European Forest Reserves

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Preface

Introduction

From 6 - 8 May 1992 the European Forest Reserves Workshop took place in Wageningen, The Netherlands. This workshop was organized by the Institute for Forestry and Nature Research, cooperating with the National Reference Centre for Nature, Forests and Landscape.

The Institute for Forestry and Nature Research (IBN-DLO) is one of the research institutes under the aegis of the Agricultural Research Service (DLO) within the Dutch Ministry of Agriculture, Nature Management and Fisheries. The National Reference Centre for Nature, Forests and Landscape (IKC-NBLF) is part of the Department for Nature, Forest, Landscape and Wildlife (NBLF) of the same Ministry. Both organizations are involved in the forest reserves programme in The Netherlands. The National Reference Centre is responsible for the selection and monitoring of the forest reserves, whereas the Institute for Forestry and Nature Research is responsible for coordinating the research in forest reserves and for analysing the data gathered.

Forest reserves

Since the beginning of this century forest reserves have been established in many European countries, frequently with formal and legal status. In most cases they are strict reserves, used for the study of natural (spontaneous) processes in forest ecosystems. The earliest permanent plot in a forest reserve was established in 1847 in Bohemia. The scientific significance of reserves increases with the ageing of the forest systems and the duration of the record from permanent plots and other forms of observation. Their practical significances increase progressively for several reasons:

- Most European forests have been managed for so long that we know little about the incidence of natural processes, such as mortality patterns, growth and regeneration in natural forests;
- Some forest areas are being abandoned to nature or less intensively managed, but the direction and character of future succession in the different compartments (tree layer, herb layer, forest floor etc.) is unknown;
- Most European forests are subjected to environmental stresses. Because benchmarks for monitoring the long-term effects at ecosystem level of environmental change are lacking, conclusions on effective forest management can not be drawn;
- Control sites for measuring the effects of management, both in managed forests and other land uses, are being promoted in many countries; forest reserves constitute experimental plots for zero management and provide information on measures that may enhance the quality of nature in forests;
- Secondary succession on former farmland which is deliberately afforested for commercial reasons or where trees establish themselves, is a widespread phenomenon in Europe, but the results of this forest succession are rarely foreseen.

In recent decades many meetings have been held to discuss virgin forests and forest reserves, such as during the XVI IUFRO world congress in Oslo, Norway in 1976, the "Urwald Symposium" of the IUFRO virgin forests group in 1982 in Vienna, Austria and in 1987 in Ort-Gmunden, Germany and the "Naturwaldreservate" symposium organized by the working party of forest reserves in Germany in 1989. One of the results of this latter was a decision to hold a workshop on forest reserves in The Netherlands.

The European Forest Reserves Workshop

The main aims of this European Forest Reserves Workshop were:

1. To review the history of European forest reserves and their aims and applications;

2. To discuss man-induced and environmental impacts on forest reserves;
3. To demonstrate the research methods applied in the Dutch forest reserve programme.

The workshop was attended by 88 participants from 17 countries. It consisted of two days of lectures and poster presentations and one excursion day. The main themes of the lectures were: history, aims and application of European forest reserves, the Dutch forest reserve programme, recent environmental impacts on forests in Europe and cultural impacts on forests.

On the excursion day two Dutch forest reserves were visited: Het Leesten and Vechtlanden. These two reserves represent the extremes of the range of forest reserves in The Netherlands.

Het Leesten is a 19th century afforestation of heathland (45 ha) largely comprising stands of exotic species, especially Douglas-fir. The area was designated as a forest reserve in 1987. The potential vegetation of the site is a Fago-Quercetum petraeae typicum. The soil parent material is loam-poor morainic preglacial material.

Most of the Vechtlanden forest reserve (11 ha) results from spontaneous tree growth on marshland and grassland from the second half of the 19th century on. The floristic composition is characteristic of a Lysimachio-Quercetum and Carici elongatae-Alnetum. The tree layer consists mostly of Quercus robur, Alnus glutinosa and Betula pubescens. The soils are humic gleysols, fimic anthrosols and arenosols.

The need for a European network of forest reserves

A special session was devoted to a discussion of the need for a European network of forest reserves.

Much information has been gathered on the factors that control the development of forest ecosystems. So far, the developments of site factors, floristic composition, vegetation structure, humus forms etc. have been studied in individual countries, using different methods and at different intensities. Some countries have developed an integrated approach to study the various factors. The advent of geographical information systems means that a powerful tool is available, which may be helpful in the spatial analysis and the evaluation of the role of the various factors. However, the methods are not yet comparable and compatible and little information is being exchanged between countries.

From a pragmatic point of view it is very important that the results of such researches are comparable at the international level. At the moment this is problematical, mainly because of a lack of coordination and because of the different methodologies employed. There is no standarization of the methodology concerning the quality and scale of the research programmes of the countries involved. The various reference systems are scattered over various countries. When combined, they may offer more complete series of forest ecosystems, but at the moment it is not clear what kind of reserves exist, where they are and who is studying them. Conclusions on management measures, derived from observations on forest reserves, are not being exchanged.

The participants discussed how the need for standardized concepts and monitoring methods could be achieved. As a result a questionniare was drawn up in order to inventory the existing European forest reserves and permanent plots that are intended for research on forest developments, the methodology applied to study these and the organizations involved.

On the last day the participants agreed on a general statement concerning the need for forest reserves.

Editing was enabled by financial support of the Commission of the European Community, DG XII for Science, Research and Development.

Mirjam Broekmeyer, Willem Vos, Henk Koop
Wageningen, March 1993.

Programme European Forest Reserves Workshop

May 6th, 1992	**European forest reserves: history, aims application and methods.**
	Chairman: Dr. W. Bücking, Forstliche Versuchs- und Forschungsanstalt Baden-Württemberg, Germany
09.00 - 10.00 hr:	Registration and coffee Installation of posters
10.00 - 10.15 hr:	Opening speech Dr. A.M. Van der Zande, Deputy Director of the Department of Nature, Forests, Landscape and Wildlife of the Ministry of Agriculture, Nature Management and Fisheries, The Netherlands
	History, aims and appliciation
10.15 - 11.00 hr:	Prof. dr. D. Mlinšek, University of Ljubljana, Slovenia - Research in virgin forests - for forestry and society in general
11.00 - 11.45 hr:	Dr. G.F. Peterken, Joint Nature Conservation Committee, United Kingdom - long term studies in forest nature reserves
11.45 - 12.30 hr:	Dr. M.T. Sykes and prof. dr. E. Van der Maarel, University of Uppsala, Sweden - Application of forest dynamics research in landscape planning and managment
12.30 - 14.00 hr:	Lunch
	Dutch forest reserves programme
14.00 - 14.45 hr:	Ms. M.E.A. Broekmeyer, Institute for Forestry and Nature Research, The Netherlands - The Dutch forest reserves programme
14.45 - 15.30 hr:	Dr. H.G.J.M. Koop, Institute for Forestry and Nature Research, The Netherlands - Monitoring forest structure and species composition using the SILVI-STAR system
15.30 - 15.45 hr:	Coffee and tea
15.45 - 16.15 hr:	Prof. dr. J. Sevink[1], Mr. R.H. Kemmers[2] and Mr. I. Emmer[1], University of Amsterdam[1] and The Winand Staring Centre[2], The Netherlands - Soil research in Dutch forest reserves
16.15 - 17.00 hr:	Discussion
17.00 - 19.00 hr:	Buffet
19.00 - 21.00 hr:	Poster presentation
20.00 - 22.00 hr:	* Meeting possible participants EC research project, draft for second call for offers AIR programme * Opportunity for IUFRO members to meet
May 7th,	**Excursion to two Dutch forest reserves**
8.00 hr:	Departure IAC Wageningen
9.00 hr:	Arrival forest reserve Het Leesten. Explanation development forest reserve, characteristics forest reserve and demonstration research-methodology.
11.15 hr:	Departure Het Leesten
12.45 hr:	Lunch

14.30 hr:	Arrival forest reserve Vechtlanden. Explanation development forest reserve, characteristics forest reserves and explanation of interpretation of data and application of results of the various researches
16.00 hr:	Departure Vechtlanden
17.30 hr:	Arrival at IAC Wageningen
20.00 hr:	Social evening

May 8th, **Human impact on forest reserves in Europe**

Chairman: Dr. W. Vos, Institute for Forestry and Nature Research, The Netherlands

Recent environmental impacts

09.00 - 09.45 hr:	Mr. G.M. Dirkse, Institute for Forestry and Nature Research, The Netherlands - Recent changes in forest vegetation in NW and Central Europe and some likely causes
09.45 - 10.30 hr:	Ir. W.P.J. Zeeman, State Forest Service, The Netherlands - Water managment as a factor in forest development
10.30 - 11.00 hr:	Coffee and tea
11.00 - 11.45 hr:	Dr. B. van Geel, University of Amsterdam, The Netherlands - Impact of climate history and expected man-induced climatic changes on forest development

Cultural impacts

11.45 - 12.30 hr:	Dr. J. Buis, The Netherlands - Cultural inheritance and forest development
12.30 - 14.00 hr:	Lunch
14.00 14.45 hr:	Dr. M. Hermy, Institute for Nature Conservation, Belgium - Effects of site history on forest vegetation development
14.45 15.30 hr:	Prof. dr. H. Ellenberg, Institut für Weltforstwirtschaft und Ökologie, Germany - Large herbivores as factors in forest succession in Central Europe
15.30 - 16.15 hr:	Discussion
16.15 - 16.30 hr:	Conclusions, follow-up of this meeting

Opening speech

A.M. van der Zande

Deputy Director of the Department of Nature, Forests, Landscape and Wildlife of the Ministry of Agriculture, Nature Management and Fisheries, The Netherlands

Ladies and gentlemen,

On behalf of the Dutch Minister of Agriculture, Nature Management and Fisheries, it is a great pleasure for me to welcome you, the participants in the European Forest Reserves Workshop.

The aim of this workshop is to exchange experience on forest reserves in different parts of Europe and to examine the desirability of harmonizing forest monitoring systems in various countries.

The theme of the workshop is not only of scientific importance. It is especially important for society as a whole and it is very topical. Awareness of the importance of forests and their ecological functions has grown considerably in the last ten years. Forest must be considered as a vital precondition for the future of mankind.

Over most of Europe forest is the natural vegetation cover. We in Europe have succeeded in almost completely destroying this natural cover. It is only during the last 100 to 150 years that Europeans have been able to reverse this deforestation into a gradual expansion of the forest area. This positive development will and should continue in the coming decades and at an accelerating pace. The need for forests and their multipurpose benefits is growing. A recent development in this respect involves exploiting the potential of forests to sequester large amounts of carbon for a reasonable price. This is very important in the policy to slow down global warming.

Agricultural developments in the world and in Europe will inevitably lead to a strong reduction in the land area used for agricultural production. Forests will certainly be one of the main alternative uses for this land. With respect to this we believe that the proposals from the European Commission, the so-called MacSharry proposals to stimulate the afforestation of agricultural lands, should be supported.

Efforts to unite common forestry activities into a real common forestry policy deserve our full support. They are a necessary and logical step towards meeting needs and exploiting opportunities at European Community level.

The proposals of the European Commission expected later this year will prove whether the 12 EC countries are aware of this challenge and their responsibilities regarding forests.

Ladies and gentlemen, at global level too, forest and its ecological function merits increasing attention.

The problems of safeguarding parts of the tropical rainforests - the richest ecosystems on earth - are well known and have also penetrated through to discussions at the highest political level. Neverthless, little progress in the conservation and sustainable development of these rainforests can be reported.

Forest conservation and sustainable development is a theme which will play an important role in the United Nations conference on environment and development this summer in Rio de Janeiro. We fervently hope that the nations of the world will take the steps necessary to agree on a legally binding global forest convention. A necessary consensus on this forest convention can only be achieved if all the nations of the world join together and also do what has to be done in their own countries.

Let us not forget that hardly any natural forest remains in Europe and that in most cases we do not even know how to restore the original forest vegetations or what kind of processes dominated these ecosystems. These are precisely the aims of the Dutch forest reserves programme. Later today some experts will give you more details about the Dutch programme. Ultimately, all the different forest types in The Netherlands will be covered by the programme - tomorrow you will be able to visit some forest reserves. The experiences of several other European countries in natural processes in forests will also be presented.

Forest reserves play an important role in Dutch forest policy. The Dutch government's policies aim at the preservation of the current forest area, at the expansion of the forest area, especially near urban centres, at the optimal fulfillment of various functions and at forests functioning at an acceptable cost.

The main functions of the Dutch forests are defined in recreation, nature, timber production, landscape and environment. 82 % of the forests will be managed for various objectives and the remaining 18 % will have nature conservation as their main function.

Ladies and gentlemen, Dutch forest policy was defined in 1986 and ratified by Parliament in 1987. Now, in 1992 we have evaluated the progress made in this policy. Although the results of this evaluation have not yet been published, one thing is already very clear: developments within the forests and forestry sector, but also outside this sector, make it necessary for us to redefine and adjust our policy. A redefinition towards achieving a more substantial role for forests in land use in The Netherlands and towards a more ecological way of forest management.

Ladies and gentlemen, in my speech I have tried to sketch the national and international context in which your workshop can be seen. For me, the importance of this workshop is therefore extremely clear. On behalf of the organizers of this workshop I would like to wish you all a successful workshop. I sincerely hope this workshop will be fruitful and may even be the beginning of a well organized European network of forest reserves.

With this wish I declare this meeting opened.

Chapter 1

The significance of forest reserves

Białowieza - a forest landscape

The Białowieza National Park (Poland) has an area of 5000 ha and lies within 125 000 ha of silviculturally managed forest. Both the park and the surrounding forest landscape consist of a complete complex of all forest communities, enabling megafauna to migrate freely between the various communities. However, in the age-old hunting area of kings and tsars, the megafauna has been strongly manipulated. The European bison, which had died out, was reintroduced in the First World War. Supplementary feeding, hunting and silvicultural management outside the central national park greatly influence the density of the megafauna.

The lynx and the wolf had almost died out, but a recent ban on hunting them has allowed their numbers to increase again. Until the First World War the population densities of European bison, red deer, roe deer and wild boar were unnaturally high, to accommodate hunting. The result of the extremely high densities was a shift in the composition of tree species. The rejuvenation of hornbeam, small-leaved lime and ash regressed, while the more browse-resistant spruce benefited. This, in combination with anthropogenic fires, and earlier grazing by livestock from the villages, means that one can no longer speak of primaeval forest.

Forest reserves in Europe: a review

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Summary

Forests play an important role in Europe's cultural and natural; heritage. Forests have major functions for wood production, recreation, hunting, protection and conservation. The total forest area of Europe diminished gradually the last centuries. Also the original forest composition has been transformed. As a result most virgin forests disappeared.

This lead to the establishment of strict nature reserves in forested areas for conservation and lateron also for the study of natural forest ecosystems. These socalled forest reserved have been established in almost all European countries. Part of them is subjected to long-term monitoring programmes, funded by national authorities. At a European level the significance of forest reserve research increases.

Keywords: forest reserve, long-term monitoring, forestry research, forest ecology

Introduction

At present, approximately one-third of the land area of Europe is covered with forests (about 160 million ha). This represents 8% of the world's total area of temperate forests. (Figure 1 shows the main coherent forest units). Virtually all these forests are secondary. Remnants of virgin forests tend to be concentrated in regions that are less suited for agriculture or other intensive land uses, and that are therefore sparsely populated (e.g. Scandinavia, mountain areas like the Alps, the Balkan and Tatra zone, zones around the Mediterranean that are not easily accessible). Countries with extensive areas like these also have the greatest percentage of forest coverage (e.g. Finland 60%, Sweden 54%, Austria 45%, Greece 45%, former Czechoslovakia 35%; see Table 1 and Figure 1), although hardly any has escaped some felling in the past. The countries of north-west Europe have only a low percentage of forest cover (e.g. Ireland 5%, United Kingdom 8%, The Netherlands 9%, Denmark 12%, apart from Iceland 1%); the forests are mostly dispersed over the country in small discontinuous units, and are not virgin. It is estimated that only about 1% are native forest areas or forests untouched for the last 200 years or more (Dudley, 1992; Figure 2).

Most virgin forests disappeared over the centuries as a result of land reclamation and intensive forest management practices (e.g. coppicing and pollarding, plantation of exotic tree species, forest grazing, removal of leaf litter). The total forest area diminished gradually and the original forest composition (trees as well as plant and animal species) has been transformed. Since the last decades of the 19th century the forested area in some parts of Europe has been gradually recovering, however. Initially this was mainly because plantations were established for timber production and later also for chips and pulp. Only a few per cent of the present European forest area may be described as unproductive forest, and these are usually inaccessible sites which cannot be economically exploited (Mayer, 1984). In recent years, however, large-scale land abandonment has caused the spontaneous development of secondary forests all over Europe, especially in hilly and mountainous areas. At this moment less than half of the original forested area of Europe is covered with secondary forest (Dudley, 1992). Consequently, a large part of the European forests

Table 1. Review of the state of forest reserves in Europe.

Country	forested area (ha) 1000	% closed forest	number of forest reserves#	forest nature conservation area (ha)*1000	area of forest reserves (ha)	average size of forest reserves (ha)	% of f.r. of total forest area
Albania	1242	32	492 (?)		120380	4-1750	10
Austria	3754	45	74 (62)		2390	32	<1%
Belgium	760	19		100			
Flanders		6 (5)			360	60	<1%
Bulgaria	3800	34		30			
Cyprus	173	19		5			
Czechoslovakia	4578	35					2%
Czech			214 (214)	25	25030	117	
Slovakia			74 (70)	67	70000	950	
Denmark	484	12	25 (10)	56	250	10	<1%
France	15075	25	22 (8)	95	1501	50-200	<1%
Finland	23225	60		1040			
Germany	10632	27	564 (564)	118	16443	31	15%
Greece	5754	45	11 (?)	660	65800	6000	1%
Hungary	1649	17	2 (2)	120	80	40	<1%
Iceland	100	1		2			
Ireland	380	5					
Italy	8063	21	100 (80)		5000	50	<1%
Luxembourg	82	32		23			
Norway	8701	28		110			
The Netherlands	355	9	27 (27)	40	828	31	<1%
Poland	8726	26	40 (?)	103	58837	50-8200	<1%
Portugal	2976	35					
Romania	6340	26	40 (40)		20000	500	<1%
Spain	12511	25		60			
Sweden	27842	54	18 (18)	200	?	?	
Switzerland	1124	28					
Ukraine	?	?	212 (65)		386696	600-16000	
United Kingdom	2178	8		52			
England			20 (20)				<1%
Scotland			10 (10)				
Wales			20 (14)		905	65	
former Yugoslavia	10500	36		560			4,5%
Croatia			250 (120)		447114	1800	
Slovenia			167 (21)		9040	55	

- Countries that returned the questionnaire are printed in bold type. Other data are based on Dudley, 1992 and UNECE/FAO, 1985.
- # in brackets, the number of strict forest reserves (used for research).

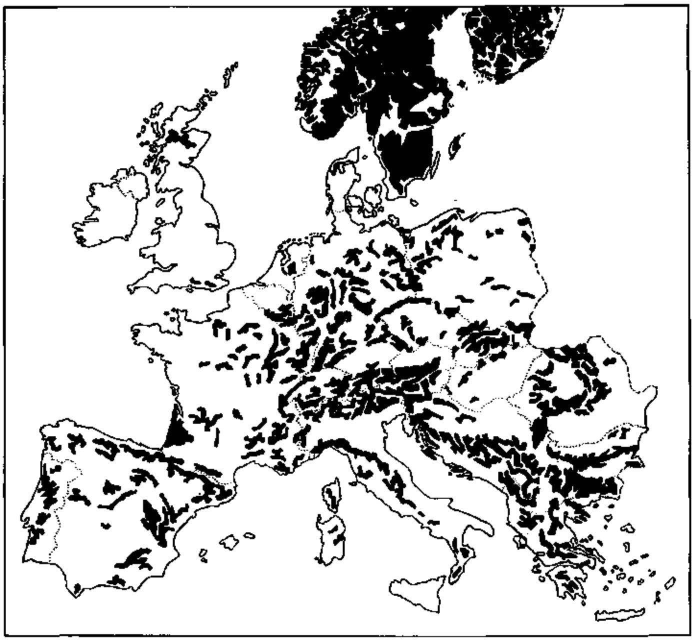


Figure 1. Main coherent forest units in Europe.

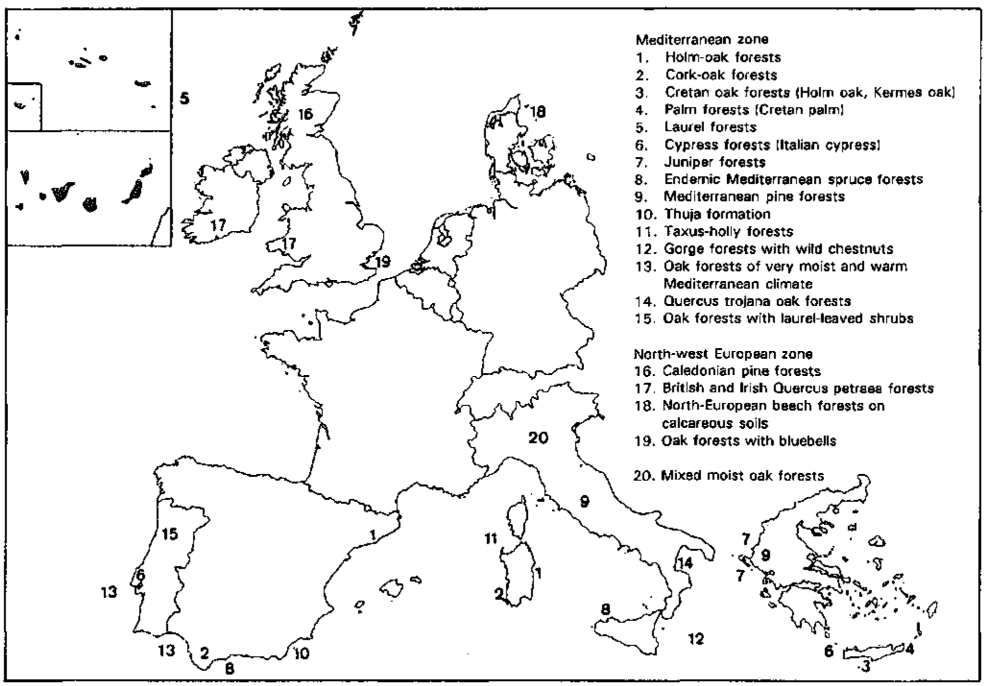


Figure 2. Main fragments of virgin forest types of the EC countries (less than 1% of the total forest area).

is relatively young and in most cases structurally homogeneous and poor in plant species composition.

Table 2 reviews the frequencies of forest functions in different European countries. Wood production is obviously the main function, except for some southern European countries where wood production is often limited due to lack of moisture and unfavourable rainfall distribution. To be effective, nature conservation requires the existence of formal regulations. Conservation is attracting interest internationally, nationally and regionally (UNECE/FAO, 1985).

Meanwhile the demand for forestry products is still present or is even growing, resulting in a net production deficiency of about 60% for the countries of the European Community (Gathy, 1990). One might expect that these market conditions would be very favourable for European forestry. But in many cases the costs are so high that products are being imported from outside the European Community (the tropics, Scandinavia, Canada, Eastern Europe). And the paper industry now often prefers recycled paper rather than pulp. In response, forest management is being extensified and forest sites are being abandoned. Together, these processes promote spontaneous forest development and also more nature-based, low-input forest management practices in Western Europe.

Table 2. Tentative frequencies of forest functions in different European countries. Figures refer to forest areas (not always closed forests) with high or medium importance of the respective functions. Data based on UNECE/FAO, 1985.

Country	Functions (%)						% of total forest area reported on (ha x 1000)
	Wood production	Recreation	Hunting	Protection	Conservation	Range	
Austria	74	?	100	?	?	9	84%
Belgium	100	10	94	0	59	12	100%
Bulgaria	65	94	96	100	17	50	100%
Cyprus	63	37	63	97	13	6	100%
Czech Republic	95	61	68	26	35	?	100%
Denmark	83	69	52	85	72	0	85%
Finland	86	56	69	12	4	31	91%
France	82	87	94	35	84	4	92%
Germany*	92	20	?	68	28	0	100%
Greece	46	3	91	93	15	66	100%
Hongary	88	82	91	76	13	?	100%
Ireland	100	1	0	0	0	0	100%
The Netherlands	83	100	65	7	13	0	56%
Norway	75	100	100	100	100	?	100%
Poland	95	58	97	16	2	0	100%
Slovakia	90	82	80	93	45	?	87%
Spain	38	9	77	74	1	9	100%
Sweden	89	71	99	8	5	11	100%
Turkey	33	1	5	66	13	10	88%
Yugoslavia (former)	89	77	95	56	33	23	100%

* Former BRD only.

Growing pragmatic and scientific interest in forests has gone hand in hand with forest plantation since the second half of last century and, since about 1970, with awareness of environmental problems . Various forest functions that were severely threatened, such as water quality control, protection against soil erosion, buffering of climate extremes and deposition of pollutants, supply of animal habitats, gene pool, etc., have been re-evaluated. The significance of forests for society and the environment has become a popular international political issue, as demonstrated on numerous occasions (e.g. the first ministerial conference on the protection of forests in Europe (Strasbourg, 1990); the intergovernmental conferences on the environment of the Council of

Table 3. Labour input in different forest research themes in European countries in 1991 (original data after Pardos (ed. in prep.), supplied by country delegates of the COST Technical Committee on Forestry and Forestry Products). Figures rounded at 1.0.

Countries	Research themes				
	Forest system		Threats		
	Ecosystem, nature conservation	Site, hydrology	Pathology & pests	Environmental problems	Fires, fire control
Austria	12	48	26	35	-
Belgium	1	11	1	3	-
Denmark	1	1	-	21	-
Finland	21	70	55	77	-
France	20	171	40	6	7
Germany	15	20	51	32	-
Ireland	4	11	6	6	-
Italy	14	7	17	6	7
Luxembourg	-	-	-	-	-
The Netherlands	17	26	6	16	-
Norway	1	4	3	9	-
Portugal	13	25	11	5	11
Spain	40	39	8	8	9
Sweden	24	31	21	27	4
Switserland	4	13	7	36	-
UK	-	54	55	36	-
(former) Yugoslavia	56	21	19	55	1
	243	552	326	377	39

Research themes						
Planning and management				Auxiliary means		
Countries	Silviculture, forest operations, forest products	Wildlife & game management	Landuse planning, economy	Biotechnology, physiology, propagation, breeding	Data-based modelling	Research management
Austria	61	9	20	35	44	2
Belgium	23	2	6	11	7	-
Denmark	21	1	18	16	2	2
Finland	240	12	78	105	79	7
France	134	16	12	122	55	5
Germany	73	12	50	50	38	12
Ireland	9	-	-	13	2	-
Italy	54	1	3	29	6	-
Luxembourg	-	-	1	-	1	-
The Netherlands	62	5	15	18	6	1
Norway	12	1	3	2	5	-
Portugal	54	1	9	33	18	2
Spain	60	-	34	63	15	-
Sweden	134	45	59	146	22	14
Switserland	8	9	-	7	2	-
UK	111	18	23	129	16	-
(former) Yugoslavia	78	4	57	64	7	-
1134		134	388	843	325	45

Europe (e.g. 1992); the European Community Conference in Maastricht (1991); the UN conferences on the environment in Stockholm (1972) and Rio de Janeiro (1992)). An indirect result has been that in many European countries it has been recommended that:

(1) remnants of virgin forests or semi-natural, old-growth forests be conserved;

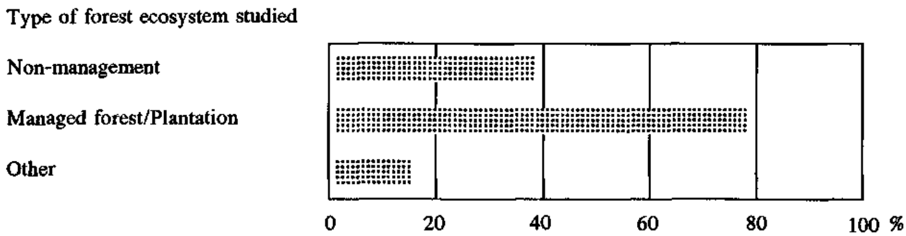
(2) natural forest development be studied in depth, and the results used in more natural and effective forest management (the New Forestry Principles).

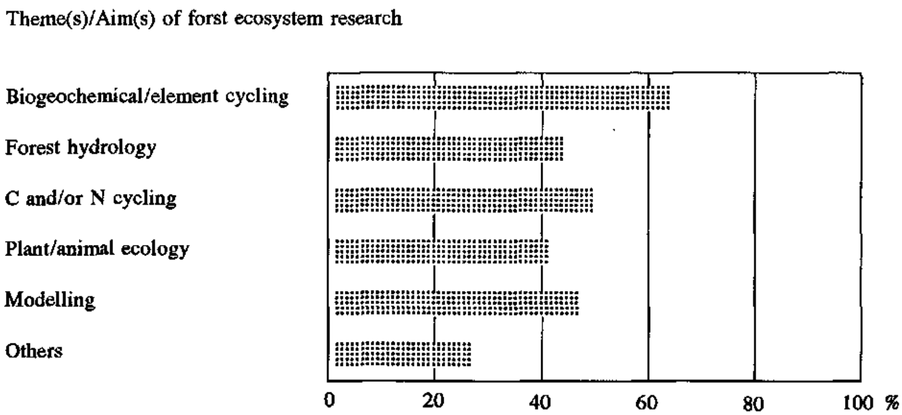
The latter was also promoted by the market-controlled need to extensify forest management practices in order to reduce costs.

At the moment in almost all European countries a considerable share of total forestry research input is in the study of forest ecosystems (Table 3 and 4). Most of it, however, is research on sites, site factors and their management (e.g. soil improvement, watershed management, erosion control).

Table 3 shows that still only about 5-6% of total labour input is concerned with structure, dynamics and performance of ecosystems and with nature conservation and management of protected areas. As results from a questionnaire distributed in preparation for the second Ministerial Conference on the Protection of Forests in Europe (June 1993 in Helsinki) show, most work on forest ecosystems is done on biogeochemical cycling and on the linkage of forest response to environmental factors. A minor part is done on non-managed forest ecosystems, and on forest plant/animal ecology (Sienkiewicz and Starr, 1992).

Table 4. Involvement in forest ecosystem research in certain European countries (data from Sienkiewicz and Starr, 1992).





In many European countries strict nature reserves have been established for proper conservation of forests of great natural value. The earliest reserves comprise virgin forests or old-growth forests, like the Zofinsky forest (97 ha) in former Czechoslovakia, which was established back in 1838, or the Fontainebleau forest in France, which has been a nature reserve since 1854. The significance of such forests for the study of natural forest ecosystems soon became apparent. As far back as 1847 a study plot was established in the virgin forest of Kubany in Bohemia, making it the oldest forest research plot in Europe. It has been protected as a strict forest reserve since 1858 (Leibundgut, 1982). Later, specific forest reserves with the main aim of research and/or monitoring of spontaneous processes were also established. Secondary forests and even planted stands were also included.

The European Forest Reserves Workshop which focused on the research in forest reserves sent out a questionnaire to obtain an overview of existing European forest reserves (including different kinds of permanent plots with the formal status of sites preserved for forest ecosystem research). The questionnaire also inquired about research methods and techniques used by the organizations involved, and about their research programmes. Twenty-three European countries were approached, 18 of whom responded. The results only partially deal with the new political realities of former Yugoslavia and Czechoslovakia.

The degree of detail and the character of the information supplied differ greatly. This is not surprising, as so do the interpretations of the forest reserve concept, the aims, number and formal status of the reserves in the various countries, the progress in establishment, the labour input, etc. Not all countries have developed a well defined research programme yet, although according to the respondents they all intend to. Consequently, the task of summarizing the results was sometimes very difficult. We nevertheless believe that the information received should be published as completely as possible.

These results will be used to prepare a second, more extended survey in the near future. This time, countries not approached in the first round (Bulgaria, Finland, Iceland, Norway and Turkey) for lack of time and of the appropriate contacts, will be involved.

Definition of forest reserves

The term "forest reserve" is a confusing one. There is no international agreement about the requirements that should be met in order to call a forest area "forest reserve". Countries use different classifications with relation to aim, management and forest type: conservation versus research, management versus non-management and virgin forests reserves versus secondary and even man-made forest reserves. At the same time in many countries with no official forest reserve programme there are well protected forest areas, where the spontaneous forest development is monitored. All these areas have been treated as forest reserves in a strict sense (see also Figure 3).

The following definition of forest reserves was given in the questionnaire: "Forest reserves are all non-intervention forests, being all sites where positively has been decided not to manage or exploit the forest and where this decision has resulted in some legal status of the reserve."

Within this definition two main conditions are unifying concepts:

(1) the status of strict forest area without any direct human influence;

(2) the status of a well protected area in order to safeguard its existence as a strict forest reserve in the long term.

Although this definition can be broadly interpreted, the questionnaire focused on strict forest reserves e.g. those used for scientific research. Therefore in this document the term "strict forest reserve" will be used for forest areas without human intervention, which are subjected to research but are not necessarily virgin or old-growth forests. Otherwise the term "forest reserve" will be used.

Many forest areas are referred to as forest reserves although they definitely do not fit the definition above, e.g.:

- forest areas that have developed gradually or "accidentally" into some kind of forest reserve, as their location or site quality was not suited for exploitation or production-oriented management;
- woodlands in nature reserves that are not managed because of a lack of money or manpower, as frequently occurs in the United Kingdom;

- forest reserves that function as such, but without a legal status, as for instance some of the forest reserves in Austria;
- forest reserves meant as such, but with a not very strict interpretation of the "non-intervention" criterion, such as in those cases where it is permitted to remove "dangerous" trees or trees that have fallen on forest roads, or to take fire-control measures, or to hunt or allow recreation;
- strict nature reserves consisting of forest.

The main aim of nature reserves is conservation of nature, but forest reserves clearly have a broader view: one of their main aims is forest research (Leibundgut, 1966). In line with this, Mayer (1976) defined rules for the establishment of forest reserves ("Waldreservate") and stated the following three general aims:
(1) Nature conservation, e.g. conservation of natural forest stands because of cultural heritage and for ethical reasons (conservation for future generations).
(2) Preservation of the ecological/biological basis, to protect the main natural forest communities, especially because of the function of rare forest communities as refuges for plant species, as natural habitats for forest animals, and because of the need to maintain areas for regeneration.
(3) Functioning as outdoor (nature) laboratories, intended for scientific research on the entire forest ecosystem, in order to provide basic knowledge for optimal silviculture.

Purpose of forest reserves

Two main aims of forest reserves have been mentioned above: science and conservation. These two are often additional, see Table 5. The general trend is well reflected by the following definition:
"Forest reserves are those areas of a forest which by the composition of their tree species and the stand structure represent the original state of the vegetation particularly well or which are likely to fulfil these conditions in the foreseeable future and where changes of any kind have to be prevented in principle. Forest reserves serve for forest research, which deduces the composition and development of forests untouched by man as guidelines for natural silviculture. They are also of use for other branches of scientific field observation. As complete forest ecosystems they are of great value to the task of nature protection. They also serve as subjects for instruction and observation." (Zukrigl, 1990a).

Scientific aim

The research programmes in forest reserves of the European countries have one or more of the following scientific aims:
- the study of time series of spontaneous processes, forest structure and plant and animal species composition in natural "outdoor laboratories";
- the study of effects of forest management compared with non-management;
- integrated ecological research (bio-monitoring) in reference areas of non-intervention compared with other, more strongly influenced forest and non-forest ecosystems;
- the monitoring of environmental impacts (air pollution, global climate change) and the effects of policy-making on these.

This scientific function of forest reserves is very important. If we know more about the spontaneous changes of forests, we will have a more realistic view of the degree of flexibility in forest management. Furthermore, if we know how managed forests differ from natural forests, we will at least have a better appreciation of the benefits and disadvantages of management.

This knowledge is not yet fully available, as most forests have been used intensively or have even been created by man, implying major impacts on the functioning of the forest ecosystem.

Table 5. Status and main aim of forest reserves.

main aim \ status	governmental research	non-governmental research
scientific	*Croatia* *Germany* *Flanders-Belgium* *Hungary* *The Netherlands* *Slovenia* Sweden	*Austria* France*
conservation	*Czech* Poland*	Italy*
both	Albania* *Denmark* *Greece* *Romania* *Slovakia* *Ukraine*	United Kingdom

* The respondents from these countries mentioned several programmes, some of which are forest reserves in a strict sense.

Countries which do have a national forest reserves research programme, are given in italics.

Only recently has western society become aware that forests not only fulfil multiple economic functions, but may have all kinus of other functions too: scientific and historical information, gene pool, amenity, water supply, climate regulation, etc. (Vyskot, 1981; Council of Europe, 1989). There is growing interest in silviculture that is closer to nature and better adapted to the natural conditions of the site and the natural succession of the forest. This is shown for instance by the European PRO SILVA movement. Therefore, the spontaneous development of forests must be be known. This is best achieved by studying unmanaged and undisturbed forest ecosystems. The development differs on different sites and in different forest types. This is why a broad spectrum of forest reserves is needed (Zukrigl, 1990b).

The reserves offer the obvious advantage of a closed forest compartment, where undisturbed long-term research is guaranteed. The research may be limited "forestry research", broader "multidisciplinary research", pure field description, laboratory and modelling research, mapping, syntaxonomic/taxonomic or process-oriented research.

Most countries mention strict forestry research as well as multidisciplinary research. The multidisciplinary research contains the study of vegetation succession, including inventories of cryptogams, mosses, mycorrhiza etc., faunal succession (inventories or studies of the population dynamics of breeding birds, mammals or soil organisms) and the study of the forest site e.g. humus forms, soil development, hydrology etc. The study of these factors, besides the research on stand structure and forest dynamics, leads to a multidisciplinary approach to the forest ecosystem. These supplementary studies are known to be very valuable compared with separate studies of the various factors. Forest reserves are especially suited for studies of the relation between forest stand, vegetation and site.

Even if the main aim is forestry research (the reserves should aim to have "natural" silviculture), multidisciplinary research techniques are mostly used (e.g. in the Netherlands and Slovenia).

[Certain foresters are not enthusiastic about forest reserves; they fear the decline of the economic base of forestry. Apart from the fact that the economic base is in many cases weak anyhow, long established strict forest reserves show that e.g. fears of non-managed forests harbouring insect pests and diseases are unfounded, as in later stages of succession the natural predators and parasites are present in the system too. Therefore, dead wood in the forest is no threat, but merely an extra stabilizing mechanism, as it helps e.g. in buffering acidification and in ensuring a steady supply of nutrients. The dynamic equilibrium in these forest stands is a "natural guarantee", although the general public may need additional information on the goals and benefits of these forest, as they are used to managed, "clean" forests (Leibundgut, 1990).]

Conservation aim

Apart from the scientific and forestry purposes of forest reserves, the conservation of particular forest ecosystems may also be important (Table 5). They may serve as:

- areas for the conservation and re-establishment of natural forest communities, including all specific species, and
- biogenetic reserves of indigenous species.

In Germany and in Austria the conservation aim is central, as demonstrated by the name "nature forest reserves". In the forest reserves programmes of e.g. Denmark, Romania and Italy the aim of nature conservation is also mentioned separately. In the United Kingdom all nature forest reserves have been established because of their value for nature conservation.

Even if nature conservation is not especially mentioned (e.g.in the Netherlands and Slovenia), forest reserves will obviously still play a role in nature conservation and the development of nature in the surroundings. In time they will develop into more natural stands or will even approximate virgin forest. Their value will increase with their undisturbed development (Mlinsek, 1976). This is particularly true for forest reserves established in forest areas with the original stand structure and plant composition. Forest reserves in formerly managed forests or forest plantations have a special significance for nature development in the surrounding forest, because of the impact of migrating plant and animal species. Dead wood will be allowed to remain in the forests, new habitats will develop and therefore the reserves will become richer in species, especially those of old-growth forests. At the same time, some species that were favoured by the former management strategy will probably disappear (Peterken, 1988).

Finally, forest reserves may also play a role because of their educational, recreational and aesthetic functions.

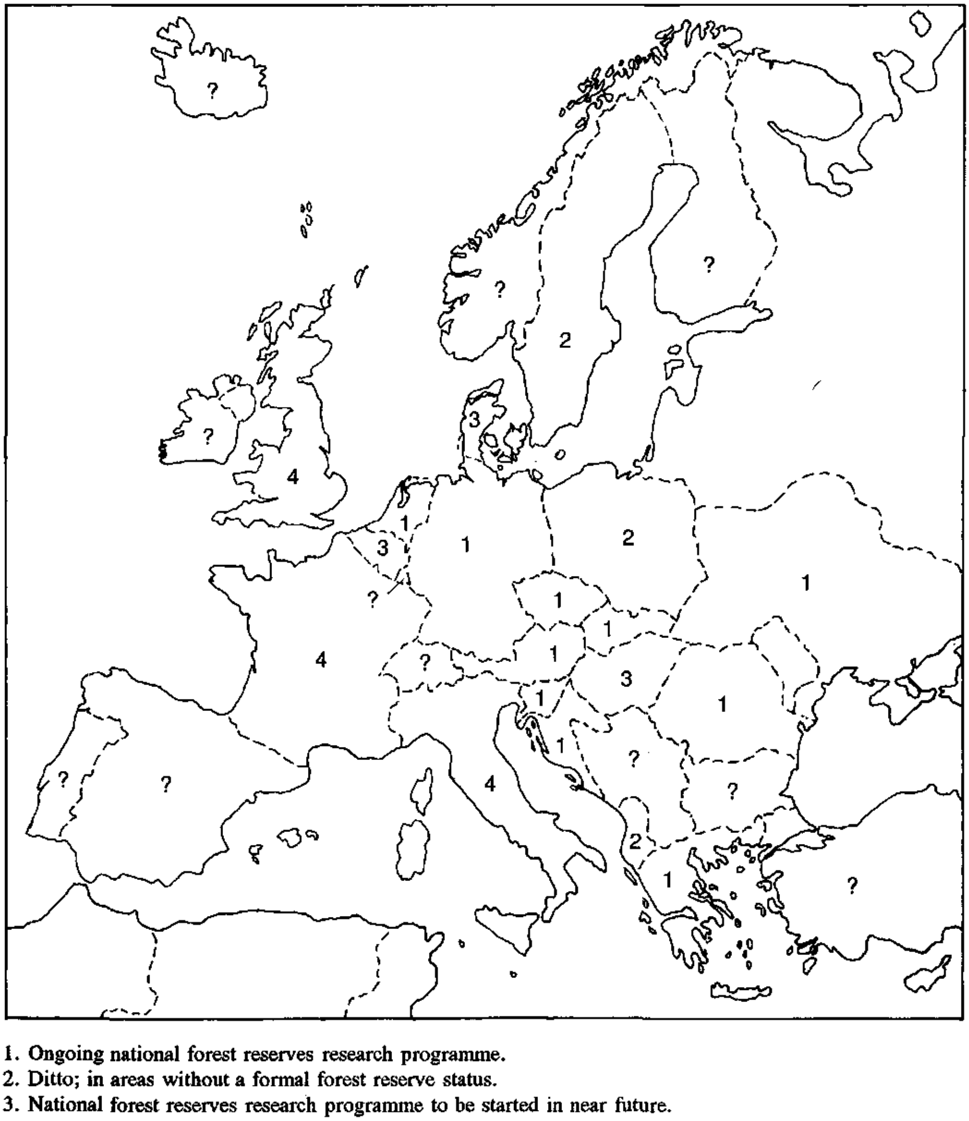
Present situation in Europe

Half the European countries in this review have a national forest reserves programme, funded by national authorities. The definition of these reserves and the intentions of the research programmes may differ greatly (see Table 5, Figure 3) The work may focus primarily on the reserve as an object of study, or on the conservation, or on both. At the same time, however, many countries without an official forest reserves programme do have well protected forest areas where the spontaneous forest development may be monitored. Thus, there too, the main functions of forest reserves are fulfilled, albeit organized less strictly.

In Austria, which has a long tradition in forest conservation and research, forest reserves are not legally protected unless they are established in nature reserves or national parks. The designation and research programme are the responsibility of individual research institutes (Zukrigl, 1990a).

Various types of protected forest areas (e.g. nature reserves and integrated biological reserves and integrated nature reserves and national parks) exist in France and Italy . There is no national coordination of the research, and several institutes may be involved in the designation and the research.

In the United Kingdom the situation is diverse. There are different levels of legal protection, depending on the forest owners. Research is mostly ad hoc.



1. Ongoing national forest reserves research programme.
2. Ditto; in areas without a formal forest reserve status.
3. National forest reserves research programme to be started in near future.
4. Ad hoc research in areas with different status; intention to coordinate research at national level.

?. Not addressed or no response.

Figure 3. State of research in forest reserves of certain European countries.

No official forest reserves exist in Poland, either, but the law on nature conservation provides for national parks, nature reserves and nature monuments. Some of these are managed as strict reserves and some of them (like the Bialowieza national park) are used for scientific research too (Mortier, 1989).

Various programmes exist in Albania, such as the one on establishing protective ecological zones and the programme on genetic improvement of forest trees. There are different categories of forest reserves. It is not clear to what extent the forest reserves really fulfil the criteria of strict forest reserves.

Sweden has many nature reserves; most, of course, are forest reserves. There is a national Swedish environmental monitoring programme within 18 forest reference areas which meet the conditions of strict forest reserves.

In Flanders (Belgium) research is being done in some nature forest reserves earmarked for conservation, on the initiative of one institute . Last year an official programme on forest reserves was started, with research as the main aim.

In Table 5, countries which use the term "forest reserve" for their protected non-intervention forest areas are shown in italics. Here again the reader should be warned about confusion in the terminology, because Flanders (Belgium) and Denmark include some managed forests in their national programmes. Mayer (1976) distinguished nature forest reserves ("Naturwaldreservate") which are strict forest reserves, and managed forest reserves ("Nutzwaldreservate") intended for the maintenance of specific forest communities.

Table 1 gives an overreview of the present state of forest reserves. The total number of forest reserves is somewhat difficult to interpret. Most respondents with an official forest reserve research programme restricted themselves to the strict forest reserves. For example, in The Netherlands and Sweden there are many more protected strict forest areas, mainly nature reserves, which are not listed here because they do not serve any direct scientific goal. On the other hand, Albania has included all protected strict forest areas, including all nature reserves. The fourth column gives the results of a survey on the role of forests in supplying environmental and other non-wood goods and services, carried out in 1981 by the joint FAO-ECE Working Party on forest economics and statistics. Data are given on forest areas intended for nature conservation, e.g. the use or management of an area in order to preserve a representative sample of an ecological community, to re-establish such a community or to protect or restore a site of cultural or historical interest (UNECE/FAO, 1985). Since 1985 the Council of Europe has been preparing a scientific study on the situation of natural woodlands and virgin forests within the Council's member states and Finland. Preliminary results were published in 1987 (Council of Europe, 1987). No detailed data were available for this document.

In the third column, forest reserves subjected to some kind of research are given in brackets. It may be obvious that those strict forest reserves form only part of all the forest reserves mentioned. A few countries, led by Germany, include all their reserves in the research programme.

The average size of a reserve varies greatly. The ranges given refer to the average sizes of various classes of protected forest areas. Also, when one figure is shown, the minimum and maximum size could differ greatly. In the Ukraine some state forest reserves are 16,000 ha. National parks in Poland have an average size of 8,200 ha, Greece has 11 forest reserves of 6000 ha each. Romania and Slovakia also have relatively large protected areas. In most other countries the average size varies between 30 and 60 ha. This size is often mentioned as a minimum area for Fago-Quercetum communities in order to be able to study the spontaneous development of the forest ecosystem representing all stages of development from regeneration until mature trees (Koop, 1981).

The selection of forest reserves

In practice, forest reserves occur in the following distinct forest types:
1. virgin forests and their remnants;
2. semi-natural forests with a long spontaneous development;
3. old-growth or formerly managed forests, mainly with native tree species;
4. secondary growth forests on abandoned farmland;
5. forest plantations, possibly with exotic tree species.

Another forest category which is often mentioned is ancient woodland; these are in fact old-growth forests. In the United Kingdom forested areas which have been continuously wooded since 1600 are referred to as ancient woodland (Peterken, 1987). Walter (1991) distinguishes three types of natural forests: (1) virgin or near-virgin forests, (2) secondary forests (unmanaged for at least for one decade), (3) old-growth open forest areas (forest parks like the New Forest in England or the 'montados' and 'dehesas' in Mediterranean countries). All these forest types are classified here as ancient woodland or old-growth forest. They are characterized e.g. by a large amount of biomass that is well distributed over the mature stand, by large amounts of dead wood, by well-developed forest soils and humus forms, and by a heterogeneous stand structure.

In most national forest reserves programmes it is predetermined which forest types will be selected as forest reserves. Some of the differences between different countries may be illustrated by some diverging definitions of national nature forest reserves and forest reserves:

- "Nature forest reserves are those areas of a forest which by the composition of their tree species and stand structure represent the original state of vegetation particularly well or which are likely to fulfil these conditions in the foreseeable future, and where changes of any kind have to be prevented on principle" (Austria);
- "Forest reserves are parts of forest land or potential forest land, which are systematically left to undisturbed natural development, and they represent a given typical or exceptional forest biotic community with its entire environment" (Slovenia);
- "Nature forest reserves are formerly managed natural forest stands where now and in the near future the undisturbed biological development is guaranteed" (Germany);
- or simply "Forest reserves are selected forest areas" (implying all possible forest types; the Netherlands).

These examples illustrate the wide range of forest types from virgin forest to man-made plantations that may be selected as forest reserves. It makes clear that not only natural forests have to be included. Nevertheless, there is a clear distinction between Central and Eastern European countries, which mainly have forest reserves in the first three categories, and north-western European countries, which also include former forest plantations. The latter will in time develop into stands with characteristics of old-growth forest too. Forest reserves are often seen as the virgin forests of the future, but that future state is not needed at this moment in order to select forest reserves for the study of spontaneous development. On the contrary, as we are facing the transformation of all kinds of production forests and abandoned pastures and fields into near-natural forests, and as nature-based management is an important policy in many countries (from an economic point of view too), it may be wise to monitor these transformations.

Which forest stands will be selected in a particular country depends mainly on the occurrence of various forest types and the main aims of the forest reserves programme. If nature conservation is a main aim, then forests of the first three categories mentioned above will largely be selected. If silviculture is a main aim, then forests with a particular management history will be selected. And if a strict selection system is applied, representative amounts of forest reserves reflecting all main existing forest types will be selected.

The criteria for selecting forest reserves are not sharply defined. However, a generally applied criterion is the forest type, which may be understood to be defined by the dominant tree species and structure. A second important criterion is in the phytosociology, although it may be

Table 6. Criteria used for the selection of forest reserves (18 responses)

CRITERIA	N	
Forest type	13	
Phytosociology/rarity/vulnerability of plant species	7	
Soil type	5	
Virgin/semi-natural	2	
Productivity	2	
Other criteria	6	

interpreted in different ways (e.g. plant rarity, vulnerability). A third criterion is soil type. Other criteria are not generally applied, as is shown in Table 6.

Some examples of selection criteria applied by different countries are:

- representation of the natural forest plant communities and a geographically balanced distribution of different forest sites (Germany);
- plant-sociological criteria ascertaining a good distribution over all forest plant communities (Slovenia);
- representation of all "ecological provinces", with at least three forest reserves per province (Romania);
- representation of all major forest plant communities (Austria);
- representation of the existing forest areas, based on site conditions, plant species composition and stand history (The Netherlands).

In practice, not every forest area meeting to these criteria is selected, however. Additional selection criteria may be:

- a high degree of naturalness;
- a late stage in the succession;
- a minimum area (ranging from 1 ha to 15 ha);
- guarantees that the forest reserve will be safeguarded in the future;
- as few disturbing influences from the surroundings as possible, recreation included;
- the potential for establishing a buffer zone with a minimum width of twice the tree height.

Countries like Germany and the Netherlands may select non-forest areas too, if these areas have the potential to eventually develop into forest.

Some respondents tried to classify the forest reserves according to the different types of forest. Even if virgin forests are still present, forest reserves of the other categories are also established. It is worth noting that (apart from the Ukraine mentioning 25 reserves in virgin forests, a total of 59,000 ha), seven countries report having forest reserves in virgin forests, with a total area of 58,207 ha; see Table 7.

Table 7. Area of virgin forest reserves (in ha) and the number of reserves.

Country	Area	Number
Albania	7,474	?
Austria	380	7
Croatia	32,424	25
Czech	12,285	105
Greece	800	1
Slovenia	344	12
Slovakia	4,500	20

Coordination of forest reserves programmes

Table 8 indicates the organizations responsible for the establishment of forest reserves. In most countries the Ministry of Agriculture is involved, especially when national forest reserves or other protected areas are concerned. Sometimes this task is in fact executed by a specific institute, as in Croatia and The Netherlands. Other respondents mentioned this institute directly (e.g. Albania, the former Czechoslovakia and Slovenia).

The establishment of forest reserves is still going on in most countries. All countries mention that in the near future more reserves will be established (from one in Greece to 400 more in Romania), dependent on their selection system.

Three countries (Belgian Flanders, Hungary and Denmark) have recently developed a national forest reserves programme, apart from various existing protected forest areas which serve as strict forest reserves (which are listed in Table 1).

In Belgian Flanders the new Forest Act of 1990 provides for forest reserves primarily intended for scientific research. A proposal for the establishment of 30 reserves has been made, but so far no reserves have been established. However, there are a few nature reserves in forested areas which are being subjected to multidisciplinary research (and thus in fact are strict forest reserves; see Figure 3). This is an initiative of one particular institute. In the future the Institute for Forestry and Game Management will probably be in charge of the research.

The same situation is encountered in Hungary and Denmark. Both governments established national forest reserves programmes in 1992. The main aim in Hungary is forestry research; the aims in Denmark are diverse, and include research. Hungary designated two forest reserves in 1989 (before the new Forestry Act), and will establish 15 more in the future. The first two are

Table 8. Tentative overview of the organizations in charge of the establishment of forest reserves and the research programme.

Country	Establishment	Research
Albania	Forest Research Institute of Tirana	Forest and Range Research Institute Tirana#
Austria	Forestry Institute, Vienna	Forestry Institute, Vienna
Belgium	Ministry of the Flemish Community	Institute of Nature Conservation*
Croatia	Ministry of Environment	University of Zagreb#
Czech	Ministry of Environment	several institutes/universities
Denmark	Ministry of Environment	several institutes/universities*
France	several ministries	several institutes/universities
Germany	Forest Administrations Bündeslander	Research Institutes of Forest Administrations#
Greece	Ministry of Agriculture	University of Thessaloniki
Hungary	Ministry of Agriculture	Forest Reserves Foundation*
Italy	several local/national authorities	several institutes/universities
The Netherlands	Min.of Agriculture and Nature Management	Institute for Forestry & Nature Research#
Poland	local/national authorities	several institute/universities
Romenia	Forest Research & Management Institute	Forest Research & Management Institute#
Slovakia	Ministry of Environment	several institutes/universities
Slovenia	Forest Management Slovenia	University of Ljubljana
Sweden	Ministry of Environment	National Environmental Protection Board#
Ukraine	Min.of National Environment Conservation	Institute of Ecology of the Carpathians#
United Kingdom	local/national authorities	several institutes/universities

Institute in charge of the research e.g. the coordinating organization. Several other organizations are also involved in the research.

* In the near future national research programmes will start, implying other coordinating research organizations.

being studied by the Forest Reserves Foundation, a non-government organization; the others will be monitored by the national Forest Research Institute. Denmark has selected 13 areas for designation in the near future. The Danish Center for Forest and Ecosystem Research might be a possible coordinating body in the future.

In Austria too, it is being attempted to stimulate the establishment of a national research centre which will coordinate the research task. The selection and protection of forest reserves should become part of the remit of the Austrian Federal Forest Administration and the term "Naturwaldreservat" should be introduced into forest legislation.

The coordination of the research programme is obviously related to national research programmes. The inventories may be carried out by various institutes, but in most cases are coordinated by one specific organization or institute, as in The Netherlands, Germany and Sweden. Otherwise, various organizations are in charge of the research (Poland, Czech Republic, Slovakia).

In France, Italy and the United Kingdom too, several institutions are involved in the research. It depends on the institute what type of research will be carried out, in which reserves and how frequently. However, all three countries intend to coordinate the research in the near future.

The Ecology Group of the Italian Botany Society is trying to coordinate a standard method for the inventory of permanent plots in Italy.

As a result of the conference on the situation and protection of ancient natural and semi-natural woodlands in Europe (Council of Europe, 1987), France is establishing an integrated research programme beginning with three sites that will be monitored for 30 months. All institutes that are currently individually involved in forest reserves research, will work together in this project. At the same time, France is stimulating the establishment of 15,000 ha integrated forest reserves within five years.

English Nature hopes to improve the coordination of the research in the National Nature Reserves in England. Regrettably, the Nature Conservancy Council, a national organization in charge of the coordination of selecting Nature Reserves, was disbanded in 1992. Therefore at the moment England, Wales and Scotland each have their own responsibility to establish reserves.

Protection of forest reserves

Forest reserves may only develop into natural forests if their undisturbed development is guaranteed for a long time. Furthermore, the long-term research will be optimized if the monitoring is repeated several times, at least for more than 50 years. Therefore, the selected areas must be protected from local environmental impacts, not only now, but also in the future. Any kind of human interference inside or in the proximity of these areas must be avoided by means of legal protection. Local human influences, like recreation, are more difficult to prohibit. And indirect human influences, like air pollution, can never be avoided either (Bernes, 1985).

Due to the objectives pursued, the ownership should be as stable as possible, which means that most forest reserves will be established in state-owned areas.

In practice, legal protection is the only way to guarantee the existence as a strict forest reserve. This is done by most countries with a national forest reserves programme. In other countries, e.g. Austria, forest reserves are not legally protected, although they may be well known to the public. These reserves may only be safeguarded with existing laws (e.g. for town and country planning or nature conservation), by locating the forest reserves in nature reserves, national parks, national landscapes, genetic reserves, etc. Forest reserves outside these areas may be protected by local regulations only, which may change from one day to the next. In Sweden and Italy, forest areas meeting the conditions of forest reserves may be protected only if they are located in national parks or nature reserves.

