycorrhizal fungi was indicated on detailed maps (scale 1:100) during each visit. Soil profiles and some soil-chemical characteristics were determined in all plots (for details, see chapter 2 and 3). In addition the communities of green plants were described and classified according to the Braun-Blanquet method (e.g. Westhoff & Van der Maarel, 1973).

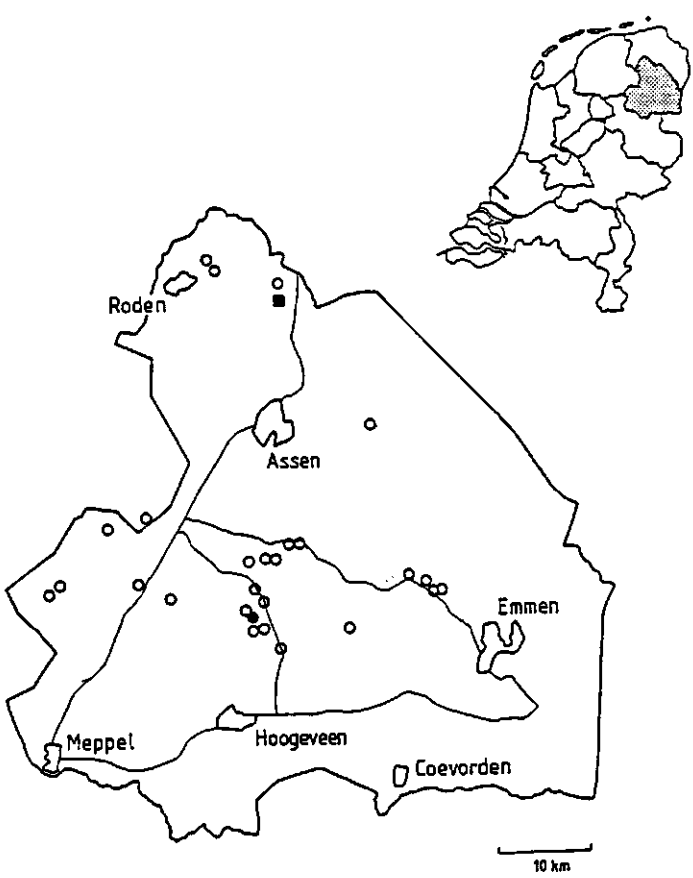


Fig. 1. Geographical situation of the studied plots. ○ = plots in roadside verges planted with Common Oak of the *Hypochaeris radicata Quercus* type; ■ = Eelde Meteolrological station; ● = Wijster Biological station.

Plots belonging to the *Hypochaeris radicata-Quercus* type were divided into three age-classes of the trees: "young" (10-20 years; 4 plots), "medium old" (20-50 years; 11 plots) and "old" (50-140 years; 10 plots). The age of the trees was determined with an

increment borer. The *Hypochaeris radicata-Quercus* type is characterized as roadside verges in open landscapes with a short, low-productive, grass-rich herb layer on rather dry to dry oligotrophic to mesotrophic soils. In the "young" plot Q54 no ectomycorrhizal fungi were found.

In addition to the 26 plots of the *Hypochaeris radicata* type (indicated in fig. 1), 23 plots belong to the *Anthriscus sylvestris* type, open to half-open roadside verges on slightly richer soils, and 4 plots to the *Mnium hornum* type, shady plots along roads through forest stands. All plots of these types belong to the "old" age class.

On the basis of vegetation relevés phytocoenological classifications were carried out for the roadside verges for ectmycorrhizal and sprotrophic fungi independently, using the computer program TWINSPAN (Hill, 1979; Jongman & al., 1989). The methods and results are discussed in extenso in chapter 2. The data on saproptrophic fungi are left out of consideration in this paper. The plots were divided into three types. Some phytocoenological and environmental characteristics are summerized in Table 1.

In the data presented here, species found in less than 3 plots were omitted. Two parameters are used: 1) the presence-degree, being the percentage of plots of a type in which a certain species was found and 2) the average maximum numbers of sporocarps per visit over three years. The maximum numbers of sporocarps encountered in one visit during three years is considered as the most reliable expression of the potential fruiting capacity of a species in a plot (Arnolds, 1981; Barkman, 1987). Consequently, the average maximum numbers of sporocarps is the best expression of the potential fruiting capacity of a species in a set of plots belonging to a certain vegetation type.

Species are considered as differential of a certain age class when 1) its presence-degree is at least twice the presence-degree in other classes or when 2) its average maximum numbers are at least thrice these numbers in other classes. The combination of presence and abundance characters in the criteria for differential species prevent the application of statistical tests.

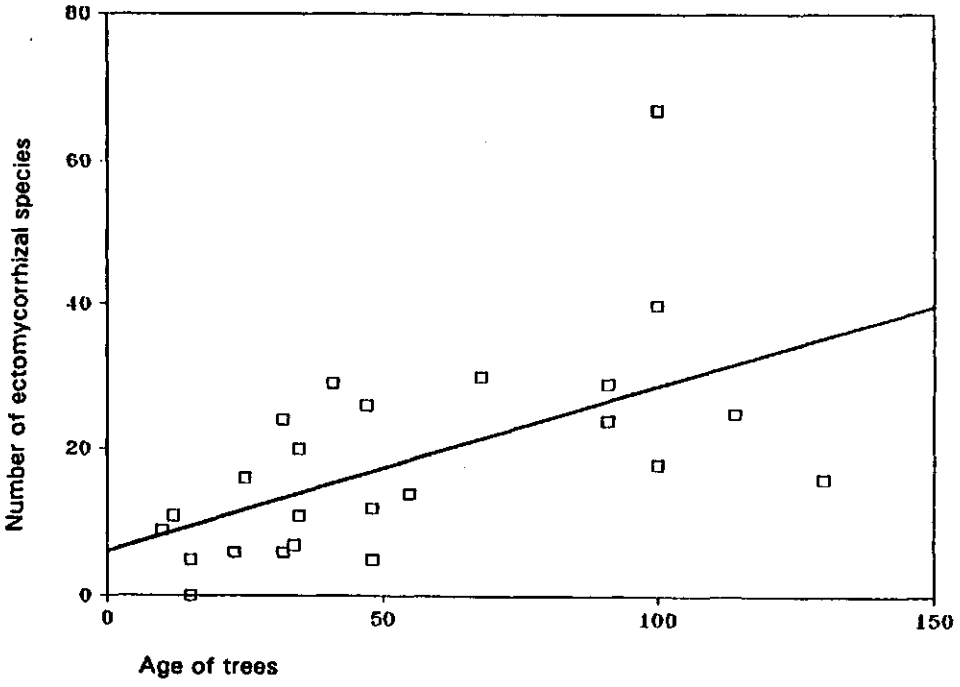
Nomenclature of phanerogams is after Heukels & Van der Meijden (1983), of bryophytes after Margadant & During (1982), of fungi mainly after Kreisel (1987). A complete list of fungi is presented in appendix 1. Taxonomic and nomenclatural notes on critical and rare species were published in chapter 8. The names of vegetation types in roadside verges are according to those presented in chapter 2 and 3, and only preliminary, without official syntaxonomic status.

3. **Results.**

The occurrence of ectomycorrhizal fungi in plots belonging to different age classes of the *Hypochaeris radicata-Quercus* type is presented in Table 2.

For comparison, data on the average maximum sporocarp numbers in the *Anthriscus sylvestris-Quercus* and *Mnium hornum-Quercus* types of roadside verges are added. These types comprise only plots with trees over 50 years old. In addition, data are presented on the average maximum numbers of sporocarps of all species, the average numbers of species per plot, and the average dry weights of sporocarps.

The number of ectomycorrhizal species in the *Hypochaeris radicata-Quercus* type strongly increases with increasing tree age. The average number of species in old plots of this type is much larger than in plots of the *Anthriscus sylvestris-Quercus* and *Mnium hornum-Quercus* types with old trees. The numbers of sporocarps strongly increase from young to medium-old plots, but are lower in the old plots of the


Number of ectomycorrhizal species
80
60
40
20
0
0
50
100
150
Age of trees

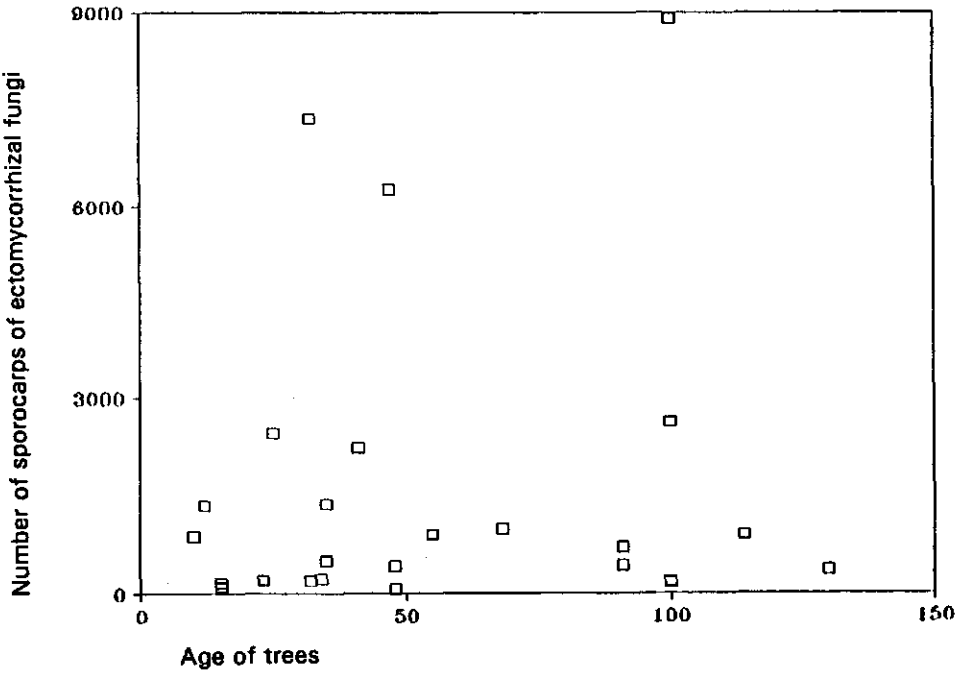

Number of sporocarps of ectomycorrhizal fungi
9000
6000
3000
0
0
50
100
150
Age of trees

Fig. 2. Relation between the number of ectomycorrhizal species and the tree age in plots of the *Hypochaeris radicata Quercus* type.

Fig. 3. Relation between the number of sporocarps of ectomycorrhizal fungi and the tree age in plots of the *Hypochaeris radicata Quercus* type.

Hypochaeris radicata-Quercus type. The latter plots produce more sporocarps than the *Anthriscus sylvestris-Quercus* and *Mnium hornum-Quercus* type, but the differences are less pronounced than for numbers of species.

The relation between tree age and number of ectomycorrhizal species in the plots of the *Hypochaeris radicata-Quercus* type is illustrated in fig. 2. Although the variation is rather large, there is a significant, positive correlation between tree age and numbers of species ($r=0.569$; $n=26$, $p<0.01$). The large variation is mainly due to the considerable heterogeneity of this vegetation type.

The relation between tree age and total numbers of sporocarps is indicated in fig. 3. The variation is very strong indeed and no significant correlation between these characteristics is found. The higher averages in medium-aged plots can be mainly attributed to two plots with very high sporocarp counts.

The species in table 2 are arranged according to their preference for age classes of trees within the *Hypochaeris radicata-Quercus* type. Six groups of differential species are distinguished.

Two species having a preference for young trees (group I), are *Laccaria tortilis* and *L. proxima*. Four other species, viz. *Hebeloma pallidoluctuosum, Inocybe lanuginosa, Naucoria bohemica, Thelephora terrestris*, probably belong to this group as well, but had to be listed in group VI (no preference) because of their low frequencies: one out of four investigated plots. *Thelephora terrestris* is found with higher presence-degree in old plots of the *Mnium hornum* type.

Five species are differential for young and medium aged trees with regard to old trees, viz. *Hebeloma mesophaeum, Inocybe lacera, I. lanuginella, Laccaria bicolor* and *Scleroderma areolatum* (group II).

A group of 10 species are found most often in plots of medium-aged trees. These 10 fungi include *Amanita muscaria, Cortinarius saniosus* and *Chalciporus piperatus* (group III). Some fungal species are present in almost all plots, but reach their maximum abundance in this age-class, viz. *Lactarius quietus* and *Laccaria laccata*. However, the latter two species also constantly occur with high densities in the old plots of the *Anthriscus sylvestris-Quercus* type.

Six species occur more in plots with medium-aged and old trees within the *Hypochaeris radicata-Quercus* type, than in plots with young trees, e.g. *Russula parazurea* and *R. amoenolens* (group IV). Three species of this group have a higher presence-degree and/or abundance in old plots of the *Anthriscus sylvestris-Quercus* type (*Russula parazurea, Xerocomus chrysenteron*) or *Mnium hornum* type (*Lactarius theiogalus*).

The largest group of 34 taxa are differential of old trees, among which *Amanita citrina, A. rubescens, Russula atropurpurea* and *R. nigricans* (group V) are common species. Interestingly, 20 of these taxa are characteristic for the *Hypochaeris radicata-Quercus* type and consequently less frequent in the *Anthriscus sylvestris-Quercus* and *Mnium hornum-Quercus* type, despite the occurrence of trees of comparable age. Only three species in group V are differential of the *Mnium hornum-Quercus* type and none of the *Anthriscus sylvestris-Quercus* type.

Twenty species show no preference for any age class within the *Hypochaeris radicata-*

Quercus type (group VI). *Hebeloma helodes* and *Naucoria bohemica* are the only species with fairly high presence-degrees in this group. The remaining species occur only in one to three plots of this vegetation type, so that no conclusions can be drawn. Thirteen species of this group are considered differential for the *Anthriscus sylvestris-Quercus* or *Mnium hornum-Quercus* type. The numbers of differential species of each group, belonging to different genera of fungi, are presented in Table 3.

A comparison of the three vegetation types with old trees (table 2, columns 3, 4 and 5) reveals also large differences in ectomycorrhizal flora. These differences were extensively described and discussed in chapter 3 and are only summarized in this paper. The average number of species per plot is considerably lower in the *Anthriscus sylvestris-Quercus* type (than the *Hypochaeris radicata-Quercus* type) and lowest in the *Mnium hornum-Quercus* type. The numbers of sporocarps are also lower in these types, but the differences with the *Hypochaeris radicata-Quercus* type are less pronounced. Among 80 species studied, the largest group of 27 species have a preference for the *Hypochaeris radicata-Quercus* type. Twelve species are differential of the *Anthriscus sylvestris-Quercus* type (often relatively weak) and only 7 species of the *Mnium hornum-Quercus* type. The remaining 34 species are either not differential (24 species) or differential of a combination of two types.

In the present study the spots of sporocarps of ectomycorrhizal fungi were indicated on detailed maps during each visit. Calculations were made of the average sporocarp distance for some selected species (belonging to early and late stage fungi and present in sufficiently large numbers) to the nearest tree and to the margin of the pavement in one plot (plot Q1, Oranjekanaal near Odoornerveen) with trees of 100 years during the year 1986 (Table 5). The table shows that the average distances from the trees is indeed larger for the early-stage fungi *Laccaria laccata* and *Hebeloma helodes* than for the four late-stage fungi studied.

However, roadside verges are a habitat liable to deform the patterns to be tested, since the root systems of trees are restricted to a narrow strip between the road and the canal and since an environmental gradient is present perpendicularly to the road. *L. laccata* and *H. helodes* are also found at the greatest distance from the pavement, so that the influence of tree roots is of uncertain significance. It is striking that sporocarps of *Russula odorata* are found very close to the road, a phenomenon also observed in other roadside verges.

4. Discussion.

4.1. *Changes in numbers of species and sporocarps.*

In open roadside verges the average number of ectomycorrhizal species increase with the age of the trees. Old trees have more differential symbionts than young and medium-aged trees. Numbers and productivity of sporocarps show an optimum in plots with medium-aged trees. The initial increase can partly be understood in view of the extension of the root system of the trees. After approx. 30 years, the soil is entirely occupied by fine roots (Keizer, unpubl. observ.). Hence, the striking succcession of species in later stages cannot be explained by root extension alone.

Our results will be compared with some published data on numbers of ectomycorrhizal fungi in forest stands of different age.

Ricek (1981) studied ectomycorrhizal macromycetes in 19 stands of *Picea abies* in Germany on former pastures, the trees varying in age from 4 to 40 years. He summarized his results in a scheme, indicating a species only if present during this primary

succession, but no specifications regarding presence-degrees or abundance in stands or groups of stands. Exact conclusions on species occurrences per stand can therefore not be drawn. In stands with trees less than 5 years old he observed only 3 ectomycorrhizal species, increasing to 6 in the age class 5 to 10 years, 17 in the age class 10 to 15 years, 29 in the age class 15 to 20 years (in which usually canopy closure was reached), up to 48 in the age class 20 to 25 years. In older stands the total number of species gradually decreased to 36 in stands of 40 to 45 years.

Hintikka (1988) compared the ectomycorrhizal fungi in 25 plots (750 m^2) with *Pinus sylvestris* of different age in Finland (Table 4). He found the minimum average number of species (10) and sporocarps (179) in young stands (5 to 15 years), increasing to 21 species and 470 sporocarps in stands between 20 and 30 years old and gradually decreasing again to 13 species and 208 sporocarps in stands older than 70 years.

Jansen (1991) investigated ectomycorrhizal fungi in 25 plots (1000 m^2; 500 m^2 in 7 plots in young stands) in plantations of the introduced *Pseudotsuga menziesii (Mirb.)Franco* in the Netherlands. The average numbers of species (16) and sporocarps (5500) were highest in young plots before canopy closure (age 8 to 18 years) and strongly decreased in older stands, 9 species and 560 sporocarps in stands between 20 and 36 years old, 8 species and 280 sporocarps in stands between 41 and 54 years old. This author observed also a strong reduction of the numbers of ectomycorrhizal root tips (from on the average 128/100 cm^3 in young stands to 30/100 cm^3 in old stands and mycorrhizal frequency (from 70% in young stand to 8% in old stands).

The results of these three investigations show all the same trends, i.e. an initial increase of species numbers and probably also of sporocarp numbers until a maximum is reached at an age of 30 to 40 years in the studied tree species, after which these numbers decrease.

Termorshuizen & Schaffers (1991) studied a total of 33 plots (1050 m^2) in planted forests of *Pinus sylvestris* on sandy soils. They found trends comparable to the preceding authors in plantations of the first and second rotation: in young stands of the first rotation (4-10 years) the average number of species was 6, of sporocarps 1190; in old stands (50-80 years) these figures were 3 and 120, respectively. In young stands (6-11 years) of second or third rotation on the average 11 species were found with 1860 sporocarps per plot; in old stands (50-80 years) 3 species with 390 sporocarps. Some 60 years old, slowly growing pine forests in the coastal dunes on sand poor in humus, were strongly deviating: they contained on the average 11 species, producing 2720 sporocarps. They found also a negative correlation between the numbers of mycorrhizas and tree age, but the mycorrhizal frequency varied only between 97 and 100 percent.

The steady increase of the number of ectomycorrhizal species with ageing trees, found in roadside verges with *Quercus*, was not observed in the studies mentioned above. The results are also conflicting with the model for ectomycorrhizal succession, proposed by Dighton & Mason (1985), that predicts an increase of species diversity until canopy closure and a strong decrease afterwards. The possible reasons for this discrepancy will be discussed in the conclusions (section 5).

4.2. *Changes in species composition.*

Our observations on ectomycorrhizal fungi in road-verges with planted oak trees of different age can be partly explained indeed using the concepts of early- and late-stage fungi. The five species, found to be differential of young stands (< 20 years) are all

considered as early-stage fungi (Dighton & Mason, 1985). Most other species in these stands belong also to this category, but they are also present in road-verges with older trees and in older forest stands (Dighton et al., 1986), e.g. *Laccaria laccata*. Only three typical late-stage fungi were found in young plots, each of them in only one plot with very low densities: *Russula parazurea*, *R. amoenolens* and *Lactarius quietus*. In addition, two species were found in young plots regularly which were not yet classified as early- or late-stage fungus, viz. *Scleroderma areolatum* and *Naucoria bohemica*. In view of their occurrence in the field, they may very well belong to the group of early-stage fungi (in the sense of Dighton & Mason, l.c.).

A noticeable difference between ectomycorrhizal succession in *Betula* and *Quercus* is the duration of different phases. Early-stage fungi are dominant with *Quercus* in trees up to 20 years old, with *Betula* in trees younger than approx. 6 years (Last et al., 1987). It is quite possible that this phenomenon is related to the maximal life-time of the trees: less than 100 years in *Betula* and over 1000 years in *Quercus*. The predominance of early-stage fungi in *Quercus* trees of 10 to 20 years may also be caused by the maintenance of ectomycorrhizal fungi already present in the tree nursery and transported in the tree-roots to the roadside verge. Dighton et al. (1986) found that in stands of *Pinus contorta* and *Picea sitchensis* in Northumberland (Great-Britain) sporocarps of early-stage fungi were also dominant in slightly older stands (4 to 10 years) than in previous experiments with *Betula*. He suggested that this difference may be dependent on both the tree species and the environmental conditions.

Two early-stage fungi, *Laccaria proxima* and *Thelephora terrestris* are present outside the young *Hypochaeris radicata-Quercus* stands in old plots of the *Mnium hornum-Quercus* type and with comparable frequency. This suggests that ectomycorrhizal succession is not (only) dependent on the age of the trees, but also on soil conditions (Mason et al., 1987; see section 4.3).

Roadside verges with medium-old and old oak trees are dominated by late-stage fungi (Tables 2, 3). However, boletes are most often found with medium-old trees, most *Russula* and *Amanita* species with old trees. The distinction of early- and late-stage fungi can often not be made on generic level. For instance, most *Laccaria* species are typical early-stage fungi, but *L. amethystea* is differential of old trees in our plots; *Inocybe lanuginella* and *I. lacera* are already present in young stand, but *I. napipes* and *I. assimilata* grow exclusively in old stands (Table 1). The succession in stands of *Betula* was only investigated during the first 15 years (e.g. Last et al., 1987). Dighton et al. (1986) analysed the succession in stands of *Pinus contorta* and *Picea sitchensis* up to a stand age of 27 years. It is evident that ectomycorrhizal development is not restricted to younger stands, at least of *Quercus robur*. The largest number of differential species are conspicuous by being characteristic for roadside verges with trees over 50 years old. Likewise, species characteristic for oak trees older than 130 years may exist, an age class not investigated thus far. Apparently, considerable ecological, and possibly physiological, differentiation exists within the group of late-stage fungi.

Other data confirm the prolonged succession of ectomycorrhizal fungi after the establishment of late-stage fungi. Data by Hintikka (1988), rearranged by the present authors in similar groups as in the roadside verges with *Quercus*, are illustrative of the succession in forests of *Pinus sylvestris* on poor, sandy soils (table 4). Species of *Laccaria*, *Thelephora* and *Inocybe* are important in young stands, *Boletus* and *Suillus* are best represented in rather young and medium-old stand, whereas *Russula* species dominate medium-old and old stands. Species characteristic for stands older than 70 years were reported. Roadside verges with *Quercus* and *Pinus* forests had only few species in

common. Some species show a similar preference, for instance *Thelephora terrestris* for young, *Boletus edulis* for medium-old and *Russula emetica* for old trees. However, striking differences exist: *Laccaria laccata* (sensu lato) is frequent under old oak trees, but absent from old pine forest; *Amanita muscaria* and *Paxillus involutus* are present in many young pine forests, but in roadverges with *Quercus* they are characteristic for medium-aged and old trees, respectively.

A comparison is presented of data on the presence-degree of species found by Hintikka (1988) and observations by Termorshuizen (1990) in young and old stands of *Pinus sylvestris* on sandy soils in the Netherlands (Table 4, columns 5 and 6). Many species, which are characteristic for older stands in Finland, behave quite differently in the Netherlands. In the latter country, some of them are even restricted to young forests, for instance *Cortinarius semisanguineus* and *Suillus variegatus*. On the other hand, *Laccaria laccata* sensu lato was present in most old stands in the Netherlands.

Comparable results were obtained by Jansen (1991), for stands of *Pseudotsuga menziesii* in the Netherlands. The early stage fungi *Laccaria proxima* and *Thelephora terrestris* were observed in most stands of all age classes (from 8 to 54 years), whereas late-stage fungi such as *Cortinarius semisanguineus*, *Paxillus involutus*, *Russula ochroleuca* and *Xerocomus badius* were present in at least 70% of the stands younger than 20 years.

4.3. *Changes in weight of sporocarps.*

The average dry weights of sporocarps of the species found in the three age classes of roadside verges of the *Hypochaeris radicata-Quercus* type were determined in order to test the observations by Dighton & Mason (1985) that sporocarps of early-stage fungi are usually smaller than those of late-stage fungi (Table 2).

The average dry weights of sporocarps of the species encountered in roadside verges with *Quercus* amounted to 0.3 $\pm$ 0.2 g in young plots, 4.5 $\pm$ 11.8 g in medium-aged plots and 1.8 $\pm$ 0.9 g in old plots. Only the difference between young and old plots was significant ($p < 0.01$, T-test). The high value and enormous standard deviation in plots with medium-aged trees is mainly due to the occurrence of *Boletus edulis* with heavy sporocarps in some of these plots. Our results agree with the observations by Dighton & Mason (1985). However, the conclusion that sporocarps in young stands are on average lighter has no general validity. Termorshuizen (1991) found the highest average sporocarp weight in young *Pinus sylvestris* (4 to 14 years) stands in the Netherlands. Therefore, the concepts of early stage fungi and fungi growing in young stands are not identical.

5. Conclusions.

On the basis of our investigation in roadside verges with oak trees of different age and on a comparison with other studies on succession of ectomycorrhizal fungi in different habitats, it is evident that the course of this succession is not uniform in different habitats.

Probably the most usual process in forest stands is a fairly rapid increase in species richness and sporocarp productivity during approx. 30 to 40 years and a more gradual decrease afterwards to an intermediate, rather constant level. In the beginning, the ectomycorrhizal flora is dominated by early-stage fungi, which to a large extent are gradually replaced by late-stage fungi, some late-stage fungi being more characteristic for rather young or medium-aged stands, others of old ones. This process was observed in

pine forests in Finland (Hintikka, 1988; Table 4).

However, in the Netherlands maximum species richness and sporocarp productivity in coniferous forests are reached in young stands up to approx. 15 years old. Part of the early-stage fungi also live in mature stands, whereas some late-stage species, found in older stands elsewhere, are mostly found in young stands in the Netherlands (Jansen, 1991; Termorshuizen, 1991).

On the contrary, in roadside verges planted with *Quercus* the species richness steadily increases with the age of the trees and the sporocarp abundance remains at a high level. Some early-stage fungi are confined to roadside verges with young trees, others are also present near old trees. Among the late-stage fungi a strong differentiation is observed in connection with the age of their partner trees.

These observations do not support the conclusions by Gibson & Deacon (1988), who suggested that succession of ectomycorrhizal fungi is primarily determined by the age of the tree root system. Alvarez et al. (1979) demonstrated that in the presence of an organic layer over the mineral soil growth and survival of *Abies concolor* seedlings is worse than in soil where this layer is lacking. They attributed this to an inhibitory effect of the organic layer on mycorrhizas. Soil factors play a decisive role in the course of succession, as suggested by Mason et al. (1987).

Environmental conditions in coniferous forests in the Netherlands mainly differ from those in Finland in the high deposition of acidifying substances and nitrogen (on the average 50 kg N ha^{-1} yr^{-1}; Heij & Schneider, 1991) and, probably as a result, an accumulation of coarse, slowly decaying litter (Kuyper 1989; Jansen, 1991). These factors are thought to be responsible for a strong reduction of sporocarp production in mature stands (Arnolds, 1991) and an acceleration of ectomycorrhizal succession, so that some fungi normally found in mature stands, now occur in young stands.

The high level of air pollution also can influence directly the nutritional status of the trees, causing a change in the allocation pattern and/or quantity of carbohydrates in the tree. This might result in a lower availability of carbohydrates in the roots and consequently a changed species composition and a lower sporocarp production in some species (Termorshuizen, 1990).

Roadside verges with oak trees in open landscapes in the Netherlands differ from forest stands mainly by the absence of a litter layer. Like forests they are exposed to "acid rain", but the fertilizing effects of the latter are, at least in part, compensated by removal of litter by the wind (cf. General discussion, fig. 1, p 251). In part of the roadside verges also the sward is removed by mowing. The absence of a litter layer and/or loss of nitrogen from the system so would lead to an extended succession in which early-stage fungi tend to maintain themselves longer and numerous late-stage fungi appear in the course of the succession.

However, the importance of nitrogen and litter, and their interaction, are not yet sufficiently known. It has been experimentally demonstrated that the use of nitrogen fertilizers reduced the species richness of ectomycorrhizal fungi in roadside verges (chapter 7), which is in good agreement with the effect of fertilizer application in forests (Kuyper, 1989; Termorshuizen, 1992). It has also been demonstrated that removal of sods in forests leads to an increase of sporocarp numbers of ectomycorrhizal fungi (Baar & Kuyper, 1993; in press). In addition, roadside verges form a relatively dynamic habitat where periodical riding, trampling and road (re)construction may locally create "pioneer" circumstances. In such places, species usually confined to early successional stages can presumably either maintain themselves or re-establish themselves repeatedly.

In view of the above discussion, it is probable that a negative effect of N-deposition on the ectomycorrhizal fungi acts via a change of soil properties.

In this context it is interesting that shady roadside verges with old trees, situated in forests (*Mnium hornum-Quercus* type), where litter accumulation is only slightly reduced relatively to the forest itself and usually no management is carried out, on the average contain only half the number of ectomycorrhizal species found in the open, exposed *Hypochaeris radicata-Quercus* type (Table 2). In addition, the *Mnium hornum-Quercus* type has few differential species and its ectomycorrhizal flora is much more similar to that of typical *Quercus* forests (chapter 5).

Some mature forest types are also reported to be extremely rich in ectomycorrhizal fungi, e.g. oak forests on acid sand dunes (Dicrano-Quercetum) in the Netherlands (Jansen, 1984), pine forests on sand dunes (Cladonio-Pinetum) in eastern Germany (Sammler, 1988; Wöldecke & Wöldecke, 1990) and beech forest on limestone slopes (Carici-Fagetum) in Western Germany (Jahn, 1986). These forest types have only few features in common, in particular the occurrence in hilly areas where part of the litter and nutrients are removed from the system by natural causes, only a thin organic top soil is developed, and the forest floor is overgrown with mainly mosses and only a few herbaceous plants. Many characteristic species of these forest types are differential species for roadside verges with old trees in open landscapes, e.g. *Russula graveolens*, *Tricholoma saponaceum* and *Lactarius vellereus* (chapter 5).

We expect that the mycorrhizal flora in the *Hypochaeris radicata-Quercus* type will change towards that of the *Mnium hornum-Quercus* type when ever litter and nutrients accumulate for some reason, and therefore that species richness and composition will change due to soil succession instead of ageing of trees.

Dighton & Mason (1985) developed a model of ectomycorrhizal succession in which species richness increases from young to medium-aged stands, then strongly decreases in old stands, to reach a very low final level. This model does not explain the series analysed by us. At least three different processes must be distinguished in connection with litter accumulation and nitrogen deposition. The different pathways of succession are schematically presented in fig. 4. According to this model, in nutrient-poor soils, the

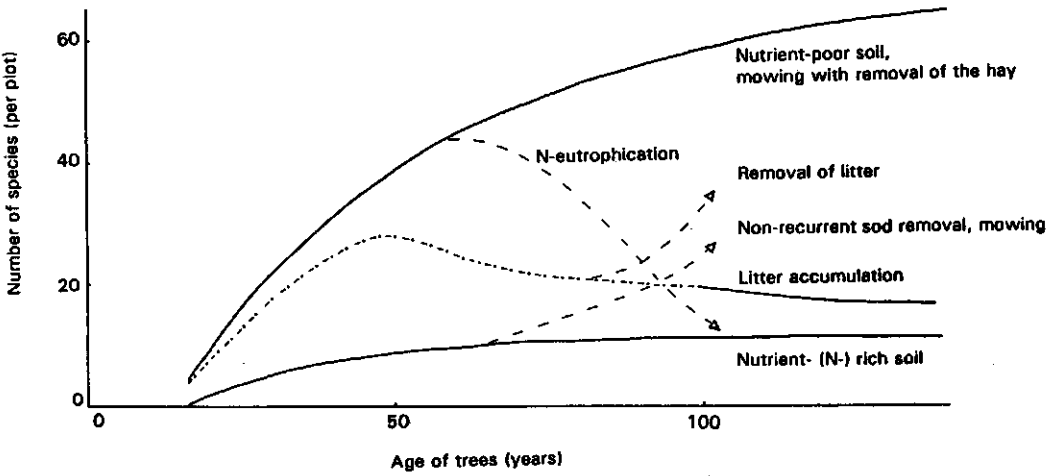


Fig. 4. Model indicating the probable course of succession of ectomycorrhizal fungi in roadside verges with ageing trees, under various circumstances. ___= observed; -·—·-·= inside forests, after Dighton & Mason (1985); - - -=probable course.

species number increases with the age of the trees, provided that no accumulation of litter and nutrients takes place. Litter accumulation and eutrophication reduce the species number. On the other hand, nature management measures like litter removal, removal of sods or yearly mowing with removal of the hay may increase the species number in situations with litter accumulation or eutrophication.

The underlying mechanism may be as follows. Compared to old trees, young ones need more mineral nutrients (nitrogen), which is in young, mineral soils with a low organic matter content rapidly available. Early stage fungi (relatively few "pioneer" species) are adapted to these circumstances. As the stand ages, more root substrate and more different (micro)habitats become available. In the course of time, an organic layer develops, where a larger proportion of the nutrients is stored. The trees need relatively less nutrients because of a more efficient internal circulation of nitrogen (Cole & Rapp, 1981; Chapin III, 1986). This, in combination of the presence of an organic layer will lead to a somewhat decreased species number.

Some symbiotic fungi of this stage are capable of releasing nutrients from soils with a high organic matter content more effectively than the early-stage fungi (Read, 1991). However, a wide variation between species must exist in this capability, as many species can be found near old trees in mineral soils (although in these sites probably more organic material is present compared to young mineral soils, due to the presence of dead tree and plant roots). The strong decrease of many ectomycorrhizal fungi from aging and old forests in the Netherlands and their maintenance in foreign (old) forests and in the *Hypocharis radicata Quercus* type roadside verges indicate that the quality of the organic material in Dutch forests has become unfavourable for many ectomycorrhizal fungi.

The concepts of early- and late-stage fungi are primarily based on physiological characteristics of species and indeed are useful to understand early phases of primary forest succession. However, they are not appropriate to describe ectomycorrhizal succession under field conditions over a longer period since

1) some early stage fungi are restricted to young trees, but others are maintained on the root systems of old trees (table 2 group I, II);
2) some late-stage fungi appear already with young trees (table 4);
3) seedlings near mature trees may be infected by late-stage fungi (last et al., 1987);
4) late-stage fungi are dominant during some 90 to 95 % of the lifetime of a tree and can be divided into several groups, living on root-systems of different age-classes.

We propose the following schematic classification of ectomycorrhizal species in view of their appearance during forest development. The groups are not primarily based on age classes of trees, but on general changes in forest architecture (Oldeman, 1990) since the duration of successional stages seems to depend on the maximum lifetime of the tree species and soil fertility in the stand. This classification is based on supposed "typical" succession series and may be altered under the influence of environmental factors (cf. fig. 4). Many species may occupy an intermediate position or occur during two or more stages (Tables 2, 4).

1. Ectomycorrhizal fungi of the innovation phase: fungi colonizing root-systems of very young trees in the absence of mature trees; low degree of host-specific association (e.g. *Betula* and *Pinus* $\pm$ 1 to 5 years; *Quercus* $\pm$ 1 to 10 years; e.g. *Thelephora terrestris*, *Laccaria tortilis*).

2. Ectomycorrhizal fungi of the canopy closure phase: fungi mainly growing in open stands of young trees without canopy closure; moderately low degree of host-specific association (e.g. *Betula* $\pm$ 5 to 10 years, *Pinus* $\pm$ 5 to 15 years; *Quercus* $\pm$ 10 to 20

years). e.g. *Suillus luteus*, *Lactarius pubescens*, some *Inocybe* species.

3. Ectomycorrhizal fungi of the aggradation phase: fungi, mainly growing in stands around canopy closure and some years afterwards; moderately high degree of host-specific association (e.g. *Betula* ± 10 to 25 years, *Pinus* ± 15 to 40 years; *Quercus* ± 25 to 50 years), e.g. *Cortinarius semisanguineus*, *Boletus edulis*.

4. Ectomycorrhizal fungi of the late biostatic phase: fungi, mainly growing in mature stands; high degree of host-specific association (e.g. *Betula* ± 25 to 50 years; *Pinus* ± 40 to 100 years; *Quercus* ± 50 to 150 (?) years), e.g. *Amanita rubescens*, *Russula nigricans*, *R. decolorans*.

(5) Ectomycorrhizal fungi of the degradation phase: fungi, mainly growing in stands with senescent trees (e.g. *Betula* ± 50 to 100 years; *Pinus* > 100 years; *Quercus* > 150 (?) years). Examples unknown, possibly *Podoscypha multizonata* (doubtfully ectomycorrhizal; cf. Jahn & Müller, 1976).

(6) Persistent ectomycorrhizal fungi: fungi occurring from the innovation phase to phase 3 or 4; low degree of host specific association, e.g. *Laccaria laccata*.

It is evident that changes in species richness and composition during ectomycorrhizal succession are not only influenced by the structure of stands and the age of the trees, but also by e.g. the soil conditions, tree species, other forest components and former land use (primary or secundary succession). The interactions between these factors are complex and still poorly understood. More data on the composition of the ectomycorrhizal flora in stands of different age-classes growing in various environments are indispensable for a better understanding of ectomycorrhizal successions. In addition, field and laboratory experiments are needed to unravel the physiological and ecological differences between groups of late-stage fungi, appearing at different moments during stand development.

Table 1. Some phytocoenological and environmental characteristics of three types of roadside verges with planted oak trees.

Phytocoenological type	*Hypochaeris radicata-Quercus* type	*Anthriscus sylvestris-Quercus* type	*Mnium hornum-Quercus* type
Number of plots	26	23	4
Age of trees (1988)	10 to 114	26 to 146	102 to 144
Phytocoenological characteristics:			
Av. nr. of plant species (± s.d.)	37 ± 9	29 ± 7	19 ± 5
Av. coverage herb layer (%) (± s.d.)	75 ± 19	72 ± 17	35 ± 11
Av. coverage moss layer (%) (± s.d.)	14 ± 16	0.5 ± 2.0	6 ± 4.7
Some differential species	*Hypochaeris radicata* *Leontodon autumnalis* *Luzula campestris*	*Anthriscus sylvestris* *Stellaria media* *Poa trivialis*	*Mnium hornum* *Deschampsia flexuosa* *Hypnum cupressiforme*
Environmental characteristics:			
Soil profile	All disturbed sandy soils with variable organic layers		
Av. litter layer (cm) (± s.d.)	0.2 ± 0.5	1.1 ± 1.3	5.5 ± 3.8
Av. pH-$CaCl_2$ (± s.d.)	4.2 ± 0.4	4.0 ± 1.0	3.3 ± 0.4
Av. Ellenberg N-indication value* (± s.d.)	5.1 ± 1.0	6.7 ± 0.6	4.0 ± 1.7
Av. hours direct sunshine (Oct) (± s.d.)	6.9 ± 4.2	3.0 ± 2.9	0
Exposure	Open, bordered by fields	Open to shady, bordered by fields, forest at one side or in forests	Shady, situated in forests

* Nitrogen availability indicating values are awarded to plant species according to Ellenberg (1979). The plots are characterized by the median of these values of the occurring plant species. The presented averages are the averages of the medians of the plots that belong to a phytocoenological type.

Table 2. Average Maximum Numbers (AMN) of sporocarps per 1000 m^2 and percentage-degrees (%) of ectomycorrhizal fungi in roadside verges planted with *Quercus robur*, belonging to different age classes and vegetation types, in Drente, the Netherlands. Only species occurring in more than two plots were included.
The following vegetation types are distinguished:
HQ = *Hypochaeris radicata-Quercus* type
AQ = *Anthriscus sylvestris-Quercus* type
MQ = *Mnium hornum-Quercus* type
The following differential species groups are distinguished within plots with old trees (> 50 years old), belonging to different vegetation types:
H = differential of the *Hypochaeris radicata-Quercus* type
A = differential of the *Anthriscus sylvestris -Quercus* type
M = differential of the *Mnium hornum-Quercus* type
HA = differential of the *Hypochaeris radicata-* and the *Anthriscus sylvestris-Quercus* type
AM = differential of the *Anthriscus sylvestris-* and the *Mnium hornum* type
O = not differential

Age of trees (years)	< 20		20 - 50		> 50		> 50		> 50		
Vegetation type	HQ		HQ		HQ		AQ		MQ		
Number of plots	4		11		10		21		4		
Av. nr. of species per plot	8		15		28		20		16		
Av. nr. of sporocarps per plot	614		1932		1619		1264		1324		
	%	AMN	%	AMN	%	AMN	%	AMN	%	AMN	
I Preference for young trees											
Laccaria proxima	100	221	36	18	50	16	38	11	75	98	O
Laccaria tortilis	50	167	0	0	10	1	0	0	0	0	O
II Preference for young and medium-aged trees											
Hebeloma mesophaeum	50	5	9	59	0	0	14	3	0	0	A
Inocybe lanuginella	25	14	27	12	0	0	0	0	0	0	O
Inocybe lacera	50	10	36	12	0	0	5	0	25	18	O
Laccaria bicolor	25	11	18	1	0	0	10	1	25	3	O
Scleroderma areolatum	100	10	82	22	40	2	52	8	0	0	HA
III Preference for medium-aged trees											
Amanita muscaria	0	0	36	23	0	0	0	0	0	0	O
Boletus edulis	0	0	36	40	40	9	10	1	0	0	H
Chalciporus piperatus	0	0	27	4	0	0	0	0	0	0	O
Clavulina coralloides	0	0	64	66	20	44	33	74	25	59	O
Clitopilus prunulus	0	0	27	19	20	1	5	0	0	0	H
Cortinarius pallidoluctuosum	0	0	9	275	10	4	0	0	0	0	O
Cortinarius saniosus	0	0	55	47	40	7	10	1	0	0	H
Laccaria laccata	100	108	100	380	90	115	90	429	100	117	A
Lactarius quietus	25	2	91	516	100	153	95	63	100	139	O
Russula pectinatoides	0	0	45	29	20	8	38	8	0	0	HA
IV Preference for medium-aged or old trees											
Cortinarius flexipes	0	0	18	2	30	4	19	2	0	0	HA
Cortinarius erythrinus	0	0	27	23	40	13	19	3	0	0	H
Inocybe mixtilis	0	0	27	8	20	5	5	0	0	0	H
Lactarius theiogalus	0	0	18	53	30	21	43	17	75	223	M
Russula amoenolens	25	1	82	70	100	59	90	33	0	0	HA
Russula parazurea	25	2	55	19	60	22	100	30	50	18	H
Xerocomus chrysenteron	0	0	27	1	50	3	71	10	25	1	A
V Preference for old trees											
Amanita citrina	0	0	0	0	60	8	33	2	25	2	H
Amanita rubescens	0	0	18	5	90	21	71	4	100	16	O
Amanita fulva	0	0	0	0	60	2	14	1	50	4	O
Cantharellus cibarius	0	0	0	0	40	19	10	2	0	0	H
Cortinarius privignus	0	0	0	0	20	20	0	0	0	0	H
Cortinarius striaepilus	0	0	27	6	50	87	29	82	25	3	HA
Cortinarius subsertipes	0	0	0	0	20	22	5	2	0	0	H
Cortinarius hinnuleus	0	0	9	0	50	42	14	3	0	0	H
Cortinarius obtusus	0	0	0	0	20	2	5	0	0	0	O
Cortinarius paleaceus	0	0	27	5	30	124	33	21	25	1	H
Hebeloma longicaudum	25	10	9	17	40	11	0	0	0	0	H
Hebeloma truncatum	0	0	0	0	20	16	0	0	0	0	H
Inocybe assimilata	0	0	9	1	20	2	29	5	25	7	HA
Inocybe napipes	0	0	0	0	20	2	10	1	50	4	M
Laccaria amethystea	0	0	9	23	40	163	33	25	0	0	H
Lactarius serifluus	0	0	0	0	50	44	38	19	0	0	H
Lactarius chrysorrheus	0	0	9	3	60	77	24	15	0	0	H

Age of trees (years)	< 20		20 - 50		> 50		> 50		> 50		
Vegetation type	HQ		HQ		HQ		AQ		MQ		
	%	AMN	%	AMN	%	AMN	%	AMN	%	AMN	
Otidea bufonia	0	0	0	0	20	4	10	10	0	0	HA
Paxillus involutus	0	0	9	1	30	12	48	27	100	82	M
Russula vesca	0	0	0	0	30	1	19	2	0	0	HA
Russula graveolens	0	0	0	0	60	30	24	10	0	0	H
Russula nigricans	0	0	0	0	100	118	52	11	0	0	H
Russula cyanoxantha	0	0	9	1	40	7	33	3	25	1	O
Russula graveolens f. purp.	0	0	0	0	20	1	14	1	0	0	O
Russula fragilis	0	0	73	11	100	69	43	8	25	2	H
Russula velenovskyi	0	0	0	0	40	5	10	5	0	0	H
Russula graveolens f. cica.	0	0	0	0	30	7	14	1	0	0	H
Russula atropurpurea	0	0	0	0	80	19	43	9	50	3	H
Russula ochroleuca	0	0	9	1	30	2	29	1	100	147	M
Russula odorata	0	0	9	0	70	8	5	0	0	0	H
Scleroderma citrinum	0	0	18	3	60	7	38	9	100	312	O
Tricholoma saponaceum	0	0	0	0	20	4	5	2	0	0	H
Tricholoma sulphureum	0	0	0	0	20	1	5	12	0	0	H
Xerocomus badius	0	0	9	1	60	8	38	6	75	10	O
VI No preference or rare species											
Amanita spissa	0	0	0	0	10	2	10	3	0	0	O
Cortinarius umbrinolens	0	0	18	1	10	3	0	0	0	0	O
Cortinarius anomalus	0	0	9	1	10	1	10	0	0	0	O
Cortinarius lanatus	0	0	0	0	0	0	19	4	25	5	AM
Cortinarius helveolus	0	0	0	0	10	6	10	19	0	0	A
Hebeloma pallidoluctuosum	25	5	0	0	10	1	0	0	0	0	O
Hebeloma helodes	25	25	36	54	30	23	29	6	0	0	H
Inocybe griseolilacina	0	0	9	1	20	8	5	92	0	0	HA
Inocybe lanuginosa	25	5	9	5	10	0	0	0	0	0	O
Inocybe petiginosa	0	0	0	0	10	10	14	35	0	0	A
Inocybe maculata	0	0	0	0	0	0	19	18	0	0	A
Inocybe albomarginata	0	0	0	0	10	1	19	7	0	0	A
Lactarius camphoratus	0	0	0	0	20	1	19	7	50	8	M
Leotia lubrica	0	0	9	73	10	1	5	1	25	7	O
Naucoria bohemica	50	6	64	9	30	3	0	0	0	0	H
Pseudocraterellus sinuosus	0	0	0	0	0	0	14	31	0	0	A
Russula ionochlora	0	0	0	0	0	0	29	3	0	0	A
Russula grisea	0	0	0	0	0	0	19	1	0	0	A
Russula laurocerasi	0	0	0	0	0	0	14	2	0	0	A
Russula emetica	0	0	0	0	0	0	5	0	50	5	M
Thelephora terrestris	25	14	9	1	10	0	5	0	50	17	M
Xerocomus rubellus	0	0	0	0	10	0	14	3	0	0	A
Xerocomus porosporus	0	0	0	0	0	0	19	2	0	0	A

Table 3. Numbers of taxa in different genera of ectomycorrhizal fungi belonging to various groups of differential taxa for three age classes of trees in roadside verges planted with *Quercus robur* in Drente, the Netherlands. The group of differential taxa were distinguished in the *Hypochaeris radicata* - *Quercus* type only, according to table 1:

Group I : Differential taxa of young trees (< 20 years)
Group II : ,, ,, of young and medium-aged trees
Group III: ,, ,, of medium-aged trees (20 - 50 years)
Group IV : ,, ,, of medium-aged and old trees
Group V : ,, ,, of old trees (> 50 years)
Group VI : Indifferent and rare taxa

	Groups of differential species				
	I+II	III+IV	V	VI	Total
Total number of differential taxa	10	16	34	20	80
Laccaria	3	1	1	-	5
Inocybe	3	1	2	4	10
Hebeloma	2	-	2	1	5
Scleroderma	1	-	1	-	2
Boletus, Xerocomus, Chalciporus	-	3	1	1	5
Lactarius	-	2	2	1	5
Cortinarius	-	4	6	4	14
Amanita	-	1	3	1	5
Russula	-	3	11	4	18
Tricholoma	-	-	2	-	2
Other genera	1	1	3	4	9

Table 4. Presence degree (in %) of selected ectomycorrhizal fungi in plots (250x3m) in stands of different ages of *Pinus sylvestris* on sandy soils near Helsinki, Finland (columns 1 to 4; after data by Hintikka, 1988), and in the Netherlands (columns 5 and 6; after data by Termorshuizen, 1990).

	FINLAND				NETHERLANDS	
Nr. of plots	7	8	4	6	14	19
Age class (year)	5-15	20-30	30-50	>70	4-13	50-80
Occurrence mainly near young trees (5-15 years) e.g.:						
Thelephora terrestris	57	—	—	—		
Laccaria laccata s.l.	100	62	25	—	100	88
Occurrence mainly near (young and) rather young trees (20-30 years), e.g.:						
Inocybe spec.	29	25	—	—		
Suillus luteus	14	37	—	—		
Gomphidius roseus	29	50	—	—	38	-
Occurrence mainly near young to middle-aged trees (30-50) years), e.g.:						
Amanita muscaria	71	62	100	16	38	-
Paxillus involutus	43	37	50	—	100	56
Occurrence mainly near (rather young and) middle-aged trees, e.g.:						
Boletus edulis	—	37	25	—		
Cortinarius semisanguineus	—	75	50	16	75	-
Tricholoma auratum	—	75	50	16		
Hygrophorus hypothejus	—	75	50	—	25	-
Rozites caperata	—	75	50	16		
Russula xerampelina	29	75	75	33		
Occurrence mainly near middle-aged and old trees (> 70 years), e.g.:						
Suillus variegatus	43	100	100	83	25	-
Russula emetica	—	25	25	16	13	13
Russula vinosa	14	100	100	100		
Russula paludosa	—	62	50	83		
Russula decolorans	14	50	100	100		
Cortinarius collinitus	14	37	75	83		
Without preference for age-class:						
Lactarius rufus	86	100	100	100	100	31
Suillus bovinus	86	75	75	67	75	13

Table 5. Average distances of sporocarps of various ectomycorrhizal fungi to the trunk of the nearest tree and to the edge of the pavement in the year 1986 in a roadside verge planted with *Quercus robur* of 100 years old (in 1988) near Zwiggelte, The Netherlands.

	n	distance to nearest tree (m)	distance to road surface (m)
Fungi of the canopy closure phase:			
Laccaria laccata	330	3.5 ±0.7	4.5±0.2
Hebeloma helodes	105	3.2 ±0.5	4.3±0.5
Fungi of the biostatic phase:			
Russula odorata	15	3.0 ±1.3	0.9±0.6
Russula fragilis	126	2.3 ±0.6	3.3±0.6
Lactarius chrysorrheus	160	2.0 ±0.9	2.5±0.8
Russula nigricans	27	1.9 ±0.8	2.6±0.8

THE EFFECTS OF VARIOUS MANAGEMENT TREATMENTS ON THE MACROMYCETES IN A ROADSIDE VERGE PLANTED WITH COMMON OAKS (*QUERCUS ROBUR L.*).

P.J.Keizer

Abstract. In a roadside verge planted with Oaks the macromycetes were studied during 5 years under 5 different treatments: a. mowing without removal of the hay, b. mowing with removal of the hay, c. removal of sods, d. N-fertilization, e. no treatment. Treatment "a" served as control. Each treatment was carried out sixfold. Besides the phanerogam vegetation, some soil properties and ectomycorrhizal samples from treatments b, c and d were analyzed as well. Sods removal caused an immediate decrease of sporocarps of mycorrhizal fungi but after 3 years the species numbers had largely recovered. However, there was some shift in species composition. After fertilization a strong decrease of ectomycorrhizal fungi occurred. The saprotrophs were strongly afflicted by sods removal. Fertilization caused lower saprotroph species numbers but the production did not change significantly. Treatments b and e showed no significant differences with the control. The soil chemistry was not influenced by the treatments except for higher concentrations of N in fertilized plots. Fertilized plots contained more mycorrhizal root tips with a relatively large proportion of the *Cenococcum*-type.

I. Introduction.

In recent years an increasing interest is observed in the impact of man-made environmental changes on semi-natural plant communities. This interest is concentrated on woods and grassland. The habitat "roadside verges planted with trees in an open landscape" differs from grassland by a greater variation in microclimate and various amounts of tree litter, from woodlands by different mycroclimate and by input of pollutants such as fertilizers from the adjacent arable fields, from both grassland and forest by soil disturbance, and pollutants produced by traffic. The vegetation of roadsides is treated variously, often by mowing once or twice a year without removal of the hay, sometimes by mowing once a year with removal of the hay and sometimes no management is carried out al all during many years. In many places the top soil layer (with the vegetation that it bears) is removed with intervals of 5 to 10 years to warrant a good drainage of rain water for reasons of traffic safety.

During mycocoenological research in this specific habitat, carried out in the province of Drente in the Northern part of the Netherlands it became evident that roadsides planted with one tree species (viz. *Quercus robur* L. or *Fagus sylvatica* L.) vary widely with regard to species composition, species richness, production, etc. of macromycetes (chapter 2, 3). From these data it was hypothesized that at least part of the observed differences are connected with differences in management. Another part of the variation in species composition seemed to be related to soil fertility, which is strongly influenced by nutrient input from the adjacent agricultural fields and atmospheric deposition.

Field experiments including various management regimes and addition of artificial fertilizer were established in order to test these hypotheses. The results may serve to select optimal types of management for macromycetes in planted roadside verges.

Nomenclature of syntaxa follows Westhoff & Den Held (1969); of vascular plants Heukels/Van der Meijden (1983); of bryophytes Touw & Rubers (1989); of Basidiomycetes Kreisel (1987), except for the genera *Inocybe* (Kuyper, 1986) and *Psathyrella* (Kits van Waveren, 1985); of Ascomycetes Cannon et al. (1985). Taxonomical notes on rare and critical species are presented in (chapter 8).

II. Material and Methods.

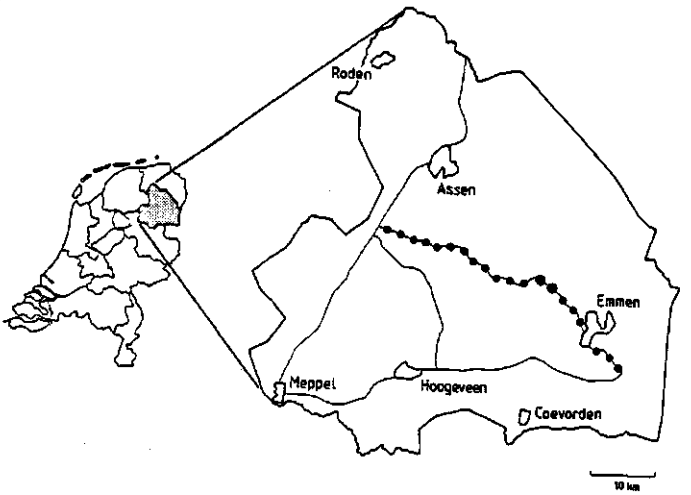
1. *The experimental setup.*

The experiment was carried out in a 5 m broad and 1.5 km long strip of grassland between a NW-SE oriented road paved with asphalt and a canal at the NE side (the "Oranjekanaal") near the village of Odoornerveen, 20 km SW of Assen, province of Drente, the Netherlands. At a more or less regular distance of about 6 m planted common Oaks (*Quercus robur* L.) of about 100 years old and about 20 m high are present.

The composition of the soil and the original sequence of the horizons have very much been disturbed by the construction of the canal and the road. Nowadays, the soil consists largely of loamy sand, intermixd with clumps of boulderclay and peat. The organic topsoil is poorly developed (less than 2 cm thick). The groundwater-table is determined by the level of the water in the canal, i.e. constantly about 0.8 to 1.0 m below the soil surface. The site is managed by the Provincial Service for the maintenance of ways and water works.

Before the start of the experiment, the verge was mown yearly in August with a flail-mower mounted on a tractor and the hay was not removed. The vegetation in the study-area was

relatively homogeneous over the entire length of the area although in the direction from the road towards the canal a zonation was noticed, which is a result of a decreasing intensity of trampling and riding and of an increasing soil moisture.



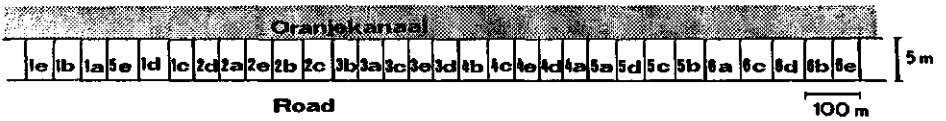


Fig. 1. Locality and schematic sketch of the study-site. Small dots indicate the Oranjekanaal; large ones the locality of the studied site.

The 1.5 km long section was divided into six plots of 250 m numbered 1 through 6. Each plot was subdivided into five subplots of 50 m numbered a through e, each with a different treatment (fig. 1). Consequently, the five experiments were carried out sixfold. Within the plots the order of the treatments was random. In each subplot, 4 to 9 trees were present. The following experiments were carried out.

a. removal of sods. In the spring of 1987 the vegetation plus the top soil (about 5 cm) was removed, followed by treatment e in the subsequent years (fig. 2);
b. mowing once a year in late summer with the aid of a light double-knife mower (type Agria 5500) and with subsequent removal of the hay. The hay was removed by hand;
c. no treatment;
d. application of artifical fertilizer combined with treatment e: in 1987 150 kg N/ha, in 1988 and 1989 300 kg N/ha, applied in 2 and 4 portions of 75 kg N/ha respectively, with monthly intervals during the growing season. In 1990 and 1991 no fertilizer was applied. The fertilizer, the so-called "Kalkammonsalpeter", is a mixture of ammonium nitrate and calcium carbonate. It contains 27% pure Nitrogen. Calcium carbonate is added to neutralize the acidification caused by the N-input. The amount of 300 kg N/ha year is commonly used in agricultural grasslands in the Netherlands;
e. mowing once a year (same equipment as in treatment b.) in late summer without removal of the hay.

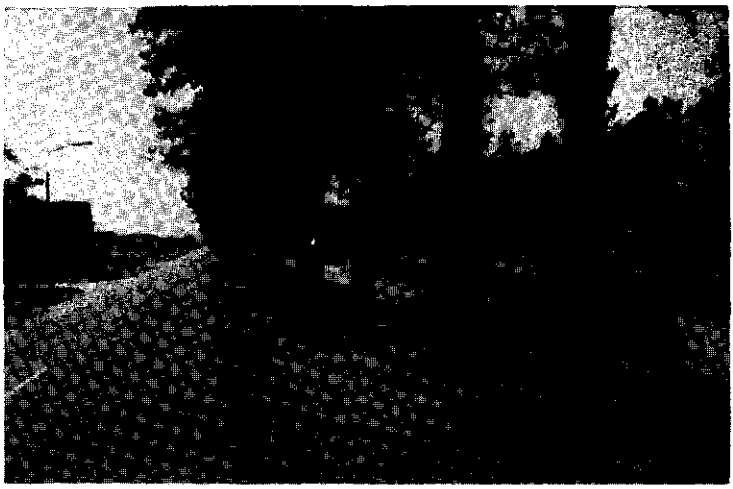


Fig. 2. Subplot where sods have been removed.

In all treatments a zone 0.7 m broad along the road was mown 4 times a year without removal of the hay, for reasons of traffic safety. This zone was included in the investigation of the vegetation and macromycetes. Treatments a, b and e were carried out by the staff of the Provincial Service for the maintenance of ways and water works. Plots with treatment e are considered as control because mowing without removal of the hay represented continuity of the management practice. In the last week of May 1987 in all subplots the cover degree of all plant, moss and lichen species was estimated (after Westhoff & van der Maarel before the start of the treatments and again in the last year of the application of the fertilizer (July 1989). The vegetation at the very edge of the road (0.2 m) was strongly deviating from the remainder of the plots, belonging to the *Polygono-Coronopion* and *Lolio-Plantaginion*, and hence was not included in this study. In the autumn of 1988 (after the last application of fertilizer), one composite soil sample was taken in each subplot from 0.0 to 0.1 m and one from 0.1 to 0.2 m depth, each consisting of 5 subsamples from random places in the subplots. The soil samples were analysed in 0.01 M $CaCl_2$ for pH, extractable Mg^{2+}, Na^+, K^+, NO_{3-}, NH_{4+}, PO_4^{3-}, N-soluble total, all according to the standard methods described by Houba et al. (1988). N-total as %, P-total and C as % were assessed after destruction in concentrated H_2SO_4. The C/N ratio refers to N total.

In November 1989, 18 mycorrhiza-samples (0-10 cm depth, 200 cm^3) were taken in the treatments a, b and d, one in every subplot. It was expected that in these treatments differences in root and mycorrhiza development would be most obvious. After cleaning the samples and the number of root tips were counted for the recognisable types of mycorrhiza, using a dissecting microscope with maximal 16x magnification. The total root length was estimated using the line intersection method of Newman (1966).

During the autumns of 1987 to 1991, all carpophores of macromycetes in the plots were

identified and counted with monthly intervals from August to November. Incidental visits revealed that fungi were absent in other periods. The extreme margins along the road and the water were not included, resulting in a surface of 50x4.5=225 m^2 per subplot. At each visit, the caps of all carpophores were removed to prevent double counting. Many carpophores were collected for identification in the laboratory. Of all species the "specific dry weight" was determined by weighing air-dry herbarium-material of representative fruitbodies. In some cases the values for specific weights given by Arnolds (1981) were used.

2. *Ecological status of fungal species.*

In this investigation a distinction between mycorrhizal and non-mycorrhizal fungi was made. Considered as mycorrhizal were most of the taxa (genera, species) listed as such by Trappe (1962). For some macromycetes it is uncertain whether they belong to mycorrhizal or saprotrophic fungi. Among the ambiguous species the following are considered here as being presumably mycorrhizal: *Clavulina coralloides* and *C. rugosa* (not listed by Trappe (l.c.) and reported as saprotrophic by Kreisel (1987)) and *Clitopilus prunulus* (possibly mycorrhizal according to Trappe (l.c.); saprotrophic according to Kreisel, l.c.). Like many true mycorrhizal species they 1) have not been observed outside the range of mycorrhiza bearing trees; 2) often prefer humus/litter-poor microhabitats such as gaps in the vegetation, steep sides of ditches, places where sods have been removed; 3) have their peak fructification-period during August-September, contrary to many true saprotrophic species which fructify during the second half of October and November. On the other hand, *Lyophyllum semitale* is regarded as a saprophyte (in agreement with Clemençon, 1986) but it may in fact be mycorrhizal as well.

III. Results and conclusions.

1. *Changes in soil characteristics.*

Within one year, the various treatments did not cause significant short-term changes in the top soil chemistry (table 1). Only the application of N-fertilizers (d) and absence of any treatment (c) produced significant effects: in the fertilized subplots the concentrations of soluble N, nitrate and ammonium have increased indeed. In the untreated subplots the total percentage of nitrogen is significantly lower than in the control and in treatment b the amount of soluble N compounds is relatively high, which cannot be readily explained.

The data for the soil layer 0.1-0.2 m are not presented since they show large similarities to the data for the topsoil. In all cases, the concentrations of soluble N, total N, total P and total C were significantly lower than in the top soil. Concentrations of extractable Mg and Na were also lower, except in the plots where sods were removed.