Other countries do have various categories of legally protected forested areas; e.g. Albania has "protective ecological zones", France has "integrated biological reserves", England has "sites of special scientific interest" and the Czech Republic has "territorial systems of ecological stability".

Research in forest reserves

Specific research programmes have been established for the study of the undisturbed, spontaneous forest development. Not all forest reserves or comparable forest areas, however, are used for research, as Table 1 shows. All programmes, except for those from Greece and Italy, focus on long-term research (monitoring programmes). However, in some countries only a basic inventory is carried out in all reserves, and just a few reserves are subject to long-term research, as in the former Czechoslovakia, Germany and Romania. This basic inventory is carried out once only and is intended to describe the state of the forest reserve at the moment of designation. The basic inventory may form the first record of the monitoring programme. It may eventually be extended with the study of forest history, former management measures, climatic, geological and geomorphological conditions, etc..

Long-term research (monitoring) is normally repeated every 5 to 10 years, or whenever manpower is available. This kind of research may be restricted to specific reserves, e.g. monitoring of vegetation in one reserve and monitoring of forest dynamics in another. In countries with a national research programme, the main reason that only a limited number of reserves are studied is lack of finances and manpower, as in the former Czechoslovakia and Slovenia. In other countries (France and Italy) this greatly depends on the involvement of research institutes. In these countries a number of different institutes are involved in the research (see Table 8). In contrast, Germany has developed a widespread network of forest reserves, some of which are studied very intensively.

Table 9 lists the main topics being studied in European forest reserves. Most topics may be studied by simple, non-destructive means in the field. The study of nutrient cycling, ecophysiology, etc. requires measures that may be destructive. This may raise the question of whether reserves should be completely safeguarded or whether this rule should be interpreted more flexibly in order to obtain additional valuable information. Nevertheless, in most programmes these actions are not being carried out (yet), for lack of finances and manpower.

Table 9. Subjects studied in European forest reserves according to 18 respondents.

SUBJECTS	N	
Forest dynamics	18	
Flora inventory	18	
Forest regeneration	17	
Vegetation succession	16	
Fauna inventory	16	
Soil description	11	
Nutrient cycling and energy flow	7	
Forest structure	4	
Eco-physiology	4	
Forest history	2	
Forest hydrology	1	
Forest valuation	1	

Practically all programmes include the study of forest regeneration, forest dynamics, and the state of flora and fauna. Thus, even if the research primarily aims at more natural forestry, multidisciplinary research methods are used. As already stated, it is especially this multidisciplinary approach which makes these programmes so valuable. Ad hoc research should be possible, e.g. after trees have been windthrown, or after fire, in order to be able to study these effects in greater detail than is possible with a monitoring frequency of 5 - 10 years.

Methods

Countries with an official forest reserves programme or comparable programmes do always study standard parameters. Even if different institutions carry out the inventories, the same measurements are taken throughout the programme. Most of the time these measurements correspond with internationally used or widespread standards, like the IUFRO codes for tree vitality, vegetation relevées according to Braun-Blanquet, or soil descriptions according to FAO guidelines.

If several institutes study their "own" specific forest reserves, as in France and Italy, each institute may use its own methods. However, in these cases too it is attempted to standardize the inventories.

Lay-out of forest reserves

Because of the various factors to be studied, in different countries the reserves may be classified according to a specific sampling scheme. Inventories are done in the entire forest reserve, core areas, transects and/or sample plots. These specific research areas/plots are mostly well-defined. The location of the permanent plots is of great importance for the long-term research. Monitoring studies strongly increase in value if the measurements can be done at the same location. The boundaries of the forest reserve itself and of the permanent plots should be marked clearly, both in the field and on maps.

The subdivision of the forest reserve into specific plots allows the parameters to be studied with a different degree of detail. The most intensive studies are restricted to those plots that are thought to be the most characteristic part of the forest reserve concerned. In this way, some research programmes work step-wise. This phased approach may also be practised at the level of all forest reserves together. If it is not possible to study all the reserves, representative reserves are selected for study in greater detail. Other reserves may then be monitored less frequently or less intensively, but in combination with the data gathered in the intensively studied reserves, these measurements may still have great scientific value.

Forest reserves in a European context

Clearly, forest reserves may play an important role in Europe's natural heritage, for the purpose of conservation, science, recreation, education and aesthetics. At a European level their significance increases. This is especially due to the fact that time series and series of different environmental and management conditions will be more complete, offering reference systems that may not be obtained within one single country. And, because forest reserves may form a coherent network of highly developed, natural units within the European Main Ecological Structure. The main arguments for a European network of forest reserves are:

- a high proportion of the ancient woodlands (virgin forests and semi-natural forests) of Europe is threatened by air pollution, intensive commercial exploitation, urbanization, mass tourism or other agents; remnants from different regions may together offer a more complete series to be preserved and to be monitored;
- series of forest ecosystems become more complete, offering reference systems that may not be obtained within one single country;
- ancient woodlands are important constituents of the old cultural landscapes of Europe, completely integrated as they were in traditional rural life; they constitute a natural European heritage with highly valued scientific, educational, cultural, recreational, aesthetic and intrinsic qualities;
- ancient woodlands are gene pools for indigenous flora and fauna;
- given that forests constitute the final stages of ecological succession on most sites, forest reserves may form a valuable coherent network of highly developed, natural units within the European Main Ecological Structure;

- most European forests have been managed by man for so long that we know little about the incidence of natural processes under different conditions, such as mortality patterns, maximum ages, growth and regeneration in natural forests; reserves from different regions offer complementary information in this sense;
- some forest areas have been abandoned or are less intensively managed than before, but the direction and character of future succession in the different compartments (tree layer, herb layer, forest floor, etc.) is difficult to predict - and therefore to handle in planning - as there is a lack of basic knowledge;
- most European forests are subject to environmental stresses, but no benchmarks for monitoring the long-term effects of environmental change at ecosystem level are known, and this hampers effective forest management and conservation measures;
- forest reserves may be used as control sites for measuring the effects of forest management at different levels of "naturalness"; they may also be used for monitoring the effects of environmental policy measures at national and international level;
- strict forest areas constitute experimental plots for zero management and provide information on measures that may enhance the quality of nature in forests;
- secondary succession on former farmland, spontaneously or resulting from afforestation for different reasons (e.g. EC policy, erosion control, ecological planning), is becoming a widespread phenomenon in Europe, but the results of this succession are difficult to predict as there is a lack of basic knowledge;
- coordination and standardization of methods and techniques, as well as the exchange of data may offer numerous benefits from the scientific, practical and financial points of view.

Conclusions

Some European countries have a long tradition in forest reserves research (e.g. the former Czechoslovakia, former Yugoslavia, Austria). In other countries the establishment of national forest reserves programmes has gathered pace during the last decade. The Netherlands, Belgium, Hungary and Denmark have recently developed forest reserves programmes. Other countries are at least trying to standardize their research in forested areas on a national scale (e.g. France, Italy and the United Kingdom).

However, at the moment the results of forest reserves research are in general not comparable at international level. There is no standardization of the aims and methods yet. Conclusions on management and conservation measures derived from observations on forest reserves are not exchanged between countries.

At the same time there is an increasing need for standardized benchmarks and controls, making the effects of forest management and conservation measurable and internationally comparable. Uniformity in methods and techniques and the exchange of results may only be achieved at a supranational level. These are essential conditions for the practice of ecologically accountable and sustainable forest management systems.

This view has been endorsed e.g. by the participants at the European Forest Reserves Workshop in the Netherlands, May 1992 (see the Declaration on Forest Reserves in this volume). Subsequently, delegates of 15 European countries expressed their interests in establishing a European network of forest reserves. The main aims of this cooperation may be the establishment of a network that is protected and reserved for long-term research, the achievement of comparable scientific results, standardized methods and techniques for forest research, and the exchange of data and practical conclusions.

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Forestry and society-oriented research on the history of virgin forests and their future needs

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Summary

Forestry science has to investigate the nature of the forests. Yet it lacks a strong historical basis for this. New trends must be followed in basic forestry research:

- To study 'untouched' nature, in order to learn and to apply research findings - in forestry as well as in general. Forestry science must become an important part of basic sciences.
- To develop a new transfer of knowledge, a new public relations service, based on 'new' knowledge which tells us what forests really are. Forestry has to help build new paradigms.

The major duties and opportunities of forestry research include:

- saving virgin forests;
- establishing new forest reserves and creating an international network of such reserves;
- enhancing research in virgin forests as well as in forest reserves in general;
- organizing comparative research in forest reserves in a combined way, i.e. strengthening interdisciplinary field laboratory research combined with laboratory research;
- translating research findings so that they can be used by foresters and as general guidelines.

This article outlines some proposals based on existing research, experience and practice.

Keywords: virgin forest, forestry research, forest management

Introduction

The local lack of fossil fuel in Europe has changed the face of wooded countries on the Continent. Woods have been felled and although some have been replaced by planted stands, catastrophes have resulted. European forests are still among the most altered forests in the world. They have been fatally degraded, and yet - in spite of everything - are still alive. As a result, people can hardly remember what natural forests really looked like in most parts of the Continent. This accounts for the early interest of European foresters in the surviving, less spoiled or even untouched forests. The disappointing results of monocultures led European foresters to turn away from man-made forests towards natural forests. It is now more than a century ago that the first forest reserves were established in Europe (in Austro-Hungary). Many of these reserves were - of course - originally created for hunting. The first observations in virgin forests of Romania, Bosnia and Bohemia, encouraged foresters to use the selective-cutting system. This movement, which started in the second half of the 20th century, was the beginning of a new attitude and of a new paradigm: 'die waldbauliche Anschaung'. This new forestry paradigm needs basic information on the preconditions for the existence of forests (what keeps forests fit).

Virgin forests, forest reserves and forests on extreme sites (such as karst areas, timberline conditions, etc.) are permanent universities for 'silvology' and biocracy (for life). Fundamental research may be carried out in these areas. The results may help in the creation of a new forestry language as well as in understanding the 'biosubstance', its structure and the truth about the forests as real green Goliaths.

Review of previous forest reserve research

The idea of preserving and studying virgin forests and doing research has evolved through various periods. The first was characterised by the preservation of certain stands or forest sections for hunting. This was particularly widespread in Austro-Hungary. The following period was closely connected with the first one. It was characterised by a stronger conservationist idea. It aimed at saving some forests for posterity, at a time that European forests were suffering large-scale devastation. The third period began when some foresters became aware of the importance of virgin forests for the study of the life of the forests. After the Second World War interest in virgin forests burgeoned. Prof. Leibundgut was one of the first promoters of this. He introduced research on forest reserves in IUFRO. The 'Virgin Forest Research' Working Party was set up later by IUFRO and chaired by Hannes Mayer, professor of silviculture in Vienna. At the same time, virgin forest research became attractive in many parts of the world. During this period interest in investigations on nature was also growing within international organisations such as UNESCO (MAB projects). In Czecho-Slovakia, the Zlatnik School contributed much to the later shift towards virgin forest research.

Parallel to the previously mentioned activities, the network of forest reserves was enriched by different biocells (commercial forests, abandoned and left to nature). This development was also stimulated by IUFRO, which simultaneously promoted the study of virgin forests. Virgin forest research was never coordinated worldwide. The movement evolved differently on each continent. MAB and IUFRO are contributing substantially to the coordination of such work, to the development of comparative research and to the promotion of interdisciplinary approaches. In this way, a new era in virgin forest (or forest reserves) research may be initiated.

European virgin forest research, North American forest research and Australian forest research are different research streams. European forest research, especially in mainland Europe, is based largely on the study of the structure of the biomass, and of the development stages - particularly the natural regeneration. The faunal components and the soil component are not always integrated. An incomplete literature review of this work is given by H. Mayer (Vienna). Prof. Leibundgut's guidelines had a strong impact on the Continental approach to research on virgin forests. Some of the characteristics of this approach are: permanent observation plots; analyses of the development phases; focus on the structure of stands, especially the social structure of the tree layer; perceiving the virgin forest as a field laboratory.

The countries most active in the research on virgin forest reserves are Switzerland (Leibundgut, Matter), Austria (Mayer, Kral, Zukrigl), Czecho-Slovakia (Prusa, Korpeľ), Poland, Slovenia (Mlinšek and co-workers), Croatia (Raus, Prpic), and Finland. In other countries, only random investigations were carried out at first. However, this has now changed: forest research programmes focusing on multidisciplinary research have been developed in Northern and North-Western European countries. However, only a few virgin forests are being studied. What is needed is a systematic European approach, even where no virgin forests remain.

The published literature reflects North American research activities in primeval forests (e.g. Andrews, 1987; IUFRO Workshop on Virgin Forest Resources in Corvallis (Oregon), 1988; various publications by Franklin et al.). Jerry Franklin, working in North-West USA, created one of the biggest research groups. The IUFRO meeting on virgin forest research in Corvallis in 1988, organised by R. Hermann, was one of the most interesting events on the topic. American primeval forest research is interdisciplinary. By comparison with Europe, it focuses more on zoological research, soil-life research, and research on dead biomass. The combined field and laboratory research is very promising. Europeans and North Americans do have one thing in common though: the transfer of research findings to the field.

Australia has been trying to save its virgin forests, especially the tropical ones. In 1990 Webb and Kikkawa edited a book on Australian tropical rain forests, to which a large group of people active or interested in primeval forest research contributed. Twenty-three people, from biologists to priests and sociologists, came up with a very diverse list of opinions, research findings and proposals.

Forest reserves as 'permanent universities'

In recent decades, the reappraisal of the position of mankind in nature has brought about some major changes. Untouched nature is becoming increasingly important, and so are the forests. Man-made forests are a long way away from the real nature of the forests. The significance of a structure close to the one in nature should be emphasized. We should learn from virgin forests and forest reserves in general. The starting point in virgin forest research is commendable, although still too anthropomorphic. It is influenced too much by forest research carried out in commercial forests, such as classic yield and growth studies, and other dendrometrically influenced research, classic studies of the structure of the biomass, etc. To amass knowledge on forests without anthropomorphic aims (i.e. 'die zweckfreie Erkenntnis') 'virgin forest universities' are needed in every country. They have to be established even where the forests have acquired an 'agricultural' character, or in areas where forests have already disappeared (such as the karst area in Slovenia).

Present state of research on forest reserves

Research on virgin forests has helped forestry to change its views slowly. It takes time to realise the magnitude of the mistakes of current forest management. Much more research on virgin forests is needed for this. Virgin forests have unique characteristics:
- They are in dynamic equilibrium. Even when damaged, they recover relatively fast.
- In virgin forests, the 'optimal stage' predominates. Decaying stages and regenerating stages are present in small proportions, on scattered, crucially distributed small sites. The different stages of development are mixed in a mosaic. The structure of the stands varies, according to which of the life functions they provide.
- There is great diversity of species even though the 'homogeneous' optimal stage predominates.
- The trees are very individual. Each tree changes its function(s) during its long life.
- The young trees of the regeneration stage are permanently in a suppressed state. Such social position is a result of strong selection and safeguards the development of the coming optimal stage.
- The decaying biosubstance, in different forms, (snags, trunks, decaying trees on the ground, etc.) enhances natural fertility. It supports life and habitats, both above and below the ground. It is life itself, because a dead tree contains more 'life' than a living tree. Generally, there is a great retention capacity in virgin forests. The biosubstances or other stored substances are not easily dissolved.
- There is intensive cycling of the bioelements and biosubstances within the ecosystem as well as between ecosystems. But in this case 'intensive' means a permanent flow of very small quantities: a process which is highly effective and 'rational'.
- In principle, the presence of virgin forests is permanent, even when winds or fire destroy them. Decomposed substances guarantee that the optimal forest stage recovers relatively easily.

From the above, some rules may be formulated on how to manage a forest or renew natural resources: reduce entropy; observe forests as processes; establish permanent forests without rotation; increase stability through diversity and flexibility, and so on.

Yet this is only the beginning of our observations. In many cases a comparison between foresters' findings in virgin forest research and research in basic sciences (e.g. Prigogine) shows presence of coincidence. A more interdisciplinary approach is needed. Even researchers in basic sciences have to leave their laboratories and investigate outdoors.

Virgin forest and forest management

Forestry is the only branch of production which at the same time teaches and practices how to combine economy and ecology. The basic rules are valuable when managing other renewable natural resources. It is not enough to have vital and economically healthy forests. They have to be a part of a balanced landscape too. In several countries foresters already have experience in how to do this, but much could still be learned from virgin nature. A new type of foresters is emerging, with new duties and tasks. Basic knowledge on the functioning of natural ecosystems will assume an 'umbrella' character. Virgin forest research and the establishment of forest reserves are an important aid:

- when educating people on what nature and its protection really mean;
- when manageing renewable natural resources in general;
- for discovering the fatal fetish of world hunger and the role of agriculture in modern society;
- for discovering the misconceptions about the socioeconomic relations of modern society;
- for enabling forestry to divorce forestry from agriculture;
- for discovering that basic sciences and forestry sciences have to grow together;
- etc.

Virgin forest processes have nothing in common with agricultural systems. Virgin forests save energy, reduce entropy and are richly diversified. Agricultural ecosystems are the opposite. They are based on artificial fertility. Virgin forests show how to preserve and how to maintain natural fertility; they are based on natural fertility.

The need for international networks of forest reserves

Each forestry approach needs its own 'virgin' forest network and its own research laboratory to practise its 'cognitive' observation work on the forest. New reserves have to be selected from the typical and specific forests of the area. Each part of the national networks should become a substantial part of a European network for permanent observation and research on forests, for various reasons:

- the study of forest life in forests abandoned by man;
- to construct a holistic approach in the forestry of the future;
- to study forest conditions under extreme life conditions;
- to ascertain the scientific value of different types of forests;
- to help establish a new database for forestry research;
- to educate and inform the general public;
- to study vital questions in forestry research and research in general, etc.

Last but not least: advanced forestry may be observed as one of the few examples of really ecologically oriented economics. Such forestry was initiated in practice in the 19th century, but only in very small areas. It is now spreading over larger areas. It therefore needs new research to support its development. The main tasks have become:

- converting forests spoiled by agriculture into real close-to-nature forests in order to save the European landscape;
- reclaiming degraded lands (considered as ecological wastelands), by close-to-nature silvicultural practice;
- establishing influential connections with other human activities dealing with the natural environment (especially landscape management, etc.);
- systematically transferring research findings into practical forestry;
- influencing public opinion;
- using every forest as a permanent laboratory, as an integral part of the landscape, etc. There are already some examples of this type of forestry organisation in various European countries (e.g. in certain peri-Alpine countries).

Some countries have started to convert forestry into an organic profession for the management of renewable natural resources, especially forestry. New forest reserves may function as catalysts in this crusade.

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Long-term studies in forest nature reserves

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Summary

British experience is that few forest reserves are used for research. Most, however, require surveillance. Research can validate surveillance methods and surveillance can validate the extrapolation of results from the few research sites to forests in general. We need to study forest dynamics in order to understand (i) natural processes, (ii) the effects of forest and other land management, and (iii) to monitor environmental change. Unmanaged (= natural) forest reserves are needed for (i) and as baselines, or controls, for (ii) and (iii). Forest dynamics can be studied by many methods. Permanent plots are required to test theories derived from other approaches and to provide basic observations of slow processes, rare events and unpredictable events. Permanent plot studies are hard to establish and sustain. Many do not survive. Simplicity, personal dedication, luck and an understanding of the limitations of human institutions and individuals are all needed to generate a long-term record. A review of permanent plot studies shows that most have value for ecological research. They have introduced reality into theories of forest development and contributed many new and unexpected observations, but their contributions at a landscape scale have been weak. Studies as short as 5-10 years have been valuable, but value increases with time. Unedited records, such as photographs, complement more precise records. Studies have been valuable for conservation even where they have not brought new basic insights. Both research and surveillance of forest dynamics would benefit from closer links between these two activities. Specific suggestions are for more photographic recording, event recording, archiving short-term records, establishing marked plots as 'sleepers', and deriving procedures for common use from research. A European register of permanent plot studies of forest dynamics would help to sustain the studies themselves and improve their application. This would complement a European register of virgin or near-natural forests.

Keywords: forest research, permanent plot, long-term monitoring

Introduction

By permission of H R H The Prince of Wales Wentworth Buller on Sept 16 1868 cut down a tree near this spot it measured 9 in in diameter reckoned to be about 163 years old.

[Inscription on a stone erected near the upper margin of Wistman's Wood, Dartmoor, a high altitude pedunculate oakwood, once a 'wonder of Devon' and now a National Nature Reserve.]

Few people go to the length of recording ecological observations on tablets on stone and, indeed, this particular record is more a monument to the observer and his influence with royalty than a serious field record. But it does form an excellent symbol for long-term ecological research in forest reserves, for it shows a proper interest in the history and origins of this unique wood; and the record itself is precise and as permanent as erosion, lichens and vandals will allow. Furthermore, although the observation was no doubt felt to be important at the time it was made, it has many defects when it is judged by modern eyes. It is neither remarkable or informative; it was not (thankfully) replicated; and it could not form the baseline observation for studies of later changes.

The studies of forest dynamics using permanent plots, concentrating especially on the structure and composition of unmanaged forest vegetation in reserves established primarily for wildlife and ecological research are reviewed. Forests change slowly over long periods, often in unexpected ways, so studies should ideally form a comprehensive, systematic and enduring programme, such as that described by Koop (this volume). In practice, however, long-term studies mostly form an uncoordinated array of separate initiatives, started and maintained for many different reasons, which collectively illustrate the limitations of human institutions and individuals at least as much as they tell us about forest dynamics. This paper examines these real-life needs and limitations, and considers their implications for existing and future plans for long-term studies.

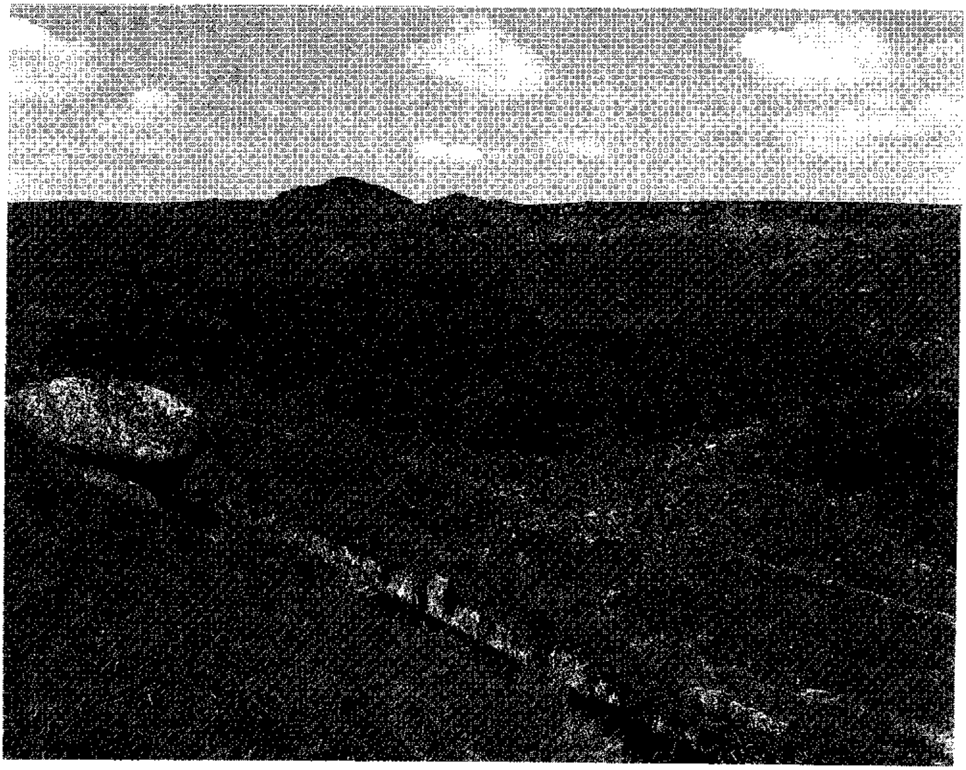

Figure 1. Wistmans Wood, Devon, England. A Quercus robur scrub growing on boulder-fields high on the moorland of Dartmoor. The stone commemorating the first attempt to discover the age of the gnarled oaks stands at the top edge of the main block of trees. Photograph Mr. P. Wakely.

British forest reserves and the need for long-term studies

In Britain the modern form of forest reserve started in the 1870s with the protection of the New Forest (1877) and Epping Forest (1878). These were typical of the Victorian reserves, being large open spaces, mostly surviving under a system of common rights, which were protected primarily as amenities and places for public recreation, but also for wildlife and their historical associations (Eversley, 1910).

Individual woods were protected after 1895 by the National Trust and from the 1920s onwards by local Authorities (e.g. Lessness Abbey Woods), natural history societies, the Royal Society for the Protection of Birds, the Society for the Protection of Nature Reserves and nature conservation trusts based in each county. These reserves were usually much smaller than Victorian preserves, but they were protected more for their wildlife. Since 1973 the Woodland Trust has acquired many woods with the broad aims of protecting wildlife, preserving amenities, establishing public open spaces and bringing neglected woodlands under sympathetic management. In 1989 the Forestry Commission established 46 Forest Nature Reserves on its own properties. Now, 13% of all ancient woodland is under some form of conservation protection (Spencer and Kirby, 1992).

Since about 1980 the forest reserve concept has become diffuse because of measures to promote nature conservation in a much wider range of woodlands. Under the Wildlife and Countryside Act 1981 perhaps 150000 ha of woodlands have been scheduled as Sites of Special Scientific Interest. Management agreements with owners try to ensure sympathetic management for nature conservation while usually accepting management for timber and other aims. Under the Wildlife and Countryside (Amendment) Act 1985 the Forestry Commission acquired a duty to take account of nature conservation in all its activities. In particular, the Broadleaves Policy of 1985 and the introduction in 1992 of special management grants for environmentally sensitive woods (e.g. ancient woodlands; all woods in National Parks) has created a climate of opinion and action in which nature conservation is a factor in the management of all woodlands, including extensive plantations. Now, although we still talk of "Forest Reserves", the reserves have ceased to be a distinct entity. They are scattered across a spectrum of management from outright non-intervention in a few strict nature reserves to wildlife-sensitive treatment of plantations and native woodlands managed principally for timber production.

Woods were first reserved for research from the early 1940s, when the Forestry Commission established Lady Park Wood (1944) and Black Wood of Rannoch (1947) as research reserves and the Universities of Oxford and Cambridge acquired Wytham, Buff and Madingley Woods for research. From 1951 onwards woodlands were protected as National Nature Resérves (NNR), in which research was of primary importance (e.g. Beinn Eighe, Yarner Wood). Research remained important in NNR woodlands until about 1970, but since then the use of such reserves for research has greatly diminished and their distinctive role has been lost.

A realistic view of forest reserves (sens. lat.) in Britain should therefore recognize that only a small and perhaps diminishing number will be used for detailed, professional research. On the other hand, an increasing number of managers (of both nature reserves and other woodlands) recognize the need to monitor the effects of their management without spending much time or resources on it.

Two forms of investigation into the dynamics of forest reserves can be distinguished:

1. Surveillance: managers need to know the rates and kinds of changes taking place so that they can manage them if necessary. This calls for simple observations and an effective archiving and data base system which can be operated by non-specialists on a large number of sites.
2. Research: this seeks new insights into forest processes, effects of management and the impact of broad environmental change. This usually requires more detailed recording and input by specialists, at least in the analysis, and can only be afforded on a small number of sites.

Research and surveillance are linked in several ways. For example, research can generate and validate surveillance methods. Surveillance provides both an early warning system for new subjects which may demand detailed research and preliminary data. With some care, surveillance can be used to validate extrapolations from the few research sites to forests in general.

Natural forest reserves

Some of the earliest British forest reserves were intended to be 'natural' (Buxton, 1898) and long-term studies were initiated in the 1940s in two of the earliest Forestry Commission nature reserves. Non-intervention was an important component of the management strategy for the early NNRs (Ovington, 1964), but few studies of natural developments were initiated. Indeed, most of the projects which could have become useful long-term studies were abandoned, lost or forgotten.

Recently, however, interest in long-term studies of forest dynamics has been revived by the maturation of some long-standing permanent plots and the establishment in unmanaged stands of some new baselines to study stand structure and composition (Peterken and Backmeroff, 1988). These long-term studies have been maintained cheaply by infrequent recording and restriction to basic features. Other long-term studies of various aspects of forest dynamics have also been published in recent years, such as those on ground vegetation (Barkham, 1992), regeneration (Pigott, 1983), ground vegetation in newly afforested land (Hill and Jones, 1978), butterfly diversity (Pollard, 1977), populations of individual bird species (Perrins, 1991) and birds in general (Marchant et al., 1990). It is now clear that long-term studies of all aspects of forest dynamics are valuable.

Support remains strong for non-intervention (= strict natural) reserves in British woodland nature reserves, for both nature conservation and scientific reasons. The benefits of such reserves are threefold (Peterken, 1991). They provide mature habitat for species which need large trees and dead wood, many of which are rare or threatened. Natural processes can be studied, both for their intrinsic interest and as controls for the study of the effects of forest management and other uses of forest land. Unmanaged woodlands can also provide locations for environmental monitoring, free from local impacts. However, the amount of research in such sites remains extremely limited.

Sources of information on forest dynamics

Permanent plots form only one method of studying the dynamics of individual forests (Hytteborn, 1986), so it is important to determine their place in the full spectrum of methods. Broadly, six approaches are available:

1. Chronosequence: stands are compared which supposedly differ only in age. Older stands are assumed to have developed via the condition which can now be observed in younger stands, i.e. space is substituted for time (Pickett, 1989), e.g. Ford and Newbould (1970) studied the chestnut coppice cycle in Ham Street NNR by comparing stands of different age.
2. Stand characteristics: age-class distributions, size-class distributions and spatial patterns are interpreted in development terms. E.g. Peterken and Tubbs (1965) reconstructed the development of beech-oak-holly wood-pastures in the New Forest from an examination of the existing stands. Retrospective permanent plots can be established by archaeological, i.e. destructive techniques (Henry and Swan, 1974, Oliver and Stephens, 1981).
3. Pollen profiles: pollen and other sub-fossil remains in organic deposits, mineral soil and bryophyte mats form a sequence which preserves the sequence of development on and around the site (Davis, 1989), e.g. Durno and McVean's (1959) study of the pinewood at Beinn Eighe. Profiles from peat deposits in small hollows give a very local history of forest dynamics (Bradshaw, 1988). The individual profile is in some respects a permanent plot.
4. Historical records: maps, documents, old photographs and other papers, combined with earthworks created by past owners and users, record the state of a forest at identifiable times and/or places. Comparisons are made with existing conditions. For example, Rixon (1975) and Rackham (1975) reconstructed the history of individual woods from such sources. Proctor et al. (1980) relocated old photographs to show recent changes in Wistman's Wood. Event records (Peterken, 1969) on forest reserves enable existing conditions to be interpreted in terms of the past without recourse to circular reasoning.
5. Modelling: forest processes and states are represented by equations which enable current trends and processes to be projected forward indefinitely. Long-term instability or stable states can be identified against given assumptions. The sensitivity of variation in parameters can be predicted. An example is the projection of Appalachian forest dynamics by Shugart et al. (1981).
6. Permanent plots: observations made in precisely relocatable plots are repeated at intervals. 'Plot' does not necessarily imply a small rectangle of forest. Any transect, line, grid of observation points of just the area visible in a photograph could be a 'plot', provided the location and boundaries of the ground under observation do not change. Impermanent plots have also been used: forests have been repeatedly sampled with no attempt to relocate plots measured earlier. This allows less precise estimates of change to be made.

Each approach has its strengths and weaknesses. Some form of understanding of past vegetation change is immediately obtained with the first four approaches. Models (5) extend understanding by allowing us to see the future within certain assumptions. Chronosequences (1) and stands (2) are readily observed, but palynological (3) and historical (4) investigations are time-consuming, and the deposits and documents may either not be available, or they may contain substantial gaps. Palynology and historical studies can, however, cover periods of hundreds of thousands of years, whereas stand studies are virtually limited to the lifetime of the dominant trees. The assumptions necessary in space-for-time substitution (1) and in overcoming gaps in historical records (4) may not be valid. Each approach furnishes only certain kinds of information.

Permanent plots suffer from the obvious disadvantage that patience is needed to obtain useful results, but set against this are several advantages. Actual change is observed directly. Depending on the frequency of observation, the demography of the whole population can be observed, not just the survivors. Casual events and their consequences can be connected. Small-scale and short-term events can be detected. New factors, such as the effects of pollution, can be observed (Falkengren-Grerup, 1990). Of course, the approaches are most informative when they are used in combination, e.g. Barkham and Hance's (1982) study of *Narcissus pseudonarcissus*, which combined modelling with permanent plots. Whilst the other methods bring some immediate understanding of how individual forests reached their present condition, permanent plots help to verify the inferences, fill in fine detail, connect causes with effects and maintain up-to-date surveillance (Franklin, 1989). As Austin (1981) said: "Ultimately, the study of vegetation dynamics is dependent on the evidence of permanent quadrats".

Permanent plot studies within the general pattern of research

How should permanent plot studies fit into the overall pattern of research on forest dynamics? Three stages to or levels of understanding seem worth recognising.

1. Casual observations of forest patterns, structure, processes and change made by visitors, researchers at the start of their investigations and managers who have no specialist interest in forest dynamics. These generate questions, hypotheses and preliminary understandings. Even on a first visit, foresters and forest ecologists formulate a view on how a forest has reached its present state and determine the probable rate and direction of current trends in its development by integrating casual observations of the sizes, shapes and distributions of trees and shrubs, using experience gained elsewhere.
2. Short-term research, designed to test hypotheses and interpretations, and generally increase the level of understanding. Chronsequence, historical and other studies which lead to immediate understanding of long-term changes would generate models of succession, stand development, etc. For example, quantitative observations of stand structure, relationships between saplings and overstorey, gap sizes and other features, generate quantitative models of stand history and possible future development which can be used both as a basis for management and as a route to understanding natural forest dynamics. This research is often exciting. It leads quickly to major advances in understanding and gives full rein to the imagination and inventiveness of the researcher.
3. Long-term permanent plots, which test understandings and models against reality and lead to substantiated or revised models. "Permanent plots" include all kinds of repeated observations. We can contrast the simplicity and clarity of models and theories with the complexity of the real world. Changes which some people think have taken taken place (e.g. decline in tree health) can be demonstrated or refuted. New changes can be detected. Detail can be observed which is obscured in chronosequence studies. This research is commonly dull and routine, taking many years to generate new perspectives. It often invalidates the neat theorizing from short-term research and substitutes sober reality instead.

As Taylor (1989) has emphasized, short-term and long-term research are fundamentally different. The former adopts the procedures of the physical sciences: research projects have the limited aim of falsifying hypotheses by means of a project having a clear beginning and end, through observations which should be repeatable in time and space. The latter is not only open-ended in time and scope, but the changes it observes may be unique in time and space. Long-term permanent plot studies enable ecologists to see 'the invisible present' (Magnuson, 1990).

Permanent plots not only test existing ideas against reality (3), but also generate new observations (1) of slow processes and unpredictable events. They allow investigators to answer new questions which arise during the course of observation.

Origin and survival of permanent plot studies

Long-term permanent plot studies have had three more or less distinct origins:

A. Projects which were initiated with explicit long-term intentions and which have been successfully maintained until they have actually become long-term.
B. Projects which were conceived as short-term studies, but which continued for much longer.
C. Single observations, surviving in files or publications, which were later repeated. These range from detailed, systematic surveys which readily qualify as 'research' to casual observations, such as photographs taken on impulse or simply to illustrate a point, which are often no less informative. Simple observations accumulate 'compound interest' with time, which far outweighs in value the limitations of the original record.

Only the first is usually regarded as long-term by institutions and the third is commonly not regarded as research by professional ecologists. Studies of all three classes will only survive to become long-term if five conditions are satisfied:

1. The observations must survive. The record can take many different forms, e.g. published papers, internal reports, research files or personal notebooks.
2. The record must be understandable in the absence of the original recorder. Methods, equipment, codes and levels of accuracy must be recorded in a form which can be understood by a later investigator without the help of the initiator.
3. The 'plots' must be relocatable, i.e. the original observations must be repeatable in exactly the same place.
4. The site must survive in a form worth studying. This does not necessarily mean that a site must be unchanged or unmanaged. Natural processes and the impacts of management are both suitable subjects for long-term studies, but investigators usually need some guarantees about management policies and information about how these policies have been implemented.
5. Some form of group or institutional memory must exist. It is possible for potentially valuable plots and clear, detailed records to survive intact without anyone remembering.

Several factors can be identified which increase the chance that these basic requirements will be met. Strayer et al. (1986) found that the primary correlates of survival and success were a dedicated individual, who felt personally responsible for the project, and a simple, accommodating design, which was easy to operate, adaptable to various uses and to which ancillary studies could be attached. This study was, however, primarily interested in permanent plots for type A and - to a lesser extent - type B research. If one places the emphasis equally on the three types of research the perspective changes somewhat. British experience with long-term studies in forests (Peterken and Backmeroff, 1988) and other habitats (Taylor, 1989; Dunnet 1991) points to the importance of the following factors:

1. A dedicated initiator is certainly important for the type A and B projects, but not type C. If this dedication lasts for more than a decade there is a good chance that worthwhile long-term observations will be published and that the project will eventually be adopted by others.
2. Equally important is a successful 'first transfer'. Unless an initial investigator maintains an interest for an unusually long period, a type A or B project will only become long-term if it passes safely into the responsibility of a second investigator who is equally enthusiastic. Researchers often keep records long after their initial research use, but projects of type C usually only become long-term if someone else recognizes the value of an old record. Carl

Olaf Tamm is exceptional in demonstrating the importance of both this and the previous point. He has been prepared to maintain a demographic study of forest meadow plants for a working lifetime (e.g. Inghe and Tamm, 1985) and he recognized the value of repeating soil observations inherited from his father (Hallbäcken and Tamm, 1986).
3. Publication establishes the value of the project and contributes to the collective memory.
4. A protected site. Although unplanned events are often worth studying, in practice most successful projects have been undertaken on reserves or in sites where the investigator has some guarantee about long-term management.
5. Clear objectives are required, but not for scientific reasons. Scientists will appreciate that research questions change over decades and long-term observations commonly pick up unexpected events, i.e. the objectives may change with time. Clear objectives are needed at the outset to attract resources to the project, for funding sources rarely back vague or open-ended projects.
6. Simple, quantitative observations are more likely to be sustained than complex, specialized observations (Franklin, 1989). Observations which seem naive when recorded for the first time (e.g. maps of trees in plots) become valuable when repeated over long periods. Observations made with specializsed equipment, according to a complex design, using fashionable classifications (e.g. of canopy strata) tend to become dated and even unrepeatable. Transects may not be a good statistical representation of a site, but they are more likely than random plots to be found by new investigators after intervals of decades.
7. Later investigations must be willing to utilize imperfect data and designs. It is almost inevitable that the design which was acceptable for the initial purposes will be seen to be deficient 40 years later (McCune and Menges, 1986).

A complete study of success and failure also requires some appreciation of why some projects have not become long-term. Projects which were initiated with long-term intentions (A) have commonly failed because records have been lost. Very many opportunities for types B and C long-term studies have been lost through neglect of archiving. Others remain unrealized in the files because their value has not been appreciated. 'Out-of-date' files are often destroyed by officials. Researchers moving from one job to the next take their 'personal' research files with them, then lose interest and contact, until finally the material is consigned to the flames by their executors. Academic specialists have sometimes been unwilling to give house-room to the musty relicts of their predecessors. With the passage of time, the initial purpose of the project is often seen to be irrelevant to modern questions.

However systematic and scientific long-term studies attempt to be, survival, success and failure depends on the care, foresight, imagination and realism of the individual people involved. If one is thinking now about establishing a new long-term study, one's chance of success will be greatly increased if human psychology is given as much weight in design as scientific rectitude.

Experience with long-term permanent plots

Mere survival is a poor measure of success. Accumulated observations are worthless if they tell us nothing of interest. Do permanent plot studies of forest reserves actually bring any benefits to ecological research which cannot be gained by quicker methods?

The earliest forest permanent plot may have been one established in 1826 in an oakwood at Bremerhus, Denmark (Madsen, 1977). The earliest to survive in an unmanaged forest appears to be one started in 1847 in Boubinsky Prales, Bohemia (Rehak, 1968). Neither was replicated, but both have yielded useful information on stand development.

Several more detailed studies are available, mainly from North America, which have measured vegetation change in permanent plots over periods of 40 years or more. All were in unmanaged forests, but some forests were supposedly stable old-growth whereas others were rapidly changing secondary or second-growth stands. Most publications present data at a stand scale, i.e. they give totals or means per unit area, but some (Foster, 1988) effectively describe change in a whole site from various kinds of plot recorded at different periods. Remarkably few present demographic details, i.e. about individual trees and shrubs, but Peterken and Jones (1987, 1989) follow the history of individuals in the recent phases of their study. One study (Avery et al., 1978) records a remarkable amount of information about thousands of individual pines, but performs no analysis.

Many valuable observation were made. Change was revealed in supposedly stable forest stands (Leak, 1987; Whitney, 1984; Parker et al., 1985) and ground vegetation (Brewer, 1980). Expected successional trends were broadly confirmed, but unpredictable perturbations were observed which appeared likely to have short-term (Stevens and Waggoner, 1980) or lasting (Phillips, 1976; Peterken and Jones, 1987) effects. Changes in structure and composition were observed which could not readily have been deduced from later stand characteristics (Hibbs, 1983; Whitney, 1984). Models of diversity through succession were found to be at variance with observed facts (Scheinter and Terri, 1981).

Some recent studies have shown, encouragingly, that permanent plot studies do not have to be long-term before they yield valuable information about forest dynamics. Thus, Runkle and Yetter (1987) showed important features of gap dynamics by repeating observations after 7 years. Romme and Martin (1982) were able to compute features of old-growth forest dynamics after recording gap creation annually for 10 years (though an extensive blowdown shortly afterwards was salutary). Harcombe and Marks (1983) observed tree deaths annually for only 5 years, but by then important features of the mortality pattern were becoming apparent. Nevertheless, the value of studies undoubtedly increases with time as the sequence of papers on Donaldson's Woods, Indiana showed. An increasingly complex pattern of temporal change was revealed (Lindsey and Schmetz, 1965; Schmetz et al., 1975; Barton and Schmetz, 1987) and new kinds of study (of log decay) (MacMillan 1981, 1987) became possible as adjuncts to the core study.

None of these studies generates the excitement of a very long-term perspective or a new general model of forest dynamics, nor do they relate to the landscape scale, though combined with other sources the permanent plots can contribute to a general view taking landscape-scale dynamics into account (Foster, 1988). Rather, they all embody sober, painstaking observations which put existing models and predictions to the test, generate new and often unexpected questions which can be tested by other means, measure routes and directions of slow and fine-scale change, reveal short-term phenomena with lasting effects and generally give the investigator an unparalleled subliminal understanding of the forest under study.

Despite these successes, it would be wrong to believe that long-term permanent plots invariably produce worthwhile insights. For example, the available information on the first 92 years (1844-1937) of an unthinned Scots pine stand near Moscow (Eytingen, 1949) showed no more about growth and thinning than standard yield tables derived from chronosequence studies. However, similar observations made on a number of plots yielded a classic demonstration of the relationship between growth, mortality and initial density (Peet and Christensen, 1980; 1987).

In these and most other studies chronosequences were either not available as an alternative and quicker approach, or they would not have been appropriate. For example, the effects of urbanizing the surroundings of an unmanaged old-growth stand in the Bronx (New York) (Rubnicky and McDonnell, 1985) could perhaps have been examined by comparing this wood with an old-growth remnant still in a rural setting, but the reference stand would have necessarily been situated many tens of kilometres away on an inherently different site. More generally, in so far as each site has a unique history of use, natural disturbance and forest responses, the chronosequence approach is suitable only as a quick means of identifying broad trends in structure and composition at a coarse spatial scale (Pickett, 1989).

Although the most valuable studies have been those based on quantitative and exactly repeatable observations, less precise forms of observation have their place. Old photographs, in particular, have preserved unedited records from which new observations have been made retrospectively. They have also expanded the scope of permanent plot studies to the landscape scale. For example, the spectacular photographs from the Rockies (Gruell et al., 1982; Gruell, 1983) give an astonishingly intimate, though totally non-quantitative, insight into changes within both forest stands and forest landscapes over a century or more.

Permanent plots can be valuable for nature conservation, even though they have only limited value for basic research. For example, plots in the Black Wood of Rannoch started in 1948 and only recorded again in 1956 and 1984 (Peterken and Stace, 1987) demonstrated that snags remained standing for decades (i.e. the dead trees one can see in the reserve do not indicate high rates of recent mortality) and that considerable amounts of regeneration had developed during the last 40 years. This helped to deflect pressure from foresters to 'manage' this non-intervention reserve because they thought it was 'dying on its feet'. As it happened, interesting research results also emerged: saplings had been recruited, not as a single-cohort flush, as might have been expected, but steadily over the years.

These and many other studies confirm that long-term studies tend to be open-ended and unpredictable. Investigators who have sustained such studies, or simply repeated observation over an interval of several years, have often become wary of models, theories and predictions (e.g. Jones, 1945; Raup, 1956). The studies which are most informative over periods of decades are not necessarily those which were intended to be long-term at the outset and the reasons why a long-term study is useful are not necessarily those which were foreseen or intended at the start. Indeed, it is inherently improbable that the questions which interest ecologists will remain unchanged over periods of decades.

Broadening the value of long term ecology

How can we break through these personal, institutional and scientific barriers to establish a wider range of enduring permanent plot studies? One way forward could be to link research and surveillance more closely. Surveillance offers the prospect of low-cost records being started and sustained in a large number of sites, which would pick up unusual and scattered events missed by research sites. Research offers detailed understanding of the dynamics of few sites and the possibility of generating cheap but reliable methods of basic recording which can be widely applied. Put together, they can enhance each other. Results from a core of a few, representative detailed research sites could be placed in context by simple but reliable observations from a large number of sites under surveillance.

Against this background, several measures could be taken to establish some form of long-term studies on a large number of sites:

1. Photographic recording. Old photographs usually yield valuable, qualitative understanding of changes in forest reserves, especially if their locations are known. New photographs form a cheap, unedited record whose particular value decades hence cannot be predicted. Series of fixed-point photographs, and indeed any photograph whose position is recorded in the files, would be the most valuable.
2. Event recording. If simple records are made of natural events, management activities and other impacts (visitors, accidents), the response to the ecosystems can be observed at a later date and interpreted without fear of circular reasoning. The basic record must describe what happened and where. The system in Britain (Peterken, 1969) now forms of component of a more comprehensive reserve management system.
3. Archiving short-term records, which may turn out to be useful. Descriptive plots from the past have been used as baselines for long-term studies (e.g. Hytteborn, 1987; Proctor et al., 1980; Whitney, 1984). Forest managers and researchers should acquire a habit of documentation. Records generated during the ordinary course of management and research should be archived. If one-off observations were filed with a record of where exactly the observations were made, many valuable long-term studies of type C would eventually be available.
4. Marked plots as 'sleepers'. Given that plots which were originally recorded as descriptions have later been valuable for long-term studies if they have survived and have been relocated, a policy of recording new descriptive plots ought eventually to yield valuable information on forest dynamics. Plot records would simply sit in the files, together with relocation instructions, until some issue arises that a second recording might illuminate. The subjects of these records should be eclectic: we do not know which will be regarded as valuable in the future,

so standardization of sleeper plots should be limited. Records should be diverse and should include informal, uncoded observations. Guidelines for plot recording of stand characteristics have been developed from experience of long-term studies (McCune and Menges, 1986).

5. Procedures for common use. Researchers involved with the few long-term, intensive research sites should develop and verify simple methods for surveillance in the generality of forest reserves. This will not only improve the reliability of surveillance, but will enable findings from research sites to be extrapolated to the wider environment. Examples of widespread surveillance methods are the transects of stand composition and structure (Peterken and Backmeroff, 1988) and Common Bird Census (Williamson and Homes, 1964), both foreshadowed by Williams (1936), and the Butterfly monitoring scheme developed by Pollard (1977).

Conclusions and action points

Mlinšek (this volume) should be supported in his call for more natural forest reserves and for at least basic long-term recording of processes and conditions. Such reserves are needed to study natural processes, form baselines for comparison with managed systems, and monitor environmental change free from direct human influence. These sites would be more valuable if they were linked to managed forests where similar long-term recording is undertaken.

The most productive approach to long-term study would be to define clearly a limited core of standardized recording, but encourage researchers to follow their interests and imaginations in adding other subjects. In forest reserves, the standard core should cover stand structure and composition. There is also a need to enlarge the number of sites with some long-term record, however incomplete and informal, through photographic recording, event recording, archiving, simple marked plots and tested procedures for common use. Long-term research sites should not be elitist and exclusive.

It would also help to establish and sustain natural forest reserves and long-term studies if registers (c.f. Hill and Radford, 1986) were made of all such sites and studies in Europe. This would also generate momentum towards the necessary standardization of the core record and enable results to be analysed across a wide geographical area. The sites included would be the counterparts of the Research Natural Area in the USA (e.g. Johnson et al., 1984).

The register of natural woodlands should develop the initial work of the Council of Europe embodied in the report produced by Gerhard Heiss (1987). Although the original proposal for this project was limited to virgin and near-virgin forests, the project was unfortunately deflected into an incomplete general review of ancient forests.

Permanent plots are needed in all major forest types. Existing permanent plots should be maintained, old plots should be rescued and new plots should be established to fill the gaps. Permanent plots should be recorded in all forest sites included in programmes of environmental monitoring, such as the Environmental Change Network developing out of experience in Britain (Heal, 1991). The European register would help researchers to co-ordinate their studies, allow coverage to be tested, record relevant publications, and facilitate survival of permanent plots by publishing their existence and recording where the data are archived.

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Aims of nature conservation and scientific functions of reserves

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Summary

Besides 17 national parks, Poland has more than 1000 designated reserves (Czubinski et al., 1977; Ochrona przyrody w Polsce, 1981). The majority of these are unmanaged forests in different stages of development, which means that several of them are more or less strict forest reserves. The problem of the rationalization of the network of reserves, which were established spontaneously over the last 90 years, and their proper use in science, education and tourism is discussed here (Faliński, 1991a, 1991b, 1992; Denisiuk, 1990).

Keywords: nature reserves, scientific functions

Introduction

Detailed and explicit formulations of the phenomena that are protected in a given reserve and of their particular functions are important prerequisites that may enable reserves to perform their specific functions. In Table 1 protected forms in Poland are listed. Table 2 reviews the surface of specific forest reserves. For each reserve, it is necessary to ascertain whether it can currently fulfil any of the six scientific and semi-scientific functions listed in the third paragraph. If a given reserve cannot perform any of these functions, e.g. because of the state of preservation, the locality, the threat of other incompatible functions (e.g. tourism), it should not be formally encumbered with scientific functions. The network of nature reserves and nature conservation will not suffer if some of the reserves do not serve scientific purposes but have educational, touristic, and environmental functions instead.

Table 1. Protected forms in Poland and total protected surface (1990).

Protected forms		Surface km_2	% of country surface
17	national parks	1.630	0.5
1001	nature reserves (incl. 531 forest reserves)	1.175	0.4
11	landscape parks	5.794	1.8
	zones of protected landscape	79.600	25.5
	Total	88.199	28.2

Poland country surface: 312.683 km^2
Woodland cover: 31%
Protect forest under all protected forms: 72%

The functions of reserves that may serve one of the five scientific purposes should be specified. Multiple functions should be avoided; if necessary, a leading function has to be indicated for a given reserve. For example, if a reserve has a scientific documentary role, it must be stated what phenomena it documents and whether it performs this function alone or within a

Tabel 2. Surface of forest reserves in Poland (1990)

Surface class		Number of reserves
<5.0 ha		64
5.1- 10.0 ha		76
10.1- 25.0 ha		129
25.1- 50.0 ha		107
50.1-100.0 ha		74
100.1-500.0 ha		73
>500.0 ha		8
	Total	531

Total surface: 35124.88 ha
Mean reserve surface: 66.15 ha

Source: Z. Denisiuk, T. Zajac (1991)

network of reserves.

The present and future purpose of a given reserve for scientific studies should be followed by detailed determination of the aim and topic of research, time and methods of conducting it, researcher(s), etc. In the case of reserves destined for experimental studies, the results of the experiments and (if relevant) the subsequent restoration of destroyed elements, or even the annulment of the reserve, must be foreseen and planned. In some cases, the reserve should be established for a certain period of time only, i.e. until the end of experimental studies.

It is the task of scientists and scientific institutions to evaluate the whole network of reserves to ascertain their scientific usefulness and to ascribe a function to each reserve. Finally, the reserve should be evaluated by the national institutions for nature conservation (in Poland: PROP - National Council for Nature Protection, and The Committee for Nature Protection of the Polish Academy of Sciences).

Information on the precisely defined scientific or semi-scientific functions of each reserve should be noted in the documentation on the reserve and shown on the information board in the reserve according to uniform standards. Adequate measures that may enable reserves to perform scientific research functions should include an elaboration of the detailed research programme, establishing e.g. permanent research plots and measurement points, and rendering the site accessible to the scientific institution - which implies establishing "true science ground" in the reserve.

Synthetic information on this subject should be published as special publications and maps that should be updated periodically.

Classification of reserves for protection

Phenomena worthy of protection in reserves are complex nature sites and biological or ecological relationships. Usually, the phenomenon is defined in relation to the purposes for which the reserve was established. Most often it is also the main or leading element of nature or ecosystem of the reserve.

For protection, it seems most appropriate to distinguish the following types of reserves:

1. Floristic and faunistic reserves, where sites with concentrations or local populations of certain plants and animals are the main subject of protection.
2. Biocenotic reserves, where it is the entire ecosystem that is to be protected, i.e. a certain biocenosis plus its abiotic environment. According to the ecosystem type, forest reserves, steppe, dune, peat and bog reserves, saline reserves and water reserves (lake, river, well-head)

can be distinguished. In some biogeographical regions there may also be desert, tundra, marine and other reserves.

3. Soil reserves, where fully developed soil profiles and types, soil and soil-formation processes are the subject of protection.
4. Geological-geomorphological reserves (also called abiotic environmental reserves), where geological or geomorphological forms and processes (such as caves, karst phenomena, geological outcrops, erosion forms, erosion phenomena) are to be protected.
5. History and nature reserves, where what is to be protected are the objects of material culture, i.e. groups of historical or archaeological objects in the environment, where they were esablished and have persisted, or in the habitats that sometimes determined these historical phenomena (e.g. tumuli, barrows in the forest, remnants of city settlement on rocks or kame hills overgrown with steppe).
6. Landscape reserves, where what is to be protected is the landscape in a broad sense, as a harmonious and beautiful structure in given habitat, and in a strict sense, as an expression of relationships between all components of nature and, possibly, material culture.

Scientific functions of nature reserves

Scientific-documentary functions

Recording of biological, ecological, physical geography phenomena as well as of some man-environment relationships.

1. Borderland localities of plants, animal, plant communities and some physical geography phenomena, which document the borders of their ranges by the network of special reserves; see for example Figure 1;
2. Dependence of biological, phytosociological, ecological, soil, and physical geography phenomena;
3. Biodiversity and variability of biological, phytosociological, ecological, soil and physical geography phenomena;
4. Occurrence of rare and endemic phenomena;
5. Occurrence of relict phenomena;
6. Course of ecological processes; soil, soil formation, geomorphological, hydrological and other processes.

Scientific research functions

1. Permanent observations of processes and phenomena (listed above);
2. Experiments designed to explain the origin and course of processes and phenomena (listed above);
3. Model objects ('model' in sense of 'norm' and sense of 'reference point').

Monitoring functions

Biological, ecological, and technical monitoring (permanent monitoring of changes in the environment based on a single concept, identical methods and technical equipment, in the network of representative sites or objects covering large territory).

Ex situ breeding

Restitution and/or reintroduction, and protection of the local endangered population in the area of its primary occurrence, planned and conducted under scientific supervision).

Scientific educational functions

Education of scientists and specialists in nature protection and environmental engineering (not to be confused with the education of the general public).

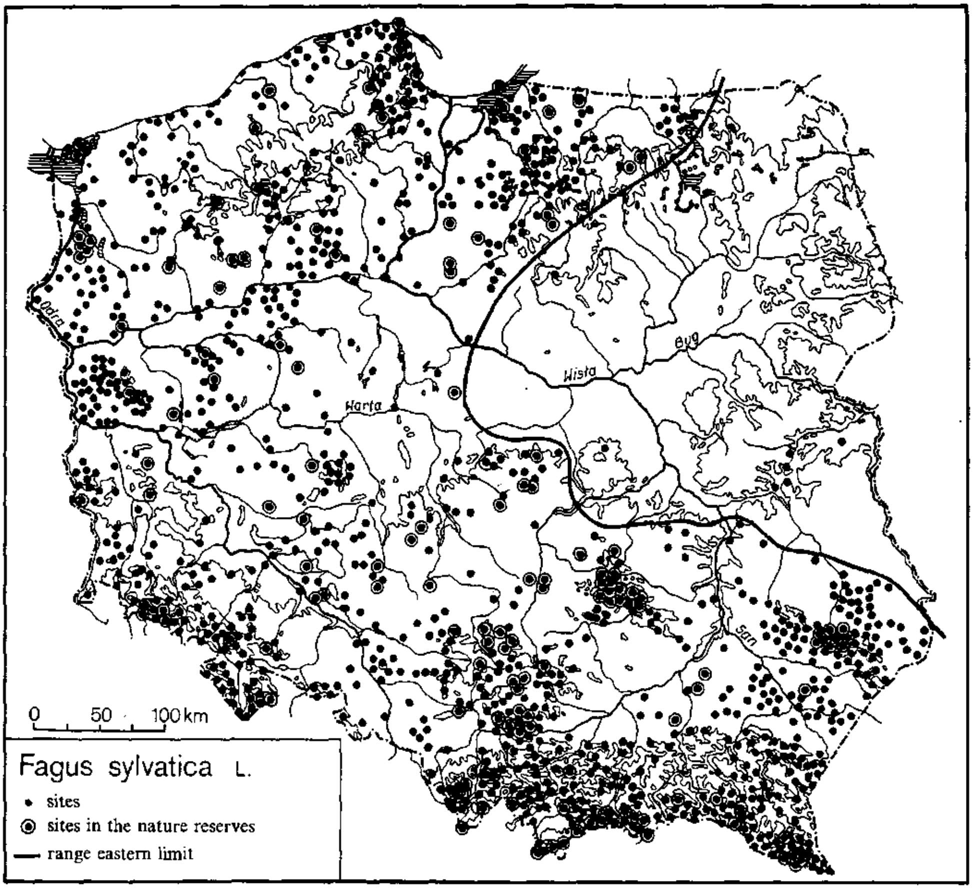

Figure 1. Location of sites of *Fagus sylvatica* in Poland.