2. *Characterization of the plant community.*

The plant community can be characterized according to Westhoff & Den Held (1969) as Arrhenatherion elatioris (especially the subassociation Luzuletosum of the association Lolio-Cynosuretum), by the presence of *Leontodon autumnalis, Anthoxanthum odoratum, Holcus lanatus, Festuca rubra, Luzula campestris, Stellaria graminea, Agrostis capillaris, Hieracium pilosella, Hypochaeris radicata, Trifolium*

Table 1. Averages with standard deviations of contents of some minerals in the soil and pH under various treatments. Mg, Na, K, NO_3-, $NH4^+$, N soluble total, P soluble and P total are expressed in mg/kg. N total as % and C as % are the fractions of the sample of N and C respectively, multiplied by 100%. * = significantly deviating from the value under treatment e with $p < 0.05$ (t-test; Mann-Whitney-test for NO_3^- and P soluble (no standard deviation in treatment e)).

Treatment	e:mowing no removal of hay	b:mowing removal of hay	a:removal of sods	d:N-fertilized	c:no treatment
pH ($CaCl_2$)	4.0±0.4	4.0±0.4	4.0±0.3	4.1±0.3	4.1±0.2
Mg	46±17	41±13	36±20	51±30	34±9
Na	22±13	18±4	18±8	20±9	18±10
K	25.8±1.6	37±11	30±18	30±15	31±10
NO_3^-	0.0 -	1.0±1.6	0.2±0.4	2.3*±1.8	0.5±0.9
NH_4+	3.7±1.0	5.3±2.3	3.5±1.6	5.3*±1.6	4.3±1.9
N soluble total	12±2.8	15±3.4	11±3.6	16*±3.0	12±4.3
N total as %	0.2±0.1	0.2±0.0	0.2±0.1	0.2±0.1	0.1*±0.0
P soluble	0.0 -	0.2±0.4	0.0 -	0.0 -	0.2±0.4
P total	215±49	216±42	225±28	298±122	207±30
C as %	3.2±2.8	2.8±1.2	3.1±0.8	3.2±0.7	2.6±0.6
C/N	17±2	15±2.6	20±3.6	17±2.8	22±13

dubium. Further some elements of the grass heath alliance Violion caninae are present: *Galium saxatile*, *Euphrasia stricta* and *Viola canina* and of the order Festuco-Sedetalia: *Aira praecox*, *Ornithopus perpusillus*, *Rumex acetosella*. The moss layer is unusually well developed with a cover degree of (10-)30-50(-70)%. Most abundant bryophytes are *Pseudoscleropodium purum* and *Rhytidiadelphus squarrosus*. After Stieperaere (1990) the name the name of the present syntaxon should be Nardo-Agrostietum tenuis.

3. *Changes in vegetation.*

After two years the vegetation had changed considerably in the plots with treatments a, d and c, compared with the "control" treatment e. There were no clear differences between treatments e and b (Table 2; at the back of this chapter). In the plots where the top soil had been removed (a) a strong development of annual vascular plants and acrocarpous mosses was observed in the second growing season, forming a pioneer community belonging to the Thero-Airion. In the third growing season the annuals were partially replaced by perennials.

The fertilized plots became darker green in colour and the plants grew more vigorously, especially the grasses *Agrostis capillaris* and *Festuca rubra*. There was a noteworthy increase in cover of *Dactylis glomerata* and *Lolium perenne* and at the same time a decrease in species number and coverage of forbs. The moss layer largely disappeared.

Dead grass material accumulated and the large plants *Cytisus scoparius* and *Phragmites australis* developed significantly in the plots without treatment (fig. 3). *Calluna vulgaris*, *Festuca ovina* and *Brachythecium albicans* decreased.

4. *Changes in mycorrhizal roots.*

In Table 3 the results of the analyses of the root samples are summarized. All data show large standard deviations. Obviously, the results of the three treatments are largely similar. It is striking that mycorrhizal infection of the tree-roots is almost 100 %, irrespective of the treatment. In the fertilized plots the total number of root tips were higher than in the other

Fig. 3. Subplot where no treatment was carried out during 3 years, resulting in strong development of *Cytisus scoparius* and *Phragmites australis*.

treatments, although this number contained a relatively large proportion (> 50%) of non-vital mycorrhizal root tips. Also the proportion of the *Cenococcum*-type mycorrhiza (of vital root tips) was higher in the fertilized plots. The number of root tips in plots where either the top soil was removed or the vegetation was mown were approximately the same. The number of root tips of type 2 (*Lactarius*) was lowest in plots where sods had been removed. Further, it can be seen that in plots where sods were removed, a relative low percentage of the mycorrhizal root tips were non-vital, whereas in N-fertilized plots this percentage was high. However, the absolute numbers of vital root tips was highest in the fertilized plots.

Table 3. Distribution of mycorrhizal roots over three management regimes. The values are averages plus standard - deviations of 6 root samples of 200 cm^3 in each treatment. No significant differences between the treatments were found (oneway anova).

treatment	a: removal of sods	b: mowing with removal of the sward	c: application of N-fertilizer
	av. ± std.	av. ± std.	av. ± std.
total root length (cm)	698 ± 483	803 ± 236	1813 ± 1908
total number of root tips in 100 cm^3	2260 ± 1301	2252 ± 810	4397 ± 3590
branching (number of root-tips/cm root length)	3.3	2.8	2.4
% mycorrhizal root tips	98.1	99.1	99.6
% non-vital mycorrhizal root tips	29.7	41.8	54.2
number of mycorrhiza types	5.5 ± 1.3	5.7 ± 0.9	5.0 ± 1.6
nr. of type 1 (*Cenococcum*)	830 ± 617	754 ± 494	1311 ± 1198
nr. of type 2 (*Lactarius*)	122 ± 96	211 ± 263	172 ± 125
% type 1 (of vital root tips)	52.2	57.5	65.2
% type 2 (of vital root tips)	7.6	16.1	8.6

5. *Changes in mycocoenoses.*

The fungal species were arranged according to niche-substrate groups (Arnolds, 1988a), viz. 1) mycorrhizal symbionts, largely according to Trappe (1962); some exceptions will be discussed above, 2) terrestrial saprophytes on litter and humus inclusive species associated with bryophytes, and 3) other, including wood-inhabiting saprophytes and parasites, and saprophytes on fungi, insects and dung (after personal observations or after Arnolds, 1982). Species of group (3) are considered as alien or facultative in the studied community and have therefore been excluded (Barkman 1976, 1987). They are listed in table 13, at the back of this chapter. Wood-inhabiting species that can also grow on dead leaves, herbaceous stems, etc. (e.g. *Tubaria furfuracea*, *Psathyrella fulvescens* var. *brevicystis*, *Crepidotus variabilis*), have not been excluded. The mycorrhizal fungi and saprophytes will be treated separately because they play fundamentally different roles in the ecosystem.

a. Mycorrhizal macromycetes.

The community of the ectomycorrhizal fungi agrees well with the *Cortinarius erythrinus* type (chapter 3) on account of the presence of *Russula pectinatoides*, *Cortinarius erythrinus*, *C. hinnuleus* and *C. flexipes*. The common occurrence of *Russula velenovskyi*, *Cantharellus cibarius* and *Laccaria amethystea* points towards the *Laccaria amethystea* subtype of this type. This subtype is indicative for nutrient-poor roadsides with old Oak trees.

In all, 83 species of mycorrhizal fungi have been observed, 68 (82%) of them already in the first year. It is a well-known fact that the fruiting process of macromycetes is strongly influenced by weather conditions (e.g. Thoen, 1976; Dahlberg, 1991). In the studied plots the numbers of species and carpophores (tables 4, 5 and 6) show strong fluctuations over the five years of research. The figures were relatively low in 1990 and in particular in 1991 due to very dry conditions during the fruiting season. The fluctuations show the same trend in all treatments and therefore they are not caused by the treatments themselves. For an evaluation of these effects

the figures within each year must be compared with each other. Significance values in tables 4, 5 and 6 are also calculated with respect to other treatments in the same year.

Table 4. Percentages of numbers of taxa of ectomycorrhizal fungi, compared with "mowing, no removal of the hay" (=100%) per treatment in 1987-1991. In parentheses are the absolute numbers of taxa.

	1987	1988	1989	1990	1991
Treatment:					
mowing, no removal of the hay	100 (42)	100 (36)	100 (43)	100 (30)	100 (23)
mowing, with removal of the hay	79 (33)	81 (29)	93 (40)	83 (25)	104 (24)
no treatment	98 (41)	83 (30)	91 (39)	83 (25)	87 (20)
N-fertilized	76 (32)	36 (13)	56 (24)	43 (13)	65 (15)
removal of sods	81 (34)	94 (34)	114 (49)	93 (28)	78 (18)
total	(68)	(55)	(66)	(49)	(39)

Table 5. Average numbers of mycorrhizal taxa per subplot (225 m²) for the different treatments in the years 1987-1991. *: difference significant ($p<0.05$) with respect to control (mown without removal of hay); **: idem ($p<0.01$; t-test).

	1987	1988	1989	1990	1991
Treatment:					
mowing, no removal of the hay	17.2	14.5	16.2	10.5	6.3
mowing with removal of the hay	13.0	10.8*	17.0	9.7	6.3
no treatment	14.8	10.0*	14.8	7.2	5.0
N-fertilized	10.7*	5.0*	7.7*	4.3**	3.7*
removal of sods	11.0**	11.5	17.2	8.3	4.5
average all treatments	13.3	10.4	14.6	8.0	5.2

The application of N-fertilizers led to a strong reduction of the species numbers, starting already in the first year of the experiments. Sod removal resulted in a strong reduction of species numbers in the first year, but a quick recovery from the second year onwards. The number of species number in this treatment appeared in 1989 even larger than in any other treatment (Table 4). The plots with removed hay and without treatment showed a significant lower average species number in only one year, viz. 1988. This phenomenon cannot be explained at present.

Table 6. Averages of the sporocarp production of mycorrhizal fungi (g dr.wt.$1000m^{-2}$) for the different treatments in the years 1987-1991. *: difference significant ($p<0.05$;t-test) with respect to control (mown without removal of the hay).

	1987	1988	1989	1990	1991
Treatment:					
mowing, no removal of the hay	1218	916	795	89	156
mowing with removal of the hay	866	778	811	175	224
no treatment	1508	1090	664	155	193
N-fertilized	947	328*	236*	56	77
removal of sods	530*	625	734	159	190

The sporocarp production (dry weight) of mycorrhizal fungi shows trends similar to the number of species (table 6): after removal of the top soil layer a sharp decline of the production in the first fruiting season and recovery in the subsequent years, with in 1990 and 1991 even a production exceeding that of the control. The production was strongly reduced in the fertilized

plots. During the last two years this effect appears less prominent. No significant changes were recorded in the production in plots where the hay was removed. There was a relatively large production in the treatments "mowing with removal" and "no treatment" during the years 1990 and 1991, which cannot yet be explained.
In all treatments, *Russula nigricans* is the most productive species, accounting for 11 to 50% of the total production. Obviously, there are great differences in the species composition of mycorrhizal fungi between the plots that have been treated differently for three years. In the fertilized plots (Table 7; at the back of this chapter) many species have decreased, e.g. *Russula nigricans*, *Cortinarius violilamellatus*, *Russula fragilis*, or have disappeared completely, e.g. *Lactarius chrysorrheus*, *Amanita rubescens*, *Hebeloma helodes*, *Russula cyanoxantha*, *Cantharellus cibarius*, *Cortinarius saniosus* and *C. erythrinus* (fig. 4). These species were still present in 1987 in these subplots. For other species no conclusion can be drawn because they were already absent in 1987, e.g. *Russula atropurpurea* (Fig. 4). They either have disappeared in the first year of the treatments or were, accidentally, already absent in these subplots before the experiment started. Other species still occur in approximately the same densities as in other plots, e.g. *Laccaria proxima, Lactarius quietus, Lactarius tabidus, Russula amoenolens* and *Xerocomus badius*. These species are thought to be relatively tolerant to nitrogen and are also present in roadside verges on rich soil where most mycorrhizal fungi of the experiment are lacking (chapter 3). Only one species shows a significant increase, viz. *Xerocomus chrysenteron*, which was not yet present in 1987 and was lacking in all other treatments.

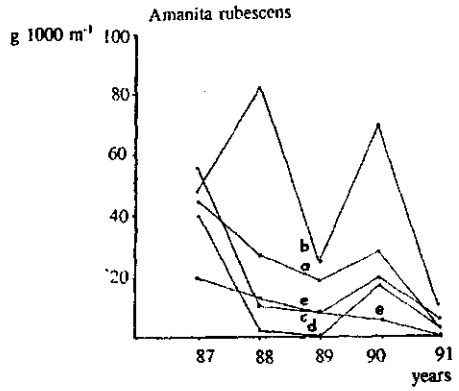
The extreme poverty in fungi during the years 1990 and 1991 seriously hampers interpretation of the trends in decrease or increase of the ectomycorrhizal fungi.

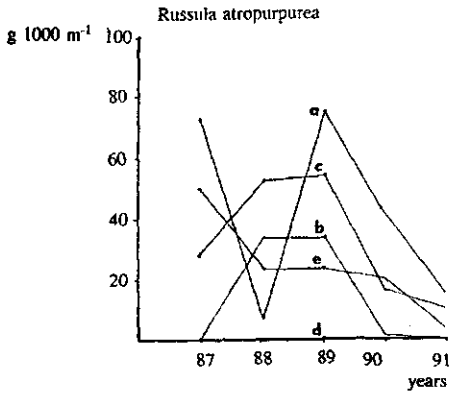
Sod removal increased the number of *Inocybe* species, known as pioneer ectomycorrhizal fungi (Kuyper, 1986). In 1987, seven *Inocybe* species were found in the plots where sods had been removed, compared to one to three in plots with other treatments. Although most species have a lower productivity in plots with removed top soil, some species seem to have been positively influenced viz. *Clitopilus prunulus*, *Cortinarius erythrinus*, *C. saniosus* and *Russula graveolens* f. *graveolens*. Between the other treatments no qualitative differences in mycorrhizal fungi could be established after three years. Numbers of carpophores of *Cantharellus cibarius*, *Lactarius quietus* and *Russula amoenolens* seem to increase by mowing (Table 7).

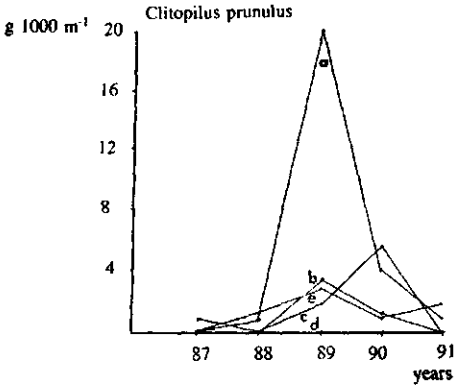
b. *Saprotrophic macromycetes*

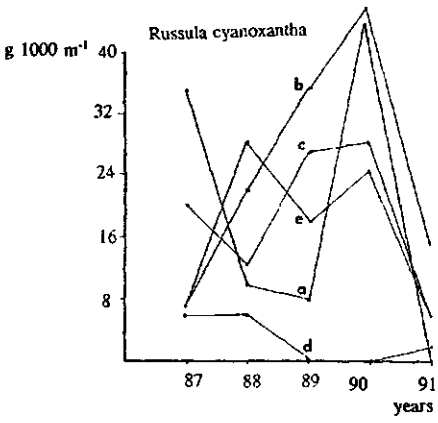
Many of the saprotrophic fungi that were found in the studied site are considered as differential species for the *Mycena avenacea Quercus* type (chapter 3), e.g. *Camarophyllus niveus, Marasmius oreades, Mycena avenacea* and *Mycena vitrea*. This community is found in exposed, roadsides on nutrient-poor soil with planted Oak trees and a grassy understorey.

A number of 104 saprotrophic taxa were recorded, 58 (56%) of them already in the first year of this study. This percentage is lower than the percentage of ectomycorrhizal species found during the first year and it suggests that fluctuations in fruiting in this functional group are larger than in mycorrhizal fungi (fig. 5). For saprophytes, like the mycorrhizal fungi, the years 1987 and 1989 were much richer in species and in sporocarp production than the other years (Tables 5, 9).









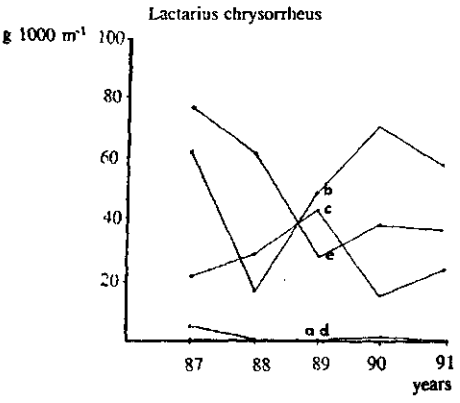


Fig. 4. Production (g.1000m^2) during the years 1987-91 of five ectomycorrhizal species with five nature management treatments in a roadside verge on nutrient-poor soil with 100 years old planted Oaks (*Quercus robur*).

a = sod removal followed by mowing once a year without removal of the hay;
b = mowing once a year with removal of the hay;
c = no treatment;
d = adding N-fertilizer in the years 1987-89 (see explanation in the text) in combination with mowing once a year without removal of the hay;
e = mowing once a year without removal of the hay.

Table 8. Percentages of numbers of taxa of ectomycorrhizal fungi, compared with "mowing, no removal of the hay" (=100%) per treatment in 1987-1991. In parentheses are the absolute numbers of taxa.

	1987	1988	1989	1990	1991
Treatment:					
mowing, no removal of the hay	100 (43)	100 (22)	100 (48)	100 (20)	100 (20)
mowing with removal of the hay	128 (55)	91 (20)	85 (40)	140 (28)	120 (24)
no treatment	74 (32)	82 (18)	75 (36)	70 (14)	100 (20)
N-fertilized	70 (30)	77 (17)	65 (31)	50 (10)	135 (27)
removal of sods	21 (9)	36 (8)	48 (23)	50 (10)	75 (15)
total	(58)	(42)	(73)	(36)	(41)

Table 9. Averages of the numbers of saprotrophic taxa per subplot (225 m^2) for the different treatments in the years 1987-1991. *: difference significant ($p<0.05$) with respect to control (mown without removal of the hay); ** idem ($p<0.01$; t-test).

	1987	1988	1989	1990	1991
Treatment:					
mowing, no removal of the hay	18.7	6.3	18.2	6.5	9.8
mowing with removal of the hay	14.7	4.8	19.8	9.1	10.1
no treatment	13.8	6.0	16.5	4.5	9.0
N-fertilized	11.5	4.7	12.0*	3.8	9.8
removal of sods	2.0**	1.3**	6.8**	4.0	6.7*
average all treatments	12.4	4.6	14.7	5.6	9.1

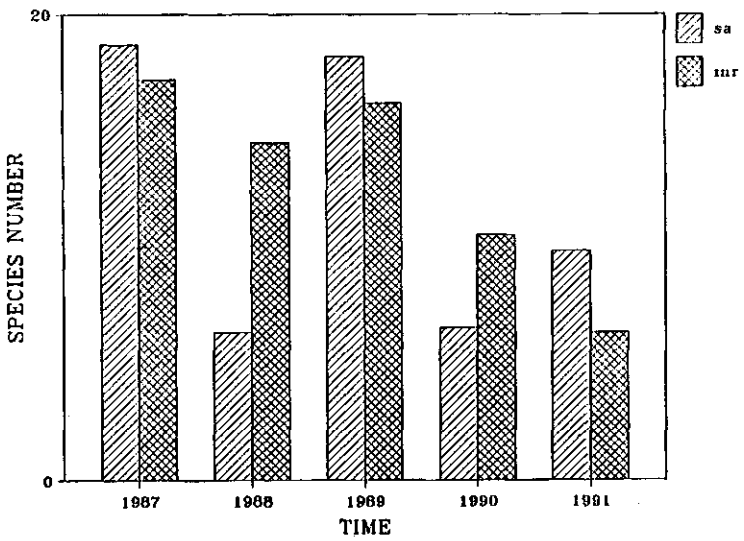


Fig. 5. Averge species numbers of saprotrofic (sa) and mycorrhizal fungi (mr) per subplot (225 m^2; n=6) in the control treatment (mowing without removal of the hay) in the years 1987-1991.

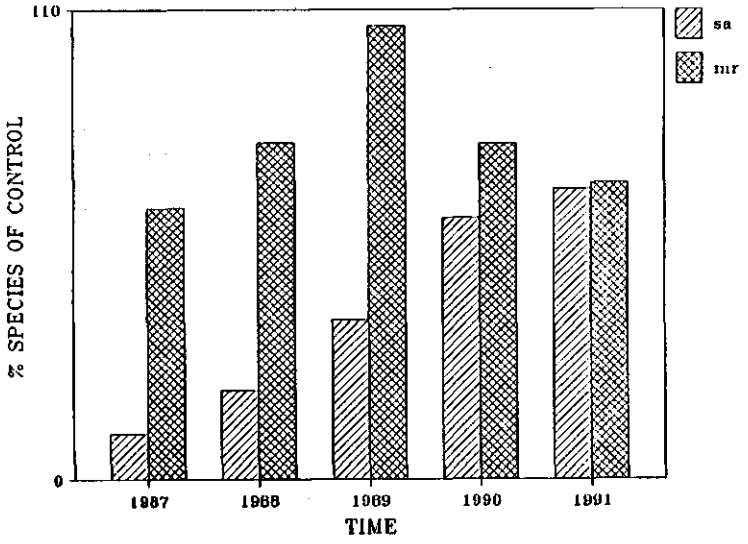


Fig. 6. Percentages of the average species numbers of saprotrophic (sa) and mycorrhizal (mr) fungi in subplots (225 m^2, n=6) where sods were removed, relative to the control treatment (mowing without removal of the hay) in the years 1987-1991.

Naturally, the removal of the top soil (including most of the decomposing litter) causes a sharp and immediate decline of the species number and sporocarp production. Although the recovery is more steady than in the ectomycorrhizal fungi, the species number in the fifth year is still significantly lower than in all other treatments (fig. 4). The species numbers in the fertilized plots were distinctly lower compared with the control during the period that the fertilizer was applied, (although significant only in 1989) but reached in the second year without fertilization (1991) already values comparable to the control. However, the species composition was still deviating.

Table 10. Averages of the sporocarp production (g dr.wt. 1000 m^{-2}) of the terrestrial saprotrophic taxa per subplot (225 m^2) for the different treatments in the years 1987-1991. *: difference significant ($p<0.05$) with respect to control (mown without removal of hay); **: idem, ($p<0.01$; t-test). Percentage of saprotrophic fungi of total fungal production in 1987, 1989 and 1991.

						% saprotrophs		
	1987	1988	1989	1990	1991	1987	1989	1991
Treatment:								
mowing, no removal of hay	189	52	92	7	30	13	10	16
mowing with removal of hay	78	61	154	7	38	8	12	14
no treatment	262	34	77	2	25	15	11	11
N-fertilized	234	27	78	4	90*	20	25	54
removal of sods	29*	1**	6	2	9**	4	1	5

As in the mycorrhizal fungi, few species determine a large share of the production of saprophytes: the five most productive species (*Marasmius oreades, Calvatia excipuliformis, Collybia dryophila, Lepista nuda, Camarophyllus niveus*; in order of decreasing productivity)

produced more than 75% of the total dry sporocarp weight of saprotrophic fungi in all treatments together. The high production in 1989 in the mown plots with removal of the hay can partially be ascribed to an accidental occurrence of *Lepista nuda*, a species with large sporocarps. The production figures of 1990 were not considered because of the extreme poverty of saprotrophs in that year.

There is no relation whatsoever between species numbers and production figures when years and treatments are compared. Compared with mycorrhizal fungi, the production of saprotrophic fungi is low, namely 10-16% of the production of ectomycorrhizal fungi in mown and untreated plots and only 1-5% in the plots where sods were taken. In the fertilized plots this share is larger (25% in 1989, the last year of application of fertilizer). Because the production of saprotrophs did not increase in that period, it suggests that fertilization afflicts the ectomycorrhizal fungi stronger than saprotrophs (Table 10).

In 1989 and 1991, the production of *Mycena leptocephala*, *M. avenacea* var. *avenacea*, *M. metata* and *Rickenella fibula* was much lower in the N-fertilized subplots than in unfertilized mown subplots. Other species disappeared completely in the fertilized plots, viz. *Camarophyllus niveus, Entoloma sericeum f. sericeum, Hygrocybe conica, , Mycena pelliculosa, M. sepia, Ramariopsis helveola, R. laeticolor, R. luteoalba* and *Rickenella setipes*. On the other hand, the N-fertilized plots contained five species of *Clitocybe*, the unfertilized plots only one or two. In particular *C. metachroa* and *C. marginella* seem to be favoured by N-fertilization. The same applies to *Mycena flavoalba, Calocybe carnea* and *Collybia dryophila* (which in 1991 produced in the fertilized plots 43% of the sporocarp production of all treatments together). The more or less ruderal species *Tubaria furfuracea* was obviously favoured both by N-fertilizers and by mowing without removal of the hay, which too may increase N-supply. So contrary to ectomycorrhizal symbionts where only one species was favoured by N-fertilization, several species of saprophytic fungi were favoured.

The greater part of the saprotrophs have disappeared after removal of the top soil, where apparently their mycelia were living. Three years afterwards, some species began to establish themselves again, probably owing to sufficient regrowth of the damaged mycelia and possibly to a slight accumulation of humus. The mycelia of species less afflicted by this treatment may live deeper in the soil, e.g. *Agaricus campestris, Calvatia excipuliformis*.

Termination of management leads to a lower production, in spite of the increased availability of dead organic matter. Especially some small species (*Mycena spp., Rickenella spp.*) tend to have higher numbers in mown plots compared with the plots of treatment c (Table 11; at the bach of this chapter).

Only a narrow strip along the road was mown. Here the herb layer remained low and open, harbouring such species as *Hygrocybe conica, Camarophyllus niveus, Mycena avenacea, Entoloma sericeum, Ramariopsis luteoalba, R. laeticolor*. In the remaining part of the plots these species tended to decrease. From a comparison between mown plots with and without removal of the hay it appeared that no obvious qualitative differences could be detected. However, some species show larger numbers in the plots where the hay was removed after mowing, compared to plots where the hay was not removed (Table 11). Continuation of the experiment will reveal the presence or absence of such trends in the future.

IV. Discussion.

1. *General effect of the treatments.*

A summary of the effects of the treatments in this experiment is presented in table 12.

Compared with the original treatment, mowing without removal of the hay, no significant effect on the mycoflora was found when the hay was removed. In fact we would expect that the species diversity of mycorrhizal fungi increases with further impoverishment of the soil. However, since the starting-point of the experiment represents a low-productive vegetation and a poor soil, a possible favourable influence of hay removal may be apparent only in the long run. For the same reason, the mycoflora in subplots without any treatment does not differ significantly from the satandard treatment. The accumulation of grass litter is in these plots a slow process. It would be expected that in the long run the numbers of ectomycorrhizal fungi, and possibly also of saprotrophic fungi are reduced in this case. In more productive grassland types a strong suppression of fruiting was observed when the sward was not removed during two or three years (Arnolds, 1980).

Table 12. Effects of different treatments on the mycoflora, compared with treatment: mowing without removal of the hay. Nsp = number of species; 0 = no effected detected; - = significant negative effect; (+) = unsignificant positive effect; (-) = unsignificant negative effect.

	Mycorrhizal fungi		Saprotrophic fungi	
	Nsp	Production	Nsp	Production
Treatment:				
mowing with removal of hay	0	0	0	(+)
no treatment	0	(-)	0	0
N-fertilized	-	-	-	0
removal of sods	0	0	-	-

There is a significant negative effect of the application of N-fertilizer on ectomycorrhizal fungi. This is in agreement with the results of many experiments of fertilization in forest stands, mostly of *Pinus sylvestris* L. or *Picea abies* (L.) Karsten (e.g. Ohenoja, 1988a, 1988b; Shubin, 1988; Menge et al., 1977; Menge & Grand, 1978; Wästerlund, 1982; Termorshuizen, 1990; Kuyper & De Vries, 1989). A hypothesis for this proces is presented by Björkman (1942). According this hypothesis the amino acid synthesis in the plant increases after extra N-uptake, causing an increased use of carbohydrates. This leads to a reduction in the supply of carbohydrates to the mycorrhizas. On the other hand, Slankis (1973; cited in Nylund, 1988) stressed the role of the phytohormone production, which might enhance mycorrhiza formation and which might be affected by fertilization.

In the Netherlands, the deposition of N averages 50 kg N/ha yr and locally (in the SE part of the country) is more than 250 kg N/ha yr (Roelofs et al., 1988). This, combined with the results of this study, makes the dramatic decline and the threatened status of so many mycorrhizal fungi (Arnolds, 1989b) understandable. In roadside verges in an open landscape a considerable proportion of the leaves of the trees is blown away in autumn. This means that large quantities of nutrients incorporated in the leaves are taken from the soil and removed from the roadside ecosystem. In addition, minerals are leached out from the upper soil layers to the ground-water. This is unlike the situation in most forests where only the latter process plays a role. In this respect, open roadsides with trees show the same properties as the Dicrano-Quercetum (Barkman,

1974), an association of oak-scrub on poor windblown sand dunes, very rich in species and carpophores of mycorrhizal species (Jansen, 1984).

There are few data available on the effects of N-fertilization on saprotrophic macromycetes. Hall (1978) found a positive effect on saprotrophs in a beech forest at a low level of NPK fertilization (340 kg/ha) but a negative effect at a level of 1700 kg/ha. Garbaye et al. (1979) and Garbaye & Le Tacon (1982) mentioned an increase of some saprotrophic species after adding NPK fertilizer to beech and spruce forests. On the other hand, Arnolds (1989c) noted a strong decline of the number of saprotrophic species but no decline of the production in grassland after application of either liquid manure or NPK fertilizers. The results of the present study agree largely with Arnolds (l.c.). Apparently, the number of species and (changes in) species composition are more sensitive parameters for changes of the nutrient level than the carpophore production.

The saprotrophic fungi form a rather heterogeneous group, including three subgroups: 1) species associated with (mainly pleurocarpous) mosses, e.g. *Rickenella fibula*, *Galerina vittaeformis*; 2) species growing on litter, e.g. *Collybia dryophila*, *Tubaria furfuracea*, *Clitocybe metachroa*; 3) species growing on humus that is incorporated in the soil, e.g. *Calvatia excipuliformis*, *Agaricus campestris*, *Camarophyllus niveus*, *Ramariopsis spp.*, *Entoloma spp.*. Especially the species of subgroups 1) and 3) are reduced by nitrogen application, the former caused by the disappearance of the moss layer, the latter for unknown reasons. Apparently they are spcialized on substrates with low N-contents. In nitrogen rich conditions they might be outcompeted by nitrogen tolerant fungi. Grasslands that are rich in saprotrophic species, the so-called *Hygrocybe*-grasslands, are typically unfertilized (Arnolds, 1980, 1989c; Rald, 1985). Many of the species disappear after application of fertilizer, and belong to subgroup 3).

If we consider specific results, we may expect the species that declined after N-fertilization in the present experiments, to belong to the fungi that have declined in The Netherlands in the past decades, because of the air pollution with ammonia and nitrogen oxides. Among the 13 species of mycorrhizal fungi that decreased after N-fertilization (table 7), 9 are mentioned by Arnolds (1985, tab. 3.2, p. 17-18). Two have not changed their frequency, one (*Laccaria laccata*) has increased in the Netherlands and 6 have decreased, but only for 2 of them (*Cantharellus cibarius* and *Clitopilus prunulus*) this decrease is statistically significant. Among the 11 species of saprophytic fungi that decreased after N-fertilization (Table 11) 6 are mentioned by Arnolds (1985, tab. 3.1, p. 15). Among them one has increased (*Rickenella fibula*), 5 have decreased, only 2 significantly (*Hygrocybe conica* and *Camarophyllus niveus*). Arnolds (1989c, p. 67) states that *Ramariopsis helveola* disappears immediately when artificial fertilizer is applied to grassland. Among the saprophytes 5 species increased in the fertilized plots. Arnolds (1985, p. 15) mentions 3 of them, 2 with an increase (*Clitocybe metachroa* and *Tubaria furfuracea*), one with a decrease (*Mycena flavoalba*). Consequently the trends in these two studies are similar.

Three years after removal of the upper soil layer the flora of mycorrhizal fungi had completely recovered, both regarding species number and production, albeit that the species composition was still different. In the saprotrophs, a strong decrease of species numbers and production was still evident five years after this treatment. It is to be expected that the moss-associated species will recover together with the development of a new moss layer, especially of the large pleurocarps. After five growing seasons only very few species of this group have returned. The litter-inhabiting species will recover as the vegetation becomes re-established and will have produced sufficient litter. It will take a long time before many species of the third subgroup have returned, in view of the fact that many species occur only in old (at least 15-20 years old) grasslands that are continously managed, by extensive grazing and/or mowing with

removal of the hay (Arnolds, 1980, 1982). Nevertheless, some of the humus-inhabiting species have already returned. Possibly these exploit deeper soil layers with a lower humus content.

2. *Comparison of the analysis of mycorrhizal roots and mycorrhizal carpophores.*

Interestingly, the large number of mycorrhizal root tips in the fertilized plots does not coincide with a large number of sporocarps of mycorrhizal fungi. Apparently, the growth of roots and number of mycorrhizal root tips seem to be enhanced whereas the development of sporocarps seems to be hampered by application of N-fertilizer (cf. Tables 3 and 6). Probably, the strong development of mycorrhiza-types that do not produce above-ground sporocarps (*Cenococcum geophilum* and possibly others) after N-fertilization contributes to this feature. These results do not fully agree with other information on this subject. Alexander & Fairley (1983) found after N-fertilization of *Picea sitchensis* (Bong.)Carriere roots a lower production, mortality and mycorrhizal infection but an increased longevity of the fine roots. Termorshuizen (1990) found no effects on mycorrhizal roots of *Pinus sylvestris* L. after N-fertilization but a decreased fruitbody production. In view of the small scale of the experiment together with the large variation in the data it seems too early to draw definite conclusions.

3. *Comparison with other mycocoenological data.*

Comparing the present study with the data on oak forests in Drente by Jansen (1984), there is a striking similarity in the flora of mycorrhizal fungi between the *Dicrano-Quercetum* and the mown and unmown unfertilized plots along the canal. 1) In the roadside verge and in the Dicrano-Quercetum the proportion of the mycorrhizal species is relatively large (41% and 45% respectively); 2) the sites have many species in common e.g. *Amanita fulva, Boletus edulis, Cantharellus cibarius, Cordyceps species, Elaphomyces muricatus, Lactarius chrysorrheus, Leotia lubrica, Psathyrella dicrani*, etc.; 3) both sites have soil properties in common: Soils without developed horizons (*Dicrano-Quercetum*) or disturbed soils (the present study area) of acid, nutrient-poor sand with a very thin to absent humus and litter layer due to wind blowing (Keizer & Sullock Enzlin, 1988). The other oak forest communities differ much more with respect to species composition and relative shares of various functional groups.
There are several mycorrhizal species that seem to be characteristic for the roadside-habitat, e.g. *Cortinarius erythrinus, C. saniosus, Russula nigricans, R. atropurpurea, R. pectinatoides, R. graveolens, R. odorata*. A more extensive comparison between roadside verges and forest communities is made in chapter 5. Saprotrophic macromycetes in the plots of the present study show many similarities to the mycocoenoses described by Arnolds (1981) from grasslands belonging to the Lolio-Cynosuretum and, to a somewhat lesser degree, the Thero-Airion. Saprotrophs, which were reported by Jansen (1984) as characteristic or differential of oak forests form a minority, although some differential species of the Dicrano-Quercetum are also present in my plots, e.g. *Psathyrella dicrani*. Consequently, the studied areas combine mycocoenological characteristics of two contrasting habitats: oak scrub on poor sand and poor unfertilized grasslands.

4. *Aspects of nature conservation and management.*

During this study 83 mycorrhizal taxa, 104 taxa on humus, litter or bryophytes and 28 species

on other substrates have been found. This is a remarkably large number, considering the restricted size of the study-area and the limited time of investigation. A fairly large proportion of the taxa is considered rare and/or threatened and therefore placed on the red data list of macromycetes of the Netherlands (Arnolds, 1989b): 18 mycorrhizal species, 12 soil-inhabiting saprotrophs and 3 species on other substrates. This site obviously is a valuable habitat for many species. The same applies to other roadside verges on poor sandy soils, planted with trees (chapter 3, 5) or verges of old alleys in estates on river-clay where a grassy, mown, unfertilized vegetation is present (Reijnders, 1968). This type of roadside verges forms only a small minority (less than 1%) of all roadsides planted with trees. Many of the mycorrhizal fungi encountered in these habitats have become rare or extinct in forests of the same tree species (Arnolds, 1989b; pers. obs.). Examples are *Hydnellum concrescens*, *Phellodon confluens* and *Cantharellus cibarius*, species of which the decline in the Netherlands is particularly well documented (Arnolds, 1989a; Jansen & Van Dobben, 1987). Especially banks of canals, planted with trees form a favourable habitat for these fungi, presumably owing to the constantly sufficient soil humidity which is an important factor for carpophore formation. Agerer (1988) found an increased number of carpophores after extra irrigation in a Norway Spruce forest.

The species composition of the saprotrophic fungi has similarities with some types of seminatural grasslands, a strongly declined and threatened habitat (Arnolds, 1980, 1982, 1985, 1989b, c). Examples of rare or threatened species found in the study area are *Ramariopsis helveola*, *R. laeticolor*, *R. luteoalba*, *Geoglossum nigritum*, *Entoloma nitidum*, *E. solstitiale*, *Hygrocybe acutoconica*. Roadsides on poor soil with mown vegetation and removal of the hay can be very rich in rare species and form a vulnerable refuge for many endangered species. However, a large majority of the roadsides planted with trees in Drente contain a ruderalized vegetation with only few trivial fungi. This study shows that a proper management can lead to a rich mycoflora in roadside verges planted with trees.

The studied area has the potential to remain rich in fungal species. However, if the herb vegetation of the roadside verges is not or wrongly managed, it will change in such a way that the mycoflora will deteriorate. Without management dead grass-leaves accumulate and catch more leaves from the trees, the bryophyte layer will be suffocated and after some years the community may develop into a species poor stand with tall grasses and herbs and finally into scrub. This, together with the influence of air pollution (N-deposition) will lead to a loss in species diversity and productivity of both mycorrhizal fungi and saprophytes. If the soil is very poor, as is the case in the present study site, mowing without removal of the plants is probably sufficient to keep a fairly high mycological diversity, but in this study only 5 species are favoured by mowing without removal of the hay and no less than 13 species by removal of the hay. In most cases mowing with subsequent removal of the hay is necessary to compensate for air pollution effects and to conserve and possibly enhance the mycological diversity. Sod removal as a management practice is undesirable in poor environments because many saprotrophic fungi characteristic for old stable grassland will disappear and it will take a long time before they return. However, when the roadside environment has become strongly enriched or polluted, removal of the top soil followed by mowing with removal of the hay is recommended, provided the sources of the enrichment or pollution are eliminated.

The proposed optimal management of roadside verges with trees, mowing with removal of the hay, is also favourable from a view-point of species diversity in the herb layer (Zonderwijk, 1974; Melman *et al.*, 1990) and the maintenance of vulnerable phanerogams. It is also in agreement with demands of traffic safety. The possible influence on animals and the economic costs in relation to alternative practices fall outside the scope of this paper.

5. Reliability of the method.

The mycoflora in this roadside proved to be diverse and many of the species appeared to occur in low densities, i.e. in one or a few subplots. The consequence is that many species have low frequencies in the different treatments (tables 7 and 11). This makes it hazardous in many instances to draw conclusions on individual species. But, on the other hand, a great number of species were subjected to the five treatments. Under the assumption that many species react in a similar way to the treatments of this experiment, it is concluded that average species richness figures give the most useful results in this case.

For the analysis of the data the total numbers of the sporocarps per year were used, multiplied by the "specific weights" to assess the production of the species. In this case, where all plots had the same frequency of visits, it gives the best representation of the biological "importance" of the various species. For a further discussion on this subject see Barkman (1976, 1987), Arnolds (1981).

It must be realized that for two reasons the presented production values can only be considered as rough estimates. First, the determination of the "specific weight" may be influenced by 1) adhering soil particles (especially in small species) and 2) availability of small numbers of some rare species which enhances the risk of weighing deviating specimens. Secondly, the plots were visited monthly, which implies that an unknown proportion of the carpophores is missed. This is mainly relevant for saprotrophic fungi since they have small and ephemeral sporocarps, often only a few days to one week, e.g. in many species of *Galerina* and *Mycena*. In some cases over 3/4 of the production may have been missed. The proportion of missed sporocarps is smaller in the case of the mycorrhizal species, with their fleshy, longer lasting sporocarps. However, the interpretation of the results of this experiment is hardly influenced by these complications since all plots were investigated in the same way, but when comparing with other mycocoenological studies some precaution is necessary.

Table 2. Frequency (= numbers of plots per treatment; n=6) and average cover of some frequent plant species before and after five different treatments.

Treatment	E mowing without removal of the hay				B mowing with removal of the hay				C no treatment				D adding N-fertilizer				A removal of the top soil			
	1987		1989		1987		1989		1987		1989		1987		1989		1987		1989	
	freq	cov	freq	cov	freq	cov	freq	cov	freq	cov	freq	cov	freq	cov	freq	cov	freq	cov	freq	cov
total cover herbs %		66		70		82		77		79		82		78		103		78		46
total cover bryophytes %		25		27		18		31		18		30		16		.2		26		6
Species frequency or cover strongly changed after "no treatment":																				
increase:																				
Cytisus scoparius	4	<1	4	<1	5	<1	4	<1	6	<1	6	5	5	<1	3	<1	4	2	6	<1
Phragmites australis	4	<1	3	2	5	1	1	1	3	<1	3	4	3	<1	2	1	3	<1	4	2
decrease:																				
Calluna vulgaris	4	<1	5	<1	5	<1	6	1	5	<1	0	0	3	<1	1	<1	2	2	3	<1
Species frequency or cover strongly changed after application of N-fertilizer:																				
increase:																				
Agrostis capillaris	6	7	6	24	5	8	6	26	6	10	6	27	6	7	6	49	6	11	6	16
Lolium perenne	3	2	6	3	0	0	6	3	1	<1	6	3	1	1	6	11	0	0	6	2
Holcus mollis	3	<1	2	<1	4	1	2	<1	4	<1	0	0	3	<1	3	7	5	1	2	<1
Dactylis glomerata	1	<1	5	1	1	<1	6	<1	4	<1	6	1	4	1	6	3	5	1	3	<1
decrease:																				
Festuca rubra	6	30	6	23	6	26	6	27	6	33	6	23	6	33	6	19	6	30	6	6
Festuca ovina	6	30	6	6	6	27	6	5	6	19	4	5	6	21	4	<1	6	16	5	2
Hieracium pilosella	3	1	2	1	4	1	5	1	4	1	3	1	5	1	2	<1	4	1	4	<1
Hypochaeris radicata	6	<1	5	<1	6	<1	5	<1	6	<1	6	<1	6	<1	1	<1	5	<1	6	<1
Pseudoscleropodium purum	6	16	6	17	6	11	6	16	6	14	6	20	6	12	4	<1	5	8	1	<1
Rhytidiadelphus squarrosus	6	7	6	10	5	6	6	15	5	5	6	10	5	3	2	<1	5	13	2	<1
Species frequency or cover strongly changed after removal of the top soil:																				
increase:																				
Aira praecox	4	<1	3	<1	5	<1	2	<1	5	<1	3	<1	5	<1	3	<1	3	<1	6	10
Holcus lanatus	2	<1	3	1	3	<1	4	<1	2	<1	3	<1	3	<1	6	1	3	<1	5	3
Ceratodon purpureus	2	<1	1	<1	4	<1	0	0	4	<1	0	0	4	<1	0	0	2	<1	4	6
decrease:																				
Anthoxanthum odoratum	6	8	6	4	6	11	6	5	6	8	6	6	6	10	6	5	6	9	6	2
Plantago lanceolata	6	1	6	2	6	2	6	3	6	2	6	3	6	2	6	2	6	2	6	<1
Hieracium laevigatum	6	1	6	<1	6	1	5	<1	6	1	5	<1	6	<1	4	<1	5	2	1	<1
Leontodon autumnalis	4	<1	6	<1	4	<1	6	<1	3	<1	6	<1	6	<1	6	1	5	<1	3	<1
Cerastium fontanum	6	<1	4	<1	6	<1	5	<1	6	<1	5	<1	6	<1	5	<1	6	<1	2	<1
Other species:																				
Achillea millefolium	6	1	6	<1	6	1	6	1	6	1	6	1	6	1	6	<1	6	<1	6	<1
Anthriscus sylvestris	1	<1	2	<1	1	<1	0	0	0	0	0	0	0	0	0	0	1	<1	0	0
Brachythecium rutabulum	5	<1	1	<1	4	<1	0	0	3	<1	0	0	3	<1	0	0	3	<1	0	0
Danthonia procumbens	1	<1	1	<1	2	1	3	<1	0	0	0	0	1	<1	0	0	1	<1	0	0
Equisetum arvense	4	<1	3	<1	2	<1	3	<1	4	<1	2	<1	3	<1	3	<1	5	<1	2	<1
Euphrasia stricta	3	<1	3	<1	2	<1	1	<1	2	<1	2	<1	1	<1	0	0	1	<1	0	0
Succisa pratensis	1	<1	3	<1	4	<1	5	1	3	<1	3	<1	1	<1	0	0	3	1	0	0
Galium saxatile	2	<1	2	<1	1	<1	3	<1	2	<1	1	<1	2	<1	1	<1	2	<1	0	0
Luzula campestris	6	5	5	<1	6	7	4	<1	6	6	4	<1	6	6	3	<1	6	7	3	<1
Plantago major	2	<1	6	1	0	0	6	1	1	<1	6	<1	2	<1	6	2	0	0	6	1
Poa annua	3	<1	1	<1	2	<1	0	0	0	0	1	<1	2	<1	0	0	3	<1	2	<1
Poa pratensis	6	2	3	<1	6	2	3	<1	6	2	2	<1	6	2	1	<1	6	4	2	<1
Polytrichum formosum	4	<1	1	<1	3	<1	1	<1	2	<1	0	0	3	<1	0	0	1	<1	1	<1
Brachythecium albicans	2	<1	1	<1	5	<1	2	<1	4	<1	0	0	4	<1	0	0	6	1	1	<1
Rumex acetosa	6	<1	5	<1	6	<1	4	<1	6	<1	5	<1	6	<1	6	<1	6	<1	3	<1
Rumex acetosella	6	<1	4	<1	6	<1	5	<1	4	<1	3	<1	5	<1	4	<1	5	1	6	<1
Taraxacum officinale	6	<1	5	<1	6	<1	5	<1	6	<1	3	<1	6	1	6	<1	6	1	6	<1
Trifolium dubium	4	<1	1	<1	3	<1	0	0	4	<1	2	<1	3	<1	0	0	2	<1	2	<1
Trifolium pratense	4	1	5	<1	5	1	4	<1	5	2	4	1	5	1	2	<1	2	<1	2	<1
Trifolium repens	4	<1	1	<1	2	<1	0	0	3	<1	0	0	4	<1	0	0	6	<1	1	<1
Viola canina	1	<1	0	0	1	<1	0	0	2	<1	1	<1	0	0	0	0	1	<1	0	0

Table 7.

Frequency (F, n=6) and number of carpophores (N) of mycorrhizal fungi in 1987 and 1989 under five treatments; duration of the treatments was three years.

Values are the total numbers of carpophores of the six 225 m2 subplots per treatment, adjusted to 1000 m2.

Treatment:	E mowing without removal of the hay				B mowing with removal of the hay				C no treatment				D adding N-fertilizer				A removal of the top soil			
Year:	87		89		87		89		87		89		87		89		87		89	
	F	N	F	N	F	N	F	N	F	N	F	N	F	N	F	N	F	N	F	N
Species increased after mowing with removal of the hay																				
Hebeloma helodes	3	4	2	36	1	1	5	76	1	1	3	10	0	0	0	0	0	0	1	12
Lactarius theiogalus	0	0	1	8	0	0	3	39	1	13	2	20	1	1	3	13	0	0	0	0
Species increased after mowing with or without removal of the hay																				
Lactarius quietus	4	24	5	36	4	46	6	44	3	3	5	8	3	6	3	18	0	0	4	5
Russula amoenolens	4	11	6	22	4	13	5	33	4	14	3	12	1	15	3	16	1	15	3	14
Species decreased after adding N-fertilizer																				
Russula velenovskyi	3	10	3	12	1	1	1	4	0	0	0	0	2	5	0	0	1	1	2	8
Species decreased after adding N-fertilizer and after sod removal																				
Russula pectinatoides	3	27	4	68	3	4	2	4	2	7	4	21	3	10	1	1	1	3	1	1
Lactarius chrysorrheus	3	45	2	16	3	37	3	29	2	3	3	26	1	3	0	0	0	0	0	0
Russula fragilis	6	19	5	46	5	11	6	49	4	8	6	19	3	4	2	4	3	4	3	4
Species decreased after adding N-fertilizer and increased after removal of the top soil																				
Clitopilus prunulus	0	0	4	4	0	0	3	5	1	1	2	3	0	0	0	0	0	0	5	32
Cortinarius erythrinus	3	34	3	33	2	1	3	7	2	1	3	9	3	10	0	0	3	2	5	127
Cortinarius violilamellatus	5	162	2	15	4	49	3	19	3	30	4	29	2	15	1	4	1	1	2	53
Cortinarius saniosus	4	41	1	2	0	0	1	1	2	5	2	13	2	2	0	0	0	0	3	60
Species decreased after adding N-fertilizer																				
Russula nigricans	6	116	6	33	6	92	6	47	5	144	4	62	6	138	4	10	6	79	6	54
Russula cyanoxantha	2	3	3	7	3	3	5	13	4	7	5	10	1	2	0	0	6	13	3	3
Cantharellus cibarius	4	203	3	10	4	195	4	102	4	119	2	7	2	61	0	0	1	1	3	10
Amanita rubescens	3	5	2	2	5	13	5	7	3	12	2	2	4	10	0	0	5	12	3	5
Laccaria laccata	4	7	1	15	2	4	4	9	2	5	2	4	2	3	1	1	2	14	5	22
Hebeloma mesophaeum	3	15	4	6	6	27	3	14	3	53	3	22	2	14	1	1	1	1	2	13
Other species:																				
Boletus edulis	3	4	3	11	2	4	1	2	1	4	1	2	1	5	2	1	0	0	5	9
Russula atropurpurea	3	10	2	5	0	0	2	7	2	5	2	12	0	0	0	0	5	16	3	16
Russula graveolens f. grav.	1	13	2	11	0	0	0	0	0	0	1	4	0	0	0	0	2	3	3	20
Clavulina coralloides	0	0	0	0	1	4	1	53	2	2	1	20	1	1	0	0	0	0	1	7
Lactarius serifluus	2	4	3	31	2	2	0	0	0	0	0	0	2	3	2	8	1	4	2	46
Xerocomus badius	0	0	4	4	0	0	2	2	1	1	2	1	4	4	1	3	1	1	1	1
Russula parazurea	2	2	4	4	0	0	1	1	5	7	4	4	2	1	5	6	2	6	2	3
Scleroderma citrinum	4	17	2	1	3	5	1	1	1	2	2	4	3	4	1	1	1	1	1	1
Russula odorata	5	7	4	14	2	6	5	9	1	1	1	11	2	4	3	5	0	0	2	4
Amanita citrina	2	3	0	0	0	0	2	3	1	2	1	3	1	1	1	1	1	1	1	1
Russula vesca	1	4	1	2	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1
Cortinarius helvolus	0	0	1	19	0	0	1	8	0	0	0	0	0	0	1	7	0	0	0	0
Paxillus involutus	0	0	1	1	0	0	2	4	0	0	1	1	1	1	1	1	1	2	2	1
Scleroderma areolatum	1	3	2	4	0	0	0	0	1	1	1	1	0	0	1	1	0	0	0	0
Inocybe albomarginata	1	10	0	0	1	1	2	9	0	0	4	8	2	10	0	0	2	7	2	9
Laccaria proxima	1	4	1	6	2	5	1	1	0	0	0	0	2	19	4	5	1	4	3	13
Hebeloma anthracophilum	1	1	1	20	0	0	0	0	0	0	1	1	0	0	1	1	0	0	1	4
Russula chloroides	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	3
Russula ochroleuca	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	1	1	1	1
Cortinarius rigidus	0	0	0	0	0	0	1	4	0	0	1	12	0	0	0	0	0	0	0	0
Inocybe dulcamara	0	0	0	0	0	0	1	2	1	50	1	7	1	3	0	0	2	5	1	2
Cortinarius lanatus	0	0	0	0	1	18	1	1	0	0	1	9	0	0	0	0	0	0	0	0
Cortinarius velenovskyi	0	0	0	0	0	0	1	1	0	0	0	0	1	2	0	0	2	5	1	2
Cortinarius striaepilus	0	0	1	1	2	4	1	23	0	0	0	0	0	0	0	0	0	0	0	0
Inocybe sindonia	0	0	0	0	0	0	0	0	1	4	1	1	0	0	0	0	0	0	1	3
Inocybe geophylla	1	1	1	1	1	7	0	0	1	15	0	0	0	0	0	0	0	0	1	4
Cortinarius rigens	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	2	5	0	0
Clavulina rugosa	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Cortinarius elatior	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Cortinarius paleaceus	0	0	0	0	1	13	0	0	1	7	0	0	0	0	0	0	0	0	1	3
Cortinarius flexipes	2	10	0	0	1	1	2	1	1	6	1	1	1	2	0	0	1	1	1	2
Inocybe grammata	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	6	1	1
Laccaria bicolor	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Cortinarius parvannulatus	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Cortinarius hinnuleus	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Alnicola bohemica	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	2	3
Inocybe fuscidula	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Inocybe xanthomelas	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0

(table 7 continued)
Species found in plot(s) of only one treatment. For each species are given the year,the treatment and the numbers o
carpophores, adjusted to 1000 m2. Inocybe umbrina (87) A:14 - Otidea bufonia (87) A:2 - Thelephora terrestris A:1 -Laccari
tortilis (89) A:13 - Inocybe umbrina (89) A:184 - Cortinarius fusisporus (89) A:1 - Cortinarius obtusus (87) B:9 - Russul
delica (87 and 89) B:1 and 7 - Russula albonigra (89) B:8 - Amanita spissa (87) C:1 - Tricholoma ustaloides (87) C:1
Amanita pantherina (89) C:1 -Boletus erythropus (87) D:1 - Xerocomus chrysenteron (89)D:36 - Elaphomyces muricatus (89)
D:1 - Inocybe rimosa (87) E:1 - Amanita fulva (89) E:1 - Hydnellum concrescens (87) E:10 -Inocybe phaeocomis (87) E:1
Laccaria amethystea (87 and 89) E: 13 and 2 - Leotia lubrica (87) E:1 - Phellodon confluens (87 and 89) E:6 and 15 - Inocyb
lacera (89) E: 1 - Inocybe hirtella (89) E:8 - Lactarius camphoratus (89) E:1

Table 11. Frequency (F, n=6) and number of carpophores (N) of saprotrophic fungi in 1987 and 1989 under five treatments; duration of the treatments was three years. Values are the total numbers of carpophores of the six 225 m2 subplots per treatment, adjusted to 1000 m2.

Treatment:	E mowing without removal of the sward				B mowing with removal of the sward				C no treatment				D adding N-fertilizer				A removal of the top soil			
	87		89		87		89		87		89		87		89		87		89	
	F	N	F	N	F	N	F	N	F	N	F	N	F	N	F	N	F	N	F	N
Species decreased after application of N-fertilizer																				
Hygrocybe conica	1	7	1	4	2	1	4	7	3	12	2	25	0	0	0	0	0	0	1	4
Ramariopsis helveola	0	0	3	15	0	0	1	10	0	0	1	1	0	0	0	0	0	0	1	7
Species decreased after application of N-fertilizer and removal of the top soil																				
Camarophyllus niveus	2	27	2	25	4	45	4	88	3	36	6	29	1	22	0	0	0	0	1	2
Mycena leptocephala	5	29	6	263	4	24	5	197	2	1	5	89	4	16	5	24	0	0	4	8
Entoloma sericeum v. sericeum	4	21	2	19	4	11	4	4	2	11	1	7	3	2	1	1	0	0	1	2
Rickenella fibula	6	63	5	170	5	41	6	279	4	71	6	165	3	10	1	2	0	0	0	0
Mycena metata	4	25	5	19	4	39	6	64	2	5	4	31	4	14	2	4	0	0	0	0
Ramariopsis luteoalba	2	44	1	1	2	53	2	4	3	13	1	4	0	0	0	0	0	0	1	1
Mycena sepia	1	1	5	19	0	0	4	30	0	0	3	7	0	0	0	0	0	0	0	0
Mycena pelliculosa	2	7	2	4	2	12	1	1	1	2	1	9	0	0	0	0	0	0	0	0
Ramariopsis laeticolor	2	5	1	1	0	0	1	22	1	18	1	3	0	0	0	0	0	0	0	0
Rickenella setipes	1	1	1	2	1	1	3	4	0	0	2	7	0	0	0	0	0	0	0	0
Species increased after removal of the top soil																				
Mycena galopus v. nigra	1	3	4	13	0	0	5	11	1	1	5	13	0	0	4	7	2	4	6	47
Species decreased after removal of the top soil																				
Marasmius oreades	4	59	2	36	3	87	2	140	3	123	3	7	2	71	2	30	1	4	0	0
Calvatia excipuliformis	2	53	3	8	3	6	3	10	3	64	3	17	3	67	4	9	2	2	1	1
Tubaria furfuracea	5	146	4	51	6	41	5	22	4	8	2	13	5	421	5	56	1	1	0	0
Collybia dryophila	6	34	6	213	4	13	6	84	4	16	5	73	4	61	5	45	0	0	3	3
Melanoleuca polioleuca	2	4	2	2	2	4	4	6	1	1	2	3	4	4	3	3	0	0	0	0
Mycena avenacea v. avenacea	2	1	5	29	3	20	6	96	1	1	4	30	2	3	5	8	0	0	1	1
Mycena filopes	3	4	5	47	2	3	6	30	2	1	4	28	2	2	6	30	0	0	3	10
Mycena epipterygia	1	1	1	16	0	0	2	15	0	0	3	10	2	18	1	15	0	0	0	0
Mycena stylobates	0	0	1	2	0	0	3	11	0	0	3	5	0	0	3	19	0	0	0	0
Galerina atkinsoniana	5	14	3	11	1	2	1	8	0	0	3	10	1	12	3	4	0	0	0	0
Mycena sanguinolenta	4	13	4	15	2	2	5	46	0	0	4	10	0	0	3	13	0	0	1	2
Other species																				
Lepista nuda	0	0	0	0	0	0	1	9	1	13	1	2	0	0	1	7	0	0	0	0
Entoloma conferendum	4	68	0	0	6	69	0	0	5	38	0	0	3	6	0	0	0	0	0	0
Psathyrella fulvescens v. brevicystis	3	69	3	19	1	4	2	82	0	0	1	5	2	8	1	4	0	0	1	2
Agaricus campestris	1	1	1	4	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Clitocybe metachroa	0	0	1	5	0	0	1	2	0	0	0	0	0	0	1	30	0	0	0	0
Clitocybe marginella	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	27	0	0	1	4
Mycena aetites*			1	9			3	70			3	77			3	34			2	6
Entoloma papillatum	4	55	1	1	3	57	3	16	4	65	3	16	3	18	1	1	1	1	1	3
Coprinus subimpatiens	0	0	1	3	0	0	1	2	0	0	1	3	0	0	0	0	0	0	0	0
Panaeolus fimicola	1	2	1	1	0	0	0	0	1	1	0	0	0	0	1	1	0	0	1	4
Psathyrella dicrani	0	0	2	4	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Entoloma sericeum v. nolanif.	0	0	1	1	0	0	2	2	0	0	0	0	0	0	0	0	0	0	1	1
Mycena galopus v. galopus	3	6	0	0	1	5	2	1	2	8	1	11	3	2	0	0	0	0	0	0
Mycena avenacea v. roseofusca	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Mycena cinerella	3	3	1	1	2	4	0	0	1	1	0	0	1	1	0	0	0	0	0	0
Mycena flavoalba	1	1	1	2	2	4	0	0	0	0	0	0	1	6	2	10	0	0	0	0
Geoglossum nigritum	1	4	0	0	0	0	1	6	0	0	0	0	1	31	0	0	0	0	0	0
Helvella lacunosa	1	1	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Helvella villosa	0	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Panaeolina foenisecii	1	1	0	0	1	1	0	0	2	1	0	0	0	0	1	1	0	0	0	0
Psathyrella frustulenta	2	7	0	0	0	0	1	2	0	0	0	0	2	4	0	0	0	0	0	0
Panaeolus sphinctrinus	1	1	0	0	1	2	0	0	0	0	0	0	1	2	0	0	0	0	0	0
Lycoperdon perlatum	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Mycena flavescens	1	1	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Clitocybe rivulosa	0	0	0	0	2	1	0	0	1	1	0	0	1	3	0	0	0	0	0	0
Conocybe siennophylla	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0
Clavaria acuta	1	4	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calvatia utriformis	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0	0
Entoloma sericellum	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1
Psilocybe inquilina	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1

* species not recognized in 1987.

(table 11 continued)
Species found in plot(s) of only one treatment. For each species are given the year, the treatment and the numbers o
carpophores adjusted to 1000 m2.
Bovista plumbea (87 and 89) A:1 and 1 - Lepista sordida (89) A: 4 - Agaricus sylvaticus (87) B:1 - Melanoleuca excis
var. iris (87) B:1 - Mycena polyadelpha (87) B:4 Psathyrella frustulenta (89) B:2 - Crepidotus variabilis (89) B:6 - Cyathu
olla (89) B:1 - Conocybe rickeniana (89) B:3 - Psilocybe montana (89) B:1 Clitocybe marginella (87) C: 1 - Nidularia farct
(87) C:1 - Psathyrella spadiceogrisea (89) C:1 - Stropharia aeruginosa (89) C:7 - Hygrocybe miniata v. mollis (89) C:1
Tephrocybe tesquorum (89) C:1 - Clitocybe odora (89) D:3 - Bovista nigrescens (87) C:1 - Pholiota carbonaria (87) C:6
Psathyrella artemisiae (87) D:1 - Clitocybe clavipes (89) D:2 - Calocybe carnea (89) D:12 - Clitocybe diatreta (89) D:6
Entoloma turbidum (89) D:1 - Entoloma lividoalbum (87 and 89) E:1 and 1 - Galerina stylifera (87) E:1 - Galerina unicolo
(87) E:1 - Psatyrella gracilis (87) E:1 - Vascellum pratense (89) E:1 - Clitocybe agrestis (89) E:2 - Hygrophoropsis auran
tiaca (89) E:1 - Hygrocybe miniata v. miniata (89) E:1 - Psilocybe semilanceata (89)E:1 - Tephrocybe ambusta (89) E:1
Mycena cinerella (89) E:1 - Marasmius androsaceus (89) E:1 - Galerina hypnorum (89) E:1 - Mycena acicula (89) E:1

Table 13. List of excluded species.

Wood-inhabiting species: Armillaria bulbosa, A. ostoyae, Coprinus micaceus, C. radians, Grifola frondosa, Hypholom
fasciculare, H. radicosum, H. sublateritium, Mycena cortiana, M. galericulata, M. polygramma, M. speirea, M. vitilis, Panellu
stipticus, Pholiota squarrosa, Pluteus atricapillus, Polyporus brumalis, P. ciliatus, Psathyrella artemisiae, P. piluliformis
Resupinatus applicatus.

Parasites on fungi: Collybia cirrhata, Collybia cookei, Collybia tuberosa, Cordyceps ophioglossoides.

Parasite on insects: Cordyceps militaris.

Saprophyte on dung: Stropharia semiglobata.

Saprophyte on feathers: Onygena corvina.

Saprophyte on burnt ground: Tephrocybe anthracophila.