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Cultural heritage and forest reserve

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Summary

Society's impacts on forests are no longer explained solely by political history. Historians are increasingly taking society as an entity as their point of departure for explaining and interpreting the past. This new view on history in general is called the layer structured view. This way of interpreting history has been developed further into a layered view on forest history: the "sandwich formula".

This view on forest history allows for different kinds of long-term trends and cycles that interfere with different kinds of interaction, at different directions and speeds. They influence society in general and forests and woodlands (and forest reserves) specifically.

The layer-structured view implies the existence of more than one way of interpreting cultural heritage in relation to forest reserves. It leads to a paradox: cultural heritage and forest reserves need different, often mutually exclusive kinds of management - conservation, préservation and reservation. It is a challenge to manage this paradox to benefit forest reserves.

Keywords: Cultural heritage, woodland archaeology, layer-structured view of forest history

Introduction

A few months ago a Dutch weather forecaster remarked: "Some time ago we were given the opportunity of using one of the world's most powerful computers, a supercomputer. We meteorologists are convinced that the earth's meteorological and climatological system can be input into a general model, a matrix. The new computer allows us to compute our matrices and weather forecasts to ten decimal places. And it is quite easy to change part of the input and see what effect this has on the output. We were astonished. Merely changing the tenth decimal place changed the output radically! To get an idea of the scale effects of such a small change: a a butterfly flapping its wings in New York could cause a deep low near the Western European Atlantic coast".

The scientist Isaac Asimov wrote several science fiction novels. One of his stories tells of a time traveller in the far future who travelled back hundreds of thousands of years in time. As he was leaving his time capsule he accidentally killed a small, very ugly creature. When he returned to his own century he found his world completely changed. His visit to the distant past had changed the course of evolution totally, and by accidentally killing the ugly creature he had destroyed the source of very large-scale future developments.

Although Asimov's story is fantastic, its philosophical implications touch all of us: we all live in a changing world and in practice we actually are able to change future developments drastically. We are all time travellers in an Asimovian sense. Therefore, we have to consider the consequences of everything we do. In fact, anything may change the course of history. In creating forest reserves in the woodlands and forests in our countries we are again intervening in and changing the course of history.
Paradoxically, philosophically speaking it is that same course of history that enables us to think of forest reserves.

A theory on forest history and cultural heritage

History is society's heritage. The history of the future is all happening today. And indeed, the discussion on forest reserves is also part of it. History and cultural heritage is everything we do, everything we create, everything we destroy, everything we change, everything we manage and decide now.

Though exaggerations, the anecdotes mentioned above illustrate the problems we are confronted with when managing forest reserves. The example of the meteorologist demonstrates the impossibility of capturing all factors influencing a system in a series of matrices. Even a small change gives quite unpredictable consequences elsewhere. Although science fiction, the second example is a good illustration of that kind of unpredictability.

Although a system might be hugely complex and although the additional predictive value of a matrix with which one tries to represent a system might be small, we cannot do without a model explaining developments in the past and predicting future developments. Understanding the past developments and factors that have led to the present situation does at least enable us to react more positively to present threats within a particular system. It is this that drives us to try to understand the past and our heritage, and the cultural heritage of the society that led to the present state of a particular site, here a forest reserve.This understanding enables us to counteract external pressure and to win over opponents of the aims of forest reserves. It also enables us to prepare convincing arguments to justify an action that probably is not optimal but is at least the second best solution. This is why it is important to try to understand the past.

In the same way as meteorologists try to create models that may reliably predict the weather, historians try to create models in order to explain historical processes and their impact on society. Up to the end of the 1970s, history was generally thought of in terms of political history, the history of kings, tsars, emperors, kingdoms, empires, wars, depressions and so on. But in the 1950s a new generation of historians emerged, particularly in France, which tried to alter the approach to history to one that is more closely related to everyday life. Since the 1980s this approach to history has been adopted all over the world. The focus of attention has shifted from states, politicians, wars, or warlords to economic situations, the man in the street, social developments, trade and commerce.

Although one cannot deny the relative importance of political developments, it is clear that other developments are at least as important as the political ones (Van der Woude, 1980). In accordance with this change in thinking about history, a new view on history - historical coincidences and the structure of history - has developed. This new look is called the layer-structured view of history. Developments in the past may be subdivided into more or less independent layers (Buis, 1985):

MAN

NATURE (e.g. FORESTS - WOODLANDS - FOREST RESERVE)

GEOLOGY

This "sandwich formula" describes forests as a result of relations between human action, the ecological and biological capacities of forests and geological development, i.e. development of the abiotic factors.

Clearly, these layers develop in different ways and directions and with different speeds: a very active "human" layer, a less active biological layer, and - from a human point of view - an almost indifferent physiological layer (the latter also relates to climate).

Of these layers the "human action" itself can be divided further into at least three interacting parts:
- forest legislation and its history;

- the forest itself and its history;
- the human use of forest and forestry products.

This model raises doubts in terms of the theory of history, e.g. about the reality of the processes of succession in vegetation (Buis, 1985; Van der Woude, 1980). Succession is generally understood as the spontaneous replacement of one type of vegetation and site by another one. The traditional view is that there is always a climax type of vegetation, which will eventually prevail regardless of the colonization processes by which it is attained.

This doctrine may be partly true, but from a historical point of view the climax may not be as simple as this, for several reasons (see the frequent discussions in the literature). Several contributions to these proceedings illustrate perfectly what is meant by the influence of the different layers in relation to history and also to the present and to the nearer or more distant future.

Different views on forests and nature reserves

From the different parts in the layer called "society" one may develop different views on forests and nature reserves and their conservation. According to the Oxford English Dictionary, conservation means "preservation from destructive influences, natural decay or waste". The impact and importance of these three factors will vary widely from site to site, and general prescriptions or even principles in relation to forest reserves, are unlikely to be applicable to every case.

In most cases, people unfamiliar with the concept of "forest reserve" will think that the immediate threat is one of "waste", one of more or less deliberate destruction. If the chosen management of sites of forest reserves is nothing else but "doing nothing" - i.e. inaction - people might think, and often actually do, that these forest sites will become go to waste and will lose their significance ... for them personally and for society as a whole.

Here, the general concept of "conservation" being a kind of "preservation from .. waste" needs to be corrected. "Waste" may however, occur in a completely different sense: the waste of historical "evidence". One has to admit that woods are not only biological but also historical "documents" that should be read before somebody destroys them (Ten Houte de Lange, 1977; Rackham, 1976). Therefore, it is necessary to identify the potential historical or archaeological value of forest reserves.

In 1974 Peterken introduced in 1974 the idea of "non-recreatability" in a biological sense when selecting forest sites for conservation. Ancient coppice woods, wood pastures and old secondary woodland all possess features which, once destroyed, cannot be re-created. In this concept, both biological and archaeological interests are served by focusing conservation on such sites rather than on others whose "destruction" is readily reversible (Peterken, 1974).

Almost every wood on an ancient site has some non-recreatable features. Its value will be enhanced if it is a complete mediaeval wood, if it contains several different types of native woodland, if its understorey is well preserved, if different parts of it have different origins or management histories, if it has earthworks or archaeological sites that tell a particular story, and so on.

"Conservation" in relation to forest reserves raises another question: what does conservation mean if one is dealing with living things managed by man? Some woods have been managed uninterruptedly for hundreds of years. Total preservation in their present state is a perfectly reasonable conservation objective. In such a case "forest reserve" almost inevitably means continuation of the management in accordance with the management of the past. "Doing nothing" or doing something differently would be a grave interruption in the course of nature and history.

In general, mediaeval woods have been neglected for periods varying between several decades and a century. This will often have caused the spontaneous erosion of some of their historical features. But provided that e.g. the coppice structure has survived, it is still possible to be rehabilitated if management is resumed. If this is not practicable, to do nothing may be the next best solution. Any other action may erode the historical features faster and more thoroughly than more "neglect". An acceptable compromise could be to resume the coppicing in a part of the wood and to leave the remainder for the time being.

It is more difficult to decide on ancient wood pasture sites and trees. Little is known about how to prolong the lives of wood-pasture trees. Their value lies in their age and in the effects of past pollarding. Therefore, the problem is not solved by establishing young trees as successors. In this case effective conservation measures must include renewed pollarding of existing trees - if they have not been neglected for too long - and starting new pollards destined to become the very old trees of future centuries.

Natural decay is practically never an imminent threat calling for action. But society will seldom accept inaction as the best conservation policy, although it is often second best. A neglected wood does lose some of its historical interest, but the decline is slow and reversible.

At the turn of the nineteenth century the idea that the amenities of the countryside could no longer safely be left in the hands of ongoing economic processes gained public acceptance. In Britain this movement began after the destruction of Hainault Forest, in The Netherlands it started around 1906 when naturalists bought Naarden lake (near Amsterdam) and its surroundings, in order to preserve it from being destroyed by the dumping of town waste.

More recently this public amenity interest in the conservation of trees and woodlands has been augmented by the specific interests of biologists and naturalists, expressed by burgeoning public or voluntary bodies such as Natuurmonumenten (nature heritage sites) in The Netherlands and the Nature Conservancy Council in Britain (Rackham, 1976). In recent years, with the rise of interest in rural history as a practical, and not a purely literary field of study, the archaeological importance of woods and trees is becoming more widely known.

These three conservation interests - public amenity, naturalness and history - generally do not coincide, as is illustrated by the following example. A grove of beeches planted on the top of a chalk down may be held sacred by the amenity lobby interested in conservation. Naturalists, knowing that it harbours little else but pigeons and stinging nettles, may not share this enthusiasm. Archaeologists may want to get rid of it before the roots of the beech have completely destroyed the Iron Age hill-fort on which it stands. On the whole, the differences in interests are only in sympathy at the local level. In matters of national policy, let alone international policy, the more influential spokesmen of the amenity interest have until recently often shown scant understanding of historical processes or sympathy with the wildlife lobby.

The idea that the countryside is somehow "natural" has given way to the equally dubious notion that it is totally artificial. Therefore, the planting of new groves is often still thought to be an adequate remedy for failure to conserve existing woods and trees (Rackham, 1976).

The historical significance of earthworks in forests

A more concrete example is shown by the significance of earthworks as a cultural heritage. The history of e.g. woodmanship and wood pasture cannot be learned from forestry books and historical documents alone, but has to be reconstructed from field and archaeological evidence too. One of the most eye-catching features of cultural heritage in forests is the occurrence of earthworks. Almost every ageing wood more than a century old, certainly those in lowland areas, contains earthworks consisting of a bank and a ditch. The former, originally being on the wood side of the earthworks, was created in order to separate the farmed land from the wood (Rackham, 1976; Rackham, 1980; Buis, 1985).

Earthworks are mainly of interest from the point of view of woodland archaeology. The methods of woodland archaeology are closely akin to those used in the study of buildings such as churches. Woods, like buildings, may have been in constant use for many centuries, and have accumulated natural changes and deliberate alterations down the years. Unfortunately, only a small part of the evidence is simple and direct. Detailed maps and dendrochronology applied to living trees enable us to go back some 400 years. Most other evidence requires circumstantial interpretation of a kind widely employed by archaeologists in other fields. A main objective is to investigate in what respect features such as earthworks and vegetation patterns are historically determined, and where chronologies of them may be constructed.

Chronologies may be based on documentary evidence, as for instance where woods with a management history continuously documented since the Middle Ages are compared with others, known to have originated later. Chronologies may be based on physical evidence too. This is shown e.g. by historical changes, as is the case when a wood contains earthworks of two types that intersect in such a way that it can be proved that one is more recent. A combination of documentary and physical evidence may be called for in the case of a wood which, though known to be mediaeval, partly overlies the ridge-and-furrow earthworks produced by ancient ploughing.

Once a provisional chronology has been established for woods having a good historical record or containing clear evidence of alteration, it may be applied to other sites (Rackham, 1976; Buis, 1985).

The work of woodland archaeologist is facilitated by a simultaneous use of as many lines of inquiry as possible. An argument involving both vegetation and earthworks is generally more convincing than one based on vegetation alone. Documentary evidence should be used wherever possible, because the dates which it provides afford a means of escaping the pitfalls of the circular reasoning which await the investigator who confines himself to field evidence alone.

Where a wood has increased in size, the old boundary nearly always survives as an internal earthwork. Where parts of a wood have been grubbed out, the old boundaries often remain as a hedge or a trace visible in the soil in the fields.

Ancient woodland boundaries have characteristically irregular outlines. Two types may be recognized: sinuous shapes, in which the boundary straggles across country in a series of curves with changes of direction every few metres, and zigzag shapes with abrupt changes of direction at longer intervals. A perfectly straight boundary (or, less often, regular curves such as circles and ovals) was usually established later than approximately 1700. Sinuous outlines are more common in mediaeval woods. Early wood margins tend to avoid streams and other natural features and seldom pay any regard to drainage patterns. Zigzag outlines may result from successive small incursions of farmland. Wooded banks follow all the irregularities of both the sinuous and the zigzag types of boundaries. This is why even complex outlines are so stable: any straightening out involves a lot of earth-moving to efface the bank (Buis, 1985).

Mediaeval wood boundaries normally have relatively massive banks and ditches with characteristics of ancient earthworks such as those in the New Forest, which are rounded, consolidated by centuries of drumming rain and of baking sun. As a general rule they are broad, (Summer, 1917; Rackham, 1976).

Wooded banks formed in later periods are progressively less massive and steeper in profile. There is a danger that they will have been crumbled by modern traffic and treading. They continued to be formed into the 19th century, by which time the boundaries were straightened, as mentioned above (Thomas, 1983).

Boundary earthworks have been a normal feature of coppice woods since the Middle Ages, and may be found all over Europe. There are several types. Different ages may be identified with the help of documentary evidence from various periods, or of evidence that they have been left behind after the enlargement of a wood, or of the evidence of intersecting boundaries of different age (Thirgood, 1981).

Conclusions

At first sight archaeologists, naturalists, foresters, and last but not least politicians, paradoxically hold contradictory points of view on forests and forest reserves. But forest reserves are always at least the second best solution to obtaining a consensus on how to manage particular sites in the future.

Management by total inaction still keeps open the option of getting back the present situation in the future. Management by restoring past types of management (e.g. coppicing, pollarding, wood pasture), or by continuing present ways of management - even when this seems to be economically irresponsible - means that archaeological and historical features and therefore the cultural heritage in a forest reserve are reasonably preserved and will not be destroyed e.g. by new afforestations.

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Chapter 2

Forest reserves programmes

Fontainebleau - a natural forest community

The strict forest reserve La Tillaie en Gros Fouteau in the 17 000 ha forest of Fontainebleau (France) has not been managed since being clear felled in 1372. The reserve is only 80 ha and consists of just two forest communities. Populations of megafauna are completely dependent on hunting management in the forest area surrounding the reserve. Nevertheless, the reserve contains a complete mosaic of all the stages of natural development of the two forest communities, including open patches. All age classes of trees, including real woodland giants and all stages of decomposition of dead standing and fallen stems are permanently present and close to one another.

Forest reserves in Romania

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Summary

The condition of Romanian forests is briefly reviewed together with the chronology of the designation of forest reserves. The classification of these reserves, their peculiarities, scientific and landscape value, as well as the permanent increase of forest reserve area are presented. The research carried out in reserves and the resulting publications are also referred to. Finally the problems currently threatening forest reserves are analysed.

Keywords: forest reserves, forest conservation, research programme

Introduction

In the geographical space that is Romania numerous relief types, geological formations and natural ecosystems (terrestrial, aquatic) of great diversity occur on quite limited areas. Scientifically they are extremely relevant and are also incomparably beautiful as landscapes.

The soil and climate of this Carpathian-Danubian region (located between Black Sea level and 2543 m altitude) are extremely favourable for forests, which in the past occupied almost 79% of this area (Giurescu, 1977). At the moment, because of historical conditions and human impact, wooded areas cover only 27% of the country and are mainly restricted to mountainous regions (60%) (Giurgiu, 1978).

Romanian silviculture usually operates with 60 native trees and 38 shrubs, plus the introduced exotic taxa. Recently, 10 groups of natural forest formations and 150 types of forest ecosystems have been described. The dominant species with zonal extension are: *Pinus cembra, Picea abies, Abies alba, Fagus sylvatica, Fagus taurica, Quercus petraea, Q.robur, Q.cerris, Q.frainetto, Q.pedunculiflora, Q.pubescens. Larix decidua, Pinus nigra, P.sylvestris, Fraxinus sp., Alnus sp., Populus alba, P.nigra, P.canescens, Salix alba* and *S.fragilis* are intrazonal species (Doniţa et al., 1990).

Despite frequent and severe disturbance, the forests of Romania still retain their natural appearance in almost 70% of the wooded areas. Very precious genetic and forest resources, relevant for species composition, structure, growth, vitality and stability, can be still found here, especially for spruce, fir, oak and beech (Enescu, 1978; Giurgiu, 1978). Unfortunately, the pure willow stands along the Danube, the riparian forests on the inner rivers and the oak forests have suffered irreparably from felling and degradation. *Ulmus spp.* have practically disappeared; fir, oak and *Pinus mugo* are severely threatened.

Forest conservation and forest reserves

After the first law to protect nature heritage was passed (1930), the Nature Monuments Commission (CMN) was established in 1932, as a branch of the Romanian Academy. For years this Commission rallied the devotion and energy of many distinguished scientists (such as P.Antonescu, Al. Borza, A. Popovici-Bîznoşanu, E. Racoviţă, Gr. Antipa, G. Vîlsan, M. Drăcea, C.C. Georgescu, E. Pop, I. Popescu-Zeletin, At. Haralamb, Val. Puşcariu, S. Paşcovschi, Al. Beldie, N. Botnariuc, N. Boşcaiu, V. Soran, V. Giurgiu, N. Doniţă and many others).

The first forest reserves preserving authentic woodland ecosystems were set up before World War II: Mociar in 1932; Pieterosul Mare in 1932; Dosul Laurului in 1938; Letea in 1938; Piatra Craiului in 1938; Bejan in 1940; Slâti-oara and Giumalău in 1941 (Pop and Sălăgeanu, 1965). In 1935 the first national park was established in the Retezat mountains, in order to preserve primaeval beech, spruce, fir, stone and mountain pine woods, as well as alpine grasslands, glacier lakes and other marvellous landscapes (Borza, 1928; Pop and Sălăgeanu, 1965).

In 1979 three well-known reserves (Pietrosul Mare-Rodna; National Park Retezat and Roşca-Letea forests in the Danube Delta) were designated biosphere reserves, and were included in the list and map of MAB-UNESCO (Figure 1).

Figure 1. Alpine landscape with Pinus mugo in National Park Retezat. Photo: S. Radu.

According to the act on environmental protection (1973) and to world criteria, the following protected areas and natural sites exist: 1) national parks; 2) natural parks; 3) natural reserves (of zoological, botanical, forestry, palaeontological, speleological, sea or mixed importance); 4) scientific reserves; 5) landscape reserves; 6) nature heritage sites (rare or endangered species, century-old trees, peculiar geological phenomena, fossil sites) outside or inside the parks and reserves. Several wooded areas have been added to these protected areas: a) certified seed sources and seed orchards; b) arboretums and dendrological collections; c) century-old forest (having a natural uneven-aged structure as well as the natural stands of pine, larch, yew, *Pinus cembra* and lilac); d) valuable stands of exotic trees (Douglas-fir, white pine, red oak, black locust); e) stands included in wildlife reserves; f) stands included in buffer areas of reserves.

Between 1955 and 1975 the total area of nature heritage sites and reserves grew from 67 000 ha to 144 000 ha, i.e. from 1.0% to 2.3% of the total forest area (Stoiculescu, 1989). The main objective was the protection of these areas. Research was done prior to their designation and protection, and is continuing.

The national forest inventory (1984) mentioned that stands which have officially been declared as nature heritage sites cover an area of 8395 ha and that 62 121 ha are scientific reserves supervised by Romanian Academy (CMN) and by Forest Research and Management Institute

(ICAS). An unofficial list of scientific reserves (in fact natural reserves) published in 1986 contains: 355 natural reserves (111 527 ha); 31 nature heritage sites (364 ha) and 13 national parks (one existent - PN Retezat - and 12 proposed) - plus 399 protected sites (Stoiculescu, 1989). The total number of strict forest reserves exceeds 111, but many other reserves (botanical, zoological, geological, landscape reserves etc,) are located in forests, surrounded by trees and protected by forest service staff.

The most relevant forest reserves include: the Letea forest (in the Danube Delta), Domogled (Figure 2), the virgin forests of Tisa and Viforia in Penteleu Mountains, the virgin forests in Retezat, Pietrosul Rodnei, Slatioara, Valea Cernei etc., Bejan (with natural hybrids of oak species), Tismana (with chestnut trees, Ciurumela (black locust) and others which are very valuable because of their composition, sturcture and authenticity.

Soon after the revolution (1989), 12 other existing but not legally recognized natural parks were designated and added to the management of the forest service by order of the Ministry of Waters, Forests and Environment (27.01.1990). These recently designated national parks are: 1) Rodna (54 400/18 400)[1]; 2) Ceahlâul (17 200/1400); 3) Bucegi (37 700/9000); 4) Piatra Craiului (14 800/6100) ; 5) Cozia (17 100/7 300); 6) Domogled-Valesa Cernei (60 100/24 400); 7) Apuseni (37 900/9600); 8) Cheile Bicazului-Haşmaş (11 600/6200); 9) Cheile Nerei-Beuşniţa (37 100/8 800); 10) Semenic-Cheile Caraşului (30 400/8600); 11) Câliman (15 300/8300) and 12) Danube Delta (the forests of Letea, Caraorman and Sfîntu Gheoerghe (9100/5211). They comprise an area of 399 400 ha and represent forest ecosystems of exceptional scientific, genetic and landscape value. The almost undisturbed natural forests also comprise the major part of these recently designated national parks. A research programme has been started in these new areas, in order to establish the boundaries of various protected sites and the appropriate management strategy.

Thanks to the efforts made during the last five decades by CMN, forest staff and other institutions to protect the forests, the human impact and degradation are less perceptible. Nevertheless, today's human pressure on the reserves (particularly from tourism) severely threatens the reserves, and vigorous law enforcement and management are required.

Forest research programme

Many scientific reports, monographs and publicity brochures have been published on each of these reserves. Many studies have been done on the scientific and landscape significance of forest reserves - and on protection measures. The results are published regularly in the CMN bulletin "Ocrotirea naturii şi a mediului înconjurâtor", in "Revista pâdurilor" (Journal of Forests), and in other university papers in Cluj, Iaşi, Timişoara, Braşov and Craiova. Many studies on the Retezat National Park - which celebrated its half century of existence in 1985 - have been published. They include two special publications.

Regional symposiums on geography, botany, ecology and nature protection have been organized during the last four decades, to coincide with study-tours. Sustained public relations and educational campaigns have been carried out too.

An integrated research programme on the present-day state and the expected development of natural reserves in our forest heritage has been developed since 1988 in ICAS (Stoiculescu, 1989). In this study a monograph has been produced for each reserve, describing the administrative and legal status, importance, the intensity of human impacts on biotope and biocenose, as well as suitable protection measures. Another research programme started this year (1992), on the preser vation and protection of endemic, rare and endangered plant and animal species in forest ecosystems.

[1]the total area including buffer zone/special protected area in ha.

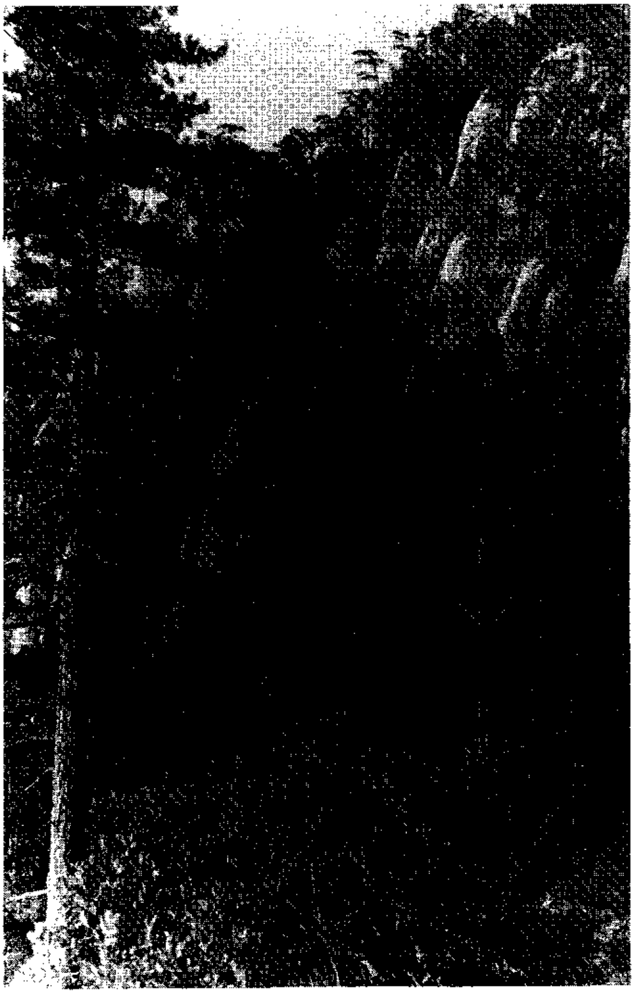

Figure 2. *Pinus nigra var. banatica* (Georg et Ion) with *Syrinhes vulgaris* L. understorey in the Domogled reserves. Photo: S. Radu.

A national monitoring programme which aims at the observation of various environmental factors (soils, waters, air and forests) has been implemented on a national scale in the last decade. Safeguarding forest reserves and preserving genetic resources (gene pools) is an essential part of the forest monitoring (Patrascoiu and Ciobanu, 1988). Unfortunately, all of Romania's forest heritage, forest reserves included, is currently being subjected to increased pressure and attack during the nation's transition to a free market economy. Forests are paying the price of transition too.

New legislation on environmental protection and other decrees affecting forests are in the pipeline. This legislation must safeguard a forest heritage that has sacrificed much to society and history. Stringent protection measures (including legislation, management, technical support, education) must stop the irreversible degradation and the disappearance of less degraded fragments of natural forest.

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The virgin forests and reserves in Slovakia

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Summary

The 332 existent state nature reserves in Slovakia include 74 forest reserves. These reserves represent the greatest and strictest degree of protection of ecosystems. The State Nature Conservation body is responsible for these reserves. To ensure good protection, scientific research is needed.

Keywords: forest reserve, nature conservation, virgin forests

Introduction

Two-thirds of the 127 876 km^2 of the Czecho-Slovakia belongs to the Hercynic system and about one-third belongs to the geologically younger system of Carpathians. The range in altitude is almost 2600 m (minimum altitude the Bodrog river in the Eastern Slovakia 94 m and the maximum altitude Gerlach 2655 m). It is possible to find all central European landscape types in Czecho-Slovakia, except the glaciers and the sea coast.

The flora of Czecho-Slovakia comprises about 3500 plant species which represent about 2500 plant communities; the fauna is represented by approximately 60 000 animal species, including 600 vertebrate species (78 mammal, about 400 bird and 65 fish).

Present network of protected areas in Slovakia

According to the Slovak National Council Act No 1./1955 on state nature conservation, the following areas can be declared as protected: national parks, protected landscape areas, state nature reserves, protected sites, protected study areas, protected natural phenomena, protected natural monuments, and protected parks and gardens.

By January 1, 1991 332 state nature reserves (including 74 forest reserves), 101 protected sites, 188 protected natural phenomena (including 40 caves), 19 protected study areas, 4 protected parks and gardens and 20 protected natural monuments were present in Slovakia. The areas are of various sizes (from one hectare to several thousands of hectares). Reserve and protected sites represent the greatest and strictest degree of protection valid for all components of ecosystems.

Care for protected parts of nature

Each protected area represents a set of various subsystems with a different level of natural diversity and of human interference. Therefore, in terms of active nature protection, different ways of protection have to be applied. At present in Slovakia the differential approach is being applied to look after small protected areas (especially reserves and protected sites) i.e. by professionally elaborating a specific regime for protection. To elaborate this specific regime (conservationist's plan of protection) it is necessary to inventory these reserves. This not only involves making a list of flora and fauna and describing inorganic nature but also includes an investigation of specific sources of negative impact on natural systems, of the degree of damage done to individual components of ecosystems, and of the prospects for restoring self-regulatory processes. It also sometimes requires measures to be implemented by the state nature conservation bodies. Without proper research and an understanding of interactions between components of geobiocenoses, every interference would merely be a purposeless routine.

The State Nature Conservation body works out a specific regime of protection and covers the costs involved in implementing it. The appropriate measures are carried out by the managers of national parks and protected landscape areas. This management is based on general principles of scientific management, with the emphasis on the individuality of ecological processes in complicated biological entities, such as small protected areas and their species gene pool.

To avoid uncontrolled interference in the evolution of reserves' ecosystems, it is necessary to elaborate a specific protection regime using a series of interventions adequate for the present conditions of ecosystems' structure and for the aims of the individual reserves and protected sites. Until recently the need for scientifically justified inventories in some reserves was tactfully postponed and, under the pretext of "not complicating the situation", ecosystems designated as reserves were left to further spontaneous evolution. Management has been reduced to marking the area and excluding visitors.

Scientific inventorying research is needed to obtain information that will enable theory to be generated. The following facts need to be underpinned by theory:

- forest ecosystems are structurally and functionally very complicated;
- the principal component of forest ecosystems (wood) is long-lasting and in natural conditions has a life-cycle of hundreds of years;
- because of the lack of understanding of population dynamics, ecological links and reciprocal exchange of matter between organisms and their environment, forest ecosystems are still little explored;
- ecosystems of reserves and the gene pool of plants and animals are still subjected to human intervention (air pollution, game, too many visitors, etc.).

These facts hamper protection and therefore the planned interventions to reserves are, in the long run, also unpredictable.

The virgin forests and forest reserves

Definition

Virgin forest is primary forest free from human intervention. A natural forest is characterized by an original tree species composition and by a different age structure, like a virgin forest, and is able to regenerate spontaneously. Yet it has visible features of human interference in biocenoses. It was formed after the mediaeval exploitation in the mountainous, poorly accessible forests. The tree species may be indigenous or exotic (with indigenous and exotic species coming from the broader area and behaving naturally due to their environmental constitution in the present tree species group and forming a naturally regenerating part of the present total wood complex).

Although there are hardly any real virgin forests in Central Europe, natural forest representing the mostly conserved remnants of the forests are usually considered under the term virgin forest, as well as those forests which are influenced by man to some extent but have their original tree species composition, are unevenly aged, and have different vertical and horizontal structures.

Forest reserve types in Slovakia

Since the end of the last century, interest in virgin forests has increased in Europe, largely for scientific reasons. At that time there were already primaeval reserves on the territory of the present Slovakia: Šalkovský les — Príboj and Ponická Huta (1895). Before World War I the following reserves were designated: Stužica (1908) virgin forest, Súľovské skaly (1907), the Szabova skala volcanic rock area (1907) (interesting botanically too) and two classic virgin forests - Dobročský prales (1913) and Badínsky prales (1913). Between the two World Wars the number of reserves in Slovakia increased to 18, however, no virgin forests were added.

In the natural range of oak in Slovakia, i.e. in the oak, beech-oak and oak-beech zones, there are a small number of natural forests. Most are even-aged forests and often young oak and mixed oak-beech forests with hornbeam. In such forest types conservation aims at protecting the rare xerothermous plants. Real virgin-like forests are found in the Kašivárová forest reserve in the Štiavnické vrchy, and partially also in the Kokošovská dubina forest reserve, where the gene pool of the valuable ecotype of oak is protected. The natural oak forests are in forest reserves Jasovské dubiny in the Slovenský kras, Príboj and Ponická huta in the Zvolenská kotlina, Boky in Kremnické vrchy, Krčmárka and Malé Brdo in the Slánske vrchy and Bujanov in the Čierna Hora. The oak forest reserves of eastern and central Slovakia suffered serious damage from oak wilt (tracheomycosis) in 1981 — 1987.

In the natural range of beech (beech vegetation zone), relatively many natural forests are present, with some partly natural forests as well. The regeneration processes take place on large areas, or in groups. The virgin forests are found in Havešová in the Bukovské vrchy, Korbeľka in Malá Fatra, Morské oko and Vihorlat on Vihorlat mountain, Raštún in Malé Karpaty, Hrádok and Hajšová in Malá Fatra, Javorníková dolina in Muráňska Planina. The natural forests are in Veľká Branica, Pripor and Šútovská dolina in the Malá Fatra, Sitno in Štiavnické vrchy and elsewhere. The area of natural beech forest is approximately 1500 ha.

The largest number of natural forests is present in the forests consisting of beech, fir and spruce. There are approximately 2000 ha of natural forest and approximately 4500 ha of natural mixed forest. The classic virgin forests include the Dobročský prales, Hrončokovský grúň in the Slovenské Rudohorie, Badínsky prales in Kremnické vrchy, Stužica, Rožok, Pľaša and Udava in the Bukovské vrchy, Beskydy, Komárnická vrchovina, Palotská jedlina and Dranec in the Laborecká vrchovina, Pod Latiborskou hoľou in the Low Tatras, Šrámková in the Malá Fatra and Padva in the Veľká Fatra.

The natural mixed forests are in the Čierna Lutiša and Kysucké vrchy in the Kysucké vrchy. Among the abovementioned forest reserves aimed at the principal forest vegetation zones, several are also being designated in the karst areas and in wet localities, with a high water table.

At present there are 74 forest reserves in Slovakia, with a total area of approximately 70 000 ha. Of this area 11% is represented by oak, 9% by beech, 45.5% by beech-fir-spruce, 20% by spruce, 14% by dwarf pine and 1.5% by alder, birch and willow forest communities. A review of forest reserves is given in Table 1.

Furthermore it is necessary to mention several forest reserves which are protected in national parks. At present there are five national parks in Slovakia (High Tatras, Low Tatras, Malá Fatra, Pieniny and Slovenský Raj) in which several forest reserves with well developed virgin or virgin-like character are present. The same is tru for the five national parks in Poland (High Tatras, Babia Góra, Pieniny, Górce and Bieszczady) and for three national parks in the Ukrainian Carpathians (including the largest beech virgin forest, of 7000 ha) and eight national parks in the Romanian Carpathians (Radu, this volume).

Forest reserves research

In contrast with other parts of Bohemia and Moravia, in Slovakia the poorer terrain conditions and less industrialization mean that part of the species composition of the forests still resembles the original conditions with a predominance of beech. On the other hand, in part of the area the species composition has been changed into monocultures, notably of spruce. It is now understood that in these monocultures it is necessary to find and enforce new measures which will link the productive and social functions of the forests without destroying them. It is impossible merely to copy or mimic the original forests, e.g. because the virgin forests have often been formed under the effect of antagonisic natural forces.

One of the main reasons why so much care is being devoted to the remnants of virgin forest is that their composition and development are being subjected to scientific research. From this research the basic natural laws valid for the existence and development of healthy and multipurpose forests are derived. Such research has been done in 25 of the best preserved reserves.

Table 1. Characteristic of the forest reserves in Slovakia (modified from Korpeĺ, 1989).

No.	Forest Reserve (geographical unit)	Size [ha]	Degree of origin	Degree of danger	Altitude [m]	Veg. level
1	Istragov (Podunajská nížina)	14.00	B(C)	b(c)	120	1
2	Kováčovské kopce	120.00	C(B)	b(c)	110-268	1+2
3	Ostrov kormoránov (Podunajská nížina)	110.00	B(C)	b(a)	130	1
4	Palárikovská bažantnica (Podunajská nížina)	38.00	B(C)	b	150-160	1
5	Rašelinisko bôĺ (Východoslovenská rovina)	11.77	B(C)	b(c)	103	1
6	Šúr (Podunajská nížina)	350.00	B(C)	b(c)	130-140	1
7	Veĺký Lél (Podunasjká nížina)	12.20	A(B)	b(c)	110	1
8	Boky (Kremnické vrchy)	176.49	A(B)	b(c)	180-589	1+3
9	Bujanov (Čierna Hora)	88.17	B(C)	a(c)	530-765	1+3
10	Kašivárová (Štiavnické vrchy)	19.46	B(C)	b	475-600	2+3
11	Kokošovská dubina (Slánske vrchy)	20.00	B(C)	b	470-520	2+3
12	Lesná (Štiavnické vrchy)	6.11	B	b(c)	550-600	2
13	Malé Brdo (Slánske vrchy)	55.56	B(C)	b	550-615	2+3
14	Sitno (Štiavnické vrchy)	45.49	A(B)	b(a)	750-1011	3+4
15	Kocúrová (Slovenské Rudohorie)	16.72	B(A)	b	510-600	3+4
16	Šivec (Slovenské Rudohorie)	57.78	B(A)	a	480-784	3+4
17	Dranec (Nízke Beskydy)	34.22	A(C)	b	330-515	4
18	Harmanec (Veĺká Fatra)	45.00	B(C)	b(c)	750-900	4+5
19	Havešová (Bukovské vrchy)	81.51	A	a	550-650	4
20	Komárnik (Nízke Beskydy)	23.65	A(B)	a	515-572	4+5
21	Kyjov (Vihorlat)	53.40	A	a	700-820	4
22	Magura (Nízke Beskydy)	76.64	B(A)	a(b)	650-900	4+5
23	Malý Milič (Slánske vrchy)	14.95	B(A)	a(b)	725-780	3+4
24	Maročká hoĺa (Slánske vrchy)	50.23	B(A)	a(b)	590-635	4
25	Oblík (Slánske vrchy)	89.58	A(B)	a	620-930	3+4+5
26	Pĺaša (Bukovské vrchy)	118.64	A(B)	a	880-1163	4+5
27	Raštún (Malé Karpaty)	18.00	B(C)	b	310-748	3+4
28	Riaba Skala (Bukovské vrchy)	94.97	A(B)	a	1050-1199	4+5
29	Rožok (Bukovské vrchy)	67.13	A	a	520-796	4+5
30	Šimonka (Slánske vrchy)	55.03	A(B)	a	830-1092	4+5+6
31	Veĺký Milič (Slánske vrchy)	67.81	B(A)	b	660-820	3+4
32	Vozárka (Slovenské Rudohorie)	76.63	C(B)	b	500-738	4+5
33	Badínsky prales (Kremnické vrchy)	30.70	A(B)	b	710-770	4+5
34	Čierna Lutiša (Kysucká vrchovina)	27.06	B(C)	b	665-904	4+5
35	Kĺak (Malá Fatra)	85.71	B(A)	a(b)	1050-1350	4+5
36	Mokrá (Stratenská hornatina)	60.20	B(C)	a	950-1188	4+5
37	Veĺký a Malý Kysel (Stratenská hornatina)	210.00	B(A,C)	b	493-1000	4+5
38	Veĺký a Malý Sokol (Stratenská hornatina)	240.00	A(B)	a	610-1138	4+5
39	Dobročský prales (Slovenské Rudohorie)	101.82	A(B)	a	700-1000	4+5+6
40	Stužica (Bukovské vrchy)	423.38	A	a	650-1220	4+5+6
41	Veĺký Javorník (Javorníky)	13.95	B	S(b)	1000-1077	5
42	Hrončokovský grúň (Poĺana)	55.22	A(B)	a	659-950	5+6
43	Juráňová dolina (Západné Tatry)	120.00	B(A,C)	a(b)	750-1300	5+6+7
44	Klenovský Vepor (Slovenské Rudohorie)	129.94	A(B)	a(b)	1100-1339	5+6+7
45	Korbeĺka (Veĺká Fatra)	86.10	A(B)	a	625-1000	5+6

Table 1. Characteristic of the forest reserves in Slovakia (modified from Korpel̆, 1989).

No.	Forest Reserve (geographical unit)	Size [ha]	Degree of origin	Degree of danger	Altitude [m]	Veg. level
46	Kornieťová (Veľká Fatra)	84.05	A(B)	a	908-1254	5+6
47	Kundračka (Veľká Fatra)	115.79	B(A)	a	900-1280	5+6
48	Lipová (Veľká Fatra)	31.27	A(B)	a	950-1260	5+6
49	Ľubietovský Vepor (Poľana)	124.60	A(B)	a	950-1277	5+6
50	Malá Stožka (Muráňska planina)	59.61	B(A)	a	805-1204	4+5
51	Padva (Veľká Fatra)	325.46	A(B)	a	850-1440	6+7
52	Pod Latiborskou hoľou (Nízke Tatry)	88.27	A(B)	a	830-1280	5+6
53	Pod Chlebom (Malá Fatra)	222.77	A(B)	a(b)	710-1350	5+6+7
54	Rozsutec (Malá Fatra)	650.00	B(A)	a(b)	800-1610	5+6+7
55	Rumbáre (Veľká Fatra)	51.59	A(B)	a	825-1125	5+6
56	Šrámková (Malá Fatra)	99.27	B(A)	a	700-1280	5+6
57	Turková (Nízke Tatry)	107.00	A(B)	a(b)	600-900	4+5+6
58	Veľká Bránica (Malá Fatra)	184.68	B(A)	a(b)	720-1300	5+6
59	Veľká Stožka (Muráňská planina)	209.55	A(B)	a	875-1342	5+6
60	Vtáčnik (Vtáčnik)	195.97	A(B)	a	1250-1345	5+6
61	Bacúšška jelšina (Slovenské Rudohorie)	4.26	B	b(c)	561	6
62	Čierny Kameň (Veľká Fatra)	34.40	A(B)	a(b)	1200-1480	7
63	Ďumbier (Nízke Tatry)	650.00	A(B)	a(b)	1200-2043	6+7
64	Jánošíková kolkáreň (Veľká Fatra)	46.81	A(B)	a	1175-1489	5+6+7
65	Javorina (Vysoké Tatry)	1700.00	B(A)	b(a)	100-2206	6+7
66	Babia Hora (Západné Beskydy)	530.33	A(B)	a	1100-1440	6+7
67	Kotlov žľab (Západné Tatry)	46.94	A(B)	b	1250-1550	6+7
68	Ohnište (Nízke Tatry)	420.00	A(C)	a(b)	900-1530	6+7
69	Osobitá (Nízke Tatry)	230.00	A(B)	b	1180-1680	6+7
70	Pilsko (Západné Beskydy)	580.00	A(B)	a	1050-1557	6+7
71	Podbanské (Vysoké Tatry)	1800.00	A,C(B)	a(b)	980-2496	6+7
72	Poľana (Poľana)	685.84	A(B)	a(b)	554-1456	5+6+7
73	Skalná Alpa (Veľká Fatra)	67.46	A(B)	a(b)	1070-1420	6+7
74	Vyšné Hágy (Vysoké Tatry)	1600.00	A(B)	b(a)	970-1898	6+7

Degree of origin:

A. very well protected original state with no traces of human influence;

B. well protected original state with minor human influence (cutting of individual trees) or recently damaged by natural catastrophes;

C. virgin forest which could have been influenced by human activity long ago or with traces of human influence; damaged by larger natural catastrophes.

Degree of danger:

a. virgin forest or state nature reserves not endangered by human influence;

b. virgin forest or state nature reserve partially endangered by recreation, industry etc;

c. virgin forest or state nature reserve seriously endangered due to the factors given above. If the protection of these forest reserves is not improved they will decline (Korpel̆, 1989).

Vegetation level:

1 oak, 2 beech-oak, 3 oak-beech, 4 beech, 5 fir-beech, 6 spruce-beech-fir and 7 spruce forest

Between three and six reserves were selected from each main vegetation and forest type. In these reserves three to six research plots of 0.5 ha were established. During 25 years various aspects of forest dynamics have been measured, at intervals of 5-10 years (Korpeľ, 1989).

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The Dutch forest reserves programme

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Summary

The Dutch Forest Reserves Programme officially started in 1983, when the first forest reserves were designated. So far, 27 reserves have been established. Each forest reserve represents a specific site type and forest type. Each year five new reserves will be established, leading to a representative network of approximately 75 reserves in The Netherlands. Most forest reserves are administered by the National Forest Service, department of the Ministry of Agriculture, Nature Management and Fisheries which is the main user of the Dutch forest reserves programme.

The forest reserves are strict reserves intended for research. An integrated research programme with a ten-year monitoring frequency has been developed. The study concentrates mainly on the forest dynamics and the development of the vegetation.

Keywords: forest reserve, forest research, monitoring

Introduction

The Netherlands is one of the least forested areas in Europe (only 10% of the total land area) and has no virgin forest. Exploitation and deforestation since the Middle Ages (cattle and sheep grazing, the need for fire-wood, timber and arable land) drastically reduced the forested area, so that it was only 1% of the total land area at the end of the 19th century. Large areas of heathland and drift sands developed. The last virgin forest, although managed to some degree, the "Beekbergerwoud", was felled in 1869. But a few old planted woodlands have been protected and managed well for several centuries, like the Speulderbos, an old beech-forest (part of which is also designated as a forest reserve, see Figure 1).

Afforestation of heathland and drift sands started in the 19th century. At present forest, either established spontaneously or planted, accounts for approximately 10% of the total area (320 000 ha). Most of the forested area is on the relatively high-lying Veluwe.

Part of the forest area is protected as nature reserves, by national or local government or by private nature conservation organizations. These are nature reserves aiming at the conservation of flora and fauna of the forest area. Forest reserves used in the sense of this article serve another goal. They are intended to be used for research on forest ecosystems in which human intervention is absent. The information gathered should, ultimately, help ensure successful forest management. Originally the Dutch government designated these forest reserves.

Motives

At the end of the 1970s there was much discussion about the "naturalness" of the Dutch forests, especially about whether it was possible to allow naturally-occuring processes to be studied. The general opinion was that little was known about spontaneous processes in forest ecosystems. The main reasons were:

Figure 1. The Speulderbos forest reserve, a floristically characteristic Fago-Quercetum, also designated as nature reserve.

- most of the Dutch forest sites were reafforested during the last century, so the stands are even-aged and of the first and second generation;
- almost all forests have been managed intensively e.g. afforested with exotic tree species; some of the soils have been tilled and fertilized, there has been intensive felling;
- the few forests that have developed spontaneously have not been monitored.

On the other hand some of the main goals of the Dutch National Long-term Forestry Plan are (Meerjarenplan Bosbouw, 1986):

- increased timber harvest from existing forests and from newly planted forests
- 18% of the total forested area will be designated exclusively for nature conservation
- basically all forests will have to be made more attractive for outdoor recreation
- most forests will be multi-functional in future, which implies the development and maintenance of the naturalness of the forests
- part of the silviculture will focus on converting even-aged, monotonous stands into mixed stands with an improved vertical structure

Because of insufficient knowledge of the forest ecosystem, many questions (e.g. on tree regeneration, species competition, structure development without management, spontaneous vegetation development) arose as to how to implement these plans in forest management.

Current research on forest structure and dynamics had solved only some of these problems: most studies were concerned with only some of the various factors that play a role in the forest ecosystem. Furthermore most research had been done in intensively managed forests and was short term. The main conclusion at the end of the 1970s was that there was a clear lack of knowledge. It was thought that long-term monitoring of the various factors that determine ecosystem development in undisturbed forests would provide some of the essential information and knowledge.

The rising costs of forest exploitation forced foresters to extensify management and therefore they became more interested in spontaneous processes, e.g. of self thinning.

Purpose of forest reserves

Approximately 80% of forests administered by the Dutch National Forest Service consists of first-generation growth. Most of these forests have been cultivated in the last 100 to 150 years. The structure of these pioneer forests is very straightforward: they are mostly even-aged monocultures. The cultivation and maintenance of first-generation forest was and still is very intensive. Younger cultures in particular demanded extremely careful (and expensive) maintenance, because they had largely to be cultivated in the absence of the protection afforded by old forests and without the humus layer such forests would have provided.

A large proportion of these forests is now ready for rejuvenation. Artificial or natural rejuvenation enables young forest of the second or third generation to grow as much as possible of its own accord. In many cases the administering body can limit itself to the initiation and discreet control of forest development. Many customary and frequently applied management methods can and indeed often must be discontinued. In this way other and less intensive methods will gain a foothold. One possibility is therefore to adopt suitable methods from abroad. But afforestation as described above differs somewhat to what is usually found in similar habitats outside The Netherlands. That is why research in the Netherlands into the approach most suited to the specific situation in the new generation of forest is also necessary. An important part of the knowledge in this field will have to be sought in the forest reserves. Natural processes and their practical application in today's and tomorrow's forest management should lead to a less extensive administration. As a result of these efforts forest managers anticipate a control that is both ecologically and economically less intensive.

Aim and definition of forest reserves

In response to the motives mentioned above the Minister of Agriculture, Nature Management and Fisheries decided that forest reserves should be established. Their main aim is to improve the understanding of spontaneous processes in forest ecosystems by means of research and monitoring. Forest reserves are selected areas of forest where no management will take place other than the protection against disturbing influences from outside the reserve (strict reserves). If people know more about natural forest dynamics, there will be a more realistic view of how much flexibility can be allowed in forest management. Furthermore, if it is known how managed forests differ from natural forests, there will be at least a better appreciation of the benefits and disadvantages of management.

So forest reserves are like outdoor laboratories for the study of natural processes in undisturbed ecosystems, although the research that is done concentrates on monitoring and describing the spontaneous processes by systematic observations and not by experiments. If forest owners could be provided with more information about these processes, this could result in extensive management and adaptation of management techniques to mimic natural processes. Thus, ultimately the relation between forest management and spontaneous processes that could be used in silviculture should be clarified.

On the other hand, strict forest reserves will contribute to the conservation of wildlife, especially by providing habitats for species associated with old growth forest. The present forest reserves are reasonably congenial to the faunal species sharing the habitat. Several of these species can exercise an important effect on forest development through their way of life. Roe deer, hares, rabbits, various bird species etc. can impede forest development and actually even stop it temporarily or permanently. The forest manager needs to be aware of this possibility, and if necessary may take appropriate measures to control the population of these species.

Organization

The Dutch forest reserves programme was initiated by the Dutch government i.e. the Ministry of Agriculture, Nature Management and Fisheries. The minister is the main user of this programme. Various departments within the Ministry have been partners in this programme from the outset. Policy, forest management and forest and nature research were involved by developing the aims and the programme.

The National Reference Centre of the Department for Nature, Forests, Landscape and Wildlife (IKC-NBLF), is responsible for selecting and designating the forest reserves. They keep in contact with the forest owners and carry out most of the inventory. So far, most of the forest reserves are owned by the Department of the National Forest Service (SBB). The concept of forest reserves has been actualized in the terrains managed by this Service. Other forest-administering organizations are gradually showing interest in allocating forest reserves in their domains too. This tendency provides strong evidence that the philosophy underlying the allocation of forest reserves is now being realized and accepted in The Netherlands. The owner is responsible for the management of the forest reserve (which consist of non-intervention) and supports the inventory.

Finally, two institutions of the Agricultural Research Department are involved. The Institute for Forestry and Nature Research (IBN-DLO) is responsible for:
- the coordination of the research programme;
- the storage and conservation of all the data collected;
- the analysis and interpretation of the data;
- specific parts of the inventory.

The Winand Staring Centre (SC-DLO) is responsible for the soil inventory and research and for the analysis and interpretation of these data. Other participants are the University of Amsterdam, which is doing research on humus form profiles and the Dutch Mycological Society which is inventorying the mycoflora (Broekmeyer and Hilgen, 1991).

The forest reserve research programme is part of various government policies (Uitvoeringsprogramma Meerjarenplan Bosbouw, 1990).

Selection of forest reserves

Because the natural processes that occur in forests differ in the various types of forest, forest reserves have to be selected in such a way that they form a representative reflection of the Dutch forest area. The main factors that determine the type of forest are: site type, species composition and forest history. These three factors form the primary selection criteria and have been implemented in the selection programme by using the following classification systems:
- Site type: is reflected in a site classification that differentiates into geological and general soil features, resulting in 13 site regions (Firet, 1985).
- Species composition: is reflected in a typology based on the potential natural vegetation. The PNV describes the composition of the vegetation after 100-200 years undisturbed development. This resulted in 33 forest vegetation types for The Netherlands (Van der Werf, 1991).
- Forest history: is reflected in a typology based on land use before afforestation and the age of the forested area. It contains 13 types (Van den Wijngaard, 1984).

A combination of these three typologies led to approximately 50 characteristic forest types. Within such a forest type a planted as well as a spontaneous forest could occur. This often occurs in The

Netherlands. Planted forest stands often consist of monotonous even-aged stands of one species, mostly planted *Pinus sylvestris*, see Figure 2. More natural forests have developed spontaneously on abandoned fields or areas not suited for cultivation. They mostly consist of secondary or young primary forest with a species combination corresponding to the PNV. However, most of the Dutch forest area is planted with exotic species, and researchers and foresters also want to know how these forests will develop in time.

If the species composition of the herb layer corresponds to the potential natural vegetation, it is called floristically characteristic. If it does not than it is called floristically uncharacteristic. If both types can be found on a site type, they will both be designated as forest reserves. Therefore both floristically characteristic as well as floristically uncharactersistics sites are included in the programme, resulting in approximately 75 characteristic forest types.

Figure 2. A floristically uncharacteristic pine forest; Nieuw-Milligen forest reserve.

Management

Forest reserves have an official status, as they are designated by the Minister. The Minister recommends the forest owner to designate and manage the area concerned as a forest reserve. Nevertheless, for judicial reasons, no direct legal status can be applied to forest reserves. Once a forested area has been designated as a forest reserve, an document concerning the rules of forest management will be drawn up with the forest owner and the local administrator. The ownership should be as stable as possible, to safeguard the reserve. If a forest reserve is selected a guarantee must be given that it will not be disturbed for at least the next 50 years. If it is in privately-owned forest area, there is a serious problem because the private owner has to guarantee the long-term research and in most cases this is very difficult. In some cases exemptions from national forest laws also have to be granted. For example, the obligation to replant if the overstorey of the reserve is destroyed by storm or disease may be removed. And development plans (for recreation, cultivation, industry) must be secured.

In addition to his usual surveys the local administrator can carry out many worthwhile inspections in a variety of areas, based on his own knowledge and proximity. In this sense a forest reserve is an open school within nature herself. This open shool should not only be the preserve of the administration. As long as excessive visiting does not disturb a forest reserve's natural growth, it is very important that as many specialists as possible be enabled to accustom themselves to these developments. In many cases it is precisely in such natural areas that particular phenomena can be studied before being explained and applied in practice. Then, perhaps, closely-supervised education in the school of nature within the forest reserves can, under certain circumstances, be made available to the public at large.

The borders of the forest reserve are not marked, so visitors will not know they are entering a forest reserve. It is of course forbidden to disturb or harvest anything from the forest, but as most reserves are designated in already protected conservation areas there is no need for additional marking of the reserves. Recreational activities are neither prohibited nor encouraged. Facilities like picknic tables, bridleways, etc. are removed. Motorways and foothpaths are not kept open unless required for fire ways.

The forest reserve is surrounded by a protection or buffer zone whose width is approximately twice the height of the trees. The management in this zone has to be adjusted to the maintenance of the forest reserve. For example, measures against insects and seed-producing exotic trees could be carried out in this zone.

So far, 27 forest reserves have been designated (see Table 1 and Figure 3). Each year five new forest reserves are selected. Their area varies from 15 to 40 hectares. By the year 2000 all 75 forest reserves should have be designated, covering 1% of the total forested area in The Netherlands.

Research programme

Intention

The study of forest reserves implies monitoring of spontaneous processes in permanent plots. Permanent plots have the advantage that they enable succession to be observed directly in detail as it takes place. On the other hand there is the limitation that you have to wait for this succession to take place, so the most interesting results will not emerge until after several decades. It is expected (and research in other countries confirms this) that these observations will be worthwhile.

The research programme has three main goals:

1. inventory of spontaneous processes (inventory);
2. analysis and interpretation of these processes and the associated factors (research);
3. analysis of the importance of these processes for the dynamics of the forest ecosystem (management).

Within the Dutch programme the most important parts of research are: vegetation development, the development of the forest structure and the study of forest dynamics. The spontaneous processes are studied from various points of view. Attention is paid to:

1. site (soil, humus profiles, hydrology);
2. forest dynamics (population development, forest regeneration, stand succession);
3. forest structure (tree position, dead wood, vitality, crown projection);

Table 1. Review of some characteristics of the present Dutch forest reserves (on 31 december 1991).

no.	NAME OF FOREST RESERVE - LOCATION	SURFACE	PNV
1	Starnumansbos - Gaasterland	53 ha	fl. Betulo-Quercetum
2	Lheebroek - Dwingeloo	39 ha	n.fl. Betulo-Quercetum
3	Galgenberg - Amerongen	48 ha	fl. Fago-Quercetum
4	Tussen de Goren - Chaam	40 ha	n.fl. Betulo-Quercetum
5	Vijlenerbos - Vaals	15 ha	fl. Luzulo-Fagetum
6	Vechtlanden - Ommen	12 ha	fl. Carici elongetae-Alnetum
7	Zeesserveld - Ommen	17 ha	n.fl.Betulo-Quercetum
8	Meerdijk - Spijk/Bremerberg	20 ha	n.fl. Lysimachio-Quercetum
9	Pijpebrandje - Speulderbos	36 ha	fl. Fago-Quercetum
10	Nieuw-Milligen - Garderen-Oost	50 ha	n.fl. Betulo-Quercetum
11	Drieduin 1 - Schoorl	25 ha	fl. Empetro-Pinteum
12	Drieduin 2 - Schoorl	20 ha	fl. Empetro-Betuletum
13	Drieduin 3 - Schoorl	28 ha	fl.Betulo-Quercetum
14	Het Leesten - Ugchelen/Hoenderloo	42 ha	n.fl. Fago-Quercetum
15	't Quin - Bergen (Limburg)	29 ha	n.fl. Betulo-Quercetum
16	't Sang - Mierlo	15 ha	fl. Carici elongatae-Alnetum
17	Grootvenbos - Deurnse Peel	40 ha	fl. Alno-Betuletum
18	Schoonloerveld - Schoonloo	28 ha	n.fl. Fago-Quercetum
19	Oosteresch - Sleenerzand	35 ha	n.fl. Betulo-Quercetum
20	Roodaam - Castricum	35 ha	fl. Convallario-Quercetum
21	Riemstruiken - Kootwijk	22 ha	fl. Fago-Quercetum
22	Zwarte Bulten - Rozendaal	45 ha	n.fl. Fago-Quercetum
23	Leenderbos - Leende	28 ha	n.fl. Betulo-Quercetum
24	De Schone Grub - St.Geertruid	15 ha	fl. Milio-Fagetum
25	Diever Zand - Smilde ..	31 ha	fl. Empetro-Pinetum/Bet.-Quer.
26	Grienden van de Dood - Drimmelen	32 ha	n.fl. Fraxino-Ulmetum
27	Kloosterkooi - Kalenberg	28 ha	fl. Alno-Betuletum

fl. = floristic characteristic
n.fl. = floristic non-characteristic
Bet.-Quer. = Betulo-Quercetum

4. forest vegetation (vegetation types and maps, vegetation succession, species compostition and dispersion, PNVs, inventory of mycoflora).