TAXONOMICAL NOTES ON MACROFUNGI IN ROADSIDE VERGES PLANTED WITH TREES IN DRENTE (THE NETHERLANDS)

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Abstract.
In this study, descriptions, drawings and observations are presented of rare, critical or less well-known macromycetes that were encountered during mycocoenological investigations carried-out in roadside verges planted with *Quercus robur* L. (53 plots) and Fagus sylvatica L. (23 plots). Special attention is paid to the genera Cortinarius S.F. Gray emend. Fr., Hebeloma (Fr.) Kumm. and Russula Pers.. *Psathyrella rhombispora* Keizer & Arnolds is presented as a new species. *Russula cicatricata* Romagn., *Russula elaeodes* (Bres.)Romagn. and *Russula purpurata* Crawsh. are reduced to formae of *Russula graveolens* Romell in Britz..

Introduction.

During the years 1986, 1987 and 1988, mycocoenological research has been carried out in 80 plots, situated in roadside verges planted with *Quercus robur* L. (53 plots), *Fagus sylvatica* L. (23 plots), *Aesculus hippocastanum* L. (2 plots) and *Acer pseudoplatanus* and *A. platanoides*. (1 plot each). The plots with *Aesculus* and *Acer* were not included in further mycocoenological research. The plots varied with respect to exposition, age of trees, vegetation type and vegetation management. Most of the plots were situated in the province of Drente, and a few in an adjacent region in the province of Friesland, all in the phytogeographical Drentian District (Weeda, 1983), in the northern part of the Netherlands. The area of research lies 10-20 m above sea-level and consists of weakly undulating glacial cover sands. A layer of boulder clay is often present at variable depths. However, in the roadside verge verges the soil horizons are always mixed up to a depth of 0.5-1 m, owing to the road construction and maintenance works.

The herb layer in the plots belongs to different grassland communities. Productivity and species composition vary with the exposition and nutrient availability from poor grassland with a relatively high moss cover (Thero-Airion, Westhoff & Den Held, 1969) to highly productive, dense, grass-dominated communities (Lolio-Potentillion). The vegetation is rather sparse to almost absent in some dark, shady plots along roads in woods. The management of the vegetation in roadside verge verges outside forests consists mostly of mowing without removal of the hay two (or more) times a year, sometimes of mowing with subsequent removal of the hay. Shaded roadside verges (in woods) are only incidentally managed. In addition the top soil and vegetation are removed in many places with intervals of ca. 5-10 years for reasons of traffic safety and road surface maintenance (to prevent water stagnating on and along the road).

A description of the plant communities, soil parameters and the results of the mycocoenological research will be published elsewhere.

The fungi dealt with in this study comprise the macrofungi. Groups with relatively small or hidden fruitbodies (e.g. the majority of the Helotiales, resupinate Aphyllophorales) have been omitted because a complete inventory would require a much more time consuming search strategy. The following groups were included: Basidiomycetes: Agaricales; Gasteromycetes; Non-resupinate Aphyllophorales and

Heterobasidiomycetes. Ascomycetes: Clavicipitales: *Cordyceps*; Elaphomycetales: *Elaphomyces*; Helotiales: *Geoglossum*, *Leotia*; Pezizales: *Helvellaceae*, *Pezizaceae*, *Tuberaceae*; Deuteromycetes: *Paecilomyces*.

The nomenclature of the Basidiomycetes is mainly after Kreisel (1987) or Arnolds (1984) if species are not mentioned in the former work. The nomenclature of the smooth spored species of the genus *Inocybe* is after Kuyper (1986) and of the genus *Psathyrella* after Kits van Waveren (1985). Ascomycetes are after Cannon et al. (1985) and Deuteromycetes after Arnolds (l.c.). Synonyms are only mentioned if names listed here deviate from the name in common use by Dutch authors.

Full understanding of mycocoenological studies is often hampered by the absence or incompleteness of descriptions of critical taxa. Therefore, descriptions and/or critical notes are given in this paper of rare and critical taxa and of collections, which disagreed with descriptions in literature. This criterion has been taken in a rather broad sense. The reason for this is firstly to provide a reference for some names used in the mycocoenological work and secondly to present the rate of disagreement with the current literature of some taxa that were accepted.

In the descriptions abbreviations of colour-codes have been used with the following meaning: "Expo" for Cailleux and Taylor (1958), "K.& W." for Kornerup & Wanscher (1978) and "Mu" for Munsell Color Company (1954).
In the microscopic descriptions Q indicates the length/width ratio of the spores and Q indicates the average of Q based on usually 10 spores of a collection.
In the figures the habit sketches are in natural size; in the microscopic drawings the bar always represents 10 μm.

All collections mentioned below are made in the selected plots and deposited in the herbarium of the Biological Station in Wijster (Wag.-W.), part of the Agricultural University Wageningen. For each collection the plot number is given, where it originates. This refers to appendix 1, where the exact place and some brief ecological notes of the plots are listed.

Species that are presented with the prefix "cf." were not included in the mycocoenological analyses.

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I. AGARICALES

Agaricus silvaticus Schaeff., incl. *A. haemorrhoidarius* Kalchbr. & Schulz.
Pileus 21-41 (-80) mm, surface of cap reddish brown squamulose with slightly darker red-brown squamules; flesh reddening when cut, rate difficult to assess, owing to rather old material.
Coll.: 87317, 88200.
Obs.: The rather small size of the pileus is characteristic of *A. silvaticus* but the dark-squamulose surface of *H. haemorrhoidarius*.
A. silvaticus is mentioned by most authors (Moser, 1978; Møller, 1949; Capelli, 1984) from coniferous woods and *A. haemorrhoidarius* from deciduous woods, but according to Pilát (1951) the former species grows in both coniferous and deciduous woods, and the latter in coniferous woods only. It turned out impossible to identify the two collections satisfactorily as one of both species.
Collections examined. - Plot Q14, 8 Nov. 1987, Keizer, 87317; Plot Q11, 28 Oct. 1988, Keizer 88200.

Clitocybe albofragrans (Harm.) Kuyp.
Pileus 25 mm, expanded, with centre depressed and margin involute, not hygrophanous, white, slightly pruinose; surface somewhat cracked with pale brownish cracks, margin not striate. Lamellae crowded, narrow, ± 2.5 mm broad, very shortly decurrent, light pinkish, with edge slightly crenulate, concolorous. Stipe 32 x 2 mm, cylindrical, pale beige with white fibrillum, therefore white-silky shining. Flesh in pileus and stipe pale brown, white on drying. Smell strong, anise-like.
Spores 4.6-5.5(-6.1)x2.8-3.2(-3.7) μm, ellipsoid, thin-walled, smooth, in exsiccata often in tetrads.
Collections examined. - Plot Q51, 31 Aug. 1987, Keizer 87063; Plot Q31, 17 Oct. 1988, Keizer 88115.
Obs.: This species is little-known, and apparently often overlooked. It is well-characterized by the combination of a white, non-hygrophanous pileus and anise-like smell. It differs from pale forms of *C. odora* in smaller basidiocarps and smaller spores. According to Kuyper (1981) it is not uncommon in the Netherlands.

Clitocybe marginella Harm.
Pileus 27-34 mm, expanded with somewhat depressed centre, when moist at centre orange-brown (K.& W. 5C5 but more greyish), towards the margin orange-beige (5C4), at extreme margin even paler; centre contrastingly darker than the remaining parts of the pileus; margin translucently striate up to 1/3 of the radius, on drying very pale beige. Lamellae crowded, shortly decurrent, pale pinkish-beige-whitish. Stipe up to 25x3.5 mm, cylindrical, somewhat flexuose, concolorous with centre of pileus, glabrous. Smell sweetish anise-like.
Spores 4.6-5.5x(2.8-)2.9-3.7 μm, shortly ellipsoid.
Collection examined. - Plot Q3, 21 Dec. 1988, Keizer 88342.
Obs.: This species is related to both *C. agrestis* and *C. diatreta*. According to Kuyper (1982) the former has a more uniformly coloured pale pileus and the latter differs in a darker orange-brown cap, which is not translucently striate, and in pink lamellae.

Conocybe cf. mairei Watl. (Fig. 1)
Pileus 12 mm, expanded with broad umbo, hygrophanous when moist, rather pale greyish ochre-brown or greyish beige, translucently striate. Lamellae rather pale brown, ("caramel coloured") with white floccose edge, rather crowded. Stipe 35x12 mm, cylindrical, base slightly broader, colour at apex white-hyaline, towards the base brownish-beige or pale ochraceous, covered with white fibrillum, at base white- tomentose; entire stipe finely pruinose. Smell and taste unknown. Spores 7.4-8.3x(4.4-)4.6-5.1 μm, Q=1.5-1.8, Q=1.65, ellipsoid, slightly thick-walled (walls ± 0.3 μm thick), with small but distinct germ-pore, ochraceous yellow-brown in NH_4OH 10%. Cheilocystidia irregularly lageniform, 30-40x7-11 μm, hyaline, thin-walled. Pleurocystidia absent.
Collection examined. - Plot F43, 6 Oct. 1988, Keizer 88221.
Obs.: *Conocybe mairei* was originally described by Kühner (1935:131) with smaller spores (6.7-)7.2(-8.2)x3.7-4.7 μm) and cheilocystidia (17-28x4.2-7 μm). Similar dimensions were given by Watling (1982:87): spores 6-7(-7.5)x3-4 μm and cheilocystidia 15-30x4-7 μm, with a relatively longer neck. The collection studied consists of only one carpophore in rather bad condition, therefore no further conclusions on its taxonomic status are drawn for the time being.

Conocybe pygmaeoaffinis (Fr.) Kühner (Fig. 2)
Pileus 20 mm, plano-convex with rather prominent umbo, hygrophanous, when moist rusty brown (Expo between F52 and F54), translucently striate up to ½ of the radius, on drying ochraceous yellow-brown (D68). Lamellae rather crowded, ± 3 mm broad, concolorous with cap (F54) or slightly paler, edge white-flocculose. Stipe 43x1.3 mm, cylindrical, at base somewhat swollen, ochraceous yellow-brown, covered with yellowish brown, shiny fibrillum, near apex powdered-flocculose (caulocystidia), darkening on handling. Context in pileus and stipe concolorous with pileus, in base of stipe dark red-brown (J42). Smell and taste not recorded.
Spores 8.5-9.1x4.6-5.2 μm, Q=1.7-1.9, Q=1.80, narrowly ellipsoid, ochraceous yellow-brown in NH_4OH, with distinct germ-pore. Cheilocystidia 30-40x7-9 μm, narrowly lageniform or narrowly fusiform.
Collection examined. - Plot Q81, 19 Sept. 1988, Keizer 88315.
Obs.: This collection differs from the description by Watling (1982) of *C. pygmaeoaffinis* by the more slender habit, the slightly narrower spores (Watling: 8.5-10x5-5.5 μm), and the narrowly fusiform cheilocystidia, not gradually tapering from a broad base. Spore size and shape of cheilocystidia are in better agreement with Maire's descriptions (in Kühner, 1935:135, 8-9x4.5-5.5 μm). *C. striaepes* (Cooke) Lundell differs in smaller spores (7-8x4-4.5 μm) and lanceolate cheilocystida.

Coprinus sclerocystidiosus M. Lange & A.H.Smith (fig. 3)
Pileus 20 mm, expanded, red-brown, covered with short hairs (setae), especially near the margin, partly withered. Lamellae black, for the greater part withered. Stipe 40x15 mm, cylindrical, somewhat swollen near the base, pale yellowish-hyaline, covered with small hairs, base somewhat tomentose.
Spores 12.5-15.0x7.3-8.5 μm, Q=1.6-1.9, Q=1.77, ellipsoid, with excentric germ-pore, dark brown in NH_4OH. Pileocystidia narrowly lageniform, thick-walled, 65-88x7.5-10.0 μm.
Collection examined: Plot F32, 18 Sept. 1988, Keizer 88063.
Obs.: This collection was kindly identified by Mr. C.B. Uljé. It is a rare species in the

Netherlands.

Coprinus subimpatiens M. Lange & A.H. Smith (fig. 4)
Pileus when young 3-4x6 mm, ovoid, soon expanding, 10-20 mm broad, broadly campanulate, with margin occasionally splitting radially, often soon desintegrating (within half a day after collecting), greyish brown (Expo C63), in centre chestnut-brown or ochrish brown (H42, H43, F43), covered with small setae. Lamellae narrow, ± 1.5 mm broad, at first pale grey-brown, then dark grey-brown, with edge white-flocculose, soon brownish black and desintegrating. Stipe 25-50x1.5-3 mm, cylindrical or slightly broader towards the base, white-hyaline or pale cream coloured, in one collection (Keizer 87234) pink (B32) at apex and greyish pink near base (C10), pruinose. Smell and taste unknown.
Spores (9.0-)9.5-15.0x(5.9-)6.0-7.5(-7.7) µm, Q=1.4-1.9 and $\bar{Q}$=1.53-1.71, not or hardly lentiform, smooth, with excentric germ-pore, dark purplish under the microscope.
Cheilocystidia of two types: vesiculose or ovoid, ± 35-65x25 µm, and lageniform, ± 30-40x10 µm. Pleurocystidia vesiculose, ± 40-50x30-35 µm.
Collections examined. - Plot F21, 30 Oct. 1986, Keizer 86187; Plot F32, 1 Sept. 1987, Keizer 87038; Plot Q22, 13 Oct. 1987, Keizer 87234; Anloo, Anderen, 29 July 1988, Keizer 88045; Plot F22, 17 Sept. 1988, Keizer 88154; Plot F43, 6 Oct. 1988, Keizer 88231; Plot F22, 16 Nov. 1988, Keizer 88319.
Obs.: The material is heterogeneous with respect to spore size: Coll. 87234 has small, slightly lentiform spores, 8.6-10.8x5.8-8.0 µm, Q=1.4-1.5 in front- and Q=1.6-1.7 in side-view. The remaining collections are more homogeneous with respect to spore size: 11-13x6.5-7.7 µm. Cheilo- and pleurocystidia could exclusively be studied in immature carpophores, which were only present in Coll. 87234. Because the characters of the pleuro- and cheilocystidia could not be studied in other collections, the spore size had to be used to identify the species of the *C. hiascens* group. All species except *C. subimpatiens* have narrower spores (Orton & Watling,1979; Uljé, 1989). Coll. 87234 is deviating by the pink colour in the stipe and in having smaller spores than the remaining collections. Yet, it is assigned to *C. subimpatiens* , which is confirmed by Mr. B.C. Uljé).

Coprinus xantholepis P.D. Orton.
Pileus when young ovoid, ca. 3x4 mm, white to cream-coloured, translucently striate, covered with a thick veil consisting of orange-brown scales, giving the pileus an orange-brown spotted appearance. Lamellae when young white, with age purplish-black and deliquescent. Stipe white, in maturity ± 25x1 mm, at base somewhat enlarged and with a zone of veil remnants. Smell and taste unknown.
Spores 6.0-6.8(-7.2)x4.5-5.5x5.3-6.0 µm, lentiform, in front view broadly ellipsoid to subglobose (Q=1.0-1.3, $\bar{Q}$=1.16), in side view ellipsoid (Q=1.2-1.4, $\bar{Q}$=1.30), with central germ-pore. Hyphae of veil irregularly diverticulate, ± 3-5 µm thick, with walls of 1 µm thick, under microscope ochre-brown.
Collection examined. - Plot Q54, 1 Sept. 1987, Keizer 87062.
Obs.: This collection is in good agreement with the original description of *C. xantholepis* by Orton (1972:150) except for the slightly larger spores in front-view. It was not recorded before from the Netherlands (Arnolds, 1984).

Cortinarius Fr.
In the Netherlands few taxonomical studies are carried out concerning this genus and

modern descriptions are scanty. Moreover, most of the species are critical in some respect. Therefore we have included descriptions of most species observed in this genus.

Cortinarius anomalus (Fr.:Fr.) Fr.
Pileus 32-42 mm, expanded, with broad, indistinct umbo, hygrophanous, when moist centre pale red-brown (Expo D56), on drying towards the margin brownish grey (D52), surface covered with white, shiny fibrils (silky). Lamellae up to 6 mm broad, moderately crowded, emarginately adnate, ventricose, pale brown ("caramel-coloured") with violaceous tinge, with concolorous margin. Stipe 40-50x6-8 mm, cylindrical, but at the base thickened, up to 13 mm, hollow, beige, at apex greyish, covered with white fibrillum, with rather inconspicuous, pale yellow velar zones in lower part of stipe and remains of cortina, brown by adhering spores. Context in pileus white with a grey zone near the lamellae; in stipe beige. Smell absent or faintly fungoid.
Spores 7.2-8.0x6.0-6.7 μm, broad ellipsoid to subglobose, Q=1.2, coarsely verrucose with small roundish or irregular warts.
Collection examined. - Plot F44, 10 oct. 1988, Keizer 88066.
Obs.: In old state this species resembles *C. valgus* which lacks any violet coloration and differs in spore form.

Cortinarius balteatoalbus R. Henry (Fig. 5).
Pileus 50-85 mm, expanded, with centre somewhat depressed or umbonate, tobacco-brown (Expo D54, E54) or somewhat paler, at margin concolorous, surface with innate, darker fibrils, in young stage viscid, later dry but with adhering leaves etc. Lamellae up to 8 mm broad, crowded, emarginately adnate, not ventricose, when young rather pale brown, later cinnamon-brown, with paler margin and sometimes serrulate, at the margin sometimes with clumps of spores like in some *Hebeloma* species. Stipe 40-65x7-13 mm, cylindrical with slightly swollen base, usually solid, pale brownish or beige, covered with pale fibrillum and appressed brown fibrils in lower 2/3 part, with some thin velar remains and near the base with one more conspicuous belt of veil. Smell weak, fruity or sweetish. Context in pileus and stipe whitish with faint brownish or pinkish hue. Chemical spot tests of pileus: KOH 5% pale brown with yellow margin; NH_4OH 10% bright yellow; in context of stipe KOH and NH_4OH both yellow.
Spores (9.0-)10.0-12.0(-12.4)x(5.3-)6.0-6.5(-6.8) μm, ellipsoid or subamygdaliform, Q=1.5-2.2, $\underline{Q}$=1.80, ornamented with fine roundish, oval or irregular warts, the area just above the hilar appendix mostly smooth. No cheilocystidia observed.
Collections examined. - Plot Q2, 15 Sept. 1987, Keizer 87138; 13 Oct. 1988, Keizer 88127.
Obs.: The size of the spores and the absence of cheilocystidia point towards *C. balteatoalbus*. My collection differs from the original description by Henry (1958) in slightly smaller basidiocarps and less involute margin of the pileus.

Cortinarius casimiri (Velen.) Huijsman (Fig. 6).
Pileus 7-42 mm, narrowly campanulate, then plano-convex with distinct umbo; hygrophanous, when moist dark brown or dark red-brown (Expo J42, J12 (in centre), E-F22, H63-64), slightly or not translucently striate, on drying grey-brown to dark grey-brown (D-E62, E43, F62), covered with white, fibrillose scales or fibres, giving the surface a delicate, silvery appearance, stronger so towards the margin. Lamellae up to 6 mm broad, emarginately adnate, sometimes broadly adnate, subdistant to distant, pale

brown ("café-au-lait") when young, without pink or violet colours, later rusty brown, with edge paler. Stipe 20-60x2-6 mm, cylindrical or sometimes broader towards the base, solid or fistulose, pinkish brown to pale lilac brown, covered with white, silky, shining fibrillum, giving the stipe a pale pinkish appearance; a white annular zone and a few white floccose remnants of the veil may be present but these fade with age. Context when moist in pileus dark brown and in the stipe pinkish brown, on drying in pileus pale beige and in the stipe pale pinkish. Smell usually indistinct, in one case earth-like and in one case sweetish.
Spores (9.7-)10.5-12.6(-13.2)x(5.0-)6.0-7.0(-7.4) μm, Q=1.5-2.1, $\underline{Q}$=1.56- 2.07, ovoid, base of spore remarkably rounded (in one case spores tapering towards the base), with ornamentation of fine punctiform or slightly irregular warts. Brown basidia present. Trama in lamella with brown, encrusting pigment.
Collections examined. - Plot Q32, 18 Sept. 1986, Keizer 86148; Plot Q2, 28 Oct. 1986, Keizer 86178; 18 Nov. 1986, Keizer 86249; 19 Aug. 1987, Keizer 87106; 15 Oct. 1987, Keizer 87242; 13 Oct. 1988, Keizer 88130; 15 Sept. 1988, Keizer 88138; Plot Q83, 24 Oct. 1986, Keizer 86181; 24 Aug. 1987, Keizer 87131; 22 Sept. 1987, Keizer 87193; Keizer 87200; 10 Oct. 1988, Keizer 88087; Keizer 88280. Plot F34, 19 Nov. 1986, Keizer 86256a; Plot F35, 6 Oct. 1988, Keizer 88101.
Obs.: This species is characterized by the combination of the dark brown pileus, pink to pale lilac tinge at the stipe and above all by the large spores. My collections are in good agreement with the descriptions by Velenovsky (1921: 464) and Huijsman (1955:20). We consider *C. subsertipes* Romagn. a synonym, although Moser (1983) placed that species in the group of *Telamonia* with a violet stipe apex and *C. casimiri* in the group without violet colours. However, Moser, (l.c.) described the stipe in the latter species as: "Stiel-Spitze blass lila...." .

Cortinarius causticus Fr. (Fig. 7)
Pileus 17-70 mm diam., plano-convex without umbo, when moist whitish with pink-brown tinge (Expo B63, B64), in old specimens warm brown, more or less like *C. obtusus* and translucently striate, on drying paler, surface viscid. Lamellae up to 6 mm broad, emarginate-adnate, moderately crowded, pale ochre-brown, then more rusty brown, at margin paler. Stipe 40-45x3-7 mm, cylindrical, somewhat tapering towards the base, white, pale ochraceous-yellow with age, with brownish (due to spores) cortina-zone, viscid when moist. Smell sweetish or strongly fungoid; taste on surface of pileus very bitter, in the other parts strongly fungoid.
Spores (6.2-)6.4-7.3(-7.9)x(3.9-)4.0-5.4(-5.5) μm , Q=1.3-1.7 and $\underline{Q}$=1.35-1.58; pale yellowish brown sub micr., minutely punctate.
Collections examined. - Plot F24, 7 Oct. 1988, Keizer 88103; 8 Sept. 1988, Keizer 88348; Plot Q2, 14 Oct. 1988, Keizer 88124.
Obs.: The three collections studied show some differences: the fruitbodies of collections 88103 and 88348 are small: pileus 17-22 mm broad and stipe $\pm$ 40x3 mm, pale ochre-yellow (old specimens) and with sweetish smell. In the other collection (88124) the fruitbodies are larger: pileus 40-70 mm broad, stipe 45x7 mm, white and the smell is strongly fungoid. The spores of the collections 88124 and 88348 are narrower (4.0-4.8(-5.0) μm) than in collection 88103 (4.8-5.5 μm). The small variant was collected under *Fagus*, the other under *Quercus*. Kühner & Romagnesi (1953:253) and Moser (1983:392) described *C. causticus* with pileus 30-60 mm wide and with considerably narrower spores, 6-9x3-4 μm. The spore size reported by Konrad & Maublanc (1932:137, 6.5-8x4-

4.5 μm) agrees with the small-spored specimen, described above. In spite of the observed differences, the three collections are called *C. causticus* because of the distinctive bitter taste being present only in the pileipellis. This species is accepted here in this broad sense because the observed differences between the three collections did not correlate.

Cortinarius comptulus Mos. (Fig. 8)
Pileus 15-28 mm, when young campanulate, soon expanding, with umbo, hygrophanous, when moist red-brown (colours like *C. striaepilus)*, only short-translucently striate, on drying paler, beginning around the centre (colours like *C. striaepilus*), surface covered with numerous white, hairy-fibrillose scales, densely fibrillose towards the margin, producing a dirty-white zone of about 3 mm broad. Lamellae up to 3 mm broad, moderately distant, emarginately adnate, weakly ventricose, when young pale brown, later darker brown, with margin white- flocculose. Stipe 40-60x3 mm, cylindrical, flesh-coloured brown, towards the base of the stipe dark brown, covered with shiny white fibrillum, therefore stipe giving a pale brown impression, with some white floccose velar remnants. Context in apex of stipe greyish, downwards brown dark brown. Smell indistinct.
Spores (6.4-)6.5-7.2(-7.5)x(4.5-)4.8-5.5(-5.6) μm, Q=1.2-1.4(-1.5), $\underline{Q}$=1.35, broadly ellipsoid with ornamentation consisting of rather coarse, roundish to elongate or irregular warts, somewhat stronger towards the apex, brown sub micr. Margin of the lamellae with hyaline, vesiculose sterile cells originating from the trama.
Collections examined. - Plot Q2, 15 Sept. 1987, Keizer 87348; Plot Q74, 10 Oct. 1988, Keizer 88249.
Obs.: This species is in macroscopic characters almost identical with *C. hemitrichus*, but readily distinguished by the smaller spores.

Cortinarius erythrinus (Fr.) Fr. (Fig. 9)
Pileus 9-45 mm, conical, then expanding with more or less prominent umbo; hygrophanous, when moist very dark brown with purplish hue (Expo J62, H42, J10), towards the margin slightly paler due to greyish, silky remnants of veil, on drying greyish brown (E52, E52/54, F21, F41) with centre much darker (J21, H61), not translucently striate. Lamellae up to 8 mm broad, emarginate-adnate, in old specimens ventricose, when young brownish, later rusty brown, moderately crowded to subdistant, with margin concolorous. Stipe 20-40x2-7 mm, cylindrical, stuffed, greyish lilac or pink-lilac (C41, C21, B21), with shiny fibrillum and often ± halfway a concolorous velar zone. Context in pileus greyish beige, in stipe pink-lilac-brownish, somewhat browner than surface of stipe. Smell indistinct.
Spores (7.0-)7.2-8.0(-8.3)x(5.0-)5.2-5.8(-6.0) μm, ellipsoid, Q=1.3-1.6, $\underline{Q}$=1.38-1.50, strongly ornamented with coarse, irregular, elongate warts, coarser towards the apex.
Collections examined. - Plot F17, 19 Nov. 1986; Keizer 86248; Plot F24, 10 Nov. 1986, Keizer 86235; Plot Q1, 18 Sept. 1986, Keizer 86152; Plot Q2, 15 Sept. 1988, Keizer 88140; Plot Q31, 20 Oct. 1986, Keizer 86176; Plot Q31, 19 Aug. 1987, Keizer 87075; Plot Q32, 18 Sept. 1986, Keizer 86153; 5 Nov. 1986, Keizer 86237; 18 Aug. 1987, Keizer 87096.
Obs.: All well-developed carpophores of this species had clearly visible, pinkish velar zones on the stipe, although Moser (1978) states that the stipe is mostly glabrous, with grey-brown veil present only in one (unnamed) variety. In the field this species is easily recognisable by the very dark cap (when moist) and the pink-lilac stipe with concolorous

context. Microscopically, the relatively small spores with strong ornamentation are characteristic.
The species presented here is *C. erythrinus* (Fr.)Fr. *sensu* Ricken (1915), Lange (1935) and Bohus (1979; as *C. erythrinus var. russulaesporus* Bohus.). Lange (l.c.) described the spores as "pale and smooth" which indicates that he probably has studied deviating or unripe specimens. The macroscopic description and the plate agree well with this species. *C. erythrinus sensu* Henry, Favre possibly represents another taxon with narrower spores (7.5-9x4-5.5 µm, Kühner & Romagnesi, 1953:305).
Although *C. erythrinus* is stated to be a vernal species (Ricken, 1915; Kühner & Romagnesi (1953), the species is during this study only encountered in the autumn and not in other periods.

Cortinarius flexipes (Pers.: Fr.) Fr. *sensu* Kühner (1961) (Fig.10)
Pileus 12-35 mm, when young conical or convex, soon expanding, often with well-developed umbo, hygrophanous, when moist dark reddish grey-brown (Expo D34, E34, F23, F43, F52, H42, H52, J21, J42), towards the margin slightly paler (C43, E52, J22, H43), translucently striate up to 1/3 of the radius, on drying slightly paler, more greyish red-brown (E43, E54, somewhat paler than H42), with darker centre, when young covered by sparse, thin, white fibrils, soon disappearing and then ± shiny, at margin frequently covered by concentrically arranged pink-greyish velar remnants. Lamellae up to 3-4.5 mm broad, in old specimens somewhat ventricose, moderately crowded, when young pink (e.g. D42), soon only pink on the edge, finally entirely pale brown to rusty brown. Stipe 20-60x2-4 mm, cylindrical, sometimes with swollen base, usually becoming fistulose, pink-brown, covered by white or violaceous white fibrillum, causing a pale pink general appearance (A41), in addition an annuliform white zone and floccose velar remnants often present, disappearing with age.
Spores (6.7-)7.0-9.2(-10.0)x(4.4-)4.6-5.2(-5.5) µm, Q=1.3-1.8, $\underline{Q}$=1.41-1.82, ellipsoid to oblong with small to coarse warts, often coarser towards the apex. Basidia with brown content present.
Collections examined. - Plot F24, 24 Aug. 1987, Keizer 87084; Plot F34, 30 Oct. 1986, Keizer 86186; 28 Oct. 1988, Keizer 88284; Plot F43, 7 Oct. 1988, Keizer 88102; Plot Q1, 5 Nov. 1986, Keizer 86236; 18 aug. 1987, Keizer 87082; Plot Q2, 13 Oct. 1988, Keizer 88253; 14 Oct. 1988, Keizer 88121; Keizer 88240; Plot Q32, 17 Sept. 1987, Keizer 87165; 13 Oct. 1987, Keizer 87295; Plot Q83, 24 Oct. 1986, Keizer 86184; 10 Oct. 1988, Keizer 88279; Plot Q84, 30 Oct. 1986, Keizer 86182.
Obs.: This species is above all characterized by the pale pinkish (and not violaceous) colour of the stipe and the arrangement of the velum on the cap (only visible in material in good condition). The dark greyish red-brown colour of the cap is also distinctive. Macroscopically much resemblance exists with *C. casimiri*, which differs in the larger spores. The mere presence of violaceous colours in the young carpophore (in the lamellae and/or in the apex of the stipe) is usually taken as decisive in the division of these species of *Telamonia*. A closely related species with violaceous colours is called *C. sertipes* Kühn. 1955 (syn.: *C. flexipes forma sertipes* Kühn. 1961, *C. contrarius* Geesink 1976). The species without violaceous but with (pale) pink colour in the stipe is called *C. flexipes*.
Cortinarius decipiens (Pers.: Fr.) Fr. is very close, but may differ in a less-developed

veil and lack of a pink tinge in the young lamellae (Persoon, 1801:298; Fries, 1821:236). However, *C. decipiens sensu* J. Lange (1938:47; pl. 103D) is in our opinion identical with *C. flexipes*.
On the other hand, the descriptions by Jansen (1984:80) under the name *C. decipiens* refer to *C. casimiri*.

Cortinarius fusisporus Kühn. (Fig. 11)
Pileus 12-13 mm, expanded with incurved margin, hygrophanous, when moist brown to yellowish brown (Expo E64), at centre darker, margin paler and somewhat fibrillose, on drying paler brownish. Lamellae pale brown ("caramel-coloured") with paler edge, emarginately adnexed, moderately crowded. Stipe cylindrical, brown with yellow-brown fibrillum, in lower half with a few dirty white velar remains. Smell insignificant.
Spores (9.2-)9.5-11.5(-11.6)x4.4-5.0(-5,1) μm, Q=1.9-2.6, $\underline{Q}$= 2.21, subcylindrical-fusiform, ornamentation consisting of fine punctiform warts.
Collection examined. - 89104.
Obs.: The long and narrow spores are distinctive for this species, but *C. semivestitus* Mos. seems to be very close to *C. fusisporus*, if not identical. *C. semivestitus* has yellowish brown velar remnants on the stipe; these are dirty white in *C. fusisporus*.
C. incisus Pers.: Fr. *sensu* Moser (1986) is considered as a synonym of *C. fusisporus*.

Cortinarius helveolus (Bull.)Fr. (Fig. 13)
Syn.: *Cortinarius basililaceus* Pearson ex P.D. Orton
Pileus 15-60 mm, campanulate or conical, then plano-convex, with prominent, acute umbo, hygrophanous, when moist ochraceous yellow-brown or warm orange-brown (Expo E56, E58 (mostly), F54), in centre somewhat more intensely, so towards the margin slightly paler by presence of thin, silky fibrils, not or slightly and shortly translucently striate, on drying pale ochre-brown to yellow-brown or straw-coloured (B66, C58, C66, D58, E56), in centre more intensely brown (C58, D58, E56). Lamellae up to 10 mm broad, emarginate-adnate, distinctly ventricose, thickish, very distant ($\pm$ 6-9 per 10 mm at margin of cap), often interveined, when young violet in most cases, soon fading to pale brown ("caramel-brown"), finally (purplish-)rusty brown, with margin concolorous or paler. Stipe 20-70x2-8 mm, cylindrical or slightly enlarged at the base, fistulose or stuffed, ground colour like moist pileus, covered by shiny, pale brown fibrils, causing a somewhat paler appearance, in young specimens with violet apex and base, fading with age, approximately half-way the stipe with a distinct, yellowish white, almost membranaceous annulus, downwards with some additional velar zones or flocci. Context in pileus concolorous with surface, in stipe violaceous in top and base of young specimens, later ochre-brown. Smell weak or distinct, musty or sweetish.
Spores (8.2-)8.8-10.2(-11.3)x(4.5-)4.7-5.6(-6.5) μm, Q=1.6-2.1 and $\underline{Q}$= 1.64-1.92, oblong, often tapering towards the base, with small, subglobose or oval warts, stronger developed towards the apex. Basidia with brown or golden-brown content present; brown extracellular pigment present in the hymenophoral trama. No sterile cells have been found in the hymenium.
Collections examined. - Plot F24, 3 Nov. 1987, Keizer 87254; Plot Q2, 15 Oct. 1987, Keizer 87277; 15 Sept. 1988, Keizer 88146; Plot Q74, 23 Jul. 1988, Keizer 88038; 10 Oct. 1988, Keizer 88199;Plot Q82, 1 Oct. 1987, Keizer 87207.
Obs.: The rather robust habit, the distant lamellae and the warm (yellowish) brown

colours indicate that this species is related to *C. hinnuleus* Fr. Some characters separate it clearly from *C. hinnuleus*, viz. the prominent, almost pointed umbo, the (often) violaceous colours of the young lamellae and stipe, the warm, more yellowish brown colour of the pileus and the persistent, almost membranaceous annular zone on the stipe. Microscopically, the spores are slightly longer, more slender and often tapering towards the base.

The descriptions of "*C. helveolus* Fr. ss. Bresadola" by Kühner & Romagnesi (1953:301) and Moser (1978:408) differ in a number of characters from the material presented here, especially in the lack of violet colours. Nevertheless, we consider these interpretations as probably conspecific with our material, on account of the well-developed annulus and distant lamellae. Both descriptions refer to plate 653 by Bresadola (1929) (although Kühner & Romagnesi (1953) with ?), which does neither show the bright yellow-brown pileus, nor any violaceous hue in lamellae or stipe.

C. quadricolor Fries (1874:378) is rather similar, but the stipe of that species was described as violaceous white without brown colours. Of this species no recent records seem to exist.

The picture of *C. hinnuleus* by Phillips (1981:138) is a misapplication of *C. helveolus*.

Orton (1984) presented *Cortinarius basililaceus* Pearson ex P.D. Orton, which was said to differ from *C. helveolus* Fr. by the non-coniferous habitat, the smell (not inodorous), yellowish veil, striate pileus, more slender stature and more elongate spores and from *C. helveolus* sensu Kühner & Romagnesi (1953) by the presence of violet colours. Except for the veil (*zona annulari ferrugineo-marginata*) Fries (1874) did not mention these characters and the violet colour in the young lamellae and near the base of the stipe of *C. basililaceus* was described as very variable. It is concluded that the description of *C. basililaceus* agrees with the description of *C. helveolus* Fr. and the interpretations of Kühner & Romagnesi (l.c.) and Moser (1978). Consequently, *C. basililaceus* is considered as a synonym of *C. helveolus*. Moreover, it seems unlikely that this species, which is apparently wide spread in at least the U.K. and the Netherlands, would not have been noticed before the fourties of this century.

Cortinarius hinnuleus Fr. (Fig. 12)
Pileus 20-65 mm, convex, soon expanding, usually with broad and blunt umbo, finally flattened to concave and then umbo not conspicuous, hygrophanous, when moist warm ochre-brown to red-brown (Expo H42, H43, D54, D64, E52, E54, E56, E58, F54, H52, H64, J34), with centre usually more intensely coloured (e.g. H52, H64, F52, H32), at margin often paler and more greyish due to a fibrillose layer, on drying ochre-brown, greyish ochre-brown or straw-coloured (B64, B72, C56, C63, C64, D56, D66, E58, E66, E68, F48), not translucently striate, often with a pattern of radial dark streaks. Lamellae up to 10-14 mm broad, in old specimens strongly ventricose, distant, sometimes veined on the sides and interveined, rather narrowly adnate, first pale brown, older darker brown because of ripening of the spores, with margin paler, whitish, especially when young, without violet or pink colours. Stipe 35-70x4-14 mm, cylindrical, tapering towards the base or basal part somewhat enlarged, fistulose or solid, brown, ± as moist cap, covered by shiny, pale brown fibrillum, giving the stipe a pale brown appearance, darker brown towards the base, with one or several white, annuliform velar zones which may fade with age, basal part often white tomentose as a "sock". Context in stipe concolorous with

surface of pileus, on drying cork-coloured, finally dark brown in basal part of the stipe. Smell distinctly musty, dusty or sweetish, but sometimes absent.
Spores (6.6-)7.0-9.0(-9.8)x(4.9-)5.1-6.1(-6.5) μm, Q=1.3-1.8, Q=1.40-1.60, ellipsoid to oblong, with oval to elongate, often branched, moderately coarse warts; ornamentation stronger developed at the apex of the spore. In one collection sterile cells were present at the edge of the lamellae (see fig. 12c.). Brown basidia present; brown extracellular pigment present in the hymenophoral trama.
Collections examined. - Plot F35, 6 Oct. 1988, Keizer 88092; Plot Q2, 28 Oct. 1986, Keizer 86179; 18 Nov. 1986, Keizer 86247; 15 Sept. 1987, Keizer 87143; 15 Oct. 1987, Keizer 87339; 15 Oct. 1988, Keizer 88136; Plot Q6, 8 Nov. 1987, Keizer 87312; Keizer 87316; Plot Q32, 14 Oct. 1987, Keizer 87236; Plot Q83, 1 Oct. 1986, Keizer 86176; Odoorn, Odoornerveen, 13 Oct. 1987, Keizer 87294; 22 Sept. 1988, Keizer 88126.
Obs.: *Cortinarius hinnuleus* is known as a variable species (e.g. Dähncke & Dähncke, 1979), which is confirmed in this research. Here, variants with a slender fusiform stipe have been united with variants with a thick-set to (slightly) bulbous stipe. Small and slender forms may be confused with *C. striaepilus* but the lamellae of the latter are more crowded and the pileus is usually translucently striate. In one collection (87143) sterile cells were observed at the edge of the lamellae. As this collection fits otherwise well into the adopted concept of *C. hinnuleus*, no taxonomic importance has been assigned to this character. This feature can be found occasionally among other species of *Cortinarius* as well and may be explained by the observation that the edge of the lamellae is the last part becoming fertile, and some basidia may fail to ripen. A closely related taxon is *C. helveolus* (see there).

Cortinarius lanatus (Mos.) Mos. (Fig. 14)
Pileus 7-38 mm, when young campanulate or conical, then expanding mostly with a prominent umbo, hygrophanous, when moist warm red-brown to dark red-brown (Expo H44, H42, H52, H43, J22, F52, F62), translucently striate up to 1/3 of the radius, at margin yellowish due to presence of a fibrillose layer, on drying ochre-brown, straw-coloured (C56, D56, C63, E56, C66) according to an irregular centripetal pattern, with small, yellow-brown, fibrillose hairy scales. Lamellae up to 4 mm broad, moderately crowded to subdistant, emarginately adnate, somewhat ventricose, when young pale brown, later rusty brown, with concolorous margin. Stipe 13-70x2-4(-5) mm, cylindrical, narrowly fistulose, ground colour rather dark brown, darker towards the base, covered by yellow-brown to straw-coloured, shiny fibrils and with a woolly, brown annular zone, downwards with several more brownish floccose velar remains. Context in all parts rusty brown, black-brown in base of stipe. Smell weak, fungoid or sweetish.
Spores (6.2-)6.9-8.3(-8.8)x(4.2-)4.4-5.0 μm, Q=(1.4-)1.5-1.9, Q=1.56-1.67, ellipsoid, pale yellowish brown sub micr., minutely punctate, somewhat stronger so towards the apex.
Collections examined. - Plot F34, 10 Nov. 1987, Keizer 87325; Plot F43, 7 Oct. 1988, Keizer 88073; Plot Q65, 24 Sept. 1988, Keizer 88266,; Plot Q82, 4 Sept. 1987, Keizer 87051; Plot Q93, 30 Oct. 1987, Keizer 87302; 21 Sept. 1988, Keizer 88056; Odoorn, Odoornerveen, 18 Nov. 1987, Keizer 87297; 1 Nov. 1988, Keizer 88195.
Obs.: Among the small *Telamonia* species with brown veil and squamulose pileus three names come into consideration, viz. *C. psammocephalus* Fr., *C. strobilaceus* Mos. and *C. lanatus* (Mos.) Mos.. Moser (1978) quoted the plate of *C. psammocephalus* by Lange

(1935:99F) under *C. strobilaceus* and apparently considered these names as synonyms. This plate shows a more squamulose pileus than the Drentian collections, and Lange observed larger spores. The description of *C. lanatus* by Moser (1978) fits better than that of *C. strobilaceus* although the differences are small. Therefore the former name has been chosen.
A closely related species, called *C. psammocephalus*, occurs in the Netherlands along lanes on clay mainly along the Rhine and its affluents. This species differs in having more prominently developed squarrulose scales on the pileus, more abundant remains of the veil on the stipe and a slightly less slender habit.
The question whether *C. psammocephalus* and *C. strobilaceus* are synonyms remains to be solved.

Cortinarius paleaceus (Fr. in Weinm.) Fr. (Fig. 15)
Pileus 8-22 mm, campanulate, later expanded, usually with well developed umbo but umbo sometimes almost absent, hygrophanous, when moist dark red-brown (Expo J32, E62, F62), towards the margin more greyish due to fibrillose veil remains, on drying pale pinkish brown, greyish beige (B61, D63), at centre darker brown (E52), margin whitish-fibrillose, covered with white hairy scales, which may disappear with age. Lamellae up to 3 mm broad, moderately crowded but sometimes more distant, emarginate-adnate, when young pale brown without lilac colours, later rusty brown, with concolorous margin. Stipe 15-40x1-3 mm, cylindrical, sometimes attenuate at the base, middle brown, covered with dirty-white or pale brownish, shiny fibrils, giving a shiny pale brown appearance, in one collection with weak lilac hue, usually with a white annular zone and several floccose veil remains below, which may disappear with age. Context in pileus and stipe pale beige when dry, reddish brown when wet. Smell usually distinct like crushed leaves of *Pelargonium zonale* (L.) Ait., sometimes more like *P. radens* H.E. Moore (=more like lemon).
Spores (7.0-)7.5-8.7(-9.5)x(4.5-)5.0-5.7(-5.9) μm, Q=1.4-1.9, Q=1.48-1.86, ellipsoid, with small punctiform warts or warts stronger developed and elongate to irregular, usually stronger at the apex of the spore, brown to rather dark brown sub micr.
Collections examined. - Plot F34, 19 Nov. 1986, Keizer 86256b; Plot Q2, 28 Oct. 1986, Keizer 86183; 15 Sept. 1987, Keizer 87152; 15 Oct. 1987, Keizer 87293; Keizer 87306; Plot Q33, 30 Oct. 1987, Keizer 87314; Plot Q74, 22 Sept. 1987, Keizer 87178; Plot Q82, 4 Sept. 1987, Keizer 87098; Plot Q83, 22 Sept. 1987, Keizer 87194; Odoorn, Odoornerveen, 13 Oct. 1987, Keizer 87331.

A discription of this species is given to enable a comparison with the closely related *C. paleiferus*.

C. paleiferus Svrcek (Fig. 16)
Pileus 20-30 mm, convex, without umbo, hygrophanous, when moist reddish brown (Expo F44-F46), towards the margin more grey due to a fibrillose layer of dirty-white veil remains; on drying pinkish grey-brown (E22), pale greyish towards the margin, covered with white hairy scales. Lamellae up to 5 mm broad, somewhat ventricose, sinuose and venose, distant, rusty brown with violet hue, emarginate-adnate. Stipe 55-60x6 mm, cylindrical, fistulose, concolorous with pileus, but apex violet, covered with white shiny fibrils, in addition with some white velar remains, at base with violet tomentum (K. & W. 18D4). Context in stipe and pileus slightly darker coloured than

surface, with smell as *Pelargonium zonale*.
Spores (8.2-)8.3-9.0(-9.2)x(5.2-)5.4-5.6(-6.0) μm, Q=1.5-1.9, $\underline{Q}$=1.58-1.85, ellipsoid to oblong, faintly verrucose, rather dark brown sub micr.
Collections examined. - plot F17, 19 Nov. 1986, Keizer 86246; Plot Q31, 17 Oct. 1988, Keizer 88214; Odoorn, Odoornerveen, 1 Nov. 1988, Keizer 88184.
Obs.: This species is distinct from the related *C. paleaceus* because the young lamellae, apex of stipe and tomentum at the base of the stipe are violet (not brownish or pale), at least in young specimens, and the lamellae are distant (not crowded).
Jansen (1984) considered these names as synonyms. However, in the present material a satisfactory distinction could be made between the two species. If old material is studied the violaceous colours may disappear and then the identification of the species becomes difficult. Yet, future research on more extensive material might prove that the species are identical.

Cortinarius parvannulatus Kühner (Fig. 17)
Pileus 10-35 m, campanulate, then expanding, mostly with obvious umbo, when moist warm brown to chestnut-brown (K. & W. 6E7, 6E8, Expo between F34-36 and E58), centre somewhat darker, in one case more ochre-brown (between D54 and D56), translucently striate, covered with small whitish hairs, towards the margin with whitish fibrillose veil, on drying yellowish brown (C56, C63). Lamellae up to 4-5 mm broad, emarginate-adnate, moderately crowded to subdistant, not ventricose, when young pale ("caramel"-)brown, often with pink-lilac hue, later darker rusty brown, margin concolorous or slightly paler. Stipe 25-65x1.5-3.5 mm, cylindrical, usually fistulose, flesh-coloured brown, covered with pale yellow-brown, shiny fibrils, (e.g. D58, C61), giving the stipe a pale yellowish brown appearance, apex lilac, fading with age; not or hardly darker towards the base, about half-way often with a conspicuous, white annular zone, downwards additional white floccose veil remnants may be present. Context in pileus and stipe concolorous with surface to slightly darker, in base of stipe dark brown. Smell of cedar-wood or as *Camarophyllus russocoriaceus* but weaker.
Spores (7.0-)7.5-9.0(-11.9)x(4.3-)4.8-5.3(-5.5) μm, Q=1.5-2.0(-2.1), $\underline{Q}$=1.60-1.73, ellipsoid to oblong, ornamentation consisting of moderately coarse, roundish, elongate or irregular warts, slightly stronger at the apex of the spore.
Collections examined. - Plot F33, 24 Sept. 1988, Keizer 88273; Plot Q2, 15 oct. 1987, Keizer 87239; Plot Q31, 28 Oct. 1987, Keizer 87267; Odoorn, Odoornerveen, 3 Oct. 1989, Keizer 89036.
Obs.: Collection Keizer 88131, 13 Oct. 1988, Plot Q2, which agrees macroscopically with the above description, differs in the size and shape of the spores (6.8-)6.9-7.5(-7.9)x5.1-5.6(-5.7) with Q=1.3-1.5 and $\underline{Q}$=1.36, and in the ornamentation consisting of coarser warts.
C. cedriolens (Mos.) Mos. with the same smell, is said to be different by the absence of an annular veil-zone (but several velar zones often present (Moser, 1978)) and absence of violaceous tinges in the top of the stipe. Both characters can vary considerably in *Cortinarius* subgenus *Telamonia*. Therefore, Lindström (1986:9), Grünert (1989:141) and Brandrud *et al.* (1990) consider these taxa as synonyms, with which view we agree.

Cortinarius privignus Fr. *sensu lato* (Fig. 18)
Pileus 21-36 mm, convex, later plano-convex with rather weak, obtuse, broad umbo,

hygrophanous, when moist warm orange-brown (Expo E58) with paler margin, not translucently striate, on drying ochre-brown (D68); margin white-silky fibrillose by remains of white veil. Lamellae up to 4 mm broad, not or slightly ventricose, narrowly and somewhat emarginate-adnate, moderately distant, rather pale brown, with margin white, without a trace of violet. Stipe 25-50x5-8 mm, cylindrical with clavate base, up to 13 mm broad, stuffed, pale brown, covered by white-silky fibrils, causing a pale beige appearance with white annuliform veil remnants in lower half of stipe. Smell none; taste not known.
Spores 7.5-8.5(-10.0)x5.0-5.5(-6.0) μm, Q=1.4-1.7(-1.8), $\underline{Q}$=1.60-1.64, $\pm$ amygdaliform, with rather coarse, elongate and branched warts, more prominent towards the apex. Brown basidia present.
Collections examined. - Plot Q2, 15 Sept. 1988, Keizer 88134; Plot Q32, 18 Sept. 1986, Keizer 86147; Keizer 86151.
Obs.: The species under consideration here is named *C. privignus*. From the descriptions in literature (Kühner & Romagnesi (1953), Moser (1978)) it is difficult to distinguish several related species viz. *C. privignofulvus* R. Henry, *C. privignus* Fr., *C. privignorum* R. Henry, *C. privignoides* R. Henry , *C. pseudoprivignus* R. Henry on the basis of (slight) differences in coloration of the pileus, degree of hygrophaneity and the shape of the stipe. All the characters mentioned are gradual and therefore an identification of our material is difficult without the possibility to compare the related species, because they all seem to be rare in the Netherlands. However, in our opinion it is doubtful whether these species are worth of distinction. The ornamentation of the spores which is studied here differs from that given by Marchand (1983:152), where punctiform warts are shown.

Cortinarius rigens (Pers.: Fr.) Fr. (Fig. 20)
Pileus 44-60 mm, plano-convex or applanate, without or with low umbo and with somewhat involute margin; hygrophanous, when moist wood-coloured brown to grey--brown (Expo B-E54) or (orange-red-)brown (E46-E58), margin not translucently striate, on drying straw-coloured ochraceous yellow-brown (B56, C64), at centre darker (C56); surface radially silky or slightly fibrillose, towards the margin with white velar fibrils. Lamellae up to 8 mm broad, not ventricose, somewhat crowded to somewhat distant, crenulate, emarginate-adnate, rusty brown, with edge paler, yellow-brown. Stipe 78-80x9-16 mm, cylindrical or irregularly inflated, gradually tapering into pointed, rooting base; hollow or solid, pale ochre-beige mixed with white, covered with white fibrillum and a few indistinct fibrillose remnants of the veil, on drying white or whitish. Smell distinct, like jodoform.
Spores (6.5-)7.0-8.7(-9.0)x(4.2-)4.9-5.6(-5.9) μm, Q=(1.4-)1.5-1.6(-1.7), $\underline{Q}$=1.53-1.61; ellipsoid, ornamentation verrucose with punctiform, sometimes elongate or irregular warts, ornamentation often stronger towards the apex of the spore.
Collections examined. - Plot Q2, 15 Sept. 1988, Keizer 88139; Odoorn, Odoornerveen, 18 Nov. 1987, Keizer 87291; 9 Nov. 1989, Keizer 89113.
Obs.: *Cortinarius rigens* as depicted by Lange (1938:100C) with stipe 4-9 mm broad fits these collections well, but is somewhat different from the description by Moser (1978) with a stipe only 3-5 mm broad. Nevertheless, Moser quoted Lange's plate for his *C. rigens*. Persoon (1801:288) originally described *Agaricus rigens* with a stipe 6.3-8.5 mm thick. He did not mention any characteristic smell. Two species are related to *C. rigens*, viz. *C. velenovskyi* R.Henry and *C. duracinus* Fr.. The former is smaller and darker and

the latter is more robust and inodorous according to Ricken (1915), Konrad & Maublanc (1924-1937), Bresadola (1927-1933), Marchand (1983) and Moser (1978). However, Bon (1988a) reported a jodoform like smell but a stipe 15 mm broad for *C. duracinus*, so that the identity of his plate remains uncertain.

Cortinarius striaepilus J. Favre (Fig. 19)
Pileus 7-25(-40) mm, convex or conical, rather soon expanding, mostly umbonate with inconspicuous and blunt to prominent, almost papilla-like umbo, hygrophanous, when moist dark reddish brown or dark yellowish brown (Expo F44, H44, H43, E54, H52, F54, F46), towards the margin paler by fibrillose covering, translucently striate up to 1/3 to 1/2 radius, sometimes more, on drying pale yellowish brown or straw-coloured (C63, C64, C62, B56 (darker), between E56 and E63, C56), centre slightly more reddish brown (E56), when young covered with very thin pale-whitish hairy remains of velum, disappearing with age, margin split and fringed in old specimens. Lamellae (L=±20-30), up to 3-6 mm broad, in old specimens ventricose, emarginate, more or less distant (± 8-10 per 10 mm at cap margin), first pale brown, ("caramel-coloured"), later more rusty brown with pale edge, sometimes edge with a very faint and soon disappearing pink flush. Stipe (20-)30-50x1.5-3 mm, cylindrical or sometimes slightly swollen at the base, hollow; apex very pale, almost hyaline, towards base darker brown, more or less concolorous with pileus, with shiny pale brown to whitish fibrillum, in addition with an annuliform velar zone and some floccose veil-remnants, base frequently white-tomentose. Flesh in drying pileus and upper part of stipe pale cork-coloured, in lower part of stem dark brown. Smell none or weakly fungoid, in one collection *Pelargonium*-like. Spores (6.2-)7.0-9.0(-11.0)x4.5-5.5 µm, Q=1.3-1.9, Q=1.45-1.75, ellipsoid or ellipsoid-oblong, with small round or elongate warts, often slightly stronger warty at the apex. Basidia with brown content present, brown extracellular pigment present in the hymenophoral trama. Collections examined. - Plot F24, 10 Nov. 1986, Keizer 86226; Keizer 86229; 7 Oct. 1988, Keizer 88090; Plot F33, 1 Oct. 1987, Keizer 87201; Plot F34, 30 Oct. 1986, Keizer 86180; Keizer 86185; 19 Nov. 1986, Keizer 86243; Keizer 86255; 10 Nov. 1987, Keizer 87329; 28 Sept. 1988, Keizer 88236; Plot F35, 22 Sept. 1987, Keizer 87199; Plot F41, 15 Sept. 1986, Keizer 86143; 10 Nov. 1987, Keizer 87323; Plot Q1, 6 Oct. 1986, Keizer 86170; 3 Oct. 1988, Keizer 88074; Plot Q2, 18 Nov. 1986, Keizer 86253; 19 Aug. 1987, Keizer 87121; 15 Sept. 1987, Keizer 87148; 15 Oct. 1987, Keizer 87240; 15 Sept. 1988, Keizer 88142; Plot Q13, 22 Sept. 1987, Keizer 87184; 3 Nov. 1987, Keizer 87263; Plot Q35, 6 Oct. 1988, Keizer 88091; Plot Q81, 3 Nov. 1986, Keizer 86242; Plot Q82, 24 Sept. 1988, Keizer 88083; Plot Q83, 1 Oct. 1986, Keizer 86175; 10 Nov. 1986, Keizer 86224; 24 Aug. 1987, Keizer 87068; 4 Nov. 1987, Keizer 87252; 8 Sept. 1988, Keizer 88161; Keizer 88174; Keizer 88317; Keizer 88354; Plot Q84, 19 Nov. 1986, Keizer 86252; Plot Q93, 29 Sept. 1986, Keizer 86177; Odoorn, Odoornerveen, 17 Sept. 1987, Keizer 87168; 22 Sept. 1988; Keizer 88267; Keizer 88112.
Obs.: This species is conceived here in a rather wide sense with 1) colours varying from warm dark red-brown to dark yellowish brown, 2) small to medium sized sporocarps and 3) spores with Q=1.45 to 1.75. All three characters are intergrading. The colour of the pileus depends on the thickness of the pale fibrillose layer, which is subject to individual variation and which tends to wear off with age. The habit of the carpophores ranges from slender to rather thick-set with rounded or umbonate cap and with base of stipe enlarged or not, but this character varies independently from the other characters studied. The spore shape varies from rather broadly ellipsoid to oblong- ellipsoid (fig. 19 b, d). All

intermediate shapes do exist (fig. 19 f), and spore shape does not not correlate with other characters. The smell is usually insignificant but in some specimens of one collection it was obviously *Pelargonium*-like (as in *C. paleaceus*). The other characters and the fact that in the same group many odourless sporocarps were present are indicative of *C. striaepilus*.

Cortinarius striaepilus J. Favre has been considered the correct name for this taxon. The description and plates match fairly well the material collected during this study. Minor differences are (1) the lamellae which were described by Favre (1948:119) as "assez serrées", whilst the lamellae of the Drentian collections are subdistant, (2) the stipe which is frequently hollow and (slightly) swollen towards the base, unlike the specimens depicted by Favre, and (3) Favre (l.c.) described the habitat as wet coniferous forests.

A species that comes close to *C. striaepilus* with respect to habit and which is known to many authors is *C. incisus* (Pers.) Fr., e.g. Moser (1978), Kühner & Romagnesi (1953), Bresadola (1930), Michael-Hennig-Kreisel (1985). Differences with the present material are that the pileus is not translucently striate and more fibrillose and that the stipe is not darkening towards the base in *C. incisus*. In the original description by Persoon (1801:310) no reference was made to a striation of the pileus in *Agaricus incisus*. It was described as a small species with a squamulose pileus and regarded by Persoon (l.c.) as close to *A. psammocephalus* Bull.. Consequently, this name will not be used for the present taxon. However, it remains unlikely that such a common species was not described earlier than 1948.

The plate of "*C. incisus* forma" by Lange (1938: 99C) lacks the darkening stipe, but the pileus is of the right colour and distinctly striate. Consequently, this plate probably represents *C. striaepilus*.

C. incisus Pers.:Fr. *sensu* Moser (1986) deviates from previous concepts of this species by the long and narrow spores. This taxon is considered by us as a synonym of *C. fusisporus* Kühner.

A closely related taxon is *Cortinarius helobius* Romagn., which differs in the complete absence of veil on the stipe and its occurrence in marshy habitats.

C. striaepilus, although listed as very rare in the Netherlands (Arnolds, 1984), is a rather common species in the studied plots. It has probably frequently been overlooked or confused with other related taxa.

Cortinarius subbalaustinus R. Henry (Fig. 22)
Pileus 15-45 mm, convex, then expanded, umbo low and broad or absent, strongly hygrophanous, when moist warm orange- or red-brown (Expo F46), not translucently striate, on drying pale orange-brown (D48) to almost straw-coloured (Expo C56, B56), margin covered by a 2 mm broad, pale, fibrillose layer. Lamellae up to 6 mm broad, not ventricose, moderately crowded, when young pale brown (C64), soon rusty brown, margin paler. Stipe 35-80x6-10 mm, cylindrical with bulbous base, up to 17 mm wide, pale brown, covered by thick, cream-coloured fibrillum, thus appearance of stipe pale beige and shiny, over the lower half some white, floccose veil remnants, bulb white-tomentose, entire stipe darkening with age. Context in pileus when moist beige, on drying white, in stipe when moist with darker and paler parts. Smell indistinct.
Spores (8.0-)8.2-9.0(-9.6)x(4.5-)4.9-5.0(-5.4) μm, Q=1.6-1.9, $\bar{Q}$=1.75, oblong, with ornamentation of fine, punctiform warts, stronger at the apex.
Collections examined. - Plot Q35, 22 Sept. 1987, Keizer 87183; 3 Nov. 1987, Keizer

87247; 7 Oct. 1988, Keizer 88094.

Cortinarius tabularis (Bull.) Fr. (Fig. 23)
Pileus 9-40 mm, convex, soon plano-convex, finally centre somewhat depressed, hardly hygrophanous, when moist greyish or ochraceous red-brown (Expo D54, D56, E56, E58), towards margin more greyish (D52), due to greyish fibrillose veil remnants, in the smallest specimen the margin weakly translucently striate, surface somewhat micaceous, not viscid. Lamellae up to 4 mm broad, emarginate-adnate, moderately crowded, pale ("caramel"-) or ochre-brown, later rusty brown, with margin serrulate, sometimes paler than the sides. Stipe 33-70x2.5-6(-9) mm, cylindrical or enlarged at the base, very pale greyish white, covered by white fibrillum and in the lower 2/3 of the stipe with pale beige or cream-coloured zones of veil, therefore general appearance white. Context when moist in pileus watery grey, in stipe pale brown; on drying in pileus white, in stipe very pale beige. Smell indistinct.
Spores (7.2-)7.5-8.6(-8.8)x(4.9-)5.6-6.5(-6.8) μm, Q=1.2-1.4, $\underline{Q}$=1.31, broadly ellipsoid to ellipsoid; ornamentation consisting of rather coarse, round or irregular warts.
Collections examined. - Plot Q2, 15 Sept. 1988, Keizer 88135; 13 Oct. 1988, Keizer 88192.
Obs.: *Cortinarius tabularis* is a rarely reported species (Arnolds, 1984) and close to *C. anomalus*, mainly different in the lack of lilac lamellae in young specimens. However, according to Lange (1938:31) intermediate forms occur and are even more common than typical carpophores. We do not support this view.
C. tabularis and *C.decoloratus* are closely related and Geesink (1972) therefore suggests that they should be considered as synonyms. The two species differ in the surface of the pileus which is dry in the former and viscid in the latter species (Moser, 1978). Whether this difference warrants a distinction on specific level cannot be decided here. The specimens found during this study had dry caps and are therefore named *C. tabularis*.

C. umbrinolens P.D. Orton (Fig. 21)
Misapplied name: *Cortinarius rigidus* (Scop. Fr.) ss. J. Lange
Pileus 12-36 mm, campanulate, then expanding with distinct umbo, hygrophanous, when moist dark brown, dark grey-brown or dark reddish brown (Expo H42, J42, H52, H64, F62), on drying pallescent to grey-brown (F62, E54), covered with scattered, small, silky hairs, more densely so towards the margin, disappearing with age. Lamellae up to 7 mm broad, distant, emarginately adnate, when young pale brown, soon dark rusty brown, with pale brown or whitish margin (but no cheilocystidia present). Stipe 30-70x3-7 mm, cylindrical or sometimes slightly swollen at the base, fistulose or solid, rather dark brown ($\pm$ as surface of pileus), covered with beige or whitish, shiny fibrillum giving the stipe a pale brown, shiny appearance, when old without fibrils and therefore darker, usually with a dirty white annular zone and some floccose veil remains. Context in pileus pale brown or cork-coloured; in stipe brown to rather dark brown, in base black-brown. Smell usually strong, dusty, like *Cystoderma amianthinum*.
Spores 6.8-10.5(-10.8)x(4.0-)4.5-6.0 μm, Q=1.4-1.9(-2.0), $\underline{Q}$=1.51-1.74, ellipsoid, ornamentation moderately verrucose.
Collections examined. - Plot Q1, 3 Oct. 1988, Keizer 88093; Plot Q43, 11 Oct. 1988, Keizer 88202; Plot Q45, 21 Sept. 1988, Keizer 88169.
Obs.: The collections can be divided into two groups concerning spore size: Coll. 88169

with spores (8.8-)9.2-10.5(-10.8)x(5.0-)5.3-6.0 μm, Q=1.7-1.9(-2.0); Coll. 88093 and 88202 with spores 6.8-8.0x(4.0-)4.5-5.0(-5.5) μm, Q=1.4-1.8. The small-spored variant has spores with coarser and more irregular warts. These microscopic differences do not correlate with variation in macroscopic characters. Several other studied collections from the herbarium at Wijster (WAG-W) appeared to have intermediate spores sizes. Therefore *C. umbrinolens* is accepted here as a separate species with an unusual variation in spore size.