The inventory of the abovementioned aspects is split into two programmes: the initial program and the basic programme (Table 2). The aim of the initial programme is to record the situation of the forest reserve at the time of designation. As part of this initial programme the primary site factors are recorded, such as macroclimate, topography, parent material and groundwater. It is carried out once, almost immediately after the designation.

The basic inventory is intended to monitor the secondary site factors such as humus profiles, groundwater fluctuations, plant communities and other slowly changing variables to record the forest dynamics and forest structure. The emphasis is on methodical observations of the spontaneous developments of biotic factors of the forest ecosystem. This is done by means of repeated sampling at ten-year intervals (Stuurman and Clement, this volume).

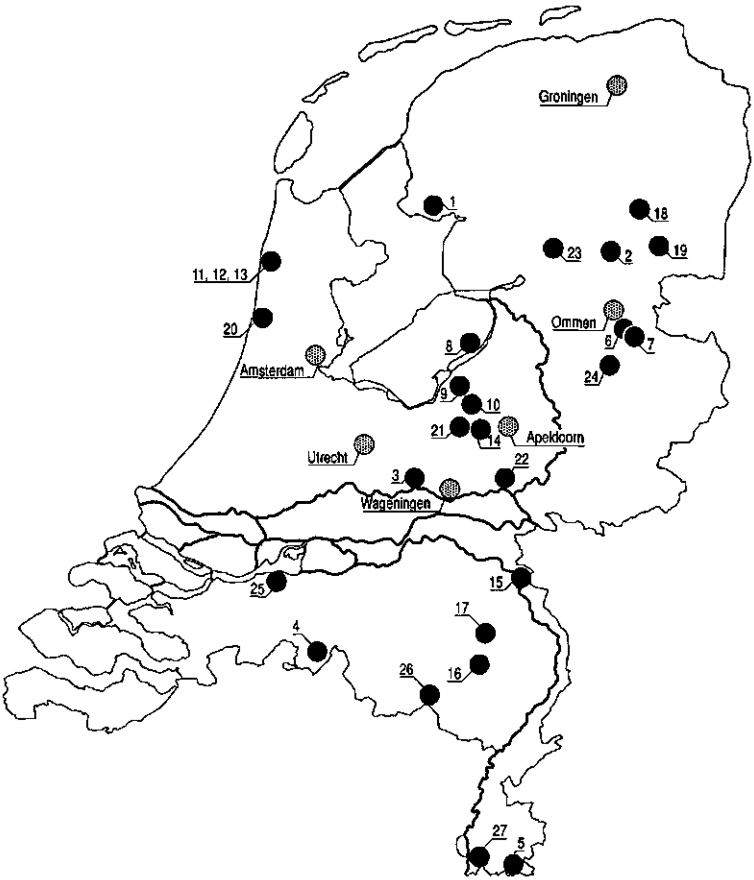

Figure 3. Location of the Dutch forest reserves. For names see Table 1.

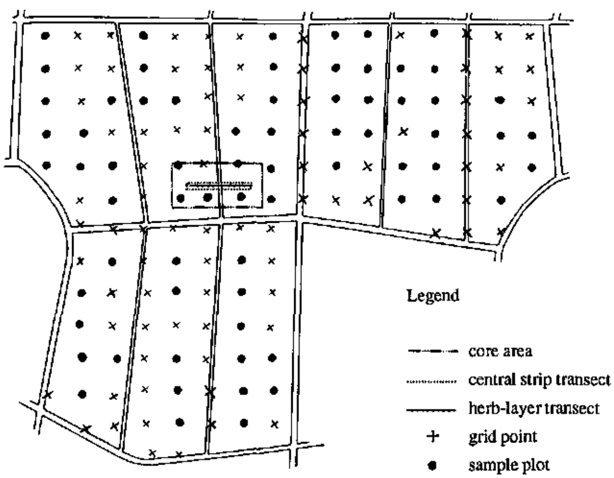

Figure 4. Lay-out of the entire forest reserve.

Table 2. Overview of the Dutch forest reserves programme.

Initial program: Lay-out of forest reserve Marking of core area and sample points Maps scale 1:2500 (base map, fieldwork map, tree-cover map) History of origin Former forest management Soil survery (soil map 1:2500)				
Basic program:				
	Site	Vegetation	Forest structure	Forest dynamics
Whole reserve	Humusform-profiles Groundwater-fluctuations	Vegetation relevés Vegetation map 1:2500 Classification of PNV's	Aerial photography 1:1000 and 1:500	Tree-species/ position/ dbh/ stem length/ height. Vitality Dead wood No. of species <5 cm. dbh
Core area		Vegetation relevés Vegetation map 1:200 Photographs herblayer Species composition and distribution Inventory of mosses and mycoflora	Tree species/ position/ dbh/ height Vitality Map crown projection Map trunks/species numbers 3-D map of trees	/

Lay-out of the forest reserve

To assist the research all forest reserves have been mapped according to a pre-set sampling scheme. Four different scales of study are used, see Figure 4.

1. The entire forest reserve of 15 - 50 ha with 50 - 70 sample points situated on a rectangular grid of 50 x 50 m.
2. The core area, a 1 hectare block, 70 x 140 m.
3. A central strip transect, one-tenth of a hectare strip, 10 x 100 m.
4. A herb-layer transect, in the middle of the strip transect, 2 x 100 m.

re 1) A 50 x 50 m grid is set up for the entire forest reserve. Approximately half of these points (50 - 70 per reserve) are selected as sample plots. Analysis of the gathered data is focused on describing the changes in structure and composition of the forest stands in time and the attendant dynamics of different populations of trees and shrubs. Also soil- and humus samples are collected at the sample plots (Kemmers et al., this volume). Data from the sample plots will also be used to map the forest structure of the entire forest reserve, in conjunction with air photographs, but this part still has to be developed.
re 2) The core area represents the most characteristic part of the forest reserve. It is situated in a

homogeneous part of the reserve and is oriented north-south. It is subdivided into seven transect strips of 10 x 140 m. A part of the central strip forms the strip transect. In the middle of this transect is the transect for the herb layer, consisting of 50 quadrats of 2 x 2 m. The analysis of the data gathered in these parts is mainly focused on the forest structure (Stuurman and Clement, this volume) and the vegetation development. The vegetation of the entire reserve is mapped with the aid of relevés; the vegetation of the core area is mapped in the herb layer transect (Koop, this volume).

The the results are analysed and published by the various participating institutions (Koop, this volume; Kemmers et al., this volume; Veerkamp and Kuyper, this volume). As mentioned earlier the interdisciplinary research will be of major importance. It will deepen insight into the various factors, their mutual relation and the role they play in the development of the forest ecosystem.

Conclusion

A forest reserve programme such as the Dutch one, and probably like those in most other European countries, is based on long-term research. In The Netherlands it has been decided to execute the basic inventory at least five times at intervals of ten years, which implies a monitoring period of at least fifty years. The monitoring of permanent plots means that the most interesting results will be released in the long run.

Policy-makers and managers should be aware of the importance of this kind of research in the interest of their own forest policies.

To warrant a good research programme there are a number of points that should be considered, at national as well as international scale:

1. standardizing of inventory methods; much progress has been made with this in The Netherlands
2. centralized data storage: all data have to be linked
3. safeguarding the reserves against development plans
4. financial safeguarding of the research programme
5. continuous publication and keeping the government and the community informed, so that all are aware and informed on the importance of forest reserves.

For specific problems, ad hoc research can be added to the research programme. The results of the basic inventory should not be used only for forest management (silviculture) but could also be used for the Dutch long-term forestry plans, such as the realization of new forests, for nature development and so on.

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Forestry Canada green plan: ecological reserves

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Summary

Most of Canada's forests remain stocked with native species. While many of Canada's forest ecosystems are sensitive to logging, other human activity may have had more profound effects. The Deciduous Forest Region has been severely impacted by agricultural and urban development, and only small remnants are protected. Other regions are variously represented by ecological reserves. Under Canada's Green Plan, Forestry Canada has established an Ecological Reserves Project to foster the continental network of protected areas. The Project will develop model reserves within the framework of a larger Model Forest Program, enhance the National Conservation Area Data Base, and promote ecological reserves through public awareness and advocacy.

Keywords: forestry, nature conservation, ecological reserves

Introduction

Canada's forest estate is remarkable for its diversity: 12 Forest Regions, 90 distinct Sections, and 131 species of native trees. Occupying 453 million hectares, it constitutes 10% of the world's total forests. This heritage has long been recognized as a major genetic resource for foresters in Canada, and in other countries where the choice of native species is more limited. Many productive forests throughout central and northern Europe are stocked with trees of Canadian origin, resulting from importation of seeds over several decades. Since 1970, when Forestry Canada became the designated authority for the Organization for Economic Cooperation and Development Scheme for the Control of Forest Reproductive Material Moving in International Trade, over 3000 certificates of origin have been issued for 33 tonnes seed of 16 species (Portlock, 1992).

Canada's commercial forests remain stocked almost without exception with native species, either as uncut original stands (some of which are referred to as old growth) or as cut and usually regenerated forests (often referred to as second growth). Some movement of genetic material has occurred in the process. While concerns have been expressed over the replacement of natural forests with plantations, forest management has not endangered any Canadian tree species. This is not to say that all biodiversity in Canada's forests is secure. Many species are sensitive to logging, in particular; where these species are already endangered, their status could become severely aggravated.

Agriculture and urban development also have caused major impacts on certain ecosystems and species. Most critically affected in this regard is the Deciduous Forest Region (Rowe, 1972) of southern Ontario. The Region is, almost exclusively, the habitat of all tree species listed by The Committee on the Status of Endangered Wildlife in Canada (Cosewic, 1991; see Table 1).

The Deciduous Forest Region has many more tree species than other Forest Regions in Canada. Considering that its southern tip is at the same latitude as northern California, it is not altogether surprising that the Region contains a high level of species diversity. What is disturbing, therefore, is that only a very small proportion is currently reserved in "highly protected" areas (Forestry Canada, 1991), far below the national average of 3.2%. The Region has some of the largest concentrations of population and industrial development in Canada, and is used intensively for agriculture. Opportunities for protection of natural ecosystems in the Region are diminishing at an alarming rate (Hackman, 1989).

Table 1. List of endangered tree species in the Decidious Forest Region.

Endangered:	cucumber tree *Magnolia acuminata* L.
Threatened:	American chestnut *Castanea dentata* (Marsh.)Borkh
	blue ash *Fraxinus quadrangulata* Michx.
	Kentucky coffee tree *Gymnocladus dioicus* (L.) K.Koch
	red mulberry *Morus rubra* L.
Vulnerable:	dwarf hackberry *Celtis tenuifolia* Nutt.
	hop tree *Ptelea trifoliata* L.
	Shumard oak *Quercus shumardii* Buckl. var. shumardii

As Turner et al. (1992) point out, conservation of natural ecosystems can be accounted for in terms of protected areas. But the degree of protection can be highly variable, and any assessment must reflect human intervention and management objectives. Turner et al. outline application of the five-category IUCN classification system to the development of a Canadian National Conservation Area Data Base (NCADB). Some 2973 protected areas, totalling 70.8 million hectares, are now listed. Despite the existence of this large number of protected areas in Canada, however, it is clear from the above example that the task of protecting Canada's diversity of ecosystems, fauna and flora is far from complete. This is as true for forests as it is for other landscapes.

The need for representivity

If Canada's biological diversity is to be maintained for conservation, scientific and educational needs, there must be a systematic approach to the selection of protected areas. The approach most widely accepted is through adequate representation of landscape units, classified to take account of factors determining ecosystem development. Several systems already exist in Canada, and currently are being used to evaluate protected area networks. The systems themselves are also under review, as frameworks for conservation and other land use planning.

Protected areas in Canada are established primarily by provincial governments, with significant contributions from federal agencies, nongovernment organizations, and others. The resulting network has thus been built under a variety of legislative instruments, and varies in selection criteria, degree of protection, management policies and other features. As Peterson (1991) has observed, the application of the concept of representativity differs among agencies in a rather fundamental manner. In some instances, representivity of landscape units is one of several criteria for consideration, including diversity, rarity and natural integrity. Many areas in Canada have been selected for these reasons. But representivity can be viewed as the underlying principle which the selection process aims to satisfy. It is the latter approach, advocated by Peterson, that will guide Forestry Canada's program for enhancing a national network of forested ecological reserves.

While each province has developed its own system, most reflect to some degree the hierarchical Ecological Land Classification System developed by the Canada Committee on Ecological Land Classification. The system comprises 15 Ecozones, 45 Ecoprovinces, 177 Ecoregions, and 5428 Ecodistricts (Wiken, 1986). Ecoregions, in particular, now appear to offer a common level of aggregation, acceptable to most jurisdictions. The use of Ecodistricts can remain optional for regional planning purposes; in some cases, well developed alternative systems are already widely used.

Despite considerable progress in recent decades, there remain several impediments to the completion of Canada's contribution to a continental network of protected areas. Among the more serious are diminishing opportunities in many important locations, a shortage of information on ecosystem function and appropriate management guidelines, and insufficient appreciation of the role of protected areas. It is to these problems that Forestry Canada is addressing a new project *entitled Ecological* Reserves.

Forestry Canada's Ecological Reserves Project

In 1991, Forestry Canada received Cabinet approval of its submission, Partners for Sustainable Development in Forestry, as a contribution to the Federal Government's Green Plan. As part of this submission, the Ecological Reserves project is committed to the preservation and protection of the great variety of complex biological systems found in Canada's forests (Forestry Canada, 1991). Its primary task is to work with the provinces, territories and other partners in the Canadian Council on Ecological Areas (CCEA) to assess how well Canada's forest ecosystems are represented in existing protected areas, and to identify and address weaknesses in the network.

As a first step is examined how Forest Regions and Forest Sections (Rowe, 1972) are represented in the NCADB. We have focused on 1874 scientific reserves, wilderness areas, national and equivalent reserves, and habitat and wildlife management areas (Categories 1, 2 and 4, IUCN 1985). More areas are covered by these Categories than are included in the National Registry of the CCEA. Much regional variation emerges. Protection in the Deciduous Forest Region amounts to 3.3%, while the highly diverse Columbia Forest Region has only 1.2% of its area protected. The Grassland Region, with its distinctive woodlands, has a mere 0.7% protection. Some Regions fare much better than average: the Subalpine Region, in British Columbia, enjoys 18.4% protection. In total, 4.7% of Canada is protected under IUCN categories 1, 2 and/4. This figure drops to 3.7% when lands in the Tundra Region are excluded. The above figures are not limited to forest ecosystems of course, but include many kinds of protected land.

Between 1992 and 1997, Forestry Canada will undertake three related initiatives. The first recognizes conservation agencies' needs for better forest-related information, and the importance of demonstrating benefits of reserves to Canadians. Action will be focused on selected Forest Ecological Reserves. One such reserve will be designated in each province and territory, wherever possible as part of the Model Forest project. In this related initiative, Forestry Canada will work with partners to establish a set of 10 Model Forests on highly productive sites that represent several major forest types in Canada. Sites will be close enough to urban areas to permit public access and information exchange. The network will also represent a variety of values, such as wildlife, biodiversity, watersheds, fisheries and carbon pools, in addition to the essential component of timber. Regional public issues such as old growth conservation, pest management, land use and forestry practices will also help to create the diversity of models needed to chart a path to sustainable forestry in Canada.

In its second initiative, Forestry Canada will provide appropriate forest information, specific to each protected area accessioned in NCADB. A Canada-wide guide will be prepared, listing protected, undisturbed forest areas for ecological research, conserving biodiversity, and monitoring effects of atmospheric change. The NCADB will be used to inform the Minister of Forestry on progress towards a continental network of protected areas, with particular regard to his Report to Parliament on The State of Forestry in Canada.

Thirdly, the completion of a continental network of protected areas will be advocated as a vital part of global conservation strategy. Regional, national, and international efforts towards this goal will be promoted through senior level policy positions, articles in professional journals, appropriate representation at key conferences, and presentations to decision-makers.

More information on Ecological Reserves, Model Forests and other aspects of the Green Plan can be obtained from Forestry Canada, Ottawa, Canada, K1A 1G5.

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The network of river system nature reserves in France and the preservation of alluvial forests

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Summary

Alluvial forests form an important part of French nature reserves. The protected alluvial forests cover an area of 17 000 ha. They are intended to be conserved and to contribute to establishing guidelines for the ecological management of river ecosystems and the exchange of information between managers of these protected areas. A special research programme has been set up to achieve this.

Keywords: Nature reserves, alluvial forests

Introduction

There are several types of forest reserve in France. A forest can be classified as a reserve using various administrative procedures either under the nature protection Act of 1976 or:
- by means of land control through the "Conservatoires des Sites Régionaux" (regional conservation bodies) e.g. purchase for protection purposes;
- by means of agreements (e.g. the agreement between the Ministries of Agriculture and Environment relating to the state-owned biological reserves (e.g. the forest of Fontainebleau) and to the biological forest reserves);
- by means of the law on nature protection of 10 July 1976 (e.g. nature reserves and voluntarily registered nature reserves). Note that particular attention is paid to the preservation of riverine forest. The long-term aim of the Ministry of Environment is to establish a significant network of alluvial forest reserves along the Rhine, Rhone and Loire .

The network of French nature reserves

The first two nature reserves in France were established in 1912 (Sept Iles) and in 1927 (Camargue) on the basis of private associations' initiatives for nature protection. They were provided with a first legislative framework by legislation of 2 May 1930 on the protection of the sites. The present scheme of nature reserves was set up under the law of 10 July 1976. On the basis of this law a decree was published in the Official Journal, indicating the boundaries, regulation and management methods of each of the reserves established. This management is delegated to bodies such as associations for nature protection, or to municipalities or public bodies.
To date, 108 nature reserves covering more than 110 000 ha have been created and registered at the Conférence Permanente des Réserves Naturelles (CPRN). The following categories of protected ecosystems exist:
- river ecosystems (17 reserves)
- wetlands (about 30 reserves)
- mountain areas (about 20 reserves)
- coastal and marine areas (about 10 reserves)
- grasslands and heathlands (about 10 reserves)
- geological sites (about 10 reserves)

Most of these nature reserves are non-forested areas, although they often include fragments of wooded areas. Apart from the alluvial forests, there are also some entirely forested reserves whose objectives are as follows:
- conservation of original fauna;
- entomological, in the case of the forest of the Massane (Eastern Pyrenees) and of the forest of Cerisy (Normandy);
- ornithological (forest reserves of the mountain range of the Vosges, aiming at preserving the habitat of the capercaillie (*Tetrao urogallus*);
- protection of high altitude forest clearings such as the formations of *Pinus uncinata* on the high plateaux of Vercors, or of *Larix decidua*, *Pinus cembra* and *Picea excelsa* of the Tueda Plan (two nature reserves in the northern Alps);
- lastly, conservation of tropical forests, in the overseas départements (Guadeloupe, Martinique, Réunion).

The network of river system nature reserves

This network operates within the CPRN and covers those nature reserves where at least part of the territory is situated in the major bed of a river. These environments are consequently directly of indirectly connected with the river, through the intermediary of the water factor (periodic flooding, or link with the water table). At the present time this network comprises 17 nature reserves (Figure 1), totalling more than 17 000 ha, of which about 3000 ha are in the major bed of a river (Table 1). Several more projects for river system nature reserves are being investigated at the moment, in particular in the Loire basin.

The objectives of the network are as follows:
- to preserve the alluvial forests;
- to collect information to establish guidelines for the ecological management of the river ecosystems;
- to encourage the exchange of information between the managers of protected river areas;
- to develop coordinated research programmes in the field of natural sciences and environmental law in river systems.

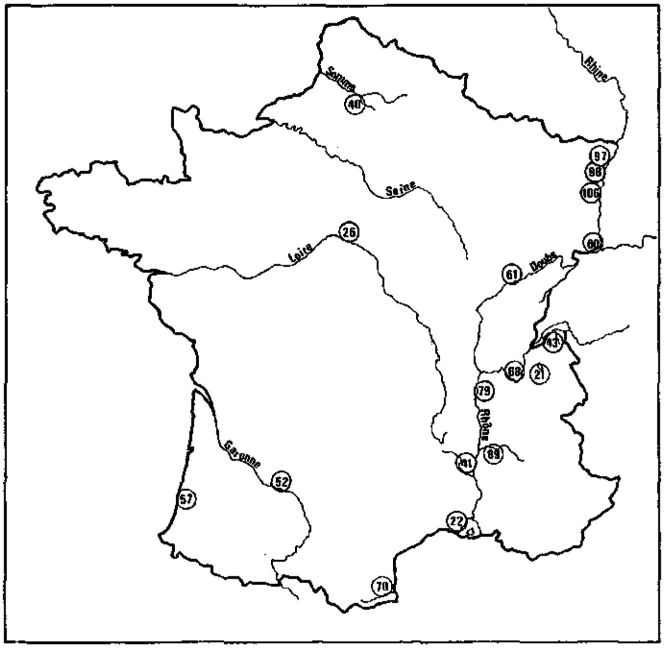
Forests in the network of river system nature reserves

The spontaneous forests preserved in the river system nature reserves cover a total area of about 1100 ha. Another approximately 200 ha of more or less anthropogenic forest can be added to this. The main kinds of forests are:
- softwood forest (willow-poplar) which corresponds to the first stage of river dynamics: about 350 ha;
- hardwood forest (ash) and mixed forest (poplar-ash) corresponding to the mature stage of the riparian forest (about 600 ha); it is in this type of forest that the structures observed are the most complex, in conjunction with an extremely complex ligneous flora;
- marsh or peat forest (alder groves): about 100 ha.

Different biogeographical areas and several catchments are represented:
- the mid-European area: Rhine basin (4 reserves) and north of the Rhône basin (5 reserves);
- the Atlantic area: Loire basin (1 reserve), Garonne basin (1 reserve), and coastal rivers (2 reserves);
- Mediterranean area: the southern Rhône basin (3 reserves) and coastal rivers (1 reserve).

Table 1. List of the fluvial nature forest reserves in France.

Name	River	Area (ha)	Year designated	Types of environment
Marais du bout du lac d'Annecy (21	Ire, Eau Morte	84	1974	riparian forest, reed belt, alkaline marsh, flowing water
Camargue (22)	Rhone	13 117	1975	lagoon, sand dunes, salt marsh
Ile de St Pryve St. Mesnin (26)	Loire	6.3	1975	forest, reed belt, mud flat
Etang de St Ladre (40)	Avre	13	1979	reed belt, pond, fen
Gorges de l'Ardèche (41)	Ardèche	1 570	1980	flowing water, karst
Delta de la Dranse (43)	Dranse	45	1980	flowing water, forest
Frayère d'Alose (52)	Garonne	47.8	1981	riparian forest
Courant d'Huchet (57)	Courant d'Huchet	656	1981	gallery forest, sand dune, marsh, flowing water
Petite Camargue Alsacienne (60)	Rhine	120	1982	abandoned meander, marsh, dry grassland, forest
Ile du Girard (61)	Doubs	95	1982	gravel bank, abandoned meander, mud flat, back swa-mp, reed belt, forest
Marais de Lavours (68)	Le Seran - Les Rousses	474	1984	alkaline marsh
Mas Larrieu (70)	Tech	145	1984	flowing water, forest, marsh, beach, sand dune, reed belt
Ile de la Platière (79)	Rhone	480	1986	flowing water, forest, side channel, dry grassland, gravel bank
Ramière du Val de Drôme (89)	Drôme	346	1987	flowing water, forest, gravel bank, side channel
Forêt d'Offendorf (97)	Rhine	60	1989	forest, side channel, abandoned meander, wet grassland
Forêt d'Erstein (98)	Rhine	180	1989	forest, side channel, abandoned meander
Ile de Rhinau (106)	Rhine	307	1991	reed belt, forest, side channel



21. Marais du bout lac d'Annecy
22. Camargue
26. Ile de St Pryve St Mesnin
40. Etang de St Ladre
41. Gorges de l'Ardèche
43. Delta de la Dranse
52. Frayère d'Alose
57. Courant d'Huchet
60. Petite Camargue Alsacienne
61. Ile du Girard
68. Marais de Lavours
70. Mas Larrieu
79. Ile de la Platière
89. Ramières du Val de Drôme
97. Forêt d'Offendorf
98. Forêt d'Erstein
106. Ile de Rhinau

Figure 1. Location of the natural fluvial forest reserves in France.

Research in the forest reserves

Several forest reserves are being subjected to pure and/or applied scientific research. Fauna and flora are being inventoried in all the protected areas. Various research themes are being pursued in the alluvial forests, particularly those along the Rhine and Rhône. Many studies are also under way in the forest reserves of Fontainebleau.

Alluvial forests

- Spatial diversity, typology based on phytosociology, dynamic method (successional stages and phases of the silvigenetic cycles), ecological interpretation (effect of the substrates, of the hydrological regimes). Comparison of the flood-prone and non-floodable zones.
- Hydrological and biogeochemical functioning. Influence of the riparian forest on the quality of the groundwater and on the filtering of floodwater according to forest composition and structure. Combined effects of the types of substrate and flooding on the bio-availability of phosphorus. Piezometric monitoring of aquifers.

- Studies on the architectural profiles of the dynamic forest and of the spatial structure of the alluvial forests in the Rhine valley.

Aquatic vegetation and functioning of the aquatic ecosystems

- Studies of the exchanges between groundwater and surface water using aquatic macrophytes as bio-indicators of the water quality.

Mycosociology

- The functional group of macromycetes (symbiosis, mycorrhiza) are used as ecological niche descriptors and detectors in an riparian environment.

Conclusion

The most diversified and structured forests of the French forest nature reserves are to be found along the river banks. This is why particular care should be paid to their conservation to ensure their continued survival.

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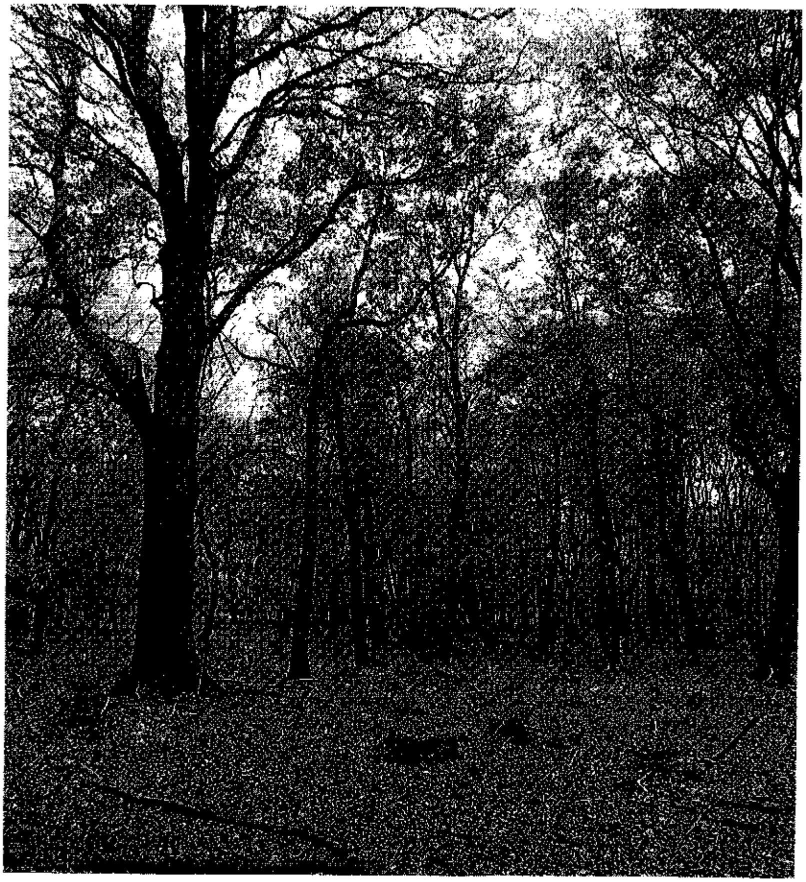
Chapter 3

Forest reserves research and other research on forest dynamics



Speulderbos - a cultural forest

The Speulder-Sprielderbos (Veluwe, The Netherlands) is an ancient area of forest, known of in the Middle Ages, which has always been used as a supply of wood. The forest used to consist of coppice and of uncoppiced indigenous tree species. The forest is renowned for its characteristic moss and lichen flora in the old uncoppiced 'boombossen' with their many crooked and gnarled trees. Over time the forest has become fragmented due to the planting of exotic tree species, especially Douglas-fir and larch, which have seeded spontaneously. Red deer, roe deer and wild boar occur in the forest. Their population densities are regulated by hunting. Douglas-fir is more resistant to browsing than the indigenous English oak, sessile oak and beech, which means that in spontaneous rejuvenation the exotic species are becoming more dominant. Since 1985 36 ha of the Speulderbos has been designated as a forest reserve.

The standardized monitoring programme for forest reserves in The Netherlands

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Summary

The Statistics section of the National Reference Centre is responsible for an important part of the inventories in the Dutch forest reserves programme. Data gathering is standardized and is done with the aid of field computers. The monitoring of the forest structure in the core area and the forest dynamics in the sample plots are explained.

Keywords: forest inventory, monitoring methods

Introduction

Within the Dutch forest reserves programme the most important parts of the study of the forest ecosystem are: vegetation development, the development of the forest structure and the study of forest dynamics. Therefore the spontaneous processes are studied from various points of view. Attention is paid to:

1. site (soil, humus profiles, hydrology);
2. forest dynamics (population development, forest regeneration, stand succession);
3. forest structure (tree position, dead wood, vitality, crown projection);
4. forest vegetation (vegetation types and maps, vegetation succession, species compostition and dispersion, PNVs, inventory of mycoflora).

In order to study these factors correctly the research programme has been divided into an initial programme and a basic programme. The aim of the initial programme is to record the situation of the forest reserve at the time of designation. The basic programme is intended to monitor secondary site factors (Broekmeyer and Szabo, this volume). Table 1 lists the inventory aspects of the two programmes. Most of these inventories are done by the National Reference Centre, which is part of the department for Nature, Forests, Landscape and Wildlife of the Ministry of Agriculture, Nature Management and Fisheries.

Organization of the inventory

The time available for the inventory is restricted, so to carry out the intitial and basic programmes a tight time schedule is required. Most parts of the inventory programme are carried out by the National Reference Centre with the help of foresters from the National Forest Service.

In the year of designation aerial photographs are taken. The following year the forest reserve is laid out: core area and grid points are marked and the maps are drawn. These maps serve as a basis for further investigation.

The sample plots and core area are inventoried in the third year or later, as are the vegetation mapping and soil survey.

Table 1. Overview of the inventory programmes. The organization doing the inventory is given in brackets. NRC = National Reference Center. WSC = W. Staring Centre for Integrated Land, Soil and Water Research. IFN = Institute for Forestry and Nature Research. DMS = Dutch Mycological Society.

Initial programme:

1. Lay-out of the forest reserve (NRC)
2. Drawing maps of the whole reserve at a of scale 1:2500 (NRC)
3. Inventory of forest history (NRC)
4. Soil survey (WSC)

Basic programme:

1. Inventory of the tree layers of the core area (NRC)
2. Inventory of the tree layers of the sample plots (NRC)
3. Inventory of the vegetation of the entire forest reserve (IFN)
4. Inventory of the vegetation of the core area (IFN)
5. Inventory of the humus form profiles (-)
6. Aerial photography: false colour photos 1:10 000 and 1:5000 (NRC)
7. Inventory of the mycoflora (in part of the reserves) (DMS)

Table 2. Estimated time required for fieldwork of the inventory programme per reserve.

Initial inventory:		
- lay-out reserve + map making:		10 working days for 2 persons
- soil survey:		12 working days for 1 person
Basic inventory:		
- core area:	tree trunks	10 working days for 2 persons
	crown projection	10 working days for 1 person
- sample plots:		20 working days for 2 persons
- vegetation entire reserve:		2 working days for 1 person
- vegetation core area:		3 working days for 1 person
- mycological investigation:		3 working days for 2 persons

Lay-out of the forest reserve

The study of the forest reserves in The Netherlands concentrates mainly on monitoring the forest structure and the development of the vegetation. To assist the research all the forest reserves are mapped according to a fixed pattern. Four different scales of study can be distinguished:

1. The whole forest reserve of 15-50 ha with 50-70 sample plots on a rectangular grid of 50 x 50 m.
2. The core area of 1 ha: a block of 70 x 140 m.
3. A central strip transect, one-tenth of a hectare strip, 10 x 100 m.
4. A herbaceous transect area in the middle of the central strip, 2 x 100 m.

The core area represents the most characteristic part of the forest reserve. It is situated in a homogeneous part of the reserve and is oriented north-south.

A 50 x 50 m grid of points is set up over the entire forest area. Approximately half of the points (50-70 per reserve) are designated as the centre of sample plots. See also Broekmeyer and Szabo (this volume).

Inventory of the initial programme

First, the sample plots and the core area are marked in the field. All points are marked underground with a detectable element. One-quarter of the points are marked by concrete posts about 15 cm above the surface.

After marking in the field three maps to scale 1:2500 are made:

- a base map, containing the most important topographical elements, border of the core area and the grid points;
- a field work map, containing all the information of the base map plus extra topographical information;
- a tree cover map, containing all the information of the fieldwork map plus tree cover at the moment of assignment (see Figure 1).

The maps are then digitized.

The forest history is described. In text and figures the general characteristics of the forest reserves are noted as well as the history of the vegetation cover over the last century, using old topographical maps. The history of former forest management is noted.

The soil survey consists of two parts. Most important for the monitoring of the sample plots are profile descriptions up to 2 m below ground level. But a 1: 5000 map is also made of the most important soil types.

All data are stored in computer files and linked to a geographical information system (ARC/-INFO).

Inventory method for the sample plots

Introduction

The inventory of the sample plots, 50 to 70 plots in each forest reserve, is aimed at monitoring the forest dynamics. Observations will be repeated every ten years. All sample plots consist of two lay-outs, see Figure 2:

1. A circle of radius of 12.6 m around the sample point (500 m^2)
2. A square of 18 x 18 m (324 m^2) subdivided into 36 squares of 3 x 3 m.

In the circle the position of trees with a diameter of more than 5 cm at breast-height (dbh) is measured, and crown characteristics are recorded. The results will be compared with air photos. In this way it will be possible to draw conclusions about the whole forest reserve using the observations of the sample plots.

In the 36 squares of 3 x 3 m the monitoring of the forest dynamics and regeneration is surveyed. Recordings of the trees with a dbh of less than 5 cm can provide information about rejuvenation. The position of younger trees is not recorded. The dynamics in rejuvenation within ten years are such that counting the young trees in areas of 3 x 3 m is considered to be adequate.

Observations

First stage: Inventory of the circle area

All trees with a dbh more than 5 cm are positioned by angle and distance related to the sample point and north (Figure 3). Tree species, appearance (single-stemmed, multi-stemmed and cluster), diameter, height of tree top and stem length, vitality as well as dead wood (origin, decomposition and position) are determined.

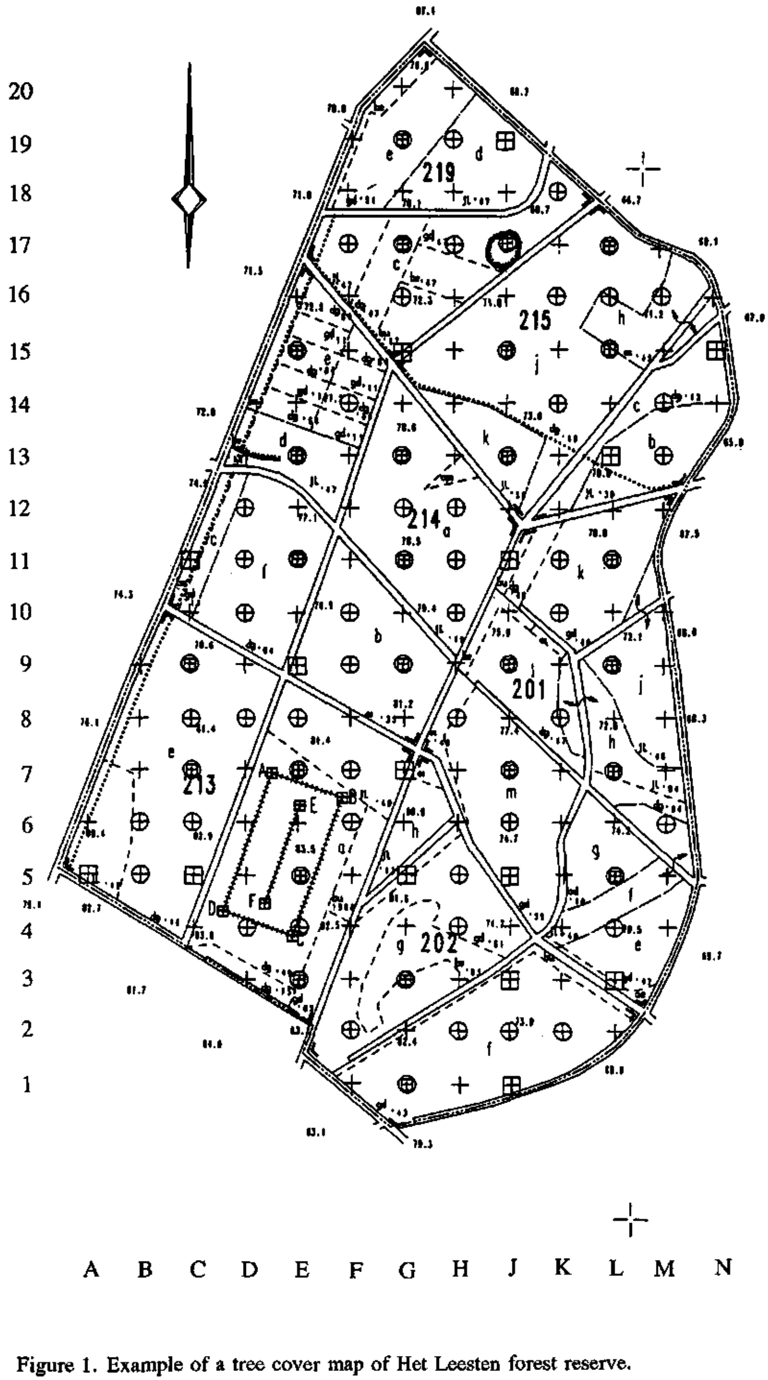


Figure 1. Example of a tree cover map of Het Leesten forest reserve.

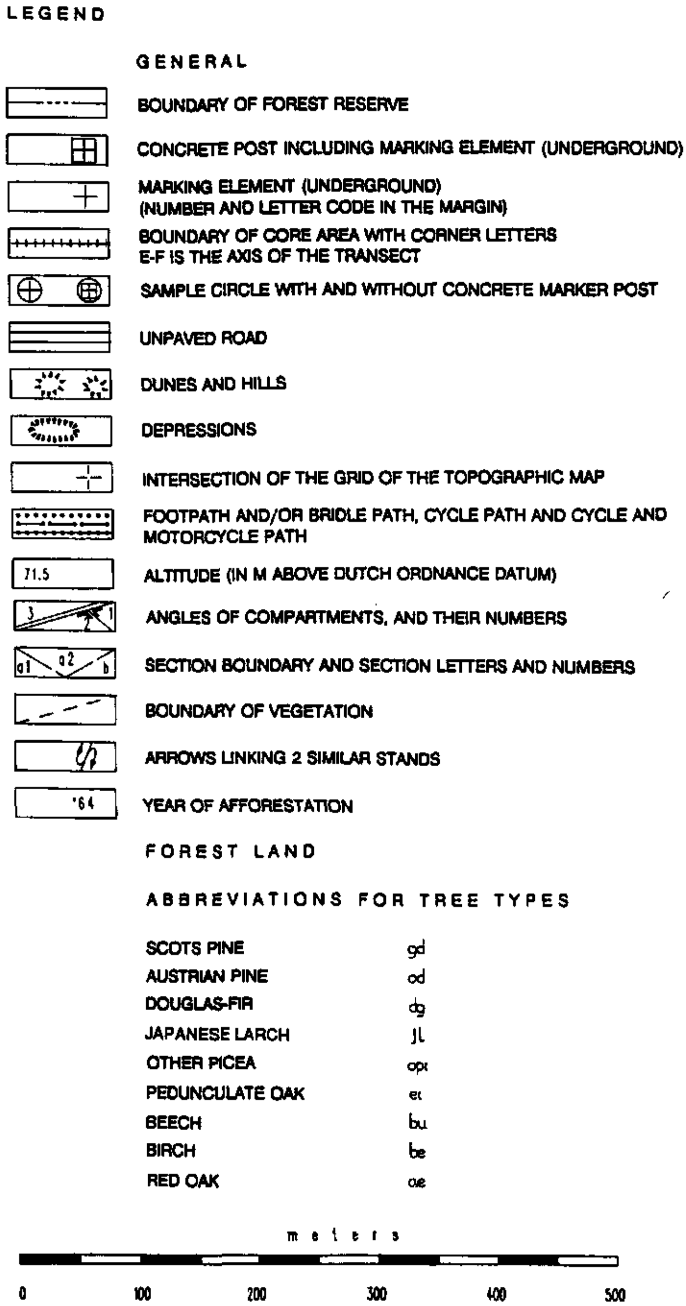
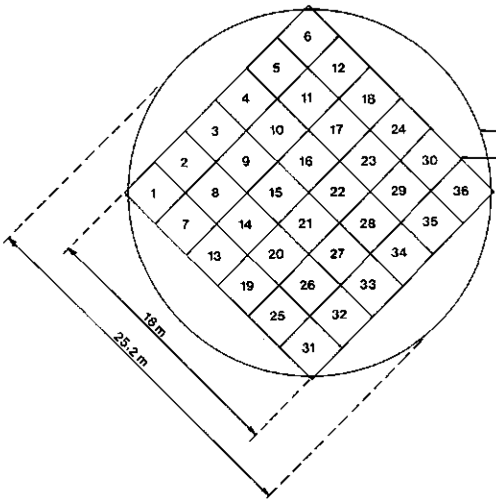


Figure 1. Legend of the tree cover map.

Second stage: Inventory of the squares

The numbers of trees (diameter less than 5 cm) differentiated by species and height classes (0.5-2 m and > 2 m) are counted. To reduce the amount of work and in view of the great dynamics over ten years, only trees more than 0.5 m tall are counted.

The data are recorded in a Husky field computer, using a database specially designed for this purpose, resulting in a data file per sample plot. The different results can be plotted into maps of living standing wood, standing plus lying dead wood, and so on.



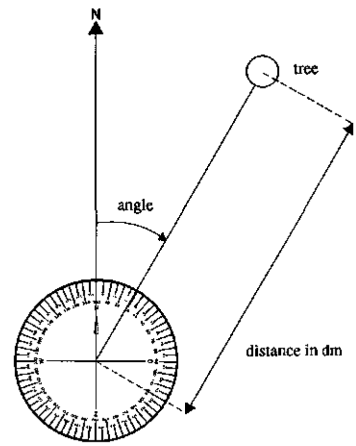


Figure 2 (left). Lay-out of a sample plot.
Figure 3 (right). Location of a tree in angle related to the north and distance from the sample point.

Example of the results

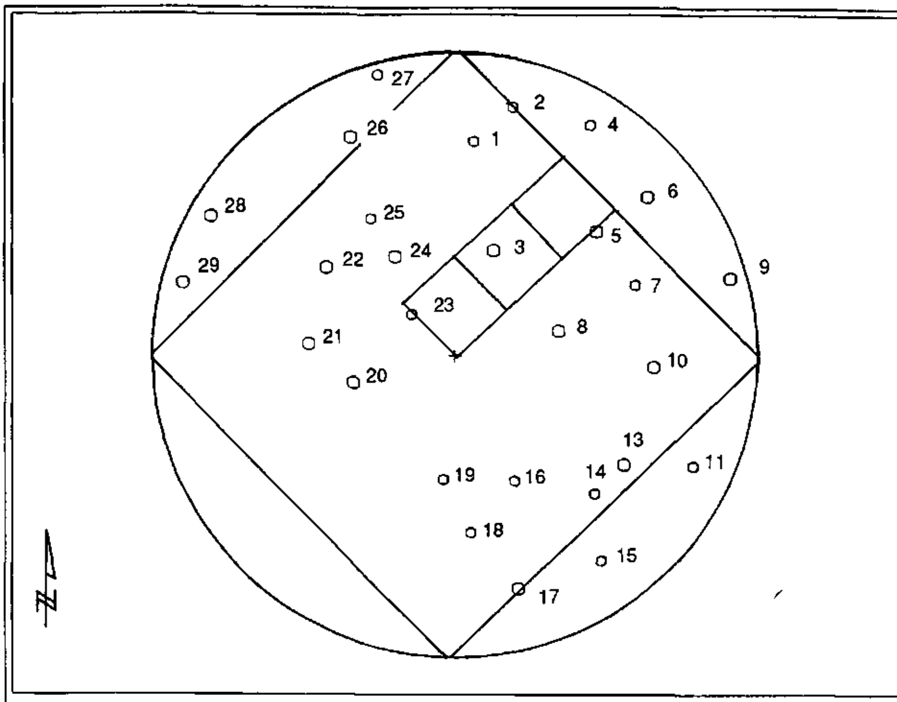
The inventory of plot H10 of forest reserve Het Leesten was carried out on 29 November 1988. Figure 4 shows a plot of the living standing trees with a diameter more than 5 cm. All these trees are larch (*Larix leptolepsis*). As can be seen, sample plot H10 is situated at the north-eastern boundary of a canopy gap (windhole): there are no trees in the south-west part of the circle. It is likely that this gap will enhance forest dynamics. The squares (3 x 3 m) 16, 17 and 18 contain respectively the larch trees nos. 23 (border), 3 and 5 (border). In November 1988 there were only 2 trees under 5 cm diameter (one Douglas-fir and one Scots pine). About three years later (February 1992) we found 32 small trees with a quite irregular distribution over the three squares (see Figure 5).

Inventory method for the core area

Introduction

The inventory of the core area is aimed at monitoring the forest structure. Observations are repeated every ten years.

The forest structure is monitored by mapping the position of the trunks and the crown projection. Lying dead wood and uprootings and their related pits are also mapped. This is done in three stages. For practical reasons the core area is subdivided into 14 strips, each 5 m wide (Figure 6). The data from the first and second stages are recorded in a field computer.



forest reserve: Het Leesten

sample plot H10 living, standing trees

nr	diam	srt
1	17	58
2	18	58
3	21	58
4	18	58
5	20	58
6	20	58
7	16	58
8	24	58
9	23	58
10	24	58
11	17	58
13	25	58
14	19	58
15	18	58
16	16	58
17	24	58
18	18	58
19	19	58
20	20	58
21	25	58
22	22	58
23	19	58
24	20	58
25	19	58
26	21	58
27	18	58
28	29	58
29	21	58

meters

0 2 4 6 8 10

- diam. 5- 9 cm
- diam. 10-19 cm
- diam. 20-29 cm
- diam. 30-39 cm
- diam. 40-49 cm
- diam. 50-59 cm
- diam. >= 60 cm

58 = Larix leptolepis

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IBN-DLO

Figure 4. Plot of the living standing wood of sample plot H10 of Het Leesten forest reserve.

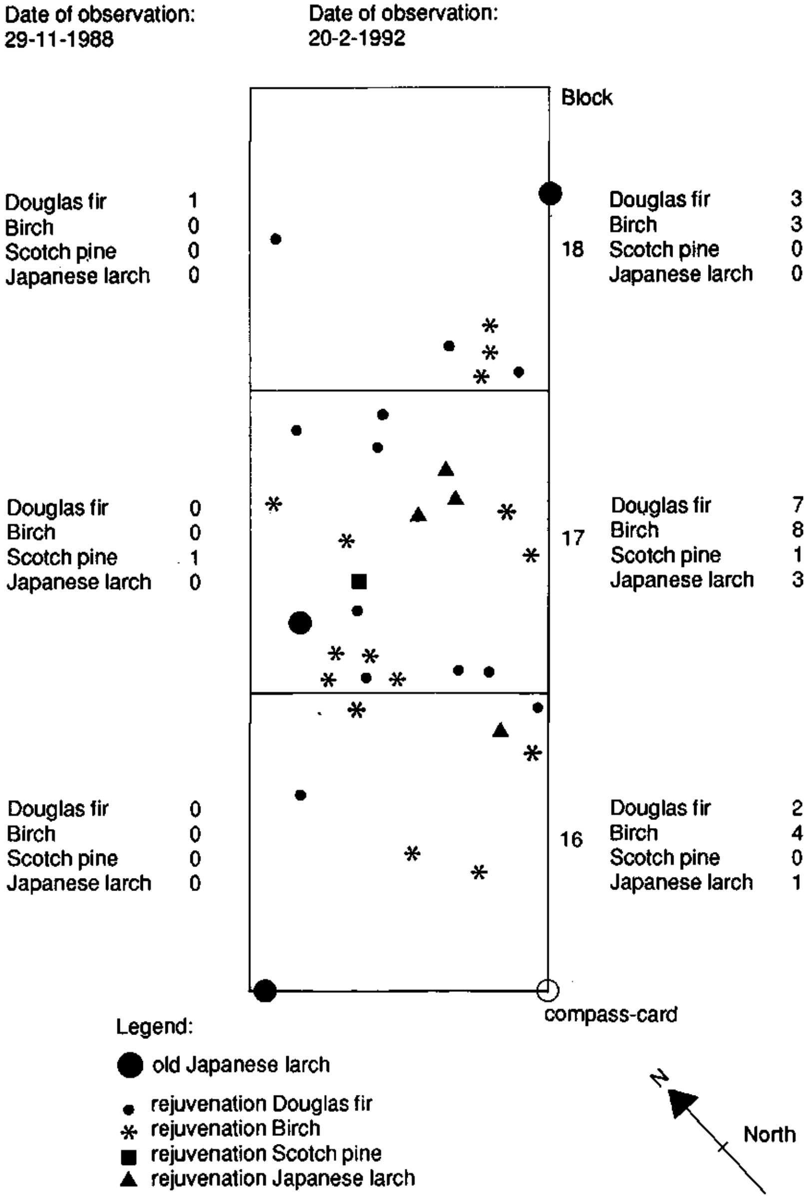

Figure 5. Regeneration on squares 16, 17 and 18 of sample plot H10.

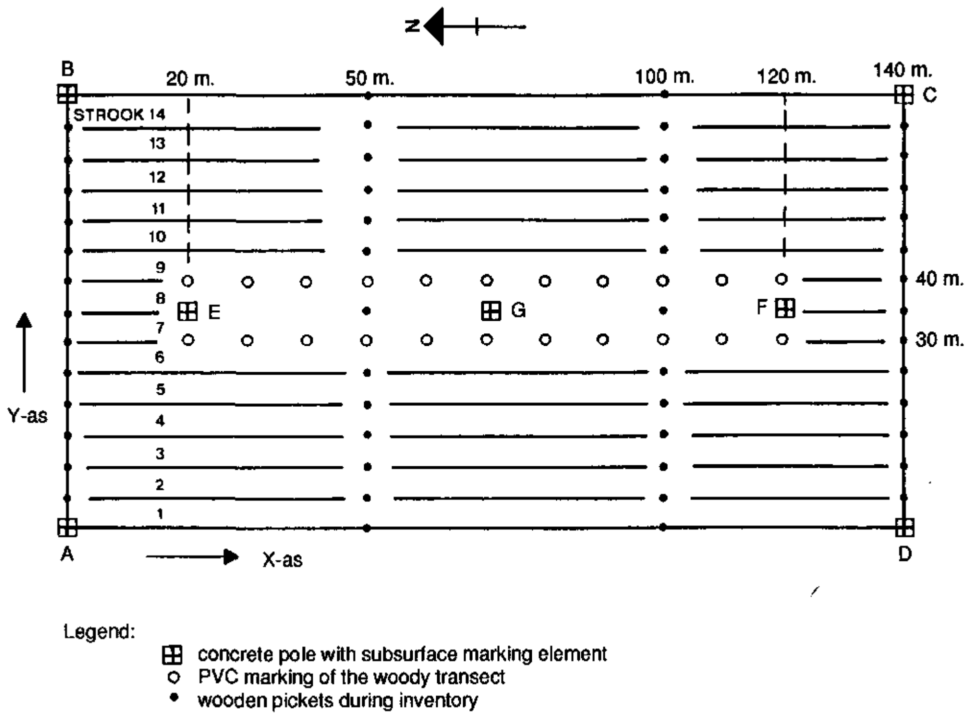

Figure 6. Lay-out of the core area.

Observations

First stage: Location of tree trunks
All trees are numbered and the position (accuracy up to 0.1 m), the diameter breast height and species of each tree are mapped. Vitality and damage are also estimated according to the international IUFRO code.
The result is a map of trunks and species.
Second stage: Height measurement
The height of the crown-top (T), the periphery (P), the crown base (C) and the first living fork (F) are measured (Koop, 1989), see Figure 7. Furthermore the trunk positions are checked. The result is a map of tree trunks and numbers. This map serves as a basis for drawing crown projections.
Third stage: Crown projection
The cover percentage of the crowns, as well as uprootings with related pits and lying dead wood are measured. The crown projection is drawn using imaginary vertical planes that touch the crown. Maps are drawn by hand on the map of tree trunks (Figure 8). The result is a crown projection map as a basis for digitizing.

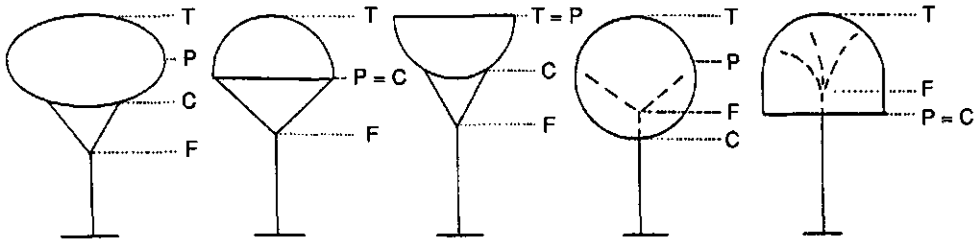

Figure 7. Measuring crown heights.

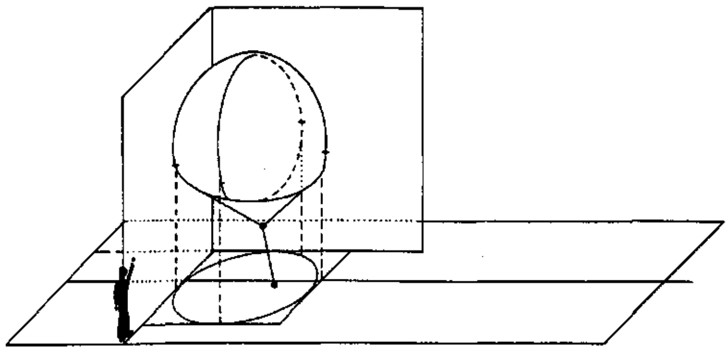

Figure 8. Determination of the crown projection.

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Soil research in Dutch forest reserves: the implications of spatial and temporal soil variability

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Summary

The plans for soil research in the Dutch forest reserves originally comprised three programmes - initial, basic and sequential - which have already been described in an earlier publication (Sevink, 1991a). The initial programme has been executed in most of the present forest reserves and serves to identify and characterize the soil conditions. The results are also being used to study the relations between parent material, soil, drainage, vegetation and humus form. A brief outline will be given of the research done so far and of the problems encountered. For the study of successional changes a research proposal comprising a study of only some soil parameters in all forest reserves (the basic programme) and a more in-depth study of relevant soil parameters in a few representative reserves (the sequential programme) was developed. Only part of this proposal has been implemented so far (measurements of water table in relevant forest reserves). The reasons for this are rather fundamental and merit further discussion, since they are relevant for all successional studies of soils. The paper concludes by examining the methodology proposed for the future research on successional changes.

Keywords: soil research, soil succession, humus forms, spatial variability

Introduction

To date, 14 reserves have been studied out of the total of 75 reserves, which are planned to be established. This research includes soil observations at 50-70 points (randomly selected from a square grid with inter-spacings of 50m) and a soil survey at scale 1:2500. The observations at sample points comprise standard soil profile descriptions and a concise description of the humus form (according to Klinka et al., 1981). With regard to the site conditions, the set of 14 reserves is fairly representative of the range in conditions encountered in The Netherlands. This implies that the data obtained allow for a first analysis of the relations between soil, drainage, vegetation and humus form in the Dutch forest reserves. The results from such analysis have been presented by Kemmers et al. (this volume).

Soil mapping units were identified on the basis of their classification according to the Dutch soil classification (De Bakker and Schelling, 1989) and using additional parameters. For a map at scale 1:2500 the observations at gridpoints were insufficient and many additional observations were often required, in particular in areas with a complex geology. It was soon realized that data obtained at these additional points were unsuited for statistical analysis, their location being far from random. This led to an intensive discussion on the role of a soil map in forest reserve research; it was concluded that soil maps are less important than earlier assumed.

The soil map shows the soil pattern within the forest reserve and thus would allow for the selection of specific soils for further research. However, because of the considerable spatial variation it was found that thorough field checks were still required to identify sites with specific soils. Moreover, the map is based on the use of differentiating criteria, i.e. on a class subdivision for a rather limited number of soil parameters. Consequently, it is far less suited for studies on the relationships between parent material, drainage, vegetation and soil than the observations at the sample points. Recently, it was therefore decided to replace the soil survey by a physiotope survey, for which a typology is currently being developed and which is assumed to require fewer observations.

The successional studies

Most of the literature on soil succession deals with processes operative in the mineral soil. The latter include processes such as podzolization, clay translocation and weathering, which have low rates, causing measurable changes in soil properties over periods ranging from centuries to milennia. Studies on successional changes in forest soils at a time scale of decades are scarce. The studies available, which we will discuss below, indicate that changes are small and mainly restricted to the humus form. This is not surprising, since such short-term changes will be connected with rapid pedogenic processes occurring in the humus form, such as litter decomposition and bioturbation.

Humus forms are noted for their spatial variability due to local differences in litter input and quality, soil climate, soil fauna activity, etc. The consequence is that a statistical approach is required for a reliable quantification of chemical and physical parameters of humus forms, and of their spatial variability - implying large numbers of samples and observations. When these two aspects are combined it becomes clear that successional studies based on sequential observations and sampling at intervals of a decade or so will encounter serious problems: changes will probably be small and thus will be hard to identify and quantify. These problems and their consequences for successional studies within the framework of forest reserve research will be discussed in more detail, using results from recent studies on humus forms and their succession in some Dutch forests.

Successional changes in soil properties

From the available successional studies it is clear that specific conditions are required for relatively rapid and significant changes to occur. Firstly, changes are fastest during initial stages of soil formation, but slow down rapidly during succession. At some stage a steady state is reached, in which soils are considered as "mature" and change very little in time. In the temperate region, most soils which started to form during the Early Holocene are to be considered as mature soils. Secondly, conditions are optimal if sites are well-drained and the parent material has a low acid-neutralizing capacity. These conditions allow for rapid leaching and acidification, and concurrent changes in litter decomposition and nutrient status.

Given the above, it is not surprising that the scarce relevant studies on soil succession, i.e. covering time spans in the order of a century, are largely confined to freely drained soils in coarse textured recent glacial deposits or recent aeolian deposits (see for example Chandler, 1942; Crocker and Major, 1955; Olson, 1958; Wilson, 1960; Van Berghem et al., 1986; James and Wharfe, 1987; Sevink, 1991b). The general trend is a development towards a podzol as a result of retarded litter decomposition and rapid acidification.

This trend was indeed observed during recent studies of soil succession under primary stands of Scots pine on inland dunes and blow-outs in the central part of The Netherlands. General trends in soil development in a representative transect through a blow-out were described by Emmer et al. (1991). Along this transect the age and density of the Scots pine trees gradually increase. Initially, mull type humus forms prevail, but mor type humus forms become dominant when trees are older than 75 years. Data on some soil parameters are presented in Table 1. The "depth of front" refers to the acidification of the mineral soil, defined as the depth to which pH values are lower than 4.4, the parent material having a pH of about 4.4. The data show that the thickness of the ectorganic layer, amounts of ectorganic matter and depth of acidification clearly increase with increasing age. However, rates seem to decline between zone c and SE. Furthermore, the pH of the LFH and A horizon, after a rapid decline, remains rather constant.

Table 1. Some parameters of soils (n=20) in the various zones of a transect representing a spontaneous primary Scot pine succession (u = mull type soils; o = mor type soils).

avg age (years)		thickness (cm)		organic matter (g.m^{-2})		pH (CaCl^2)		front[#] (cm)
		LFH	H	LFH	15 cm[*]	LFH	A	
8^u	avg	0.1	0	25	720	3.5	4.4	1
	cv%	120	-	40	26	3	2	165
40^u	avg	0.3	0	555	1087	3.4	3.7	12
	cv%	192	-	79	24	5	8	41
40^o	avg	5.8	414	5447	1302	3.0	3.1	25
	cv%	47	49	49	21	3	5	41
80^o	avg	7.7	2469	7495	1550	3.0	3.0	56
	cv%	51	64	53	21	4	3	44
100^o	avg	9.5	2156	7163	1350	2.9	3.0	63
	cv%	32	40	26	17	4	2	37

[#]) explanation see text
[*]) top 15 cm of mineral soil

Table 2 presents data on the amounts and accumulation rates of some elements in the ectorganic horizons of soils in recent inland dunes under primary Scots pine stands (for their general description, see Van Berghem et al., 1986). The data show that amounts increase with increasing age. However, they also illustrate that accumulation rates expressed as the percentage increase relative to the amount present (reserves) are generally small. For example, the annual percentage increase of Ca in the LF horizon is about 1.1% after 55 years, whereas it will be about 0.8% after 120 years. For K, the values are about 0.2% and 0.4% respectively.

The studies mentioned above concern soil development under natural or semi-natural tree stands (i.e. indigenous species, not planted). This will not be the case in many of the forest reserves in The Netherlands, since most stands have been planted and exotic species abound. In such stands, distinct changes in tree species composition are to be expected during succession, with concurrent changes in litter input, litter quality and nutrient uptake.

Miles (1985) reviewed the effects of rather drastic man-induced changes in tree species composition and concluded that these may be significant. However, the changes described by Miles generally concern periods of some decades or more. Moreover, it is unlikely that the vegetational changes in the forest reserves will be as drastic as those induced by man. It is therefore concluded that the rates of changes in soil properties caused by changes in tree species composition will probably be close to those observed in the natural stands.

Spatial variability

In the past considerable attention has been paid to spatial soil variability and the methodology to be employed for its study (see for example Nielsen and Bouma, 1985; Webster and Oliver, 1990). However, the spatial variability of humus forms has received very little attention and only a few in-depth studies on this topic have been published (Quesnel and Lavkulich, 1980; Arp and Krause, 1984). Consequently, little is known about the spatial variability of humus forms in the Dutch forest reserves.

Table 2. A) Amounts of Ca, Mg, K and Na in kg.ha^{-1} and B) their accumulation rates in kg.ha^{-1}.y^{-1}, in the ectorganic horizons of soils under primary Scots pine stands of increasing age.

A

age	hor	Ca	Mg	K	Na
15	LF	28.14	15.40	23.06	3.84
30	LF	63.60	16.60	25.10	4.77
55	LF	78.80	34.22	62.06	6.46
	H	28.20	7.33	7.05	1.97
91	LF	111.35	40.36	64.54	7.31
	H	33.50	8.29	7.98	3.19
120	LF	156.42	50.80	72.54	8.38
	H	54.55	16.00	17.00	6.50

B

interval	hor	Ca	Mg	K	Na
0-15	LF	1.88	1.03	1.54	0.26
15-30	LF	2.36	0.08	0.14	0.06
30-55	LF	0.61	0.70	1.44	0.07
	H	1.13	0.29	0.28	0.08
55-91	LF	0.90	0.17	0.10	0.02
	H	0.15	0.03	0.03	0.03
91-120	LF	1.55	0.36	0.28	0.04
	H	0.72	0.27	0.31	0.11
0-120	LF	1.30	0.42	0.60	0.07
	H	0.45	0.13	0.14	0.05

From recent research in primary stands of Scots pine on aeolian sands near Kootwijk some data are available on the variability of a number of relevant humus form parameters. In three plots with stands of identical age (about 70 years), soil was described and sampled at about 50 grid points (rectangular grid with an interspacing of 15 m). The organic matter content of the aeolian sands varies, enabling two types of parent material to be distinguished: "stuifzand" (wind-blown sand) A and B, which are respectively very low and low in organic matter. Moreover, in some soils a buried podzol occurs within a depth of 180 cm (soil type P).

In Table 3 data are presented on the thickness, loss on ignition (loi), organic matter content (om in kg/m^2), electric conductivity of water extracts (1:10 ectorganic horizon; 1:2.5 mineral horizons) and pH of 149 soil profiles. The data clearly illustrate the often considerable spatial variability within the plots. Table 4 is more interesting; it provides information on the significance of mean values in relation to the number of samples. The first two colums show the numbers of samples required to reduce the possible error to less than 10% and 20% respectively (at a confidence level of 95%). The last column shows the possibe error (at a confidence level of 95%), if the mean value is based on 50 samples. The data show that for several relevant parameters even 50 samples are not sufficient to reduce the error to less than 10%.

In Figure 1 data are presented on concentrations of extractable elements in bulked samples (20 subsamples) of L/F and H horizons in soil types A, B and P, in the various plots. Although the data do not allow for a thorough statistical analysis, they indicate that spatial variability is considerable and that if n = 150, errors may still exceed 10%. The data concern monospecies

Table 3. Mean value, standard deviation and coefficient of variation of some parameters of soils in aeolian sands near Kootwijk.

		hor	avg	sd	cv%	
thickness	cm	F	4.20	1.06	25	
		H	3.20	1.76	55	
		E	0.79	1.34	169	
		B	4.67	3.11	66	
loi	%	F	82.95	10.50	13	
		H	48.01	10.89	23	
		E	5.02	2.42	48	
		B	1.55	0.56	37	
om	$kg.m^{-2}$	L	0.18	0.08	44	
		F	1.75	0.74	42	
		H	2.43	1.30	53	
Ec25	$\mu S.cm^{-2}$	LF	231	63	27	
		H	114	32	28	
		0-5	74	18	24	
		5-10	43	10	23	
		15-20	36	10	28	
		30-35	37	9	25	
		65-75	35	10	29	
H (H_2O)#	$\mu mol.l^{-1}$	LF	83	39	47	4.1*
		H	190	62	33	3.7*
		0-5	163	41	25	3.8*
		5-10	80	29	37	4.1*
		15-20	48	19	40	4.3*
		30-35	40	15	37	4.4*
		65-75	29	8	26	4.5*

#): proton concentration in water extract
*): geometric mean of pH

stands with a groundcover dominated by *Deschampsia flexuosa*, a vegetation which deviates from that in most forest reserves. Mixed stands with a very varied groundcover are fairly common and in such stands spatial variability of the humus form is likely to be much more pronounced. Unfortunately, there are hardly any systematic studies on the spatial variability in such stands.

Some indication for the effects of species composition on humus form properties is provided by a comparative study of first generation forest plantations in the Flevopolders (Sevink et al., 1989). As shown in Figure 2, within less than 30 years differences in tree species composition were found to lead to prominent differences in humus form properties. Similar conclusions were reached in other studies (Miles, 1985; Boerboom, 1963; Wardenaar and Sevink, 1992).

Although humus form properties in mixed stands are likely to vary considerably, ranges will be less than those observed in the Flevopolders. Tree species composition, for example, will be less diverse and mixed litters rather than monospecies litter will prevail. However, no reliable predictions of the numbers of samples required to be able to quantify parameters such as those presented in Table 4 can yet be made; they have to be based on future research in representative mixed stands.

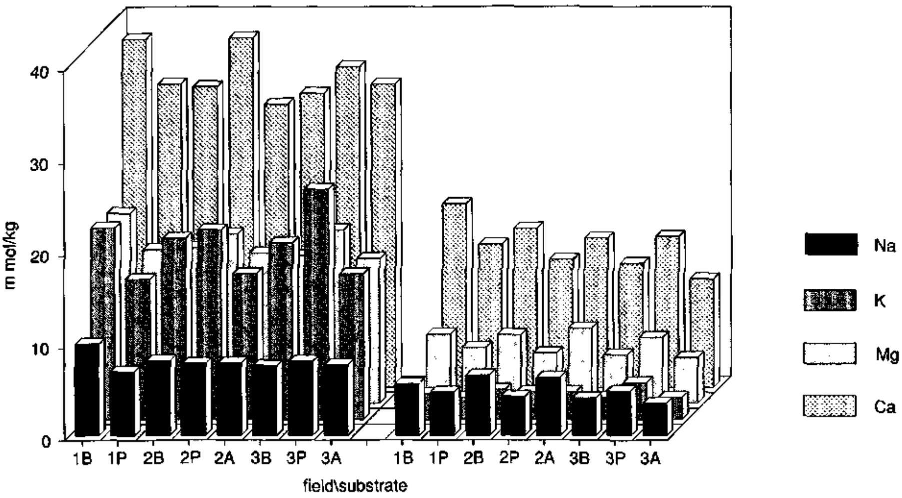

Figure 1. Extractable elements in mmol.kg^{-1} for various soils (A, B and P) and plots (1, 2 and 3) at Kootwijk. Left: L + F horizons; right: H horizons. For each sample n = 20.

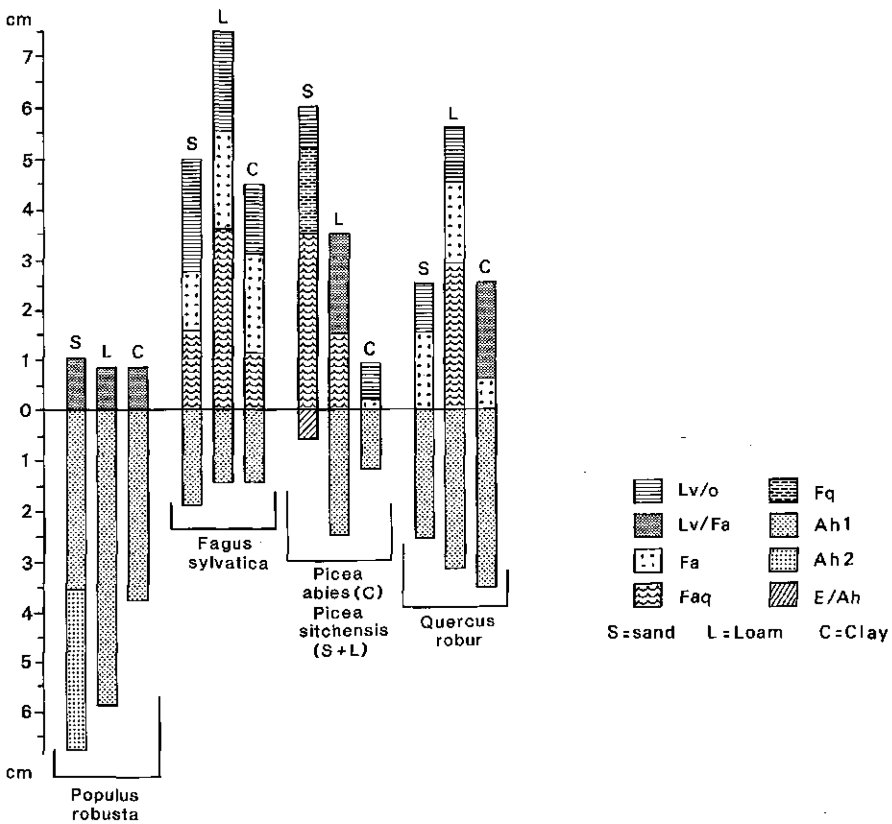

Figure 2. Soil horizons in a number of tree stands on different parent materials in the Flevopolders.

Table 4. Numbers of samples required for maximum errors of 10 % (n10) and 20 % (n20), and maximum error in %, if n = 50 (δ50), at 95 % confidence levels.

		hor	n10	n20	δ50 (%)
thickness	cm	F	18	5	6
		H	85	21	13
		E	810	202	40
		B	125	31	16
loi	%	F	5	1	3
		H	15	4	5
		E	65	16	11
		B	38	9	9
om	$kg.m^{-2}$	L	54	14	11
		F	51	13	10
		H	81	20	13
Ec25	$\mu S.cm^{-2}$	LF	21	5	6
		H	22	6	7
		0-5	16	4	6
		5-10	15	4	6
		15-20	23	6	7
		30-35	18	4	6
		65-75	24	6	7
H (H_2O)#	$\mu mol.l^{-1}$	LF	63	16	11
		H	30	8	8
		0-5	18	4	6
		5-10	38	10	9
		15-20	45	11	9
		30-35	38	10	9
		65-75	19	5	6

#): proton concentration in water extract

Research methodology

The successional research thus has to cope with the problem that changes in soil properties will be small and hard to identify and quantify in many of the stands concerned, assuming that data are collected at intervals of a decade. When using longer intervals these problems will decrease, but in that case another problem is likely to surface, which is that administrations are not very eager to finance research whose results will only become available in the distant future.

Assuming that the Scots pine stands described above are fairly representative of monospecies forest stands, some statements can be made about the number of samples required to identify and quantify changes in soil properties. The parameters that can generally be established with relative ease in the field or laboratory include the thickness and ash content of the ectorganic and endorganic horizons, organic matter contents expressed in weight/surface area, and pH and EC of individual soil horizons. The data presented suggest that 50 samples are generally sufficient to quantify significant changes. 'Significant' in this case implies a change of more than 10% (at a significance level of 95%).

Nutrient availability and nutrient reserves are important parameters, but their quantification is much more laborious and expensive, requiring chemical analyses of a larger number of samples. The exact numbers are hard to predict, but will be in the order of 50 or more.

It should be stated that fewer data are required to statistically test the significance of observed changes in the parameters mentioned above. Furthermore, the analytical work could be alleviated by analysing bulk samples. However, in that case the significance of observed differences cannot by analysing bulk samples. However, in that case the significance of observed differences cannot be tested statistically. The best and most realistic alternative therefore seems to be to sample a large number of soils and to bulk these samples into a smaller number of composite samples (for example 10), thus reducing the analytical work and costs, but allowing for statistical tests. It should be emphasized that such methodology is inappropriate for the analysis of the spatial structure of the changes observed and their relation to changes in vegetation composition.

For mixed stands, data allowing for a fairly reliable estimation of sample numbers required are still missing and it must be concluded that there is a serious gap in our knowledge of soil variability in mixed stands. Pending future research on this topic, the most realistic approach seems to be to avoid stands with a very varied composition (in terms of litter quality) and to apply the sampling methodology described above, i.e. sampling large numbers of soils and bulking into composite samples.

Conclusions

A critical examination of the start programme was required, largely because of the sheer number of forest reserves. As a result the soil survey will be replaced by a less expensive and time-consuming physiotope survey. Initial results from a statistical analysis of the available systematic set of soil data are promising and suggest that the methodology employed - soil descriptions at gridpoints - is adequate and should be continued.

The original plans for successional research were too ambitious and were seriously hampered by the lack of adequate knowledge on soil succession and soil variability in forest stands. The methodology to be employed has to account for both the spatial variability and the successional changes anticipated in these reserves. It also has to aim at a reduction of labour and costs to levels that administrations find acceptable.

Assuming that the forest reserves are monitored at intervals of 10 years, it is concluded that 50 samples will probably be sufficient to identify significant changes in soil parameters. Furthermore, for financial reasons, research should be done in only a limited number of forest reserves, which should meet one or more of the following criteria: initial soils, likely to show distinct changes in species composition over time periods of decades, a species composition which is not too complex (with regard to litter quality).

It is regrettable that successional research on stands with a more complex genesis or species composition has to be excluded because of their unsuitability for relatively short-term successional studies. It is to be hoped that administrations will realize that although successional processes proceed at slower rates than 5- or 10-year plans, they merit study.

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Soil survey and humus form research in Dutch forest reserves

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Summary

This paper presents the results of research on a representative set of 14 out of 75 reserves, where soil survey and humus form research have already been done in an initial programme. The main aim of this study was to examine whether the distinct humus layers can be predicted from parent material, drainage state and vegetation. The method of collecting and statistically analysing data is described. The regression model resulting from the analysis is presented and some of its aspects are illustrated. Finally the results are discussed.

Keywords: humus forms, soil survey, horizon characteristics

Introduction

Present-day Dutch forests were planted in a period of unemployment and an increasing demand for pit-props in the second half of the 19th century and the first decades of the 20th century. As a result, the forests are characterized by a simple structure and a poor tree species diversity.

Recent long-term planning in Dutch forestry (Meerjarenplan, 1986) aims at developing more diversity both in tree species composition and in forest structure. Forest development will thus largely be controlled by spontaneous processes. Hardly anything is known about this. Therefore more information on spontaneous processes will be valuable to forestry management. In 1983 the Dutch Government decided to establish Forest Reserves and an extensive research programme was developed to study spontaneous forest succession (Broekmeyer and Szabo, this volume).

Nutrient cycling is an important process in forest development. The humus layer is an important compartment in nutrient cycling, being an interface between vegetation and physiographic factors. It is thought that the development of the humus form contains important information about nutrient cycling (Vos and Stortelder, 1988).

An initial programme aims at doing soil surveys in approximately 75 forest reserves over a 15-year period. The purpose of this survey is to establish actual humus forms and their dependence on physiography and vegetation. In the basic programme a sequential study will be done in a representative set of sites to focus on reserves of organic matter and macronutrients (Sevink et al., this volume). The results of the basic programme will be extrapolated to the initial programme.

Methods

Introduction

Soil properties can be considered to be a function of independent state factors (Jenny 1941; Jenny, 1980). Vegetation and the physiographic state factors climate, parent material and drainage state control soil development. The humus layer as an interface between physiographic factors and vegetation plays a key role in this process. Litter and nutrients will accumulate if decomposition is impeded and homogenization is prevented by unfavourable physiographic site conditions. Mor-like humus forms, characterized by horizon differentiation, are a reflection of these vegetation-controlled ecosystems. Sites with favourable conditions for decomposition show mull-like humus forms, characterized by homogenization of horizons and nutrient transfer (Vos and Stortelder, 1988). It is hypothesized that parent material, drainage state and vegetation all have distinct influence on the development of humus forms. The purpose of this study is to establish actual humus forms and their dependence on physiography and vegetation.

Data collection

The aim is to select forest reserves representing the spectrum of the independent state factors parent material and drainage state in The Netherlands. Data were collected from 14 reserves (Figure 1). In each reserve the data were collected from grid points (called sample points) using a random sampling technique. Approximately 60 points per grid were sampled.

Soil profile data on parent material, drainage state, soil characteristics per horizon and thickness of distinct horizons were collected from bore holes. Special attention was paid to the description of the humus form (Van der Werff and Mekkink, 1992). Thicknesses of ecto-organic and endo-organic layers were described according to Klinka (1981). Within the ecto-organic horizon a distinction was made between the litter layer (OL), the fermentation layer (OF) and the humified layer (OH). No further distinction within each layer was made for statistical analysis. Dominating tree species in the surroundings of the sample point were noted.

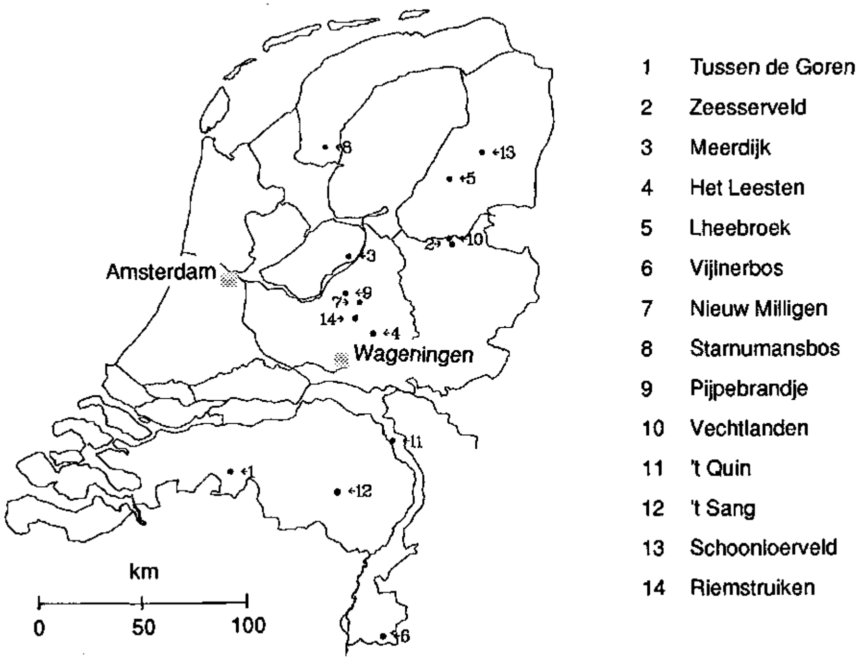

Figure 1. Location of 14 forest reserves where soil data were collected.

Mapping

The sampled grid points were used to define soil mapping units. Boundaries between mapping units are based on visible land characteristics. In the case of doubt additional borings were made. A geological map describing the distribution patterns of distinct parent material, and a soil map describing the distribution of soil types according to De Bakker and Schelling (1989) and the drainage state were made for each forest reserve.

Statistical analysis

A multiple linear regression technique was used to test significant differences between the thicknesses of distinct humus layers as response variables dependent on parent material, drainage state and vegetation as qualitative predictor variables (Lane et al., 1987). Thicknesses of layers were log-transformed to correct for skew distributions.

Data were stratified according to the predictor variables. Parent material was stratified according to geogenetic and geochronological criteria. For statistical purposes seven strata increasing in mineral richness were discerned (see Table 1). Each stratum consists of different geological units, aggregated together by expert judgement. Drainage state was stratified according to five classes of Mean Highest Water-table (MHW; see description of the models). Vegetation data were stratified at the level of the dominant tree species in the surroundings of the sample point.

Results

General

The result of the regression analysis consists of two multiplicative models for the thicknesses of the OF and OH horizons. The models predict the thicknesses of the horizons, given certain values for parent material, tree species and drainage state. The estimates of the effects given for the different predictors are proportional.

A stepwise selection of predictors, considering interactions between them, was carried out on the three main predictors. Only statistically significant predictors and interactions were added to the models and non-significant ones were dropped. Significance was tested using variance ratio and F-probability. Because the number of samples differs greatly between different values of the predictors (see Table 1) the predictors are not orthogonal. This means that variance ratio and F-probability depend on the sequence of the predictors in the model. Therefore not only different combinations of predictors and interactions, but also different sequences were tested. In all cases parent material proved to be very significant and was put first in both models. Vegetation appeared to be statistically significant for borizons as well, but drainage status turned out to be statistically significant for the OH horizon only.

Table 1. Samples according to parent material.

Parent material	Pleistocene	Holocene	Clay	Loam	Sand	Number of samples
A Aeolic (drift sand)		x			x	210
B Aeolic (cover sand)	x				x	325
C Fluviatile	x				x	86
D Anthropogenic		x			x	42
E Aeolic (loess)	x			x		46
F Fluviatile	x	x	x		x	34
G Marine		x	x		x	43+
						786

There appeared to be some slightly statistically significant interactions between predictors. But because their significance was weak, they were not incorporated in the models.

Regression models

The models resulting from the regression analysis are given below:

OF horizon (R^2 = 46.2):

$$Th = 4.08 \times \left\{ \begin{matrix} 1 & \textit{for } A \\ 0.74 & \textit{for } B \\ 0.77 & \textit{for } C \\ 0.81 & \textit{for } D \\ 0.66 & \textit{for } E \\ 0.63 & \textit{for } F \\ 0.27 & \textit{for } G \end{matrix} \right\} \times \left\{ \begin{matrix} 1 & \textit{for } PS \\ 0.90 & \textit{for } QR \\ 1.98 & \textit{for } LK \\ 0.96 & \textit{for } PM \\ 0.99 & \textit{for } FS \\ 1.34 & \textit{for } PA \\ \ldots & \textit{for } .. \end{matrix} \right\}$$

OH horizon (R^2 = 27.9):

$$Th = 1.67 \times \left\{ \begin{matrix} 1 & \textit{for } A \\ 1.06 & \textit{for } B \\ 1.23 & \textit{for } C \\ 1.20 & \textit{for } D \\ 0.80 & \textit{for } E \\ 0.47 & \textit{for } F \\ 0.38 & \textit{for } G \end{matrix} \right\} \times \left\{ \begin{matrix} 1 & \textit{for } D1 \\ 1.12 & \textit{for } D2 \\ 1.29 & \textit{for } D3 \\ 1.48 & \textit{for } D4 \\ 0.91 & \textit{for } D5 \end{matrix} \right\} \times \left\{ \begin{matrix} 1 & \textit{for } PS \\ 0.87 & \textit{for } QR \\ 0.41 & \textit{for } LK \\ 0.56 & \textit{for } PM \\ 1.08 & \textit{for } FS \\ 0.95 & \textit{for } PA \\ \ldots & \textit{for } .. \end{matrix} \right\}$$

where:

Th = Thickness (cm)
A..G= Parent material (Table 1)
PS = *Pinus sylvestris*
QR = *Quercus robur*
LK = *Larix kaempferi*
PM = *Pseudotsuga menziesii*
FS = *Fagus sylvatica*
PA = *Picea abies*

Drainage status	MHW[1]
D1	> 80
D2	40-80
D3	25-40
D4	15-25
D5	< 15

The models consist of a constant which is multiplied by proportional values for each predictor. Ratios are given in braces for each value of the predictor. In the presentation of the models only the most frequent tree species were included, but in the calculations we used all species.

Parent material

The effect of parent material on the thicknesses of the OF and OH horizons is given by the first column in braces in both models and is illustrated by Figure 2. A distinction can be made between mineral-poor sands (A, B, C, D) and mineral-rich loam and clays (E, F, G).

Mineral-poor sands

- Total thickness stabilizes when there is equilibrium between input of fresh fallen litter and output by decomposition and homogenization with mineral subsoil.
- Increasing thickness of the OH horizon suggests a rate of decomposition increasing with increasing richness of parent material. Homogenization processes seem to be limited.

Comparing Figure 2 with the estimates for the poor sands in the models suggests a somewhat different order in the thicknesses of OF and OH layers. Figure 2 is based on average thicknesses within the strata, irrespective of tree species and drainage state. Estimates in the model are based on all combinations of values of the predictors that occur. Since the predictors are orthogonal some differences may occur.

Mineral-rich loam and clays

- Decreasing thickness of both layers with increasing mineral richness of parent material suggests decomposition and homogenization increase with the mineral subsoil.

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[1]Mean Highest Water Table in cm below soil surface.

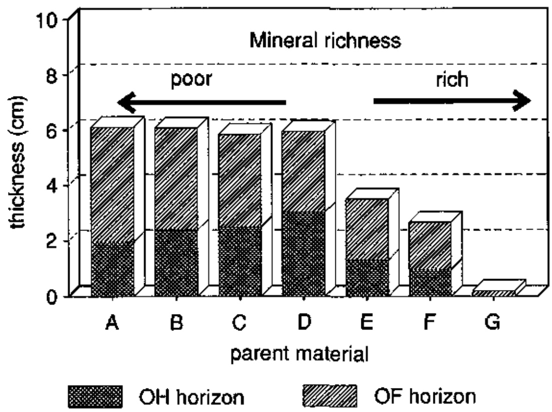

Figure 2. Thicknesses of OF and OH horizons in relation to parent material.

Vegetation

The effect of vegetation on the thicknesses of the OF and OH horizons is given by the last column in braces in both models and is shown by Figure 3.

- Litter from different tree species decomposes differently on the same parent material, generating different humus forms. This is illustrated by the estimates in the models for *Quercus robur* and *Larix kaempferi*, which differ by a factor of two.
- There is a considerable heterogeneity of humus form characteristics (see Figure 3).

Drainage status

The effect of drainage status on the thickness of the OH horizon is given by the second column in braces in the model for the OH horizon and is shown by Figure 4.

- Total thickness stabilizes at an equilibrium level independent of drainage status, unless the conditions become dry, suggesting decreased litter production caused by shortage of water.
- Poor drainage results in moist conditions, which favour decomposition processes generating an increased thickness of the OH layer, unless the MHW exceeds 15 cm (see general model).

Discussion and conclusions

Discussion

Although the influence of the predictors on thickness of the ecto-organic horizons is evident, some comments need to be made. At the moment only 14 of the 75 forest reserves have been surveyed, so conclusions can only be tentative. On some kinds of parent material the number of samples was rather small (see Table 1). In the coming years, when more reserves are surveyed, more data will be available.

The percentages of variance accounted for by the models (R^2) suggest that other factors might cause variation as well. In the future, analysis factors such as age, fertilization and base status should be included in the statistical analysis.

In this study the influence of the predictors on the ecto-organic layers was examined. When homogenization processes depend on mineral richness of parent material, as can be concluded from the decreasing thickness of the OH horizon with increasing mineral richness, the development of the Ah horizon in the mineral subsoil must be dependent on the same factor. In future

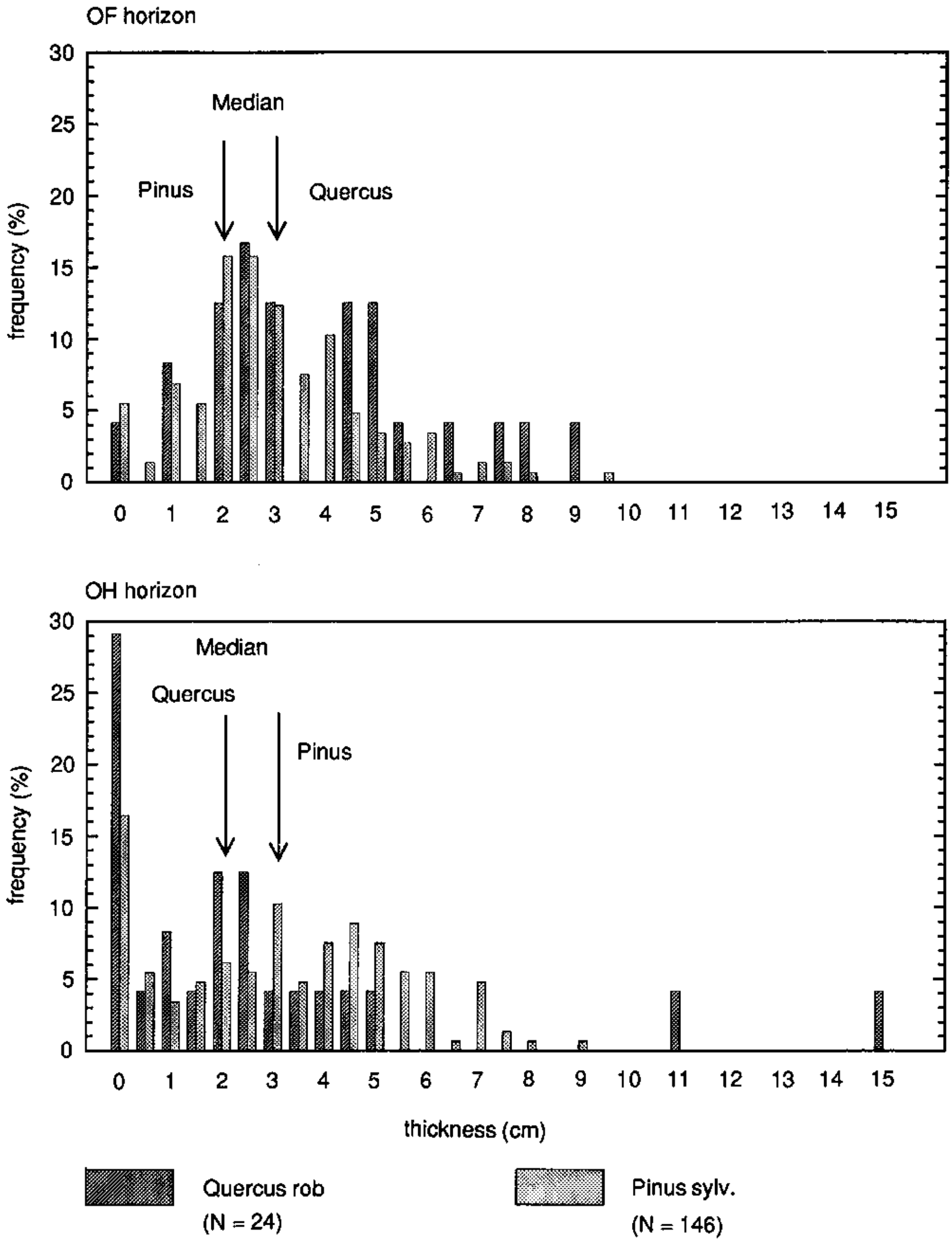

Figure 3. Frequency distribution of thicknesses of OF and OH horizons on Pleistocene aeolian sand (B).

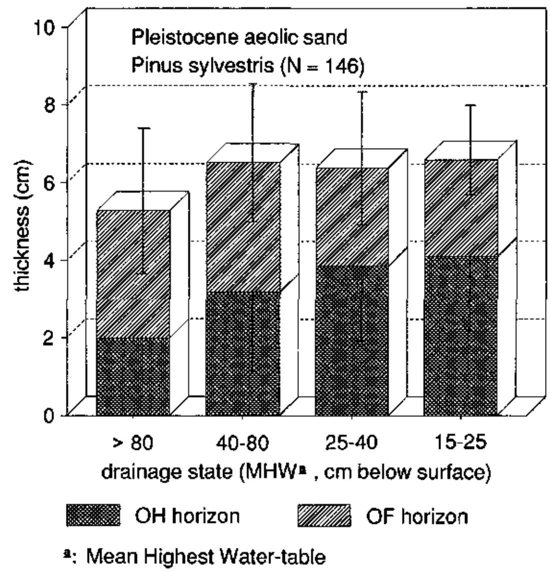

Figure 4. Thicknesses of OF and OH horizons in relation to drainage status.

analyses, the properties of the Ah horizon and their relation to parent material and other predictors should be examined as well.

The results suggest that the important pedogenetic process of homogenization of organic matter and the underlying mineral horizon is primarily dependent on parent material and drainage status and, to some extent, on vegetation. Vegetation, like parent material, seems to be important in decomposition processes.

Conclusions

Four main conclusions can be drawn from this study:

- Thicknesses of layers can only partly be predicted by parent material, drainage status and tree species. A considerable part of the variation is not accounted for by the models. Other factors such as age, fertilization or base status (pH) might cause some variation as well.
- Parent material has a distinct influence on the OF horizon; so does tree species, but less so.
- In decreasing order of importance, parent material, tree species and drainage status have a distinct influence on the OH horizon.
- Spatial variability in the plots studied appeared to be considerable.

The results imply that there are perspectives for using humus forms as predictors of nutrient cycling, which is an important process in forest development. Future research should focus on analysing the nutrient status of different humus horizons, so that humus form and nutrient status can be linked in forestry management.

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Mycological investigations in forest reserves in The Netherlands

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Summary

Mycological investigations were carried out in 16 Dutch forest reserves from 1988 to 1990. Within each reserve an area of 100 m x 10 m subdivided into ten blocks of 10 m x 10 m was investigated. A total of 540 species was recorded: one of these was new to science and six others were new to Dutch mycoflora. Wood-inhabiting fungi were very well represented, whereas ectomycorrhizal symbionts were uncommon. Forest reserves on fertile soil were much richer in species of all functional groups than reserves on nutrient-poor soils. On the basis of a direct ordination technique the relevant ecological factors for ectomycorrhizal, litter saprotrophic, and wood-inhabiting fungi were tentatively identified. A refined ecological classification of ectomycorrhizal and litter saprotrophic fungi gave additional strength to this interpretation. On the basis of mycofloristic composition a transition from coniferous stands towards deciduous forest is inferred. Finally some predictions are made about future mycological development in forest reserves.

Keywords: mycological investigation, forest reserves, ecological classification

Introduction

At present most forests in The Netherlands are managed rather intensively. There is, however, an increasing tendency to allow forests to develop more naturally - one of the advantages of this is that it reduces management costs. More "natural" forests are thought to have a greater diversity of tree species, a more varied age structure, and a more marked vertical and horizontal structure than managed forests. However, not much is known about natural processes in Dutch forest ecosystems. Since 1983 various forest reserves have been selected for study in order to clarify these processes. The term 'forest reserve' is somewhat misleading, as it suggests forests that already have a high degree of 'naturalness', whereas it actually refers to forest areas which are no longer being managed, so that spontaneous processes can be studied (Broekmeyer and Szabo, this volume).

The forests selected as forest reserves are intended to reflect the various forest associations that occur in The Netherlands. At present the selected forest reserves show various degrees of anthropogenic influence. A research programme has been set up for forest reserves in The Netherlands (Broekmeyer and Hilgen, 1991). Mycological research was not part of the original programme, but a grant from the Prins Bernhard Fonds enabled such research to be done in 16 reserves.

Fungi have various important ecological functions in forest ecosystems, as ectomycorrhizal symbionts, decomposers of litter and wood, and parasites of trees. Mycorrhizal fungi are ubiquitous in forest ecosystems. Almost all forest tree species form ectomycorrhiza, with the remaining tree species usually forming vesicular-arbuscular mycorrhiza. The ectomycorrhizal fungi enhance nutrient and water uptake by increasing the soil volume that is exploited. Some ectomycorrhizal fungi are able to take up organic nitrogen and phosphorus. They can also protect the tree against aluminium and heavy metals, and provide physical and/or chemical protection against root pathogens. Ectomycorrhizal fungi are provided with carbohydrates from the trees (Brundrett, 1991; Read, 1991; Vogt et al., 1991).

Ectomycorrhizal fungi show different degrees of specificity for tree species and/or soil conditions. As different mycorrhizal fungi might not be equally effective in all respects, a diverse mycorrhizal flora is extremely important for forest health (Kuyper et al., 1990). In the last twenty years most ectomycorrhizal fungi in The Netherlands have decreased, and almost 50 % are now on the Red Data List (Arnolds, 1989, 1991). At the same time the vitality of many Dutch forests, especially those on nutrient-poor soils where trees are obligately ectomycorrhizal, has also declined.

Fungi are also very important as decomposers of organic material. Their hyphal growth form, enzymatic abilities, and tolerance of acidic conditions give them a definite advantage over bacteria in many forest ecosystems. Only fungi (Basidiomycetes and a few groups of Ascomycetes) possess ligninolytic enzymes. The lignocellulosic matrix in litter and wood, which generally constitutes 70-80 % of fresh organic material, can only be degraded by fungi (Swift, 1982; Rayner and Boddy, 1988). During the decomposition process, mineral nutrients such as nitrogen, phosphorus, and cations are mineralized, leading to efficient recycling of nutrients and carbon. Changes in the decomposition process as a result of anthropogenic influences may therefore have serious consequences for the functioning of forest ecosystems.

Finally, some fungi are known as tree parasites. They can enter trees via roots or above ground. Several of these fungi are necrotrophic parasites, being able to persist by switching to a saprotrophic mode of life after the tree has been killed (Rayner and Boddy, 1986). It is not always easy to classify a species as a wood parasite or a wood saprotroph. We will therefore combine both groups of wood-inhabiting fungi and consider litter saprotrophic species a separate category.

Forests are very rich in fungal species. According to Arnolds and de Vries (1989) 1994 fungal species occur mainly in forests. As species belonging to different functional groups or guilds (ectomycorrhizal symbionts; litter saprotrophs; wood-inhabiting fungi) are dependent on different and independent nutrient and energy sources, they are excellent indicator species of nutrient availability, soil pH, litter and humus characteristics, naturalness of the forest, etc. (Kost, 1991).

The mycological investigations in Dutch forest reserves were set up in order to:

- record the initial fungal species composition in 16 reserves
- assess the importance of forest reserves for the conservation of fungi (Winterhoff, 1989)
- assess the similarity between reserves on the basis of mycofloristic composition of the different functional groups
- generate testable hypotheses on the role of fungi in successional processes (Cromack, 1981).

The results of these investigations have already been published in Dutch (Veerkamp, 1992). The main findings are summarized here. Mycological investigations in forest reserves have also been carried out in the Federal Republic of Germany (Kost and Haas, 1989). The German research, which was more qualitative, was done in reserves of various sizes (ranging from 8 to 97 ha) and for periods of different duration.

Material and methods

In all, 16 Forest Reserves (FR) were investigated (see Figure 1). They were selected on the basis of historical considerations, site conditions, and actual vegetation (Broekmeyer and Szabo, this volume). A brief characterization of these reserves is provided in the Appendix.

Only a small part within each reserve was investigated, using the myco-coenological method as developed at the Biological Station in Wijster (Barkman, 1976; Jansen, 1981). The representative area ('Minimum Area') in forests is considered to be 1000 m^2 (Winterhoff, 1984). In these reserves the central transect of 100 m x 10 m within the core area was used. Detailed data are also available on the floristic composition and forest structure in this transect. The transect was subdivided into ten blocks, each measuring 10 m x 10 m. This subdivision provides a better insight into the spatial distribution of fungi within the plot and hence allows a better assessment to

Figure 1. Forest reserves investigated in the years 1988-1990.

be made of changes in future investigations, as most changes are expected to occur on spatial scales much smaller than plot size.

The investigations took place from 1988 to 1990. The plots were visited 2-3 times a year in late summer and autumn (August-November). The vernal aspect was assessed only once, in Meerdijk FR. During the visits all Agaricales, Gasteromycetes, and conspicuous Aphyllophorales and Ascomycetes were noted. Less conspicuous corticioid fungi were investigated in 1989. Only incidental attention was given to small Ascomycetes. The carpophores of larger fungi were counted or estimated. Abundance of corticioid fungi and small Ascomycetes was expressed as the number of branches on which a certain species was found. Herbarium material of rare and interesting species is conserved at the Wijster Biological Station (WAG-W). Using the relevés a synthetic relevé for each plot was made, in which the parameter AMAC (Absolute Maximum Abundance of Carpophores) was indicated. The synthetic relevés have been published elsewhere (Veerkamp, 1992).

As the functional groups (ectomycorrhizal symbionts; litter saprotrophs; wood-inhabiting fungi) rely on independent carbon and nutrient sources, it seems plausible that their occurrence in the forest reserves will be governed by different environmental factors. For that reason a Direct Gradient Analysis (Bray and Curtis, 1957) was done for the functional groups separately, on the basis of presence/absence data.

Results and discussion

Species richness

A total of 540 species was recorded. As mycological considerations did not play a role in the selection of forest reserves, these results can be assumed to reflect the fungal species richness of forests in The Netherlands. Arnolds and de Vries (1990) listed 1994 fungal species for forest ecosystems in The Netherlands, implying that 27% of them have been found on a (cumulative) area of 1.6 ha. By comparison the research in forest reserves in Germany yielded 1158 species on 387 ha (Kost and Haas, 1989).

Of these 540 species seven turned out to be new records for The Netherlands: *Flammulaster limulatus* (Weinm.: Fr.) Watl. (Starnumansbos FR), *Mycena longiseta* Höhn. (Vijlenerbos FR), *Athelopsis glaucina* (Bourd. & Galz.) Parm. (Vechtlanden FR), *Hyphoderma macedonicum* (Litsch.) Donk (Riemstruiken FR), *Sistotrema pistilliferum* Hauerslev (Drieduin 3 FR), and *Hypoxylon semiimmersum* Nitschke (Roodaam FR). Furthermore in Het Leesten FR an undescribed species of *Marasmiellus* was found, provisionally named *M. lateralis*.

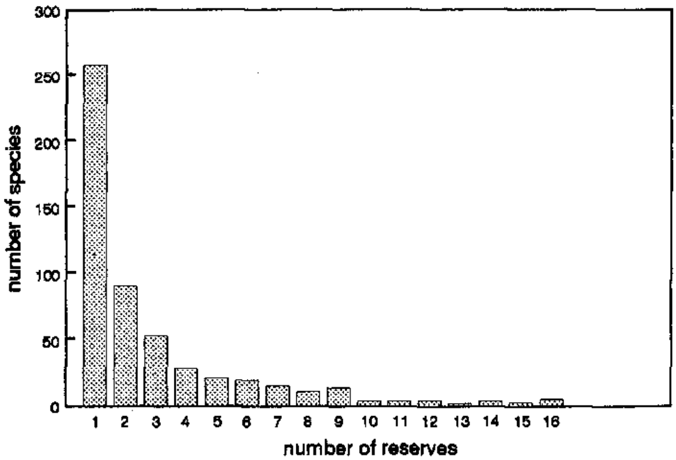

Figure 2. Distribution of the number of species over the number of reserves.

Commonness and rarity of species in forest reserves is indicated in Figure 2 and 3. About 50% of all species were recorded in one forest reserve only. Of these species, about 50% were only found in one block within a reserve, implying that 25% of the species were recorded from one block only. Such relative rarity of a large part of fungal species is not uncommon. Keizer and Arnolds (1990) recorded 27% of wood-inhabiting Aphyllophorales in marshy forests only once. De Vries (1990) also noted a very great spatial variability of wood-inhabiting fungi in coniferous forests. Only five species were found in all reserves: *Mycena galericulata* (Scop.: Fr.) Quél. (146 blocks), *Dacrymyces stillatus* Nees: Fr. (104 blocks), *Hyphoderma praetermissum* (P. Karst.) J. Erikss. & Strid (74 blocks), *H. puberum* (Fr.) Wallr. (60 blocks), and *Trechispora vaga* (Fr.) Liberta (51 blocks).

The number of fungal species per reserve varied from 45 (Nieuw Milligen FR) to 206 (Vechtlanden FR). There were no significant differences in species richness between floristically characteristic and floristically non-characteristic (Broekmeyer and Szabo, this volume) reserves ($t = 1.17$; $p > 0.05$). In Germany the number of fungal species per forest reserve varied from 65 to 422 (Kost and Haas, 1989). The numbers were not related to size of the reserve investigated ($r = 0.003$; $p > 0.05$).

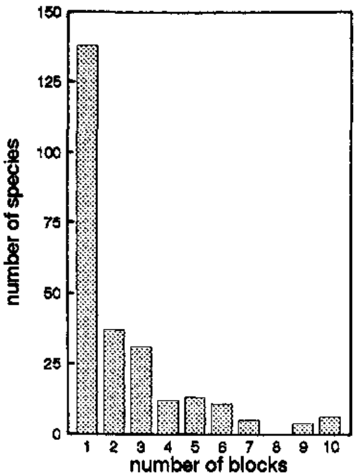

Figure 3. Distribution of the number of species found in only one reserve over the number of blocks.

Forest reserves can be sites where rare and threatened fungi occur, even though these sites are neither designed nor managed for species conservation. During our investigations we found 26 species on the Dutch Red Data List (Arnolds, 1989). The number of threatened species per reserve varied from zero to nine (Vechtlanden FR) and was, on average, 2.0 (i.e. 2% of the average number of species). Floristically characteristic reserves did not contain more threatened species ($t = 1.22$; $p > 0.05$). In Germany 82 species on the German Red Data List were found in forest reserves, ranging from zero to 17 per reserve (average 7.7, i.e. 3.6% of the average number of species; Winterhoff, 1989). These numbers are higher than those from The Netherlands, not only because a larger area was investigated for longer (resulting in more species per area), but also because the reserves themselves are already more natural than the Dutch reserves.

Numbers of species in different functional groups

The distribution of the fungal species among the main functional groups is indicated in Table 1.

Table 1. Distribution of fungal species among functional groups in Forest Reserves and in all forested habitats (based on Arnolds and De Vries, 1989).

	Absolute number		Percentage	
	Reserv.	Forests	Reserves	Forests
ectomyc. fungi	86	650	16	32
litter fungi	168	632	31	32
wood fungi	286	712	53	36

Ectomycorrhizal fungi are strongly underrepresented in forest reserves by comparison with a general ecological statistics for forest fungi, whereas wood-inhabiting fungi are extremely well represented. In fact, 40% of all wood-inhabiting fungi that occur in The Netherlands were found during this inventory of 1.6 ha (out of a forested area of 283 000 ha). The corresponding figures for ectomycorrhizal and litter saprotrophic fungi are much lower (13% and 24% respectively).
The species numbers of the functional groups in different forest reserves are given in Figure 4. The species richness of the three functional groups correlates statistically significantly (ectomycorrhizal fungi - litter saprotrophs: rank correlation: $r = 0.73$; $p < 0.05$; ectomycorrhizal fungi -

wood-inhabiting fungi: r = 0.81; $p < 0.05$; litter saprotrophs - wood-inhabiting fungi: r = 0.54; $p < 0.05$). Although these correlations are very high, we should not overestimate their importance. Such correlations will certainly not hold when we compare one site over a number of years (instead of several sites simultaneously). In the German forests all three functional groups were also statistically significantly correlated, but in Sweden Tyler (1985) reported a negative correlation between richness of ectomycorrhizal and litter saprotrophic fungi in beech forests.

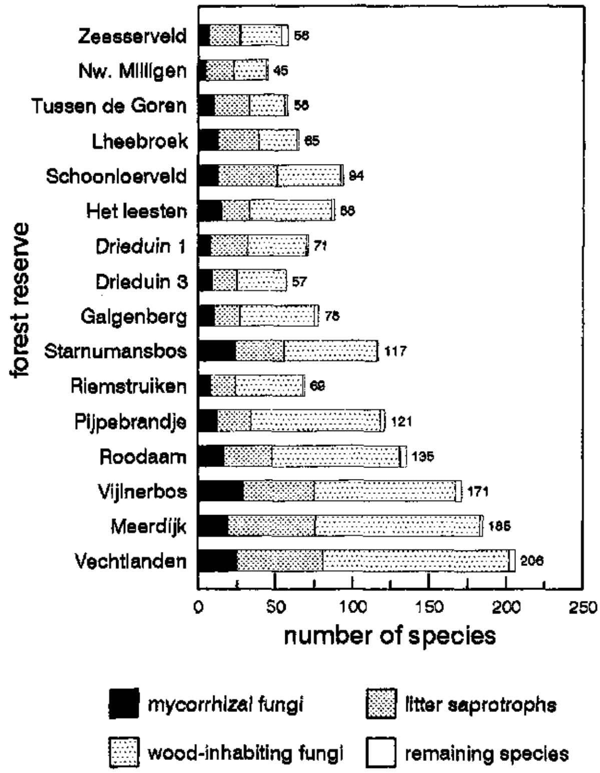

Figure 4. Distribution of the number of species over the functional groups per reserve.

Because of this strong correlation a general rule can be derived that at present in forest ecosystems in The Netherlands the average number of ectomycorrhizal fungi (13.6) is half that of the number of litter saprotrophs (28.3) and the average number of wood-inhabiting fungi (55.9) is double that of soil-inhabiting saprotrophic fungi. As far as ectomycorrhizal fungi are concerned these data compare unfavourably with species lists from former times, in which all groups tend to be present in equal proportions. The shift can be explained by a dramatic decrease of ectomycorrhizal fungi caused by eutrophication and acidification, and a largely independent increase of wood saprotrophic fungi as a consequence of the ageing of Dutch forests and a decrease in forest management (Arnolds, 1989). According to Kost (1991) a ratio of litter saprotrophic to ectomycorrhizal fungi greater than 2 would indicate larger nutrient fluxes and an increased availability of mineral nitrogen.

In Germany the three functional groups are more or less equally represented (ectomycorrhizal fungi: 73.3 species; litter saprotrophs: 60.9 species; wood-inhabiting fungi: 80.1 species). Only 2 (out of 15) German forest reserves had a ratio of litter saprotrophs to ectomycorrhizal fungi larger than 2.0, and only 2 had more than 50% wood-inhabiting fungi (Kost and Haas, 1989).

The more or less constant ratio between the functional groups can be used to explain

deviations in relative numbers among functional groups in various forest reserves. The relative contribution of ectomycorrhizal fungi in Zeesserveld and Nieuw Milligen Forest Reserves is much lower than average, but is average in Tussen de Goren FR (all are pine forests on poor acidic soils). The first two reserves have a large grass cover (*Deschampsia flexuosa*) in the herb layer, suggesting that grasses suppress ectomycorrhizal fungi (Timbal et al., 1990; Baar et al., 1992b). Tussen de Goren FR is richer in ectomycorrhizal fungi, although it has a large cover of *Molinia caerulea*. However, almost all mycorrhizal fungi were found at the edge of ditches within this reserve, where there is no accumulation of litter and no grass cover. We cannot explain the paucity of species in Drieduin FR 1 and 3, as these forest types are expected to harbour a diverse ectomycorrhizal flora (Sammler, 1988; Wöldecke and Wöldecke, 1990).
Figure 4 furthermore indicates that broadleaved forests on poor sandy soils are generally more species-rich than coniferous forests, with mixed forests being slightly more diverse. In broadleaved forests on fertile soils more species were found than in such forests on poorer soils (see below).

In coniferous forests the percentage of wood-inhabiting fungi is somewhat lower than expected. Until recently such forests were managed as plantation forests; this suggests that the variety of organic debris on the forest floor is very poor (mainly branches, no trunks or stumps). The great species richness of wood-inhabiting fungi on fertile soils is statistically correlated with amount of dead wood on the forest floor (rank correlation: $r = 0.69$; $p < 0.05$) and furthermore is related to a greater tree species diversity and a larger variety of woody substrates in different stages of decomposition (Jahn, 1979; Barkman et al., 1983).

Ordination of ectomycorrhizal fungi

The similarity between Meerdijk and the other forest reserves was zero or (as in the case of Vechtlanden FR) only slight. This resulted in an ordination that had most reserves clustered together. For that reason the first axis was made on the basis of the second most dissimilar pair of reserves (Figure 5). The position of Meerdijk FR was subsequently determined, but the procedure implies that its position cannot be wholly correct.

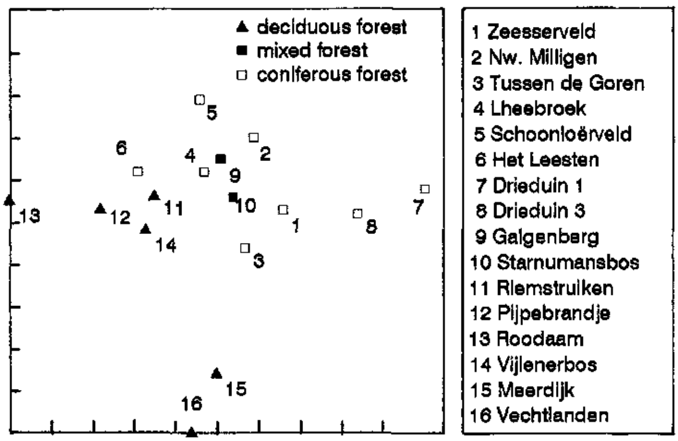

Figure 5. Ordination of forest reserves on the basis of mycorrhizal fungi.

There is no clear separation between coniferous and broadleaved forests. This cannot be explained by the spontaneous growth of broadleaved trees in coniferous stands, as to date this only occurs to an appreciable degree in Galgenberg and Starnumansbos forest reserves. A likely explanation is that the ectomycorrhizal flora in coniferous forests tends to resemble that of broadleaved forests. In forests with a thick ectorganic layer, and most clearly so in Douglas-fir stands (Het Leesten FR), the ectomycorrhizal flora includes some species that were formerly found only in deciduous forests, e.g. *Lactarius theiogalus* (Bull.: Fr.) S.F. Gray, *Russula ionochlora* Romagn., *R. parazurea* J. Schaeff., *R. nigricans* Fr., *Inocybe napipes* J. Lange, and *Xerocomus chrysenteron* (Bull.) Quél. In a certain sense the ectomycorrhizal flora (and the saprotrophic flora too) indicates such stands are developing towards broadleaved forests, even before deciduous trees have become established (cf. Vogt et al., 1990). Species that are most typical of coniferous forests (and occurred in very poor wind-blown oak and beech forests as well) have become very rare. Both factors result in a weak separation between deciduous and coniferous forests.

In order to explain the ordination we subdivided the ectomycorrhizal flora into a number of groups, resulting in the following classification (see Table 2).

Figure 6 shows this classification for some reserves. Most forest reserves, e.g. Zeesserveld, Het Leesten, and Pijpebrandje, are characterized by species that occur on nutrient-poor to slightly

Table 2. Classification of ectomycorrhizal fungi.