Cortinarius valgus Fr. (Fig. 25)
Pileus 15-24 mm, convex to plano-convex, not or weakly hygrophanous, at centre reddish brown (Expo F52), towards the margin paler, greyish red-brown (D52, D54), surface with white shiny fibrils and with radially oriented, very thin, dark brown fibrillose covering, at extreme margin greyish by velar covering. Lamellae emarginate, rather narrow, up to 3-4 mm broad, moderately crowded to subdistant, at first loam-coloured grey-brown with violaceous tinge, later rusty brown with paler margin. Stipe 33-45x4-5 mm, cylindrical or slightly broadened towards the base, hollow with age, pale beige-brown, paler than pileus, indistinct violaceous greyish colour sometimes present at apex, covered with pale beige fibrillum, and in the lower half some dirty-whitish velar zones. Context in pileus cork-coloured, in the apex of the stipe greyish or greyish with lilac flush; downwards pale brown, slightly darkening towards the base. Smell absent or slightly raphanoid when cut.
Spores 7.2-8.8(-9.0)x4.8-5.6(-5.7) μm, Q=1.4-1.6, Q=1.49-1.52, ellipsoid to oblong, with rather fine verrucose ornamentation. Cheilocystidia absent.
Collections examined. - Plot Q2, 15 Oct. 1987, Keizer 87241; 14 Oct. 1988, Keizer 88225.
Obs.: Our description agrees well with the description in Moser & Keller-Dilitz (1983). However, in the present material no cheilocystidia were found, although Moser (l.c.) mentions them as "often frequent". The spore size is rather variable, although the two collections studied come from the same place: in coll. 87241: 7.2-7.7(-7.8)x4.8-5.0 μm, Q=1.49 and in coll. 88225: 8.0-8.8(-9.0)x(5.3-)5.4-5.6(-5.7) μm, Q=1.52. These values fall within the variation reported by Moser (1983:350) and Moser & Keller-Dilitz (1983:45). The species was also observed in a roadside verge outside the studied plots on nutrient-poor sandy soil with *Fagus* and there the carpophores were considerably larger: pileus 20-50 mm, stipe 50-70x3-8 mm.
Cortinarius valgus is a little-known species and has probably often been overlooked. It was not recorded before from the Netherlands (Arnolds, 1984; Arnolds & al., 1989b) and has been found several times since.

Cortinarius velenovskyi R. Henry (Fig. 26)
Pileus 11-45 mm, convex, then plano-convex, usually without, but sometimes with indistinct low umbo, with margin often incurved, hygrophanous, when moist dark red-brown or chestnut-brown (Expo F-H52, H42, H34-36, F23, F48), towards the margin sometimes somewhat paler (E44-46), only short translucently striate, up to 1/4 of the radius, on drying ochraceous yellow-brown, orange yellow-brown (Expo E58, D56, F42), paler towards the margin (C66, D56, C58-68), surface with greyish bloom caused by a fine white fibrillose layer which fades with age but remains visible for a long time especially at the margin; pattern of drying irregularly centripetal, i.e. margin dries first. Lamellae emarginate, subdistant, up to 6 mm broad, at first pale brown ("café-au-lait")

with edge yellowish, when older rusty brown and ventricose. Stipe 20-60x4-9 mm, cylindrical, often tapering towards the base and rooting, the root sometimes short and indistinct, solid or fistulose, when moist pale beige (Expo A62), covered with white fibrillum, on drying white; few white, soon disappearing veil remains may be present. Context in pileus pale brownish, in stipe beige, paler towards the base. Smell usually iodoform-like but sometimes with rancid or cedar wood component.
Spores (7.0-)7.5-9.0(-9.7)x(4.2-)4.8-5.5(-6.0) µm, Q=1.4-1.8(-1.9), Q=1.47-1.76, ellipsoid, ornamentation finely verrucose with mostly punctiform warts; few brown basidia present; trama with brown incrusting pigment.
Collections examined. - Plot F34, 28 sept. 1988, Keizer 88123; 28 Oct. 1988, Keizer 88188; Plot Q82, 24 Sept. 1988, Keizer 88084; Odoorn, Odoornerveen, 18 Nov. 1987, Keizer 87256; Keizer 87296; 22 Sept. 1988, Keizer 88100; Keizer 88113; 1 Nov. 1988, Keizer 88182.
Obs.: This species is different from *C. rigens* and *C. obtusus* (both with iodoform-like smell) in the relatively dark colours and grey-fibrillose layer on the pileus. In addition, *C. obtusus* has a striate cap when moist. *Cortinarius velenovskyi* is a little-known species, not reported before from the Netherlands (Arnolds, 1984; Arnolds & al., 1989).
C. velenovskyi was described two times by Henry (1940, 1967). The first description refers directly to the description by Velenovsky (1917) of *C. obtusus*. The second description is an extension of the first, but differs in the description of the smell, which is "faible" ("weak") in the first and "de bois de crayon, d'*H. russocoriaceus*" ("of cedar-wood, of *Camarophyllus russocoriaceus* (Berk. & Miller)Lange"), sometimes mixed with iodoform or radish, in the second description. The plate of *C. velenovskyi* in the publication of 1967 shows rather pale (dried out?) specimens. In our opinion the two descriptions do not differ substantially and therefore we do not agree with Gaugé (1974, 1977) who created a new name (*C. fragrantior* Gaugé) for the species described by Henry (1967).
The specimens studied here differ from the description by Henry (1967) in having a smell which is predominantly iodoform-like.

Cortinarius violilamellatus Pearson ex P.D. Orton (Fig. 24)
Carpophores often (sub)cespitose, growing in clusters of (1-)3-10. Pileus 13-35 mm, campanulate, soon expanding with broad to pointed umbo, hygrophanous, when moist dark reddish grey-brown or red-brown (Expo H22-J22(-J26), H52, H12, F52), centre slightly darker, margin translucently striate, when dry wood- to straw-coloured, ochraceous yellow-brown (C63-C64, B56, somewhat yellower than E46), paler towards the margin, surface slightly innately fibrillose, especially so at the margin, sometimes with sparse whitish hairy scales, more distinct towards the margin. Lamellae distant, sometimes irregularly veined, emarginate, 3-6 mm broad, not or slightly ventricose, at first pinkish violet or purplish, with edge remaining violet for some time, later entirely rusty brown with paler edge. Stipe 35-60x(2-)3-6 mm, cylindrical, sometimes slightly enlarged and tapering towards the base, hollow, concolorous with pileus, but appearance somewhat paler due to shiny pale brown fibrillum, darker to the base, the apex sometimes showing a violet hue, with whitish floccose velar remnants in lower half. Context in pileus coloured like surface, in the stipe yellowish brown, downwards dark brown. Smell distinct, as *Pelargonium zonale* or *Cortinarius paleaceus*.
Spores (8.0-)8.9-10.3(-11.0)x(4.0-)4.3-5.0(-5.1) µm, Q=(1.8-)1.9-2.3(-2.5), Q=1.85-

2.44, narrowly amygdaliform or slightly fusiform, frequently with small depression just above the hilar appendix, minutely punctate or verruculose. Basidia with brown content present; brown extracellular pigment present in the hymenophoral trama. No sterile cells observed in the hymenium.
Collections examined. - Plot F24, 10 Nov. 1986, Keizer 86228; 7 Oct. 1988, Keizer 88095; Plot F34, 19 Nov. 1986, Keizer 86254; 1 Oct. 1987, Keizer 87289; 28 Oct. 1988, Keizer 88286; Plot Q32, 18 Sept. 1986, Keizer 86149; Plot Q35, 10 Nov. 1986, Keizer 86225; 22 Sept. 1987, Keizer 87189; Keizer 87197; 3 Nov. 1987, Keizer 87260; 7 Oct. 1988, Keizer 88080 (type; Odoorn, Odoornerveen, 13 Oct. 1987, Keizer 87233; Keizer 87311; 19 Nov. 1987, Keizer 87304; Assen, Kloosterveen, 13 Oct. 1988, Keizer 88335 (leg. E. Arnolds).
Obs.: The combination of *Pelargonium*-like smell, violaceous colours in the young lamellae, rather small size, sparse whitish velar remnants on the cap and especially the ± fusiform spores are characteristic for this species. Besides, the (sub)cespitose growth of the carpophores in open grassy vegetation on nutrient-poor sandy soil seems to be characteristic as well.
It clearly differs from *C. sertipes* and *C. pulchripes* in much narrower spores and the *Pelargonium*-like smell. *C. fusisporus* Kühner may be related but the smell is absent, the veil is dirty whitish and the spores are longer with Q=2.1-2.5 while most spores have Q=2.3. Moser (1983) mentions three species with Pelargonium-smell, viz. *C. paleacens*, *C. paleiferus* and *C. rigidus* Fr. ss. Kühn. & Romagn.. The first species has more abundant white hairy scales on the pileus and no violaceous colours in the lamellae when young which are more over crowded. The second has more distant (Marchand, 1983) and violaceous lamellae when young like in the present species, but the spores are broader and the pileus is covered with white hairy scales. *Cortinarius rigidus* ss. Kühn. & Romagn. has crowded lamellae without violaceous colours and smaller spores (7.2-9.5x4.2-5.7 μm).
Orton (1984) describes this species as occurring in coniferous forests. In our opinion, no taxonomic value can be ascribed to ecological preferences. The morphological characters of the specimens found during this study fit sufficiently well the description in Orton (l.c).

Cyphellostereum laeve (Fr.:Fr.) D.Reid (Fig. 55)
Coll.: 87303.
Fruitbody irregularly ear-shaped, ±5-10 mm long, outer surface whitish, inner surface (hymenium) cream-coloured, dorsally attached to bryophytes: *Dicranella heteromalla*, *Isopterygium elegans*, *Mnium hornum*.
Spores (4.0-)4.5-5.2(-6.2)x(1.8-)2.0-2.5(-2.7) μm, Q=(1.8-)2.0-2.7, Q=2.27, pip-shaped, often in tetrads. Basidia 4-spored. Cystidia 30-40x3.5 μm, narrowly fusiform with blunt apex, thin-walled, hyaline. Hyphae 2-2.5 μm broad, septa without clamp-connections.
Obs.: Macroscopically this species is rather similar to *Mniopetalum globisporum*, which differs among other things in the globose spores.
C. laeve has been recorded only a few times in the Nethewrlands (Arnolds, 1984).

Entoloma lividoalbum (Kühn. & Romagn.) Kubicka (Fig. 27)

Pileus 45-65 mm, convex to plano-convex without prominent umbo; hygrophanous, when moist yellowish grey-brown (Expo E64) or more greyish brown, shortly translucently striate (± 5 mm), on drying paler (C72-74). Lamellae moderately to strongly ventricose, distant, crenulate, pink, with edge concolorous. Stipe 40-55 x 10-15 mm, cylindrical or slightly broader towards the base, yellowish white to white, silvery white striate. Context in all parts greyish white. Smell indistinct; taste somewhat farinaceous with bitter after-taste.
Spores (7.5-)8.0-9.0x6.5-8.0 µm, isodiametrical to slightly oblong, Q=(0.9-)1.1-1.3, Q=1.17-1.23, mostly 5-angled. Pigment in pileipellis diffuse, intracellular; clamp-connections present.
Collections examined. - Plot Q82, 24 Sept. 1988, Keizer 88088; Odoorn, Odoornerveen, 17 sept. 1987, Keizer 87164.
Obs.: This species is very rare in the Netherlands. It was reported by Noordeloos (1988:102) from two localities only. Our collections differ in slightly narrower spores.

Entoloma undulatosporum Arnolds & Noordel. (Fig. 28)
Pileus 9-19 mm, plano-convex with weak or small, pointed umbo, hygrophanous, when moist dark grey-brown (Expo E41, F41), translucently striate, on drying somewhat paler, then silvery silky shining, sometimes radially splitting. Lamellae up to 3.5 mm broad, ventricose, distant, dark grey-brown like pileus or slightly paler (between D61 and D63), with edge paler, crenulate. Stipe 25-32 x 1-4 mm, cylindrical, grey-brown, at apex paler and with minuscule white squamules, downwards glabrous or somewhat silver-white, striate, fistulose or solid. Smell absent or weakly farinaceous.
Spores (8.0-)8.2-10.0(-10.5) x 5.0-6.5(-7.0) µm, 6-8 angled in side-view, Q=1.3-1.7(-2.0), Q=1.43-1.61. Basidia 4-(2-)spored. Cheilocystidia absent. Pigment in pileipellis diffuse, intracellular. Clamp-connections present.
Collections examined. - Plot Q74, 22 Sept. 1987, Keizer 87177; Plot Q83, 29 June 1987, Keizer 87011; 8 Sept. 21988, Keizer 88318.
Obs.: My collections differ in some respects from the description by Noordeloos (1988), viz. in the silvery striate stipe and relatively narrow spores. The undulate outline of the spores is regarded as distinctive for this species. However, *E. undulatosporum* comes close to *E. subradiatum*. The study of more material is needed to assess the taxonomic status of both taxa.

Hebeloma (Fr.) Kumm.
"Il n'est pas de genre où la taxonomie des espèces soit plus embrouillée. C'est un véritable chaos". (Favre, 1960). It seems that little has changed since, despite recent revisions of the genus (Bruchet, 1970; Boekhout, 1982). The taxa that could be distinguished in the present material agreed rather well with the concepts of Boekhout (l.c.), which, for the time being, have been adopted. Particularly the taxa which belong to the species complex *H. crustuliniforme sensu lato* are difficult to separate (see there). The extremes in this complex are widely different, but most of the differentiating characters are not correlating in many less typical collections.

Hebeloma anthracophilum Maire (Fig. 29)
Pileus 6-25 mm, convex to plano-convex, sometimes umbonate, when young with involute margin, pale pinkish brown (Expo C56), paler towards the margin. Lamellae 1-1.5 mm broad, ventricose, moderately crowded, narrowly adnate, purplish grey-brown,

with white-floccose margin. Stipe 20-35x1.5-3.0 mm, cylindrical, at base slightly rooting, narrowly fistulose, apex cream-coloured, downwards brownish, at base dark brown, at apex white-floccose, downwards glabrous. Context in pileus and apex of stipe white, downwards in stipe darker brown. Smell faint to absent, taste unknown.
Spores (9.3-)9.5-10.3(-11.2)x(4.7-)4.9-5.9(-6.1) μm, Q=1.7-2.0(-2.1), $\underline{Q}$=1.72-2.00, ellipsoid-subamygdaliform with loose exosporium, enveloping the complete spore, except for the hilar appendage; inner sporewall (epispore) thick-walled, with coarse roundish or irregularly shaped warts, rather dark brown sub micr.. Cheilocystidia 30-40x4-6 μm, $\pm$ cylindrical, not or hardly enlarged at base or apex, thin-walled.
Collections examined. - Plot Q93, 30 Oct. 1987, Keizer 87268; Odoorn, Odoornerveen, 13 Oct. 1987, Keizer 87338; 31 Oct. 1989, Keizer 89100.
Obs.: This species shows much resemblance with *H. spoliatum* in the microscopical characters. Macroscopically, the distinctly rooting stipe and more uniformly red-brown pileus of the latter are distinctive. We agree with Boekhout (1982) in considering *H. calyptrosporum* Bruchet synonymous with *H. anthracophilum*. The only differences mentioned by Bruchet (1970) are the habitat (growing on burnt places or not) and the stipe turning brownish with age or not. Differences in habitat alone cannot serve as distinguishing characters and a discolouring of the stipe with age is so common in the genus *Hebeloma* that it is certainly not sufficient to distinguish taxa on the level of species, if it is of any use at all.

Hebeloma crustuliniforme sensu lato.
It appeared to be difficult to identify *Hebeloma* species of the group of *H. crustuliniforme* ($\pm$ section *Denudata* (Fr.) Sacc.). This group as a whole is characterized by carpophores without veil, with long ($\pm$ 50-100 μm), narrowly clavate to capitate cheilocystidia and amygdaliform spores with at most partially loosening perispore.

In order to separate taxa in a more or less objective way, groups have been distinguished in the 30 available collections, following the method described by Arnolds (1974): the groups were distinguished on the basis of characters that will be mentioned below, independent from previous species concepts in the literature. Subsequently, these groups were compared with taxa (species) described in literature. The advantage of this method is that individual collections are not "forced" to match the description of a certain taxon. The following characters have been used: (1) habit, i.e. size and shape of the fruitbody; (2) colour of the pileus; (3) stipe hollow or not; (4) lamellae weeping at the margin or not, droplets watery or milk-white; (5) size and shape of the cheilocystidia; (6) size and shape of the spores; type of ornamentation; loosening of the perispore or not; reaction with Melzer's reagent; (7) smell.

The characters 3 and 4 appeared to be too variable, even within collections, to be useful, although they are considered by some authors as rather important (e.g. Bruchet, 1970; Moser, 1978). In general, the stipe tends to become hollow as the sporocarp ages. Moreover, slender carpophores tend to have less often hollow stipes. Also the formation of droplets at the margin of the lamellae appears to be age-dependent (old specimens cease guttation) and varies with weather conditions. Dry weather hampers the excretion of liquid. This liquid can turn milky white after some time, which again makes the character dependent of the moment of collecting of the fruitbody.

Because mycocoenologists, unlike taxonomists, are often forced to study fruitbodies in far from optimal conditions, most value has been assigned in this study to microscopic characters, assuming that they are less influenced by external factors than

macromorphological characters. In our opinion, the characters of weeping lamellae and the presence of a cavity in the stipe as well as the density of the white floccose squamules covering the stipe, discussed in Boekhout (1982), together with so-called ecological characters, have been overestimated in literature, thus contributing to the confusion in this group.

On the basis of the shape and size of the cheilocystidia three groups could be distinguished with (a) cheilocystidia rather short, e.g. 40-60 μm, the majority slenderly clavate with somewhat ventricose base, frequently with (sub-)capitate apex; (b) cheilocystidia 40-80 μm long, except for the very short ones (< 40 μm, always present together with the longer cystidia) usually not ventricose but with more or less parallel walls near the basis, very gradually broadening towards the apex; apex frequently furcate or ± irregularly shaped; (c) cheilocystidia up to 100 μm long, not ventricose near the base, hardly broader towards the apex to slenderly clavate, or a minority of the cystidia irregularly capitate. These groups were identified as *H. helodes*, *H. longicaudum* and *H. crustuliniforme* ss. str. respectively.

Some of the above-mentioned characters correlated rather well with the different form and size of the cheilocystidia.

(1) Habit of the fruitbody: *Hebeloma crustuliniforme* ss. str. has large and relatively thick-set carpophores, with context in the pileus relatively thick (up to more than 10 mm in centre) and with thick stipe (over 6 mm, near base over 10 mm thick). *H. helodes* and *H. longicaudum* generally have smaller pilei and more slender stipes.

(2) Colour of the pileus: *H. crustuliniforme* has a ± uniform pale brown or alutaceous pileus; the other two species usually have a darker reddish brown centre contrasting with a pale margin.

(6) Size and shape of the spores: *H. longicaudum* has relatively broad spores with Q=1.56-1.71, whereas *H. crustuliniforme* and *H. helodes* have more slender spores with Q=(1.69-)1.72-1.92(-2.14) respectively (Fig.30).

Differences in consistence of the stipe (3), weeping of lamellae (4) and smell (7) did not correlate with the size and shape of the cheilocystidia; all specimens had a raphanoid smell. The differences in characters of the spores (6) other than size and shape, such as type of ornamentation, colour (sub micr.), loosening of the outer spore-wall and a dextrinoid reaction with Melzer's reagent, described by Boekhout (l.c.) and Bruchet (l.c.), could not be confirmed by the study of the present material.

Hebeloma crustuliniforme comes closest to *H. helodes*. Robust carpophores of the latter with long cystidia can only be separated from the former by the darker and contrasting centre of the pileus, and this hardly warrants a distinction on specific level. It seems, however, that this problem occurs in only a minority of the collections. For further details, see descriptions of the individual species.

Hebeloma crustuliniforme (Bull.) Quél. *sensu* Boekhout (Fig.32)

Pileus 38-80 mm, convex, then expanding, at centre pale beige yellowish (Expo A62), towards the margin gradually paler (A61), viscid when moist, with age turning dirty ochre yellowish. Lamellae ± 6 mm broad, narrowly adnate, moderately distant, pale brown to pale purplish brown, margin white-floccose, without droplets. Stipe 70x6 mm, cylindrical but at the base enlarged up to 10 mm broad, whitish with white floccose squamules, mainly in the apical part, narrowly fistulose. Context whitish. Smell raphanoid. Spores (9.5-)9.7-10.5(-10.6)x5.5-5.9(-6.0) μm, Q=1.6-1.8, Q=1.75, often

with loosening perispore (not at apex), therefore seemingly thick-walled, rather coarsely verrucose; pale yellowish brown sub micr., not discolouring in Melzer's reagent. Cheilocystidia 50-100x2.5-3 μm, long, slender, more or less cylindrical, slightly enlarged in the apical part, up to 6 μm broad, the short ones somewhat ventricose near the base, the long ones with parallel walls throughout
Collection examined. - Plot F41, 28 Oct. 1988, Keizer 88201.
Obs.: This collection has been called *H. crustuliniforme* on account of the long (up to 100 μm) cheilocystidia, the more or less uniformly coloured, pale pileus and the rather robust habit of the carpophores. The species is accepted here in the sense of Boekhout (1982) and not in the sense of Bruchet (1970). Their interpretations of *H. crustuliniforme* differ in the range of the length of the cystidia: 40-60(-70)x4(-5) μm according to Bruchet (l.c.) and 35-95x2-9 μm according to Boekhout (l.c.).
H. crustuliniforme ss. Bruchet (l.c.) possibly represents *H. longicaudum*.

Hebeloma helodes J. Favre (Fig. 33)
Syn.: *Hebeloma fragilipes* Romagn., *H. oculatum* Bruchet, *H. velutipes* Bruchet, *H. helodes var. capitatum* prov. Boekhout.
Pileus 20-100 mm, convex, soon expanding, finally sometimes somewhat depressed, with centre orange to brown-yellow or reddish ochre-brown (Expo B56, C64, E52, D58, E32, E54, C-B56, C46), paler towards the margin, pinkish beige (B52, A21-22, C63), viscid when moist. Lamellae up to 7 mm broad, moderately to slightly crowded, sometimes ventricose, narrowly adnate or emarginate, rather pale brownish, "caramel"-coloured, pale "café-au-lait" (B32, C64), margin white-floccose, sometimes guttating hyaline droplets or with brown spots (aggregations of spores where drops have evaporated), but often no trace of guttation visible. Stipe 40-100x3-12 mm, cylindrical or with somewhat broader base, mostly fistulose with narrow or wide cavity, in the latter case with a hanging strand in the cavity, sometimes stuffed, whitish or cream-coloured, on handling dirty pale brown, white-floccose, mainly at the apex. Context in the pileus with a grey watery zone above the gills, in the stipe white. Smell weakly or distinctly raphanoid.
Spores (9.0-)10.5-13.3(-14.8)x(5.0-)5.6-7.0(-7.7) μm, narrowly amygdaliform, Q=(1.5-)1.7-2.1(-2.4), Q=(1.69-)1.72-1.92(-2.14), perispore (in ammonia 10%) often loosening in part of the spores, not so at the apex, sometimes with some hyaline blisters, usually with fine warts, the biggest spores often with only weak ornamentation. Cheilocystidia 30-70(-90)x(2-)3-8(-16) μm, ventricose at the base, apical part clavate to (frequently) capitate, usually thin-walled.
Collections examined. - Plot F14, 30 Oct. 1987, Keizer 87313; Plot F15, 26 Aug. 1987, Keizer 87126; Plot F16, 13 Nov. 1986, Keizer 86232; Plot F21, 30 Oct. 1986, Keizer 86192;19 Nov. 1986, Keizer 86260; 24 Sept. 1988, Keizer 88120; Plot F24, 22 Sept. 1987, Keizer 87181; 3 Nov. 1987, Keizer 87255; Plot F41, 4 Sept. 1987, Keizer 87123; Plot Q2, 13 Oct. 1988, Keizer 88223; Plot Q11, 19 Nov. 1986, Keizer 86259; Keizer 86273; Plot Q26, 18 Sept. 1986, Keizer 86155; Plot Q33, 20 Oct. 1986, Keizer 86173; 22 Oct. 1988, Keizer 88308; Plot Q35, 10 Sept. 1986, Keizer 86141, 24 Oct. 1986, Keizer 86189; 10 Nov. 1986, Keizer 86231; 7 Oct. 1988, Keizer 88157; Plot Q43, 29 Sept. 1986, Keizer 86112, Plot Q83, 8 Sept. 1988, Keizer 88175; Odoorn, Odoornerveen, 1 Nov. 1988, Keizer 88257.
Obs.: For an evaluation of the differences of this species with *H. longicaudum* and *H. crustuliniforme*, see the discussion under the *H. crustuliniforme* group.

Typically, the cheilocystidia of *H. helodes* are rather short and slender. Other types of cheilocystidia have been encountered in several collections: (1) Cystidia up to 60 μm long, clavate and frequently with thickened walls in the middle part. This variant is identical with *H. fragilipes* Romagn., which was regarded by Boekhout (1982) as a variety of *H. helodes* (Fig. 32 l.). (2) Cystidia long and slender (up to 90-100 μm), only slightly clavate. This variant is identical with *H. oculatum* Bruchet and was regarded by Boekhout (l.c.) as a form of *H. helodes*. (3) Cystidia in addition to the typical ones broadly clavate to capitate, with heads up to 12(-16) μm broad; distinguished by Boekhout (l.c.) as *H. helodes* var. *capitatum* prov.. Until the study of extensive material shows the contrary, we consider these as taxonomically insignificant variants.

Bruchet (1970) used the name *H. velutipes* for the present species. He apparently did not know *H. helodes* J. Favre because he did not mention it explicitly. Two collections of *H. helodes* J. Favre, one of them being the lectotype (coll. G.K. 9139, 30-8-1939, Tourbière du sentier, Herb. G.), the other collected and identified by the author (coll. G.K. 7721, 29-9-1941, Haut Marais des Pleiades, Herb. G.), have been studied here in order to compare some of the microscopic characters (Fig. 33). The spores differed somewhat between the two collections, and were (9.3-)9.6-10.0(-10.7)x(4.9-)5-5.5(-5.7) μm, Q=1.7-1.9, $\underline{Q}$=1.8 and (10.4-)10.5-11.7(-12.5)x(5.3-)5.4-5.9(-6.0) μm, Q=1.9-2.1, $\underline{Q}$=2.0 respectively, narrowly amygdaloid, perispore loosening in part of the spores, ornamentation consisting of fine warts, pale brown in ammonia 10%. Cheilocystidia 35-65x4-5 μm, in majority cylindrical with more or less capitate apex, 7-11 μm wide, sometimes slightly ventricose at the base, some slightly thick-walled. These collections show in our opinion sufficient similarities with the collections described here to justify the name *H. helodes*. Consequently we consider *H. velutipes* Bruchet as a later synonym of *H. helodes*.

Probably, this common species has been included by most authors in *H. crustuliniforme* (*sensu lato*) until recently. It seems likely that still an older name exists somewhere in the literature because it is remarkable that such a common and wide- spread species is "discovered" as late as 1948 in montane peat-bogs.

Hebeloma longicaudum (Pers.:Fr.) Kumm. (Fig. 34)

Pileus 28-35 mm, convex, then plano-convex, often with broad and low umbo, with margin at first involute, pale orange-pinkish brown (Expo D54, E54 or paler: C64) with paler margin (D52 or much paler), or ± uniformly pale beige (A61) with somewhat paler margin, viscid when moist. Lamellae narrowly adnate or emarginate, 3-5 mm broad, moderately crowded, pale beige-brown, with age purplish brown, with edge white-floccose, sometimes slightly serrulate, sometimes weeping. Stipe 35-60x6-10 mm, usually cylindrical but base often bulbous, up to 15 mm wide, fistulose or stuffed, cream-coloured, downwards pale brownish, entirely white-pruinose or floccose, but less distinctly so to the base. Context in the pileus and stipe very pale beige to white. Smell raphanoid.

Spores (10.0-)10.5-12.2(-12.6)x(5.9-)6.3-7.3(-7.5) μm. Q=1.5-1.8, $\underline{Q}$=1.56-1.71, usually rounded, sometimes tapering or papilla-like, perispore sometimes somewhat loosening (in ammonia 10%), with ornamentation consisting of fine, punctiform warts, pale brown sub micr., not dextrinoid. Cheilocystidia 40-80x8-11 μm, usually slenderly clavate, gradually broadening towards the apex, apex frequently lobed or bifurcate, usually not ventricose at the base, sometimes slightly ventricose towards the base of short

cystidia, sometimes a few slightly thick-walled.
Collections examined. - Plot Q1, 6 Oct. 1986, Keizer 86172; Plot Q2, 22 Seopt. 1986, Keizer 86156; Plot Q43, 6 Oct. 1987, Keizer 87215; 12 Oct. 1988, Keizer 88089.
Obs.: The combination of the non-ventricose and frequently lobed or furcate cystidia and the relatively broad spores is characteristic for this species. For a more detailed comparison of this species with *H. helodes* and *H. crustuliniforme*, see the observations under the *H. crustuliniforme* group.

The name *H. longicaudum* was rejected by Boekhout (1982:97), but on the basis of an incorrect interpretation of the rules of nomenclature. He compared his description with Fries' description in Epicrisis (1838:181), but that is not relevant from a nomenclatural point of view. Fries sanctioned *Agaricus longicaudus* in 1821(:248) on the basis of Persoon's diagnosis from 1801(:332), which consequently should be regarded as the basis for (neo)typification. Both descriptions differ considerably from the concept in the Epicrisis. *Agaricus longicaudus* Pers. fits the present fungus well (although the description is very short and therefore an irrefutable interpretation cannot be given). The combination of a pale leather-coloured pileus, a white, cylindrical stipe and punctate lamellae (due to dried excreted droplets!) suggests a *Hebeloma* near *H. crustuliniforme*. The small pileus and slender stipe exclude *H. crustuliniforme sensu stricto*. It should be noted that Persoon's description concerns a slender variant (pileus ± 40 mm, stipe ± 100x4-6 mm), as depicted by Lange (1938:119E). However, more thick-set variants are equally wide spread and represent in our opinion the same taxon. This interpretation of *Agaricus longicaudus* is in agreement with widely accepted interpretations by Konrad & Maublanc (1924-37: pl.79), J. Lange (l.c.) and Bruchet (1970:77).

Hebeloma spoliatum (Fr.) Gillet (Fig. 35)
Pileus 7-35 mm, convex to plano-convex, warm red-brown (Expo F48, F-H36, E26), on drying more yellowish red-brown (E56), towards the margin paler, pinkish beige (C63), viscid. Lamellae up to 5 mm broad, crowded, emarginate to narrowly adnate, not or slightly ventricose, pale purplish brown, margin white-floccose, not weeping. Stipe 22-35x1-5 mm (exclusive of the rooting part), cylindrical with rooting base, upper half pale beige to whitish, downwards greyish brown (± E68), solid, floccose. Flesh in pileus white, above the lamellae greyish, in stipe cream-coloured in upper part, becoming brownish more downwards. Smell faintly raphanoid; taste bitter.
Spores (8.6-)9.4-10.6(-10.7)x(5.0-)5.2-5.9(-6.1) µm, Q=1.7-2.0(-2.1), Q=1.75-1.85, ellipsoid with loosening perispore which envelopes the complete spore, except for the hilar appendix, epispore thick-walled with coarse, rounded or elongate warts, rather dark brown sub micr.. Cheilocystidia 25-50 µm long, ± cylindrical or apex slightly enlarged, base sometimes slightly ventricose, sometimes with slightly thickened walls.
Collections examined. - Plot F32, 22 Oct. 1986, Keizer 86190; 13 Nov. 1986, Keizer 86233; Plot Q2, 13 Oct. 1988, Keizer 88128.
Obs.: This rare species, well characterised by the rooting stipe, shows microscopically much similarity with *H. anthracophilum*, which has no rooting base of the stipe. The interpretation of Boekhout (1982), which has been followed, deviates from Bruchet (1970); the latter author mentions that the perispore is not loosening.

Gröger (1987) distinguished two taxa within *Hebeloma spoliatum* on the basis of habitat preference: 1. *H. spoliatum* Fr. in the original sense of Fries (1838) i.e. occurring in mountainous pine forests and 2. *H. danicum* Gröger (= *H. spoliatum* as interpreted by

various modern authors e.g. Bruchet (1970), Romagnesi (1983), Weholt (1983)), which occurs in beech forests. We do not support this view because ecological differences alone do not warrant a distinction on specific level.

Hebeloma truncatum (Schaeff.:Fr.) Kumm. (Fig. 36)
Pileus 28-80 mm, hemispherical, then plano-convex, with broad umbo or not umbonate, rather irregularly shaped, red-brown, then more yellowish brown (Expo E58, D56) towards the margin slightly paler, smooth, dry. Lamellae up to 8 mm broad, ventricose, rather crowded, emarginate adnate, at first pale cream-colour, then with colour of milk-chocolate, margin white-floccose and sometimes serrulate, without droplets. Stipe 30-55x4-22 mm, mostly tapering to the base, sometimes with tendency of rooting, fistulose, apex whitish to beige, densely white-floccose, downwards brown to dark brown, slightly flocculose. Context pale cork-coloured in cap, darker brown in stipe. Smell raphanoid. Taste unknown.
Spores (8.0-)8.5-10.2(-10.4)x(4.1-)4.5-5.0(-5.2) μm, Q=1.7-2.1 and $\underline{Q}$=1.79-2.01, oblong to amygdaloid, finely punctate without loosening exospore. Cheilocystidia 25-45 mm long, sometimes more or less cylindrical, more often with both apex and base ventricose, frequently some cystidia with thickened walls.
Collections examined. - Plot Q2, 28 Oct. 1986, Keizer 86193; 15 Sept. 1988, Keizer 88085; 14 Oct. 1988, Keizer 88235; Plot Q32, 18 aug. 1987, Keizer 87028.
Obs.: According to Bruchet (1970), the cheilocystidia are more cylindrical and longer. However, the spores and the colour and habit of the sporocarps point to *H. truncatum*.

Inocybe albomarginata f. *longispora* f. nov. prov. (Fig. 38)
Pileus 24-48 mm, plano-convex, then expanding with faint umbo, dark reddish brown sometimes with greyish tinge (Expo J22, J42), paler towards the margin (D44-E58), with appressed squamules, at margin not rimulose, no velipellis observed. Lamellae thin, crowded, up to 5 mm broad, pale (yellow-)brown, soon darker, narrowly adnexed, with white-flocculose edge. Stipe 46-52x5-9 mm, cylindrical but towards the base sometimes enlarged up to 11 mm, subbulbous, pale beige-isabella, pinkish orange or pale brown (A22-C56), longitudinally striate, pruinose to about 2/3 radius. Context whitish in the pileus, more reddish in the stipe, especially near the cortex. Smell and taste unknown.
Spores (8.0-)8.3-10.0(-10.3)x(4.0-)4.1-4.8(-5.0) μm, oblong, Q=(1.8-)1.9-2.3, $\underline{Q}$=2.04-2.13, smooth, $\pm$ regular but sometimes with a faint depression, brown. Basidia 4-spored. Pleurocystidia 50-68x12-17 μm, lageniform, with 1-2 μm thick, pale, faintly yellowish walls, crystalliferous at apex, cheilocystidia as pleurocystidia, roundish cells abundant.
Obs.: Macroscopically this taxon fits well in *I. albomarginata* and shows some resemblance with *I. grammopodia*. The former has smaller spores ((6.0-)6.5-8.0(-8.5)x4.0-5.0 μm, Q=1.4-1.7, $\underline{Q}$=1.5-1.7 (Kuyper, 1986)) and the latter has larger spores with a conical apex and more (sub-)cylindrical pleurocystidia. Since this taxon grows in the same place where typical *I. albomarginata* is present and intermediate variants might occur, we decided to name it provisionally and on the taxonomic level of forma.

Inocybe amethystina Kuyp. (Fig. 38)
Pileus 6-13 mm, broadly campanulate, soon plano-convex with indistinct umbo, brown, then pale grey-brown (Expo F62 to C62), woolly fibrillose, near centre with scales darker than the surface of the pileus, with some remains of veil. Lamellae up to 2 mm broad, narrowly adnate, rather dark brown, with white-floccose edge. Stipe up to 28x2 mm,

cylindrical, hardly broader at the base, upper half pinkish-violet, downwards pale beige, in older carpophores violet colour only visible at the apex, only apex (± 1/10) pruinose, downwards brown-fibrillose. Smell indistinct.
Spores 9.3-10.3x4.5-5.2 μm, Q=1.9-2.2, Q=1.99, oblong-amygdaliform, with the abaxial side more rounded than the adaxial side. Pleurocystida 40-50x11-15 μm, narrowly lageniform, with 1.5-2.0 μm thick, yellow walls and some crystals at apex.
Collection examined. - Plot F24, 7 Oct. 1988, Keizer 88296.
Obs.: The identification was confirmed by Kuyper. This collection differs in several respects from Kuyper's description (1986:136), viz. in very small carpophores, narrower spores and smaller pleurocystidia.

Inocybe assimilata (Britz.) Sacc.
Syn. *I. umbrina* Bres.
Collections examined. - Plot Q2, 15 Sept. 1987, Keizer 87328; Plot Q4, 29 June 1987, Keizer 87016; Plot Q31, 19 Aug. 1987, Keizer 87069; 15 Sept. 1987, Keizer 87151; Plot Q34, 29 June 1987, Keizer 87350; Plot Q93, 8 Sept. 1986, Keizer 86157; 30 Oct. 1987, Keizer 87270.
Obs.: The shape and size of the spores are rather similar to those of *I. soluta* Velen. (= *I. brevispora* Huijsman). The two species differ among other things (such as structure of surface of pileus and shape of the base of the stipe) in the colour of the spore-print: in *I. assimilata* dark tobacco brown (Expo H63), in *I. soluta*, slightly more yellowish tobacco-brown (F63).

Inocybe huijsmanii Kuyp. (Fig. 39)
Pileus 8-15 mm, convex or campanulate without prominent umbo, ochraceous grey-brown, orange-brown to pale ochraceous isabella (Expo D63, E54, Mu 2.5 YR 7/4-6/4), radially fibrillose, fibrils not diverging, with some indistinct patches of veil around centre, at margin with remains of cortina. Lamellae 1.5-2 mm broad, not or slightly ventricose, moderately to slightly crowded, narrowly adnate, pale brown with pink-lilac hue, edge white-floccose. Stipe 20-31x1.5-2.5 mm, cylindrical with slightly enlarged base, pale beige or isabella ochraceous, entirely or only at apex with a lilac hue (Mu 2.5 YR 7/3-7/4), covered with white fibrils. Context in pileus and apex of stipe pinkish-lilac, in the other parts white. Smell spermatic.
Spores 8.0-9.0(-9.4)x4.2-5.0(-5.7) μm, Q=1.5-2.1, Q=1.65-1.97, ellipsoid or somewhat amygdaliform, in coll. 88304 often with a depression at the adaxial side. Pleurocystidia narrowly lageniform or narrowly fusiform, with walls 1.0(-1.5) μm thick and usually crystals at apex.
Collections examined. - Plot F21, 24 Sept. 1988, Keizer 88272; Plot F24, 7 Oct. 1988, Keizer 88304; Plot F43, 6 Oct. 1988, Keizer 88357.
Obs.: Collection 88304 unites some characters of both *I. huijsmanii* and *I. griseolilacina*: it shows a more or less smooth pileus surface with yellowish brown colours and lacks a *Pelargonium* smell (*I. huijsmanii*), but it shows violaceous colours and some subcapitate pleurocystidia (*I. griseolilacina*; cf. Kuyper, 1986:133-134). The spores deviate from other collections in the relatively narrow ellipsoid-subamygdaliform shape with frequently a depression in the adaxial wall. For the time being, this collection has been called *I.* cf. *huijsmanii*. Spores of all collections were smaller than those reported for *I. huijsmanii* by

Kuyper (1986:135). The species was not recorded before from the Netherlands (Arnolds, 1984; Arnolds et al., 1989).

Inocybe mixtilis (Britz.) Sacc. (Fig. 43)
Collections examined. - Plot F24, 24 aug. 1987, Keizer 87102; Plot F43, 6 Oct. 1988, Keizer 88219; Plot Q13, 22 Sept. 1987, Keizer 87191; Plot Q32, 18 Aug. 1987, Keizer 87097; 25 Nov. 1986, Keizer 86262; Plot Q65, 24 Sept. 1988, Keizer 88302b; Plot Q83, 29 June 1987, Keizer 87013.
Obs.: The present material is in good accordance with the descriptions by Stangl (1981, 1989), but the spores in the present material are more strongly nodulose than depicted by Stangl (l.c.).

Inocybe pseudoasterospora Kühner & Boursier var. *microsperma* Kuyp. & Keizer (Fig. 40)
Collections examined. - Plot Q63, 18 Sept. 1988, Keizer 88152; Plot Q93, 20 Aug. 1986, Keizer ThK2695; 21 Sept. 1987, Keizer 87173.
Obs.: This taxon agrees macromorphologically well with *Inocybe pseudoasterospora* but has smaller spores.
The reader is referred to the complete description by Kuyper & Keizer (1991). This description is based on more extensive material than the collections cited above.

Inocybe spec. (Fig. 41)
Pileus 9 mm, plano-convex without obvious umbo, brown to rather dark brown (Expo F63), at centre slightly more reddish brown; surface radially innate-fibrillose, fibrils hardly diverging towards the margin. Lamellae narrowly adnate, moderately crowded, (greyish) brown with grey brownish flocculose edge. Stipe 20x1 mm, cylindrical but at base bulbous, 2.5 mm broad, brown, slightly paler than the pileus, with bulb white-tomentose, otherwise smooth. Smell not observed.
Spores 9.4-11.1x4.5-5.0 μm, Q=2.0-2.3, $\underline{Q}$=2.17, smooth, narrowly amygdaliform, with remarkable apical papilla. Pleurocystidia 50-55x12-14 μm, with walls up to 2 μm thick, yellow in KOH 10%, often crystalliferous at apex. Cheilocystidia similar to pleurocystidia; paracystidia pyriform or broadly clavate, hyaline, thin-walled. Caulocystidia not observed.
Collection examined. - Plot Q45, 21 Sept. 1988, Keizer 88170.
Obs.: A relatively large proportion of the spores seems to be mis-shaped, with very long apex, or to the contrary much shorter, for instance 8.3x5.5 μm. This feature, together with the fact that the collection consists of only one small specimen, leads to the decision to let it unnamed. This specimen may be related to *I. phaeocomis* because of its small habit, spore-size, but differs a.o. by the absence of violaceous colours in the stipe, the absence of brown paracystidia, the apical papilla of the spores and its distinct bulbous base of the stipe (pers. comm. Th.W. Kuyper).

Laccaria bicolor (R. Maire) P.D. Orton (Fig. 43a,b)
Coll.: Q62, 4 Oct. 1987, K87210; Q38, 18 Sept. 1988, K88053; F21, 28 Oct. 1988, K88305.
Obs. *L. bicolor* has violaceous tinges in the lamellae and the basal mycelium, in ideal cases. However, the intensity of the violaceous colour is variable and specimens are met

without this colour at the basal tomentum and with only a lilac-pink hue in the lamellae, which come very close to typical *L. proxima* (see also obs. under *L. purpureobadia).*

Laccaria laccata (Scopoli:Fr.)Cooke (Fig. 43e)
Coll.: Q93, 8 Sept. 1986 K86134; Q33, 31 Aug. 1987, K87036.
This species is readily distinguished from *L. proxima* by the smoother pileus, less striate stipe and especially the globose spores with long spines (> 1 μm). According to Mueller (1991) the correct name for this taxon is *Laccaria laccata var. pallidifolia* (Peck)Peck. The typical variety, however, seems hardly distinct from *L.proxima.*

Laccaria proxima (Boud.)Pat. (Fig. 43c)
Collections examined. - Plot Q33, 3 Dec. 1986, Keizer 86275; Plot Q37, 7 Oct. 1987, Keizer 87288; Plot Q93, 8 Sept. 1986, Keizer 86135.
Obs.: Three taxa around *L. proxima* can be distinguished in the field, which all are characterized by small scales on the cap, striate stipe and, microscopically, broadly ellipsoid-subglobose spores with small spines (< 1 μm), viz. *L. bicolor, L.proxima* and *L. purpureobadia* (see obs. under *L. purpureobadia).*

L. purpureobadia Reid (Fig. 43d)
Coll.: Odoorn, Odoornerveen, 6 Oct. 1986, Keizer 86169; Q31, 28 Oct. 1987, Keizer 87266.
Obs.: This taxon, which is characterized by the dark purplish brown colours of pileus and stipe, was found twice, and in one case it grew mixed in a large group of typical *L. proxima.* The fruitbodies of both "species" were identical except for the dark colours in *L. purpureobadia* (like the water painting in Reid, 1966: pl. 5 and the photograph in Phillips, 1981:53). In Fig. 43 it is shown that the spores of the collected *L. proxima, L. bicolor* and *L. purpureobadia* are largely similar. Consequently, if these taxa are only characterized by (rather variable) colours, it becomes questionable whether a distinction on specific level is desirable in this case. It would seem that the rank of variety is more appropriate, but mating experiments have shown the interindependency of these species (Fries & Mueller, 1984), except for *L. purpureobadia,* which was not tested. In conclusion, although it seems that the species differ in only one character (colour of carpophore and mycelium) which would point to a distinction on the level of variety, the specific status is maintained because of the proven intersterility of most of the collections belonging to the taxa distinguished on the basis of their morphology.

Leccinum oxydabile (Sing.) Sing.
Pileus 30-42 mm, convex to hemispherical, hazel-brown (Expo E-F62), at margin and in young specimens slightly paler, slightly tomentose, near centre with very fine hairy scales. Tubes up to 7 mm long, at first white, soon greyish-brown, often ochraceous yellow-brown. Stipe 95x12 mm, slightly tapering upwards, cream-coloured, covered with warts which are white and small near apex, coarser downwards and with purplish brown tips near base spotted greenish blue. Context white, after a few minutes becoming pink, in extreme base of stipe dirty yellow. Smell absent, taste not tested.
Spores 17.0-9.5x6.0-6.5 μm, fusiform.
Collection examined. - Plot Q2, 15 Sept. 1988, Keizer 88137.
Obs.: The pinkish discoloration of the context, rather pale pileus and the broad spores are

distinctive for this species. This collection fits well with the description by Watling (1970:53). The sporocarps grew between small, yearly mown birches. Most records of *L. oxydabile* from the Netherlands concern *L. variicolor* Watling (= *L. oxydabile* ss. Sing. 1967) or *L. roseofractum*. *Leccinum oxydabile* was not reported with certainty before.

Mycena aetites (Fr.) Quél.
Collections examined. - Plot Q53, 5 Nov. 1986, Keizer 86214; Odoorn, Odoornerveen, 2 Nov. 1989, Keizer 89071; 11 Nov. 1983, Keizer 89090.
Obs.: For descriptions of *M. aetites* the reader is referred to Kühner (1938) and Maas Geesteranus (1988).
With the help of the keys by Maas Geesteranus (l.c.) it is rather simple to identify this species. In the field, however, it may show much resemblance with variants of the very common *M. leptocephala* which sometimes has a hardly perceptable chlorine-like smell, especially during cold and wet weather. Moreover, inodorous variants of both species seem to exist (Maas Geesteranus, l.c.). Field characters to separate *M. aetites* from *M. leptocephala* are among other things: 1) the stouter habit, 2) the more rigid consistency, 3) the more narrowly adnate lamellae that are usually darker grey in the latter species. In mycocoenological work, one is forced to identify large numbers of carpophores so that it is impossible to check every carpophore under the microscope. In this study, small specimens of *M. aetites* might have been mistaken for *M. leptocephala* in some cases.

Mycena filopes (Bull.:Fr.) Kumm.
Collection examined. - Plot Q2, 17 Nov. 1988, Keizer 88325.
Obs.: The typical *M. filopes* with grey-brown pileus with a pale margin is common and well-known. Another taxon exists which is more or less similar (Arnolds, 1982: 409 f.f.) except for the pink pileus. It is usually called *M. filopes var. metata* (Fr.) ss. Oort (according to Arnolds on variety level) or *M. metata* (Fr.) Kumm. ss. Oort. Although all intermediates exist between a grey-brown, pinkish grey-brown, greyish pink and pink pileus, the extremes seem to be rather different in several aspects. How subtle the difference in colour can be, is illustrated when fig. 7a (third fruitbody) and fig. 7b (first fruitbody) by Arnolds (1982) are compared. Minor differences beween these two taxa, apart of those given by Arnolds (l.c.), are: 1) the greyish taxon has a more (narrowly) parabolical pileus, the pinkish taxon has a slightly more campanulate-expanded pileus; 2) in the greyish taxon the dark colours in the centre of the pileus are more contrasting to the pale whitish colour of the margin; 3) the greyish taxon tends to grow solitary while the pinkish form usually occurs in groups of for instance 5-10 carpophores in an area of 1 dm^2. These characters are correlated, but in each character intergradations seem possible. The possibility to distinguish the taxa by using differences in the shape of the cheilocystidia, as proposed by Maas Geesteranus (1980), was rejected by Arnolds (l.c.). We support this last view and therefore recognize them as varieties, named var. *filopes* and var. *metata*, respectively.

Maas Geesteanus (1984) proposed another distinction of the species of this group, mainly on the basis of differences in the cheilocystidia and of the excrescences on top of them. Maas Geesteranus (l.c.) suggested that *M. sepia* consists of two different taxa: *M. sepia* J. Lange (considered synonymous with *M. filopes*) and *M. sepia* ss. Lundell, named *M. septentrionalis* Maas G.. The differences between *M. metata* and *M. filopes* were elaborated extensively, but many of the mentioned characters seem variable.

In this study, where large numbers of carpophores had to be identified, preferably for the greater part in the field, the distinction of the species as proposed by Arnolds (1982), largely based on habit and colour characters was preferred. See also *M. vitrea*.

Mycena spec.
Pileus 9 mm, paraboloid, greyish brown (Expo E62), paler towards the margin, translucently striate, on drying paler. Lamellae ± 1 mm broad, narrowly adnate, pale grey-brown, paler towards the edge. Stipe 30x1 mm, cylindrical but slightly swollen towards the base, ± concolorous with the pileus, smooth, but apex slightly pruinose and at base somewhat tomentose-hairy. Smell unknown. Growing on a buried cupule of beech.
Spores (5.5-)7.0-8.0x4.5-5.0 µm, pip-shaped or oblong, hyaline, amyloid. Basidia (1-)2-3(-4) spored. Cheilocystidia 25-35 x 12-16 µm, broadly clavate or ± vesiculose with usually rounded apex, thin-walled; no pleurocystidia observed. Hyphae of pileipellis diverticulate. Cells of cortex of stipe smooth; no caulocystidia observed.
Collection examined. - Plot F21, 23 July 1988, Keizer 88021.
Obs.: This specimen deviates from *M. leptocephala* (as described by Maas Geesteranus, 1988) by 1) smaller spores: (5.5-)7.0-8.0x4.5-5.0 µm versus (8.1-)9.4-11.2x4.5-6.5 µm and 2) the absence of caulocystidia. For the time being it remains unnamed because our collection consists of a single sporocarp in rather bad condition.

Mycena vitrea (Fr.) Quél.
Syn. M. sepia J. Lange
Collections examined. - Plot Q34, 5 Nov. 1986, Keizer 86125; Odoorn, Odoornerveen, 13 Oct. 1987, Keizer 87235; 1 Nov. 1989, Keizer 89088.
Obs.: *Mycena vitrea* has been distinguished in this study from *M. filopes* on account of two macroscopic characters, viz. the dark pileus with only slightly paler, not contrasting margin and the somewhat stouter habit. Using the key presented by Maas Geesteranus (1980), the problem arose that the cheilocystidia did not agree entirely with one of the described and depicted types, owing to their great variation even within one lamella, which renders this character of limited value. Therefore we refrained from the use of cystidial characters and we agree with Arnolds (1982) who came to the same conclusion. Arnolds (l.c.) noted that in his *M. filopes* collections, 18% had mainly 4-spored basidia whereas in *M. sepia* 82% of the collections was 4-spored. Consequently, this feature cannot be used as a distinctive character, at most as an additional character in doubtful cases.
Coll. 89088 had 4-spored basidia and coll. 87235 had 4- and 2-spored basidia with a majority of 4-spored ones.
See also observations under *M. filopes*.

Pluteus pallescens P.D. Orton (Fig.44)
Pileus 27 mm, plano-convex, without umbo, hygrophanous, when moist rather dark (greyish) brown (Expo F63), margin strongly striate, on drying paler grey-brown (E63), dull. Lamellae free, 4 mm broad, somewhat ventricose, salmon-coloured pink with white-floccose edge. Stipe 65x4 mm, cylindrical, creamy white, striate lengthwise, fistulose. Spores (5.8-)6.3-7.2(-7.8)x(5.0-)5.7-6.2(-6.5) µm, Q=1.0-1.2, $\underline{Q}$=1.13, (sub)globose, thick-walled with ± 0.4 µm thick walls. Pleurocystidia 30-70x15-39 µm, broadly

utriform to ± vesiculose, thin-walled, rather sparse. Cheilocystidia 30-50x15-25 μm, more or less similar to pleurocystidia but smaller and often broader clavate. Pileipellis consisting of sphaeropedunculate and broadly clavate cells.
Collection examined. - Plot Q22, 15 sept. 1987, Keizer 87136.
Obs.: This collection fits well with the description by Huijsman (1955) of *P. umbrinellus* (misapplied name according to Orton (1960) and Vellinga & Schreurs, 1985) and the plate by Bresadola (1927-1933:544-2)). The specimen found here was not as dark brown as mentioned by Moser (1978) and Vellinga (1990). On account of the lack of olivaceous colours and the broad pleurocystidia it is called *P. pallescens*, which is a rare species in the Netherlands.

Psathyrella fulvescens (Romagn.) A.H. Smith var. *brevicystis* Kits van Wav. (Fig. 45)
Collections examined. - Plot Q24, 8 Sept. 1986, Keizer 86140; Plot Q72, 26 Sept. 1988, Keizer 88142; Plot Q88, 25 Sept. 1986, Keizer 86160.
Obs.: It seems that still some confusion exists about this extremely common taxon. It is difficult to identify with the aid of the *Psathyrella*-monograph by Kits van Waveren (1985), owing to differences between his descriptions and drawings of the pleurocystidia and the pleurocystidioid cheilocystidia ("lageniform or fusoid") and the usual shape of these cells. The cystidia are usually more or less ventricose with a rounded cylindrical apical part, as figured by Arnolds (1982:438, *sub nomine P. trivialis*) and in fig. 45 of the present study. They may be called (narrowly) utriform or obtusely fusiform. Consequently, this species may therefore also be placed in sect. *Spadiceogriseae*, subsect. *Lutenses*. The macroscopic characters and other microscopic characters of the material found during this study agree with the descriptions by Arnolds (l.c.) and Kits van Waveren (l.c.).
Among the large numbers of carpophores of this species, growing on pieces of wood, often some specimens with an irregular and strongly wrinkled pileus were present. They could key out as *P. reticulata* (Romagn.) Sing., but all other characters agreed with *P. fulvescens* var. *brevicystis*. Therefore, *P. reticulata* may very well be only a variant of the latter taxon.

Psathyrella cf. fulvescens var. *brevicystis*. (Fig.46)
Pileus 9 mm, paraboloid or obtusely conical, colour on drying pale brownish yellow (Expo B-C 62) towards the centre more yellowish (C63); towards the margin relatively thick remnants of the veil present as white-floccose teeth. Lamellae 2 mm broad, not ventricose, broadly adnate, pale greyish brown with white-floccose edge. Stipe 50x1.0-1.3 mm, cylindrical, pale cream to almost white, with white-floccose veil remains, at base pale brownish (on handling).
Spores 9.2-9.8(-10.0)x5.0-5.7 μm, ellipsoid-oblong, Q=1.7-1.9, $\underline{Q}$=1.80, dark (reddish) brown in NH_4OH 10%, germ-pore present. Pleurocystidia 40-50x12-14 μm, fusiform to narrowly utriform, frequently with subacute apex, thin-walled, hyaline. Cheilocystidia 27-35x9-13 μm, similar to the pleurocystidia but smaller, in addition sphaeropedunculate cells present on the lamella-edge.
Collection examined. - Odoorn, Odoornerveen, 18 Aug. 1987, Keizer 87092.
Obs.: Differences with typical *P. fulvescens* var. *brevicystis* are: the well-developed veil; the absence of a conspicuous ochre-brown colour during the process of drying; the somewhat larger spores; the cystidia with more slender and more pointed apex. The

collection consists of only one specimen for which reason we refrain from further conclusions.

Psathyrella rhombispora nov. spec. (Fig. 47)
Pileus 15 mm latus, late campanulatus, obtuse umbonatus, hygrophanus, quando uvidus cinereo-brunneus, quando vero desiccat colore stramineo. Lamellae purpureo-fuscae, acie albo-flocculosa, subconfertae. Stipes 20x1.5-2.0 mm, cylindraceus, albidus, fistulosus. Sporae (8.2-)8.3-9.8(-10.0)x(4.2-)4.3-5.0 μm, Q=1.7-2.0, $\underline{Q}$=1.90, ellipsoideae vel rhomboideae, saepe cum apiculo satis magno, poro nullo. Basidia 16-23x7-8 μm, (1-)2-3(-4) sporigera, fibulata. Pleurocystidia 35-50x9-13 μm, plerumque utriformia, cheilocystidia utriformia 35-55x12-17 μm, modice numerosa, cheilocystidia sphaeropedunculata 15-25x10 μm, rara. Habitat: terrestris in solo arenoso. Typus: The Netherlands, Prov. Drente, Anloo, plot Q65, 10 Nov. 1987, Keizer 87234, Herb. WBS.

Pileus 15 mm, expanded, broadly campanulate with broad umbo, hygrophanous, when moist grey-brown (Expo F64), at centre more reddish brown, on drying straw-coloured (C63) at centre more ochre-coloured, no velar remains observed. Lamellae purplish brown, with edge white-floccose, ventricose, narrowly adnate, moderately crowded. Stipe 20x1.5-2.0 mm, cylindrical, slightly broader downwards, shiny, whitish, near the base pale beige, with some white-floccose velar remains, fistulose. Smell insignificant. Spores (8.2-)8.3-9.8(-10.0)x(4.2-)4.3-5.0 μm, Q=1.7-2.0, $\underline{Q}$=1.90, ellipsoid to rhomboid, frequently with a fairly large hilar appendix, without germ-pore, rather light red-brown in H_2O, somewhat darker in NH_4OH 10%, rather variable in shape and size. Basidia 16-23x7-8 μm, (1-)2-3(-4)-spored, spheropedunculate, with basal clamp. Pleurocystidia 35-50x9-13 μm, (narrowly) utriform to obtusely fusiform, pleurocystidoid cheilocystidia (narrowly) utriform to obtusely fusiform, occasionally apically bifurcate, 35-55x12-17 μm, frequently slightly thick-walled with pale brown walls (in NH_4OH), rather scarce, spheropedunculate cheilocystidia scarce. Hymenophoral trama pale yellow-brown at the base of the lamella, gradually less pigmented towards the edge.
Collection examined: - Plot Q65, 10 Nov. 1987, Keizer 87234.
Obs.: The specimen agrees in macroscopical appearence and pleurocystidia with the descriptions of *P. fulvescens* var. *brevicystis* in Kits van Waveren (l.c.) and Arnolds (l.c.), among other things because of the reddish brown centre of the pileus. However, the spores differ markedly in shape, a large proportion of the spores being rhomboid and tapering in a fairly large hilar appendix and in the absence of a germ-pore.

The present species belongs to the section *Spadiceogriseae* subsection *Spadiceogriseae* on account of the in majority (narrowly) utriform pleurocystidia and the rather scarce pleurocystidioid cheilocystidia. *Psathyrella clivensis*, (as described by Orton (1960), Kits van Waveren (l.c.), not by Smith, 1972) is one of the few *Psathyrella*-species which (almost) lacks a germ-pore. It differs in: 1) the shape of the spores: ellipsoid to subphaseoliform in *P. clivensis* and ellipsoid to rhomboid in *P. rhombispora*; 2) the spores of *P. clivensis* are 5.5-6.0 μm broad, the spores of *P. rhombispora* are more slender, 4.3-5.0 μm broad; 3) the bases of the spores of *P. clivensis* are rounded with a small hilar appendix; in *P. rhombispora* they are often tapering in a large hilar appendix; 4) the basidia are 4-spored in P. clivensis but in majority 2-3 -spored in *P. rhombispora*. In addition, the habitat of *P. clivensis* is chalk grassland; the present species was found on

nutrient-poor sandy soil.

It is after some hesistation that this species was described as new, because the collection consists of only one specimen. It is obvious that there exists not yet a clear view of the possible variation of the studied characters. However, the noted differences with other (related) species, especially in the morphology of the spores, warrant in our view a distinction on specific level.

In the current literature no description could be found that sufficiently fits this material.

We thank Dr. E. Kits van Waveren, who kindly studied the present material and gave valuable suggestions and opinions on this species.

Psathyrella seymourensis A.H. Smith (Fig. 48)

Pileus 6-17 mm, hemispherical or paraboloid, hygrophanous, when moist dark brown (Expo ± J42), translucently striate up to 1/3 of the radius, on drying pale grey-brown (C63) with slightly darker centre (E68), some remnants of the veil present near the margin. Lamellae up to 2 mm broad, narrowly to rather broadly adnate, subdistant, pale (brownish) grey (J78), edge white. Stipe 15-23x1-2 mm, cylindrical, apical part white, downwards pale brown (E42-52), sometimes near base dark brown (J42), covered with small floccose veil remains.

Spores 8.0-9.1(-9.3)x5.0-5.8(-6.0) µm, Q=1.4-1.7(-1.9), Q=1.55, slightly lentiform, in side-view ellipsoid-oblong, in face-view frequently subtriangular with largest width below middle, sub micr. dark chocolate brown. Pleurocystidia 30-45x9-14 µm, lageniform, thin-walled, hyaline. Cheilocystidia 35-40x9-11 µm ± similar to the pleurocystidia, frequent, in addition sphaeropedunculate to clavate cells, 15-30x10-14 µm.

Collection examined. - Plot F16, 13 Nov. 1986, Keizer 86222.

Obs.: This species is very rare; the description by Kits van Waveren (1985:266) was based on three collections.

Psilocybe bullacea (Bull.:Fr.) Kumm. (Fig. 49)

Pileus 7-24 mm, plano-convex or convex, soon becoming applanate, sometimes with slightly depressed centre, hygrophanous, when moist warm red-brown (Expo F44 (slightly more brown) or F54), with paler margin, translucently striate up to 1/3 of the radius, on drying ± orange-brown (D56-58), viscid and gelatinous pellicle slightly separable, near the margin with white, dentate veil remnants. Lamellae broadly to rather narrowly adnate, up to 2 mm broad, not ventricose, crowded, greyish pink-brown with paler edge. Stipe up to 10x1-2 mm, cylindrical or flattened and then up to 4 mm broad, concolorous with the pileus or slightly darker, white fibrillose, squamulose below an annular zone of veil. Smell indistinct.

Spores (7.4-)7.5-8.1(-8.5)x(4.7-)4.9-5.7(-6.0) µm, Q=1.3-1.7, Q=1.49, ellipsoid-oblong, slightly lenticular, differences beween side and face view about 0.5 µm, thick-walled with walls ± 0.6 µm thick, sub micr. (purplish) brown. Basidia 4-spored. Cheilocystidia 27-37x6-11 µm, irregularly lageniform, thin-walled, hyaline. Pleurocystidia not observed. Pileipellis an ixocutis of up to 300 µm thick, made up of hyphae of 2-4.5 µm wide, the thin hyphae hyaline, the thicker ones with brown encrusting pigment. Clamp- connections present in all tissues.

Collections examined. - Plot Q3, 14 Oct. 1988, Keizer 88205; 21 Dec. 1988, Keizer 88333.