10	Species associated with coniferous and deciduous trees on nutrient-poor to somewhat nutrient-rich soil
12	Species associated with coniferous and deciduous trees on nutrient-poor soil
13	Species associated with coniferous and deciduous trees on nutrient-poor soil without a litter layer
20	Species associated with conifers on nutrient-poor to somewhat nutrient-rich soil
22	Species associated with conifers on nutrient-poor soil
23	Species associated with conifers on nutrient-poor soil without a litter layer
30	Species formerly associated with deciduous trees on nutrient-poor to somewhat nutrient-rich soil
32	Species formerly associated with deciduous trees on nutrient-poor soil
33	Species formerly associated with deciduous trees on nutrient-poor soil without a litter layer
40	Species of nutrient-rich soils with a high pH and base saturation
50	Species of nutrient-rich marshy forests

nutrient-rich soils, usually with a well-developed ectorganic layer (groups 10, 20, and 30). Such species are *Paxillus involutus* (Batsch: Fr.) Fr., *Xerocomus badius* (Fr.: Fr.) Gilb., *Russula ochroleuca* Pers., and *Lactarius hepaticus* Plowr. in Boud. Of these, only the last species is restricted to coniferous forests. *Paxillus involutus* and *Xerocomus badius* are fairly insensitive to pine needle extracts (Baar et al., 1992a).

Species characteristic of nutrient-poor soils with a very thin litter layer, e.g. *Cortinarius obtusus* (Fr.: Fr.) Fr. and *Dermocybe crocea* (Schaeff.) Mos. (both associated with coniferous and broadleaved trees), and *D. semisanguinea* (Fr.: Fr.) Wünsche and *Rhizopogon luteolus* Fr. in Fr. & Nordh. (associated with conifers only) are found in Drieduin 1 and Drieduin 3 forest reserves. *Amphinema byssoides* (Pers.: Fr.) J. Erikss., a corticioid species that was recently discovered to be ectomycorrhizal (Ingleby et al., 1990), is also restricted to these reserves. This species prefers base-rich (and especially calcium-rich) sites, but it is probably not sensitive to higher levels of available nitrogen.

The grass-rich pine forests are extremely poor in ectomycorrhizal fungi. Only Tussen de Goren FR is somewhat richer, with *Russula coerulea* Fr., *R. sardonia* Fr., and the rare and threatened *R. paludosa* Britz. growing along ditches. Most deciduous forests are also depauperate in diagnostic species. In Pijpebrandje FR no ectomycorrhizal fungi that are exclusive to beech were found, whereas in Riemstruiken FR only *Lactarius quietus* (Fr.) Fr. can be considered an exclusive species for oak. However, exclusive oak symbionts were found in FR Roodaam, together with species that are characteristic of forest soils with a thin to very thin litter layer, such as *Russula vesca* Fr., *R. pectinatoides* Peck, *Lactarius chrysorrheus* Fr., and *Amanita citrina* (Schaeff.) Pers. Many of these species now find their optimal habitat along roadsides, where

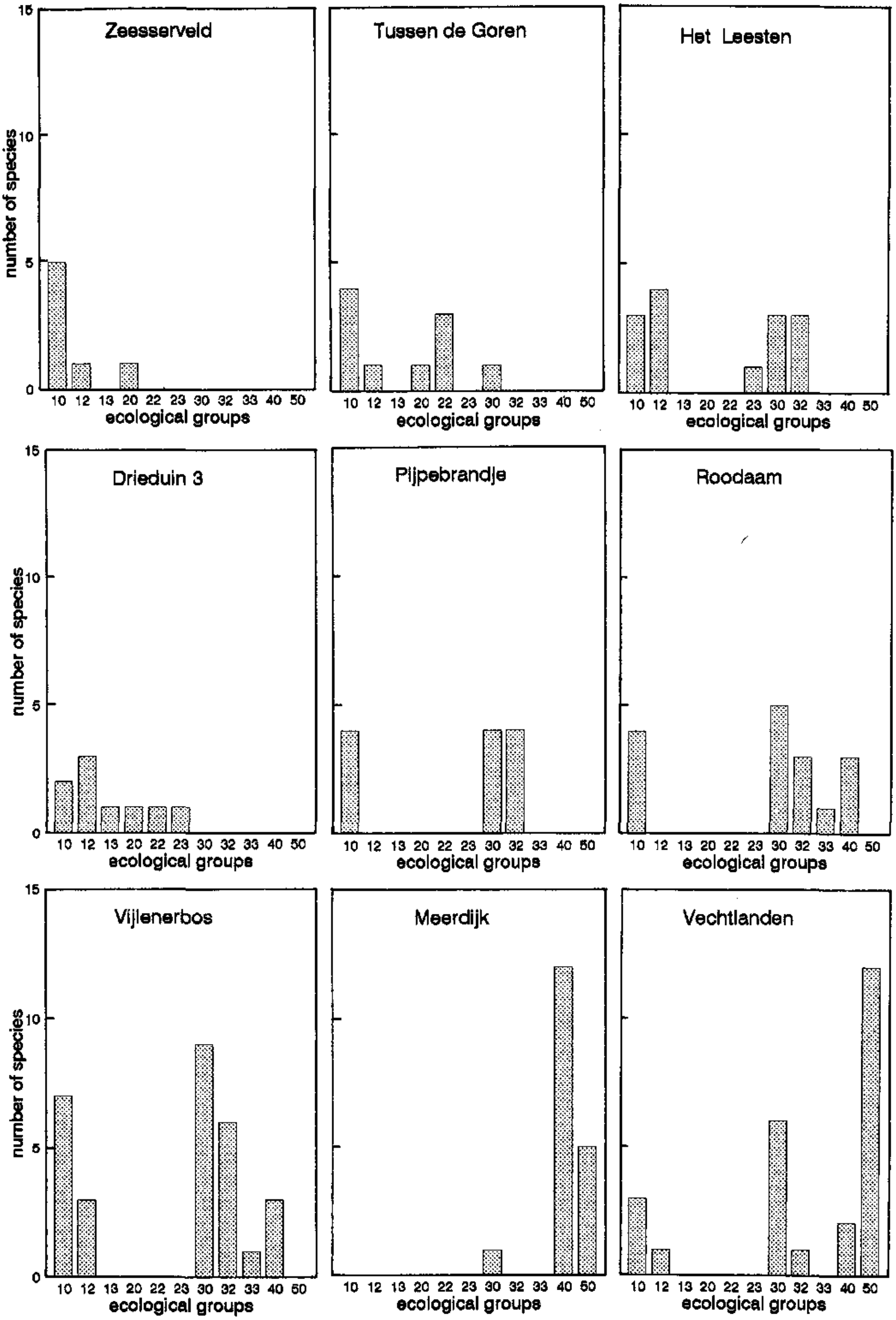

Figure 6. Number of mycorrhizal fungi of different ecological groups.

leaves are blown away and no plant litter accumulates. The presence of a somewhat higher base saturation (and especially the presence of calcium) is indicated by species like *Inocybe bresadolae* Mass. and *Scleroderma areolatum* Ehrenb. Richer soils are also found in Vijlenerbos FR with *Amanita phalloides* (Fr.: Fr.) Link, *Dermocybe sanguinea* (Wulf.: Fr.) Wünsche (very rare in The Netherlands), and *Russula densifolia* Gillet.

More fertile sites occur in Meerdijk FR and Vechtlanden FR. The following species that are exclusively associated with alder occur in both reserves: *Cortinarius alnetorum* (Velen.) Mos., *Lactarius obscuratus* (Lasch: Fr.) Fr., *Naucoria escharoides* (Fr.: Fr.) Kumm., *N. subconspersa* P.D. Orton, and *N. scolecina* (Fr.) Quél. Meerdijk FR is further characterized by species that are commonly found on nutrient-rich clay, often associated with poplar, e.g. *Cortinarius sertipes* Kühner, *C. saturninus var. bresadolae* Mos., *Hebeloma collariatum* Bruchet, *Inocybe squamata* J. Lange, and *Inocybe praetervisa* Quél. Vechtlanden FR has some other symbionts of alder and willow, but these taxa occur on somewhat wetter soils, e.g. *Cortinarius bibulus* Quél., *C. helvelloides* (Fr.: Fr.) Fr., *Entoloma sericatum* (Britz.) Sacc., *Naucoria alnetorum* (Maire) Kühn. & Romagn., and *N. salicis* P.D. Orton. On drier sites in Vechtlanden FR some indifferent species of hardwoods were found.

The first axis of the ordination is interpreted as representing nutrient status of the soil (probably base saturation or cation availability, and not nitrogen availability). The second axis could represent an axis of litter accumulation.

Ordination of litter saprotrophic fungi

In this ordination (Figure 7) there is a good separation between deciduous and coniferous stands, with mixed stands being intermediate. All coniferous stands lie close together and are fairly similar, indicating that they possess some kind of standard flora. Most deciduous forests are also fairly similar to these coniferous stands. As far as can be judged from older data, the differences in species composition of litter decomposers between coniferous and deciduous forests were formerly probably larger. Here too a transition of coniferous stands towards deciduous forests can be noted. Only Roodaam, Vechtlanden, and Meerdijk forest reserves possess a different saprotrophic mycoflora.

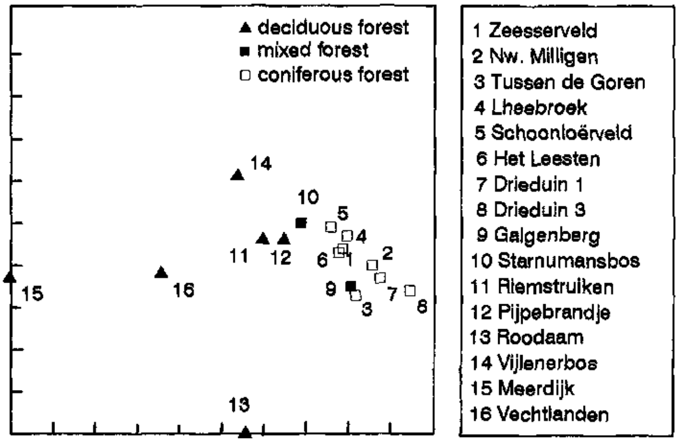

Figure 7. Ordination of forest reserves on the basis of litter saprotrophs.

Within the saprotrophic flora we recognized a number of different ecological groups. As fungi play a paramount role in litter decomposition and the resultant formation of the humus profile (Klinka et al., 1981), the kind of humus profile was one of the main classification criteria. A

number of separate substrates were also recognized. This resulted in the following classification (see Table 3).
Species belonging to subgroup 53 still form a rather heterogeneous ensemble. It consists partly of species that could not be assigned to one of the other subgroups of 5, e.g. *Mycena amicta* (Fr.: Fr.) Quél. and *Clitocybe phaeophthalma* (Pers.) Kuyp.
Raithelhuber) are mainly found in reserves with a well-developed moss layer, e.g. Schoonloër-veld FR. Group 40 is rare in coniferous forests, but well represented in broadleaved forests,

Table 3. Classification of saprotrophic fungi.

10	Saprotrophic species on mosses
20	Saprotrophic species on peat
30	Saprotrophic species that can also be found on twigs and small woody debris
40	Saprotrophic species on almost undecomposed herbs, leaves, stems or fruits. These species usually have a very restricted host range
50	Saprotrophic species with a wide range, occurring on mull, moder, and mor
51	Saprotrophic species, mainly on mor and moder
52	Saprotrophic species on mor
53	Saprotrophic species on nutrient-enriched mor and moder
55	Saprotrophic species on mull

Figure 8 shows the species composition of some reserves on the basis of this ecological grouping. Moss-decomposing species (belonging to the genera *Galerina* Earle and *Rickenella*especially on rich soils. A majority of the litter saprotrophic fungi (68%) could be assigned to groups 50 to 55 and hence (hypothetically) related to the humus profile.

Species of group 50 still more commonly occur in broadleaved forests than in coniferous forests, where only a few species of this group, e.g. *Mycena filopes* (Bull.: Fr.) Kumm., are present. The ratio between subgroups 51 (characteristic of mor and moder, e.g. *Clitocybe ditopa* (Fr.: Fr.) Gillet, *C. marginella* Harm., *C. metachroa* (Fr.: Fr.) Kumm., *Collybia butyracea* (Bull.: Fr.) Kumm., *Mycena galopus* (Pers.: Fr.) Kumm., *M. sanguinolenta* (A. & S.: Fr.) Kumm.) and 52 (characteristic of mor, *Clitocybe vibecina* (Fr.) Quél., *Entoloma cetratum* (Fr.: Fr.) Mos., *Hygrophoropsis aurantiaca* (Wulf.: Fr.) Maire, *Marasmius androsaceus* (L.: Fr.) Fr.) is striking. This (weighted) ratio, based on frequency data (number of blocks within a reserve; not shown in Figure 8) instead of presence data, is about 1:2.5 in poor coastal coniferous forests, about 1:1.5 in inland Scots pine forests, and about 1:1 in larch and Douglas-fir stands. In broadleaved forests the ratio is larger than 2:1. Group 55 occurs mainly in FR Meerdijk and Vechtlanden; diagnostic species include *Clitocybe foetens* Melot, *Conocybe* species, *Helvella* species, *Entoloma juncinum* (Kühn. & Romagn.) Noordel., and *Pluteus* species.

In the ordination the first axis represents the humus profile (mull-moder-mor). We cannot yet explain the second axis.

The largest number of saprotrophic fungi on fine organic debris was found on nutrient-rich mull soils. This observation remains true if we consider only species from groups 50 to 55, most directly connected with the humus profile. The observation that mull soils are richer in litter-decomposing species than mor and moder soils might seem intuitively strange, as decomposition in mor (and moder) is considered to be almost exclusively affected by fungi (especially by the ligninolytic Basidiomycetes), whereas in mull soils bacteria play a large role (Swift et al., 1979). Tyler (1985) also observed a larger number of saprotrophic Basidiomycetes on mull. However, species number may not be the best measure to assess the relative performance of litter-decomposing fungi in different forests. We must at least take into account the number of fruiting bodies and especially the dry matter production of fruiting bodies (Hering, 1982). On this basis fungi are indeed better represented in mor and moder. Furthermore, the larger turn-over of organic matter

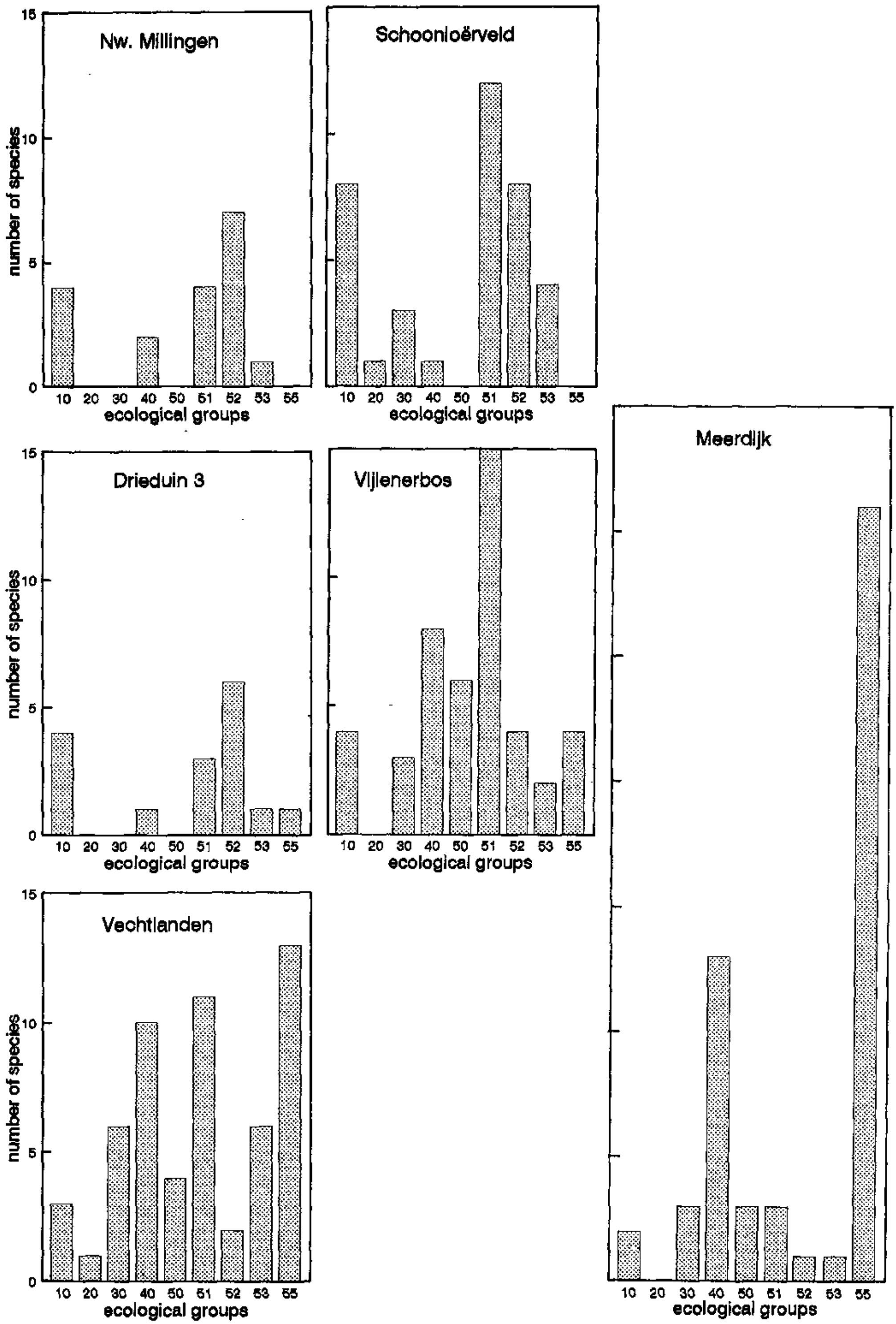

Figure 8. Number of litter saprotrophs of different ecological groups.

in mull soils could probably contribute to a larger species diversity as well. Fungal activity in mor is limited by the amount of easily assimilable carbon, and hence on mor sites only a small part of the organic matter is available.

Ordination of wood-inhabiting fungi

There is a very good separation between coniferous and deciduous forests (Figure 9). All deciduous forests, whether on poor or on fertile sites, are clustered closely together, even though the stands on fertile sites have a much greater species diversity. Galgenberg and Starnumansbos forest reserves, both mixed stands, are clustered with the coniferous stands, which can be explained by the fact that most of the wood on the forest floor is from conifers. We cannot interpret the second axis.

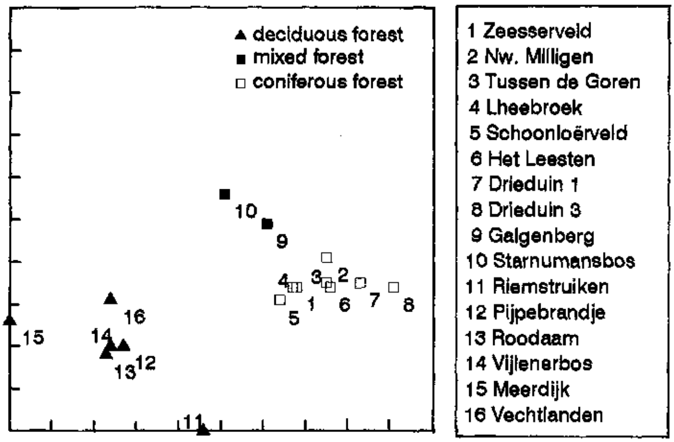

Figure 9. Ordination of forest reserves on the basis of wood-inhabiting fungi.

Even though the separation softwood - hardwood is apparently very important in determining the species composition of wood-inhabiting fungi, we note that some species (*Schizopora paradoxa* (Schrad.: Fr.) Donk, *Hyphoderma puberum* (Fr.) Wallr., *H. setigerum* (Fr.) Donk), which are usually considered hardwood species, were repeatedly found on coniferous wood. Such species shifts are almost certainly caused by the greater nutrient dynamics in the wood and possibly also a higher pH, as the same phenomenon (hardwood species on coniferous wood) was also noted in a liming experiment in a Scots pine forest in Harderwijk (Veerkamp and de Vries, unpublished observations).

The species composition of wood-inhabiting fungi in coniferous forests also shows a tendency towards that of a broadleaved forest, although at a slower rate than the other fungal groups.

That nitrogen and cations play a role in influencing wood quality and hence in species composition is clear when we compare Drieduin 1 and Drieduin 3 forest reserves with inland Scots pine stands (FR). Three species that are characteristic of these two coastal reserves are absent or extremely uncommon outside this area. They are: *Diplomitoporus flavescens* (Bres.) Domanski, *Peniophora pini* (Schleich.: Fr.) Boidin, *Sistotrema muscicola* (Pers.) Lund. in Lund. & Nannf. Others, like the somewhat ruderal *Resinicium bicolor* (Kirby et al., 1990), together with the ectomycorrhizal corticioid fungus *Amphinema byssoides* (Pers.: Fr.) J. Erikss. have been found in limed stands in the central parts of the Netherlands too.

Meerdijk and Vechtlanden forest reserves are characterized by species that almost exclusively occur on wood that decomposes rapidly. Most of these fungi belong to the Agaricales and non-resupinate Aphyllophorales, e.g. *Delicatula integrella* (Pers.: Fr.) Fayod, *Pluteus thomsonii* (B. &

Br.) Dennis, *Crepidotus cesatii* (Rabenh.) Sacc., *Steccherinum bourdotii* Saliba & David, and *Polyporus badius* (S.F. Gray) Schwein.

It was not attempted to create an ecological classification, because the current knowledge of wood-inhabiting fungi is too limited.

Conclusions and predictions

Although these reserves were designated only recently, a first inventory yielded the following conclusions:

1. Most forest reserves, especially those on originally acidic, nitrogen-poor, sandy soils, are already depauperate in mycorrhizal species,. Forest reserves on more fertile sites are less depauperate. This impoverishment should be attributed to nitrogen-rich and acidic deposition, which is far more detrimental to ectomycorrhizal fungi on mor soils than on mull soils (Meyer, 1962).
2. The litter saprotrophic fungi are useful to indicate the kind of humus profile. Mor, moder, and mull profiles each have their characteristic fungi. As a result of the general eutrophication of Dutch forests, the differences in litter saprotrophic species of coniferous and deciduous forests are rather small.
3. The forest reserves are already very rich in wood-inhabiting fungi. Presence of softwood and hardwood is the main factor that determines species richness.
4. Within the coniferous stands there is a shift in species composition of all functional groups towards a species composition that is more characteristic of broadleaved forests.

On the basis of these conclusions we venture to make the following predictions about the future mycological development in Dutch forest reserves:

1. With further succession of the forest the mycorrhizal flora will become poorer, as most mycorrhizal species (especially those with a restricted host range) are sensitive to litter accumulation, especially if the litter is rich in both nitrogen and lignin. We therefore disagree with Kost (1991) who suggested that forest reserves will yield favourable conditions for a great diversity of ectomycorrhizal fungi. However, a decrease in nitrogen deposition will have enhance the richness and abundance of ectomycorrhizal fungi, and this effect will certainly outweigh the decline of ectomycorrhizal fungi as a consequence of successional processes.
2. Changes in the ectomycorhizal flora towards species that are commonly associated with broadleaved trees will precede and assure establishment of deciduous trees, provided that the light climate is conducive to seedling establishment (Perry et al., 1992).
3. Changes in the litter saprotrophic flora will precede changes in the ectorganic profile. Species that are characteristic of mor sites will decline and species characteristic of moder and mull sites will increase. The changing species composition will enhance nutrient cycling and decomposition rates and further affect competition between coniferous and broadleaved trees.
4. Wood-inhabiting fungi will initially be less affected by successional processes, and the species composition of this guild will reflect the history of these stands for a longer time than other groups of fungi. From a longer-term perspective species that are characteristic of coarse woody debris (logs, snags, uprooted trunks) will establish and this will contribute to the naturalness of such reserves.
5. A further refinement of indicator values, if possible even quantitatively expressed, will make these predictions more explicit.

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Appendix. List of Forest Reserves investigated and their main characteristics. Abbreviations and explanations. FC (according to Broekmeyer, 1992): +: floristically characteristic; -: floristically non-characteristic; PNV: Potential Natural Vegetation (according to Van der Werf, 1991); Ect-organic Layer: -: Absent; (+) thin (< 3 cm) and locallly absent; +: moderately thick (3-5 cm); ++: thick (> 5 cm).

Forest reserves	Dominant tree species with age (years)	FC	PNV	Ectorganic layer
Zeesserveld	Pinus sylvestris (75)	—	Betulo-Quercetum roboris	+
Nw Milligen	Pinus sylvestris (45)	—	Betulo-Quercetum roboris	++
Tussen de Goren	Pinus sylvestris (75)	—	Betulo-Quercetum roboris molinietosum	++
Lheebroek	Pinus sylvestris (65)	—	Betulo-Quercetum roboris	++
Schoonloërveld	Larix leptolepis	—	Betulo-Quercetum roboris molinietosum	++
Het Leesten	Pseudotsuga mensiesii (40)	—	Fago-Quercetum petraeae	+
Drieduin 1	Pinus nigra (60)	+	Cladonio-Pinetum sylvestris	(+)
Drieduin 3	Pinus nigra, P. sylvestris (60)	+	Cladonio-Pinetum sylvestris	(+)
Galgenberg	Pinus sylvestris (95), Quercus robur	+	Fago-Quercetum petraeae	++
Starnumansbos	P. sylvestris, Q.robur, Betula pubescens	+	Fago-Quercetum petraeae molinietosum	++
Riemstruiken	Quercus robur (>90)	+	Fago-Quercetum petraeae	++
Pijpebrandje	Fagus sylvatica (>90)	+	Fago-Quercetum petraeae	++
Roodaam	Quercus robur	+	Convallario-Quercetum dunense	(+)
Vijlnerbos	Betula pendula, Quercus robur, F.sylvatica	+	Luzulo-Fagetum	+
Meerdijk	Populus robusta (25), Alnus glutinosa	—	Lysimachio-Quercetum/Fraxinio-Ulmetum	—
Vechtlanden	Alnus glutinosa (55), Betula pubescens (55)	+	Lysimachio-Querc./Carici elongtae-Alnetum	(+)

The SILVI-STAR link to a geographical information system; a tool for spatial analysis in digitally recorded forest reserves

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Summary

The SILVI-STAR forest monitoring system provides detailed information at the tree level typically in 1 ha plots. From these size measurements and attribute values 3-D representations are obtained of tree form and forest structure. The applicability of SILVI-STAR is indicated for a broad range of studies in forest reserves. Two applcations are highlighted.

Estimation of daily direct and diffuse irradiance is mediated by simulated fisheye photographs and allows e.g. analysis of patterns in the herblayer with respect to light availability. Change detection in spatial characteristics within forest reserves between succesive recordings is realized by linking SILVI-STAR to a geographical information systm what allows e.g. statistical analysis of gap dynamics.

Keywords: *forest reserve, SILVI-STAR, irradiance, geographical inforamtion system*

Introduction

There is a gap between forest modellers who start with mono-species even-aged stands and ecologists who try to elucidate the functioning of ecosystems by monitoring forest dynamics in forest reserves. The latter collect large amounts of detailed information and often have difficulties with the interpretation of their short time series. The modellers on the other hand are satisfied with much less detailed data on forest structure and focus on long-term prediction. Generally, time series for model validation fail and there are very few appropriate forests where such series can be collected, because most forests have been exploited.

Descriptions of time series on forest structure and species composition collected in forest reserves are used to calibrate and validate models of present and future forest. Just because nowadays forest modellers are satisfied with data collected in homogeneous forest patches does not mean that there is no need for detailed data from heterogeneous forest mosaics.

Forest modellers are beginning to simulate more complex structured and mixed species forests, and because the first visual impact of forests as well as of most silvicultural treatments is structural, there is a tendancy to translate the output of forest models into structured images of forests (Mohren and Burkhart in prep, 1993). The SILVI-STAR monitoring system has been developed to bridge this gap. It describes the complex reality of a heterogeneously structured forest and is derived from existing techniques of forest monitoring such as remote sensing, profile analyses, tree chartings and permanent quadrat survey in combination with vegetation mapping and ground photography (Koop 1989).

Data are collected from hierarchically nested plots in:
(i) a forest type area (10-40 ha) where forest structure is charted as forest patches in different height classes;
(ii) a core area (1 ha) where forest structure is recorded in terms of the volumes occupied by trees and their spatial arrangement;
(iii) a transect area of 50 adjacent 2 x 2 m permanent quadrats in which herb layer coverage and species composition is assessed.

The three-dimensional model of the forest structure obtained from (ii) provides a link with explanatory simulation techniques.

For an explanation of the role of the SILVI-STAR monitoring system in the core area and circle plots of the Dutch forest reserves, see Broekmeyer's contribution in these proceedings.

For each tree in the core area a restricted number of spatial coordinates are measured: the tree base, four extreme peripheral points of the crown projection and the heights of the tree base, the first living branch, the base of crown, the periphery height and the height of the top of the tree. These coordinates describe a three-dimensional tree model made up of quarters of ellipses between these coordinates. Tree attributes include species, stem diameter and crown cover. See Koop (1989) for a detailed description of the model.

The model is compatible with other methods for monitoring forest. Forest profile drawings can be digitized and tree bases can be mapped. All the data are stored in the ORACLE database system from which they can be recalled and presented graphically in various ways. Application programs have been developed for light simulation and the detection of shifts in patterns of crown projections.

Light simulation within heterogeneous forests

Direct and diffuse radiation can be estimated by using photographs taken with a fisheye lens (Anderson 1964). The hemisphere as seen from a point within the core area is partly obstructed by the trees in the core area, by the forest stands around the core area and by the relief of core area and surroundings.

A fisheye photograph can be simulated for any point within the three- dimensional forest model (Figure 1). This procedure allows all individual trees to be scanned, to compute the hemispherical coverage (Koop 1989, 1993, Bijlsma 1990). The pattern of absorption/transmission of light by the topography and the pattern of canopy gaps and forest patches of different height surrounding the core area are derived from the mapping of the forest type area, resulting in a digital terrain model stored in the ARC/INFO GIS.

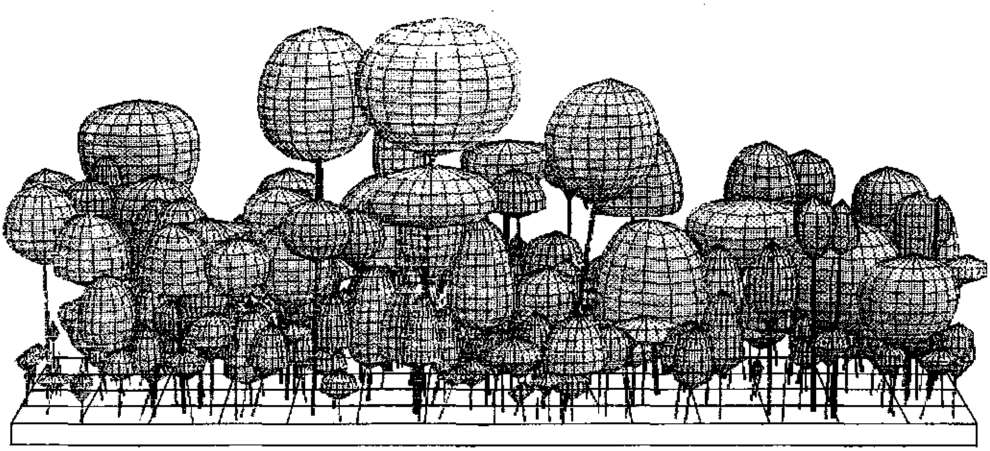

Figure 1. Three-dimensional SILVI-STAR model of a 140 x 70 m core area in a tropical rainforest in Northern Sumatra.

An ARC/INFO coverage of the pattern of height classes of the regeneration mosaic (forest structure map) is used to add the height of each regeneration patch to the actual terrain elevation, resulting in a new model that approaches the relief of the upper tree canopy. A grid of terrain elevations derived from this canopy model is used to assess the part of the hemisphere that is covered by terrain elevations and forest stands outside the core area. A complete hemispherical picture is obtained by adding those parts of the hemisphere obscured by individual trees in the

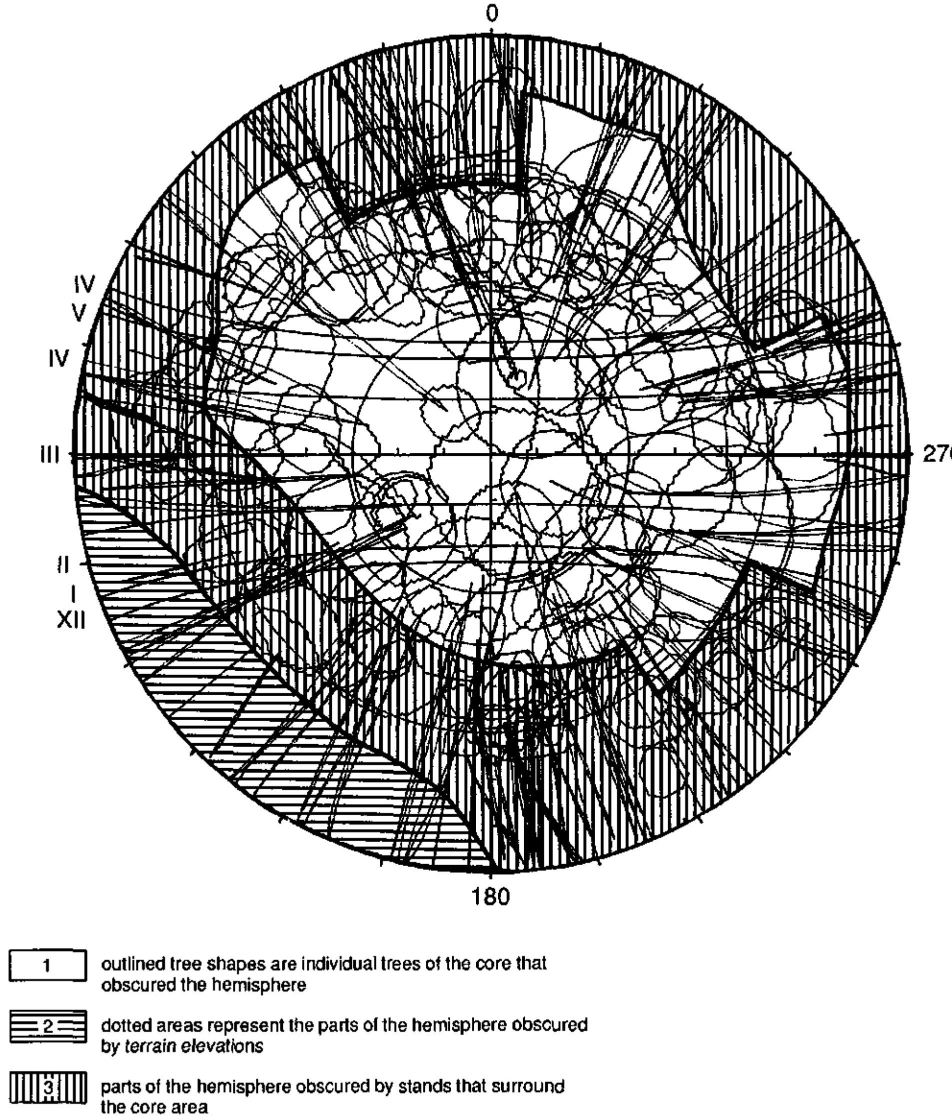

Figure 2. Complete hemispherical picture as an intermediate visual product of the simulation procedure.

core area to the part covered by terrain elevations and stands that surround the core area (Figure 2).

Calculating the daily amounts of light penetration for a large number of grid points, for example on the forest floor, enables light contour maps to be made, using ARC/INFO. These maps give the pattern of averaged daily radiation (diffuse or direct) values that reach the forest floor or any other height level over a specified time period (Figure 3). This approach solves the problem of the dynamic behaviour of sunflecks.

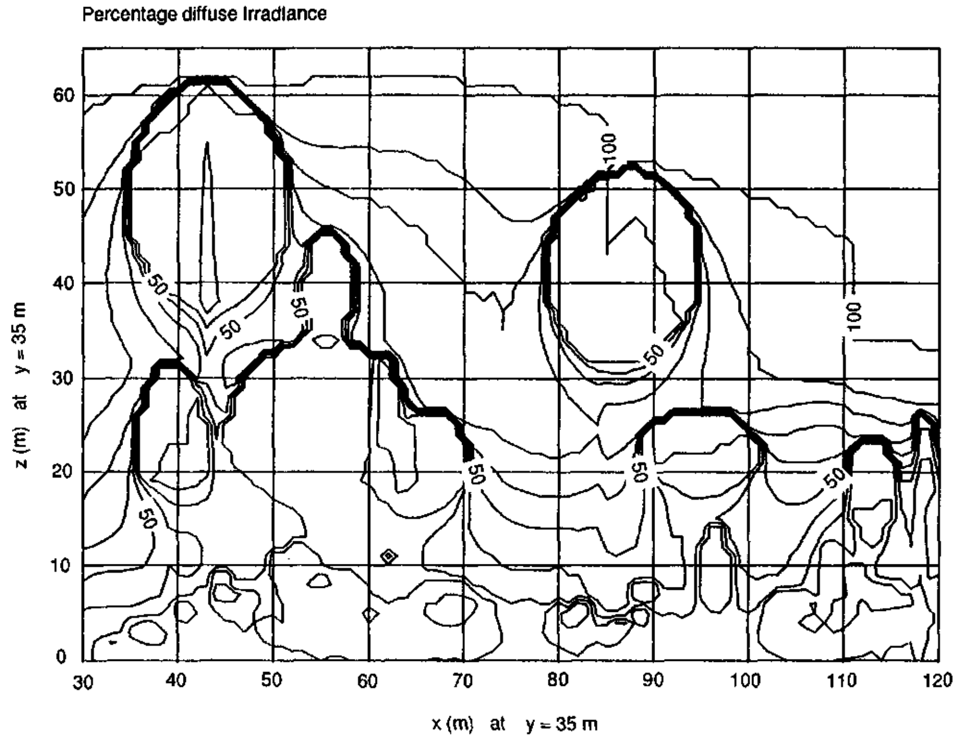

Figure 3. Vertical plane in the centre of the core area with simulated pattern of diffuse light penetration.

Koop and Sterck (in prep. 1993) describe the validation of the SILVI-STAR light simulation for complex structured canopy in a tropical rainforest in French Guiana. So far the light simulations have been used to interpret herb layer dynamics, e.g. CANOCO (Jongman et al. 1987) processing of cover data of herbs using the simulated light values as explanatory environmental variables.

A new project is under way to explain the population dynamics of herbaceous species using individual energy budgets in which the radiation component plays an important role. Patterns of herbaceous species or tree species regeneration on the forest floor will also be elucidated. Light calculations can be made, to explain differences in individual tree growth. The light penetration at points on the surface of individual tree crowns can be simulated and related to tree growth.

Processing and spatial analyses of structure measurements

The need for spatial analysis originates from interest in gap size distributions, shifting mosaic and tree base patterns, comparisons of vegetation maps, etc. It has been satisfied by linking the ARC/INFO geographical information system with the SILVI-STAR attributes in the ORACLE database (Bijlsma 1991). In an ARC/INFO data layer (coverage) each line segment (arc) and each polygon arising from an intersection operation on all crown projections, is uniquely identified in such a way that arcs and polygons are properly assigned to their tree number(s) or to a gap.

This procedure is illustrated by selections from the Otterskooi forest reserve (140 x 70 m) in The Netherlands, recorded in 1983. Figure 4 shows the selection of arcs belonging to crown projections of ash (Fraxinus). Figure 5 shows selections of polygons belonging to both understorey or potential trees and trees established in the canopy; a 10 x 10 m grid has been added for reference. Figure 6 is an apparent view from above of the Otterskooi forest reserve

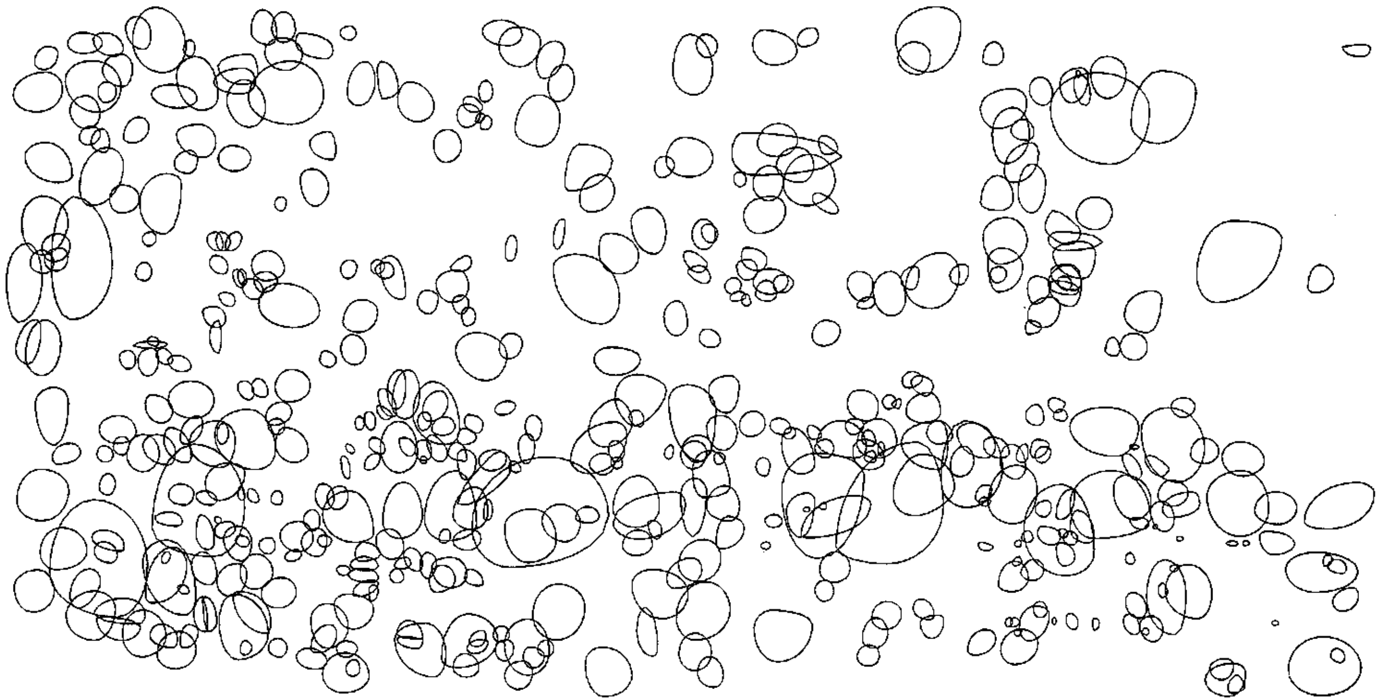

Figure 4. ARC\INFO selection of arcs belonging to crown projections of ash (Fraxinus) in the core area of the Otterskooi forest reserve (140 x 70 m) in The Netherlands, recorded in 1983.

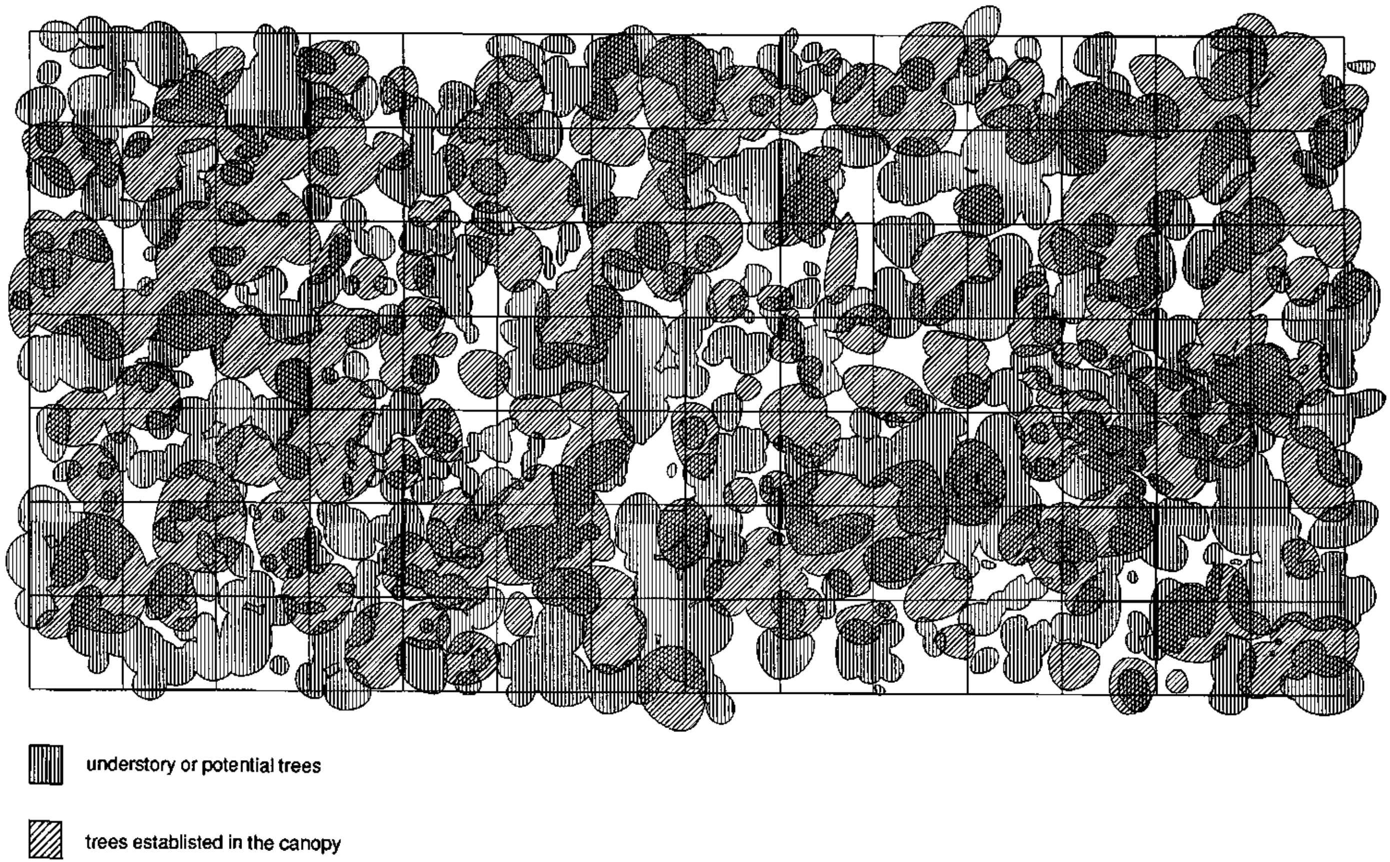

Figure 5. Selections of polygons belonging to understorey or potential trees (vertical hatching) and trees established in the canopy (diagonal hatching) in the core area of the Otterskooi forest reserve (140 x 70 m) in the Netherlands, recorded in 1983.

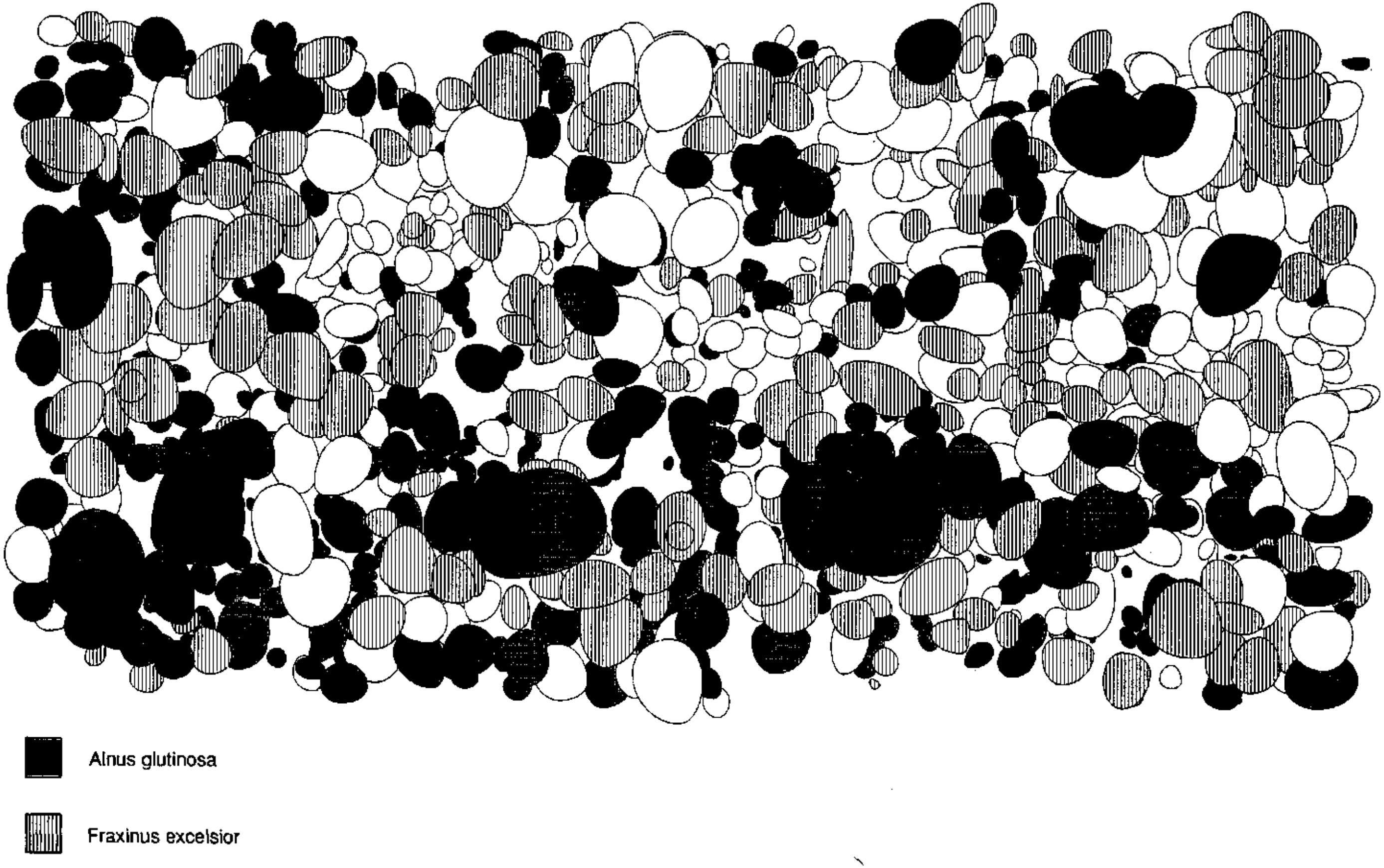

Figure 6. Apparent view from above resulting from a selection of crown projection polygons conditional on tree height; alder (Alnus; black) and ash (hatched) are indicated in the core area of the Otterskooi forest reserve (140 x 70 m) in The Netherlands, recorded in 1983.

resulting from a selection of crown projection polygons conditional on tree height; alder and ash are indicated.

The ARC/INFO-ORACLE link with SILVI-STAR will be applied:
- to detect change, using overlay capabilities;
- for pattern analysis using spatial statistics;
- for the incorporation and simultaneous analysis of environmental data using multivariate methods

Conclusion

SILVI-STAR has proved to be applicable in a wide range of forest types: primaeval forest such as the Bialowieza national park (Poland), several West European semi-natural forests, and tropical rainforests. The system is compatible with other monitoring systems, e.g. forest profile drawings can be digitized, and it includes the IUFRO codes developed by Mayer and Leibundgut. A more user-friendly and commercially supported version of SILVI-STAR would make it easier to run the program in other hardware environments. Therefore the SILVI-STAR monitoring method might offer a suitable starting point for standardizing the forest monitoring methodology in Europe.

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Significance of forest reserves for studies of the population and evolutionary genetics of forest trees

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Summary

Forest reserves may play an important role in studies of the population and evolutionary genetics of forest trees. Not only are they experimental objects in which evolution in the presence of minor human impact can be investigated, but, from the practical point of view, they are also important sources of material for gene pool conservation and breeding programmes. In Slovakia two case studies have investigated the genetic structure of natural and managed Norway spruce and common beech populations. Less genetic diversity and heterozygosity, more gene flow and greater differentiation among populations was found in Norway spruce than in common beech. Statistically significant differences between natural and managed forests in spruce and the absence of these differences in beech may be ascribed to different regeneration systems used for these species.

Keywords: isozymes, genetic variation, heterozygosity, tree population characteristics

Introduction

Forest tree species possess a relatively high level of genetic variation and - as predominantly outcrossing organisms - a high degree of individual heterozygosity. The genetic diversity in trees is generally twice that in herbaceous plants.

In European forest tree species the migration routes in the postglacial period were more complicated than those in the North American tree species. Many mountain ridges (Alps, Carpathians and others) cut across the main south-north migration routes. Patterns of genetic variation in forest tree species in Central, South-East and Western Europe depend on four factors:

1. the number and types of glacial refuges generating genetic differentiation as a result of isolation, mutation, selection and genetic drift;
2. migration routes during the postglacial period;
3. selection and genetic drift in the present distribution range;
4. human activities in recent centuries.

Forest reserves currently represent an indispensable part of the natural heritage in all European countries. They are significant not only because they provide the possibility to investigate the growth and yield processes of natural forest ecosystems, but also because they enable genetic structure, variation and differentiation and the biodiversity of populations of native and indigenous tree species to be studied. In most cases, forest reserves represent climax forests with indigenous tree species that are best adapted to local ecological conditions.

Forest reserves in the Carpathians

The Carpathians stretch 2000 km from the Danube river in western Slovakia to the Danube river in the southern Romania. The Carpathian forests cover in total about 8 million ha, from altitudes of 300 m up to the tree line at 1500 - 1800 m (Slovakia 1.5 million ha, Poland 0.5 million ha, Ukraine 0.5 million ha and Romania 5.5 millon ha).

The network of natural reserves in the Carpathians is fairly well developed. It covers five national parks in Slovakia, four national parks in Poland, two national parks in Ukraine and one national park in Romania, as well as numerous forest reserves with indigenous tree species and primary genetic resources and structures. In some parts of the Carpathians (Ukraine, Romania) there are, however, many more well developed natural (virgin) forests that are not yet protected. In this respect the Carpathians may be considered a very well preserved region, with extremely important reserves of forest genetics. The Carpathian forests have a much more natural character (original tree species composition and natural regeneration) than is known from other parts of Europe (e.g. Hercynic part of Czecho-Slovakia).

Two case studies

Recently, the genetic structure and the diversity of natural populations of the two most common and economically important tree species Norway spruce (*Picea abies* KARST.) and common beech (*Fagus sylvatica* L.) were studied.

Norway spruce

An investigation was done in five natural populations (virgin forests), five managed forest stands within the natural range of Norway spruce in Slovakia and four managed forest stands outside that range (see Figure 1). The work aimed at tracing possible differences in the genetic structure and the heterozygosities in Norway spruce populations in natural and managed forest. The genetic analyses were based on genotyping 50 trees per population using isozyme analysis of dormant buds. The multilocus genotypes were based on 10 isozyme loci (ACO, DIA-B, DIA-C, LAP-A, LAP-B, GOT-A, GOT-B, GDH, PGI-B, SKDH-B).

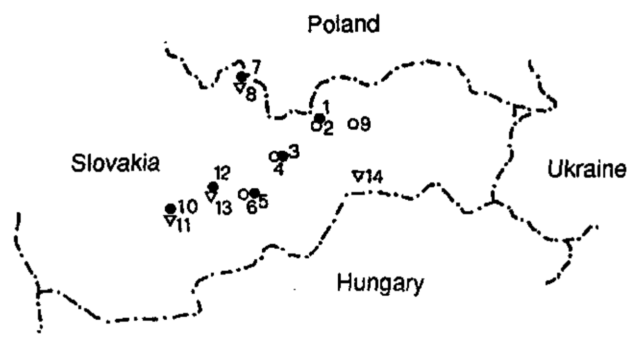
The results show that the virgin forests differ substantially from managed stands (especially from artificially regenerated ones) in having a greater gene diversity and greater heterozygosity, as well as changed allelic structures. The mean expected heterozygosities were $H_e = 0.352$ in virgin forests, $H_e = 0.380$ in naturally regenerated manged forests, and $H_e = 0.306$ in artificially regenerated man-made forests. A clustering of populations after genetic attributes shows a similarity of adjacent pairs of virgin forests and naturally regenerated stands (see Figure 2, the virgin forests are asterisked).

The only way of investigating the migration routes of tree species seems to be to analyse the characteristics of the population genetics (allelic frequencies, diversities, heterozygosities and mutual similarities) of natural populations (e.g. virgin forests) of indigenous tree species within the entire natural range.

It was shown earlier that there are significant differences in allelic frequencies of individual parts of the natural range of Norway spruce and Silver fir. Bergmann (1983) found range-specific alleles (e.g. GDH-A, and LAP-B_4) in Norway spruce in the eastern Carpathians, demonstrating that they must originate from refuges other than those in the western Carpathians or Western Europe. Furthermore, Bergmann et al. found range-specific differences (e.g. in IDH-A, IDH-B, SKDH-A and 6PGDH-A) among the silver fir populations from parts of this species' natural range (Bergmann and Kownatzki, 1988; Bergmann et al., 1990).

Common beech

A comparison of the genetic structure and diversity of common beech was based on the analysis of 55 Czecho-Slovakian populations (15 from the Hercynic area, 40 from the Slovak Carpathians). Twenty of these were considered to be virgin or virgin-like forests, having the original genetic structure. The genetic analyses comprised the genotyping of 50 - 60 trees per population, using isozyme analyses of dormant buds. The multilocus genotypes were based on 7 - 12 isozyme loci



1 ● TANAP - Biela Voda (virgin forest)
2 □ TANAP - Tatranske Matliare (managed forest)
3 ● Chopok (virgin forest)
4 □ Chopok (managed forest)
5 ● Poľana (virgin forest)
6 □ Poľana (managed forest)
7 ● Babia Hora (virgin forest)
8 ▾ Babia Hora (man-made forest)
9 □ Levoča (managed forest)
10 ● Vtáčnik (virgin forest)
11 ▾ Vtáčnik (man-made forest)
12 ● Zvolen (virgin forest)
13 ▾ Zvolen (man-made forest)
14 ▾ Zádiel (man-made forest outside the natural range)

Figure 1. Location of the Norway spruce stands investigated in Slovakia (virgin forests and man-made forests).