Obs.: These collections differ in several respects from previous descriptions. Ricken (1915), Orton (1969), Geesink (1972), Guzmán (1983), Watling & Gregory (1987), and

described or illustrated this species with a ± hemispherical or paraboloid cap and only Guzmán (l.c.) mentioned that older specimens become applanate or depressed. The specimens described here very soon become applanate. The lamellae in these collections are not exclusively broadly adnate but also sometimes narrowly adnate. The same is drawn by Geesink (l.c.). The habitat is decribed as manure or arable fields (Ricken (l.c.), Watling & Gregory (l.c.), Guzmán (l.c.), bonfire places (Geesink, l.c.), other organic debris (Watling & Gregory (l.c.), Guzmán (l.c.)). Only the last author and Orton (l.c.) explicitely mentioned dung as habitat. The specimens described here grew on (old) horse dung. Arnolds (1982) regarded *P. bullacea* as a synonym of *P. montana*, in our opinion incorrectly so. Differences between these species are, besides the habitat: the generally stouter habit and the presence of whitish dentate veil remnants at the margin of the pileus of the former species.

Russula decipiens (Sing.) Svrcek (Fig. 50)
Pileus 50-125 mm, convex, then expanding with slightly depressed centre and mostly somewhat involute margin, sometimes more funnel-shaped, colour rather variable, between cream-coloured beige and brick-red, often on a pale buff groundcolour, with a cloudy, often-concentric pattern of orange red to mostly brick-red (e.g. Expo D-E16), sometimes completely pale beige (A73, B72, C64) when older or only with a faint orange-pink colour at the margin, dull and white-pruinose when young, not viscid. Lamellae up to 10-12 mm broad, rather ventricose, narrowly adnate, near stipe frequently forked, subdistant, in large specimens ± 7 per 10 mm at the margin of the pileus, at first pale yellow, then apricot-yellow. Stipe up to 60x30 mm, cylindrical to (more often) club-shaped, white, with age and on handling yellowish grey-brown. Context in cap and stipe white, very firm, in stipe slowly turning brownish in age. Smell weak, fruit-like (± as *R. fellea*), taste sharp (but mild in coll. 86199). Reaction with $FeSO_4$ dirty orange. Spore print dark yellow (IVd-)IVe (according to Romagnesi, 1967).
Spores (7.2-)7.4-9.4(-10.1)x(6.0-)6.2-8.0 µm, Q=1.2-1.3(-1.4), Q=1.23, broadly ellipsoid, ornamentation variable, mostly with isolated warts or warts arranged in crests or connected with lines, rather blunt and ± 0.5 µm high, but a minority of the spores (sometimes a rather large proportion) with coarse, blunt, isolated warts, up to 1.0(-1.2) µm high. Pileocystidia numerous, rather variable, some up to 50 µm long, with suddenly enlarged apex, 7-9 µm broad, but in majority longer and gradually broader towards apex up to 10-12(-14) µm broad, frequently 1-2 septate, contents granular, dark in sulfovanillin. Hyphae of the cutis inconspicuous, cylindrical, 1.5-3.0 µm broad.
Collections examined. - Plot Q13, 4 Aug. 1986, Keizer 86125; 10 Sept. 1986, Keizer 86130; 1 Oct. 1986, Keizer 86167; 24 Oct. 1986, Keizer 86199; 24 Aug. 1987, Keizer 87112; 23 July 1988, Keizer 88031; 29 Sept. 1988, Keizer 88071.
Obs.: Since there exists some confusion with regard to the delimitation of this species and *R. maculata* and, to a lesser extent, *R. veternosa*, a description of *R. decipiens* is given. The colours of the pileus of *R. maculata* and *R. decipiens* show large overlap, although the red colours tend to fade more often in the latter species. The greyish or brownish discoloration of the flesh is often difficult to assess with certainty. Both species seem to occur in the same habitats. The main difference is the presence of numerous large pileocystidia in *R. decipiens*, whereas these are smaller and less abundant in *R. maculata*.

R. veternosa is macroscopically rather similar, but differs among other things in a

paler spore print. Of these three species *R. decipiens* seems to be the most common in the Netherlands.

Russula graveolens Romell in Britz.

Many problems arose with the identification of taxa within the *R. xerampelina* complex, which is well-characterized by the green reaction of the context with $FeSO_4$, the fishy smell and the brown discoloration of stipe and lamellae. Many characters show a large variation in this group, giving a carpophore or group of carpophores often a seemingly characteristic habit. However, often the extremes of a certain character are connected by intermediates (although these intermediates seem to be less frequent then the "extreme" variants) and none of the characters studied appear to be mutually correlated. Thus, following the criteria proposed by Kuyper (1988), at least two independent characters must be present to separate a species from another, it would be impossible to maintain a specific status for many of the variants observed during this study.

On the other hand, the intuitive feeling exists that it is hardly realistic to unite such different variants into one species. In modern literature (Moser, 1983; Romagnesi, 1967; Einhellinger, 1985; Marchand, 1977; Bon, 1988b) this problem is reflected in the differences in species concept in this group.

Before Romagnesi's (1967) monograph the different variants were usually considered as varieties of one variable species (e.g. Schaeffer, 1952) which is in our opinion still the best taxonomic solution except for some characteristic and constant taxa like *R. xerampelina* (Schaeff.) Fr., *R. pascua* (Mϕller) J. Schaeff. and *R. faginea* Romagn., which deserve the rank of species. In order to give the possibility to compare the present data with other studies, some names proposed in the modern literature will be adopted here.

Romagnesi (1967) was the first one who tried to disentangle tentatively and eloquently the species of the *R. xerampelina* complex. Generally, he has been followed by the later authors except by Moser (1983) who presented only a very brief key for the *Xerampelinae*.

On the other hand Bon (1988b) presents a large number of taxa (39 species and varieties!) based on minute differences. The result of such extensive splitting must be that different names will be in vogue with different mycologists or groups of mycologists for the same taxon, each of them forced to find small differences in their own way. This procedure renders many mycological data, which are usually not provided with descriptions of the collections presented, of diminished value.

In this study the taxonomic classification by Einhellinger (1985) has been followed, which is based on Romagnesi (1967), but neglecting some doubtful "species". The taxa named here can be recognized only by macroscopical characters like the colour of the pileus, size and consistence of the fruitbody.

Other macroscopic characters like colour of the stipe (with/without red), discoloration of the flesh and stipe (always brownish), reaction with $FeSO_4$, smell, and separability of the cutis are more or less constant throughout the material or vary widely within collections and do not correlate with any other character.

The colour of the spore print generally is an important character in *Russula*. However, it appeared that within this group there was only little variation in the collections studied; spore-prints varied between IId-IIIa(-IIIc) according to the system of Romagnesi (l.c.). Unfortunately, spore prints were not produced by many young, old and damaged

carpophores. Study of more material might show some value of this character.

Microscopic characters appear to be remarkably constant throughout the material. This is true for the spores (shape, size, properties of the ornamentation), the dermatocystidia (shape, size, number of septa) and hyphae in the epicutis. So it appears that these characters, which are normally so useful in the study of the genus *Russula*, fail largely in this particular group.

In view of the observed patterns of variation in the collections studied, it is to our opinion not possible to distinguish taxa in the rank of species, bearing in mind the criteria used by Kuyper in (1988). In this context the taxa observed should be considered as formae: taxa where (single) character differences show limited intergradation.

Probably speciation within the *Xerampelina*-group is going on at present and has in most cases not yet resulted in morphologically well-defined species (with some exceptions, mentioned above). Therefore the taxa described here are distinguished as formae of *R. graveolens* Romell in Britzelmayer (1893), the oldest available species epithet in this group. There is no indication that the older name *R. barlae* Quél. belongs to the group of *R. xerampelina* and this name is rejected as a *nomen dubium*, in agreement with e.g. Krieglsteiner (1987:24).

The four formae that are distinguished, are keyed out as follows.

1. Pileus predominantly green, olive-green, yellowish or brownish green. 2
- Pileus predominantly purplish red, red, brick-red or brownish violaceous. 3

2. Pileus small (± 40-50 mm), firm, pileus rather dark brownish green to dark olive green or olive brown (sometimes with reddish or purplish hue)
R. graveolens f. elaeodes
- Pileus rather large (up to 75-100 mm), somewhat less firm, pileus middle to pale olive green to yellow, sometimes a faint purplish hue present at the margin of the pileus, in centre often more brownish. *R. graveolens f. cicatricata*

3. Pileus rather large (up to 80-100 mm or more), dark purple-violaceous to (dark) reddish brown, sometimes mixed with olivaceous colours, in centre usually darker, surface of pileus in wet weather viscid, in dry situations dull, almost ± granular, habit often much like *R. atropurpurea*, less often like *R. vesca*.
R. graveolens f. graveolens
- Pileus smaller (± 35-45 mm), often less expanded, (brick-) red to purple, but large overlap with f. *graveolens*; often, the surface of the pileus is remarkably dull-velvety granular. *R. graveolens f. purpurata*

Each of the formas will be described in more detail below.

Russula graveolens forma *cicatricata* (Romagn. ex) Keizer & Arnolds forma nova
A typo differt pileo olivaceo, luteo yel brunneo-virido pro parte maximo. - Holotypus: "France, Coye-la-Forêts (Oise), 13 Aug. 1960, Romagnesi 60-69" (in herb. Romagnesi). Pileus ± 40 (young) - 75 - 100 mm or more, convex, then plano-convex with depressed centre, with different shades of olive-green or olive-brown to brown (Expo C78, D76,

E76, D78, D88), towards the margin paler (e.g. B84, A84, A86, A76, D83 or K.&W. 4C5, 5E7, 5D8), sometimes with a concentric zone with purplish colours or this colour present in "cloudy" patches (D64, D54, D52), surface dull to almost velvety, sometimes cracked in small patches towards the margin, in one case more or less concentrically arranged grooves present. Lamellae up to 8 mm broad, not ventricose, moderately distant, a few forked, cream-coloured, narrowly adnate or slightly emarginate. Stipe 32-60x12-25 mm, cylindrical or often broader towards the base, white, in one case with red colour at one side of the base of the stipe, discolouring brownish on handling and with age. Context spongy in the stipe, firmer in the pileus, white, turning brownish. Smell distinctive, fishy, like other members of the *Xerampelina*- complex. Chemical spot test: $FeSO_4$: blue-green. Spore print: IId-IIIa according to the system of Romagnesi (1967). Spores 8.0-10.5x6.5-7.5(-8.0) μm, with Q=1.1-1.3(-1.4), $\underline{Q}$=1.23, broadly ellipsoid, with ornamentation of coarse warts or spines, usually isolated but sometimes connected by a thin line, mostly acute, sometimes blunt, 1.0-1.3(-1.5) μm high, amyloid, supra-hilar spot obvious, amyloid. Dermatocystidia usually abundant, 80-100x3.5-7.0(-8.0) μm, frequently 1-septate, cylindrical or narrowly clavate, contents $\pm$ granular, with weak SV reaction. Pileipellis with hyphae 2.5-4.5 μm broad, usually cylindrical, sometimes inflated, up to 6(-13) μm.

Collections examined. - Plot Q11, 15 Sept. 1986, Keizer 86127; Plot Q32, 18 Aug. 1987, Keizer 87034; 3 Oct. 1988, Keizer 88343; Plot Q64, 19 Sept. 1988, Keizer 88147; Plot Q82, 4 Sept. 1987, Keizer 87074; 1 Oct. 1987, Keizer 87219; Plot Q83, 8 Sept. 1988, Keizer 88162.

Obs.: *Russula cicatricata* was described by Romagnesi (1967:694) as a species ad interim, without Latin diagnosis and therefore invalidly published.

Romagnesi (l.c.) stated that the concentric furrows in combination with olive colours and a certain amount of ampulliform hyphae in the cutis are characteristic for *R. cicatricata*. This seems to be a solid base for a species, but according to our observations these characters are not reliable. The concentric furrows or cracks have been found only once (coll. 87074) and it seems to be a character which develops in dry weather conditions. Marchand (1977) also indicated that this character can be variable, even in specimens of one collection, and that the character may disappear after collecting.

The greenish colour is the most striking feature, but this colour can be mixed with a purple hue. It is clear that carpophores of this species can contain various quantities of purple pigment; the more purple pigment present, the more brownish is the pileus. On the other hand, the pileus of forma *graveolens*, usually purple red-brown, can contain a variable proportion of olive or brownish colours. Such intermediates with colour of the pileus between greenish and purplish, are a minority among the studied collections. Occasionally, one can find purple and green carpophores so close together that one has to assume that they originate from the same mycelium. In the present material the hyphae of the cutis are usually cylindrical, but in two collections a small minority is inflated (coll. 88162 and 88147). This character also occasionally occurs in specimens which have been called f. *graveolens* and f. *purpurata* on account of the colour of the pileus.

In conclusion, none of the characters which are in use to determine f. *cicatricata* is reliable under all circumstances, and it is especially difficult to separate it from f. *graveolens*. A good plate is given by Marchand (1977: 480).

Russula graveolens forma *elaeodes* (Bres.) Arnolds & Keizer comb. nov.

Basionym: *Russula xerampelina* var. *elaeodes* Bres., Iconogr. mycol. 9: 420. 1929.
Pileus ± 30-40 mm, convex, then plano-convex to depressed, olive-green, olivaceous green-brown, or greyish (Expo E76, D74, E82), sometimes mixed with a faint purplish hue, short-sulcate at the margin (1-2 mm), surface moderately dull. Lamellae up to 4 mm broad, somewhat crowded, pale yellowish or cream-coloured. Stipe 20-25x7-10 mm, ± cylindrical or broader towards the base, whitish but discolouring strongly, brownish on handling and with age. Context spongy in the stipe, firm in the pileus, white, turning brownish. Smell characteristic for the group, ± fish-like, not strong. Chemical spot test: $FeSO_4$: blue-green. Spore print: not obtained. Spores 8.0-9.5(-10.2)x6.2-8.3 µm, Q=(1.0-)1.1-1.3, $\underline{Q}$=1.20, broadly ellipsoid to subglobose, ornamentation consisting of rather dense to scattered, usually isolated spines and warts, some may be connected by lines, amyloid, 1.0-1.3 µm high, suprahilar spot distinct, amyloid. Dermatocystidia 60-100x4-6 µm, more or less cylindrical or narrowly clavate, occasionally with a septum, content granular or hyaline, with weak SV-reaction. Hyphae of pileipellis 2.0-4.5 µm broad, usually more or less cylindrical, sometimes inflated in places.
Collections examined. - Plot Q11, 24 Sept. 1988, Keizer 88133; Plot Q83, 1 Oct. 1986, Keizer 86166; Plot Q84, 29 July 1988, Keizer 88011.
Obs.: The main differences between f. *elaeodes* and f. *cicatricata* are (1) the small, slender habit and (2) the less dull, almost grabrous surface of the pileus of the former. Possibly the pileus is darker than in f. *cicatricata*. This taxon is well-illustrated by Phillips (1981:105, lower right).

Russula graveolens Romell in Britz. forma *graveolens*
Pileus 45-83 mm, young convex, then plano-convex with depressed centre, in centre dark brown-purple, purplish red-brown, sometimes mixed with olivaceous colour (Expo H23), towards the margin paler, red purple-brownish (D23-24, E23-24, E34, D18), surface varying from smooth and viscid to dull and almost velvety, in part densely cracked. Lamellae up to 10 mm broad, narrowly adnate, not ventricose, distant, pale yellowish, cream-coloured, with age margin sometimes becomes brownish. Stipe 40-80x13-25 mm, ± cylindrical or broader towards the base to clavate, white, frequently with red colour at one side near the base, turning brown on handling and with age. Context firm in pileus and spongy in stipe, white, turning brownish. Smell characteristic for the group, fish-like, taste mild. Chemical spot test: $FeSO_4$ blue-green. Spore print IId-IIIb (mostly IId), in one case (IIIb-)IIIc. Spores (8.1-)9.0-10.5x6.5-8.0(-8.2) µm, Q=1.1-1.3(-1.4), $\underline{Q}$=1.26, broadly ellipsoid, with ornamentation of usually isolated spines, rarely connected, mostly acute, some broader and blunt, up to 1.0-1.3(-1.5) µm high, amyloid, supra-hilar spot distinct, amyloid. Pileocystidia abundant, 80-100 x (3.5-)4.5-7.0 µm, frequently with a septum, cylindrical or narrowly clavate, contents granular. Hyphae of cutis 2.5-5.0(-7.0) µm broad, mostly ± cylindrical, rarely inflated up to 7.0 µm wide.
Collections examined. - Plot Q12, 18 Sept. 1988, Keizer 88144, Keizer 88145; Plot Q13, 23 July 1988, Keizer 88019; 7 Oct. 1988, Keizer 88156; Plot Q84, 1 Sept. 1986, Keizer 86128; 9 Oct. 1986, Keizer 86164.
Obs.: For a discussion on the separating characters from f. *cicatricata* see under that taxon.

Russula megacantha Romagn. ad int. is, in agreement with Krieglsteiner (1987), considered a synonym, because the only reported difference, a slightly coarser and wider spore ornamentation, is not reliable since all kinds of transitions occur. Representative illustrations of *f. graveolens* were published by Marchand (1977: pl. 479), Einhellinger

(1985: pl. 25) and Lange (1940: pl. 190A).

Russula graveolens forma *purpurata* (Crawshay) Keizer & Arnolds comb. nov.
Basionym: *Russula purpurata* Crawshay, The spore ornamentation of *Russula* (1930: 103).
Pileus 33-45 mm, convex, then plano-convex, centre at most slightly depressed, deep purplish red or dark brownish purple (K.&W. 10F8 or Expo J62) with olive-brown tinge, towards the margin usually purplish red (K.& W. 10D8 or Expo E16), in one case more olive-brown (Expo J62), sometimes with yellowish spots, more or less viscid when moist, normally dull, almost velvety to minutely granular. Lamellae narrowly adnate, ± 2 mm broad, moderately crowded, not ventricose, pale yellowish or cream-coloured occasionally forked. Stipe 23-40x9-13 mm, ± cylindrical to clavate, white, base reddish at one side, on handling and with age brownish. Context white, remarkably firm, especially in stipe turning brownish. Smell rather weak, fish-like, as other members of the group. Chemical spot test: $FeSO_4$ blue-green. Colour of spore print unknown.
Spores 8.5-9.4x6.5-7.5 μm, Q=1.1-1.4, $\underline{Q}$=1.25, broadly ellipsoid, with ornamentation of usually isolated warts or spines, up to (0.7-)1.2-1.3(-1.5) μm high respectively, sometimes connected by lines, supra hilar spot distinct, amyloid. Dermatocystidia cylindrical to narrowly clavate, up to 80-100x4-6(-8) μm, frequently with 1-2 septa, with granular contents. Hyphae of cutis 3-5 μm wide, more or less cylindrical, with frequent inflations up to 7-10 μm wide.
Collections examined. - Plot Q4, 4 Oct. 1987, Keizer 87228; Plot Q13, 22 Sept. 1987, Keizer 87185; Plot Q82, 24 Sept. 1988, Keizer 88344; Plot Q84, 9 Oct. 1986, Keizer 86165.
Obs.: The delimitation of *R. graveolens* f. *purpurata* and *R. amoenoides* Romagn. seems to be very weak: the only separating character is the dull, ± pruinose cap in *amoenoides* and a more glabrous cap in *f. purpurata*. Einhellinger (1985) described the surface of the pileus of f. *purpurata* as "ausgesprochen matt" ("distinctly dull"). We regard *R. amoenoides* as a synonym. This forma was well depicted in Einhellinger (1985: pl. 25).

Russula grisea Fr. ss. str.
Collections examined. - Plot F15, 2 Aug. 1988, Keizer 88008; Plot F43, 24 Aug. 1987, Keizer 87108; Plot Q82, 4 Sept. 1987, Keizer 87104; 1 Oct. 1987, Keizer 87204.
Obs.: *Russula grisea* is closely related to *R. parazurea* and *R. ionochlora*. There is also some accordance in habitat: preferably growing along alleys. However, *R. grisea* usually occurs on neutral or calcareous soils (personal observations, Einhellinger, 1985), whereas *R. parazurea* and *R. ionochlora* prefer acid soils.
The "key-character" (in Romagnesi, 1967) to separate *R. grisea* from the other two species is the colour of the spore print. Unfortunately, old specimens often fail to produce a spore print and moreover, it is impossible to test all carpophores in mycocoenological research. The pink colour in damaged parts of the context, the bright orange reaction with $FeSO_4$, the ornamentation of the spores (warts isolated or in chains but not forming a network) and the hyphae of the cutis which are normally multiseptate with elongate, terminal cells offer sufficient additional characters to separate it from the other species of the subsection *Griseineae*.

Russula ionochlora Romagn.
Collections examined. - Plot F4, 22 Sept. 1987, Keizer 87187; Plot F34, 1 Oct. 1987, Keizer 87223; Plot Q63, 23 Oct. 1988, Keizer 88186; Plot Q82, 28 Oct. 1988, Keizer 88185; Plot Q85, 19 Sept. 1988, Keizer 88108.
Obs.: This species can be easily confused in the field with *R. parazurea* and *R. grisea*. The distribution of pink-lilac and olive-greenish colours on the pileus is often characteristic for this spcies: typically the centre is greenish, towards the margin passing into pink-lilac colours, often mixed with grey. The stipe often has a faint pink hue as in *R. grisea*, but this was never observed in *R. parazurea*. The spore print is paler than the spore print of *R. grisea* (Romagnesi, 1967). Microscopically, the spores with small isolated warts and especially the presence of septate hyphae in the cutis are characteristic. The cells of these hyphae are more or less isodiametrical, constricted at the septa and the terminal cell is often relatively short. The abundance of these multicellular hyphae varies considerably but they seem to be always present (cf. Romagnesi, l.c.).

Russula parazurea J. Schaeff. ex J. Schaeff.
Collections examined. - Plot F21, 19 Nov. 1986, Keizer 86270; Plot F22, 25 Nov. 1986, Keizer 86265; Plot F33, 19 Nov. 1986, Keizer 86269; Plot F41, 19 Nov. 1986, Keizer 86268; Plot Q5, 2 Aug. 1988, Keizer 88009; Plot Q71, 25 Nov. 1986, Keizer 86266.
Obs.: This species proved to be very variable with respect to colour and surface of the pileus, more so then generally acknowledged in literature. All variants are considered as caused by environmental conditions and hence without taxonomic significance. Typically, the pileus is dark blue-greenish grey and pruinose. These specimens preferably grow on or along footpaths in forests. In open areas, the pileus is usally dark grey when growing between tall grasses, but in direct sunshine it usually fades very soon to shiny yellowish, buff or straw-colour. Under adhering leaves or grasses the original greenish-grey colour often remains. Frequently, specimens with violet or brick-red (e.g. Expo F44, C43) pileus can be found as well. Late in the season, from November onwards, the cutis becomes cracked, ± like *R. virescens*, and then shows often brownish or ± violaceous colours. This feature, already noticed by Schaeffer (1952), is only observed in places where other forms have been found before, and is consequently considered as a variant, induced by low temperatures. The species is relatively constant in microscopical characters with as most important feature the spore ornamentation which consists of warts in rows or crests, connected with lines, forming a more or less closed network. Among the related species in the subsection *Griseinae* this species has the most obviously reticulate spore ornamentation. In addition, the dermatocystidia often show a characteristic subapical constriction. In the field the lack of any pink colour in the stipe and the yellowish cream colour of the lamellae may help the identification.

Tricholoma scalpturatum (Fr.) Quél. var. *scalpturatum*
Collection examined. - Plot Q14, 18 Sept. 1988, Keizer 88148.
Obs.: We agree with Bon (1984) and Marchand (1986) to consider *T. scalpturatum* and *T. argyraceum* as different on the level of variety, the main separating character being the pale colour of the pileus in the latter. The microscopical features are more or less identical according to Bon (l.c.) and Marchand (l.c.). However, Moser (1978) gives different spore-sizes: 5-6(-7)x3-4 μm and 7-9x4-5 μm respectively. The spores of this collection measure (4.1-)4.2-4.8(-5.4)x2.8-3.2(-3.3) μm, and are somewhat smaller than

the spore sizes cited above.

Tubaria furfuracea (Pers.:Fr.) Gillet incl. *T. hiemalis* Bon, *T. romagnesiana* Arnolds
Collections examined. - Plot F22, 16 Nov. 1988, Keizer 88320; Plot F24, 10 Nov. 1986, Keizer 86205; Plot F43, 10 Nov. 1986, Keizer 86204.
Obs.: In Kühner & Romagnesi (1953:243) three "small" species within *T.furfuracea* ss. lat. are distinguished: *Naucoria segestria*, *N. furfuracea*, *N. pellucida*. Arnolds (1982) followed this concept, although doubting whether the specific rank is deserved here. He changed the names in *Tubaria furfuracea* ss. str., *T. hiemalis* and *T. romagnesiana*. After our experience the diagnostic characters (shape of cheilocystidia: capitate or not; very slight differences in spore-size; width of the hyphae in the trama of the lamellae) show large overlap. Even within one single fruitbody cheilocystidia may be found either of the "*hiemalis*"-type (capitate) or cylindrical-clavate or irregularly cylindrical. Therefore, we prefer to consider *Tubaria furfuracea* as one, rather variable, species.

APHYLLOPHORALES

Ramariopsis kunzei (Fr.) Corner (Fig. 56)
Syn.: *R. tenuiramosa* Corner
Carpophores solitary or gregarious, up to 25 mm high, sparsely to strongly branched with 3 to 50 tips in one carpophore, branches ± 1 mm thick, with rounded axils, dirty white-yellowish to pale brownish beige (Expo B64, A62), on drying paler, stipe slightly darker, minutely velvety, base tomentose. Smell indistinct. Spores in mass white.
Spores (3.5-)3.6-4.7(-4.8)x3.0-4.2(-4.4) μm, Q=1.0-1.3, Q=1.13, globose, subglobose or broadly ellipsoid, finely echinulate, with one oil-drop. Clamp-connections present.
Collections examined. - Plot Q2, 14 Oct. 1988, Keizer 88234; Plot Q38, 22 Oct. 1988, Keizer 88244.
Obs.: The carpophores found here could not be unambiguously assigned to *R. kunzei* or *R. tenuiramosa*. The drawings of the habit by Corner (1950) of these species look rather different, but our collections include intermediate carpophores. Besides, he stated under *R. kunzei* (p. 642) that it is an extremely variable species. Maas Geesteranus (1976) inclined to consider *R. tenuiramosa* a modification of *R. kunzei*. The two collections differ in spore-size: coll. 88324 has spores of 3.5-4.0x3.0-3.4 μm, coll. 88244 of 3.5-4.7(-4.8)x(3.0-)3.5-4.2(-4.4) μm. These values fall within the range given by Corner (l.c.) for *R. kunzei*.

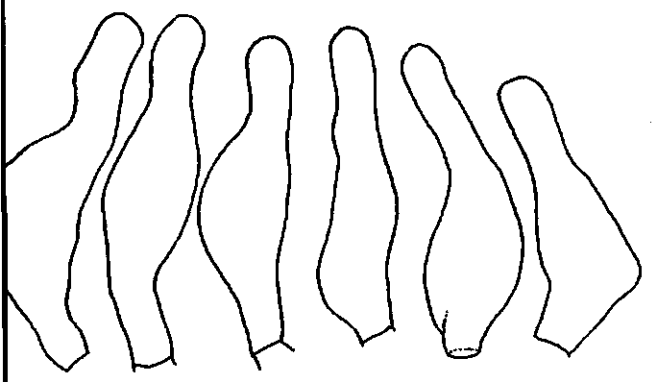
ASCOMYCETES

Helvella cf. corium (Weberb.) Massee
Ascocarp stalked-cupulate; excipulum 10 mm wide, grey to dark grey, villose-granulose, hymenium brown-black. Stipe 7x1.5 mm, cylindrical, somewhat paler than excipulum, grey, villose-granulose.
Spores 17.5-18.7x11.5-12.0 μm, ellipsoid, with one large oil-drop. Paraphyses 3.5-4.0 μm broad cylindrical, apical part enlarged, up to 7.0 μm, septate, apical cell 70-140 μm long, content diffuse greenish (in NH_4OH 10%).
Collection examined. - Plot F43, 6 Oct. 1988, Keizer 88230.
Obs.: The ascocarp is not as dark as on plate 239 in Boudier (1905-10).

Helvella cupuliformis Dissing & Nannf. (Fig. 57)
Ascocarp 25 mm high, stalked-cupulate, excipulum 18 mm broad, roundish, with margin strongly incurved, grey (Expo D81, D61), rugose-tomentose, hymenium dark brown-grey (H-J32, central part F64). Stipe 15x2.5 mm, towards the base broad (up to 8 mm) and partially split, ivory-white or cream-coloured, at apex tomentose, at base finely tomentose. Smell none.
Spores 17.5-20.3x10.3-11.3 μm, elliptical with one large oil-drop. Paraphyses 3 μm broad, cylindrical but apical part irregularly enlarged, up to 5 μm, contents pale greyish, sub micr. in NH_4OH 10%. Hairs of excipulum multicellular, cells 14-22x14-17 μm, inflated.
Collection examined. - Odoorn, Odoornerveen, 17 Sept. 1987, Keizer 87167.
Obs.: This specimen has been called *H. cupuliformis* on account of the white stipe. The microscopic characters seem to be identical with *H. villosa*.

Otidea alutacea (Bres.) Massee
Apothecia 15-40 mm broad and up to 30 mm high, irregularly cup-shaped, often more or less stalked, split at one side; excipulum pale brownish beige, alutaceous (Expo D63, but more greyish and somewhat paler or K.&W. 5D4), finely granulose; hymenium concolorous or a little more reddish.
Spores (12.0-)12.3-15.0(-15.5)x(5.7-)6.0-6.5(-7.0) μm, ellipsoid, smooth, usually with two oil-drops, obliquely uniseriate. Asci 160-200 (or more) x 9.0-12.5 μm, cylindrical; paraphyses 2-3 μm thick, apical part slightly thicker, curved, sometimes slightly lobed.
Collections examined. - Plot Q32, 3 Oct. 1988, Keizer 88220; Plot Q83, 8 Sept. 1988, Keizer 88178.
Obs.: The specimens agree well with the plates in Boudier (1905-10: pl. 327), Bresadola (1927-33: pl. 1228-2), Breitenbach & Kränzlin (1981: pl. 60), Dennis (1978: pl. 8B), but not so well with the illustration in Phillips (1981:270), which looks like *O. concinna* (Pers.)Sacc. on account of the yellow colour present in the excipulum. However, the spores are given as 12-15x6-7 μm, which is in agreement with the spore-size given above for *O. alutacea*. The spores of *O. concinna* as reported by Maas Geesteranus (1967) are smaller: 9.8-11.8x5.4-5.8 μm.

Otidea bufonia (Pers.) Boud.
Apothecia up to 40 mm broad and high, irregularly cup-shaped and deeply split at one side, indistinctly stalked; excipulum dark brown (Expo H32 - J21), finely velvety; hymenium darker than excipulum, blackish brown (J41 but darker).
Spores 13.4-15.6x5.8-7.2(-7.9) μm, ellipsoid, smooth, with two oil-drops, obliquely uniseriate; asci 150-200 (or more) x 9-12 μm, cylindrical; paraphyses 2-3 μm broad, apically enlarged up to 4 μm broad and slightly bent or straight, septate with cells of 15-40 μm long.
Collections examined. - Plot F44, 8 Sept. 1988, Keizer 88177; Plot Q22, 13 Oct. 1988, Keizer 88358; Plot Q83, 10 Sept. 1986, Keizer 86138.
Obs.: Among the large, dark brown *Otidea* species, in the literature two species are mentioned, one with large and one with smaller spores. Three names seem to be available for them: *O. bufonia*, *O. cochleata* and *O. umbrina*. The description of *Peziza umbrina* in Persoon (1801) is very short: "*magna cespitosa contorta umbrina*". Boudier (1905-10) and Bresadola (1927-33) used the name *O. umbrina* for the small-spored taxon (spores 15-16x7-8 μm and 14.7-17x6.5-8 μm respectively). However, Dennis (1978) and Maas Geesteranus (1967) mentioned *O. umbrina* as a (possible, Maas Geesteranus) synonym under the large-spored *O. cochleata* (spores 16-18x7-8 μm and 17.7-20.7x9.9-10.8 μm respectively).
It is clear that Persoon's very briefly described *P. umbrina* is variously interpreted and in the absence of authentic material is better regarded as a *nomen dubium*. The material of this study material fits well with the small-spored species and is therefore called *O. bufonia*.



g. 1

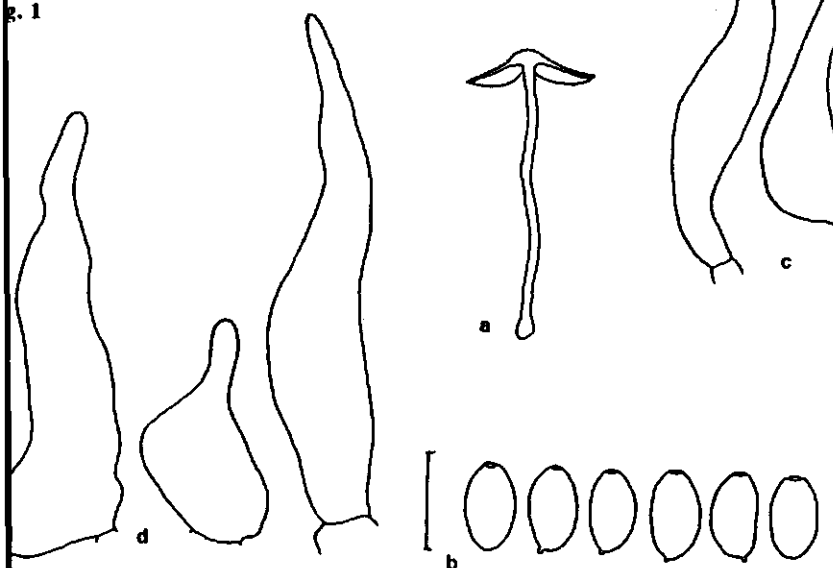


fig. 2

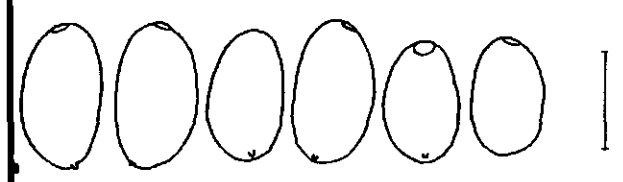


fig. 3

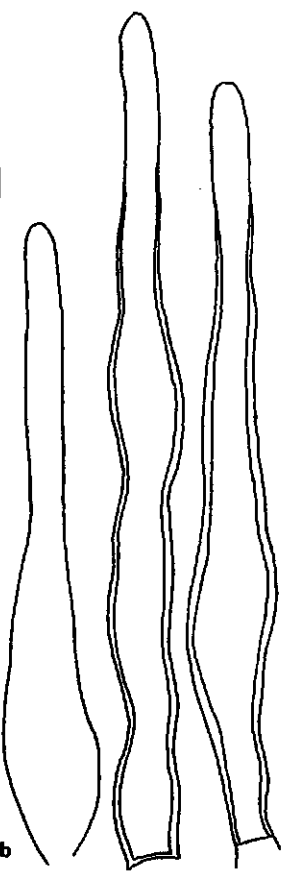


Fig. 1. Conocybe cf. mairei. a. spores; b. cheilocystidia (88221).

Fig. 2. Conocybe pygmaeoaffinis. a. habit; b. spores; c. cheilocystidia; d. caulocystidia (88315).

Fig. 3. Coprinus sclerocystidiosus. a. spores; b. pileocystida (88063).

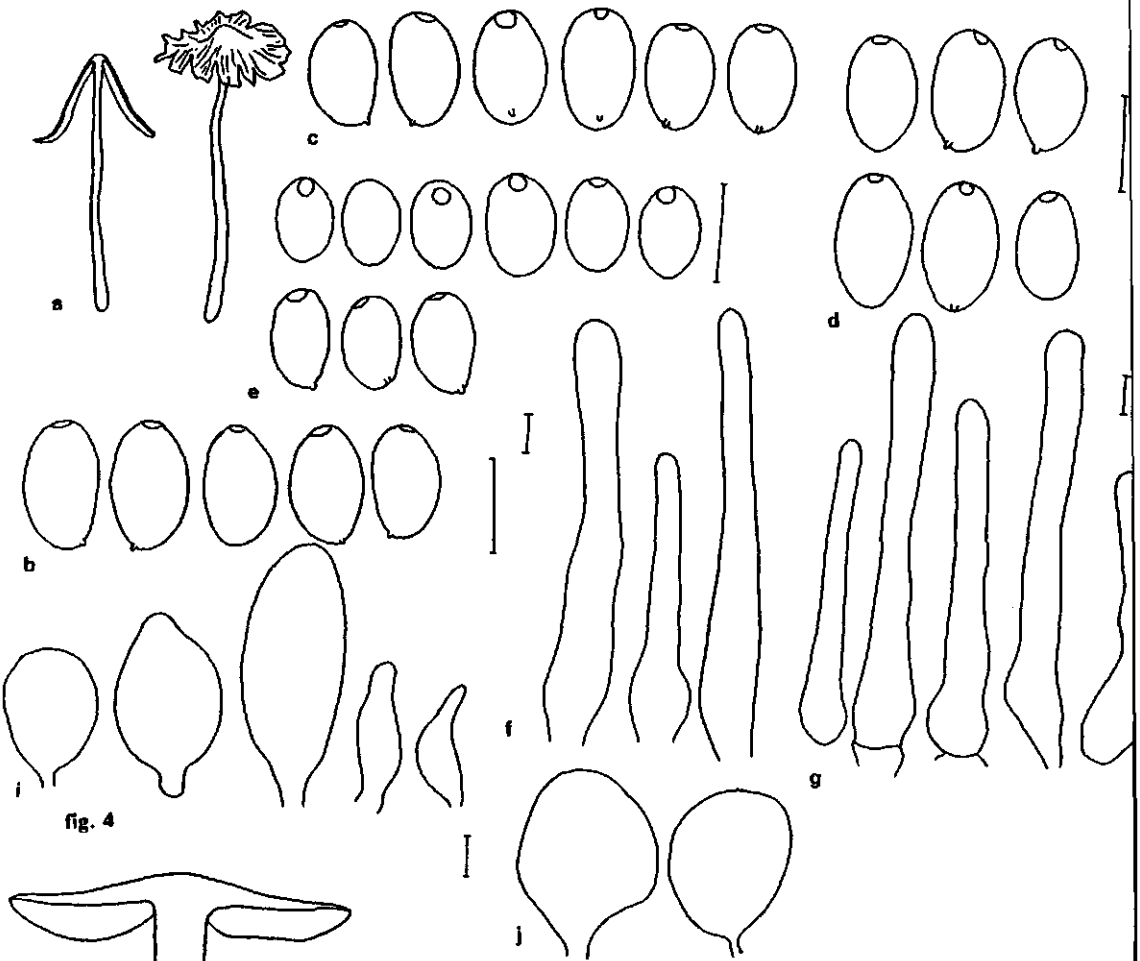


fig. 4

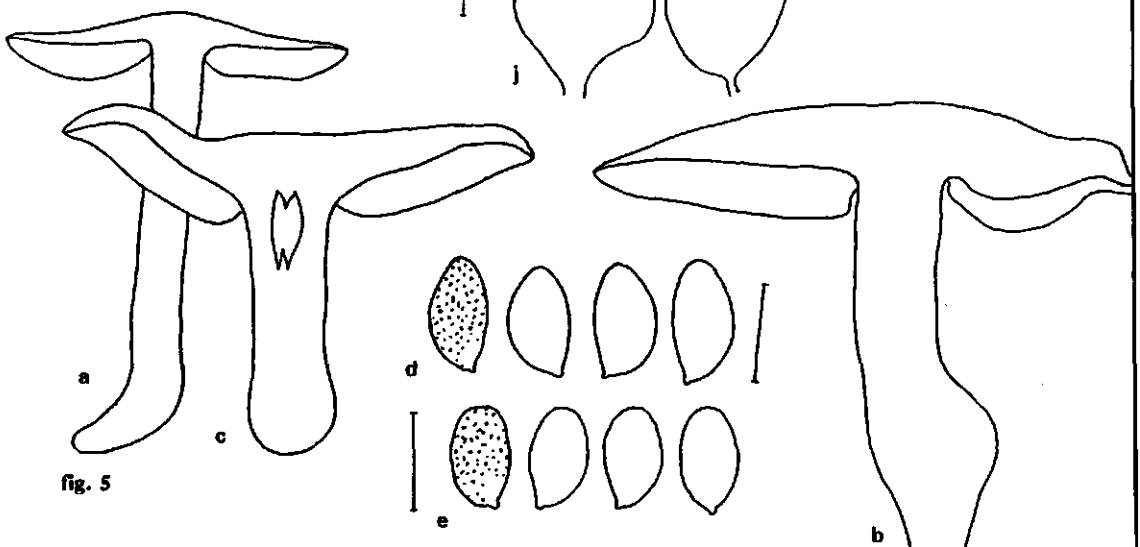


fig. 5

Fig. 4. Coprinus subimpatiens. a. habit; b, c, d, e. spores; f, g, h. pileocystidia; i. cheilocystidia; j. pleurocystidia (a, d, g. 88234; b. 88319; c, f. 88231; e, h, i, j. 87038).

Fig. 5. Cortinarius balteatoalbus. a, b, c. habit; d, e. spores (a, d. 87284; b. 88127, c. 87138).

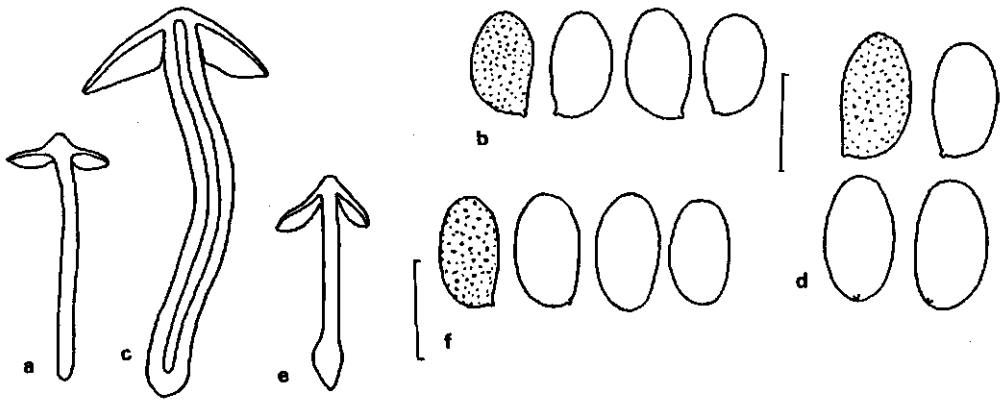


fig. 6

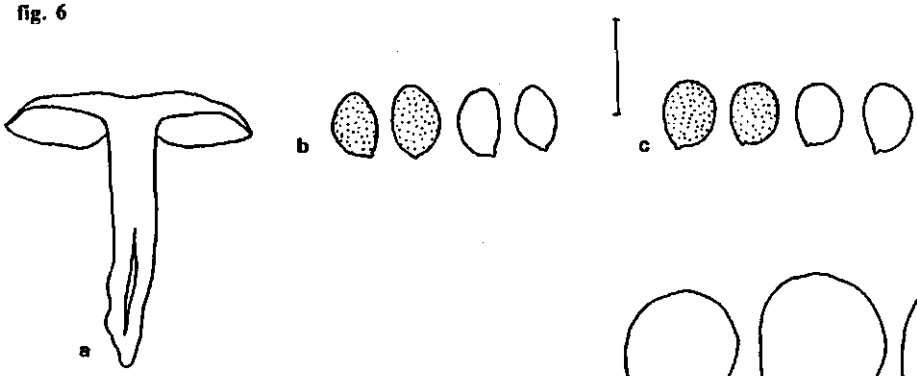


fig. 7

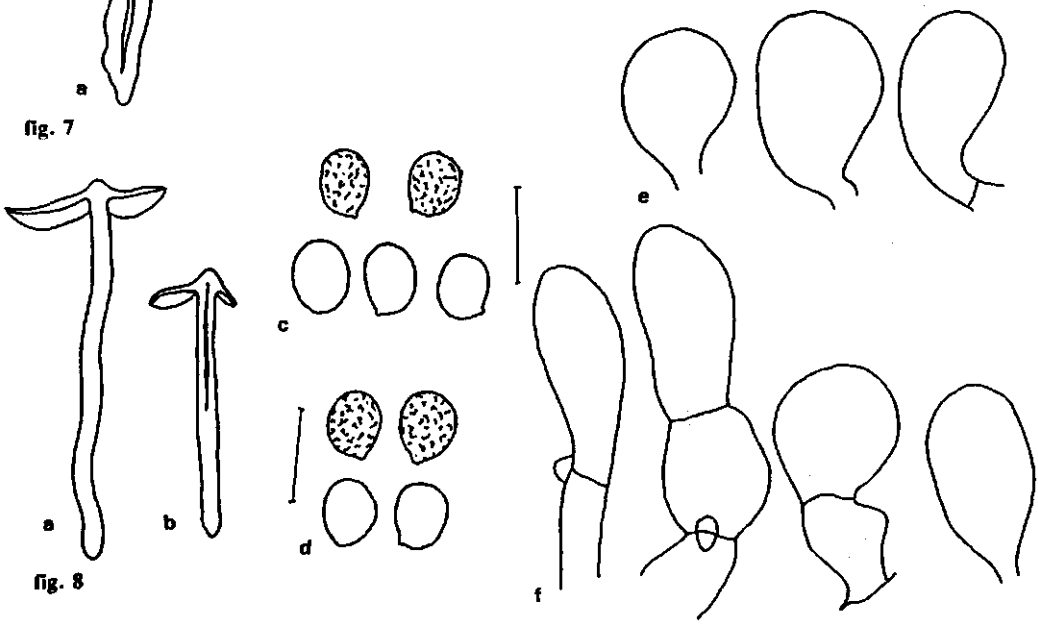


fig. 8

Fig. 6. Cortinairus casimiri a, c, e. habit; b, d, f. spores (a, b. 87193; c, d. 87200; e, f. 87290).

Fig. 7. Cortinarius causticus. a. habit; b, c. spores (a, b. 88124; c. 88103).

Fig. 8. Cortinarius comptulus. a, b. habit; c, d. spores; e, f. sterile cells in lamella edge (a, c, e. 88249; b, d, f. 87348).

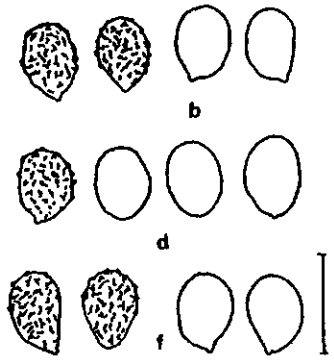


fig. 9

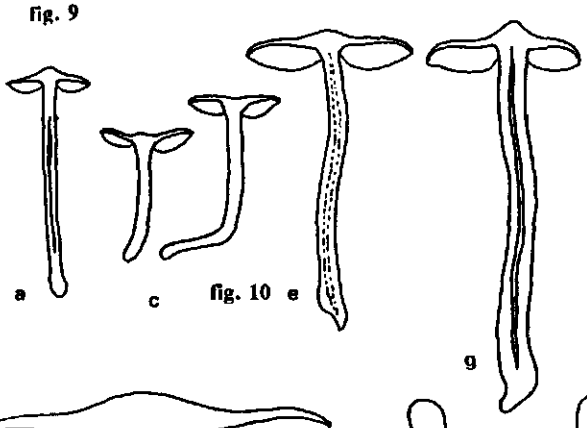
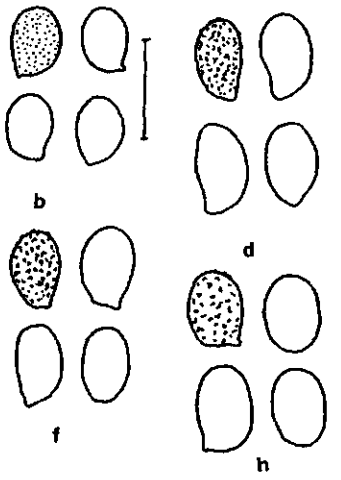


fig. 10



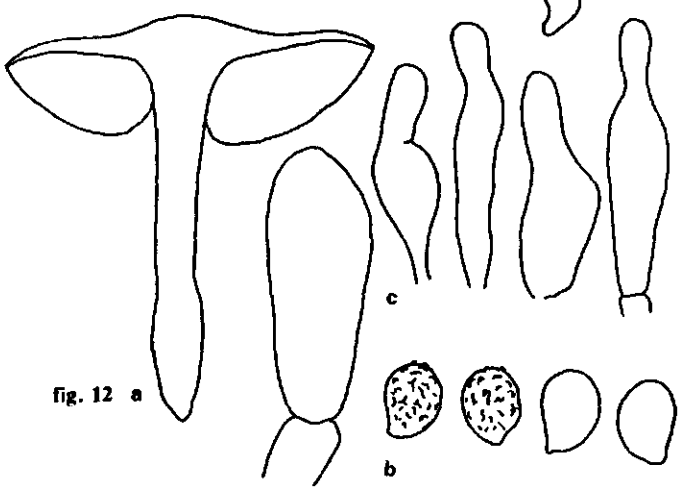


fig. 12 a

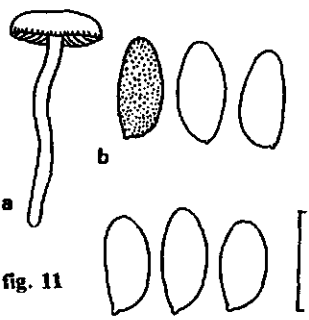


fig. 11

Fig. 9. Cortinarius erythrinus. a, c, e. habit; b, d, f. spores (a, b. 86152; c, d. 88140; e, f. 86237).

Fig. 10. Cortinarius flexipes. a, c, e, g. habit; b, d, f, h. spores (a, b. 86184; c, d. 87295; e, f. 87165; g, h. 88121).

Fig. 11. Cortinarius fusisporus. a. habit; b. spores (89104).

Fig. 12 a-c. Cortinarius hinnuleus. a. habit; b. spores; c. sterile cells in lamella edge (87143).

Fig. 12 d-i. Cortinarius hinnuleus. d, f. habit; e, g. spores; C. hinnuleus var. griseascens. h. habit; i. spores (d, e. 87312; f, g. 88126; h, i. 86238).

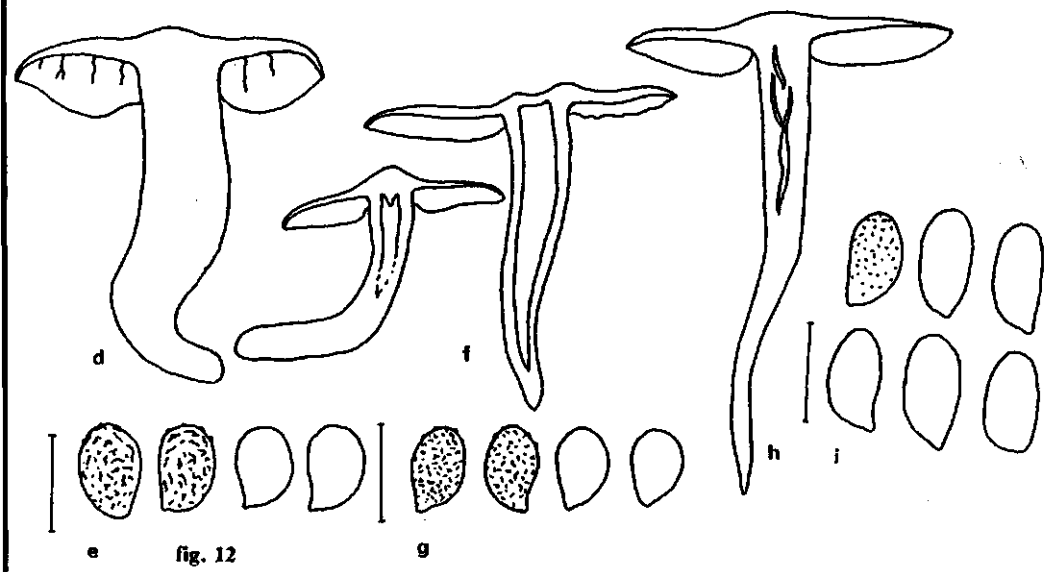


fig. 12

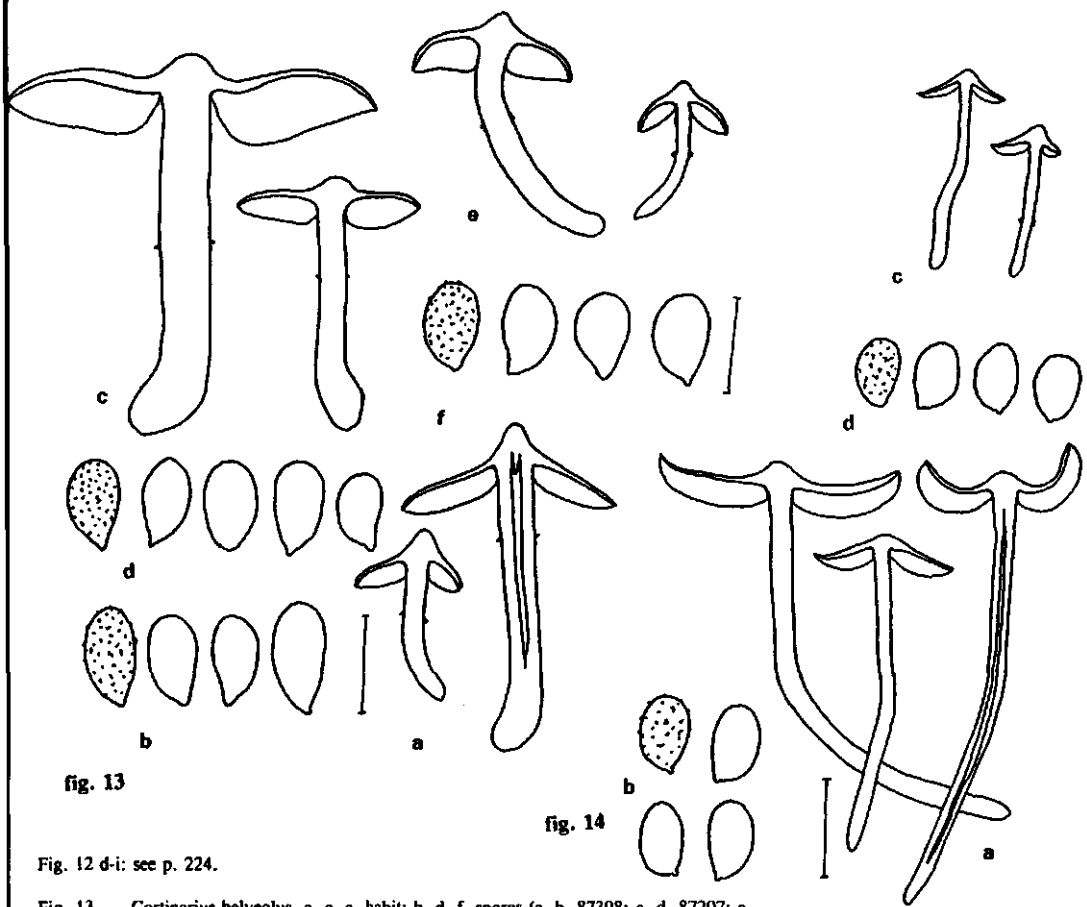


fig. 13

fig. 14

Fig. 12 d-i: see p. 224.

Fig. 13. Cortinarius helveolus. a, c, e. habit; b, d, f. spores (a, b. 87308; c, d. 87207; e, f. 88146).

Fig. 14. Cortinarius lanatus. a, c. habit; b, d. spores (a, b. 88195; c, d. 87051).

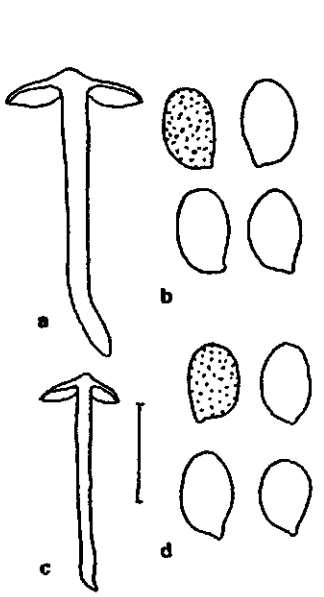


fig. 15

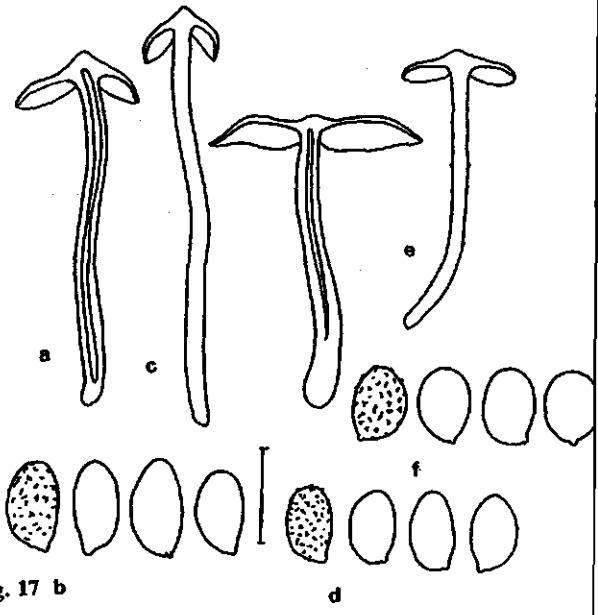


fig. 17 b

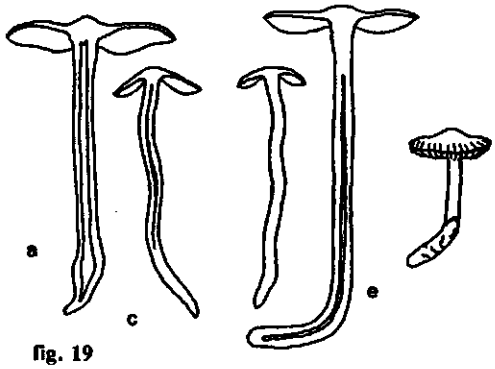
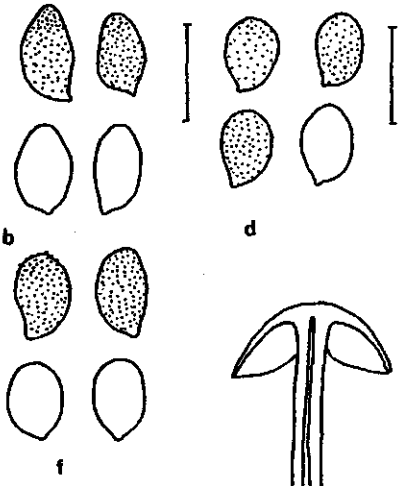


fig. 19



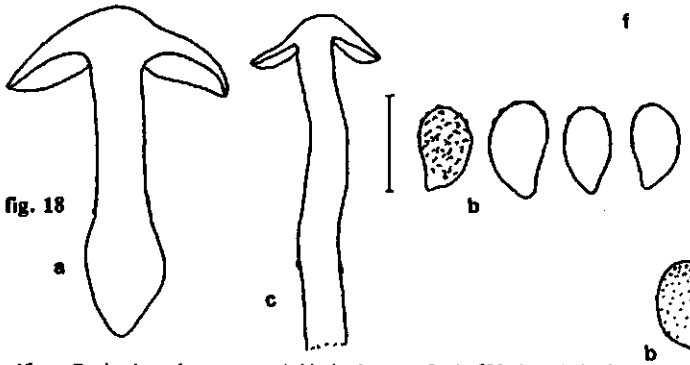


fig. 18

fig. 16

Fig. 15. Cortinarius paleaceus. a, c. habit; b, d. spores 8a, b. 87306; c, d. 87194).

Fig. 16. Cortinarius paleiferus. a. habit; b. spores (86246).

Fig. 17. Cortinarius parvannulatus. a, c, e. habit; b, d, f. spores (a, b. 87197; c, d. 87239; e, f. 88131).

Fig. 18. Cortinarius privignus. a, c. habit; b. spores (a, b. 86147; c. 86151).

Fig. 19. Cortinarius striaepilus. a, c, e. habit; b, d, f. spores (a, b. 87168; c, d. 88142; e, f. 87252).

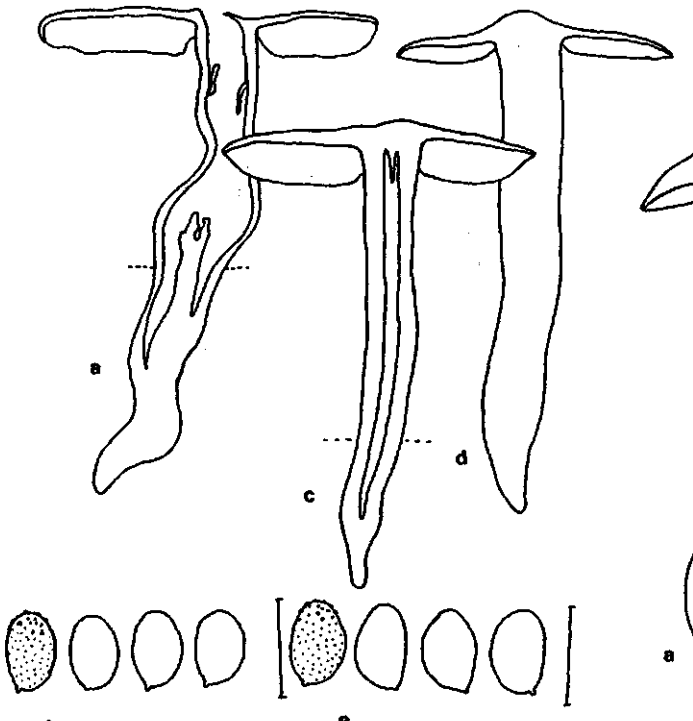
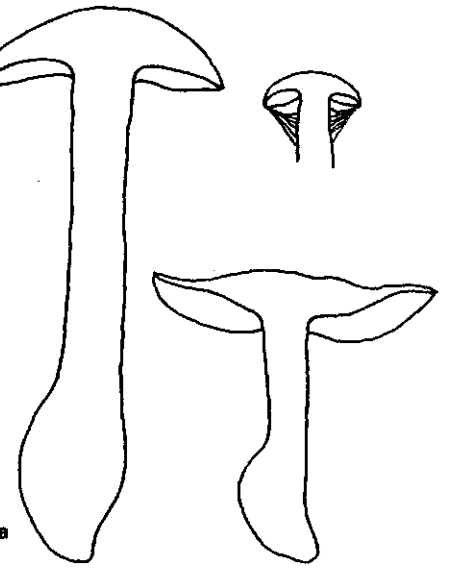


fig. 20



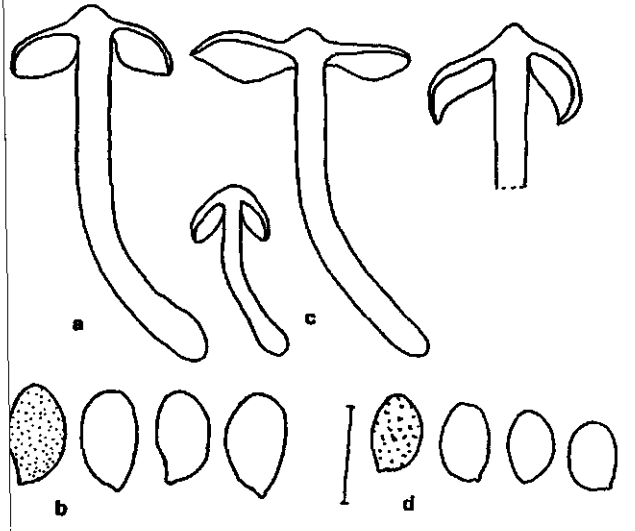


fig. 21

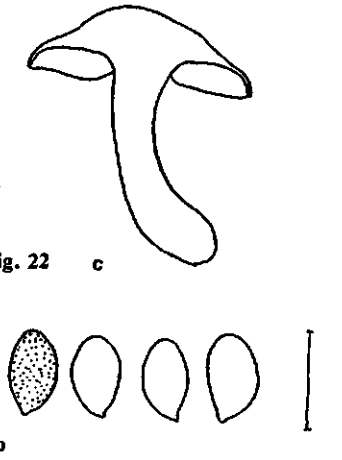


fig. 22

Fig. 20. Cortinaris rigens. a, c, d. habit; b. spores (a, b, c. 87291; d, e. 88139).

Fig. 21. Cortinarius rigidus Fr. ss. lange. a, c. habit; b, d. spores (a, b. 88169; c, d. 88203).

Fig. 22. Cortinarius subbalaustinus. a, c. habit; b. spores (a, b. 87183; c. 88094).

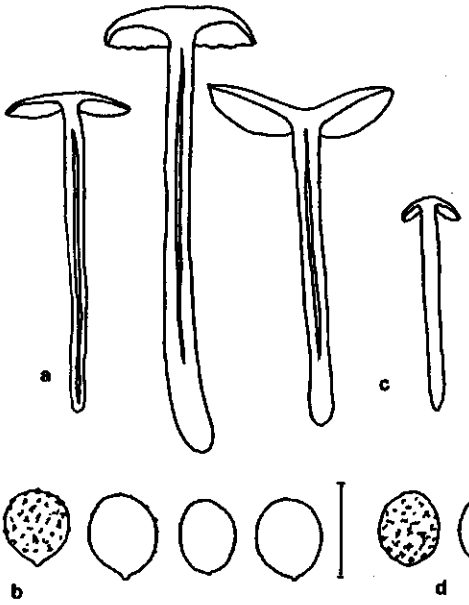


fig. 23

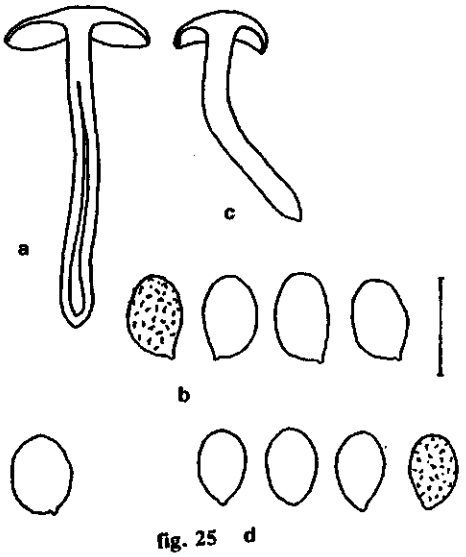


fig. 25

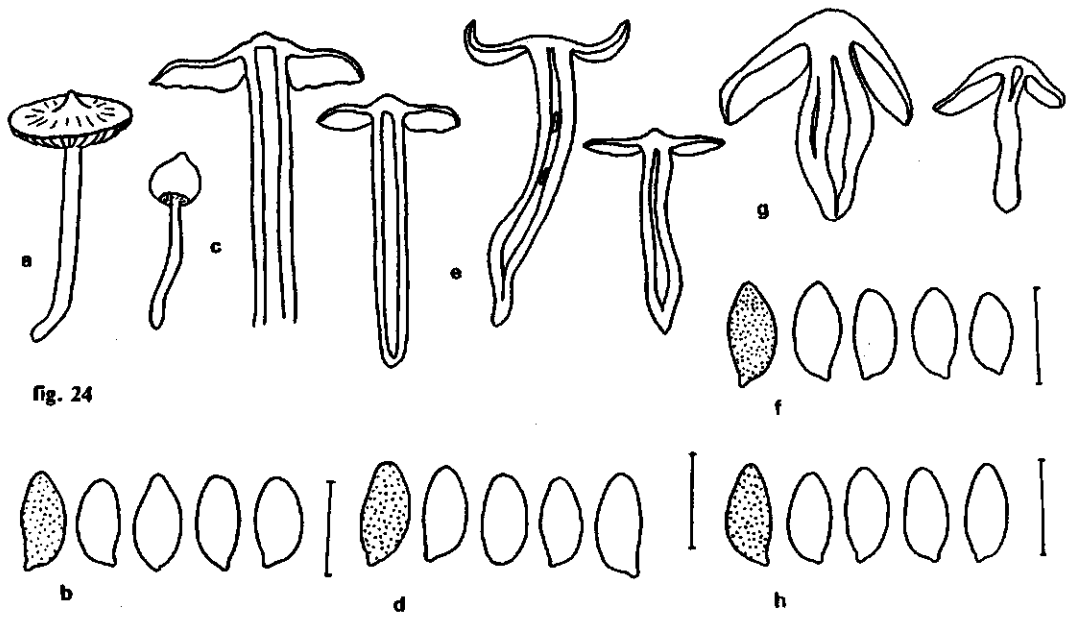


fig. 24

Fig. 23. Cortinarius tabularis. a, c. habit; b, d. spores (a, b. 88192; c, d. 88135).

Fig. 24. Cortinarius tramitum. a, c, e, g. habit; b, d, f, h. spores (a, b. 88080; c, d. 87233; e, f. 87179; g, h. 86225).

Fig. 25. Cortinarius valgus. a, c. habit; b, d. spores (a, b. 88235; c, d. 87241).

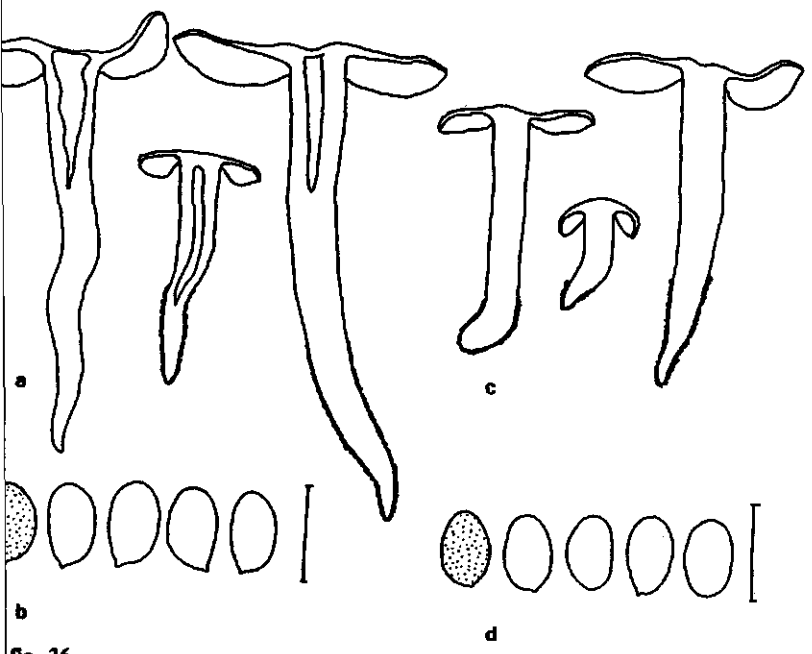


fig. 26

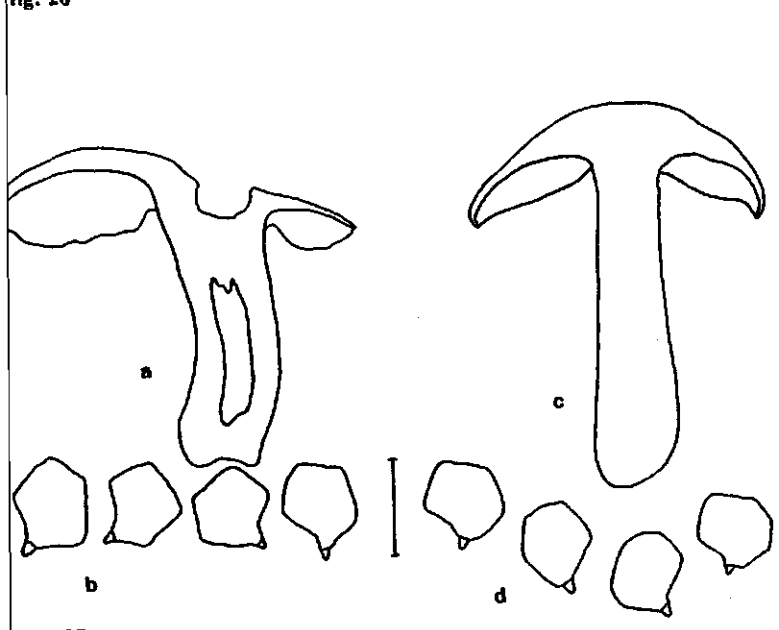


fig. 27

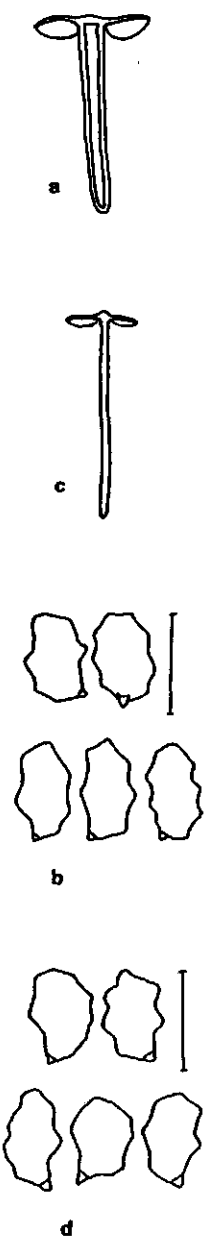


fig. 28

Fig. 26. Cortinarus velenovskyi. a, c. habit; b, d. spores (a, b. 88182; c, d. 88100).

Fig. 27. Entoloma lividoalbum. a, c. habit; b, d. spores (a, b. 88088; c, d. 87164).

Fig. 28. Entoloma undulatosporum. a, c. habit; b, d. spores (a, b. 87011; c, d. 87177).

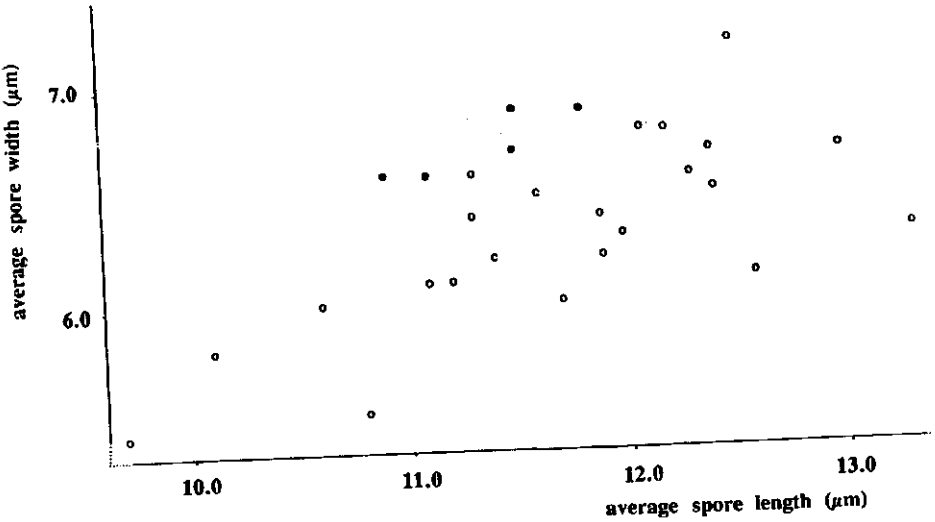


fig. 30

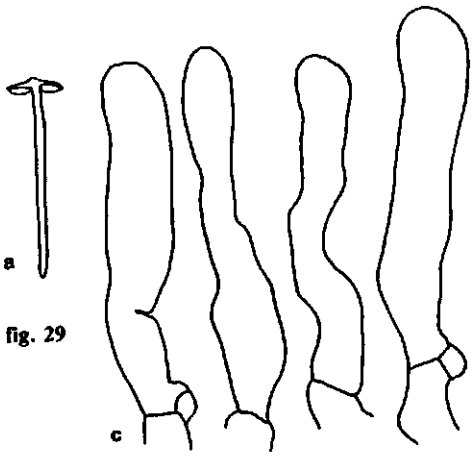
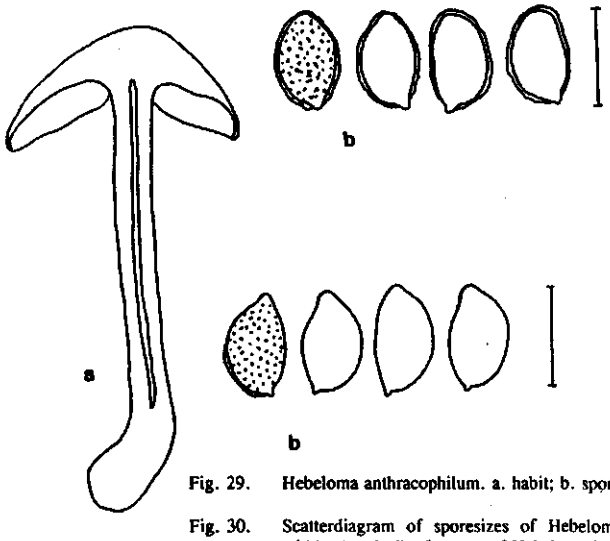


fig. 29



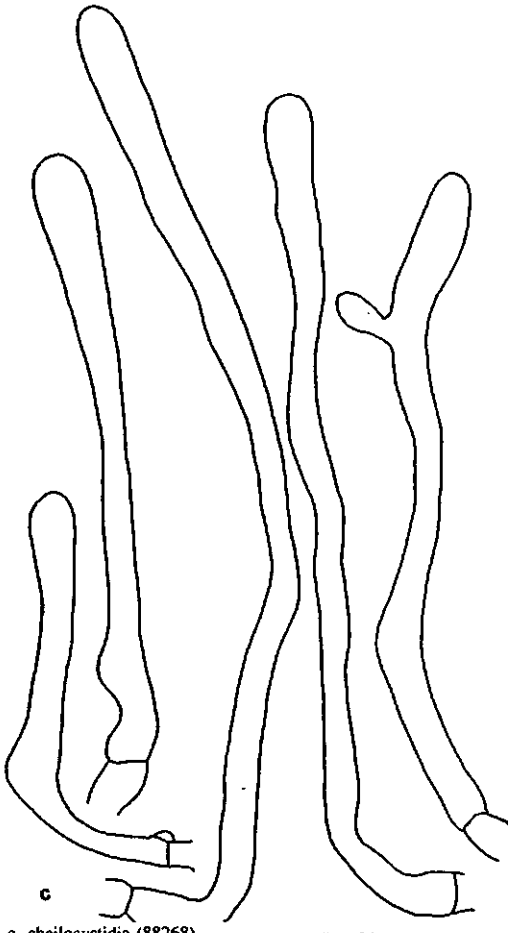


fig. 31

Fig. 29. Hebeloma anthracophilum. a. habit; b. spores; c. cheilocystidia (88268).

Fig. 30. Scatterdiagram of sporesizes of Hebeloma species. Lengths (horizontal) and widths (vertical) of spores of Hebeloma helodes (o), H. longicaudum (•) and H. crustuliniforme s. str. (c). Each symbol represents the average values of 10 spores of a collection.

Fig. 31. Hebeloma crustuliniforme. a. habit; b. spores; c. cheilocystidia (88201).

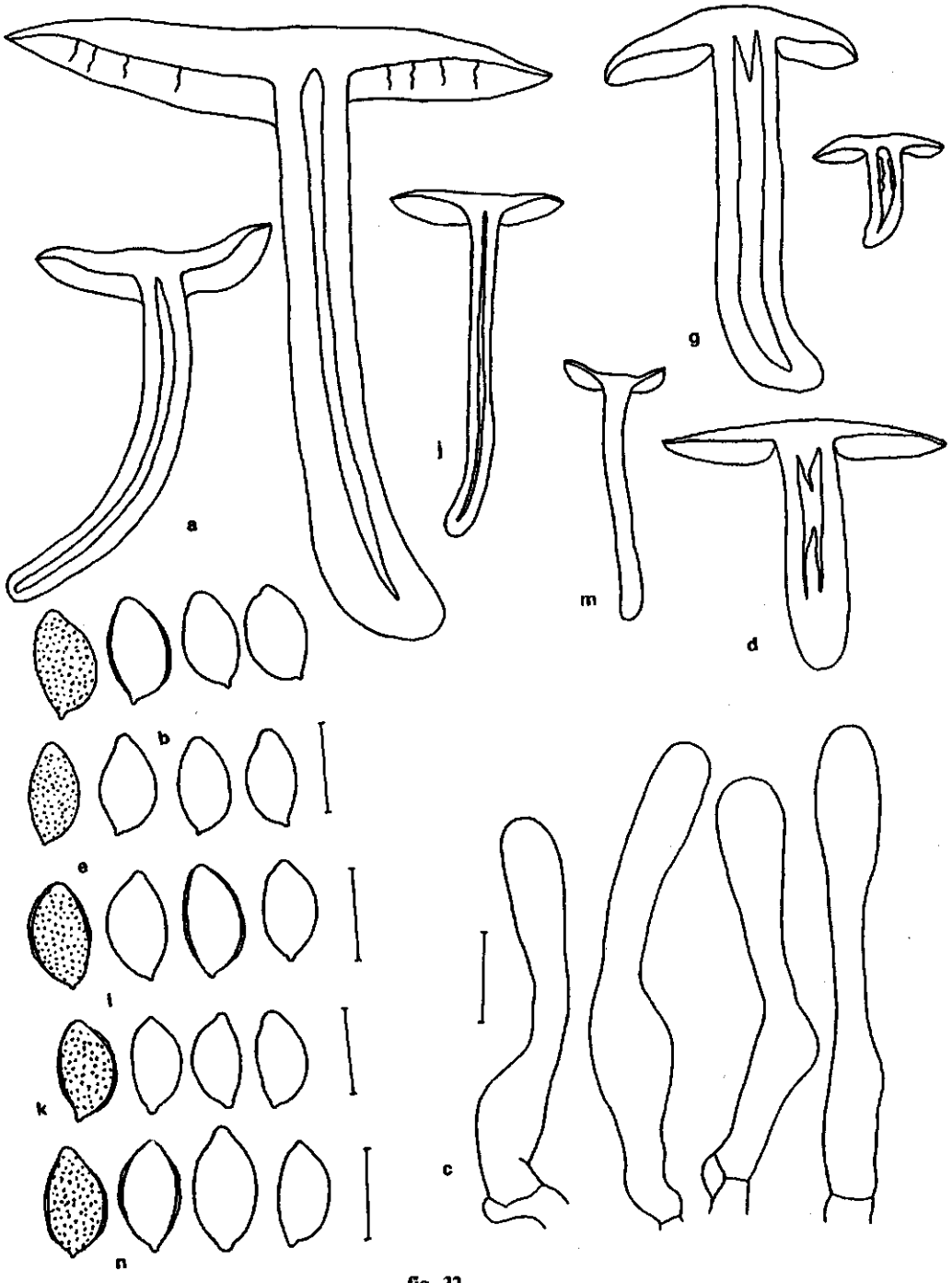


fig. 32

Fig. 32. Hebeloma helodes. a, d, g, j, m. habit; b, e. h, k, n. spores; c, f, i, l, o, p. cheilocystidia (a, b, c. 87313; d, e, f. 87126; g, h, i. 88120; j, k, l. 87255; m, n, o. 86173; p. 86276).

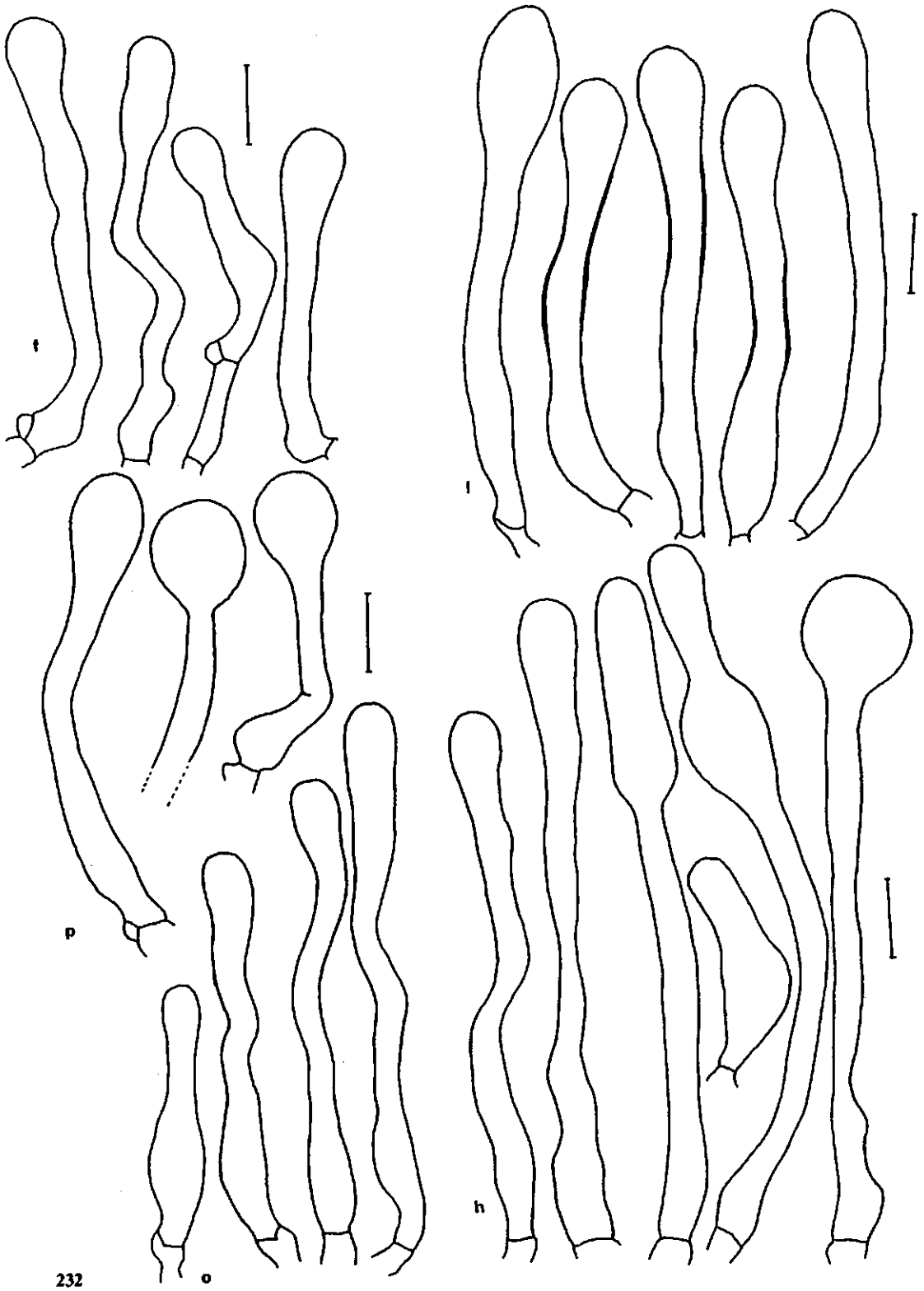


Fig. 32 (continued; see p. 231).

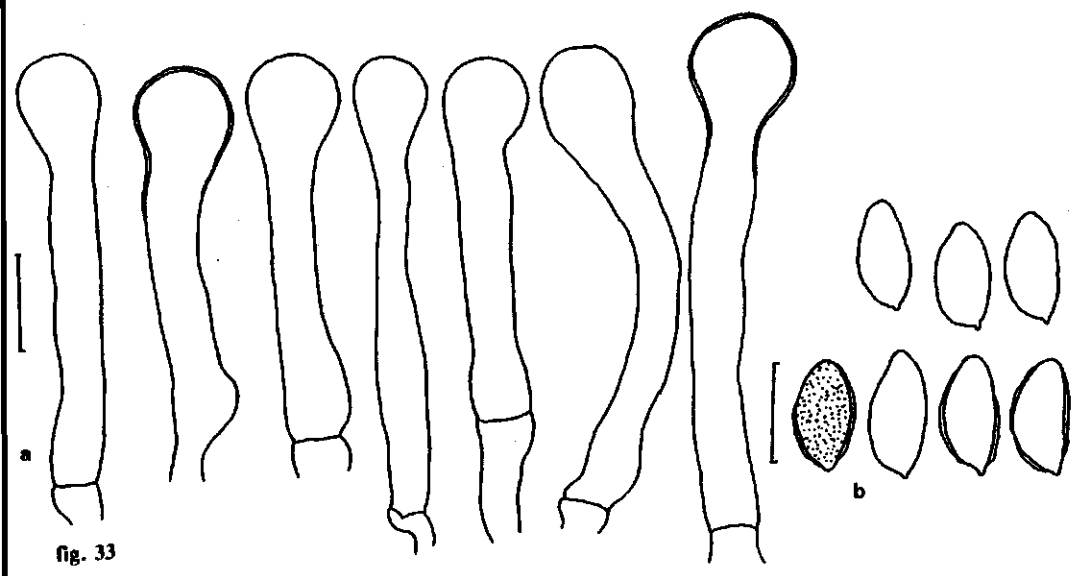


fig. 33

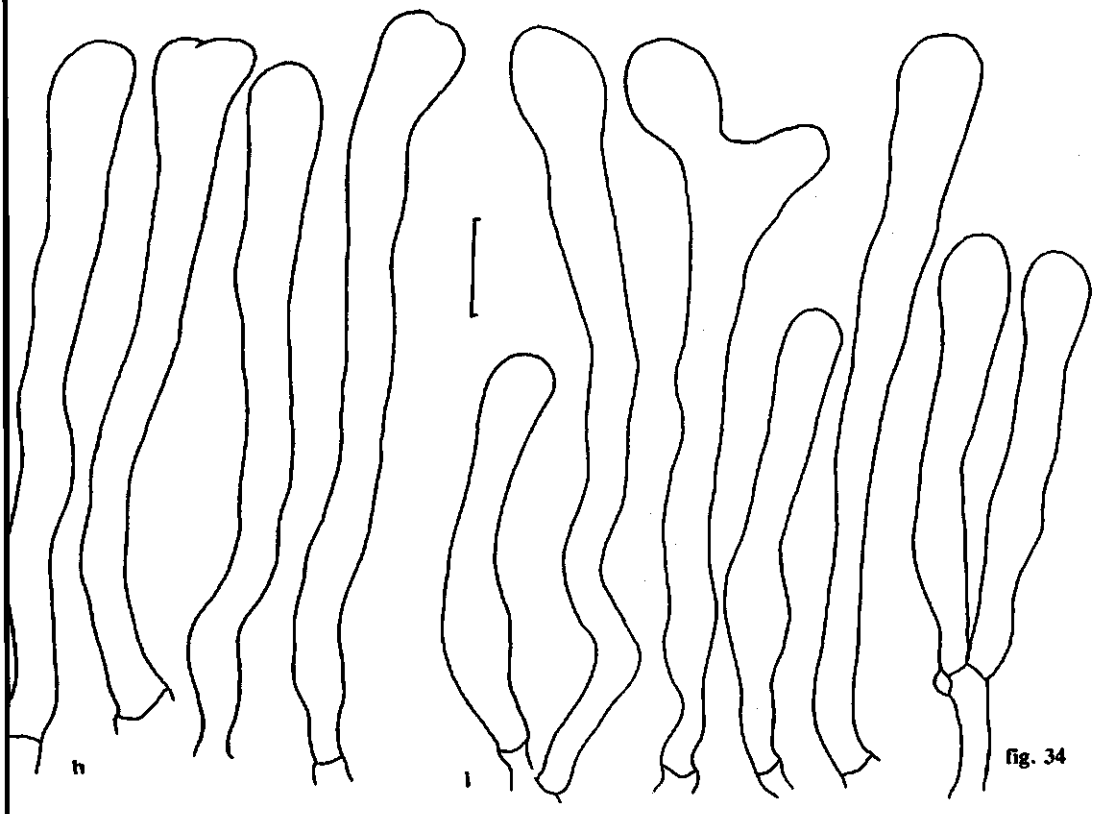
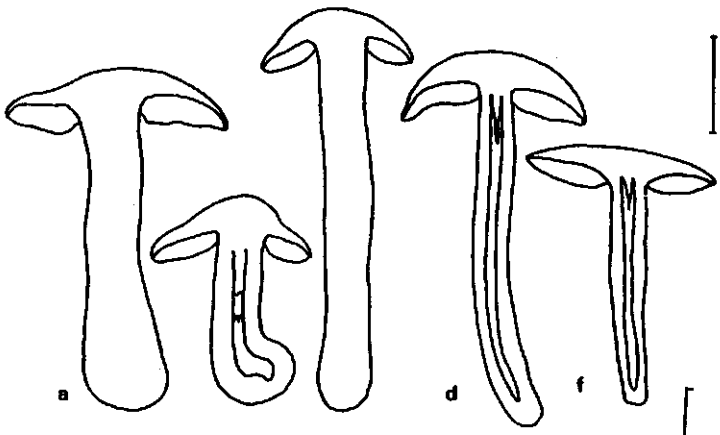


fig. 34

Fig. 33. Hebeloma helodes. a. cheilocystidia; b. spores (leg. J. Favre, GK 7721, Haut Marais des Pleiades, Switzerland, 29-9-1940, herb. G.).

Fig. 34 h, i (see p. 234). h i



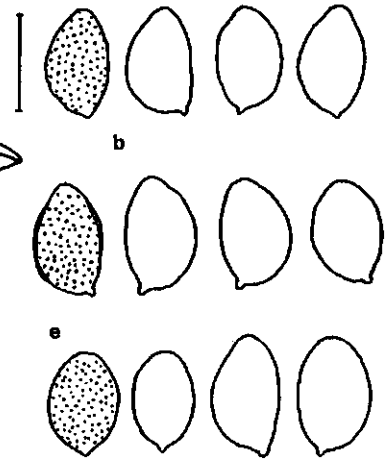
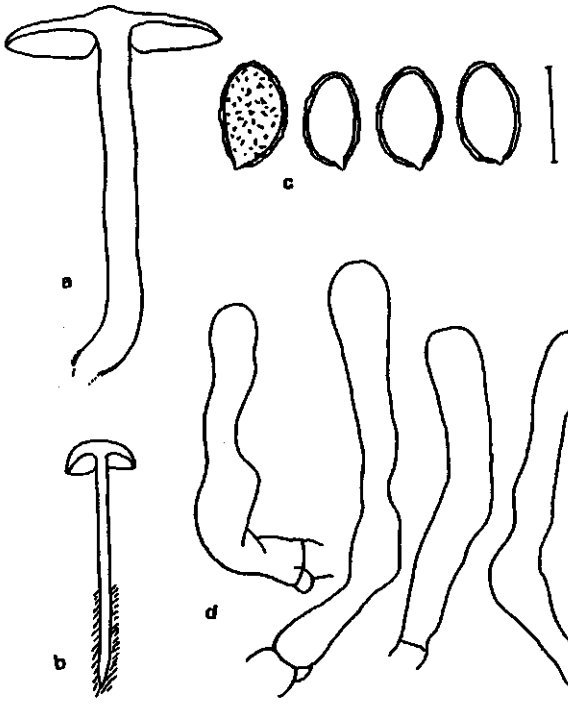


fig. 34



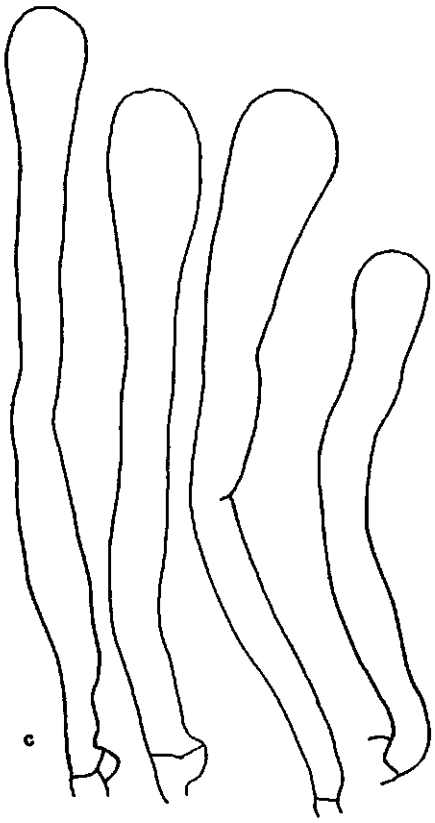


fig. 35

Fig. 34. Hebeloma longicaudum. a, d, f. habit; b, e, g. spores; c, h, i. cheilocystida (a, b, c. 87215; d, e, h. 88123; f, g, i. 86172).

Fig. 35. Hebeloma spoliatum. a, b. habit; c. spores; d. cheilocystidia (a, b, c. 88128; b. 86233).

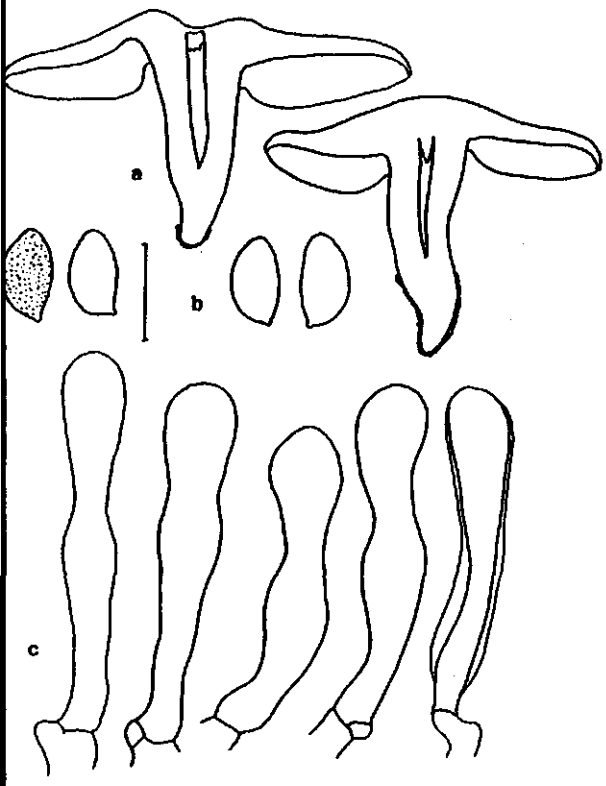


fig. 36

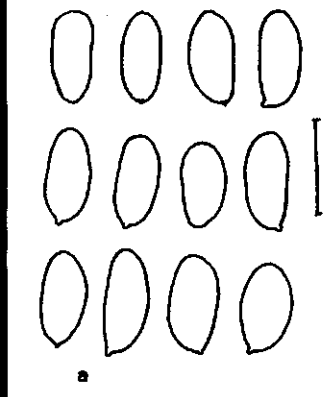


fig. 37

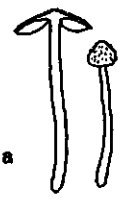
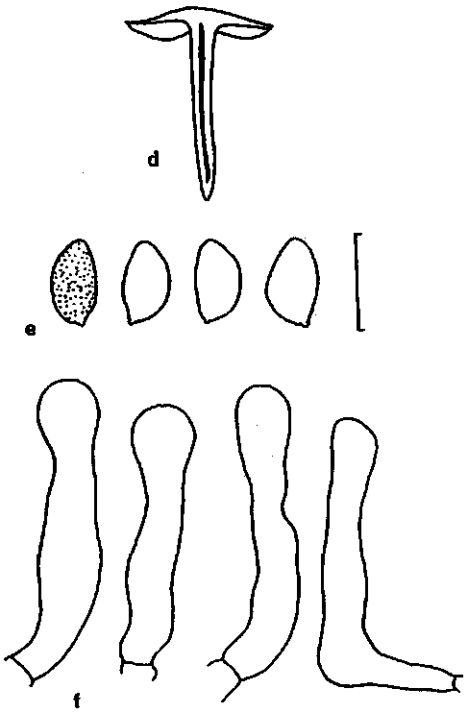


fig. 38



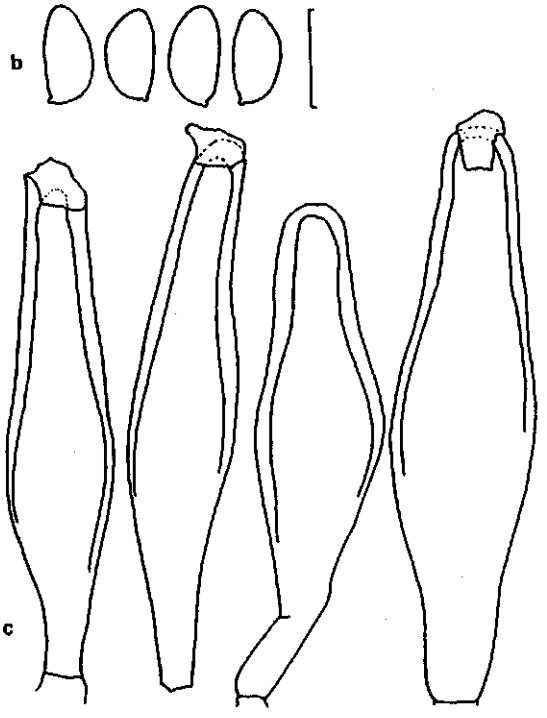


Fig. 36. Hebeloma truncatum. a, d. habit; b, e. spores; e, f. cheilocystidia (a, b, c. 88085; d, e, f. 87028).

Fig. 37. Inocybe albomarginata f. longispora. a. spores (88356).

Fig. 38. Inocybe amethystina. a. habit; b. spores; c. pleurocystidia (88296).

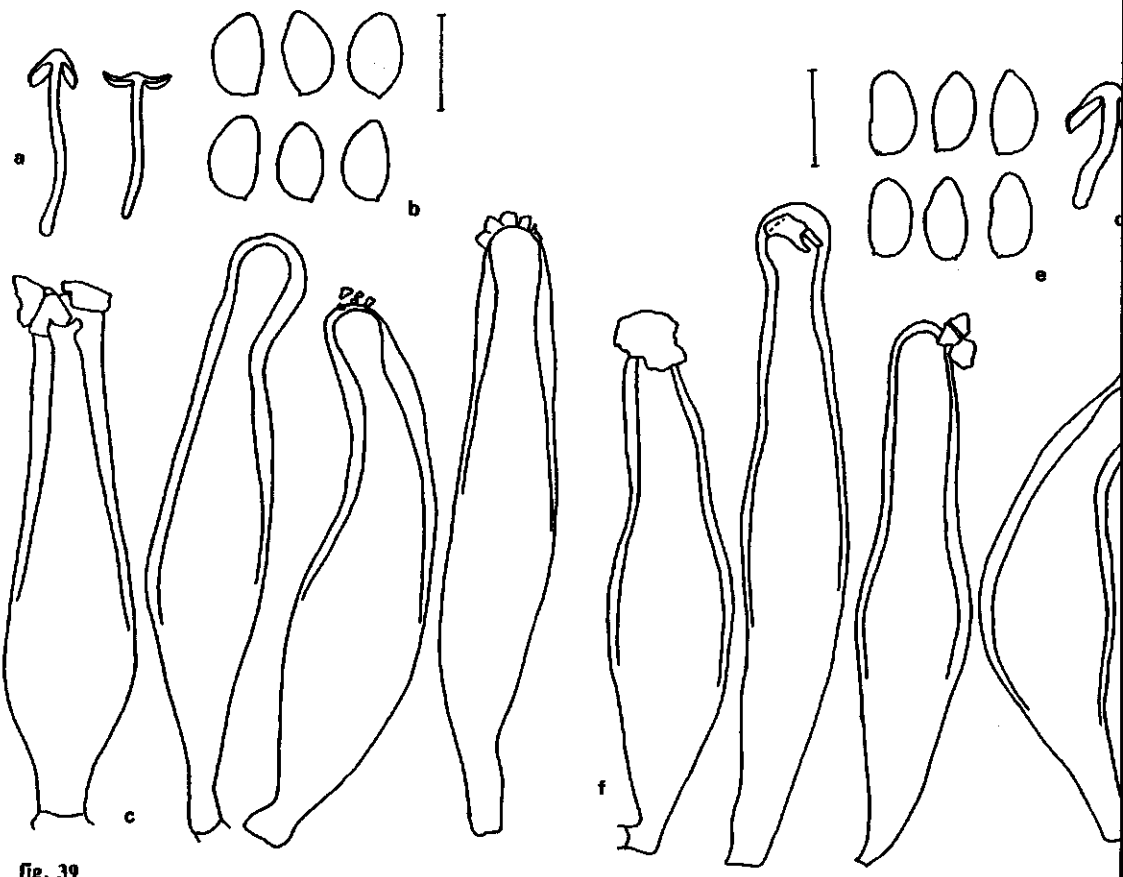


fig. 39

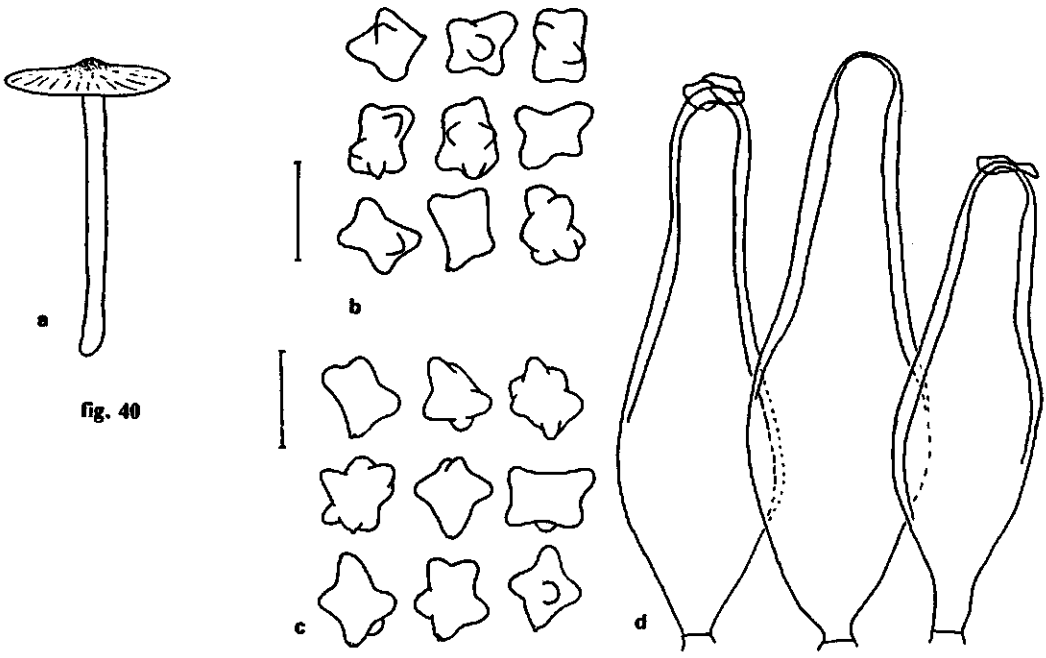


fig. 40

Fig. 39. Inocybe huijsmanii. a, d. habit; b, e. spores; c, f. pleurocystidia (a, b, c. 88272; d, e, f. 88304).

Fig. 40. Inocybe pseudoasterospora var. microsperma. a. habit; b, c. spores; d. pleurocystidia (a, b. 87173; c, d. 88152).

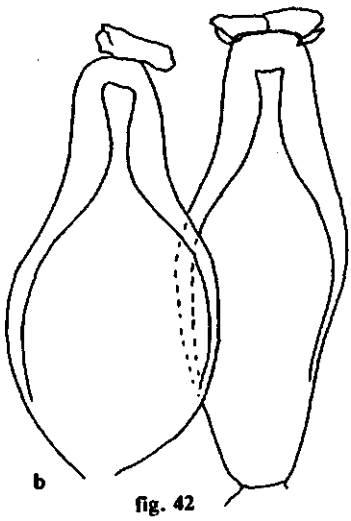


fig. 42

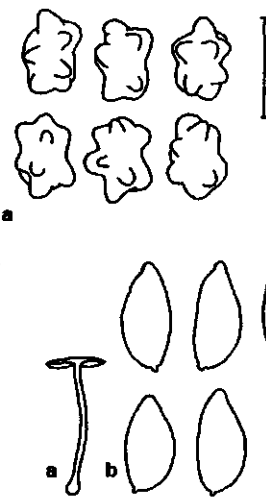
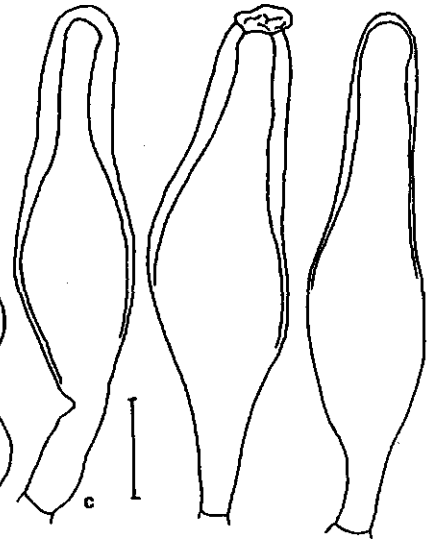


fig. 41



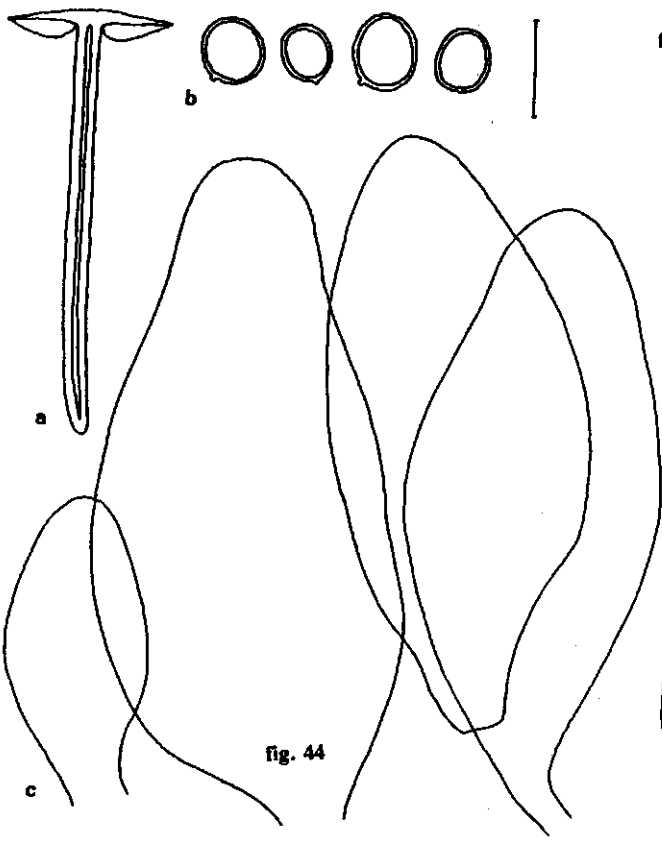
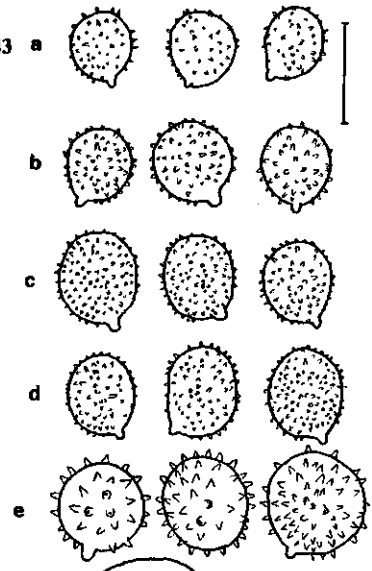


fig. 44

fig. 43



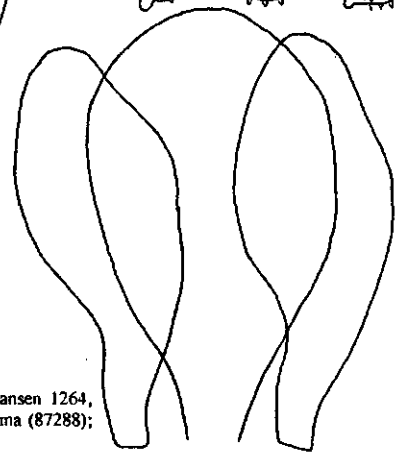


Fig. 41. Inocybe spec. a. spores; b. pleurocystidia (88170).

Fig. 42. Incoybe mixtilis. a. spores; b. pleurocystida (88302b).

Fig. 43. Laccaria, spores. a. L. bicolor (87210); b. L. bicolor (leg. A.E. Jansen 1264, St.-Anthonis, The Netherlands, 23-10-1985, herb. WBS); c. L. proxima (87288); d. L. purpureobadia (87266); e. L. laccata (87036).

Fig. 44. Pluteus pallescens. a. habit; b. spores; c. pleurocystida; d. cheilocystidia (87136).

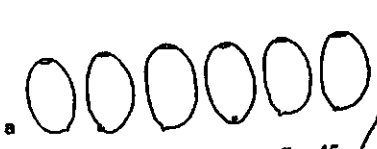


fig. 45

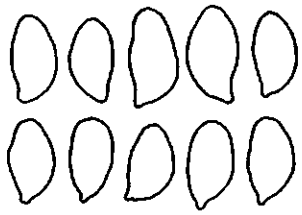
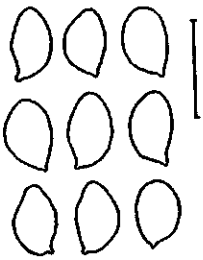


fig. 47



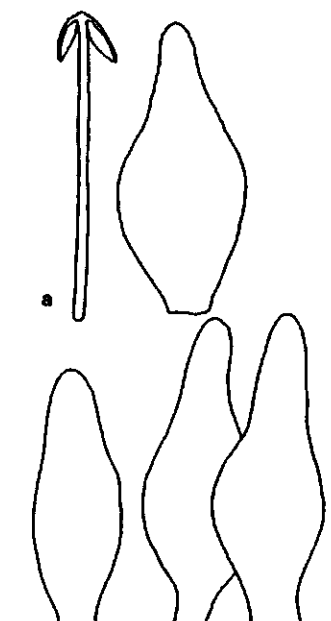


fig. 46

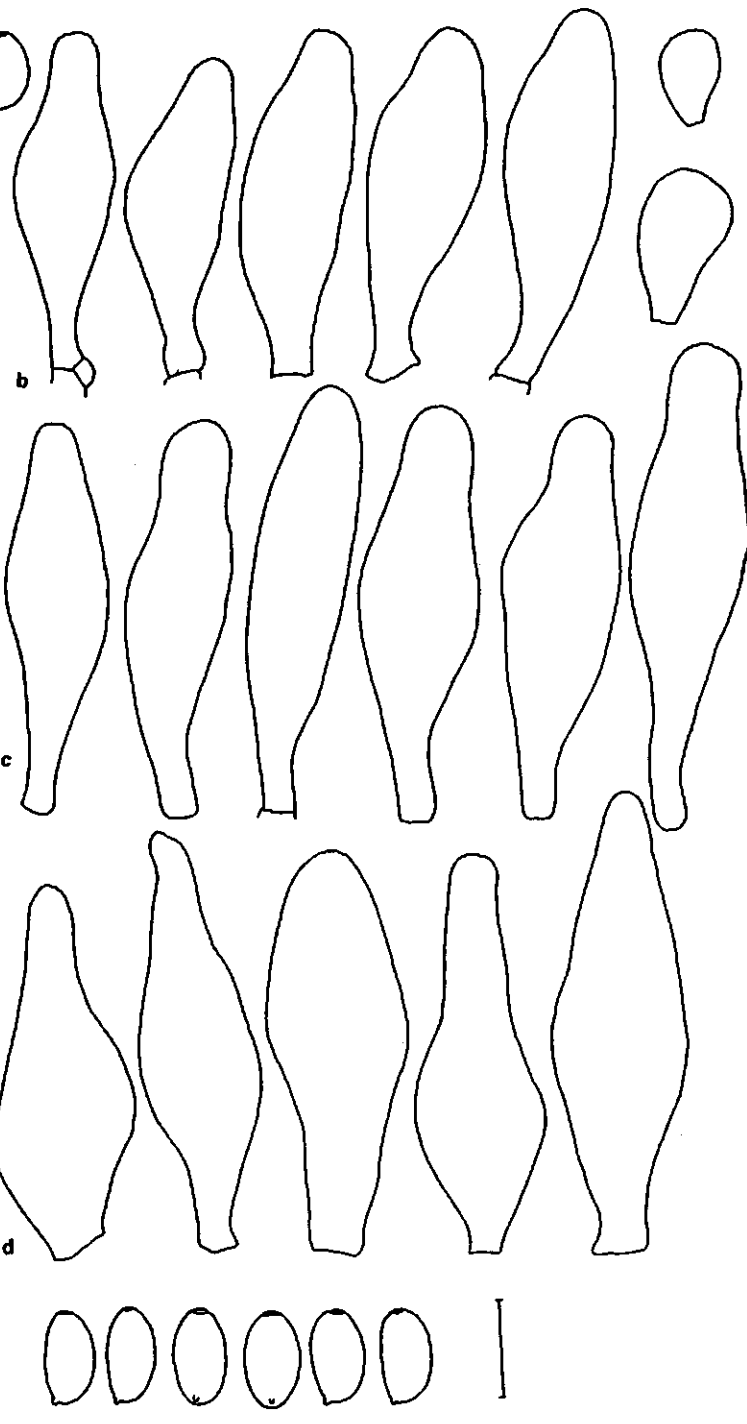


Fig. 45. Psathyrella fulvescens var. brevicystis. a. spores; b. cheilocystidia; c. pleurocystidia (86140).

Fig. 46. Psathyrella cf. fulvescens var. brevicystis. a. habit; b. spores; c. cheilocystidia; d. pleurocystidia (87092).

Fig. 47. Psathyrella aporos nov. spec. a, b. spores (a. 87324; b. 88314).

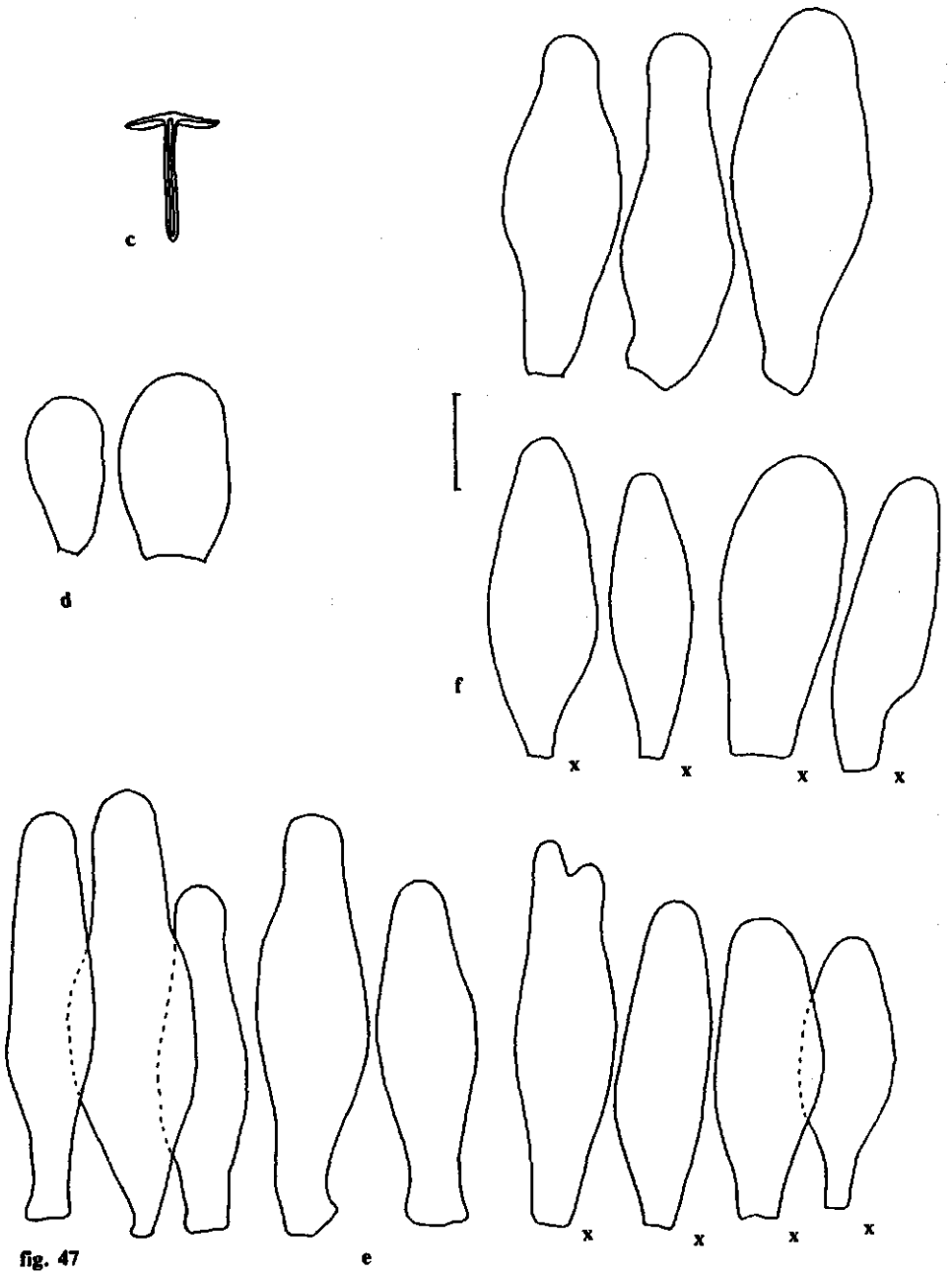


Fig. 47 (cont.) Psathyrella aporos nov. spec. c. habit; d. cheilocystidia; e. pleurocystidia; f. cheilocystidia (marked with x: kindly studied and drawn by Dr. E. Kits van Waveren). (c-g. 87324)

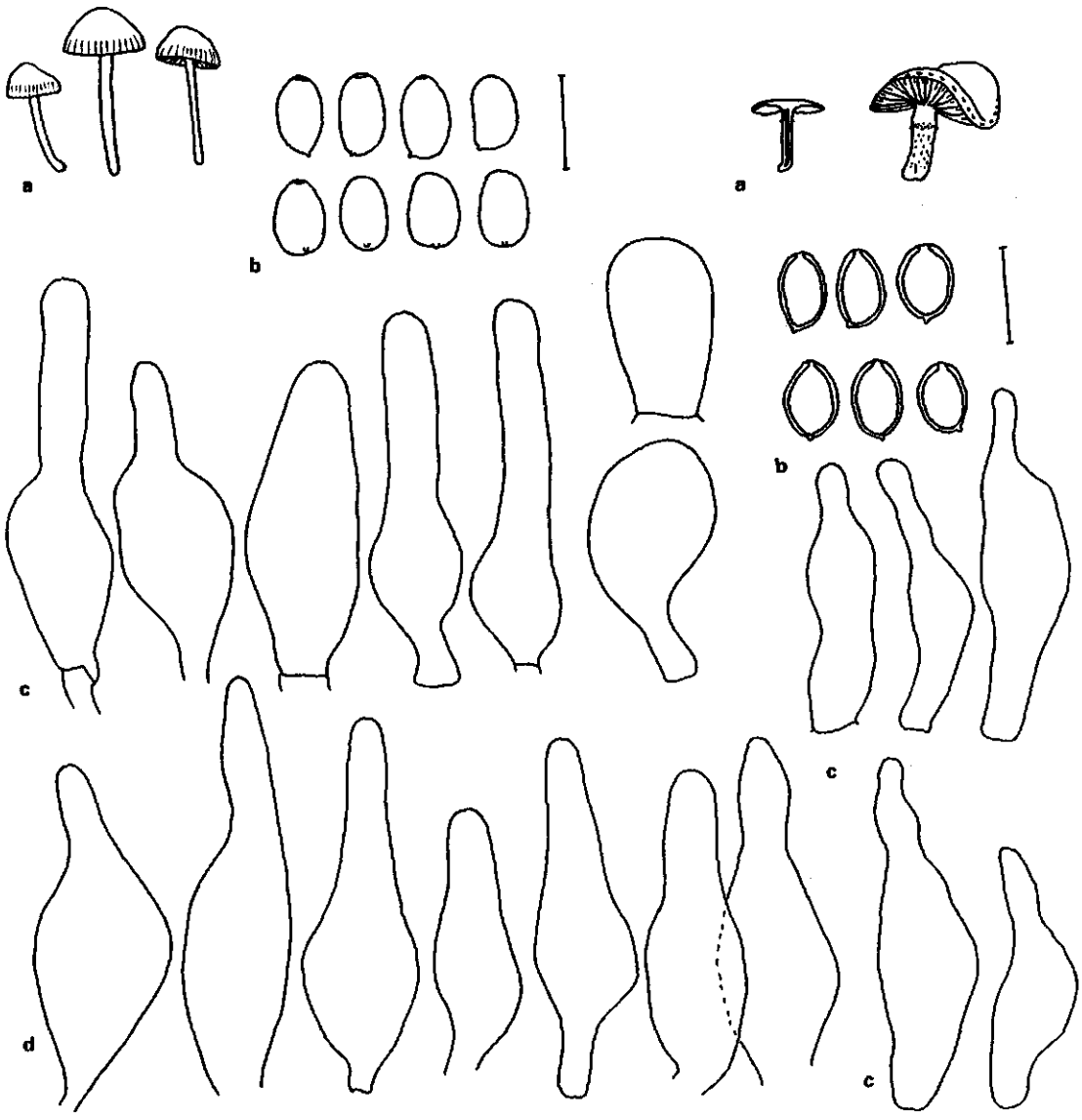


fig. 48

fig. 49

Fig. 48. Psathyrella seymourensis. a. habit; b. spores; c. cheilocystidia; d. pleurocystidia (86222).

Fig. 49. Psilocybe bullacea. a. habit; b. spores; c. cheilocystidia (88333).

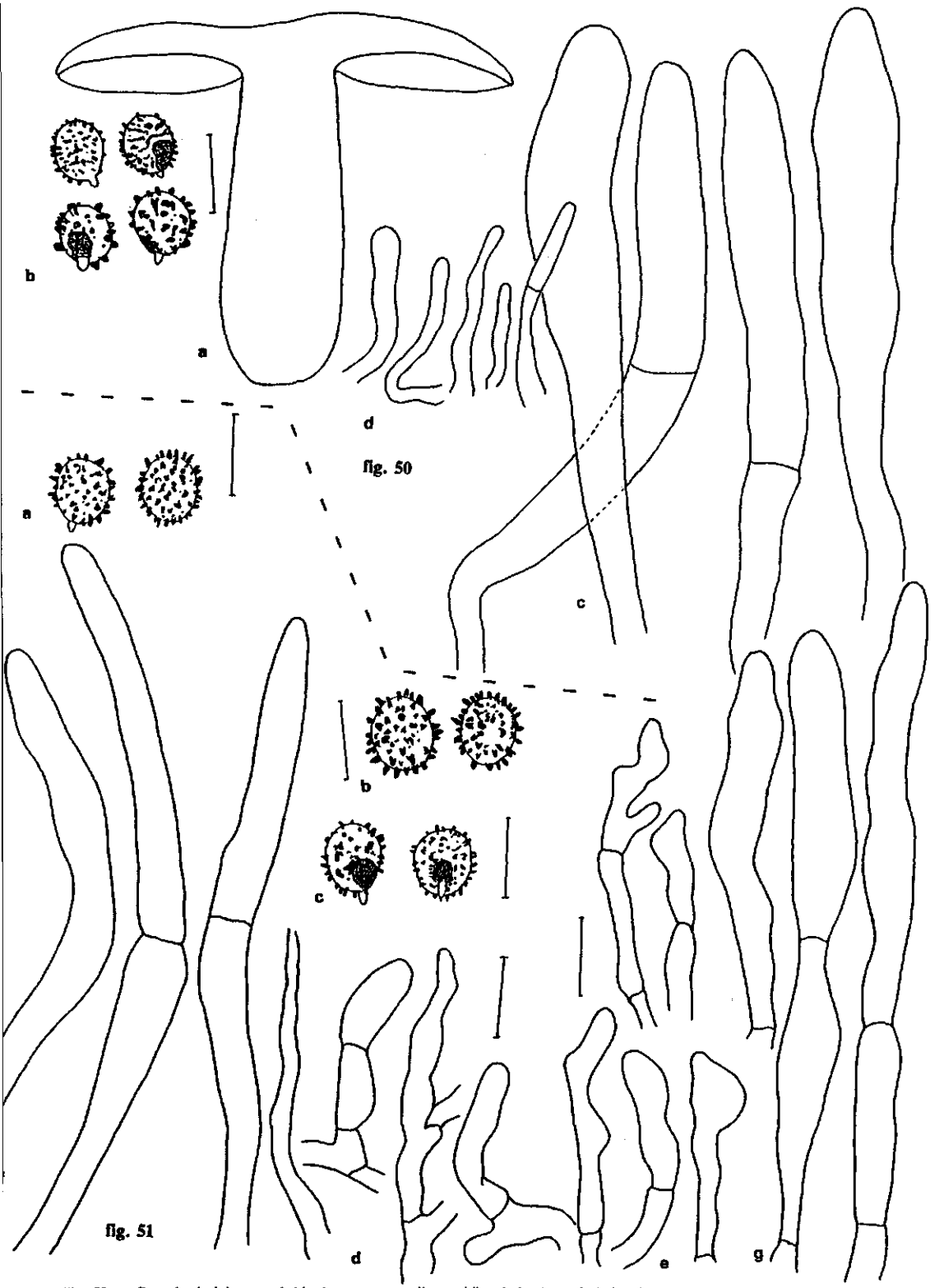


Fig. 50. Russula decipiens. a. habit; b. spores; c. pileocystidia; d. hyphae of pileipellis (86130).