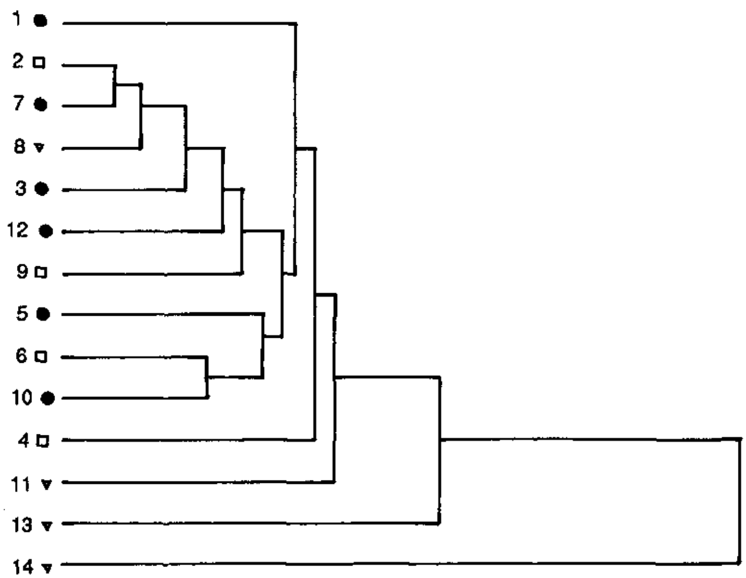


Figure 2. Clustering of populations based on similarity of genetic attributes (see Figure 1 for the names).

(ACP-A, GOT-A, IDH, MDH-A, MDH-B, MNR-A, PX-A, PX-B, PGI-A, PGM-A, 6-PGDH-A, SOD-A).

The mean expected heterozygosities of the beech natural populations (virgin forests) and of the managed forest stands were almost identical. The mean expected heterozygosities based on 12 loci in the virgin forests and the managed forests were $H_e = 0.317$ (n = 5), and $H_e = 0.317$ (n = 8) respectively, and those based on 7 isozyme loci in larger sample sets were $H_e = 0.282$ (n = 14), and $H_e = 0.290$ (n = 24) respectively. This is not surprising, as all the populations investigated originated from natural regeneration. The genetic structure of managed populations of beech would therefore only be influenced by silvicultural treatments. Small differences were also found when the adjacent populations (virgin vs. managed forests and e.g. at different altitudes) were compared.

Comps et al. (1991) compared the genetic differentiation of common beech populations from Central and Southern Europe in relation to their ecological conditions. The results from Central Europe did not show any correlation with ecological factors, whereas in Southern Europe (Croatia) the allelic frequencies in some loci (e.g. PX-B) were correlated with altitude. In order to find out whether a migration in the postglacial period might have influenced the genetic composition of beech populations in Central Europe, additional analyses of beech populations from the east Carpathians have to be done. Some 20 - 25 natural populations (virgin forests) from the Ukrainian Carpathians, 25 - 30 populations from the Roumanian Carpathians and some 5 to 10 from south-eastern Poland are to be included in this study. These investigations were started last winter by analysing the first 10 Ukrainian populations from the northern side of the Carpathians. Preliminary results indicate that there are minor differences between the allelic frequences and heterozygosities of the beech virgin forests in the western and Ukrainian Carpathians.

Hypotheses

There are some significant differences between the two model tree species discussed here, with regard to their biological properties (mating system, gene flow) as well as to forest management practices in the past:

Norway spruce:

- differences in allelic frequencies between populations are greater;
- significant differences between virgin and managed populations, as a result of artificial regeneration;
- gene flow is greater;
- genetic diversity and heterozygosities are lower;

Common beech:

- the differences in allelic frequencies between populations are smaller;
- no significant differences occur between virgin and managed forests, because regeneration is natural;
- gene flow is less;
- genetic diversity and heterozygosities are higher.

Significance of forest reserves for the population and evolution genetics of forest trees

Apart from their significance for the investigation of growth and yield processes and forest ecosystem development, forest reserves have, without doubt, enormous significance for studies of population and evolution genetics. They are in fact the only experimental objects in which evolution can be investigated in the presence of minor human impact.

From the point of view of genetics forest reserves may be useful for:

- maintaining a high degree of biodiversity in existing ecosystems;
- gene pool conservation *in situ* - utilization of genetic resources for breeding programmes;
- investigations of migration routes in the postglacial period;
- investigations of genetic structures and diversities of natural populations (virgin forests);

genetic structures and diversities may be considered to be measures of the extent to which these populations have adapted to local ecological conditions.

Information obtained from the analyses of genetic structures of forest reserves may be applied in:

- the design of forest reserves: because of gene flow from neighbouring stands (populations), only the larger natural reserves are of significance,; gene flow does not influence the genetic structure of old growths at present, but may influence the genetic structure of progenies in subsequent generations;
- the design of forest reserve networks: population and evolution genetics should be taken into consideration when determining the size and representativeness of individual forest reserves; the distribution of forest reserves should reflect these prerequisites as well as the migration routes in the postglacial period;
- the comparison of genetic structure and processes, at population level in both one-species and mixed natural (virgin-like) forests.

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Gap size differentiation and the area of forest reserve

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Summary
The article proposes a method for calculation of the minimal area of a forest reserve, based on the frequency distribution of gap size. Also, as an example, the minimal area of a forest reserve is calculated for the mixed forests of the lower montane belt of the West Carpathians.

Keywords: forest reserve, gap size distribution, minimal area of forest reserve, state of equilibrium

Introduction

Numerous ecological investigations conducted in natural forests have revealed a cycle of changes taking place in every part of a forest community. This cycle consists of young trees taking over an area, growing, ageing and dying. Features of physical environment, species composition and population structure change in this cycle (Leibundgut, 1959; Sprugel, 1976; Korpel, 1980; Korpel, 1987; Whitmore; 1982; Stewart; 1986; Nakashizuka, 1987; Taylor et al., 1987; Aplet et al., 1988; Boone et al., 1988; Newton and Smith, 1988; Koop, 1989). Therefore, the forest is not in equilibrium throughout. It is a mosaic of many patches in different phases of development, which change independently of each other. The forest attains the state of equilibrium only when it consists of hundreds of patches that are in different stages of development (Shugart and West, 1981).

The minimal area of forest still in the state of equilibrium is an important concept for the appropriate protection of forest communities in reserves and national parks. The protected area should be large enough for regeneration, growth, and ageing to proceed with an intensity slightly changing in time.

Materials and methods

Theoretical background

Canopy gaps originating because of the death of trees are one of the most important factors affecting the species composition, structure and dynamics of forest community. The creation of differently sized gaps results in light and moisture conditions being variable on the forest floor and increases the differentiation of the herb layer (Minckler et al., 1973; Nakashizuka, 1985; Moore and Vakant, 1986; Collins and Pickett, 1987; Collins and Pickett, 1988; Pompa and Bongers, 1988). Depending on their area, gaps can be invaded by species with different ecological demands and biological features (Barden, 1981; Runkle, 1982; Whitmore, 1982; Denslow 1987; Shugart, 1987, Lawton and Putz, 1988; Martinez-Ramos et al., 1988; Pompa and Bongers, 1988). Gap size also modifies the growth rate and population structure of trees (Brokaw, 1987; Uhl et al., 1988).

The variability in the size of gaps observed in forest communities is the result of two processes: (1) their creation after tree death, and (2) their disappearance in consequence of the growth of suppressed saplings and newly established seedlings, and the expansion of crowns of adjacent trees. Each part of the forest mosaic has its own intensity of these two processes and the result is a particular gap size. Only if forest consists of many patches in which gaps of different size originate can we speak about the gap size distribution of the whole forest.

It can be assumed that every type of forest is characterized by a specific frequency distribution of gap size. The quasi-equilibrium state can be defined as a situation in which parameters of this distribution are nearly stable in time and space. It means, for instance, that the probability of origin of a gap or the frequency of gaps of a certain size, and the average area of gaps only vary inconsiderably when a forest is observed in time or different fragments of the same forest are compared. To find the minimum area of forest, the acceptable variation around the equilibrium should be defined (Shugart and West, 1981).

Let's assume that the frequency distribution of gap size is known, and that the origin of a gap of certain size is a random event independent of the presence of other gaps. The number of gaps that must be present in a forest if the values of their distribution are to remain within preordained bounds can be estimated. It can be approximated by analysing the relationship between gap number and the width of confidence intervals for mean, median and other parameters of gap size distribution. Afterwards, on the basis of the estimated gap number (n), mean gap area (a), and the fraction of forest area in gaps (f), the minimal area of forest in quasi- equilibrium (MAF) and the minimal area of forest reserve (MAFR) can be calculated from the formulas:

MAF = n a f (1)

MAFR = MAF + bz (2)

where bz is the area of buffer zone, the width of which depends on the forest type and character of areas surrounding the reserve.

Study area

The method was applied in the Carpathian beech forest (Dentario glandulosae-Fagetum) in the Babia Gora National Park in Poland. This forest type is the most common one in the lower montane belt of the West Carpathians, and its phytocoenoses, which cover large areas in the Babia Gora massif, have never been logged (Celinski and Wojterski, 1978).

Methods

The measurements were obtained along parallel transects situated 50 m apart and perpendicular to the contour lines between 950 and 1050 m above sea level. The total length of the transects was 6 km, so the investigated area was approximately 30 ha. The areas of canopy gaps which were larger than 20 m^2 (Runkle, 1982) and which were intersected by these transects, were measured if the undergrowth of trees was lower than 5 m. The lower limit of gap size equals the area covered by spruce and fir crowns of average dimensions. Crowns of these coniferous species are smaller than crowns of beeches. The length (greatest distance between gap edges) and gap width (greatest distance perpendicular to the length) were recorded for each gap. Gap area was estimated from dimensions using the formula for an ellipse. The line intersect method (Runkle, 1985) was used to calculate the proportion of land area in gaps.

The probability of intersection of a gap was proportional to the square root of the gap's area. To obtain the gap size distribution corresponding with the real frequency the raw results were recalculated appropriately. Then the frequency distribution of gap size was compared with lognormal distribution, using a X^2 test (Puchalski, 1980), as it appears that this theoretical distribution well describes the differentiation of gap area for many forests (Runkle, 1982; Foster and Reiners, 1986; Arriaga, 1988a; Arriaga, 1988b; Lawton and Putz, 1988). The relationship between the number of gaps and the width of confidence interval was analysed for the mean of lognormal distribution. It should be remembered that the mean of lognormal distribution corresponds with the median gap size. On the basis of this relationship the number of gaps that should be present in the forest investigated if that forst is to remain in quasi-equilibrium was assesed and MAFR was calculated.

Results and discussion

The transects intersected 83 gaps, whose areas ranged from 20 to 2330 m^2. Most gaps were between 50 and 100 m across (Figure 1). Their average area was 179 m^2. The standard deviation and coefficient of variation were 248 m^2 and 138% respectively, and they reflect the great variability of the gap size.

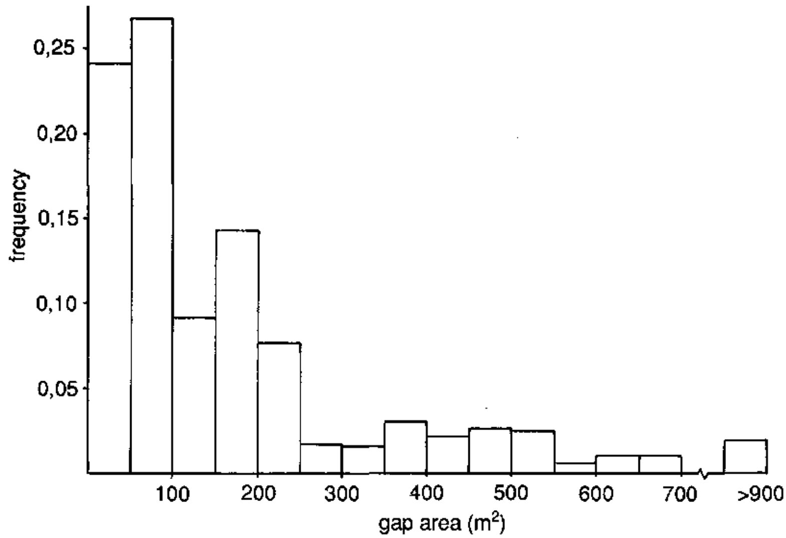

Figure 1. Frequency distribution of the areas of gaps in the old-growth spruce-fir-beech forest in the Babia Gora National Park.

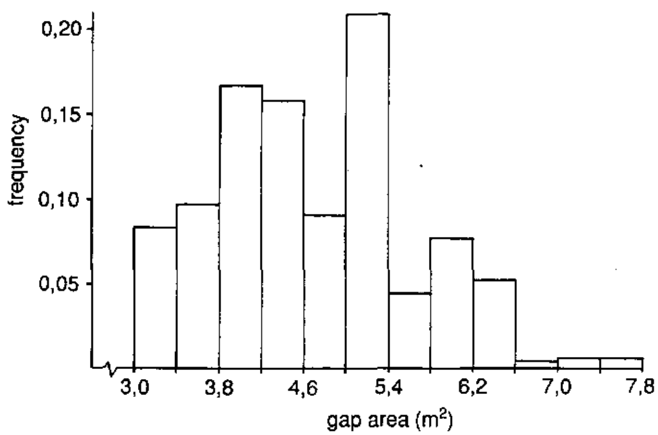

Figure 2. Frequency distribution of ln of the areas of gaps.

The frequency distribution of gap size does not differ significantly from the lognormal distribution 4.68 + 0.96 (mean + standard deviation (n = 83, df = 7, $p > 0.2$) (Figure 2). Gaps covered 17.0 + 2.3% of the forest area. The accuracy of estimation of median gap area (mean in lognormal distribution) increases rapidly with the gap number up to around 100 gaps (Figure 3). The width of confidence interval (p = 0.95) narrows to 21.6 % at 100 gaps. Increasing the number of gaps from 100-200, 200-300, 300-400 and 400-500 reduces the width of

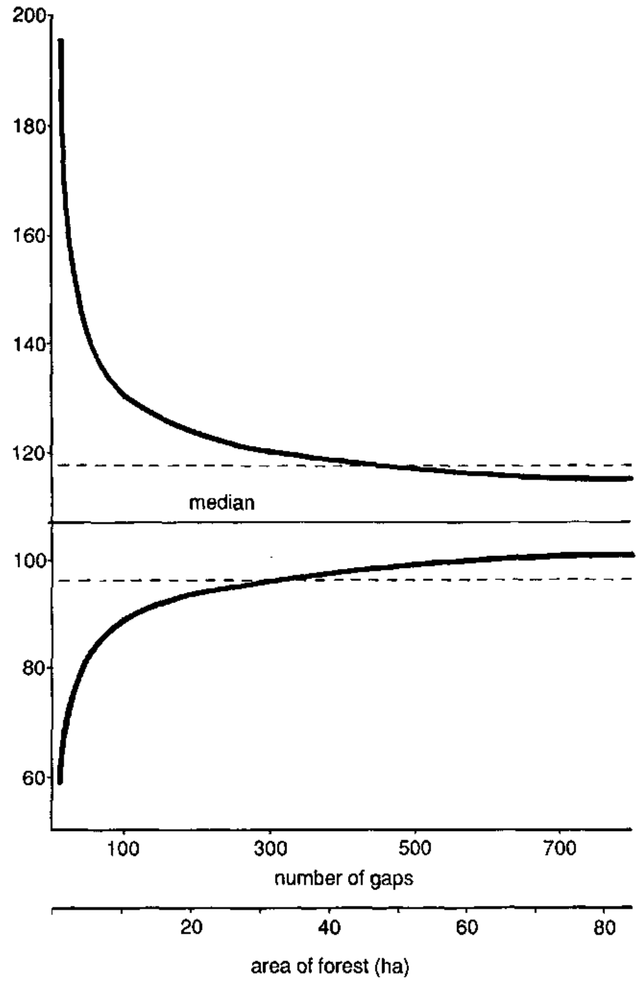

Figure 3. Relationship between the width of confidence interval for the median gap area ($p = 0.95$) and the number of gaps, and between the width of confidence interval and the area of forest calculated for different numbers of gaps according to formula (1) when the mean gap area is 179 m^2, and the proportion of gaps in the total area is 17%.

confidence interval by respectively 6.6, 2.8, 1.5 and 1.2%. Increasing the number of gaps even more only slight improves the accuracy of assessment of median gap area and does not result in any significant change of gap size distribution. On the contrary, 400 gaps are sufficient to estimate the median of gap area with 10 % accuracy, which is the accepted level in many ecological studies. Thus, the Carpathian beechwood attains quasi-equilibrium when the area covered by this forest contains 400 gaps. Assuming that the average area of a gap is 179 m and that these 400 gaps should cover 17 % of the total forest area, the MAF equals 42.1 ha.

Forest reserves in the West Carpathians are usually surrounded by managed plantations of trees. To eliminate or diminish external influence a buffer zone should be established around the reserve. It should not be less than 40 m wide, which is the height of the tallest trees in Carpathian beechwoods. Such a zone assures that every tree growing in the MAF remains within the reserve after death. Encircling the MAF by a 40 m protective belt results in an MAFR of at least 51.8 ha if the reserve is circular.

The calculation of MAFR was based on the assumption that gap creation is a random process which does not depend on the presence of other gaps. But other research suggests that this assumption is not entirely justifiable. Lawton and Putz (1988) ascertained that gaps aggregated in some parts of a tropical cloud forest. Homogenous fragments of mountain spruce-fir-beech forests in Central Europe cover areas ranging from hundreds of square metres up to several hectares, depending on the phase of development (Mayer, 1971; Mayer et al., 1980; Mayer and Neumann, 1981; Korpel, 1982). Probably the gap area increases with the ageing of the tree stand because the growth rate of trees diminishes and the intensity of dying off accelerates. It can be concluded that gaps of similar area aggregate in natural forests on a scale corresponding with the area occupied by phases of stand development. Thus the calculated MAFR may be underestimated because the assumption of randomness of gap origin does not correspond exactly with the pattern observed in some forests.

The problem of the minimal area a forest should cover in order to be in a state of equilibrium has fascinated many ecologists. Those working in montane mixed forests of Central Europe suggest that these forests attain a state of equilibrium when the forest covers at least 50 ha (Zukrigl et al., 1963; Mayer, 1971; Mayer et al., 1980; Mayer and Neumann, 1981; Korpel, 1982). This figure is very similar to that obtained for forests of Babia Gora, which represent the same type of plant community.

Using a model of forest, Shugart and West (1981) concluded that a forest approaches a state of biomass quasi-equilibrium when it contains 50 to 100 patches, each of which is the result of independent small-scale disturbance such as the fall of a tree. The results obtained for mixed Carpathian beechwood suggest that its MAF should be much larger: about 176 times that of the largest gap measured.

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Research on dead wood in Bavarian nature forest reserves

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Summary

A project to inventory fauna and flora in the forest nature reserves of Bavaria has been under way since 1986. Dead woody material, a characteristic of forests designated for nature, is important in this research. The total amounts of dead woody material have been determined on systematically arranged circular sample plots. "Photo-eclectors" were used to appraise the quality and quantity of arthropod coenoses of deadwood in a reproducible manner. The total amounts of dead wood varied greatly in the three nature forest reserves studied. In all areas, dead wood proved to be a habitat intensively used by arthropods. The analysis of the indicator group of saproxylic beetles showed the areas qualified for nature protection. Not only quality and quantity of woody debris, but also the impact of forest history and faunistic tradition are major factors for an ecological assessment.

Keywords: forest reserves, dead wood, saproxylic beetles

Introduction

A "Concept of Forest Ecological Research" has been developed for Bavaria. It focuses on the long-term survey of nature forest reserves and involves all essential compartments of forest ecosystems: soil, soil vegetation, shrubs and forest trees and also parts of the fauna. The main objective of this concept is to derive nature-oriented strategies for management and nature conservation in commercial forests. Dead wood plays an important role in this context. The types and volume of dead woody material are determined on systematically arranged circular sample plots. Saproxylic insects are collected, mainly to be used as indicators.

Research areas

The concept has been tested in selected forest nature reserves in Bavaria, three of which are presented here (Table 1).

Table 1. Forest Nature Reserves

Forest nature reserves state forest office	Vegetation unit	Tree species investigated (age of stand)
Waldhaus, Forstamt Ebrach	Luzulo-Fagetum	Beech (125 - 300 years)
Seeben, Forstamt Krumbach	Galio-Carpinetum luzuletosum	Oak (100 - 150 years)
Wettersteinwald, F.Mittenwald	Piceetum subalpinum	Spruce (140 - 260 years)

Classification of dead wood

Tree species: Tree species determine decay processes by the biological, chemical and physical characteristics of their wood.

Log sizes: Thick layers of bark and woody material are important for insulation and microclimate adjustment: Inside thick stems the fluctuation of temperature and humidity is smaller and the conditions for saproxylic plants and animals are more stable than in thin branch wood. At the same time, thick stems offer a wide diversity of abiotic factors and decomposition classes.

Abiotic factors of decay: Low insolation combined with high precipitation and total soil contact of downed barkless stems result in substrate conditions completely different to those that develop for example on standing stems that are losing bark and are exposed to sunlight. Derksen (1941, see Albrecht, 1991) was able to distinguish between the stump insects and stem insects on beech wood.

Decomposition classes: progressive biological decomposition and mechanical decay cause
- decrease in specific gravity,
- increase in pore volume,
- decrease in holocelluloses,
- changes in color, macroscopic patterns and mechanical consistency of wood
- successions of saproxylic plants and animals.

There are many approaches to classification, mostly oriented on special ecological questions or specific cases. The classification system shown in this paper is based on a scale of four decomposition classes and involves five dead wood types which also consider the criteria "size of log" and "abiotic factors of decay".

Volumes of dead wood

The volume of dead wood was inventoried by sample plots and classified as shown above. Dead wood is not homogeneously distributed over the area, but mostly accumulated in clusters. Total volumes vary between 8 and 100 m^3 per ha. One-third of the 84 m^3/ha woody material that had accumulated in "Wettersteinwald" forest reserve was standing and two-thirds were downed. Small pieces of dead wood were not important (1.0 m^3/ha). In commercial forests only small volumes of dead wood were found: for example, (4 m^3/ha) in the buffer zone of the "Waldhaus" reserve. This shows how deficient in dead wood commercial forests have become. See Figure 1.

Trapping methods

Instead of manually trapping insects (by debarking, dissecting the stems, sieving rotten wood), methods that do not damage on habitats, are effective and less dependent on manpower were investigated. Open and closed "dead wood eclectors" (photo-eclectors) were used (Funke, 1977). The closed type includes a portion of the stem 1 m long. All invertebrates hatching out of this stem during the investigation period are recorded. This reveals the relationships to the volume or type of dead wood investigated.

The open type furthermore records invertebrates which hunt on stem surfaces (for example spiders, crane flies) or bore into stems.

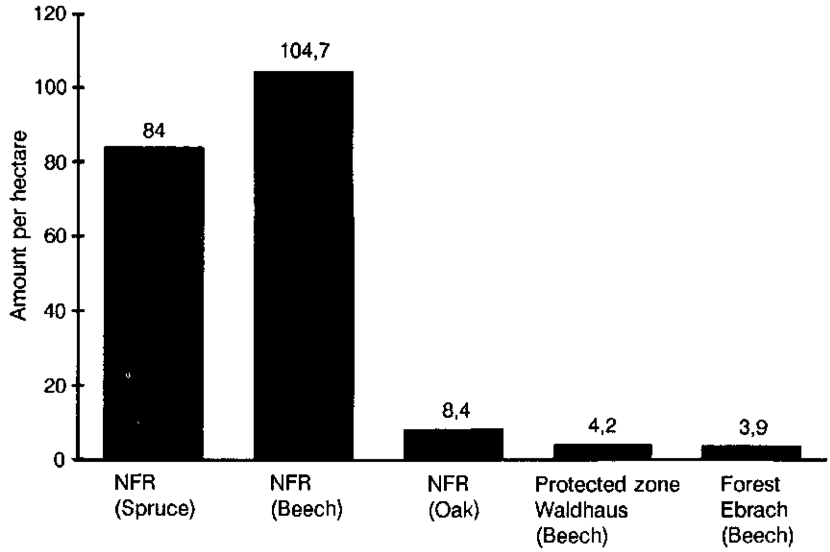

Figure 1. Amount of dead woody material in three forest nature reserves and two commerçial forests.

Results and discussion

Species groups

The trapped animals were determined at the taxonomic level of orders. Remarkably, the percentage of individuals in these orders is very similar for all three tree species studied (spruce, oak, beech). In contrast, the population densities are very different. The smaller population densities on spruce trees in Wettersteinwald are presumably caused by the unfavourable climatic conditions in the Alps (low average temperatures): see Figures 2 and 3.

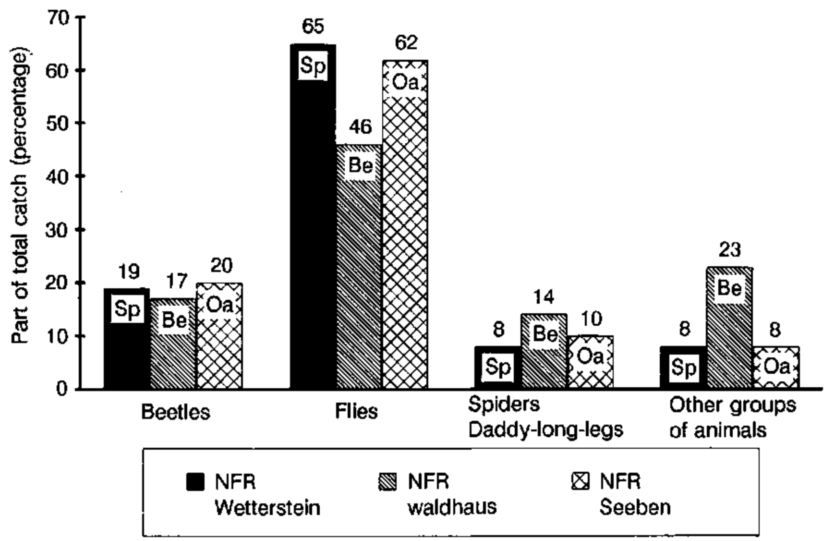

Figure 2. Share of animal groups in the total catch.

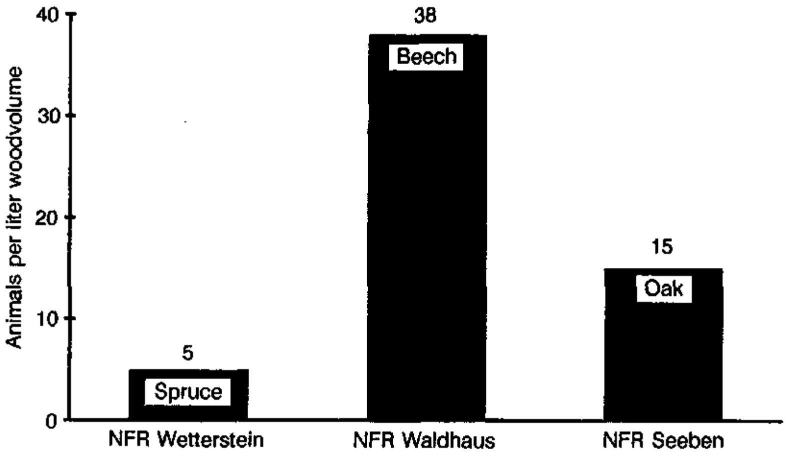

Figure 3. Amount of catch per litre of biocoenosis.

Saproxylic beetles

A comparison of the numbers of recorded saproxylic beetles with dead wood volume revealed that the "Seeben" reserve has only a small volume of dead woody material and fewer endangered species. Clearly there is too little dead wood in "Seeben" and it is not sufficiently diverse to serve as a habitat for very specialized species.

The "Wettersteinwald" reserve provides a marked contrast. A close look at the endangered species shows that most of them belong to the most endangered classes in the red data books. The occurrence of "virgin forest relict species" shows that the "Wettersteinwald" forest nature reserve plays a prominent part in species conservation. In the protected area and its surroundings there must always have been large amounts of dead and old wood which provided even very specialized saproxylics with suitable habitats.

Conclusions

Dead and dying wood of all types and stages provide habitats used by many arthropods. Nature forest reserves contribute in diverse ways towards the conservation of saproxylic beetles. The amounts and forms of dead wood are very important but vary from reserve to reserve depending on the land use histories.

A large number of endangered species and specialists are restricted to reserves with a continuous dead wood tradition, for example in the "Wettersteinwald". Dead and dying wood, especially big logs, were never in short supply here. This kind of reserve can be considered an important refuge and "core area for resettlement". By contrast, the necessary amounts and forms of dead wood have not yet accumulated in the reserves which have until recently been commercial forests.

To ensure saproxylic protection a forest nature reserve must be a minimum of 100 ha; the variety of highly differentiated dead wood types must be continuously conserved over long periods and must be accessible to insects over wide areas of forest. In this context Ammer (1991) has proposed allowing volumes of dead woody material to accumulate gradually in commercial forests too, to as much as 10 to 20 m^3/ha.

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Small neglected stands - an opportunity to study forest dynamics

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Summary

The recent stand structure and floristic composition of two less intensively managed pine stands in Germany are described. Their stand history has been traced back using dendro-ecological methods and historical records. When the results were combined the forest dynamics became apparent. The invasion of oak seems to be the most important process, because this will change the characteristics of the forest ecosystem. The value of such stands for long-term study is pointed out.

Keywords: pine-oak forest, floristic composition, dendro-ecology, historical records, stand development, forest dynamics

Introduction

Brandenburg, situated in the northeastern lowlands of Germany, is well known for its extensive pine forests. The predominating poor sandy soils, in the past often additionally degraded by litter raking etc., are adequate habitats for *Pinus sylvestris*. In addition, forest management has encouraged this fast-growing tree for economic reasons - and is still doing so, even on better soils. Since the pine is grown intensively using normal rotation techniques such as clear cutting, the forests have developed a compartmentalized appearance.

In contrast, West Berlin changed its forest policy soon after World War II, designating forests mainly as recreation and nature conservation areas (SEN STADT UM 1991). Mixed forest stands were built up by planting deciduous trees, but trees also invaded spontaneously. In 1986 a multidisciplinary research project[1] on forest ecosystems close to conurbations was started in West Berlin, investigating representative forest sites. Since the reunification of Germany, stands in adjacent Brandenburg have been included. The main goal of this project is to assess the vitality of the trees and the influence of long-term emissions on forest ecosystems. But the sampled data on soil, climate, pollution impact, vegetation e.g. are also intended to serve as benchmarks when monitoring future developments.

The research stands

In order to study forest dynamics two stands were chosen to combine analysis of recent stand structure and floristic composition, and data derived from dendro-ecological studies as well as from historical records.Both stands have one striking feature in common: for some time they have been excluded from the general forest management routines, and this has encouraged autonomous processes. Both stands are surrounded by younger pine plantations; around the Berlin stand there are also mixed stands. The stock on acidic sandy soils (the pH of the A horizon is between 3.2

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[1]The research was done as part of the multidisciplinary project 'Forest Ecosystems close to Conurbations' (Ballungsraumnahe Waldökosysteme, MAB 2) financed by the Federal Environmental Agency (Umweltbundesamt, 1986-1988) and by the Administration for Urban Planning and Environmental Protection Berlin (Senatsverwaltung für Stadtentwicklung und Umweltschutz Berlin, 1986-1992). Bert Kronenberg, Sabine Schindler and Birgit Seitz assisted with the field work and data processing.

and 3.3) is far above the water table and can be classified as Pino-Quercetum. Basic stand parameters are given in Table 1.

Table 1. Basic stand parameters of both plots.

locality	GR 91	BÄ 3321 east	west
basal area [m^2 ha^{-1}]	24.9	35.1	39.9
density trees [ha^{-1}]	625	850	800
density Pinus [ha^{-1}]	150	850	550
max. hight Pinus [m]	24.1	23.2	25.5
max. age Pinus [y]	130 (-160)	75	115

Example 1: Berlin, Grunewald, Compartment 91 a (GR 91)

Stand history (according to Tigges, 1990): In 1822 the compartment was fenced and left to regenerate naturally. In 1830 clumps of Scots pine saplings were reported on parts of the area. But as regeneration was considered to be insufficient for silviculture, additional pines were planted. In 1888 a first cutting was done. In 1930 miserable looking juvenile pines and oaks below the pine-overstorey are mentioned. In the course of the 30s further cuttings were done. No records survive for the period during and shortly after World War II. In 1949 the stand was described as an open pine stand, but a kind of understorey is also mentioned. In 1961 the height of Scots pine is given as approximately 19 m (Von Lührte, 1991, p. 54), but no oaks are mentioned. Weiss (1981) reported that the compartment was partly fenced again circa 1975 and this allowed a vigorous field and shrub layer to develop.

Stand structure: On one 400 m^2 plot, tree position, breast-height circumference and tree height were measured. Crown projection and crown base were estimated visually. From this data a map of crown projections and a cross section (Figure 1 and 2) were drawn. It is evident that *Quercus robur* and *Q. petraea* have filled the space between the old *Pinus sylvestris* trees, while *Sorbus aucuparia* and *Prunus serotina* are only found in the vicinity of the pines.

Age Structure: Since the age (130 to 160 years) and origin of the pines are known, cores for tree-ring analysis were taken from five oaks, one mountain ash (*Sorbus aucuparia*) and one black cherry (*Prunus serotina*) in the understorey. It was found that the larger oaks are between 43 and 49 years old, while the smaller ones are younger (about 38 years). The biggest black cherry is about 35 years old and one of the mountain ashes is 40 years old. It can be concluded that all trees of the second tree layer established themselves between 1943 and 1957.

Ground vegetation: Ground vegetation was investigated annually from 1986 to 1991 on the 400 m^2 plot where the structure analysis was carried out (Seidling, 1990) using the Braun-Blanquet method (1964, modified according to Barkman et al., 1964). As shown by Table 2 *Deschampsia flexuosa* dominates in the field layer, fluctuating slightly over time (this is partly caused by the activities of wild boar). In addition to other herbs and grasses ten tree species were found within five summers. Different deciduous tree species occured as saplings, but all seedlings of *Pinus sylvestris* died within the first year. Only three deciduous tree species have succeeded in entering the shrub and second tree layer within the last twenty years and it seems that they will dominate in future too. Scots pine is unable to regenerate under present conditions, even though this plant community (Pino-Quercetum; PNV according to Tüxen, 1956) is supposed to have 40 % Scots pine (Grenzius et al., 1991).

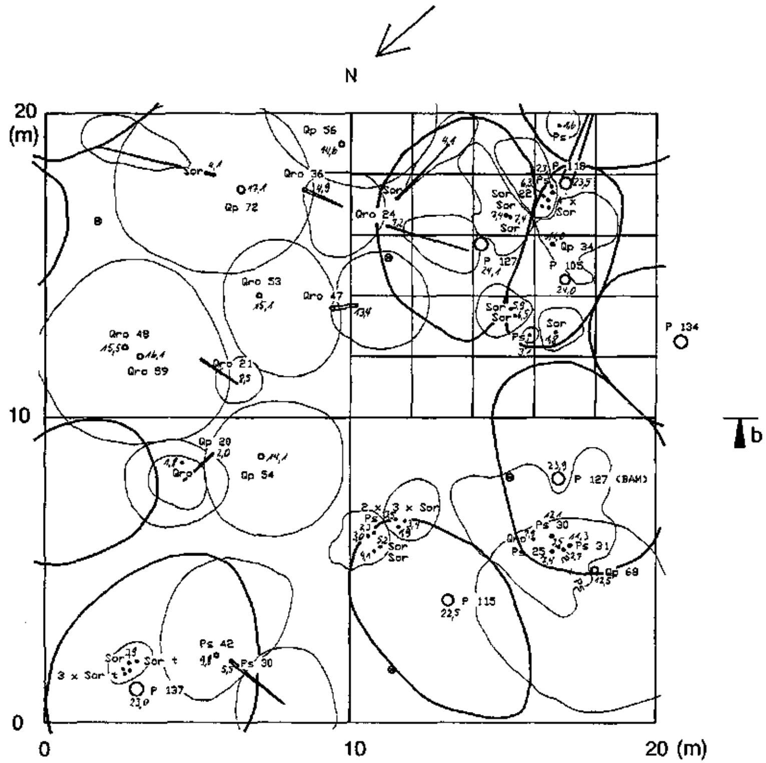

Figure 1. Crown projection GR 91: P115 22,5: Pinus sylvestris, circumference: 115 cm, height: 22,5 m; Qro: Quercus robur; Qp: Quercus petraea, Sor: Sorbus aucuparia, Ps: Prunus serotina, trees with BHC < 20 cm and height > 2 m, only height is given; ⊗ tree stump.

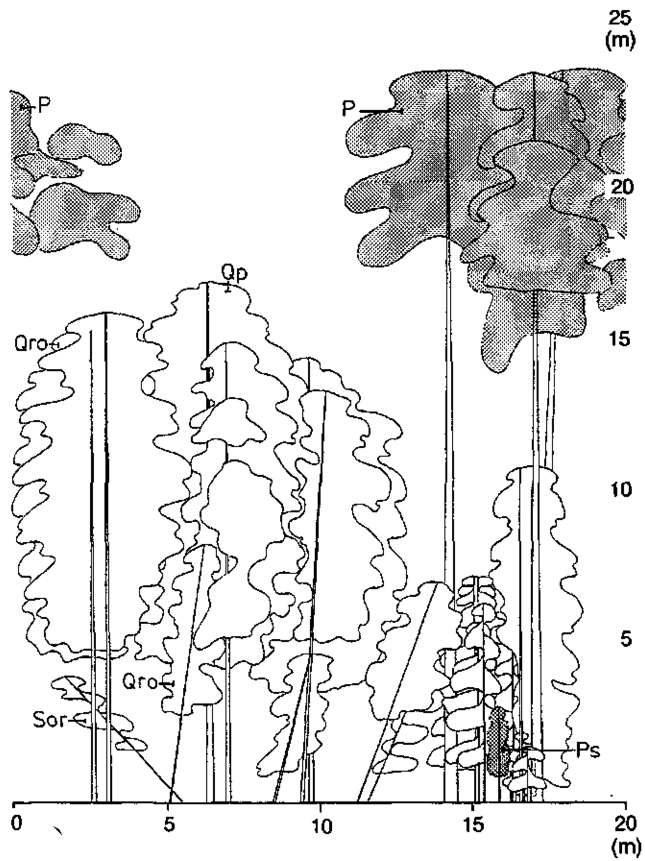

Figure 2. Side view: GR 91: upper part b of Figure 1 (depth: 10 m), abbreviations see Figure 1.

Table 2. Relevés (Braun-Blanquet 1964) of both stands: Berlin: Grunewald, compartment (Jagen) 91 (GR 91), Brandenburg: Bärenklau, compartment (Abteilung) 3321 a7 (BÄ 3321).

locality	GR91	GR91	GR91	GR91	GR91	BÄ3321
year	1986	1987	1988	1990	1991	1990
area [m²]	400	400	400	400	400	400
cover [%], tree layer 1	20	25	20	25	25	40
cover [%], tree layer 2	60	70	75	75	75	<1
cover [%], shrub layer	5	1	2	5	3	<1
cover [%], herb layer	35	45	50	15	25	65
cover [%], moss layer	1	1	1	2	1	25
n species, herb layer	17	17	17	16	20	11
1 Pinus sylvestris Ia	2b	2b	2b	2b	2b	3
2 Quercus petraea Ib	3	3	3	3	3	
3 Quercus robur Ib	2b	2b	2b	3	3	
4 Prunus serotina Ib	+b	2a	2a	2b	2a	
5 Sorbus aucuparia Ib		+b	+b	+b	+a	
6 Pinus sylvestris Ib						+r
7 Sorbus aucuparia II	+b	+p	+p	+a	1p	
8 Prunus serotina II	+b	+p	+r	1b	1b	
9 Quercus robur II	+r	+r	+p	+r	+r	
10 Betula pendula II						+r
1 Quercus robur et petraea	+p	+p	1p	1p	+p	1p
2 Prunus serotina	2m	2m	2a	2a	2a	+r
3 Sorbus aucuparia	2m	2m	2m	2m	2m	
4 Quercus rubra	+r	+p	+p	+r		
5 Pinus sylvestris						+p
6 Pinus sylvestris seedling		+p	1p	+p	+p	+p
7 Betula pendula	+p			+r		
8 Betula pendula seedling					+r	
9 Acer pseudoplatanus	+r	+p	+r	+p	+p	
10 Acer platanoides		+r				
11 Taxus baccata					+r	
12 Fagus sylvatica seedling					+r	
1 Deschampsia flexuosa	2b	3	3	2a	2b	3
2 Carex pilulifera	+p	+p	+p	+p	+p	1p
3 Danthonia decumbens	+p	1p	1p	+p	+p	+r
4 Agrostis tenuis	1p	2m	2m	1p	+p	
5 Luzula multiflora	+p	+p	+p	+p	+p	
6 Galium hercynicum	1p	2m	2m	+p	1p	
7 Viola riviniana	+p	+p	+p	+p	+p	
8 Rumex acetosella	2m	1p	1p	+p	+p	
9 Hypericum perforatum	+p	+p	+p	+r	+r	
10 Moehringia trinervia	1p	1p	+r			
11 Impatiens parviflora	+r					
12 Poa pratensis			+p			
13 Epilobium angustifolium					+r	
14 Senecio sylvaticus					+r	
15 c.f. Vicia sp. seedling					+r	
16 Vaccinium myrtillus						2a
17 Calluna vulgaris						1p
18 Festuca ovina						+p
19 Melampyrum pratensis						+p
20 Dryopteris carthusiana						+r

locality		GR91	GR91	GR91	GR91	GR91	BÄ3321
year		1986	1987	1988	1990	1991	1990
area [m²]		400	400	400	400	400	400
1	Pleurozium schreberi	x	2m	2m	2m	2m	2b
2	Pohlia nutans	x	2m	1p	2m	2m	2m
3	Hypnum cupressiforme	x	2m	2m	2m	2m	2m
4	Dicranum scoparium	x	+p			+p	+p
5	Scleropodium purum	x	+p	1p	1p	1p	
6	Polytrichum formosum	x	1p	+p			
7	Plagiomnium affine	x	+p		+p		
8	Atrichum undulatum	x	+r				
9	Dicranum polysetum						1p
10	Dicranella hetromalla						+p

Example 2: Brandenburg, Revier Bärenklau, Compartment 3321 a7 (BÄ 3321)

This stand is situated in Brandenburg approximately 30 km north of Berlin.

Stand history: No historical records about this ca. 0.3 ha stand are available, therefore its history can only be reconstructed by tree ring analysis. Fire marks can be found on some of the pine stems, evenly distributed over the area.

Stand structure: The parameters mentioned above were recorded on two adjacent 400 m² plots. The stand structure gives the impression of a very dynamic stand, although it consists only of Scots pine and birch (Figures 3, 4 and 5) and is close to being mono-layered.

Age structure: The pine trees differ in age, but this is not easily distinguishable from their dimensions. The spatial distribution of age classes shows a wave-like process (Figure 6): the oldest trees can be found in the western part, while in the eastern part pines 69 - 74 years old predominate. Below the older trees is a layer of spindly 25 - 40 year old pines and birches, which are remnants of the last two regeneration waves, the earlier of which may coincide with the ground-fire mentioned above. Each age class started growth under different (unfortunately unknown) general conditions; this can be seen from the steepness of the growth curves (Figure 7). Together with the competition this has resulted in pine trees of almost uniform size, especially those that are between 69 and 94 years old. The large numbers of dead trees aged 25 - 94 years indicates intensive stand dynamics with ongoing self-thinning.

Ground vegetation: Ground vegetation was investigated in 1990 on the eastern half of the plot only (BÄ 3321 east). As in GR 91, the forest floor vegetation is dominated by *Deschampsia flexuosa*, while *Vaccinium myrtillus* is co-dominant. *Calluna vulgaris* is present too (Table 2), indicating that more light reaches the forest floor here. In contrast to GR 91 *Pinus sylvestris* exists not only as seedlings but also as saplings. Deciduous tree species are much rarer, because there are fewer sources of diaspores in the surroundings. But they are not entirely absent and *Quercus robur* and *Q. petraea* in particular are invading the plot. It is not clear why oaks did not grow up in the past. Browsing by roe deer is a possible explanation.

Discussion of the results

For both pine-(oak)-forests on comparatively poor sandy soils (Pino-Quercetum) the following conclusions can be drawn from our studies:

1. If there is any seed source within the range of vectors (e.g. jays) *Quercus robur* and *Q. petraea* will spontaneously invade almost pure pine stands (GR 91). Within the last 40 years oak has established more successfully than young pines or birches, which were reported to be present in the understorey in 1930 and 1961. Today both species are very rare in the understorey of the whole compartment (28 ha) where the 400 m² research plot is situated. Oak seems to change the characteristics of the whole ecosystem (light climate, litter layer, etc.) in

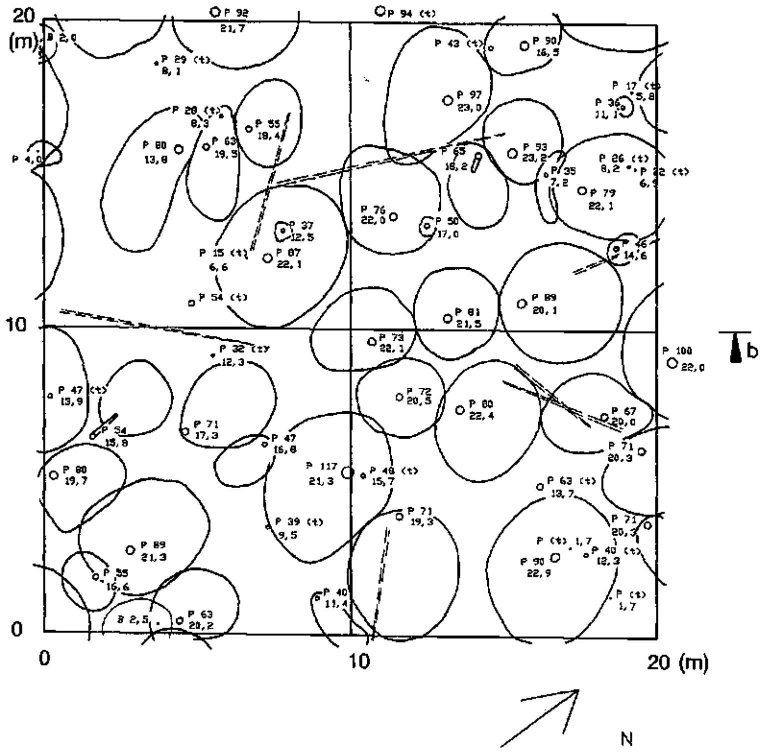

Figure 3. Crown projection BĂ 3321, western part. Abbreviations see Figure 1, B: Betula pendula.

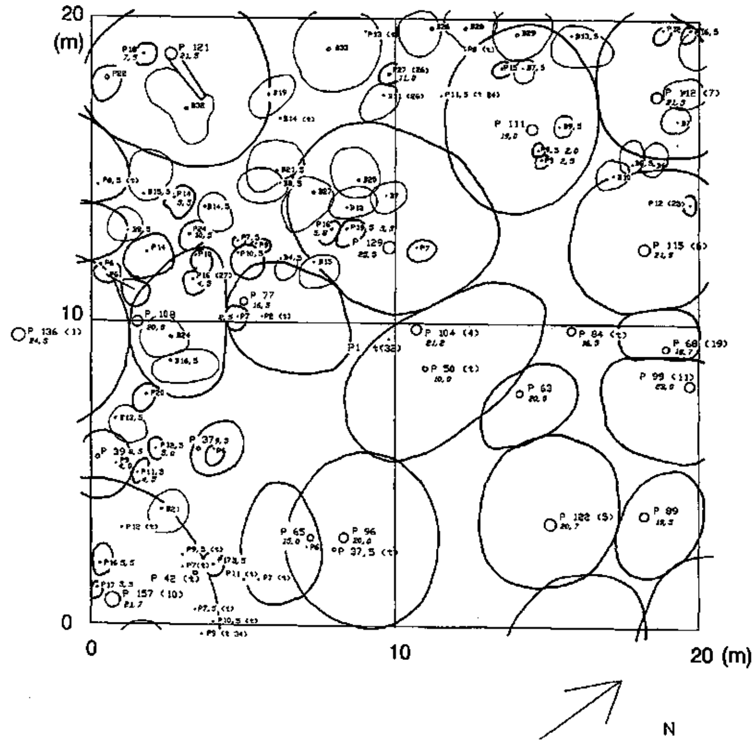

Figure 4. Crown projection BĂ 3321, eastern part. Abbreviations see Figure 1 and 3.

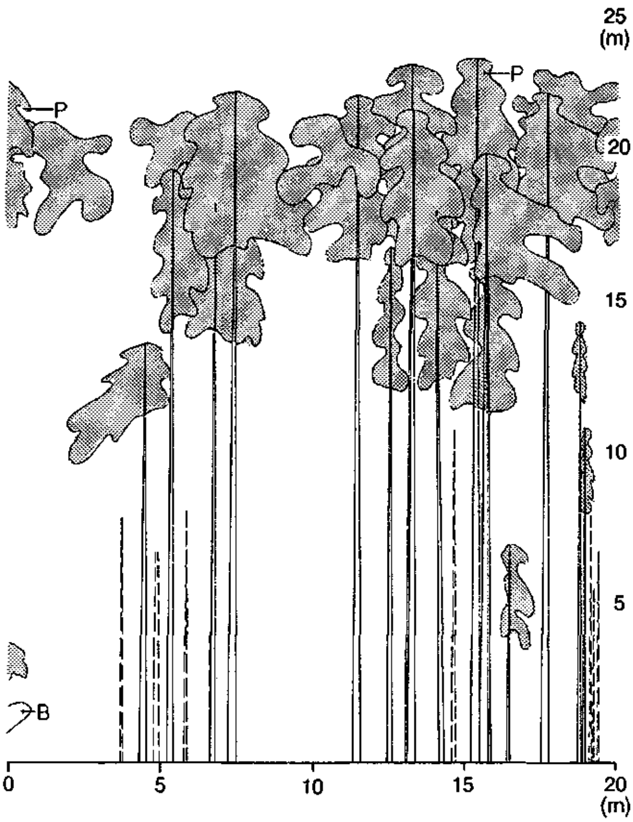

Figure 5. Side view: BÄ 3321, eastern part: upper part b of Figure 4 (depth: 10 m). Abbreviations see Figure 1 and 3.

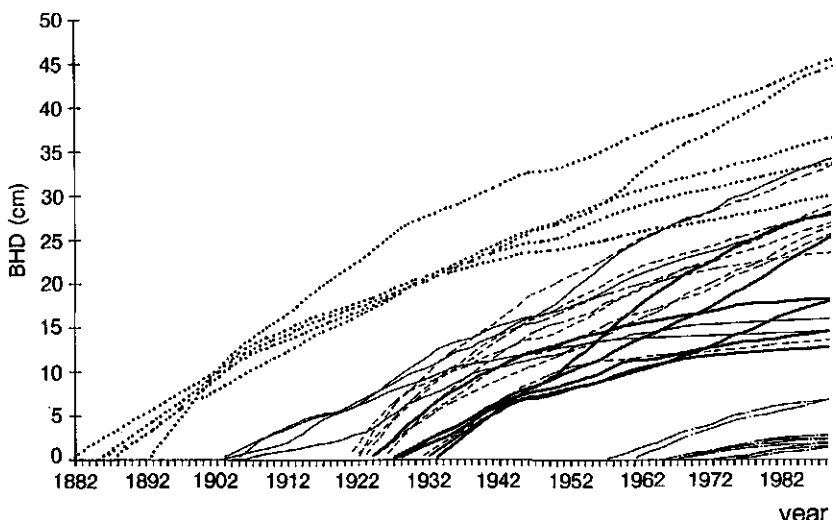

Figure 6. Spatial distribution of 4 cohorts of pines from BÄ 3321. The quadrats represent the eight 10 x 10 m subplots of Figures 3 and 4.
For each cohort the year of establishment (derived from tree ring analysis) is given below.

such a way that Scots pine or birch may no longer be able to regenerate. Because oak is long-lived it will predominate for a long time. The failure of pine (and birch) may largely be due to the damping-off of seedlings caused by fungi (Vaartaja, 1952) or to insufficient light in later stages. Only fire or other greater disturbances may enable *Pinus sylvestris* to reoccupy a certain area (e.g Bulygin, 1982; Sannikov, 1983; Lust, 1988; Scamoni, 1988).

2. As well as old pine and younger oak only two small, short-lived tree species (mountain ash and black cherry) have been able to act temporarily as a kind of stopgap (GR 91). It is not yet possible to predict the future of other tree species such as *Acer pseudoplatanus*, which occur as seedlings or small saplings, since no specimens taller than 20 cm have been observed; however, some authors (e.g. Sachse, 1989) think they will play a role in future forests, benefitting from nitrogen input (ca. 20 kg ha^{-1} y^{-1} at GR 91, Marschner, 1990).
3. In BÄ 3321 pine and birch have regenerated successfully in the last twenty years, but oak has been unable to reach the shrub or tree layer. This is surprising, given that there is one old specimen ca. 200 m away and there is ongoing diaspore input - as evidenced by seedlings and small saplings on the plot. Game pressure may be high and oak may suffer from browsing more than pine or birch, which regenerated about 30 years ago (cf. Ellenberg, 1989).
4. As often observed, tree populations regenerate in waves (e.g. Ertelt, 1967; Sprugel, 1976; Whipple and Dix, 1979) leading to approximate discrete age classes, which can be described in terms of the 'invasion (or, better 'regeneration') window' according to Johnstone (1986). In addition to annual variations in climate, the state of the ecosystem and occurrence of disturbances open and close these windows, which differ for each species in a certain forest.

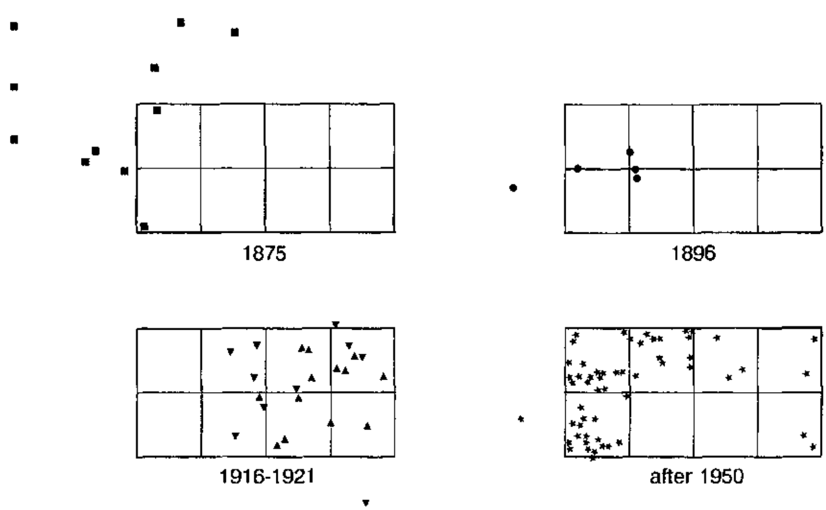

Figure 7. Diameter (cm at breast height) of selected pines from BÄ 3321 as a function of time (years). Note the different steepness of juvenile growth, e.g. of 1992 cohort and 1972 cohort.

Conclusions

Long-term observations are necessary when studying forest dynamics, primarily because of the longevity of trees (Likens, 1989). Investigations of processes within a stand should start with mapping stand structure (e.g. distribution and dimensions of trees, shrubs, dead logs, etc.). The resulting picture is far from simple and already provides an insight into stand dynamics (Köstler, 1955; Bücking et al., 1986; Koop, 1989; Oldeman, 1990). Because the early phase of the tree life-cycle takes place within the herb layer or even within the moss layer, these compartments must be studied (Bücking and Reinhardt, 1984), if only to get information about ongoing processes of tree regeneration. The composition of the herb layer is also a valuable indicator of soil properties, past and present management measures or the light regime (e.g. Schmidt, 1991).

For a better understanding of the present stand and of its future its history should be considered as well. In addition to historical documents there are two natural records which can be used: pollen and tree rings. Pollen deposited in peat bogs or in the raw humus layer of forests gives a retrospective view of species compositions back to prehistoric times or merely to the start or end of clearing activities a few centuries ago (Scamoni, 1935; Davis, 1989), and can even be applied to verify the virgin character of forests (Kral, 1988; Kral and Mayer, 1968). Analysis of tree rings, which are the manifestation of previous diameter growth enables the tree's age to be determined and its individual life history to be traced, giving information about stand dynamics (competition, wounding, climatic events, etc. see Schweingruber (1983). Various authors have demonstrated the usefulness of dendro-ecological methods for reconstructing forest history. For example, Henry and Swan (1974) traced the vegetational history of an undisturbed forest back to 1665 by analysing dead and living trees. Many of these studies have had practical relevance for future forest management, e.g. for fire control (Day, 1972), avalanche protection (Brang, 1988) or natural regeneration after storms (Hytteborn et al., 1987), but studies have also been done at ecosystem level (Whittaker and Woodwell, 1969). In combination with research on the forest's present state, such retrospective methods can effectively lengthen the observation period, allowing longer-lasting processes to be evaluated, as our examples show.

In most cases the structure and composition of managed forest stands are almost entirely steered by man. In both stands described above autonomous developments have occurred in recent decades, therefore they are of special interest, because they enable us to observe succession in forests without management.

1. They can provide practical recommendations for the new 'nature conforming' forestry, based on natural stand dynamics (Zukrigl, 1991).
2. They could serve as a starting point for long-term monitoring of different aspects and may even answer questions which will arise in future (Bråkenhielm, 1991; Sukopp et al., 1986).
3. They can be valuable themselves as unmanaged areas in our man-made countryside - for nature conservation and for public experience of natural processes. These intensively investigated stands should therefore serve as a kind of 'germ-cell' for ongoing research on forest dynamics and should be kept free from silvicultural interventions. Since the stands studied evolved from pine stands on poor soils, classic for the eastern part of Germany, they should be integrated into the existing network of forest reserves of eastern Germany, which mainly consists of old stands under special conditions (wet soils, etc., cf. Knapp and Jeschke, 1991).