Fig. 51. Russula graveolens f. cicatricata. a, b, c. spores; d, e. hyphae of pileipellis; f, g. pileocystidia; a, d, f. 87034; b. 87219; c, e, g. 88162).

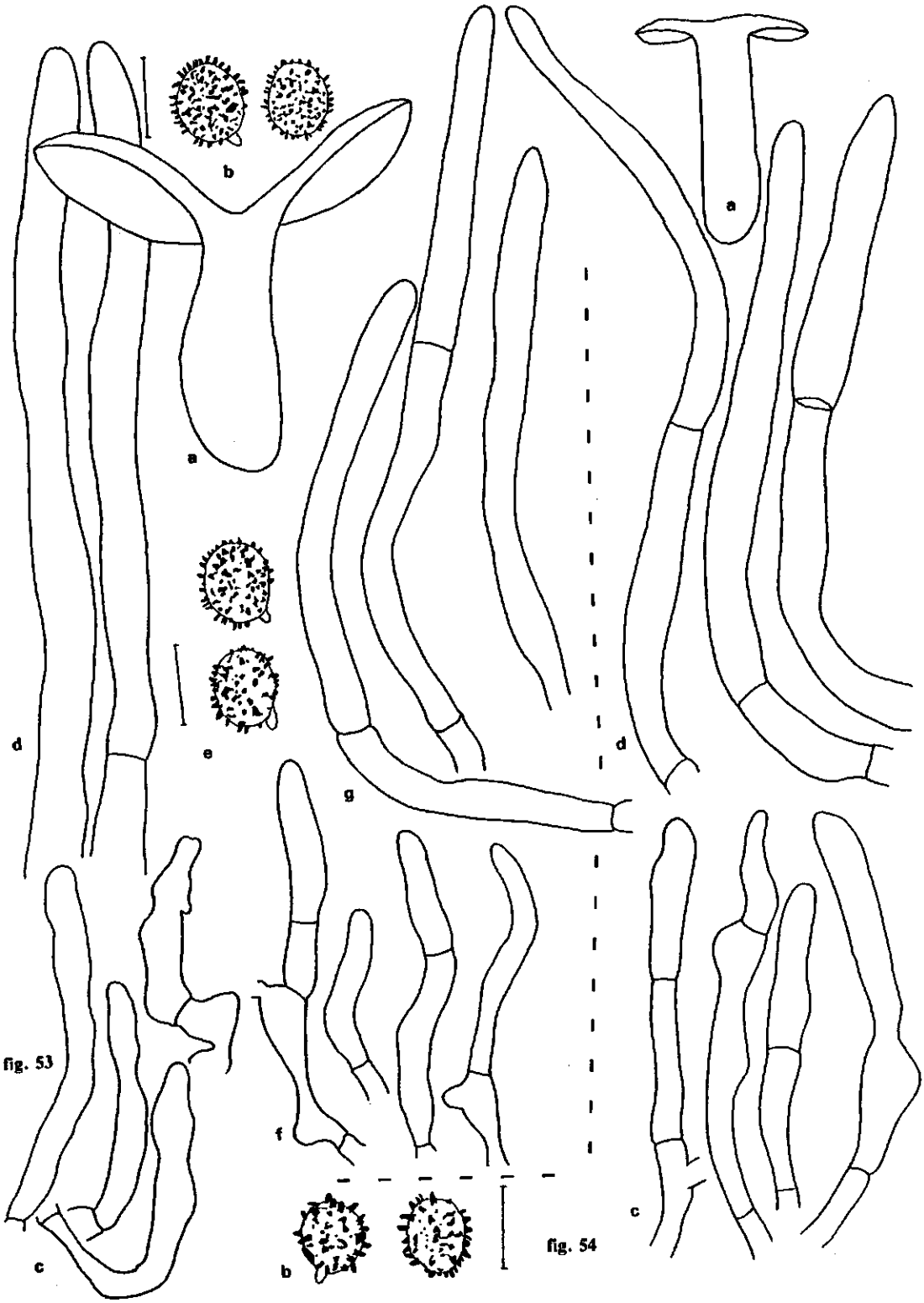


Fig. 53. Russula graveolens f. graveolens. a. habit; b, e. spores; c, f. hyphae of pileipellis; d, g. pileocystidia (a, b, c, d. 86164; e, f, g. 88019).

Fig. 54. Russula graveolens f. purpurata. a, d. habit; b, e. spores; c, f. hyphae of pileipellis; d, g. pileocystidia (a, b, c, d. 87186; e, f, g. 87228).

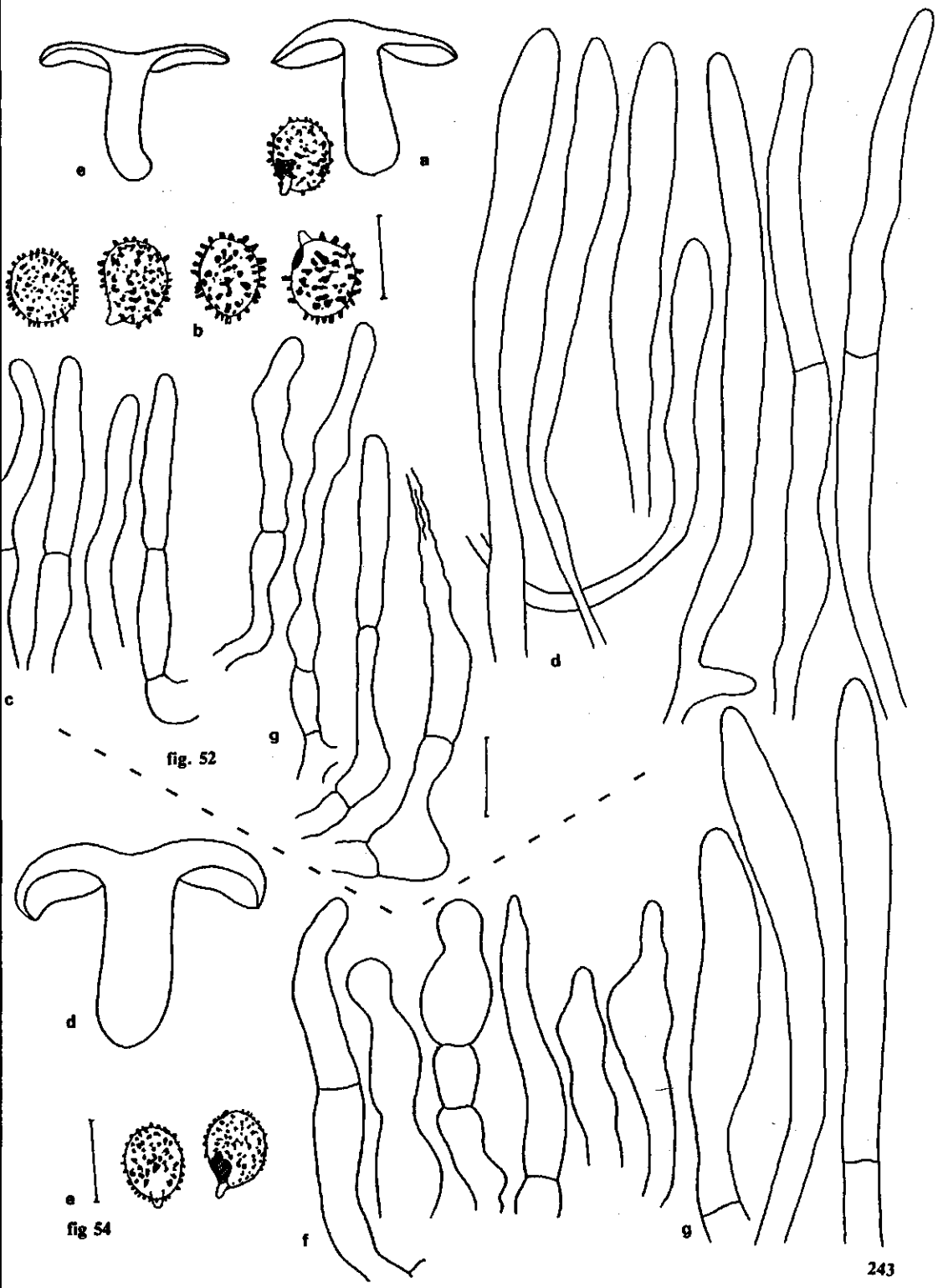


Fig. 52. Russula graveolens f. elaeodes. a, e. habit; b, f. spores; c, g. hyphae of pileipellis; d, h. pileocystidia (a, b, c, d. 88133; e, f, g, h. 86166).

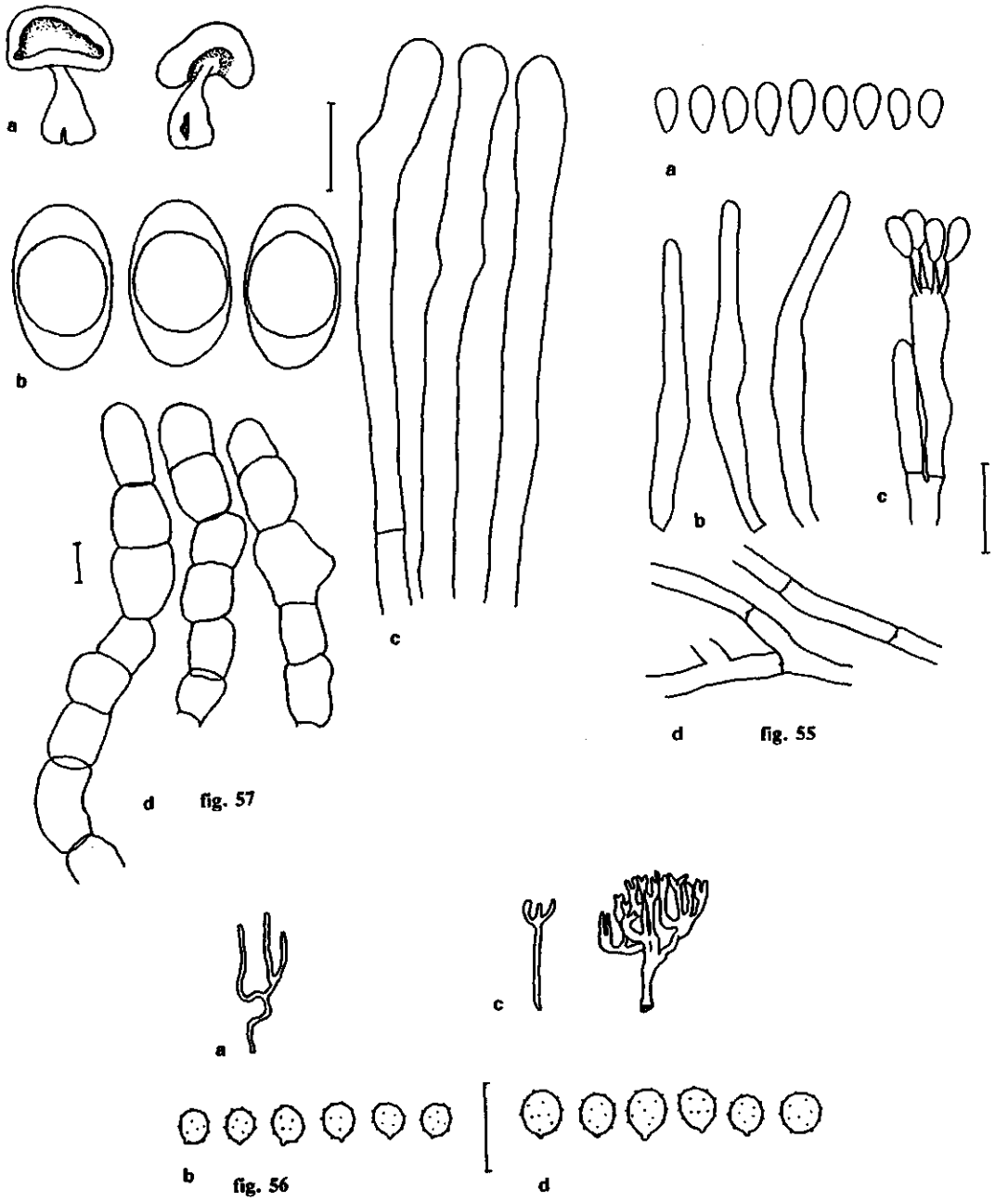


Fig. 55. Cyphellostereum laeve. a. spores; b. cystidia; c. basidium; d. hyphae (87303).

Fig. 56. Ramariopsis kunzei. a, c. habit; b, d. spores (a, b. 88324; c, d. 88244).

Fig. 57. Helvella cupuliformis. a. habit; b. spores; c. paraphyses; d. hairs of excipululum (87167).

GENERAL DISCUSSION

Introduction.

Traditionally, mycologists spend most of their time in forests, and, consequently, they mostly study the macromycetes that occur in forests. Extremely artificial habitats, which are sometimes not attractive from a scenic point of view, such as roadside verges, have been, at most, accidentally visited from a mycological viewpoint. In the literature the mycological value of some particularly rich roadside verges is rarely mentioned, e.g. in old estates in the alluvial clay area in the Netherlands (Arnolds, 1968; Reijnders, 1968, 1975). From roadside verges planted with trees on nutrient-poor sandy soil no data existed except incidental observations. However, these observations indicate that part of such roadside verges contain a rich and interesting mycoflora, including some rare and endangered species. The fact that roadside verges form an artificial habitat which differs profoundly from any other habitat offers interesting possibilities for both ecological research and for the conservation of species.

Composition of the mycoflora.

In the present study, various aspects concerning the mycoflora in roadside verges that are planted with Beech (*Fagus sylvatica*) or Common Oak (*Quercus robur*) are described. In total, 76 plots of 100 m length and a variable width, but on average 3.4 m broad, and 1500 x 4.5 m^2 for the field experiment were investigated, together 9.1 km of roadside verges, with a surface of 3.3 ha, all on sandy soils in Drente, the Netherlands.

The number of species and sporocarps that were found during the investigation are presented in table 1.

	Number of species	% of all Dutch species of the functional group	Number of sporocarps (rounded)
Ectomycorrizal fungi	164	20	82000
Saprotrophic fungi	275	11	146000
All fungi	439	13	228000

Table 1. Numbers of species, percentages of all species of the ecological group in the Netherlands (after Arnolds & de Vries, 1989) and number of sporocarps found during the study of macromycetes in roadside verges in Drente. The extremely high numbers of the small *Mycena polyadelpha* in some plots were not included in the sporocarp numbers given here, because the former were only estimated.

The total number of Macromycete species that was encountered, amounts to 439, i.e. 13% of the total number of species in the Netherlands (after Arnolds & de Vries, 1989; see appendix 1). For ectomycorrhizal species these figures are 164 and 20% respectively.

In my opinion, these numbers are remarkably high, especially for the ectomycorrhizal fungi, taking into account the following aspects:

1. the investigation was carried out in a study area of 3.3 ha which is far less than 1 $^{o}/_{oo}$ of the country but where 13 % of the indigenous species were found;

2. a relatively uniform habitat type was investigated: roadside verges on sandy soil, planted with trees;
3. only two ectomycorrhizal tree species are present in the plots;
4. woody substrates are hardly available due to the removal of most of the dead wood from roadside verges;
5. not all groups of macromycetes were included, e.g. resupinate lignicolous basidiomycetes or most inoperculate ascomycetes were not treated.

In the species-rich plots, from 30 to over 60 ectomycorrhizal species were found. This is much more than can be found nowadays in any homogeneous forest stand in the Netherlands. In addition, some species which are characteristic for old unfertilized grasslands, were found in roadside verges.

During the present study 57 species were found that are considered to be threatened in the Netherlands (classes 1, 2, 3 and 4 after Arnolds, 1989); among them four which are threatened with extinction (class 1), viz. *Boletopsis leucomelaena, Leucopaxillus giganteus, Lyophyllum semitale, Phellodon confluens*. This clearly illustrates the high mycological value of some roadside verges as the last refuges for endangered species. They are important especially for ectomycorrhizal fungi, of which some species nowadays are restricted to roadside verges.

The species-rich roadside verges are only a small minority of all roadside verges present in the area. The far majority are eutrophicated, with only a few, trivial fungal species present. The species-rich roadside verges on nutrient-poor soil should therefore be carefully protected and obtain the status of protected nature reserves.

The most important roadside verges studied during the present investigation are the following (for exact locality, see appendix 2):
1. Large parts of the verges of the Oranjekanaal (plots Q1, Q2, Q32);
2. Gieterweg, between Rolde and Gieten (plot Q4, Q65);
3. Mensingeweg, between Roden and Lieveren (plot Q83).
Other important roadside verges in Drente that were not included in this study, but are of the same species-rich kind, are among others:
1. Friesche laan in estate "Vennebroek" near Paterswolde (Keizer & Sullock Enzlin, 1988);
2. Noordwillemsvaart near Assen - Kloosterveen;
3. Norgerweg between Roden and Roderesch.

Of these roadsides, only the Friesche laan is included as part of a nature reserve.

Roadside verges, as a habitat for macromycetes, owe their main significance to the presence of ectomycorrhizal symbionts. Among these the largest proportion of rare and threatened species is found. In some roadside verges also some rare grassland species are present.

It is obvious that the necessary knowledge of the distribution of mycologically important roadside verges is still far from complete, nor is it known which fungal species are present in these places. Therefore, an inventory of roadside verges planted with trees is urgent. The most valuable parts should be designated as nature reserves and should be managed in an appropriate way with the aim of species preservation and maximalization of species diversity of macromycetes.

	Roadside verges	Forests	Indifferent
Ectomycorrhizal fungi Total	44	40	16
Beech and Oak	20	11	10
Beech	14	3	4
Oak	10	26	2
Saprotrophic fungi Total	24	60	24
Beech and Oak	14	31	20
Beech	7	8	2
Oak	3	22	2

Table 2. Numbers of differential fungal species in Dutch forests and roadside verges with Beech and Oak.

In table 2 the numbers of differential species for roadside verges, Dutch Oak and Beech forests and indifferent species are presented (chapter 5). A large number of ectomycorrhizal species are differential for roadside verges. The data for Oak forests also show considerable numbers of differential species, but many of these were found by Ypelaar in 1972-'73. Some of these species have since disappeared (Arnolds, 1992c). Among the saprotrophic fungi, only a few are differential for roadside verges. Nine out of the fourteen differential saprotrophs for roadside verges with Beech or Oak are species normally found in grasslands.

Communities of fungi and green plants.

In this study, communities have been distinguished on the basis of green plants according to Westhoff & van der Maarel (1973). Communities of ectomycorrhizal fungi and saprotrophic fungi were distinguished separately, on the basis of the same methods (cf. Winterhoff, 1984). The communities are named after a characteristic and common species (table 3). These names of the communities are only applicable in the studied area. In other geographical areas, on other soil types and with other tree species, different plants and fungi will probably be found. Therefore, no official syntaxonomical status is claimed for these communities.

Vegetation types in roadside verges with Beech:
Festuca rubra-Fagus type, subtype of *Elytrigia repens*.
Festuca rubra-Fagus type, subtype of *Festuca ovina*.
Mnium hornum-Fagus type, subtype of *Poa trivialis*.
Mnium hornum-Fagus type, subtype of *Dryopteris*.
Vegetation types in roadside verges with Oak:
Hypochaeris-Quercus type, subtype of *Hieracium pilosella*.
Hypochaeris-Quercus type, subtype of *Lotus corniculatus*.
Anthriscus-Quercus type, inops variant.
Anthriscus-Quercus type, typical variant.
Deschampsia flexuosa-Quercus type.

Communities of ectomycorrhizal fungi in roadside verges with Beech:
Russula fellea type, subtype of *Boletus edulis*
Russula fellea type, subtype of *Inocybe napipes*
Inops type
Communities of ectomycorrhizal fungi in roadside verges with Oak:
Xerocomus rubellus type, inops variant
Xerocomus rubellus type, typical variant
Russula ochroleuca type
Cortinarius erythrinus type, subtype of *Laccaria amethystea*
Cortinarius erythrinus type, subtype of *Boletus edulis*
Hebeloma mesophaeum type, inops variant
Hebeloma mesophaeum type, typical variant

Communities of saprotrophic fungi in roadside verges with Beech:
Mycena avenacea type
Collybia butyracea type, subtype of *Lepista nebularis*
Collybia butyracea type, subtype of *Psathyrella artemisiae*
Communities of saprotrophic fungi in roadside verges with Oak:
Psathyrella fulvescens type, subtype of *Clitocybe vibecina*
Psathyrella fulvescens type, subtype of *Lycoperdon foetidum*
Mycena avenacea type
Collybia cookei type

Table 3. Survey of the syntaxonomical communities of green plants, ectomycorrhizal fungi and saprotrophic fungi in roadside verges planted with Beech and with Oak in Drente, the Netherlands.

From a comparison between fungal communities and plant communities (chapter 4), it appeared that the latter correspond better with communities of saprotrophic fungi than with communities of ectomycorrhizal fungi. This indicates that the saprotrophic fungi react more like green plants to environmental variables than the ectomycorrhizal fungi.

Although all communities are well characterized by differential species, they differ widely regarding the number of species present and the number of endangered species. Among the latter, the largest number of threatened species is present in the roadside verges. Similarities between mycocoena of ectomycorrhizal species and phytocoena, and the environmental variables of both make it possible to predict with a high degree of probability where a valuable mycoflora can be expected. In Drente, places with characteristics of the *Festuca-rubra-Fagus* type, subtype of *Festuca ovina* and the *Hypochaeris-Quercus* type, subtype of *Hieracium pilosella* will probably show a rich mycoflora. This offers a possibility for a quick diagnosis of a region as to the frequency and localization of stations where a rich and diverse macrofungal flora probably occurs.

In both roadside verges planted with Oak and those planted with Beech most fungi are found in plots where the organic layer is thin to absent, with an open exposition and with a vegetation indicating low nitrogen availability (Ch. 2 and 3). Many fungal species are especially adapted to live in these circumstances. In places where organic material has accumulated or with a more ruderal vegetation, indicating high nitrogen availability, the mycoflora generally is poorly developed with only few differential species.

Relations with the surrounding landscape.

Roadside verges have to be considered as very open ecosystems with many relations to the surrounding landscape. Year after year nutrients are removed with the leaves that are blown away in the autumn (fig. 2) and with the hay that is removed after

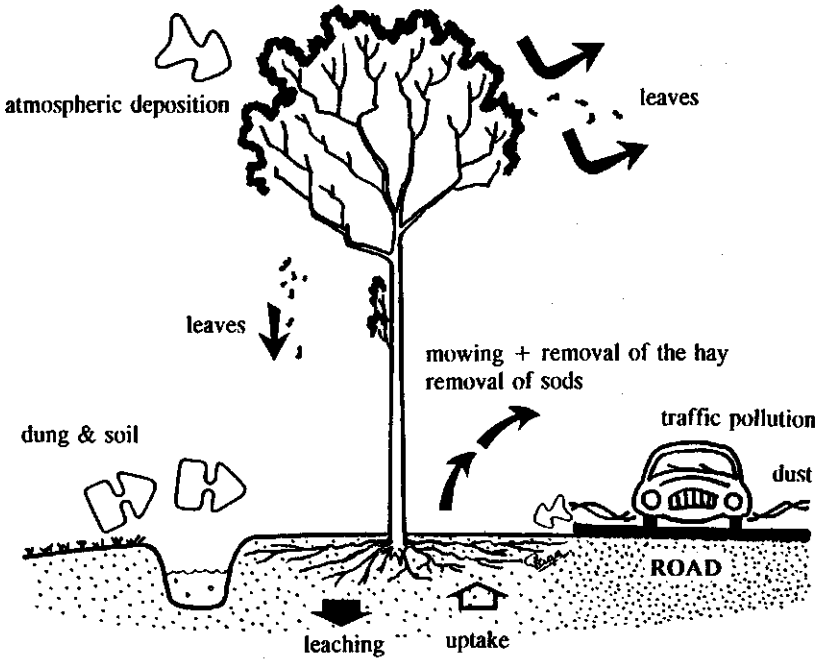


Fig. 1. Schematic view of various in- and outputs of nutrients in the roadside verge habitat.

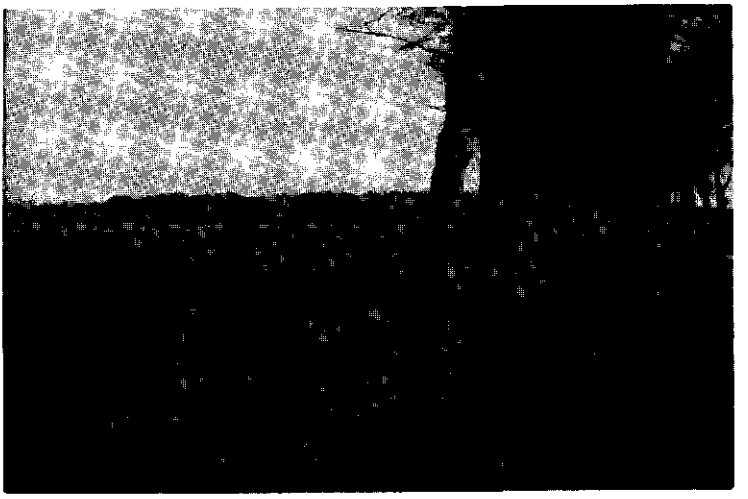


Fig. 2. Roadside verge near plot F13 just after fall of leaves. Leaves are absent from the roadside verge and are blown into the adjacent fields.

mowing. But on the other hand, this habitat is also subject to nutrient-enriching influences, e.g. pollution of the air (deposition of nitrogen compounds); fertilizer, dung and soil particles blown in from the adjacent agricultural fields; incidental dumping of chopped branches or rubbish (fig. 1).

In open roadside verges where the vegetation is mown with removal of the hay, the nutrient-poor status of the soil is maintained and accumulation of an organic layer is prevented. The more general importance of such environmental circumstances is also demonstrated by the fact that forests rich in ectomycorrhizal fungi often are situated on nutrient-poor soils without a well-developed organic layer (chapter 7). If fertilizing or litter accumulating effects dominate, the ectomycorrhizal flora will become impoverished (chapter 6).

Grasslands on nutrient-poor soils can be rich in saprotrophic fungi (Arnolds, 1982). The studied roadsides contain elements of both habitat types. However, in most roadside verges the soil is eutrophicated (probably mainly by input from the adjacent arable fields and dust and pollution caused by traffic, in combination with mowing without removal of the hay) to such an extent that the above-described removal of nutrients is no longer able to maintain the oligotrophic character of the site. In this case special measures are necessary to restore and maintain the oligotrophic status of the sites with their valuable flora of plants and fungi, if this were a management aim.

Nature management.

The actual situation of the roadside management will briefly be discussed below. The vegetation in the majority (48) of the investigated plots is mown one or two times per year (usually in June and September), in 11 plots the vegetation is mown once a year with subsequent removal of the hay and in 17 plots no management is carried-out. The latter is the case along forest roads and paths. For apparent reasons of traffic safety, in most plots a strip of 0.5 to 1 m broad along the road is mown more frequently. In many roadside verges, the upper soil layer (approx. 10 cm) including the vegetation is removed with irregular intervals, but on the average once in approximately seven years. This measure is carried out to prevent the accumulation of stagnant water on the road, but often also in places where this would not occur. Probably, these figures represent the actual situation of roadside management in Drente where most roadside verges are mown with the aid of a flail mower, without removal of the hay.

Clearly, these measures influence the vegetation and the inhabiting fungi. In order to determine the effects of the various measures, a field experiment was set up (chapter 7) in a roadside verge on nutrient-poor soil along a canal. The treatments "mowing with removal of the hay", "removal of the sods" and "no treatment" were compared with "mowing without removal of the hay" (the control), which was the management practice before the start of this experiment. In addition, artificial fertilizer was added to approximately simulate nutrient input from adjacent arable fields.

Refraining from any management measure leads to changes in the vegetation and generally to an impoverished mycoflora. In the experimental plots, a strong increase of *Cytisus scoparius* (L.)Link and *Phragmites australis* (Cav.)Trin. ex Steudel, an accumulation of dead organic material, and a decrease in the cover of bryophytes was observed. Fungi characteristic of grasslands with a short turf and those that are associated with bryophytes decreased. The difference in mycoflora between mown plots with and without removal of the hay was not clear from this experiment, perhaps because of the nutrient-poor situation in the plots, resulting in a small biomass production and therefore a

relatively small amount of accumulating dead organic matter. However, in other places, outside the studied plots, where the sward is not removed over many years, eutrophication of the vegetation can be observed and at the same time an impoverishment of the mycoflora (this study; unpubl. pers. obs.).

Fertilizing caused a decrease in ectomycorrhizal species and a shift towards eutraphent saprotrophic species. It is therefore concluded that any nitrogen input excludes most ectomycorrhizal and oligotraphent saprotrophic fungi. In roadside verges with a high input of nitrogen and where the hay is not removed, a quick ruderalization can be observed. Here the mycoflora is poorly developed.

Removal of sods causes a drastic decrease in the fungi. The ectomycorrhizal fungi recover rather quickly but after five years the numbers of saprotrophic species are still lower compared with the control. Species known to occur in old, unfertilized grasslands seem to be especially vulnerable to this disturbing treatment. Therefore removal of sods should only be carried out from a nature management point of view in order to remove a polluted upper soil layer, followed by mowing with removal of the hay.

From the above considerations, it is concluded that mowing once a year in late summer, or twice a year in more productive sites, with subsequent removal of the hay is the optimal management system in order to favour and maintain a rich mycoflora in roadside verges with planted trees.

Many of the roads, including the roadside verges are managed by the municipal authorities. Most of them are ignorant of the eventual mycological value of roadside verges. More information on optimalization of roadside management by including the fungal status of the verges may increase the willingness of the local authorities to apply this and contribute to a higher natural value in the roadside verges.

Succession.

In the present study, plots were studied with Oaks varying in age between 15 and 140 years old. It appeared that the number of ectomycorrhizal species was strongly and positively correlated with increasing age of the trees (chapter 6). This is unlike what happens in forests, where repeatedly an initial increase of species number was noted, followed by a decrease. The decrease often starts after canopy closure in the stand and is strongly accelerated under the influence of acid precipitation including nitrogen deposition (Jansen, 1989; Termorshuizen & Schaffers, 1991). The most striking feature is that in the roadsides studied species considered as characteristic for early successional stages are also present in old plots, e.g. *Hebeloma mesophaeum, H. helodes, Laccaria laccata, L. proxima, Scleroderma areolatum.*

The question arises whether the decreasing species number in ageing forests or the increasing species number in ageing roadside verges represents the "natural" situation. If forest types rich in ectomycorrhizal fungi are compared with species-rich roadside verges, it appears that these generally have in common a thin to lacking organic layer and a nutrient (nitrogen)-poor soil. Apparently the accumulation of organic material prevents the development of many ectomycorrhizal species. Thus, in the succession of ectomycorrhizal fungi the ageing tree (-root system) as well as changes of soil properties play a role. The exact interaction, however, between organic matter and nitrogen in the soil on the one hand and the formation of ectomycorrhizas by tree roots and fungi on the other needs to be further researched.

For the occurrence of saprotrophic fungi, the quality and quantity of the organic matter play the most important role. The plant species and the part of the plant (leaves,

twigs, etc.) from which the litter originates, the concentrations of various minerals and the microclimatic circumstances influence their species composition. Although the succession of saprotrophic fungi was not treated in this study, it is our impression that a succession of these fungi is not directly related to the age of the trees but more to the development of soil conditions (Arnolds, 1981; Ricek, 1981). The time interval between significant soil disturbance events, in roadside verges usually sod removal, is an important factor. Many terrestrial saprotrophs need stable soil conditions, apparently because of the development of certain organic compounds. During the eutrophication of an originally oligotrophic site, there is a shift in species composition towards eutraphent species, e.g. *Clitocybe metachroa, Calocybe carnea.* The total species number changes relatively little.

Suggestions for further research.

1) An inventory of surviving, mycologically rich, roadside verges is urgently needed. It will enable us to add to our knowledge on the species composition in various roadside verge habitats. This knowledge is also necessary in order to protect and/or manage valuable sites correctly and to advise the responsible authorities concerning the optimal management of sites. Even nature conservation organisations are often unaware of the mycological importance of some old alleys near estates and roadside verges in old landscapes (Keizer & Sullock Enzlin, 1988).

This research seems to be especially relevant for roadside verges along the big rivers. Their ectomycorrhizal flora is extremely rich in rare species and many species in the Netherlands are restricted to this habitat (Arnolds, 1968; Reijnders, 1968). Roadside verges on nutrient-poor soils in this area seem equally endangered (by eutrophication and mis-management) as in the pleistocene Drentian area. However, no systematic mycocoenological studies have been carried out in this habitat, yet. Other environmental variables in addition to the most important environmental variables found in the present study, other environmental variables, may possibly play a role in the explanation of the distribution of fungal species, e.g. lime content and water capacity of the soil.

2) Although in the Netherlands the majority of the planted roadside verges are lined with Oak and Beech, some other ectomycorrhizal trees are frequently used for this purpose, e.g. Birch (*Betula* species), Lime (*Tilia* species), Poplar (*Populus nigra* and its hybrids and species such as *P. alba, P. canescens, P. tremula*) and occasionally coniferous trees. The study of these roadside verges is promising since it is possible that the mycoflora in this habitat is richer in species, perhaps with unique elements, than forests comprising the same trees.

3) It is striking that the plots richest in fungal species were often situated along canals, e.g. the Oranjekanaal in Drente. Also, outside the studied plots, a surprisingly rich ectomycorrhizal mycoflora is frequently present on banks of canals planted with trees. This suggests that these places have special properties which favour the mycoflora. A possible explanation is the constant presence of water, enabling the mycelia to produce carpophores. In the present study too few plots were situated along canals, to reach final conclusions. An extension of the present study especially on banks of canals could reveal special properties of that habitat.

4) Another striking result of this study was the negative correlation between the thickness of the organic layer (A_0+A_{00}) and the occurrence of many ectomycorrhizal fungi and

grassland fungi. Moreover, the question as to factors particularly unfavourable for the fungi (or their fructification) remains largely unsolved. Possible factors are:
1. inhibition of exchange of gases between the environment of the mycelium and the atmosphere (Meyer, 1982);
2. release of substances toxic for the fungi from the litter layer, e.g. terpenoid substances, polyphenolic compounds (Kuiters et al. 1985; Kuiters, 1987);
3. competition for some minerals (P ?) by humus and litter inhabiting saprotrophic fungi (Read, 1991);
4. a toxic effect of the relatively large amount of nitrogen compounds that are stored in litter and that are released after its decomposition (Kuyper, 1989).

Field experiments where extracts of litter and humus are artificially added in places where the litter has been removed should be combined with laboratory experiments to test the behaviour of various ectomycorrhizal species to the presence of a host tree, an organic food source, and several saprotrophic fungi under limiting concentrations of N and P.

5) From the present study it appeared that many ectomycorrhizal species occur more frequently in the "roadside verge-environment", than in forests of the same tree species, e.g. *Russula amoenolens, R. pectinatoides, R. odorata*, several *Inocybe* species, etc.. It is suggested that these species, at least partially, have their optimum in forest communities that are either extinct, or only present in a very fragmentary form in the Netherlands, or that still occur in other regions in Europe. For an understanding of the autecology of these species it is necessary to study them in their "natural" habitat as far as possible. This also could throw some light on the question why so many ectomycorrhizal fungi coexist in a relatively homogeneous habitat such as the studied roadside verges.

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THE ECOLOGY OF MACROMYCETES IN ROADSIDE VERGES PLANTED WITH TREES.

SUMMARY.

In this thesis phytocoena and mycocoena of ectomycorrhizal fungi and saprotrophic fungi in roadside verges planted with trees are described independently. An attempt is made to indicate which environmental variables are most important in the distinguished communities. Parasitic fungi on trees, arthropods and other fungi and saprotrophic lignicolous species were not included in community definition.

In roadside verges in the phytogeographical Drenthian district 76 plots were selected, 53 planted with Common Oak (*Quercus robur*; "Oak plots") and 23 with Beech (*Fagus sylvatica*; "Beech plots").

12 beech plots were situated in an open landscape ("open") and 11 along roads inside forests ("shady"). These plots varied widely with regard to soil fertility.

The oak plots were divided into 34 open plots, 10 shady plots and 9 "half-open" plots, i.e. bordered at one side by forest. In the open plots three age-classes were distinguished: 5 plots with young trees (up to 20 years old), 12 plots with middle aged trees (20 to 50 years old) and 17 with old trees (more than 50 years old). In the remaining plots old trees were present. In oak plots, too, there is a large variation regarding the soil fertility. Plots were always 100 m long, irrespective of the width of the verge and were selected on the basis of a sufficient lengthwise homogeneity of the phanerogam vegetation. A large number of environmental variables was measured.

Vegetation relevés were made in 1987 according to the Braun-Blanquet method. For mycological purposes, the plots were visited during the autumns of 1986, '87 and '88 once every 3 to 4 weeks. All fungi were counted and identified.

The data were processed with the aid of the computer programmes TWINSPAN for vegetation classifications and CANOCO for ordinations and correlations with environmental variables.

In the beech plots 134 species of green plants, 105 species of ectomycorrhizal and 153 species of saprotrophic fungi were found.

On the basis of the green plants two vegetation types could be recognized, one with open and one with shady plots. The former was divided into two subtypes, one with a poor and one with a semiruderal vegetation. Using the ectomycorrhizal fungi the plots were divided into a species poor and a species rich type with two subtypes. The former did not correspond with a vegetation type but the latter two subtypes corresponded to a limited extent with vegetation types. The two communities that were recognized among the saprotrophic fungi corresponded well with the vegetation types. The better correspondence of communities of vascular plants with those of saprotrophs than with those of ectomycorrhizal fungi indicates that plants and saprotrophs react more in the same way to the environmental factors than the ectomycorrhizal fungi.

Environmental factors important for plants and saprotrophs are exposition of the plot, thickness of the organic layer, sodium concentration and Ellenberg N-indication values. Important for ectomycorrhizal fungi are: higher nitrate, potassium and magnesium concentrations for the species poor type and "openness", thickness of the organic layer and age of the trees for the other types.

In the oak plots 198 green plant species, 144 ectomycorrhizal and 214 saprotrophic species were found.

Three main vegetation types were distinguished, the *Mnium hornum* type of forest roads, the semiruderal *Anthriscus sylvestris* type of open to shady plots and the *Hypochaeris radicata* type of open, rather nutrient poor plots. For the ectomycorrhizal fungi, four types were recognized: the *Xerocomus rubellus*-, the *Russula ochroleuca*-, the *Cortinarius erythrinus*- and the *Hebeloma mesophaeum* type, characteristic for shady plots, semiruderal open to shady plots, open nutrient poor plots and open plots with young trees respectively. In the ordination, the environmental factors tree age, exposition of the plot and Ellenberg N indication values were most important. In the plots of the *R. ochroleuca* type a thicker organic layer and larger amounts of soluble and total nitrogen were present.

Based on the saprotrophic fungi, three communities were distinguished: the *Psathyrella fulvescens*-, the *Mycena avenacea*- and the *Collybia cookei* type. The latter is a small, weakly characterized type. The *P. fulvescens* type comprises shady to open plots with several vegetation types, the *M. avenacea* type open plots with a short, grassy vegetation. Most important environmental factors for the distinction of the types were "openness", tree age, Ellenberg N-indication values and thickness of the organic layer. The communities of saprotrophic fungi corresponded better with the vegetation types than the communities of mycorrhizal fungi.

The classification of the oak and beech plots together on the basis of the green plants is largely analogous to the classifications of oak and beech plots separately. For the saprotrophic fungi, Ellenberg N values, thickness of the organic layer and the openness of the plots are determining factors in the classification of the plots. However, for the classification of the plots using the ectomycorrhizal fungi the tree species is the most important parameter. Within the oak and beech group, the classification resembles the classifications of oak and beech plots separately. In plots with eutraphent vegetation non-host-specific ectomycorrhizal fungi dominate. In such plots the ectomycorrhizal mycoflora of oak and beech plots is more or less similar.

A comparison of the fungal communities of roadside verges with forest communities of the same tree species was made. Comparison with Dutch oak forest communities revealed that 42 ectomycorrhizal species were found to be differential for roadside verges and 39 for forests. 16 species were indifferent. Among the saprophytes, 24 species were differential for roadside verges, at least 62 for forests and 24 were indifferent. Only the Dicrano-Quercetum showed resemblance with some types of oak plots. The main difference with the other types of oak forest is the larger number of ectomycorrhizal fungi in roadside verges. Regarding the saprotrophic fungi, roadside verges differ profoundly from forests. Terrestrial raw humus inhabiting and lignicolous fungi are mostly restricted to forests, whereas typical grassland fungi were mostly found in roadside plots.

Dutch oak forest communities showed more similarity with the roadside verge communities than those from other parts of Europe. Generally, communities with little or no organic layers on nutrient-poor soils have a large proportion of ectomycorrhizal species in common with the analogue roadside communities.

A classification is presented for ectomycorrhizal roadside fungi based on their assumed restricted occurrence in the roadside habitat. In roadside verges a number of

threatened fungi occur that presumably have disappeared from forests with the same tree species.

In 25 plots of the *Hypochaeris radicata-Quercus* type with trees of three different ages successional series were studied. The number of ectomycorrhizal species increases with the tree age. This is in contrast to data from forests in the literature, where the species number decreases after an initial increase. The differences in soil and the management practices in roadside verges may explain this discrepancy. Eutrophication and litter accumulation cause a decrease in the species number, resulting in low species numbers in eutrophicated places and/or in thick litter layers, even under old trees.

A new, preliminary classification of ectomycorrhizal fungi regarding their respective optima during the sucession of the site, based on the data from roadside verges is presented.

In a homogeneous roadside verge with 100 year old Common Oaks along a canal the effects of various management treatments were studied. During the years 1987-'91, 5 different treatments were applied: a. mowing without removal of the hay, b. mowing with removal of the hay, c. nonrecurrent removal of sods in combination with mowing without removal of the hay, d. N-fertilization during the first 3 years in combination with mowing without removal of the hay, e. no treatment. Treatment "a" served as control. Each treatment was carried out sixfold in plots of 50x4.5 m^2. The phanerogam vegetation, some soil properties and ectomycorrhizal samples from treatments b, c and d were analyzed as well.

Removal of sods caused an immediate decrease of sporocarps of mycorrhizal fungi but after 3 years the species numbers had largely recovered. However, there was some shift in species composition. After fertilization a strong decrease of ectomycorrhizal fungi occurred. The saprotrophs were significantly afflicted by removal of sods. Fertilization resulted in a decline in saprotroph species numbers but the production did not change significantly. Treatments b and e showed no significant differences with the control. The soil chemistry was not influenced by the treatments except for higher concentrations of N in fertilized plots.

In eight open beech plots, viz. four in plots rich in ectomycorrhizal species on nutrient-poor soil and four in species-poor and nutrient-rich soil, root samples were taken. In the field-experiment root samples were taken two years after the start of the treatments b, c and d.

In the beech plots a positive correlation was found between the number of mycorrhizal root tips and the number of ectomycorrhizal species found during the fieldwork. However, there was no correlation with the biomass production of the sporocarps. A non-significant negative correlation was found between tree vitality and the number of mycorrhizal root tips. No significant correlations at all were found between the treatments mowing with removal of the hay, removal of sods and fertilization regarding: total root length, number of mycorrhizal root tips, degree of ramification, percentage of mycorrhizal root tips and number of types of mycorrhizal root tips. In fertilized plots the samples contained more mycorrhizal root tips with a relatively large proportion of *Cenococcum*.

In this study, descriptions, drawings and observations are presented of rare,

critical or less well-known macromycetes that were encountered in the oak plots, the beech plots, and in the experimental site. Special attention is paid to the genera *Cortinarius* S.F. Gray emend. Fr., *Hebeloma* (Fr.) Kumm. and *Russula* Pers.. *Psathyrella rhombispora* Keizer & Arnolds is presented as a new species. *Russula cicatricata* Romagn., *Russula elaeodes* (Bres.)Romagn. and *Russula purpurata* Crawsh. are reduced to formae of *Russula graveolens* Romell in Britz..

DE ECOLOGIE VAN PADDESTOELEN IN MET BOMEN BEPLANTE WEGBERMEN.

SAMENVATTING.

Het onderzoek aan levensgemeenschappen in Nederland is van oudsher grotendeels gebaseerd geweest op de producenten, dwz. de groene planten. Dit is terecht, daar de groene planten als het ware het skelet, de basis vormen van de levensgemeenschap, waar alle andere organismen van afhankelijk zijn. De afbraak van het geproduceerde organische materiaal is voor een belangrijk deel de taak van de fungi. De Fungi (Schimmels) zijn betrekkelijk zelden in het systematisch onderzoek van levensgemeenschappen betrokken, alhoewel zij in veel vegetatietypen een essentiële rol spelen.

Dit is wel begrijpelijk gezien het feit dat de Fungi door hun verborgen leefwijze en sterk fluctuerende verschijnen binnen en tussen jaren minder gemakkelijk toegankelijk zijn voor onderzoek vergeleken met de groene planten. Daarbij zijn vele soorten slechts met behulp van verspeide, niet gemakkelijk toegankelijke literatuur en na microscopische studie te determineren.

Het grootste deel van de "schimmelplant" leeft als een nauwelijks zichtbaar mycelium in het substraat en kan niet op naam gebracht worden. Daarvoor zijn de vruchtlichamen (paddestoelen) noodzakelijk. We nemen dan aan dat de aantallen, of drogestof productie van de paddestoelen een maatstaf vormen voor de biologische activiteit van de betrokken soorten. Om onderzoekstechnische redenen worden alleen die soorten beschouwd die met het blote oog zichtbare vruchtlichamen vormen, van minimaal 1 tot 2 mm groot, de zg. Macrofungi. Schimmels die geen, zeer kleine, of ondergronds blijvende vruchtlichamen vormen, blijven buiten beschouwing. Het effect van deze onzekerheden in het onderzoek op de resultaten blijft voorlopig nog onbekend.

Het mycocoenologisch onderzoek (het onderscheiden van paddestoelengemeenschappen) heeft zich voor een belangrijk deel onwikkeld in het Biologisch Station te Wijster (Dr.). Uitgangspunt vormen de vegetaties van groene planten. In diverse Drentse vegetatietypen zijn de daarin voorkomende paddestoelen kwantitatief onderzocht, bijvoorbeeld jeneverbesstruwelen, graslanden en vochtige heide, moerasbossen, eikenbossen, berkenbossen, beukenbossen, dennenbossen.

Uit fragmentarische waarnemingen was eerder gebleken dat in sommige met bomen beplante wegbermen vele, deels zeldzame paddestoelen voorkomen. Wegbermen en kanaalbermen waren echter nooit systematisch mycologisch onderzocht. Het wegbermmilieu is in vergelijking met andere vegetatietypen buitengewoon kunstmatig en onderhevig aan sterke microklimatologische variatie en een sterke invloed van het omringende land. Daarom lijken met bomen beplante wegbermen bij uitstek geschikt voor onderzoek aan diverse omgevingsvariabelen.

Ook in kwantitatief opzicht maken wegen een belangrijk deel uit van het landschap (tabel 1). De wegen (buiten de bebouwde kom en exclusief de bermen) beslaan bijna 1% van het landoppervlak van Nederland, inclusief de bermen benadert dit de 2%. Door hun lintvorm en verspreide ligging vormen ze echter een belangrijk onderdeel in de opbouw en de aanblik van het Nederlandse landschap.

	Lengte verharde + onverharde wegen (km)	Geschat oppervlak bermen (ha)	Lengte kanalen (km)	Geschat oppervlak bermen/taluds (ha)
Nederland	70000	35000	2500	2500
Drente	5000	2500	500	500

Tabel 1. Lengte en oppervlakte van wegen en bermen in Nederland en Drente (afgerond). Bron: Centraal Bureau voor de Statistiek.

Vooral op het zandplateau in Drente zijn veel van de wegen en kanaaltaluds beplant met bomen, voor het grootste deel Zomereiken, in mindere mate Beuken en weinig met andere boomsoorten.

In dit proefschrift worden de vegetatietypen en de paddestoelengemeenschappen in met bomen beplante wegbermen onafhankelijk van elkaar beschreven en wordt een poging gedaan aan te geven welke milieuvariabelen de belangrijkste rol spelen bij het tot stand komen van de gemeenschappen.

Bij de verwerking van de gegevens zijn de ectomycorrhizasymbionten en de saprotrophe fungi apart behandeld. De tot de eerste groep behorende soorten gaan een associatie aan met een plant (boom) waarvan beide partners profiteren door uitwisseling van voedingsstoffen. De soorten van de tweede groep leven van dood organisch materiaal, zoals strooisel, humus, dood hout, etc.. Parasieten op bomen, insecten en andere fungi evenals soorten van dood hout zijn wel bestudeerd, maar hebben niet bijgedragen aan de definiëring van de gezelschappen.

Op het zandplateau van Drente zijn in totaal 76 proefvlakken in wegbermen bestudeerd, waarvan 53 met Zomereiken en 23 met Beuken beplant. Van de met beuken beplante proefvlakken zijn er 12 in open landschap gelegen ("open") en 11 langs in bos gelegen wegen ("beschaduwd"). De proefvlakken vertonen grote variatie in vruchtbaarheid van de bodem. De met Zomereiken beplante bermen zijn verdeeld in 34 open en 10 beschaduwde en 9 halfbeschaduwde, dwz. aan één zijde aan bos grenzende proefvlakken. In de open proefvlakken worden drie leeftijdscategoriën onderscheiden: 5 proefvlakken met jonge bomen (tot 20 jaar oud), 12 met middeloude bomen (20 tot 50 jaar oud) en 17 met oude bomen (50 jaar en ouder). De overige proefvlakken bevatten oude bomen. Ook hier is een grote variatie in de bodemvruchtbaarheid. De proefvlakken waren steeds 100 m lang, onafhankelijk van de breedte van de berm en zijn geselecteerd op homogeniteit van de groene planten vegetatie. En groot aantal omgevingsvariabelen is gemeten.

De vegetatie is in 1987 opgenomen volgens de Braun-Blanquet methode. De proefvlakken zijn in de herfsten van 1986, '87 en '88 eens per 3 tot 4 weken bezocht. Bij ieder bezoek zijn alle paddestoelen geteld en gedetermineerd.

De verkregen gegevens zijn bewerkt met behulp van de computerprogramma's TWINSPAN voor vegetatieklassificaties en CANOCO voor ordinaties en correlaties met de milieuvariabelen.

In de met beuken beplante proefvlakken (hoofdstuk 2) werden 134 soorten groene planten, 105 soorten ectomycorrhiza vormende en 153 saprotrophe fungi gevonden.

Op grond van de groene planten zijn in de proefvlakken twee hoofdgroepen onderscheiden: het *Festuca rubra* type met overwegend open proefvlakken en het *Mnium hornum* type met beschaduwde proefvlakken. De eerste groep kan verdeeld worden in twee subtypen, één met een semiruderale, op voedselrijke bodem duidende vegetatie en één met een grazige, op schrale bodem duidende vegetatie. De proefvlakken van het *Festuca rubra* type hadden een dunnere strooisel- en humuslaag en een grotere "openheid", uitgedrukt als het potentiëel aantal uren directe zonneschijn in oktober, dan die van het *Mnium hornum* type. In het schrale subtype van het *Festuca rubra* type waren de Ellenberg-stikstof waarden en de concentraties van magnesium en nitraat lager dan in het semiruderale subtype.

De proefvlakken zijn met behulp van de ectomycorrhizafungi in twee groepen te verdelen: het soortenrijke *Russula fellea* type en het soortenarme inops-type. Het eerste type onderscheid zich van het tweede vooral door lagere concentraties van nitraat, kalium en magnesium in de bodem en door lagere Ellenberg-stikstofwaarden.

Twee groepen van proefvlakken zijn gevonden, gebruik makend van de terrestrische saprophyten: het *Mycena avenacea*- en het *Collybia butyracea* type. De dikte van de humus- en strooisellaag en de "openheid" waren lager in het eerste type. De indeling op grond van de saprophyten komt veel sterker overeen met de onderscheiden vegetatietypen dan die op grond van de ectomycorrhizafungi.

Diverse verschillende abundantiematen beïnvloeden de uiteindelijke uitkomst van de classificaties en ordinaties maar in geringe mate, doordat bij deze methoden presentie/absentie belangrijker zijn dan abundantie.

In de met eiken beplante proefvlakken (hoofdstuk 3) zijn 198 soorten planten, 144 soorten ectomycorrhizafungi en 214 soorten saprotrophe fungi aangetroffen.

De proefvlakken zijn verdeeld in drie vegetatietypen: het *Mnium hornum* type, het *Anthriscus sylvestris* type en het *Hypochaeris radicata* type. Het eerste type wordt gevonden langs beschaduwde boswegen met een dikke organische laag, het tweede op open of beschaduwde plaatsen, maar met een semiruderale vegetatie (hogere Ellenberg-stikstof waarden dan in de overige groepen) en het derde in open proefvlakken met een matig schrale tot schrale vegetatie met gemiddeld jongere bomen dan in de overige groepen.

Op basis van de ectomycorrhizafungi zijn vier typen onderscheiden: het *Xerocomus rubellus*-, het *Russula ochroleuca*-, het *Cortinarius erythrinus*- en het *Hebeloma mesophaeum* type. Deze typen zijn respectievelijk kenmerkend voor beschaduwde proefvlakken, open tot beschaduwde proefvlakken met semiruderale vegetatie, open proefvlakken met schrale, grazige vegetatie en open proefvlakken met jonge bomen. De omgevingsvariabelen boomleeftijd, expositie en Ellenberg-stikstof waarden zijn het belangrijkst voor de indeling van de proefvlakken.

De proefvlakken zijn op grond van de saprotrophe fungi in drie groepen te verdelen: het *Psathyrella fulvescens* type, het *Mycena avenacea* type en het *Collybia cookei* type. Het eerste type omvat proefvlakken met oude bomen op open tot beschaduwde plaatsen met hogere Ellenberg-stikstofwaarden, een dikkere organische laag, en een vochtigere bovenste bodemlaag met een lagere pH($CaCl_2$) dan de andere typen. De *Mycena avenacea* type proefvlakken zijn open, met een schrale vegetatie en middeloude

bomen. Het *Collybia cookei* type is vrij heterogeen met overwegend jonge bomen.

De indeling van de proefvlakken op grond van de saprophyten komt beter overeen met de vegetatie typen dan de indeling op grond van de ectomycorrhizafungi.

Enkele proefvlakken met oude Eiken op schrale bodem met een dunne tot ontbrekende organische laag blijken buitengewoon rijk aan ectomycorrhizafungi te zijn, met een relatief groot aantal zeldzame en bedreigde soorten. Deze bermen combineren zeldzame fungi van bossen op schrale bodem met soorten die kenmerkend zijn voor schrale, onbemeste graslanden. Het open karakter van deze bermen helpt de instand houding van deze situatie.

De indeling van de Eiken- en de Beuken-proefvlakken tezamen (Hoofdstuk 4) op grond van de groene planten blijkt grotendeels analoog te zijn aan de indelingen van Eiken- of Beuken-proefvlakken apart. Ook bij de indeling met behulp van de saprophyten blijken in beide gevallen de Ellenberg-stikstofwaarden, de dikte van de organische laag en de "openheid" van de proefvlakken bepalend te zijn voor de indeling in groepen. De indeling op basis van de ectomycorrhizafungi echter is in de eerste plaats afhankelijk van de boomsoort. Hierbinnen lijken de onderscheiden groepen weer op de groepen die gevonden zijn in de Eiken- of Beuken-proefvlakken.

In proefvlakken met een eutraphente vegetatie domineren de weinig waardspecifieke ectomycorrhizafungi, waardoor onder zulke omstandigheden de mycoflora van deze fungi in Eiken- en Beuken-proefvlakken sterk op elkaar lijkt.

De paddestoelgemeenschappen in de Eiken- en Beukenbermen zijn vergeleken met literatuurgegevens van bosgemeenschappen gedomineerd door deze boomsoorten in en buiten Nederland (Hoofdstuk 5). Vergeleken met Nederlandse bostypen blijken 42 soorten ectomycorrhizafungi differentiërend te zijn voor bermen, 39 soorten voor bossen. Slechts 16 soorten zijn indifferent. Van de saprophyten zijn 24 soorten differentiërend voor bermen en minstens 62 voor bossen. 24 soorten zijn indifferent.

Van de Nederlandse eikenbossen vertoont wat betreft de ectomycorrhizafungi alleen het Dicrano-Quercetum enige overeenkomst met (de soortenrijkere typen van) Eikenbermen, hoewel een deel van de Eikenbosgegevens uit het begin van de zeventiger jaren stamt en sindsdien de flora van deze fungi in deze bossen sterk is verarmd. Het belangrijkste verschil met de overige typen Eikenbos is dat het aandeel van de ectomycorrhizafungi in de bermen hoger is.

Eikenbossen blijken wat betreft de saprotrophe fungi sterk te verschillen van de bermen. Soorten die kenmerkend zijn voor een dikke organische laag en houtbewoners komen meer in het bos voor, terwijl de graslandsoorten die in de wegbermen zijn gevonden, in de bossen nagenoeg ontbreken. Van de buitenlandse bostypen vertonen de typen op schrale bodem, waar ondergroei en strooisel schaars zijn of ontbreken, in mycologisch opzicht de grootste overeenkomst met de bermen.

Van Nederlandse Beukenbossen op voedselarme bodem ontbreken oude gegevens. De meeste overeenkomst bestaat tussen Beukenbossen op schrale bodem met weinig ondergroei en sommige Beukenbermen.

Een indeling is gepresenteerd van ectomycorrhiza soorten die in bermen voorkomen, op basis van hun veronderstelde gebondenheid aan het specifieke bermmilieu. In bermen komen tal van bedreigde soorten fungi voor die - naar aangenomen kan worden - in bossen met dezelfde boomsoorten verdwenen zijn.

De aanwezigheid van wegbermen met Eiken van sterk verschillende leeftijd onder overigens vergelijkbare omstandigheden maakt het mogelijk veronderstelde successiereeksen te bestuderen (Hoofdstuk 6). Daartoe zijn 25 proefvlakken van het *Hypochaeris radicata* type met Eiken van drie leeftijdsklassen (zie boven) geselecteerd. Het aantal soorten ectomycorrhizafungi blijkt bij stijgende boomleeftijd voortdurend toe te nemen. Dit is in tegenspraak met successiemodellen die in de literatuur gepresenteerd zijn, waarbij het aantal soorten na een aanvankelijke stijging weer afneemt. Het betrekken van bodemvariabelen alsmede het uitgevoerde beheer in de diverse successiemodellen is noodzakelijk voor een beter begrip.

Processen als eutrophiëring (milieuverontreiniging) en strooiselophoping (ontbrekend maaibeheer in bermen of ouder en dichter worden van bossen, mogelijk in combinatie van vertraagde strooiselafbraak) buigen de oorspronkelijk stijgende lijn in het soortenaantal van de ectomycorrhizafungi af. Het resultaat is een laag soortenaantal op plaatsen met een geëu-trophiëerde vegetatie of met een dik pakket strooisel op de bodem, ook onder oude bomen.

Een nieuwe, voorlopige klassificatie van ectomycorrhizafungi voor het moment van verschijnen gedurende de successie is voorgesteld.

In de berm langs het Oranjekanaal, waar 100 jaar oude Eiken staan, is een veldexperiment uitgevoerd om het effect te bepalen op vegetatie en fungi, van verschillende beheersmethoden, die in de practijk worden toegepast (Hoofdstuk 7). Proefvlakjes van 50 x 4,5 m zijn in zesvoud als volgt behandeld: a. maaien zonder afvoer van het maaisel; b. maaien met afvoer van het maaisel; c. eenmalig afplaggen, gevolgd door maaien zonder afvoer van het maaisel; d. bemesting met stiksof-kunstmest gedurende drie jaar in combinatie met behandeling a.; e. geen enkele behandeling. Behandeling a diende als controle. De aantallen fungi zijn gedurende de jaren 1987 - '91 vervolgd.

Afplaggen veroorzaakte een onmiddellijke afname van het aantal vruchtlichamen van ectomycorrhizafungi. Na drie jaar was het soortenaantal ongeveer weer op het oude peil, zij het dat de soortensamenstelling nog verschilde van de controle. Na bemesten werd een sterke afname van de ectomycorrhizafungi waargenomen.

De saprophyten werden gedecimeerd door afplaggen. Ook na vijf jaar is het herstel nog niet volledig. Bemesting veroorzaakte lagere soortenaantallen saprophyten en een verandering van soortensamenstelling, maar de productie veranderde niet significant.

De behandelingen b. en e. vertoonden geen significante verschillen met de controle voor saprotrophe en ectomycorrhizafungi. Sommige onbehandelde proefvlakjes groeiden echter dicht met Brem, zodat plaatselijk het open grasland-karakter van de vegetatie verdween.

De chemie van de bodem is door de behandelingen niet beïnvloed, behalve hogere concentraties van N in bemeste proefvlakjes.

Om te onderzoeken of de geconstateerde verschillen in ectomycorrhizafungi ook in de mycorrhiza's in de grond aanwezig zijn, zijn in acht open beukenbermen wortelmonsters onderzocht, vier in soortenrijke proefvlakken op schrale bodem en vier in soortenarme proefvlakken op voedselrijke bodem. In het veld-experiment zijn wortelmonsters verzameld twee jaar na de start van de behandelingen b, c en d.

In de beukenbermen (Hoofdstuk 2) is een positieve correlatie gevonden tussen het aantal gemycorrhizeerde worteltoppen en het aantal soorten ectomycorrhizafungi (gevonden bij de inventarisatie), echter niet met de drogestof productie van vruchtlichamen. Een

niet-significant negatief verband is gevonden tussen de boomvitaliteit en het aantal worteltoppen.

In het veld-experiment (Hoofdstuk 7) zijn geen significante verschillen geconstateerd tussen de behandelingen in: totale wortellengte, aantal worteltoppen, vertakkingsgraad, percentage gemycorrhizeerde worteltoppen, aantal verschillende typen mycorrhiza's. In bemeste proefvlakjes bevatten de monsters meer gemycorrhizeerde worteltoppen met een relatief groot aandeel van *Cenococcum*.

De hier gehanteerde soortsopvattingen zijn verantwoord en geïllustreerd aan de hand van beschrijvingen en afbeeldingen van, en taxonomische opmerkingen over een aantal zeldzame of kritische soorten Macrofungi, die gedurende het onderzoek werden aangetroffen (Hoofdstuk 8). Speciale aandacht kregen de genera *Cortinarius* S.F. Gray emend. Fr., *Hebeloma* (Fr.)Kumm. en *Russula* Pers.. *Psathyrella rhombispora* Keizer & Arnolds wordt als nieuwe soort gepresenteerd. *Russula cicatricata* Romagn., *Russula elaeodes* (Bres.)Romagn. en *Russula purpurata* Crawsh. worden als formae van *Russula graveolens* Romell in Britz. beschouwd.

Appendix 1. SPECIES-LIST MACROFUNGI

List of species encountered during the mycocoenological study of roadside verges planted with trees.
Species without abbreviation have only been found in the management experiment.
A-Taxonomical group: Ag=Agaricales, Aph=Aphyllophorales, G=Gasteromycetes, Asc=Ascomyc
B-Ecological group: S=saprophyte, M=Ectomycorrhizal symbiont, P=parasite.
C-Substratum: H=humus + litter, W=wood, C=coprophytic, F=fungi, B=bryophytes.
D-Of the humus-inhabiting species: F=usually found in Forests; G=usually found in gras
Spc.wt (mg)=specific (air dry) weight in mg; A: data after Arnolds (1981).
*=Taxonomic and/or nomenclatorial notes in chapter 8.

A	Species	Abbrev.	Spc.wt (mg)	B	C	D	%Fag	%Que
Ag	Agaricus arvensis Schaeff.	Agararve	4075.00	S	H	G	4	4
Ag	Agaricus campestris L.	Agarcamp	1230.00A	S	H	G	0	4
Ag	Agaricus semotus Fr.	Agarsemo	380.33	S	H	G	0	4
Ag	Agaricus silvaticus Schaeff.*	Agarsilv	563.33	S	H	F	0	4
Ag	Agrocybe firma (Peck)KÜhner	Agrofirm	180.00	S	H	F	13	0
Ag	Agrocybe pediades (Fr.)Fayod	Agropedi	94.00	S	H	G	0	2
Ag	Agrocybe praecox (Pers.:Fr.)kumm.	Agroprae	327.00A	S	H	G	17	6
Ag	Alnicola bohemica (Vel.)Sing.	Naucbohe	34.00	M			22	23
Ag	Alnicola melinoides (Bull.:Fr.)KÜhner	Naucesch	53.00	M			0	4
Ag	Amanita citrina (Schaeff.)Pers.	Amancitr	1617.50	M			17	26
Ag	Amanita fulva Sing.	Amanfulv	776.67	M			13	21
Ag	Amanita muscaria (L.)Sing.	Amanmusc	1893.75	M			22	8
Ag	Amanita pantherina (D.C.:Fr.)Krbh.	Amanpant	2027.00	M			22	4
Ag	Amanita porphyria Alb.&Schw.:Fr.		1200.00	M				
Ag	Amanita rubescens Pers.(:Fr.)	Amanrube	3826.00	M			87	57
Ag	Amanita spissa (Fr.)Kumm. var. spissa	Amanspis	1960.00	M			26	6
Ag	Anellaria semiovata: see Panaeolus fimiputris							
Ag	Armillaria bulbosa (Barla)Kile&Watling	Armibulb	1050.00	S	W		0	2
Ag	Armillaria obscura (Schaeff.)Herink	Armiobsc	1190.00	S	W		43	25
Ag	Asterophora lycoperdoides: see Nyctalis asterophora							
Ag	Baeospora myosura (Fr.:Fr.)Sing.	Baeomyos	13.00	S	W		0	2
Ag	Bolbitius vitellinus (Pers.:Fr.)Fr.	Bolbvite	9.00	S	H	G	0	6
Ag	Boletus edulis Bull.:Fr.	Boleedul	14383.67	M			39	19
Ag	Boletus erythropus (Fr.:Fr.)Krbh.	Boleeryt	4321.00	M			17	2
Ag	Boletus piperatus Bull.:Fr.	Chalpipe	641.20	M			17	6
Ag	Calocybe carnea (Bull.:Fr.)Donk	Calocarn	113.00A	S	H	G	13	6
Ag	Calyptella flos-alba (Velen.)W.B.Cooke	Calyflos	.04A	S	H	G	0	4
Ag	Camarophyllus niveus (Scop.:Fr.)Karst.	Camanive	118.00A	S	H	G	0	6
Ag	Camarophyllus russocoriaceus (Berk.&Miller)Lange	Camaruss	34.00	S	H	G	0	2
Ag	Chalciporus piperatus: see Boletus p.							
Ag	Clitocybe agrestis Harmaja	Clitagre	100.50	S	H	G	4	4
Ag	Clitocybe albofragrans (Harmaja)Kuyper*	Clitalbo	176.67	S	H	G	0	2
Ag	Clitocybe amarescens Harmaja	Clitamar	138.00	S	H	G	0	4
Ag	Clitocybe candicans (Pers.:Fr.)Kumm.	Clitcand	32.67	S	H	F	4	9
Ag	Clitocybe clavipes (Pers.:Fr.)Kumm.	Clitclav	790.67	S	H	F	4	6
Ag	Clitocybe costata KÜhner&Romagnesi	Clitcost	370.00	S	H	F	4	2
Ag	Clitocybe diatreta (Fr.:Fr.)Kumm.	Clitdiat	67.00A	S	H	F	22	19
Ag	Clitocybe ditopa (Fr.:Fr.)Gill.	Clitdito	63.00	S	H	F	0	8
Ag	Clitocybe fragrans (With.:Fr.)Kumm.	Clitfrag	214.86	S	H	F	0	4
Ag	Clitocybe gibba (Pers.:Fr.)Kumm.	Clitgibb	647.67	S	H	F	0	6
Ag	Clitocybe lignatilis (Pers.:Fr.)Karst.	Clitlign	10.00	S	W	F	0	2
Ag	Clitocybe marginella Harmaja*	Clitmarg	96.88	S	H	G	17	26
Ag	Clitocybe metachroa (Fr.)Kumm. sensu Kuyper	Clitmeta	82.17	S	H	F	17	49
Ag	Clitocybe obsoleta (Batsch)Quél.	Clitobso	210.00A	S	H	F	0	2
Ag	Clitocybe odora (Bull.:Fr.)Kumm.*	Clitodor	757.00	S	H	F	4	2
Ag	Clitocybe rivulosa (Pers.:Fr.)Kumm.		203.00A	S	H	G		
Ag	Clitocybe vibecina (Fr.)Quél. sensu Ricken	Clitvibe	757.00	S	H	F	13	17
Ag	Clitopilus cretatus: see C.scyphoides							
Ag	Clitopilus prunulus (Scop.:Fr.)Kumm.	Clitprun	644.40	M			26	11
Ag	Clitopilus scyphoides (Fr.)Sing.	Clitcret	6.00	S	H		0	4
Ag	Collybia amanitae (Batsch)Kreisel	Collcirr	.30	P	F		30	15
Ag	Collybia butyracea (Bull.Fr.)Kumm.	Collbuty	125.00	S	H	F	52	40

Ag	Collybia cirrhata: see C. amanitae						
Ag	Collybia cookei (Bres.)J.D.Arnold	Collcook	12.50	P	F	13	6
Ag	Collybia dryophila (Bull.:Fr.)Kumm.	Colldryo	148.00A	S	H F	43	77
Ag	Collybia maculata (Alb.&Schw.:Fr.)Kumm.	Collmacu	1126.00	S	H F	9	0
Ag	Collybia peronata Bolt.:Fr.)Kumm.	Collpero	547.67	S	H F	22	4
Ag	Collybia tuberosa (Bull.:Fr.)Kumm.	Colltube	9.00	P	F	13	8
Ag	Conocybe cryptocystis: see C. subpubescens						
Ag	Conocybe filaris (Fr.)KÜhner	Conofila	11.20	S	H F	0	4
Ag	Conocybe kuehneriana Sing.	Conokueh	3.20	S	H G	4	0
Ag	Conocybe mairei (Kuehner ex)Watl.*	Conomair	26.00	S	H G	4	0
Ag	Conocybe ochracea sensu auct.: see C. kuehneriana						
Ag	Conocybe pubescens (Gill.)KÜhner	Conopube	10.30	S	H G	0	2
Ag	Conocybe pygmaeoaffinis (Fr,)KÜhner*	Conopygm	13.50	S	H G	0	4
Ag	Conocybe rickeniana P.D.Orton	Conorica	16.00	S	H G	0	2
Ag	Conocybe rickenii (J.Schaeff.)KÜhner	Conorick	34.00	S	H G	0	2
Ag	Conocybe semiglobata (KÜhner ex)Watl.	Conosemi	6.70	S	H G	0	6
Ag	Conocybe sienophylla (Berk.&Br.)Sing.	Conosien	5.85	S	H G	0	2
Ag	Conocybe siliginea (Fr.:Fr.)KÜhner	Conosili	29.00	S	H G	4	2
Ag	Conocybe subpubescens P.D.Orton	Conocryp	142.00	S	H G	0	2
Ag	Coprinus comatus (MÜll.:Fr.)pers.	Coprcoma	4012.50	S	H G	4	0
Ag	Coprinus domesticus (Bolt.:Fr.)S.F.Gray	Coprdome	59.00	S	H F	13	8
Ag	Coprinus friesii Quél.	Coprfrie	3.20A	S	H G	0	6
Ag	Coprinus micaceus (Bull.:Fr.)Fr.	Coprmica	313.33	S	W	9	6
Ag	Coprinus miser Karst.	Coprmise	.20A	S	C	0	2
Ag	Coprinus patouillardii Quél.	Coprpato	58.67	S	C	0	2
Ag	Coprinus plicatilis (Curt.:Fr.)Fr. ss. lat.	Coprplic	18.00A	S	H G	13	4
Ag	Coprinus radiatus (Bolt.:Fr.)Pers.	Coprradi	.20A	S	C	0	2
Ag	Coprinus sclerocystidiosus M.Lange&A.H.Smith*	Coprscle	33.00	S	W	4	0
Ag	Coprinus stercoreus (Scop.)Fr.	Coprster	.20	S	C	4	2
Ag	Coprinus subimpatiens M.Lange&A.H.Smith*	Coprsubi	33.00	S	H G	17	4
Ag	Coprinus urticaecola (Berk.&Br.)Buller	Coprurti	7.60A	S	H G	0	6
Ag	Coprinus xantholepis P.D.Orton*	Coprxant	2.00	S	H G	0	2
Ag	Cortinarius anomalus (Fr.:Fr.)Fr.*	Cortanom	250.00	M		4	8
Ag	Cortinarius balteatoalbus R.Henry*	Cortbalt	1306.33	M		0	2
Ag	Cortinarius casimiri (Velen.)Huijsm.*	Cortsubs	100.11	M		9	6
Ag	Cortinarius causticus Fr.*	Cortcaus	52.00	M		4	2
Ag	Cortinarius comptulus Mos.*	Cortcomp	53.00	M		0	4
Ag	Cortinarius elatior Fr.	Cortelat	5661.50	M		0	4
Ag	Cortinarius erythrinus (Fr.)Fr.*	Corteryt	142.33	M		26	21
Ag	Cortinarius flexipes (Pers.:Fr.)Fr.*	Cortflex	47.28	M		17	17
Ag	Cortinarius fusisporus KÜhner*		23.00	M			
Ag	Cortinarius helveolus (Bull)Fr.*	Corthelv	347.78	M		0	6
Ag	Cortinarius hemitrichus Fr.	Corthemi	79.00	M		0	4
Ag	Cortinarius hinnuleus Fr.*	Corthinn	510.57	M		13	17
Ag	Cortinarius lanatus (Mos.)Mos.*	Cortlana	94.38	M		9	9
Ag	Cortinarius obtusus Fr.	Cortobtu	183.36	M		9	6
Ag	Cortinarius paleaceus (Fr. in Weinm.)Fr.*	Cortpale	146.75	M		30	26
Ag	Cortinarius paleiferus Svrcek*	Cortpalf	209.00	M		17	2
Ag	Cortinarius parvannulatus KÜhner*	Cortparv	79.50	M		4	4
Ag	Cortinarius privignus Fr.*	Cortpriv	276.50	M		0	4
Ag	Cortinarius rigens (Pers.:Fr.)Fr.*	Cortrige	749.60	M		0	2
Ag	Cortinarius rigidus (Scop.)Fr. sensu Lange: see C. umbrinolens						
Ag	Cortinarius saniosus (Fr.)Fr.	Cortsani	117.00	M		30	23
Ag	Cortinarius striaepilus Favre*	Cortstri	35.31	M		30	28
Ag	Cortinarius subbalaustinus R.Henry*	Cortsubb	362.33	M		0	2
Ag	Cortinarius subsertipes: see C. casimiri						
Ag	Cortinarius tabularis (Bull.)Fr.*	Corttabu	194.40	M		0	2
Ag	Cortinarius torvus (Fr.:Fr.)Fr.	Corttorv	466.67	M		0	2
Ag	Cortinarius umbrinolens P.D. Orton*	CortrigL	141.17	M		0	6
Ag	Cortinarius valgus Fr.*	Cortvalg	532.29	M			
Ag	Cortinarius velenovskyi R.Henry*	Cortvele	294.00	M		4	2
Ag	Cortinarius violilamellatus Pearson ex P.D. Orton*	Corttram	119.00	M		9	4
Ag	Crepidotus cesatii (Rabh.)Sacc.	Crepspha	9.00	S	H F	4	0
Ag	Crepidotus luteolus (Lambotte)Sacc.	Creplute	55.75	S	W	4	0
Ag	Crepidotus sphaerosporus: see C. cesatii						
Ag	Crepidotus variabilis (Pers.:Fr.)Kumm.	Crepvari	21.00	S	H F	43	17
Ag	Cyphellostereum laeve (Fr.)Reid*24	Cyphlaev	4.00	S	B	4	0
Ag	Cystoderma amianthinum (Scop.:Fr.)Fayod	Cystamia	88.00A	S	H F	0	2
Ag	Cystoderma jasonis (Cooke&Massee)Harmaja	Cystlong	78.00	S	H F	9	2
Ag	Delicatula integrella (Pers.:Fr.)Fayod	Deliinte	1.60	S	H G	9	2
Ag	Dermocybe cinnabarina (Fr.)WÜnsche	Cortcinb	12.50	M		0	2
Ag	Dermocybe cinnamomea (L.)WÜnsche	Cortcinm	118.00	M		0	4
Ag	Entoloma caccabus (KÜhner)Noordel.	Entocacc	23.00	S	H F	0	2

Ag	Entoloma cephalotrichum (Orton)Noordel.	Entomoll	.33	S	H	F	0 2
Ag	Entoloma cetratum (Fr.)Mos.	Entocetr	59.00	S	H	F	0 4
Ag	Entoloma conferendum (Britz.)Noordel.	Entoconf	128.00	S	H	G	9 6
Ag	Entoloma hispidulum (M.Lange)Noordel.	Entohisp	1.40	S	H	G	0 4
Ag	Entoloma juncinum (Kühner&Romagn.)Noordel.	Entojunc	35.00	S	H	F	0 2
Ag	Entoloma lividoalbum (Kühner&Romagn.)Kubicka*	Entolivi	901.00	S	H	G	0 2
Ag	Entoloma molliusculum: see E. cephalotrichum						
	Entoloma nitidum Quél.		14.41	S	H	F	
Ag	Entoloma papillatum (Bres.)Dennis	Entopapi	26.00A	S	H	G	0 6
Ag	Entoloma rhodocylix (Lasch:Fr.)Mos.	Entorhod	8.00	S	H	F	13 4
Ag	Entoloma sericellum (Fr.:Fr.)Kumm.		8.60	S	H	G	
Ag	Entoloma sericeum (Bull.)Quél. var. s. f. nolaniforme (Kühner)Noordel.	Entosern	37.00	S	H	G	0 8
Ag	Entoloma sericeum (Bull.)Quél. var. s. f. s.	Entosers	86.00A	S	H	G	13 19
Ag	Entoloma solstitiale (Fr.)Noordel.		65.00	S	H	G	
Ag	Entoloma subradiatum (Kühner&Romagn.)Mos.	Entosubr	114.25	S	H	F	17 2
Ag	Entoloma turbidum (Fr.)Quél.	Entoturb	112.20	S	H	F	4 4
Ag	Entoloma undulatosporum Arnolds&Noordel.*	Entoundu	23.00	S	H	G	0 4
Ag	Entoloma xanthocaulon Arnolds&Noordel.	Entoxant	38.38	S	H	G	0 2
Ag	Flammulaster carpophiloides (Fr.)Earle	Flamcarp	4.00	S	H	F	17 0
Ag	Flammulina velutipes (Curt.:Fr.)Karst.	Flamvelu	75.00	S	W		0 2
Ag	Galerina allospora: see G. luteofulva						
Ag	Galerina cinctula P.D.Orton	Galecinc	1.30	S	H	F	0 2
Ag	Galerina heterocystis (Atk.)A.H.Smith	Galehete	7.67	S	H	G	0 2
Ag	Galerina hypnorum (Schrank:Fr.)Kühner	Galehypn	2.40	S	B		26 23
Ag	Galerina luteofulva P.D.Orton	Galeallo	4.50A	S	H	F	0 2
Ag	Galerina pseudocamerina Sing.	Galepseu	4.67	S	H	F	0 2
Ag	Galerina pumila (Pers.Fr.)M.Lange ex Sing.	Galepumi	2.10	S	H	F	0 2
Ag	Galerina unicolor (Fr.)Sing.	Galeunic	15.00	S	H	F	0 2
Ag	Galerina vittaeformis (Fr.)Sing.	Galeatki	11.00	S	B		4 15
Ag	Gymnopilis penetrans (Fr.:Fr.)Murr.	Gymnpene	50.00	S	W		4 4
Ag	Gymnopilus junoninus (Fr.)P.D.Orton	Gymnspec	157.50	S	W		0 2
Ag	Gymnopilus spectabilis: see G. junoninus						
Ag	Gyroporus castaneus (Bull.:Fr.)Quél.	Gyrocast	1734.00	M			0 2
Ag	Hebeloma anthracophilum Maire*	Hebeanth	173.30	M			4 2
Ag	Hebeloma crustuliniforme (Bull.)Quél.*	Hebecrus	1053.00	M			4 0
Ag	Hebeloma helodes Favre*	Hebehelo	727.80	M			39 28
Ag	Hebeloma longicaudum (Pers.)Kumm.*	Hebevelu	816.00	M			13 9
Ag	Hebeloma mesophaeum (Pers.)Quél.	Hebemeso	198.00	M			26 11
Ag	Hebeloma pallidoluctuosum Gröger&Zschieschang	Hebelati	694.00	M			4 4
Ag	Hebeloma latifolium (=H. sacchariolens p.p.): see H. pallidoluctuosum						
Ag	Hebeloma spoliatum (Fr.)Gill.*	Hebespol	357.00	M			4 2
Ag	Hebeloma truncatum (Schaeff.:Fr.)Kumm.*	Hebetrun	1465.50	M			0 4
Ag	Hemimycena delectabilis (Peck)Sing.	Hemidele	1.50	S	H	G	0 4
	Hygrocybe acutoconica (Clements)Sing.		195.00A	S	H	G	
Ag	Hygrocybe conica (Scop.:Fr.)Kumm.	Hygrconi	132.00A	S	H	G	0 2
Ag	Hygrocybe miniata (Fr.)Kumm. var. miniata	Hygrmini	52.00A	S	H	G	0 4
Ag	Hygrocybe miniata (Fr.)Kumm. var. mollis (Berk.&Br.)Arnolds		57.20	S	H	G	
Ag	Hygrophoropsis aurantiaca (Wulf.:Fr.)Maire	Hygraura	70.00A	S	H	F	0 4
Ag	Hypholoma fasciculare (Huds.:Fr.)Kumm.	Hyphfasc	274.00A	S	W		9 32
Ag	Hypholoma radicosum Lange		536.00	S	W		
Ag	Hypholoma sublateritium (Fr.)Quél.	Hyphsubl	825.00	S	W		4 2
Ag	Inocybe albomarginata Velen.*	Inocalbo	246.00	M			4 9
Ag	Inocybe amethystina Kuyper*	Inocamet	10.67	M			4 0
	Inocybe assimilata (Britz.)Sacc.*	Inocumbr	249.00	M			17 19
Ag	Inocybe asterospora Quél.	Inocaste	260.00	M			4 0
Ag	Inocybe brunneoatra: see I. fuscidula						
Ag	Inocybe calospora Quél.	Inoccalo	18.67	M			0 2
Ag	Inocybe cookei Bres.	Inoccook	120.00	M			4 4
Ag	Inocybe cryptocystis Stuntz	Inoccryp	225.00	M			0 2
Ag	Inocybe dulcamara Kumm.		176.16	M			
Ag	Inocybe eutheles: see I. sindonia						
Ag	Inocybe fastigiata: see I. rimosa						
Ag	Inocybe flocculosa (Berk.)Sacc.	Inocfloc	130.50	M			13 4
Ag	Inocybe fuscidula Velen.	Inocfusc	122.00	M			17 4
Ag	Inocybe geophylla (Sow.:Fr.)Kumm.	Inocgeop	68.00	M			17 4
Ag	Inocybe glabripes Rick.	Inocglab	77.00	M			4 0
Ag	Inocybe grammata Quél.	Inocgram	488.00	M			4 2
Ag	Inocybe griseolilacina Lange	Inocgris	56.67	M			0 8
Ag	Inocybe hirtella Bres. var. bispora Kuyper	Inochirt	420.00	M			4 2
Ag	Inocybe huijsmanii Kuyper*	Inochuij	23.33	M			13 0
Ag	Inocybe lacera (Fr.)Kumm.	Inoclace	184.33	M			13 17

Ag	Inocybe lanuginosa (Bull.:Fr.)Kumm.	Inoclasa	100.00	M		4	4
Ag	Inocybe maculata Boud.	Inocmacu	1160.00	M		13	8
Ag	Inocybe microspora: see I. glabripes						
Ag	Inocybe mixtilis (Britz.)Sacc.	Inocmixt	154.00	M		22	11
Ag	Inocybe napipes Lange	Inocnapi	278.00	M		26	11
Ag	Inocybe obscura: see I.phaeodisca						
Ag	Inocybe ochroalba Bruylants	Inococbr	176.00	M		9	0
Ag	Inocybe ovalispora: see I. albomarginata						
Ag	Inocybe petiginosa (Fr.)Gill.	Inocpeti	18.67	M		30	8
Ag	Inocybe phaeocomis (Pers.)Kuyper var. ph.	Inocphae	25.00	M		0	2
Ag	Inocybe praetervisa Quél.	Inocprae	31.00	M		4	2
Ag	Inocybe pseudoasterospora KÜhner var. microsperma Kuyper&Keizer*	Inocpseu	278.00	M		0	4
Ag	Inocybe rimosa (Bull.:Fr.)Kumm.	Inocrimo	390.00	M		4	4
Ag	Inocybe sindonia (Fr.)Karst.	Inocsind	87.00	M		22	2
Ag	Inocybe spec.*	Inocspec	21.00	M		0	2
Ag	Inocybe splendens R.Heim	Inocsple	80.00	M		0	2
Ag	Inocybe umbrina: see I. assimilata						
Ag	Inocybe variabillima Speg.	Inoclala	68.60	M		0	9
Ag	Inocybe xanthomelas KÜhn.&Bours.	Inocxant	193.57	M		4	4
Ag	Laccaria amethystea (Bull.)Murr.	Laccamet	180.00	M		48	23
Ag	Laccaria bicolor (Maire)Orton*	Laccbico	133.25	M		4	13
Ag	Laccaria laccata (Scop.:Fr.)Berk.&Br.*	Lacclacc	365.67	M		87	92
Ag	Laccaria proxima (Boud.)Pat.*	Laccprox	186.67	M		48	47
Ag	Laccaria purpureobadia Reid*	Laccpurp	262.00	M		0	4
Ag	Laccaria tortilis (Bolt.)Cke.	Lacctort	15.89	M		4	6
Ag	Lactarius blennius (Fr.)Fr.	Lactblen	701.88	M		61	0
Ag	Lactarius camphoratus (Bull.)Fr.	Lactcamp	320.00	M		13	15
Ag	Lactarius chrysorrheus Fr.	Lactchry	1677.22	M		4	23
Ag	Lactarius necator: see L. turpis						
Ag	Lactarius quietus (Fr.)Fr.	Lactquie	912.00	M		4	89
Ag	Lactarius rufus(Scop.:Fr.)Fr.	Lactrufu	1149.00	M		4	0
Ag	Lactarius serifluus (D.C.:Fr.)Fr.	Lactseri	740.00	M		9	25
Ag	Lactarius subdulcis (Bull.:Fr)S.F.Gray	Lactsubd	915.40	M		35	0
Ag	Lactarius tabidus Fr.	Lactthei	361.00	M		39	32
Ag	Lactarius theiogalus: see L. tabidus						
Ag	Lactarius turpis (Weinm.)Fr.	Lactneca	2202.73	M		0	2
Ag	Lactarius vellereus (Fr.)Fr. var. v.	Lactvell	5920.00	M		0	4
Ag	Leccinum oxydabile (Sing.)Sing.*	Leccoxyd	1675.00	M		0	2
Ag	Leccinum quercinum Pil.	Leccquer	3090.00	M		0	2
Ag	Lepiota cristata (Bolt.:Fr.)Kumm.	Lepicris	500.00	S	H F	4	0
Ag	Lepiota ventriosospora Reid	Lepivent	1855.00	S	H F	4	0
Ag	Lepista flaccida (Sow.:Fr.)Pat.	Lepiinve	1980.00	S	H F	9	6
Ag	Lepista nebularis (Batsch:Fr.)Harmaja	Lepinebu	1160.00	S	H F	9	8
Ag	Lepista nuda (Bull.:Fr.)Cooke	Lepinuda	3160.00A	S	H F	9	19
Ag	Lepista sordida (Schum.:Fr.)Sing.	Lepisord	253.33	S	H G	0	2
Ag	Leucopaxillus giganteus (Fr.)Sing.	Leucgiga	13668.00	S	H G	0	2
Ag	Lyophyllum decastes (Fr.:Fr.)Sing.	Lyopdeca	1718.00	S	H F	4	2
Ag	Lyophyllum semitale (Fr.)KÜhner		135.00	S	H F		
Ag	Macrolepiota procera (Scop.:Fr.)Sing.	Macrproc	13000.00A	S	H G	0	4
Ag	Marasmiellus vaillantii (Pers.:Fr.)Sing.	Maravail	2.50	S	H F	9	17
Ag	Marasmius androsaceus (L.)Fr.	Marasandr	2.60A	S	H F	4	4
Ag	Marasmius epiphylloides Rea	Maraepis	.70	S	H F	0	2
Ag	Marasmius epiphyllus (Pers.:Fr.)Fr.	Maraepip	16.00	S	H F	4	2
Ag	Marasmius graminum (Lib.)Berk.	Maragram	2.00	S	H G	9	11
Ag	Marasmius oreades (Bolt.:Fr.)Fr.	Maraorea	438.00A	S	H G	13	28
Ag	Marasmius recubans Quél.	Mararecu	.35	S	H F	4	0
Ag	Marasmius rotula (Scop.:Fr.)Fr.	Mararotu	2.40	S	H F	13	2
Ag	Megacollybia platyphylla (Pers.:Fr.)Kotl.&Pouz.	Oudeplat	554.00	S	H F	13	9
Ag	Melanoleuca excissa (Fr.)Sing. var. iris (KÜhner) Boekhout		461.00A	S	H F		
Ag	Melanoleuca polioleuca (Fr.:Fr.)KÜhner&Maire	Melapoli	145.00	S	H G	9	4
Ag	Melanotus philipsii (Berk.&Br.)Sing.	Melaphil	.80A	S	H G	0	11
Ag	Mycena abramsii Murrill	Mycpraec	36.67	S	H F	4	2
Ag	Mycena acicula (Schaeff.:Fr.)Kumm.	Mycacicu	1.25	S	H F	0	4
Ag	Mycena adcendens (Lasch)Maas G.	Mycadcen	.10	S	H F	4	17
Ag	Mycena adonis (Bull.:Fr.)S.F.Gray	Mycadoni	9.20A	S	H G	0	2
Ag	Mycena aetites (Fr.)Quél.*	Mycaetit	22.00	S	H G	4	2
Ag	Mycena avenacea (Fr.)Quél. var. a.	Mycavena	10.00	S	H G	30	36
Ag	Mycena avenacea (Fr.)Quél. var. roseofusca KÜhner	Mycavenr	45.50	S	H G	4	2
Ag	Mycena capillaris (Schum.:Fr.)Kumm.	Myccapil	.03	S	H F	26	0
Ag	Mycena cinerella Karst.	Mycciner	11.00	S	H F	39	57
Ag	Mycena epipterygia (Scop.:Fr.)S.F.Gray	Mycepipt	24.00	S	H F	0	2
Ag	Mycena filopes (Bull.:Fr.)Kumm. var. f.*	Mycfilof	9.33	S	H F	57	77

Ag	Mycena filopes (Bull.:Fr.)Kumm. var. metata (Fr.) sensu Oort*	Mycfilom	14.00	S	H	F	26	36
Ag	Mycena flavescens Velen.	Mycflave	4.40	S	H	F	17	17
Ag	Mycena flavoalba (Fr.)Quél.	Mycflavo	4.50A	S	H	G	17	17
Ag	Mycena galericulata (Scop.:Fr.)Quél.	Mycgaler	165.33	S	W		48	72
Ag	Mycena galopus (Pers.:Fr.)Kumm. var. alba Rea	Mycgaloa	17.00	S	H	F	0	4
Ag	Mycena galopus (Pers.:Fr.)Kumm. var. g.	Mycgalog	8.67	S	H	F	91	75
Ag	Mycena galopus var. nigra Rea 17		8.67	S	H	F		
Ag	Mycena haematopus (Pers.:Fr.)Kumm.	Mychaema	95.67	S	W		4	8
Ag	Mycena leptocephala (Pers.:Fr.)Gill.*	Myclepto	22.00A	S	H	G	70	62
Ag	Mycena mucor (Batsch:Fr.)Gill.	Mycmucor	.20	S	H	F	4	2
Ag	Mycena oortiana KÜhner ex Hora	Mycoorti	52.00	S	W		4	6
Ag	Mycena pearsoniana Dennis ex Sing.	Mycpears	18.00	S	H	F	0	4
Ag	Mycena pelliculosa (Fr.)Quél. var. p.	Mycpelli	14.50	S	H	G	0	2
Ag	Mycena polyadelpha (Lasch)KÜhner	Mycpolya	.05A	S	H	F	4	26
Ag	Mycena polygramma (Bull.:Fr.)S.F.Gray var. p.	Mycpolpo	49.00A	S	W		4	28
Ag	Mycena polygramma (Bull.:Fr.)S.F.Gray var. pumila Lange	Mycpolpu	20.00	S	H	F	4	2
Ag	Mycena praecox: see M. abramsii							
Ag	Mycena pura (Pers.:Fr.)Kumm. var. p.	Mycpurap	43.00A	S	H	F	22	25
Ag	Mycena rorida (Scop.:Fr.)Quél.	Mycrorid	42.00	S	H	F	0	2
Ag	Mycena sanguinolenta (Alb.&Schw.:Fr)Kumm.	Mycsangu	4.20A	S	H	F	35	40
Ag	Mycena speirea (Fr.:Fr.)Gill.	Mycspeir	1.65	S	H	F	0	15
Ag	Mycena spec.*							
Ag	Mycena stylobates (Pers.:Fr.)Kumm.	Mycstylo	10.00	S	H	F	0	30
Ag	Mycena vitilis (Fr.)Quél.	Mycvitil	20.00	S	H	F	74	96
Ag	Mycena vitrea (Fr.)Quél.*	Mycsepia	18.00A	S	H	G	26	30
Ag	Naucoria escharoides: see Alnicola e.							
Ag	Naucoria spp.: see Alnicola							
Ag	Nyctalis asterophora Fr.	Astelyco	9.33	P	F		0	15
Ag	Oudemansiella platyphylla: see Megacollybia p.							
Ag	Oudemansiella radicata: see Xerula r.							
Ag	Panaeolina foenisecii: see Panaeolus f.							
Ag	Panaeolus acuminatus (Schaeff.)Quél.	Panaacum	90.00	S	H	F	0	2
Ag	Panaeolus fimicola (Fr.)Quél.	Panafimi	34.00A	S	H	F	4	6
Ag	Panaeolus fimiputris (Bull.:Fr.)Quél.	Anelsemi	130.00	S	C		0	2
Ag	Panaeolus foenisecii (Pers.:Fr.)Schroet.	Panafoen	62.00	S	H	F	0	4
Ag	Panaeolus rickenii Hora	Panarick	52.00	S	H	F	0	2
Ag	Panaeolus sphinctrinus (Fr.)Quél.	Panasphi	62.00A	S	H	F	4	6
Ag	Panellus serotinus (Pers.:Fr.)KÜhner	Panesero	1038.00	S	W		0	4
Ag	Panellus stypticus (Bull.:Fr.)Karst.	Panestyp	11.11	S	W		4	2
Ag	Paxillus involutus (Batsch:Fr.)Fr.	Paxiinvo	997.08	M			61	34
Ag	Pholiota gummosa (Lasch)Sing.	Pholgumm	184.00	S	W		0	2
Ag	Pholiota lenta (Pers.:Fr.)Sing.	Phollent	270.00	S	W		4	0
Ag	Pleurotellus hypnophilus (Berk.)Sacc.	Pleuherb	5.80	S	H	G	4	4
Ag	Pleurotus ostreatus (Jacq.:Fr.)Kumm.	Pleuostr	6330.00	S	W		4	0
Ag	Pluteus atricapillus (Batsch)Fayod	Plutatri	966.67	S	W		13	8
Ag	Pluteus nanus (Pers.:Fr.)Kumm.	Plutnanu	45.00	S	H	F	0	2
Ag	Pluteus pallescens P.D.Orton*	Plutpall	74.00	S	H	F	0	2
Ag	Pluteus phlebophorus (Ditmar.:Fr.)Kumm.	Plutphle	42.00	S	H	F	9	2
Ag	Pluteus podospileus Sacc.&Cub.	Plutpodo	56.00	S	H	F	9	0
Ag	Psathyrella artemisiae: see P. squamosa							
Ag	Psathyrella candolleana (Fr.:Fr.)Maire	Psatcand	385.00	S	H	F	22	11
Ag	Psathyrella cotonea (Quél.)Konr.&Maubl.	Psatcoto	461.00	S	W		0	2
Ag	Psathyrella dicrani (A.E.Jansen)Kits van Wav.	Psatdicr	41.00	S	H	F	0	4
Ag	Psathyrella frustulenta (Fr.)A.H.Smith	Psatfrus	81.67	S	H	F	9	13
Ag	Psathyrella fulvescens (Romagn.)A.H.Smith var. brevicystis Kits van Wav.*	Psatfulv	98.50	S	H	F	57	55
Ag	Psathyrella gossypina (Bull.:Fr.)Pearson&Dennis	Psatgoss	43.00	S	H	F	9	4
Ag	Psathyrella gracilis (Fr.)Quél.	Psatgrac	79.20	S	H	F	0	8
Ag	Psathyrella lutensis (Romagn.)M.Bon	Psatlute	16.00	S	H	F	4	2
Ag	Psathyrella microrhiza (Lasch.:Fr.)Konr.&Maubl.	Psatmicr	30.67	S	H	F	30	6
Ag	Psathyrella panaeoloides (Maire)Arnolds	Psatpana	25.67	S	H	G	17	2
Ag	Psathyrella piluliformis (Bull.:Fr.)P.D.Orton	Psatpilu	29.00	S	W		13	21
Ag	Psathyrella prona (Fr.)Gill. f. p.	Psatpron	13.00A	S	H	G	4	4
Ag	Psathyrella pygmaea (Bull.:Fr.)Sing.	Psatpygm	3.67	S	W		4	2
	Psathyrella rhombispora Keizer&Arnolds*		16.40	S	H	?		
Ag	Psathyrella seymourensis A.H.Smith*	Psatseym	30.00	S	H	G	4	0
Ag	Psathyrella spadiceogrisea (Schaeff.)Maire	Psatspad	121.23	S	H	F	26	8
Ag	Psathyrella spec.*	Psatspec	16.67	S	H	?	4	0
Ag	Psathyrella squamosa (Karst.)A.H.Smith	Psatarte	85.00	S	H	F	26	21
Ag	Psathyrella tephrophylla (Romagn.)M.Bon	Psatteph	880.00	S	H	F	0	2
Ag	Psilocybe bullacea (Bull.:Fr.)Kumm.*	Psilbull	36.33	S	C		0	2
Ag	Psilocybe crobulus (Fr.)M.Lange ex Sing.	Psilcrob	7.00	S	H	F	4	6

Ag	Psilocybe inquilina (Fr.:Fr.)Bres.	Psilinqu	3.80	S	H	G	9 0
Ag	Psilocybe montana (Pers.:Fr.)Kumm., incl. P. muscorum (P.D.Orton)Mos.	Psilmusc	8.70A	S	B		0 6
Ag	Psilocybe semilanceata (Fr.)Kumm.	Psilsemi	57.57	S	H	G	9 11
Ag	Resupinatus trichotis (Pers.)Sing.	Resutric	2.50	S	W		4 2
Ag	Rickenella fibula (Bull.:Fr.)Raith.	Rickfibu	4.30A	S	B		43 43
Ag	Rickenella setipes (Fr.:Fr.)Raith.	Rickseti	5.20A	S	B		13 17
Ag	Ripartites tricholoma (Alb.&Schw.:Fr.)Karst.	Ripatric	19.00	S	H	F	4 9
	Ripartites helomorphus (Fr.)Karst.		51.80	S	H	F	
Ag	Russula albonigra (Krbh.)Fr.		5454.00	M			
Ag	Russula amoenolens Romagn.	Russamoe	913.75	M			39 77
Ag	Russula atropurpurea (Krbh.)Britz.	Russatro	4681.67	M			22 36
Ag	Russula brunneoviolacea Crawsh.	Russbrun	835.00	M			4 0
Ag	Russula chloroides (Krbh.)Bres.	Russchlo	1087.00	M			0 2
Ag	Russula cyanoxantha (Schaeff.)Fr.	Russcyan	2640.71	M			9 25
Ag	Russula decipiens (Sing.)KÜhner&Romagn.*	Russdeci	10797.50	M			0 2
Ag	Russula delica Fr. emend. Bres.	Russdeli	4898.50	M			0 4
Ag	Russula densifolia Gill.	Russdens	2559.20	M			0 2
Ag	Russula emetica (Schaeff.)Pers.:Fr.	Russemet	584.67	M			4 6
Ag	Russula fellea Fr.	Russfell	2700.00	M			70 0
Ag	Russula fragilis (Fr. ut var.)Fr. sensu Romagnesi	Russfrag	654.00	M			13 53
Ag	Russula graveolens Romell in Britz. f. cicatricata (Romagn. ex)Keizer&Arnolds*	Russcica	2301.38	M			0 11
Ag	Russula graveolens Romell in Britz. f. elaeodes (Bres.)Keizer&Arnolds*	Russelae	500.00	M			0 6
Ag	Russula graveolens Romell in Britz. f. graveolens*	Russgrav	2301.33	M			0 21
Ag	Russula graveolens Romell in Britz. f. purpurata (Crawsh.)Keizer&Arnolds*	Russpurp	1055.67	M			0 9
Ag	Russula grisea Fr. ss. str.*	Russgris	2401.50	M			9 8
Ag	Russula ionochlora Romagn.*	Russiono	1306.00	M			13 11
Ag	Russula laurocerasi Melz.	Russlaur	1605.00	M			0 6
Ag	Russula lutea (Huds.:Fr.)S.F.Gray	Russcham	1616.80	M			9 4
Ag	Russula mairei Sing.	Russmair	998.00	M			57 2
Ag	Russula nigricans Fr.	Russnigr	5002.00	M			30 40
Ag	Russula ochroleuca Pers.	Russochr	1215.80	M			52 26
Ag	Russula odorata Romagn.	Russodor	428.60	M			4 17
Ag	Russula parazurea J.Schaeff. ex J.Schaeff.*	Russpara	3105.75	M			78 68
Ag	Russula pectinatoides Peck	Russpect	1400.22	M			13 28
Ag	Russula solaris Ferdinandsen&Winge	Russsola	802.17	M			4 0
Ag	Russula velenovskyi Melz.&Zv.	Russvele	972.50	M			26 11
Ag	Russula vesca Fr.	Russvesc	2674.50	M			4 13
Ag	Stropharia aeruginosa (Curtis:Fr.)Quél.	Stroaeru	169.00A	S	H	F	9 8
Ag	Stropharia albocyanea (Fr.)Quél.	Stroalbo	57.00	S	H	F	4 4
Ag	Stropharia caerulea Kreisel	Strocyan	436.67	S	H	F	13 6
Ag	Stropharia coronilla (Bull.:Fr.)Quél.	Strocoro	222.00A	S	H	G	4 0
Ag	Stropharia inuncta (Fr.)Quél.	Stroinun	117.00A	S	H	G	4 0
Ag	Stropharia semiglobata (Batsch:Fr.)Quél.	Stroaemi	139.00A	S	C		4 4
Ag	Stropharia squamosa (Pers.:Fr.)Quél.	Strosqua	248.00	S	H	F	0 2
Ag	Tephrocybe ambusta (Fr.)Donk.	Tephambu	17.00	S	H	G	0 2
Ag	Tephrocybe atrata (Fr.:Fr.)Donk	Tephatra	18.80	S	H	G	0 2
Ag	Tephrocybe tylicolor (Fr.:Fr.)Mos.	Tephtesq	31.00	S	H	F	9 19
Ag	Tricholoma flavobrunneum: see T. fulvum						
Ag	Tricholoma fulvum (D.C.:Fr.)Sacc.	Tricflav	637.50	M			0 2
Ag	Tricholoma saponaceum (Fr.)Kumm.	Tricsapo	1144.00	M			4 6
Ag	Tricholoma scalpturatum (Fr.)Quél. var. s.*	Tricscal	460.00	M			0 2
Ag	Tricholoma sulphureum (Bull.:Fr.)Kumm.	Tricsulp	1098.33	M			0 6
Ag	Tricholoma ustale (Fr.:Fr.)Kumm.	Tricusta	873.33	M			39 0
Ag	Tricholoma ustaloides Romagn.		1085.00	M			
Ag	Tricholomopsis rutilans (Schaeff.:Fr.)Sing.	Tricruti	135.00	S	W		0 2
Ag	Tubaria conspersa (Pers.:Fr.)Fayod	Tubacons	23.00	S	H	F	0 2
Ag	Tubaria furfuracea (Pers.:Fr.)Gillet*	Tubafurf	86.67	S	H	F	100 36
Ag	Tylopilus felleus (Bull.:Fr.)Karst.	Tylofell	2766.00	M			0 2
Ag	Xerocomus badius (Fr.)KÜhner ex Gilb.	Xerobadi	5565.00	M			43 34
Ag	Xerocomus chrysenteron (Bull.)Quél.	Xerochry	1757.00	M			57 45
Ag	Xerocomus porosporus Imler	Xeroporo	935.00	M			0 8
Ag	Xerocomus rubellus (Krbh.)Mos.	Xerorube	800.83	M			0 8
Ag	Xerocomus subtomentosus (L.)Quél.	Xerosubt	2088.00	M			4 2
Ag	Xerocomus truncatus: see X. porosporus						
Ag	Xerula radicata (Rehl.:Fr.)Dörfelt	Ouderadi	407.50	S	W		9 0
Aph	Antrodiella semisupina (Berk.&Curt.)Ryv.&Johansen	Antrsemi	279.00	S	W		4 2
Aph	Bjerkandera adusta (Willd.:fr.)Karst.	Bjeradus	423.00	S	W		0 2
Aph	Boletopsis leucomelaena (Pers.)Fayod	Bolsubs	5237.00	M			4 2
Aph	Calocera cornea (Batsch.:Fr.)Fr.	Calocorn	.52	S	W		

Aph	Cantharellus cibarius Fr.	Cantciba	544.91	M		4	0
Aph	Clavaria acuta: see C. falcata						
Aph	Clavaria falcata Pers.:Fr	Clavacut	15.00	S	H F	4	4
Aph	Clavulina coralloides (L.)Schroet.	Clavcris	819.00	M		0	2
Aph	Clavulina cristata: see C. coralloides					0	4
Aph	Clavulina rugosa (Bull.:Fr.)Schroet.	Clavrugo	33.25	M		4	0
Aph	Clavulinopsis luteoalba (Rea)Corner	Clavlute	10.00	S	H F	13	28
Aph	Clavulinopsis spp.: see Ramariopsis					0	2
Aph	Hapalopilus rutilans (Pers.:Fr.)Karst.	Hapanidu	2657.00	S	W	4	0
Aph	Hydnellum concrescens (Pers.)Banker	Hydnconc	1820.00	M		0	2
Aph	Hydnellum spongiosipes (Peck)Pouz.	Hydnspon	6110.00	M		4	2
Aph	Hydnum repandum L.:Fr.	Hydnrepa	1515.67	M		0	4
Aph	Phellodon confluens (Pers.)Pouz.	Phelconf	1568.50	M		0	4
Aph	Polyporus badius (S.F.Gray)Schw.	Polybadi	1700.00	S	W	4	2
Aph	Polyporus brumalis (Pers.)Fr.	Polybrum	380.00	S	W	9	8
Aph	Polyporus ciliatus Fr.:Fr. ss. str.	Polycili	131.00	S	W	4	0
Aph	Polyporus varius (Pers.):Fr.	Polyvari	3370.00	S	W		
Aph	Pseudocraterellus sinuosus (Fr.)Reid	Pseusinu	141.54	M		0	2
Aph	Ramaria stricta (Pers.:Fr.)Quél.	Ramastri	370.00	S	W	9	11
Aph	Ramariopsis corniculata (Schaeff.:Fr.)Corner	Clavcorn	51.76	S	H G	35	32
Aph	Ramariopsis helveola (Pers.:Fr.)R.H.Petersen	Clavhelv	10.00A	S	H G		
Aph	Ramariopsis kunzei (Fr.)Corner*	Ramakunz	6.23	S	H G	4	2
Aph	Ramariopsis laeticolor (Berk.&Curt.)R.H.Petersen	Clavlaet	11.00A	S	H	0	2
Aph	Spongiporus subcaesius (David)David	Tyrosubc	93.00	S	W	0	2
Aph	Thelephora terrestris Ehrh. ex Willd.:Fr.	Thelterr	50.00	M		0	2
Aph	Trametes versicolor (L.)Pil.	Tramvers	660.00	S	W	0	2
Aph	Tremella mesenterica Retz.:Fr.	Tremmese	632.00	S	W	0	6
Aph	Tyromyces subcaesius: see Spongiporus s.					22	11
G	Anthurus archeri (Berk.)E.Fischer	Antharch	900.00	S	H F	0	6
G	Bovista nigrescens Pers.:Pers.	Bovinigr	1650.00	S	H G	0	2
G	Bovista plumbea Pers.	Boviplum	200.00	S	H G	0	4
G	Calvatia excipuliformis (Scop.:Pers.)Perdeck	Calvexci	1896.00	S	H F	0	11
G	Crucibulum laeve (Huds.)Kambly in Kambly&Lee	Cruclaev	10.00	S	H F	4	0
G	Cyathus olla Batsch:Fr.	Cyatolla	50.00	S	H F	13	0
G	Cyathus striatus (Huds.)Wild.:Pers.	Cyatstri	36.00	S	H F	0	6
G	Hymenogaster tener Berk.&Br.	Hymetene	30.00	M		0	2
G	Lycoperdon foetidum M.Bon	Lycofoet	775.00	S	H F	0	11
G	Lycoperdon perlatum Pers.:Pers.	Lycoperl	686.00	S	H F	4	6
G	Mutinus caninus (Huds.:Pers.)Fr.	Muticani	105.00	S	H F	13	6
G	Octavianina asterosperma (Vitt.)Kunze	Octaaste	1078.00	M		0	2
G	Phallus impudicus (L.)Pers.	Phalimpu	4830.00	S	H F	9	4
G	Scleroderma areolatum Ehrenb.	Sclereo	1707.83	M		30	57
G	Scleroderma citrinum Pers.	Sclecitr	4962.00	M		61	40
G	Sphaerobolus stellatus Tode:Pers.	Sphastel	.50	S	H F	4	8
G	Vascellum pratense (Pers.:Pers.)Kreisel	Vascprat	563.33	S	H G	0	4
Asc	Cordiceps militaris (L.)Link	Cordmili	152.00A	P	I	13	21
Asc	Cordiceps ophioglossoides (Ehrh. ex Pers.)Link	Cordophi	213.00	P	F	4	4
Asc	Cordyceps canadensis Ellis&Everh.	Cordcana	190.75	P	F	0	2
Asc	Elaphomyces muricatus Fr.	Elapmuri	4300.00	M		4	4
Asc	Helvella corium (Weberb.)Massee*	Helvcori	50.00	S	H F	4	0
Asc	Helvella crispa (Scop.)Fr.	Helvcris	948.00	S	H F	4	2
Asc	Helvella cupuliformis Dissing&Nannf.*		183.00	S	H F		
Asc	Helvella lacunosa Afz.	Helvlacu	195.00	S	H F	17	11
Asc	Helvella villosa (Hedw.)Dissing&Nannf.	Helvvill	104.00	S	H F	4	0
Asc	Hydnotria tulasnei (Berk.&Br.)Berk.&Br.	Hydntula	701.00	M		4	2
Asc	Leotia lubrica (Scop.)Pers.	Leotlubr	237.67	M		4	8
Asc	Leucoscypha leucotricha (Alb.&Schw.)Boud.	Leucleuc	3.00	S	B	4	0
Asc	Mycolachnea hemisphaerica (Wigg. ex S.F.Gray)Maire	Mycohemi	85.00	S	H F	0	4
Asc	Neottiella vivida (Nyl.)Dennis	Neotvivi	44.00	S	B	0	2
Asc	Octospora humosa (Fr.)Dennis	Octohumo	3.60	S	B	0	2
Asc	Otidea alutacea (Bres.)Massee*	Otidalut	636.00	M		0	4
Asc	Otidea bufonia (Pers.)Boud.*	Otidbufo	173.33	M		4	8
Asc	Peziza limnaea Maas G.	Pezilimo	34.00	S	H F	0	2
Asc	Pulvinula constellatio: see P. convexella						
Asc	Pulvinula convexella (P.Karsten)Pfister	Pulvcons	7.50	S	H F	4	0
Asc	Tarzetta catinus (Holmsk.)Korf&Rogers	Pustcati	50.00	S	H F	4	0
Asc	Tarzetta cupularis (L.)Lambotte	Tarzcupu	26.50	S	H F	13	6
Asc	Tuber maculatum Vitt.	Tubemacu	40.00	M		4	0
FI	Paecilomyces farinosus (Holm)Brown&Smith	Paecfari	7.50	P	I	17	17

Appendix 2. LIST OF PLOTS

Survey of the plots, where the described species originate. All plots are situated in the province Drenthe, the Netherlands, except plots F15 and Q5, which lie in the province Friesland.
F = roadside verge planted with Beech; Q = roadside verge planted with Common Oaks; Age = age of trees (in 1988);
Exp. means exposition of the plot: + = in open landscape, ± = half shady, — = shady;
Pav. refers to the pavement of the roads: A = asphalt, B = bricks, N = no pavement.

Plot-nr.	Municipality	Near village	Coordinates on the topographic map	local name	Age trees	Exp.	Pav.	Description of the vegetation
F11	Peize	Altena	227,3-571,6	Lieverseweg	58	+	B	poor grassland
F12	Rolde	Deurze	237,5-556,7	Rolder Hoofdweg	78	+	A	mod. poor grassl.
F13	Beilen	Wijster	232,2-537,1	Bruntingerweg	37	+	A	mod. poor grassl.
F14	Beilen	Bruntinge	234,7-536,5	Hamweg	37	+	A	poor grassland
F15	Ooststellingwerf	Wateren	219,7-548,2	Bosweg	51	+	A	poor grassland
F16	Diever	Wateren	217,4-546,3	Oude Willem	51	+	A	mod. poor grassl.
F17	Anloo	Annen	244,7-563,7	Anlooerweg	54	+	A	poor grassland
F21	Vries	Rhee	234,4-561,4	N 870	66	+	A	mod. rich grassl.
F22	Sleen	't Haantje	252,6-537,5	Slenerweg	63	+	A	mod. rich grassl.
F23	Anloo	Annen	244,8-563,7	Eexterweg	61	+	A	rich grassland
F24	Peize	Peize	229,5-573,5	Zuurse weg	57	+	B	mod. rich grassl.
F25	Odoorn	Klijndijk	253,1-539,1	Odoornerzijtak	41	+	A	rich grassland
F31	Havelte	Havelte	211,7-531,2	Linthorst-Homanlaan	140	—	B	poor woodland
F32	Diever	Diever	217,9-542,1	Bosweg	55	—	B	poor woodland
F33	Gasselte	Gieten	246,3-555,5	Houtvester Jansenweg	66	—	A	± absent
F34	Anloo	Eext	245,6-561,6	Annerweg	81	—	A	poor woodland
F35	Eelde	Eelde	235,7-572,5	Hooghullen	70	—	A	rich woodland
F36	Odoorn	Klijndijk	253,4-539,3	Odoornerzijtak	41	—	A	rich woodland
F40	Ruinen	Hoogeveen	228,6-529,7	Spaarbankbos	44	—	N	poor woodland
F41	Gasselte	Gieten	245,3-557,6	Gieterveld	69	—	N	poor woodland
F42	Havelte	Havelte	211,7-531,2		72	—	N	± absent
F43	Eelde	Eelde	245,2-557,4	Hooghullen	82	—	N	mod. rich woodl.
F44	Roden	Roden	225,1-571,1	Mensingebosch	81	—	N	± absent
Q1	Sleen	Schoonoord	247,8-541,2	Oranjekanaal Z.Z.	100	+	A	poor grassland
Q2	Westerbork	Zwiggelte	235,5-545,0	Oranjekanaal N.Z.	100	+	A	poor grassland
Q3	Westerbork	Zwiggelte	236,2-545,0	Oranjekanaal Z.Z.	100	+	A	poor grassland
Q4	Anloo	Gieten	243,5-557,2	Gieterstraat	110	+	A	poor grassland
Q5	Ooststellingwerf	Wateren	219,7-548,0	Oude Willem	55	+	A	poor grassland
Q6	Vledder	Frederiksoord	209,0-540,1	Vledderweg	91	+	A	poor grassland
Q11	Assen	Deurze	236,9-556,6	Rolder Hoofdweg	113	+	A	poor grassland
Q12	Diever	Wateren	215,4-547,2	Waterenweg	130	+	B	mod. poor grassl.
Q13	Roden	Foxwolde	226,3-574,7	Roderwolderweg	114	+	B	mod. poor grassl.
Q14	Vledder	Vledder	209,9-541,1	Vledderweg	91	+	A	poor grassland
Q21	Assen	Deurze	236,6-556,6	Rolder Hoofdweg	113	+	A	rich grassland
Q22	Westerbork	Westerbork	236,5-541,5	Zwiggelterstraat	98	+	A	mod. rich grassl.
Q23	Ruinen	Pesse	225,3-532,2	Eursinge	112	+	A	rich grassland
Q24	Ruinen	Kraloo	225,5-533,8	Kralooerweg	70	+	A	rich grassland
Q26	Sleen	't Haantje	252,5-537,5	Oranjekanaal Z.Z.	116	+	A	rich grassland
Q31	Beilen	Ter Horst	230,9-540,1	Ter Horst	41	+	B	poor grassland
Q32	Odoorn	Odoornerveen	251,9-538,5	Odoornerzijtak	68	+	A	poor grassland
Q33	Beilen	Drijber	234,0-534,5	De Hullen	25	+	A	mod. poor grassl.
Q34	Odoorn	't Haantje	252,6-537,5	Oranjekanaal N.Z.	26	+	N	mod. poor grassl.
Q35	Peize	Altena	227,8-572,6	Hooghaar	47	+	B	poor grassland

6	Beilen	Klatering	232,9-543,5	Klatering	15	+	A	mod. poor grassl.
7	Beilen	Klatering	233,0-543,5	Klatering	15	+	A	mod. poor grassl.
8	Diever	Dieverbrug	218,6-540,6	Dieverbrug	10	+	A	poor grassland
9	Beilen	Beilen	234,6-544,0	Eursing	12	+	A	mod. rich grassl.
1	Beilen	Wijster	231,6-538,8	Beilerweg	48	+	A	mod. poor grassl.
2	Odoorn	Odoornerveen	248,8-540,8	Oranjekanaal N.Z.	32	+	A	mod. poor grassl.
3	Beilen	Wijster	230,5-537,6	Looveen	32	+	N	poor grassland
4	Beilen	Hooghalen	232,6-548,2	Stationsstraat	34	+	A	mod. poor grassl.
5	Beilen	Wijster	231,3-537,1	Boerkoelweg	35	+	B	mod. rich grassl.
6	Beilen	Wijster	231,8-536,9	Marsweg	35	+	B	mod. rich grassl.
1	Zweeloo	Witteveen	241,5-536,0	Bosweg	48	+	B	mod. poor grassl.
2	Odoorn	Odoornerveen	251,5-538,9	Torenweg	23	+	A	rich grassland
3	Sleen	Noordsleen	249,9-534,8	Middelesweg	28	+	A	rich grassland
4	Dwingeloo	Dwingeloo	222,3-538,1	Lheeweg	15	+	A	rich grassland
1	Zweeloo	Schoonoord	246,3-540,2	Oranjekanaal Z.Z.	116	±	B	rich grassland
2	Dwingeloo	Lheebroek	226,5-539,8	Lheebroek	76	±	B	mod. poor grassl.
3	Havelte	Havelte	210,9-531,3	Busselterweg	146	±	B	rich grassland
4	Havelte	Havelte	212,1-531,6	Overcingelaan	85	±	B	rich grassland
5	Anloo	Gieten	243,9-557,4	Gieterstraat	110	±	A	mod. poor grassl.
1	Zweeloo	Schoonoord	245,9-540,0	Oranjekanaal N.Z.	116	±	A	rich grassland
2	Westerbork	Zwiggelte	236,8-545,0	Oranjekanaal N.Z.	100	±	A	mod. poor grassl.
3	Havelte	Havelte	210,6-531,3	Busselterweg	125	±	B	mod. rich grassl.
4	Roden	Alteveer	225,3-570,3	Melkweg	106	±	A	mod. poor grassl.
1	Ruinen	Pesse	224,9-532,1	Leeuwte	110	—	A	ruderal
2	Assen	Assen	235,4-556,9	Steendijk	110	—	B	mod. rich grassl.
3	Roden	Roden	225,6-571,6	Mensingeweg	97	—	A	mod. rich woodl.
4	Anloo	Gieten	243,6-557,3	Gieterstraat	100	—	A	poor woodland
5	Havelte	Havelte	212,1-531,3	Van Helomaweg	140	—	A	rich grassland
7	Havelte	Havelte	212,1-530,8	Boskampsbrugweg	143	—	B	mod. rich woodl.
8	Ruinen	Rheebruggen	216,9-553,2	Rheebruggen	114	—	B	mod. poor woodl.
2	Havelte	Havelte	211,6-530,0		144	—	N	poor woodland
3	Ruinen	Hoogeveen	228,6-529,9	Spaarbankbos	105	—	N	poor woodland
4	Roden	Roden	225,4-571,5	Mensingebosch	102	—	N	poor woodland

Glossary

For terms referring to taxonomic descriptions of Macromycetes see: Vellinga (1988).

Aggradation phase: a developmental phase in a forest stand, following the innovation phase, which starts immediately after canopy closure and ends when the trees reach maturity and self-regeneration of the forest starts (Oldeman, 1990). Although the ecological circumstances in the artificial roadside verge habitat differ strongly from forests, the term may indicate the developmental phase of trees in roadside verges as well (chapter 6).

Early stage fungi: ectomycorrhizal fungi that 1) are capable of mycorrhiza formation with tree seedlings under sterile (axenic) conditions and that persist after outplanting or 2) form mycorrhizas spontaneously with seedlings in first generation plantations (Deacon et al., 1983).

Ectomycocoenon: abstraction of a set of similar (or strongly related) ectomycocoenoses (after Arnolds, 1981).

Ectomycocoenosis: the concrete stand of ectomycorrhizal (Macro-) fungi in a given area (analogous to mycocoenosis; after Arnolds, 1981). Preliminary term, only used in chapter 4).

Ectomycorrhiza: association between green plant roots and a fungus characterized by 1) a fungal sheath or mantle which encloses the root in a fungal tissue and 2) a Hartig net which is a plexus of fungal hyphae between epidermal and cortical cells (Harley & Smith 1983).

Environmental variables: set of varying ecological properties of the environment of an organism, determining its growth possibilities.

Half open or **half shady plots**: plots bordered at one side by forest and by the other side by open area.

Late stage fungi: ectomycorrhizal fungi that 1) do not persist on seedlings after outplanting or 2) will not colonize seedlings in first generation plantations (Deacon et al., 1983).

Macromycetes (Macrofungi): those fungi forming reproductive organs (sporocarps or carpophores), which are individually visible to the naked eye, that is larger than about 1 mm (Arnolds, 1981). In practice, almost all Basidiomycetes, many Ascomycetes (Pezizales, Tuberales, some Sphaeriales, some Helotiales) and a few Deuteromycetes are included in the Macromycetes.

Mycocoenology: study of fungal communities.

Mycocoenon: abstraction of a set of similar (or strongly related) mycocoenoses (after Arnolds, 1981).

Mycocoenosis: the concrete stand of (Macro-) fungi in a given area (Arnolds, 1981).

Open plots: plots situated in an open landscape.

Parasitic: feeding on living tissues, without causing its immediate death.

Phanerogams: plants with obvious flowers.

Phytocoenon: abstraction of a set of similar (or strongly related) phytocoenoses (after Arnolds, 1981).

Phytocoenosis: Plant community. Spatially delimited group of plants which influence each other, that is in a certain equilibrial state and that lives in a more or less homogeneous habitat (after Westhoff & den Held, 1969).

Sapromycocoenon: abstraction of a set of similar (or strongly related) sapromycocoenoses (after Arnolds, 1981).

Sapromycocoenosis: the concrete stand of ectomycorrhizal (Macro-) fungi in a given area (analogous to mycocoenosis; Arnolds, 1981). Preliminary term, only used in chapter 4).

Saprotrophic: feeding on dead organic material.

Semiruderal: a vegetation with a high productivity often on disturbed sites.

Shady plots: plots that are situated inside forests.

Succession: the non-seasonal, directional and continuous pattern of colonization and extinction on a site by species populations (Begon et al., 1986).

Curriculum vitae

Peter-Jan Keizer werd geboren op 4 maart 1957 te Veldhoven. Aan het Nieuwe Lyceum te Bilthoven werd het diploma V.W.O.-B gehaald. Het lidmaatschap van de Nederlandse Jeugdbond voor Natuurstudie heeft de belangstelling voor de veldbiologie zeer gestimuleerd. In 1976 begon hij aan de Rijksuniversiteit Utrecht met de studie Biologie B1*, algemene Biologie met specialisatierichting oecologie. Tijdens de doctoraalfase werden de volgende doctoraalonderwerpen gevolgd: botanische oecologie, vegetatiekunde, ethologie, didactiek van de Biologie. Gedurende die tijd verrichtte hij onderzoek aan de reproductie-oecologie van kortlevende planten in relatie tot de moslaag in een kalkgrasland; mycocoenologie en taxonomie van houtbewonende Aphyllophorales (fungi) in moerasbossen in Drente; het effect van de Vos op het broedsucces van de Wulp. Diverse cursussen aan de universiteit werden geassisteerd en mede opgezet. In 1985 studeerde hij af (cum laude). Vervangende militaire dienst werd uitgevoerd bij het (toenmalige) Rijksinstituut voor Natuurbeheer met als taken: het verzamelen en interpreteren van oude mycologische gegevens, het vervolgen van populaties van de Cantharel in geselecteerde proefvlakken, het uitvoeren en vervolgen van beheersexperimenten in bossen, vegetatiekundige opnamen maken ten behoeve van de zg. Bosstatistiek. Van 1986 tot 1990 werd aan de toenmalige Landbouwhogeschool, later Landbouwuniversiteit, Wageningen het onderzoek uitgevoerd dat tot dit proefschrift heeft geleid. Het onderzoek vond plaats in het Biologisch Station te Wijster (Dr.). In 1991 heeft hij vegetatiekundig onderzoek uitgevoerd in opdracht van de provincie Gelderland. Vanaf 1993 is hij medewerker bij Rijkswaterstaat t.b.v het opstellen van Milieu Effect Rapporten voor voorgenomen rivierdijkverzwaringen.

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Cover: *Phellodon confluens*, in the Netherlands a rare species of nutrient-poor roadside verges.


GEDRUKT OP 100% CHLOORVRIJ GEBLEEKTE CELLULOSE CERTIFICAAT