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Vegetation diversity and soil pH in ranking forest habitats

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Summary

Three criteria were used to characterize 18 forest sites in Bialowieza primeval forest (north-eastern Poland), Kozienice forest (central Poland), and Swierklaniec forest (Silesia, southern Poland): (1) mean pH-H_2O value of 0-5 cm humus layer; (2) number of herbaceous species per 1 m^2; (3) number of tree and shrub species per 1 m^2. Two- and three-dimensional grids of forest habitats allowed us to distinguish several groups of similar forest sites. For 15 sites in Bialowieza and Kozienice forests, a statistically significant correlation between the number of plant species and soil pH was observed ($r = 0.82$, $df = 13$, $p < 0.01$). Three Silesian transects deviated strongly from this pattern, probably because the balance between the soil and vegetation had been disrupted by pollution. The results indicated that the method could be an efficient tool in forest inventory and monitoring.

Keywords: forest type classification, habitat ranking, soil pH, herb layer

Introduction

Many papers have been written on the relationship between soil pH and various soil characteristics. On the one hand, pH plays an important role in various soil processes such as carbon and nitrogen transformation (Billett et al., 1990a; Klinka et al., 1990), NH_4/NO_3 ratio (Like and Klein, 1985), ion solubility and leaching (e.g. Rechcigl and Sparks, 1985; Billett et al., 1990b), phosphorus availability (Tabatabai, 1985), Al, Fe and Mn toxicity (Kazda and Zvacek, 1989) or heavy metal activity (Brümmer and Herms, 1983). On the other hand, soil pH is influenced by biochemical processes of mineralization and humification (Tabatabai, 1985), nitrification, nutrient uptake and leaching (Binkley and Sollins, 1990; Gijsman, 1990; Verstraten et al., 1990). Most of these relationships have a feedback character.

All this indicates the key position of soil pH among the elements and processes of the ecosystem. Although pH is a logarithmic measure of H^+ concentration, its values in the field have a normal distribution and when plotted against other soil properties (e.g. cation adsorption) a straight line fits the data (Daubenmire, 1974). In this paper we describe an attempt to use forest humus pH in combination with an index of plant species richness to characterize forest habitats in Poland. We assumed that the pH of the humus layer represents broader ecological conditions, and may be closely related to other stand traits like vegetation.

Study area

Three forests were chosen for the study: (1) Bialowieza primeval forest (north-eastern Poland, 52°43'N, 23°50'E), (2) Kozienice forest (central Poland, 51°40'N, 21°26'E), and a Silesian forest near Tarnowskie Góry city (in Silesia industrial centre, southern Poland, 50°27'N, 18°52' E), see Figure 1. Each forest was represented by 3-12 research plots, giving a total of 18 plots. The following codes are used throughout the text:
Bialowieza primeval forest:
B1-B3, B4: coniferous forest (Vaccinio vitis-idaeae-Pinetum, Vaccinio myrtilli-Piceetum);

B5-B7, B8: mixed-coniferous forest (Calamagrostio arundinaceae-Piceetum, Querco-Piceetum);
B9-B10, B11-B12: deciduous forest (Tilio-Carpinetum typicum, Tilio-Carpinetum stachyetosum);
Kozienice forest:
K1-K3: coniferous forest (Leucobryo-Pinetum);
Silesian forest:
S1-S3: coniferous forest (Leucobryo-Pinetum).

Figure 1. Location of the study area.

Methods

Phytosociological study

The phytosociological analyses were done on transects 52 m long and 2 m wide, thus the area of relevés was 104 m^2 on each research plot. The relevés were done in August 1991. The abundance of given species was estimated in the Braun-Blanquet scale.

Seven associations and subassociations were distinguished, according to Sokolowski (1980) and Matuszkiewicz (1981, see Study area). All the habitats studied were characterized by the similar (fresh) humidity conditions.

Analysis of pH

The sampling was performed simultaneously with the phytosociological relevés on the transects 52 m long and 1 m wide located in the middle part of the relevés. On each transect a total of 104 volumetric samples of 5 cm^3 each were collected from the 0-5 cm surface layer. Fresh samples were mixed with 10 ml distilled water. After 5 hours the suspension was analysed with a MEDICAT 1202 SM pH meter and the combination electrode. The total number of pH samples was 1872.

For further analysis the number of vascular plant species found on a relevé, and the arithmetical mean of 104 pH values obtained at each transect were used. The cluster analyses were performed according to the average linkage between groups method (Milligan, 1980).

Results

Eighteen sets of data were characterized by 9 to 31 species of herbaceous vascular plants, and 1 to 8 woody species in tree and shrub strata per 104 m^2. The mean pH H_2O ranged from 3.67 to 4.82, and the standard deviation between 0.14 and 0.76. All parameters are given in Table 1. The number of species on relevés was converted to N/m^2 to obtain the mean number of species on the transect per m^2. The transects were classified into several specific groups according to these criteria.

One-factor (linear) ranking of forest habitats

If we took only one criterion (i.e. number of herbaceous species) into account, we were able to distinguish three groups of habitats (Figure 2). The poorest sites (below 0.15 species/m^2) included 11 transects: B1-B4, B8, K1-K3, S1-S3. The intermediate ones (from 0.15 to 0.24 species/m^2) included transects B5-B7. The group of the richest forest habitats included transects B9-B12 with ≥ 0.25 species per m^2.

When the criterion of the average value of humus layer pH was applied, the transects were grouped into three pH intervals (Figure 2). The most acid group (below 4.0) comprised transects B1-B8, K1-K3. The intermediate one (pH 4.0 - 4.5) was represented by transects S1-S3 and B9-B10. The least acid one included transects B11 and B12.

The nonparametric test for association proved that there was no statistically significant association between the mean pH and mean number of species per m^2 on 18 transects (Kendall's $\tau = 0.2907$, $p = 0.0818$).

Two-factor ranking of forest habitats

Using the species richness and the mean pH values as coordinates, a two-dimensional ordination of forest habitats was created (Figure 3). There was a statistically significant correlation between the mean pH of the humus and the number of herbaceous species per m^2 ($r = 0.591$, df = 16, $p < 0.01$). The statistical significance of the correlation increased when three strongly deviating Silesian transects (S1-S3) were excluded from the computation ($r = 0.821$, df = 13, $p < 0.01$).

The cluster analysis showed that two principal groups of forests, the coniferous and mixed-coniferous one and the deciduous one, were composed of five smaller groups of forest habitats (Figure 3): an acid coniferous group (B1-B4, B8, K1-K3), a mixed-coniferous group (B5-B7), two deciduous forest groups (B9-B10, the poorer one, and B11-B12, the richer one), and one group of Silesian transects (S1-S3, changed coniferous group). These groups seemed to accord with the intuitive impression of similarities between transects.

Three-factor ranking of forest habitats

When the mean number of woody species/m^2 was used a trend similar to that in two-dimensional ordination was noticed (Figure 4). However, this approach allows a more subtle clustering of transects. A synthetic characterization of nine distinguished groups of habitats is as follows (see Figure 4):

1. B11-B12 virgin deciduous forest (Tilio-Carpinetum stachyeto-sum) in the Bialowieza National Park;
2. B9-B10 virgin deciduous forest (Tilio-Carpinetum typicum) in the Bialowieza National Park;
3. S2-S3 coniferous forest (Leucobryo-Pinetum, 90 yrs old) in Silesia, with a very loose canopy closure, severely affected by industrial pollution;

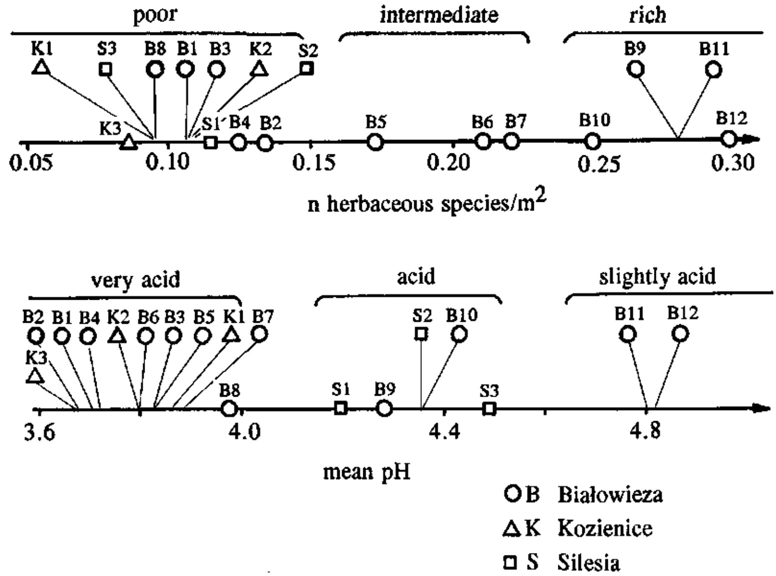

Figure 2. Single-factor ranking of forest habitats according to the mean number of herbaceous species/m^2 and the mean pH values on the transects. B - Bialowieza: 1-4 coniferous forest, 5-8 mixed-coniferous forest, 9-12 deciduous forest; K1-3 - Kozienice coniferous forest; S1-3 Silesian coniferous forest.

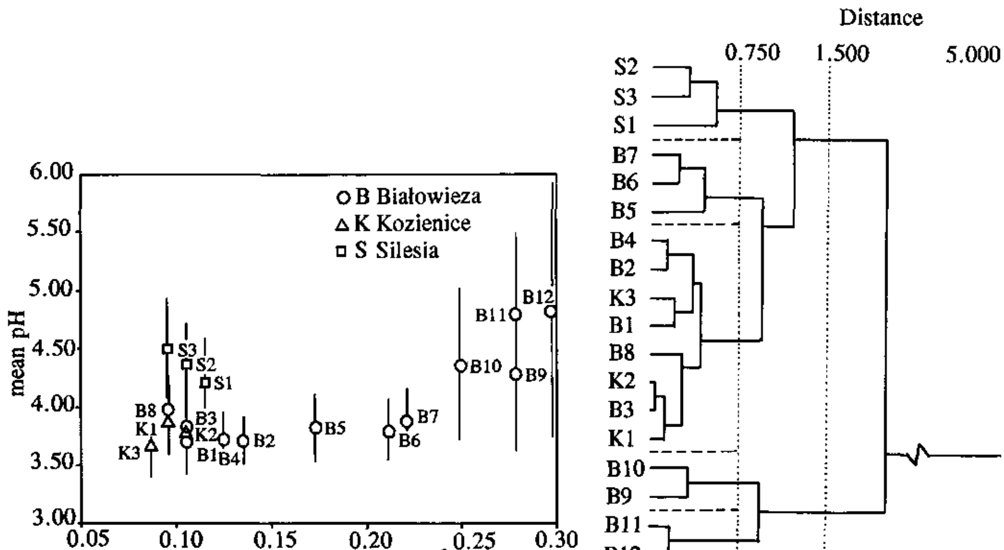

Figure 3. Two-factor ranking of forest habitats and the tree diagram joining transects according to standardized values of N herbaceous species per m^2, and of the mean pH. The correlation coefficient was $r = 0.591$, $p < 0.01$ for all 18 points, and $r = 0.821$, $p < 0.01$ without Silesian S-points. See Figure 2 for transect symbols.

4. S1 young (60 yrs) coniferous forest (Leucobryo-Pinetum) in Silesia, with a dense canopy cover, severely affected by industrial pollution;
5. K3 young (50 yrs) coniferous forest (Leucobryo-Pinetum) in Kozienice Forest, with a dense canopy cover;
6. B1-B2 older (80-150 yrs) coniferous stands in Bialowieza Primeval Forest (Vaccinio vitis-idaeae-Pinetum) and K2 in Kozienice Forest (Leucobryo-Pinetum); two very open stands (transect B3 with relatively high abundance of species from the Dicrano-Pinion class and K1, with much cover of the grass *Deschampsia flexuosa*) were combined in a separate subgroup;
7. B5-B6 virgin mixed-coniferous forest (Calamagrostio arundinaceae-Piceetum) in the Bialowieza National Park;
8. B4 virgin coniferous forest (Vaccinio myrtilli-Piceetum) in the Bialowieza National Park;
9. B8 virgin mixed-coniferous forest (Querco-Piceetum) in the Bialowieza National Park; for details see Table 1.

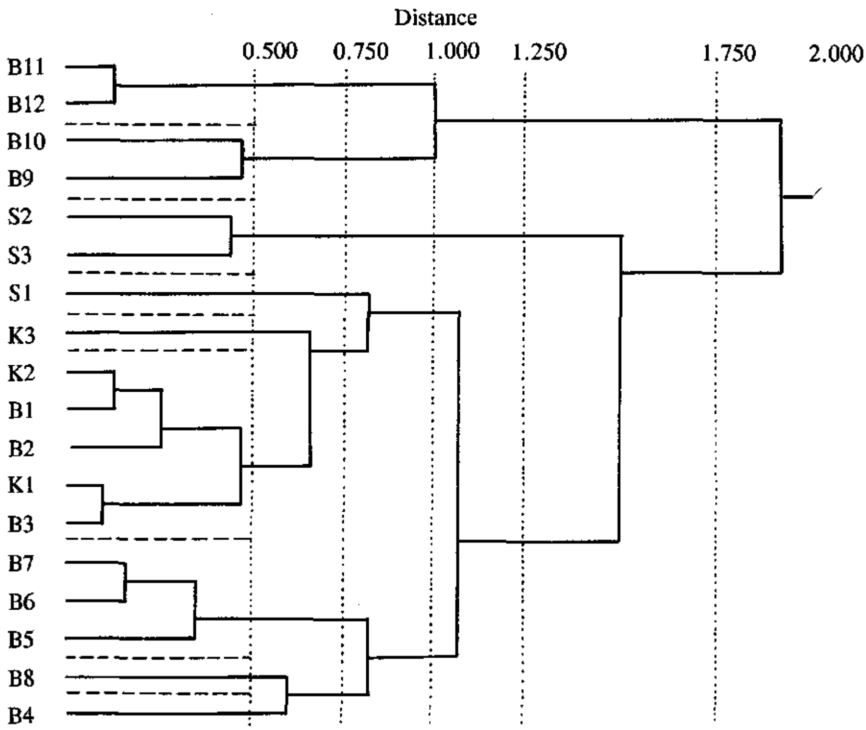

Figure 4. Tree diagram joining transects according to standardized values of N herbaceous species per 1 m^2, N woody species per m^2 and of the mean pH. See Figure 3 for transect symbols.

Discussion and conclusions

No single criterion, e.g. the number of species or the mean pH, was sufficient to characterize forest habitats. On one hand, the criterion of richness of species distinguished neither a separate group of Silesian transects nor two various deciduous groups. On the other hand, the criterion of mean pH did not differentiate between the coniferous and the mixed-coniferous stands, and did not separate two poorer deciduous plots from the Silesian plots (Figure 3). It seems, however, that the combination of these two simple parameters would be an efficient way of forest habitat characterization. Both methods of forest characterization applied (two- and three-factor) made it possible

Table 1. Four synthetic parameters describing 18 forest transects in Poland.

Transect no.	Mean no. of spp/m^2 herbaceous	woody	Mean pH N=100	SD
Bialowieza primeval forest: coniferous forest				
B1	0.106	0.02	3.71	0.21
B2	0.135	0.02	3.70	0.14
B3	0.106	0.03	3.83	0.21
B4	0.125	0.04	3.72	0.16
Kozienice forest: coniferous forest				
K1	0.096	0.03	3.87	0.19
K2	0.106	0.02	3.80	0.21
K3	0.087	0.01	3.67	0.18
Silesian forest: coniferous forest				
S1	0.115	0.03	4.20	0.26
S2	0.106	0.05	4.36	0.23
S3	0.096	0.06	4.49	0.30
Bialowieza P.F.: mixed-coniferous forest				
B5	0.173	0.04	3.83	0.22
B6	0.212	0.04	3.80	0.18
B7	0.221	0.04	3.89	0.20
Bialowieza P.F.: deciduous forest				
B8	0.096	0.05	3.97	0.22
B9	0.279	0.05	4.28	0.47
B10	0.250	0.04	4.36	0.45
B11	0.279	0.06	4.80	0.47
B12	0.298	0.06	4.82	0.76

to aggregate the habitats studied into several groups: the typical well separated groups of pure coniferous and pure deciduous forests, and intermediate groups including the other habitats. Most of them followed the positive correlation between the number of species and the humus layer pH. Generally, the higher the mean pH, the larger the standard deviation (Table 1) which is the measure of variety of transects. The results of the two- and three-factor rankings of forest habitats applied confirm Lindgren's (1969) contention that "the close correlation between the vegetation type and the soil type can also be shown by the pH variations". A conservative supposition is that the variety in pH reflects the variability of habitat, which is responsible for the creation of a mosaic of microhabitats. We can endorse the contention of Kolasa and Biesiadka (1984) that such heterogeneity indisputably favours an increase in species diversity.

The slight deviation from the observed pattern in three plots of transects B5-B7 may be explained by the presence of species from other communities, which is reported to be a phenomenon typical for Calamagrostio arundinaceae-Piceetum (Sokolowski, 1980). Three Silesian habitats deviated remarkably from this general pattern, which suggests that the balance between the soil and vegetation has been distrupted by pollution.

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Chapter 4

Research on "natural" forest management

New Forest - a park landscape

The New Forest (England) has an area of 37 500 ha and was described in the Domesday book of 1087 as a hunting ground of William the Conqueror. As a result of the annual grazing of livestock (mainly horses, but also cattle and sheep) and of red and fallow deer it has become a grazed park landscape.

The rejuvenation of trees was severely hindered by the grazing, but the periodic reduction in livestock herds during periods of collapse in the meat market gave rejuvenation a chance. Besides grazing, the felling of trees, and the thinning of the forest and the burning of heathland to allow sufficient food supply for the cattle, have contributed to the patchwork of forest, heath, meadow and scrub. As a result of the grazing, margin vegetations have developed, forming the transition from forest to open grazing vegetations, especially on rich sites. Many organisms are bound to the specific habitat of the margin vegetations.

Recent structural changes in the beech forest reserve of Groenendaal (Belgium)

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Summary

In 1983, a 215-year-old beech stand in the state owned Zoniën Forest (Flanders, Belgium) was designated a strict forest reserve. Stand structure analysis started in 1986, i.e. before the spring tempests of 1990. Subsequently, it was possible to evaluate the impact of the gales as a factor driving actual forest dynamics. It was also found that a steady structural change is still going on; there is considerable diameter growth of the upper storey trees.

Keywords: forest dynamics, beech forest, gales

Introduction

In Belgium, there is no tradition of forest reserves. However, one of the oldest forest stands in Flanders has been excluded from all silvicultural treatments since 1983. At that time the beeches in this forest were over 200 years old and were coming to the end of their lifespan. Therefore rather rapid changes in forest development were expected (Van Den Berge et al., 1990).

Before the severe gales of spring 1990 a preliminary evaluation of structural characteristics was done.

Materials and methods

The forest reserve of Groenendaal is located in the middle of the famous Zoniën Forest. This forest, only about 15 km from the centre of Brussels, extends over more than 4300 ha and can globally be characterized as a beech forest. The annual temperature averages 9.4° C, yearly precipitation totals 838 mm. The geological substrate consists of Tertiary sandy deposits, covered by a Quaternary loam layer several metres thick over most of the forest.

The central part of the research stand, inside a buffer zone of 50 m, is an 10.5 ha in size.

The soil type can be generally classified as grey brown podzolic, i.e. a severely lessivated loamy soil. The humus type is moder. Groundwater is out of the reach of tree roots, but because there is a fragipan of paleoperiglacial origin (Langohr and Vermeire, 1982) in the subsoil there is a temporary perched water table, which has resulted in a secondary pseudo-gley, beginning from a depth of 0.35 - 0.40 m.

The plant association belongs to the Milio-Fagetum Noirfalise and Roisin, and more particularly to the subhumid subassociation athyrietosum or caricetosum, with frequent presence of e.g. *Carex remota* JUSL. ex L. and *Athyrium filix-femina* (L.) ROTH.

The stock of game is small. Of the large game species only the roe deer *Capreolus capreolus* is present, but at low density (ca. 4-5 ex. pro 100 ha).

Historical documents allow to date the origin of the stand as the second half of the 18th century (± 1770). Most of it was probably planted.

In general the stand structure is composed of an upper storey of old beeches *Fagus sylvatica* L. and a few oaks *Quercus robur* L. and *Q. petraea* (Mattuschka) Lieblein; a substorey is all but absent. The understorey consists of spontaneously regenerated young beeches (10 - 50 years old), irregularly distributed.

Recent structural changes are referred to in the full silvicultural inventory of the old stand made in 1986, supplemented by strip transect analyses and stem-disk analysis on an old uprooted beech (spring 1990) from the buffer zone.

Results and discussion

Upper storey structure

Table 1 gives the silvicultural characteristics of the old stand, before (1986) and after the spring tempests of 1990.

Table 1. Inventory of the old stand, before and after the spring tempest of 1990.

	Tree species	Stem number		Basal area		Standing volume	
		ha^{-1}	%	$m^2.ha^{-1}$	%	$m^3.ha^{-1}$	%
1986	Beech	50	94.3	27.3	95.5	688	96.6
	Oak	3	5.7	1.3	4.5	24	3.4
	Total	53	100.0	28.6	100.0	712	100.0
1990	Beech	45	84.9	24.3	85.0	605	85.0
	Oak	3	5.7	1.3	4.5	24	3.4
	Total	48	90.6	25.6	89.5	629	88.4

After the spring gales of 1990, stand characteristics changed considerably. The stem number of the upper storey was reduced to 48, the basal area to 25.6 m^2 and the standing volume to 629 m^3 per hectare - i.e. decreases of respectively 9.4, 10.5 and 11.6 %. As a result, the amount of necromass increased considerably (almost quadrupled, cf. Table 2), and became comparable with that in other famous European forest reserves (Figure 1).

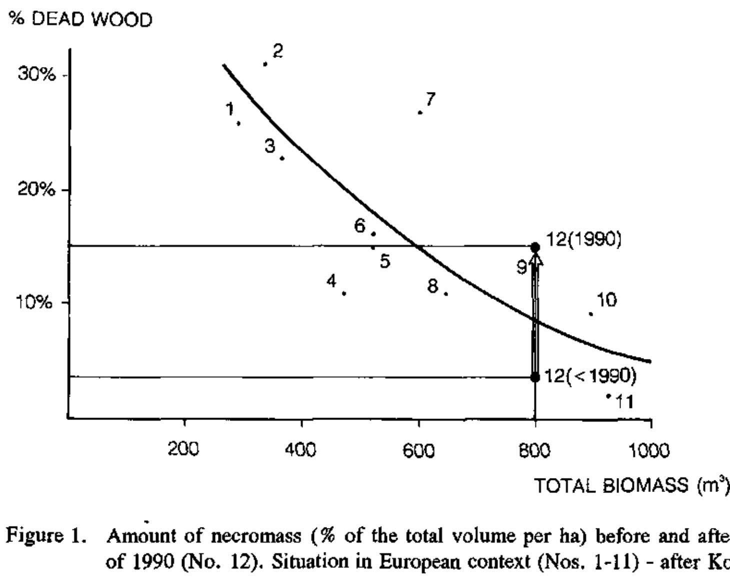

Figure 1. Amount of necromass (% of the total volume per ha) before and after the spring tempests of 1990 (No. 12). Situation in European context (Nos. 1-11) - after Koop (1983).

Table 2. Volume of necromass, before and after the spring tempests of 1990.

Tree species	1986		1990	
	$m^3.ha^{-1}$	%	$m^3.ha^{-1}$	%
Beech	28.2	96.9	109.5	376.3
Oak	0.9	3.1	1.3	4.5
Total	29.1	100.0	110.8	380.8

With regard to susceptibility to windthrow, no statistically significant influence of diameter, or of height, basal area or height:diameter ratio (levels of significance respectively : 0.63, 0.61, 0.11 and 0.62) - (Figure 2 a-d) could be detected.

Taking into account the exceptional force of the gales of spring 1990, the question arises of whether wind damage does not largely occur independently of stand characteristics but is more random, caused by local turbulence effects. In this context, the irregular canopy closure of the old stand (1986) must undoubtedly be seen as a factor decreasing storm stability, although windthrown trees are well scattered throughout the research area.

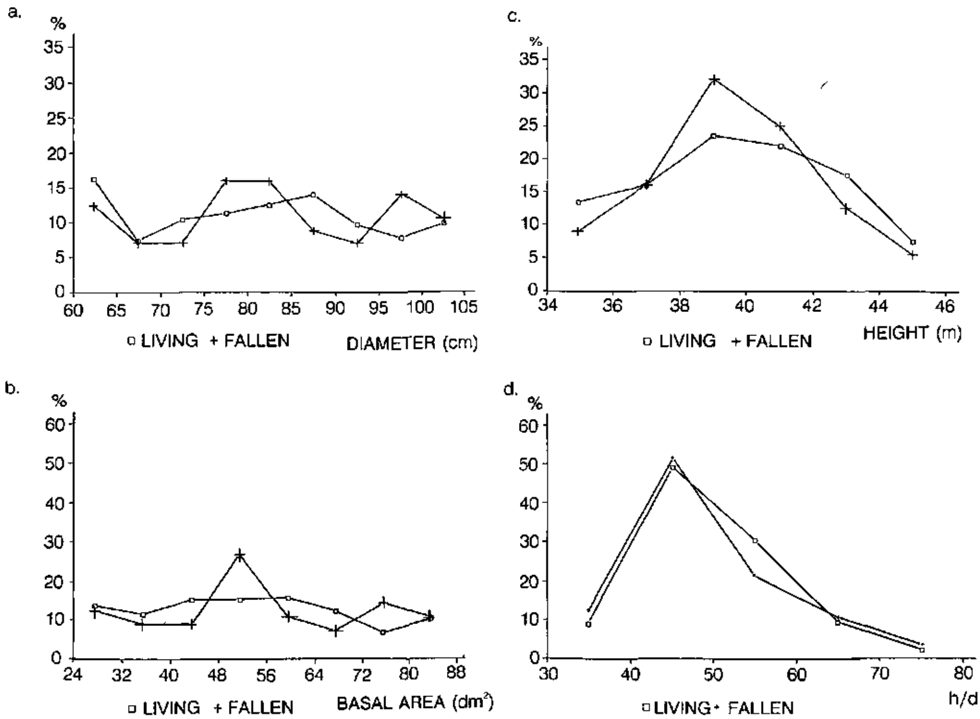

Figure 2a. Distribution of the fallen beeches in spring 1990 over diameter classes, compared with the distribution of 1986.

Figure 2b. Distribution of the fallen beeches in spring 1990 over height classes, compared with the distribution of 1986.

Figure 2c. Distribution of the fallen beeches in spring 1990 over basal area classes, compared with the distribution of 1986.

Figure 2d. Distribution of the fallen beeches in spring 1990 over h/d classes, compared with the distribution of 1986.

The vitality of the individual trees is still good, as can be deduced from the large current increment with regard to age and stem number (1986-1990 : 6.3 $m^3.ha^{-1}.yr^{-1}$); stem disk analysis shows a steady gauge of annual rings throughout the last 100 years.

Diameter class distribution (Figure 3) is quite symmetrical, indicating a vital population. So it can be expected that diameter growth will continue for a long time hence, in contrast with height growth.

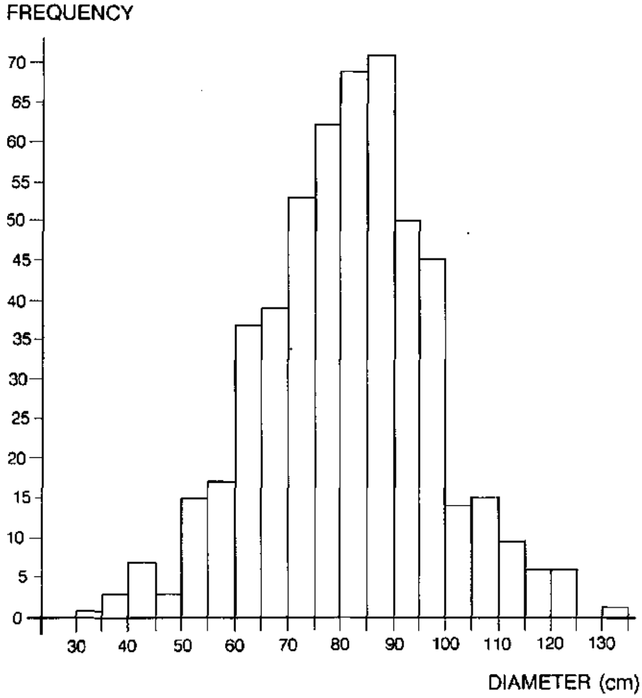

Figure 3. Diameter class distribution for beech, 1986.

Conclusions

It can be concluded that the vitality of the trees is still good at an age of 215 years, resulting in a steady structural change expressed as diameter growth.

Severe gales appear to be the forces driving actual stand dynamics, creating canopy gaps of different sizes and enabling a new surge of regeneration.

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Conversion management towards more natural forests: evaluation and recommendations

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Summary

In The Netherlands almost all forests are planted, but the demand for more natural forests is increasing. A conversion management can accelerate the development from a planted forest towards a more natural forest.

Several methods of conversion management are evaluated and recommendations for conversion managament are given.

Keywords: conversion management, natural forest

Introduction

In The Netherlands almost all forests have been planted and the demand for more natural forests is increasing. In the very long term more natural forests will develop spontaneously if plantations are not managed. However, research in European forest reserves has revealed that it takes several generations of trees before an uneven-aged population of trees has developed spontaneously (Koop, 1986). Therefore it takes centuries for a plantation to change into the uneven-aged mosaic of forest patches which is characteristic of natural forests (Koop 1981a, 1981b).

As long as the first even-aged generation of trees forms a closed tree canopy, a new generation of trees will be prevented from establishing. The second generation of trees can only establish if the first-generation stand collapses. Studies on old spontaneously recolonized clearings have shown that the first collapse phase is restricted in time to several decades, and occurs over the whole area of the previous regeneration unit. Measured against the maximum potential longevity of trees under natural conditions, the differences in tree age in the second generation are small.

The more tree species with a potentially different maximum lifespan there are in the second generation, the less the first-generation homogeneity will be transmitted to the second generation. Tree falls caused by storm and disease are spread over time, so in the long run the regeneration waves will be interrupted and cease, just as simulated by the gap-model of Bormann and Likens (1979).

In the case of beech-dominated sites in The Netherlands, the natural reference site of the historically documented 1372 clearcut in the forest of Fontainebleau is very relevant and confirms the validity of the predictions mentioned above. Only now as the second generation is being replaced by the third, have the processes of collapse and regeneration spread in space and time. At the moment, all size classes including dead trees and open phases are represented next to each other in the forest mosaic. In terms of age classes, however, after more than 600 years the population structure is still discontinuous and shows a regeneration gap of 150 years (Koop, 1989).

The need for conversion management

Many species depend on certain phases in the forest developmental cycle. Specific plant and animal species, such as fungi, woodpeckers and larvae of certain large beetles depend on dead wood. Some ants depend on canopy gaps, and bird and insect species may depend on the edges between gaps, young forest and old forest. Only a mature mosaic offers favourable conditions within easy reach of these species every year, enabling them to develop viable populations. Hence ecological values in terms of biodiversity largely depend on the mature forest mosaic. If intervention is avoided, this state will only be reached after a very long time. A method of active conversion management is needed to shorten this time.

Evaluation of the first examples of conversion management

In order to obtain a more natural forest, since 1980 different kinds of conversion management have been practised in planted forests on poor sandy soils in The Netherlands. The effectiveness of this conversion management so far has been evaluated by Koop et al. (1990) and Siebel (1992). Forest structure and species composition after management measures were monitored with the SILVI-STAR monitoring system (Koop, 1989) and compared with those of more natural forests. The conversion management measures studied were:
- various intensities of thinning throughout the original stand;
- making gaps of various sizes by cutting clusters of trees.

The conclusions to be drawn on the basis of the evaluation are:
- Thinning too many trees spread over a great part of the original stand causes trees to rejuvenate almost everywhere. The opportunity of partitioning the even-aged stand into a mosaic of uneven-aged developmental phases similar to the mosaics in more natural forests will be lost. Therefore, initially the canopy should be kept as closed as possible in most of the stand, to prevent an even-aged regeneration of the stand as a whole.
- Making gaps of variable size is the best management measure to accelerate development towards a more natural mosaic.
- Small gaps less than half the tree height are rapidly filled by the crown expansions of neighbouring trees and therefore have little effect on rejuvenation.
- The trees were cut down using chain saws, or were pulled down or pushed over by machines. A preliminary evaluation indicates that pulling trees down or pushing them over is hardly worth the extra costs, because sooner or later after the original stand homogeneity has been fragmented, spontaneous uprooting by wind will take place as well. Storms caused additional tree falls, especially at the edges of gaps, but there were no severe losses of trees in the original stands (Figure 1).
- Attempts to reduce the role of exotic deciduous species like *Prunus serotina* and *Quercus rubra* at the same time in mixed stands often fail when these species are dominant. Under conditions of sufficient light supply they easily recover from cutting and large numbers of seedlings emerge from the seedbank. Therefore these species should be diminished by individual cutting or ringing before bigger gaps are made and light conditions for rejuvenation are improved.
- The rapid establishment of a dense herb layer by species like *Pteridium aquilinum*, *Rubus fruticosus* or *Urtica dioica* depending on the forest type may delay tree rejuvenation and thereby retard the development of an uneven-aged forest mosaic.
- Forest grazing may also delay rejuvenation in canopy gaps. If there are few canopy gaps, they may be grazed too heavily.

Guidelines for conversion management

The main goals of conversion management are:
- to create a better starting point for spontaneous forest dynamics than the existent homogeneous man-made plantations;
- to speed up development towards a mature mosaic as a condition for greater biodiversity.

The conversion management that involves making canopy gaps of various sizes is most effective.

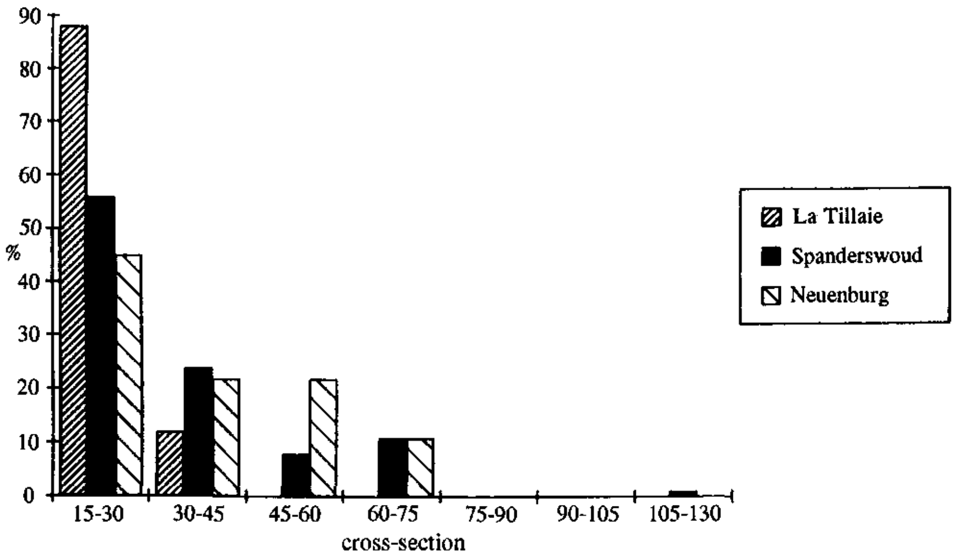

Figure 1. Size distribution in m diameter of canopy gaps in the natural reference forest of Fontainebleau in France (after Faille et al., 1984) and the Neuenburg Urwald in Northern Germany (after Koop, 1981) and the conversion management experiment in the Spanderswoud in The Netherlands (after Siebel, 1992).

The number of gaps per ha and the size distribution of gap is derived from size distributions of regenerating patches in natural forest mosaics on comparable site types. Only a few big gaps of up to three times tree height and progressively more smaller gaps of half to twice tree height are planned (Figure 2). The smallest canopy gaps are ignored because they are rapidly filled by neighbouring trees. If there is rapid establishment of dense herb layers, which delay rejuvenation, the biggest gaps may also be ignored.

Thus canopy gaps are made over 10-15% of the surface. Existent canopy gaps, such as windthrows, are incorporated in the target percentage of canopy gaps and are sometimes enlarged. By planning new canopy gaps on the edge of forest stands and over forest roads the man-made pattern of stands is deliberately erased.

The other parts of the planted stand are kept as closed as possible. Thus in some places natural regeneration of trees is stimulated and in others it is suppressed. In a later phase new canopy gaps may occur spontaneously in the closed parts of the forest, or can be made. This increases the differentiation in age classes of regeneration. Exotic conifer tree species can be eliminated by planning canopy gaps in patches that have large numbers of these trees.

One-third of the felled trees, the thickest, are left as dead wood on the forest floor after being felled or as standing dead wood after being ringed. The rest of the trees are harvested. The extraction of trees is justified by the fact that in natural forests thick trees form the important slowly decaying dead wood compartment that is the habitat for certain species, but most of the forest floor in canopy gaps is not covered by dead wood. A practical argument is that harvesting some of the trees allows at least part of the cost of conversion management to be recouped. The trees can be cut by chain saw or can be pulled down or pushed over by machines (Van der Burg and de Vries, 1992)

Whether subsequent treatments are necessary after 10 to 15 years depends upon further spontaneous partitioning of the stand by windthrow. The criterion is that 10-15% of the stand should be in an open phase (less than 2 m tall). If a larger area is already open because it has been prone to spontaneous collapse, no extra treatment is necessary. Successive treatments should be continued until an area of 50% of the original planted stand has been converted by making

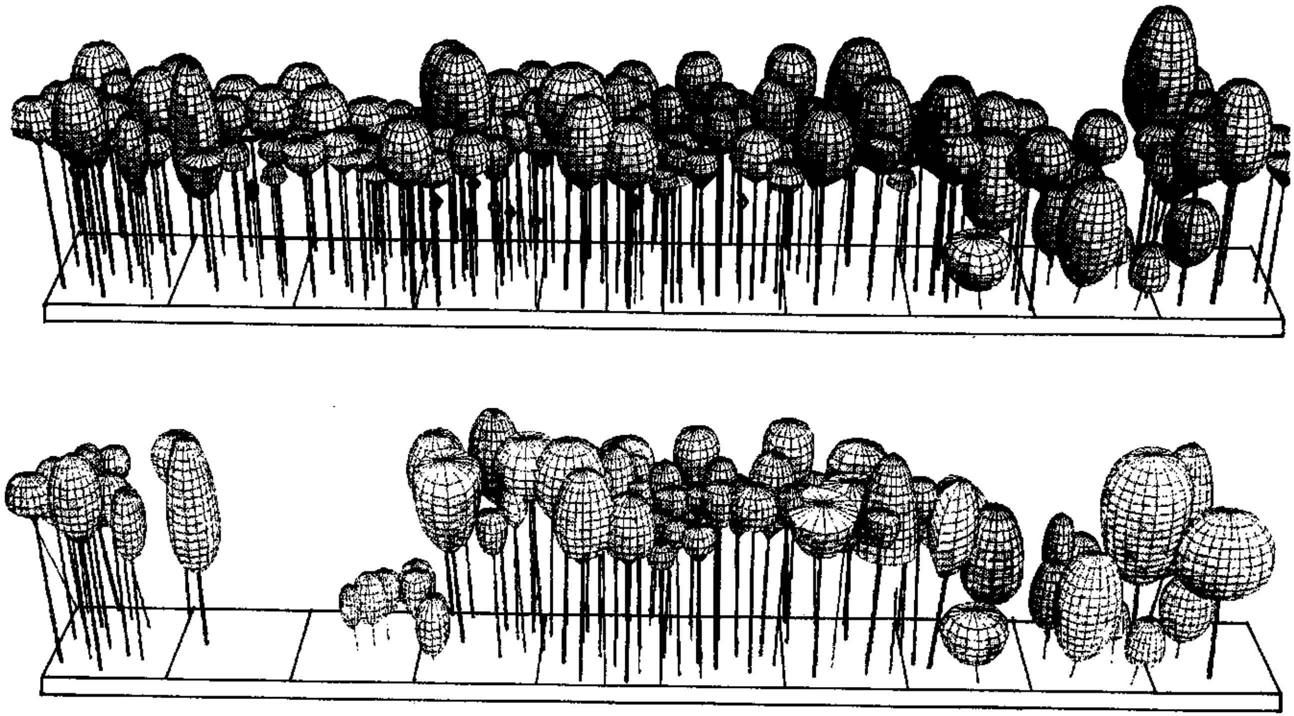

Figure 2a. Example of a transect in which forest development after conversion management measures is being monitored according to the SILVI-STAR system. Changes in forest structure in a young Pinus stand (Spanderswoud, The Netherlands). In 1982 a small clearing was made at the beginning of the transect, and at the end of the transect Pinus trees were cut where young oaks (Q) and birches (B) were growing (after Siebel, 1992).
1982 reconstruction (upper 3D drawing)
1991 reconstruction (lower 3D drawing)

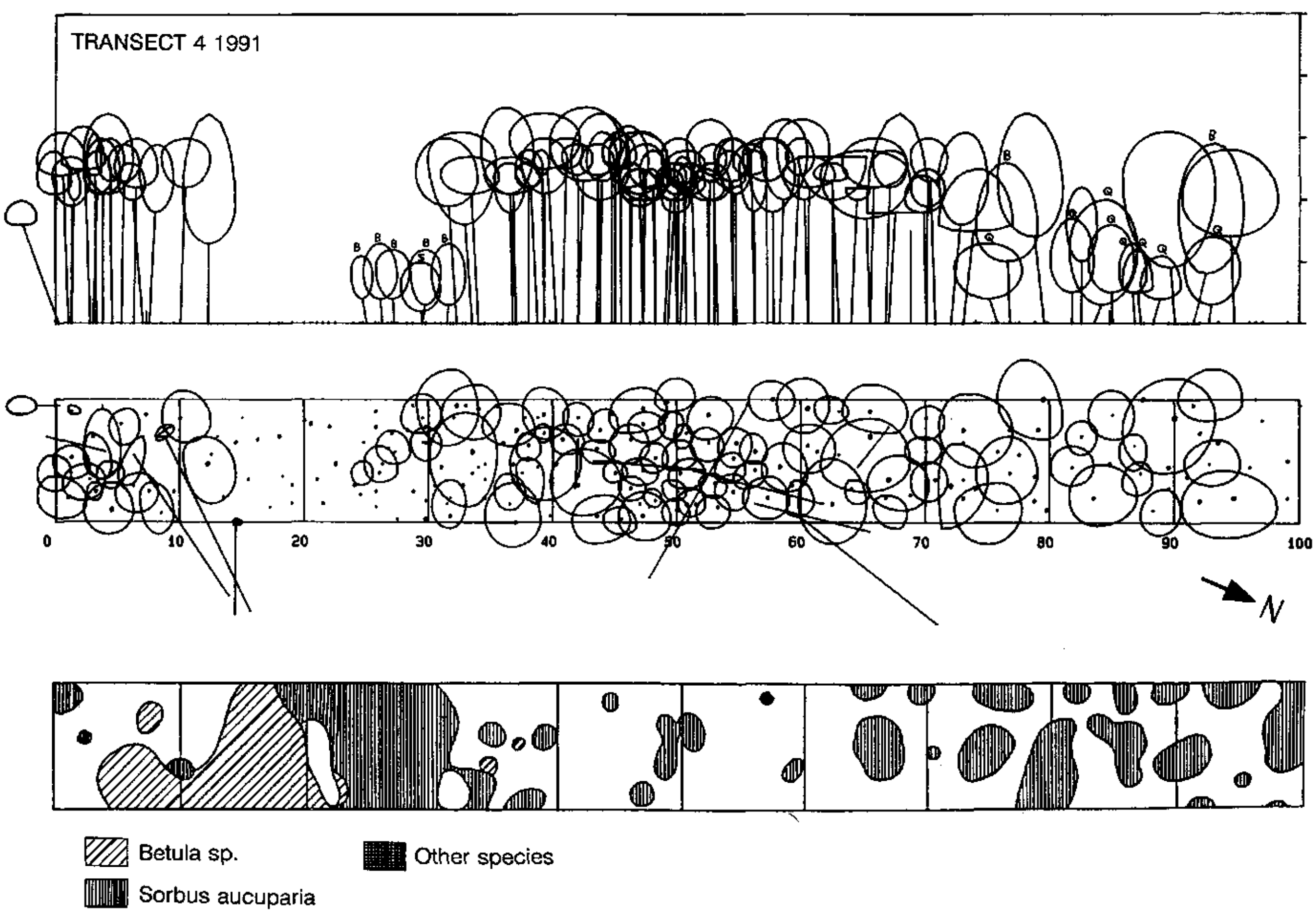

Figure 2b. Ground plan, side view and pattern of rejuvenation of the same transect as in Figure 2a. Variation in developmental phases is emerging.

canopy gaps. The 50% remaining by then is fragmented by the man-made or spontaneous gaps into a patchwork of varying coherence. This remaining part will collapse as the whole stand would have done without conversion management. But now half of the stand already consists of a mosaic of forest patches of different age.

New experiments and demonstration projects

Experiments in the conversion management described above have been carried out in Scots pine (*Pinus sylvestris*) plantations, which cover large areas in The Netherlands, in three nature reserves scattered throughout the country (Koop and Hilgen 1992; Van der Burgh and de Vries, 1992). Another experiment is under way in old beech woodland. These experiments are being used as demonstrations for forest managers. Information on conversion management is available from the National Reference Centre for Nature, Forest, Landscape and Fauna (IKC-NBLF) of the Ministry of Agriculture, Nature Management and Fisheries.

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Maximizing woodland conservation value through management

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Summary

The site history of Burnham Beeches is described. This deciduous forest consisting mainly of beech and oak has been managed and grazed for a long time. When management was abandoned the structure of the forest and also the species composition changed. In the last 10 years management specifically for conservation has been established which will also return the site to its former appearances.

Keywords: woodland management, nature conservation, pollarding

Introduction

Of the land surface in Britain 10% is wooded but only 1.5% of this is ancient semi-natural woodland (Peterken, 1991). These woods are believed to originate in or before the sixteenth century. Many different organisms, both plants and animals, have been identified as indicator species which can be used to distinguish such woodlands. But, in a country with such a high population density as Britain, no woodlands can claim to be untouched by the influence of man. Prehistoric clearance of trees gave way to the active management of woods as a renewable resource for timber, fodder etc. which was prevalent during the mediaeval period. The history of Britain has been punctuated by events which directly or indirectly affected the woodlands. Wars have had a great impact, with timber being required for ships during the Spanish Armada and for pit props during the world wars. In peace times the management of trees for domestic use has had a pronounced effect on the landscape.

Burnham Beeches: its vegetational history

Burnham Beeches is an ancient woodland just 40 km west of London. It is owned by the Corporation of London who provide the funding to manage it both as a public open space and as an area of high conservation value. The influence of man has had a profound impact on the character of the woodland. It is due to this influence that the site is so valuable in terms of nature conservation.

Burnham Beeches is 240 ha in area and, until approximately 100 years ago, almost all of it was grazed by cattle, sheep and pigs. The northern two- thirds of the site was a mixture of different woodland types. Dominated by *Fagus sylvaticus* with *Quercus petraea* and *Quercus robur* in places, parts were managed as standard woodland, parts as coppice (from which stock were excluded at least at certain times) and approximately 100 ha as wood pasture. The wood pasture consisted of pollarded *Fagus* and *Quercus* with grazing land underneath. A pollard is a tree cut just above head height on a 12-15 year cycle. This produces a crop of timber, like coppicing, but the new shoots are above the reach of the grazing animals. At the peak there were probably around 3000 pollards at Burnham Beeches (Le Sueur, 1931). The act of pollarding rejuvenates the tree, allowing it to live for hundreds of years if cut regularly. The great age of the trees and their physical shape makes them ideal habitats for numerous invertebrates and lower plants.

The southern part of the site was more open than the north and was a mixture of heathland and acid bogs. The heathers (*Calluna vulgaris* and *Erica tetralix*) were widespread, *Juniperus communis* was abundant in the drier areas and *Sphagnum* and various wetland plants dominated the bog areas. Along with these plant communities were the associated fauna. Birds such as the nightjar and nightingale bred on the site, the population of adders was healthy and many rare invertebrates were to be found. There are detailed descriptions from Victorian times (e.g. Grote, 1858; Forbes, 1898), outlining the appearances of the different areas and in addition there are many paintings and early black and white photographs. Lists from visiting naturalists give an impression of the plant and animal life and Druce (1926) gives a detailed list of plants in his county flora.

As fossil fuels became more readily available and the transportation networks improved, the need for wood decreased and pollarding and coppicing ceased. Fewer people kept domestic animals and grazing also finally ceased. The lack of woodland management and grazing has had a significant impact on Burnham Beeches. Encroachment of pioneer species e.g. *Pinus sylvestris* and *Betula spp.* took place and by 1986 all the bog and heath areas had become overgrown, with just patches of *Sphagnum* or heather remaining under the trees. The wood pasture was equally overgrown with very few grassland species to be seen. The neglected pollards, left uncut for nearly 200 years, were mostly hollow stems at risk of being pulled apart by the heavy branches on top. The number of pollards had declined to around 500-600. The site was managed as a public

Figure 1. Pollards which have not been cut for approximately 200 years with much secondary woodland surrounding them.

park for recreation with conservation measures being incidental. Many of the rare or locally important plants and animals had been lost or were at very low populations. A change in personnel led to increased awareness of the value of the site for conservation. Restoration of the various habitats was initiated along with survey and monitoring work. Non-management of the site would have led to a predictable result: Loss of the wetlands due to drying out by tree evapotranspiration, loss of heathland by shading out, loss of wood pasture by encroachment of pioneer tree species and collapse of pollards, and, overgrowth of coppice losing the characteristic ground flora. In addition, holly (*Ilex aquifolium*) previously kept down by grazing is increasing in the south of the site. It shades out all other ground flora and produces very sterile conditions. *Rhododendron ponticum*, planted in the north of the site in Victorian times is also spreading dramatically and has the same effect as the holly.

Recent survey work has shown that Burnham Beeches is very important for saproxylic invertebrates. Being in the top 10 sites in Britain it is also very valuable for bryophytes, lichens and fungi. (See Harding and Rose, 1986 for further discussion of the conservation status of pasture woodlands). This high value can only be maintained by management; indeed, managing will probably further increase the status of the site.

Figure 2. Trees repollarded in 1989. Large limbs have been removed but smaller branches have been retained. The secondary woodland has been cleared from around them.

Present management

Because of the interest in maintaining a diversity of habitats on the site and in order not to lose any more of the unusual species, a policy of intensive management is being employed. This is not viewed as being detrimental, rather it is essential if the woodland is to retain any of the characteristics for which it is famous - it is possible to manage a site actively for conservation. Peterken (1991) comments that, 'Due to neglect of traditional management, most woods are now probably less diverse than they were.'

In the last six years the following work has been undertaken at Burnham Beeches:

1. Heath clearance - 3 ha cleared so far round the existing 16 *Juniperus communis* trees resulting in increased growth and fruiting. Small patches of heather are now expanding and the adder population is increasing. Further clearance is planned.
2. Wetland clearance - 3 ha cleared so far of invading trees resulting in immediate growth by *Sphagnum*, reappearance of species e.g. *Narthecium ossifragum* and *Eleocharis multicaulis* the latter not recorded on the site since Druce (1926). Further clearance is planned.
3. Reintroduction of hazel coppice rotations, resulting in increased populations of spring flowers, e.g. *Primula vulgaris*, *Viola sp.* etc.
4. Reintroduction of pollarding and restoration of wood pasture.

The reintroduction of pollarding is the most difficult part to undertake. There are very few written records of how woodland pollarding was carried out and, in addition, the trees had not been cut for nearly 200 years making the task considerably more difficult. Experimental work was carried out in an area of young *Fagus*. The experience gained was then employed in recutting the ancient trees. Success is now very good in both groups of trees. The two most important factors influencing success seem to be:

1. amount of light reaching the canopy;
2. amount of canopy removed during cutting.

Thus, encroaching scrub and small trees are removed from round the pollards at the time of cutting. Some limbs are always retained on the tree, even in young individuals. In the old trees only the large branches are removed and the smaller, younger branches are retained.

The next step is to reintroduce grazing and this is planned initially for a 6 ha plot within the old wood pasture area. In time this should encourage a range of grasses and herbs and help to restore the habitat to that illustrated in some of the old prints. If the grazing proves successful, much more of the site will be put under this form of management in the future.

Of course parts of the site will not be managed so intensively and will be left as woodland stands of *Fagus* or *Quercus* and some as areas of secondary woodland with *Betula spp.*, *Sorbus aucuparia*, etc. Detailed monitoring of vegetation and invertebrates is being carried out during the restoration work.

The plans for management include some elements which are not strictly of a 'woodland' nature, i.e. wetland restoration. However, these habitats are an integral part of an essentially woodland site. By managing the whole area the conservation status of the site will be maintained and increased. The site will also become more interesting for visitors. Lack of management would lead to a far less diverse woodland with an understorey primarily of holly and *Rhododendron*. Coupled with this would be an inevitable loss of plant and invertebrate species.

Conclusions

Nearly all woodlands of high conservation value in Britain have such a status because of their active management, either present or past. In a highly industrialized country such as England so many environmental conditions have changed, pollution levels have risen and water tables have dropped, so that it is just not possible to consider returning the woodlands to their wild wood state. In fact, the practice of pollarding native trees, leaving the resulting timber to decay naturally and introducing large herbivores at low densities must be nearer to the wild wood scenario than a woodland dominated by aliens such as *Acer pseudoplanatus* or *Pseudotsuga menziesii* with an understorey of *Rhododendron*.

Forest reserves/non-intervention areas

The expression 'forest reserve' is a rather unfortunate one which has become adopted in much of Europe to mean an area of non-intervention management. A reserve is a term applied to an area kept for special use and, strictly speaking, a Forest in English is a piece of ground (not necessarily woodland) owned, or previously owned, by the King/Queen and maintained for hunting particularly deer.

The term non-intervention can mean a variety of different things according to the situation, e.g. from almost total non-interference for example in the Sasso Fratino Reserve in Italy of 764 ha with a buffer area of woodland of 4574 ha surrounding it where limited access is granted to a few scientists only, to small areas in Britain and The Netherlands where free access is possible and other activities, e.g. hunting, may take place.

One important point to remember is that non-intervention areas are not necessarily synonymous with conservation areas. A conservation area is somewhere 'containing a noteworthy environment and specially protected by law against undesirable changes' (Oxford English Dictionary, 1991). Non-intervention areas are not necessarily important in conservation terms when they are designated and the changes that take place may at times be undesirable.

Non-intervention areas may be politically useful in maintaining patches of woodlands which would otherwise be lost to agriculture or development, but certainly in many instances management is more valuable than non-management, as long as it is aimed at increasing/maintaining the conservation status of the site.

Watkins (1990) has pointed out that 'managed woods usually contain a richer variety of habitats within a limited area and thus more species than unmanaged woods.' Rackham (1976), commenting about woodland management, said that, 'To do nothing is seldom the best conservation policy'. He goes on to say that it may often be second best but, where resources are limited, a compromise may be to manage at least part of the site in an appropriate way.

Burnham Beeches is considered to be an area of high conservation value due to its complex mosaic of habitats, many of which are in decline in southern Britain, and its increasing list of rare invertebrates, fungi and plants. Non-intervention would cause some very 'undesirable' changes to take place and cause a significant decrease in conservation value. This is true for large numbers of woodlands. Management does not necessarily mean planting even-aged trees in rows and spraying all the undergrowth. It can mean creating the right environment for threatened species.

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Forest development in relation to forest grazing

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Summary

A deterministic simulation model that describes forest succession on dry sandy soils in The Netherlands under various grazing pressures is being developed. The simulation model will be used to evaluate the prospects of using large herbivores to develop and maintain open woodlands on poor sandy soils. Within the same project a clipping experiment is in progress to quantify the effect of defoliation on the growth and mortality of oak and beech seedlings. This article reviews the different parts of the project.

Keywords: forest development, forest grazing, modelling, regeneration

Introduction

The project 'Forest development in relation to forest grazing' is part of the Research Programme on Forest Grazing, which is a joint research project of the Institute of Forestry and Nature Research (IBN-DLO), Wageningen Agricultural University and the Winand Staring Centre for Integrated Land, Soil and Water Research (SC-DLO). The main aim of the Research Programme on Forest Grazing is to investigate whether large herbivores (roe deer, red deer, Highland cattle, ponies) can be used as a management tool to develop and maintain open woodlands on dry sandy soils in The Netherlands. The project, which began in 1991 and will run until 1995, is partly funded by the Ministry of Agriculture, Nature Management and Fisheries.

The project includes subprojects on the most important processes in the herbivore-forest system. Experiments are being done on animal condition, food selection, food requirement, natural regeneration and effects of trampling. A food preference model is being tested in the field in 30 ha compartments with one species of herbivore per enclosure. Habitat use is monitored by radio tracking in a large enclosure of 1200 ha and in the same enclosure interspecific relations between the different herbivore species are being studied.

The project puts great emphasis on a quantitative description of the processes which play a role in forest development under the influence of herbivores. The processes are being integrated in a simulation model, which describes the forest development on dry sandy soils under various grazing pressures.

Forest grazing

The success of using large herbivores as a management tool in forest ecosystems is mainly determined by the influence of the herbivore on the natural regeneration. This effect on natural regeneration is being studied in the subproject 'Forest development in relation to forest grazing'.

Grazing by large herbivores increases the mortality of the seedlings. It is hypothezised that on the dry sandy soils in The Netherlands the survival of oak seedlings is crucial for forest to develop from pioneer conifers to mixed deciduous stands. Survival of the oak seedlings will thus be the critical factor determining the maximum allowable grazing pressure.

The main aim of this subproject is to create a simulation model which describes forest succession under various grazing pressures. In addition, clipping experiments are being done, in an attempt to quantify the effect of grazing on the growth and mortality of seedlings.

Development of the simulation model

The simulation approach describing forest succession under different grazing pressures consists of three submodels. Figure 1 illustrates the main interactions between herbivore, forest and soil, together with the corresponding submodels.

The forest succession model describes the forest succession on dry sandy soils in The Netherlands. The model is based on existing models of forest dynamics (see Bartelink, 1990), using the JABOWA/FORET approach (Botkin et al, 1972; Shugart, 1984; Shugart and West, 1977). In these so-called GAP-models, forest dynamics is based on the growth and mortality of individual trees. The forest succession model differs from existing succession models in being more explanatory, because population dynamic processes such as natural regeneration, growth and mortality are quantified on the basis of physiological processes. Experiments are in progress to quantify the influence of light and moisture on the growth and mortality of seedlings. The growth of individual trees is based on light interception, whole-tree carbon balance and assimilate allocation.

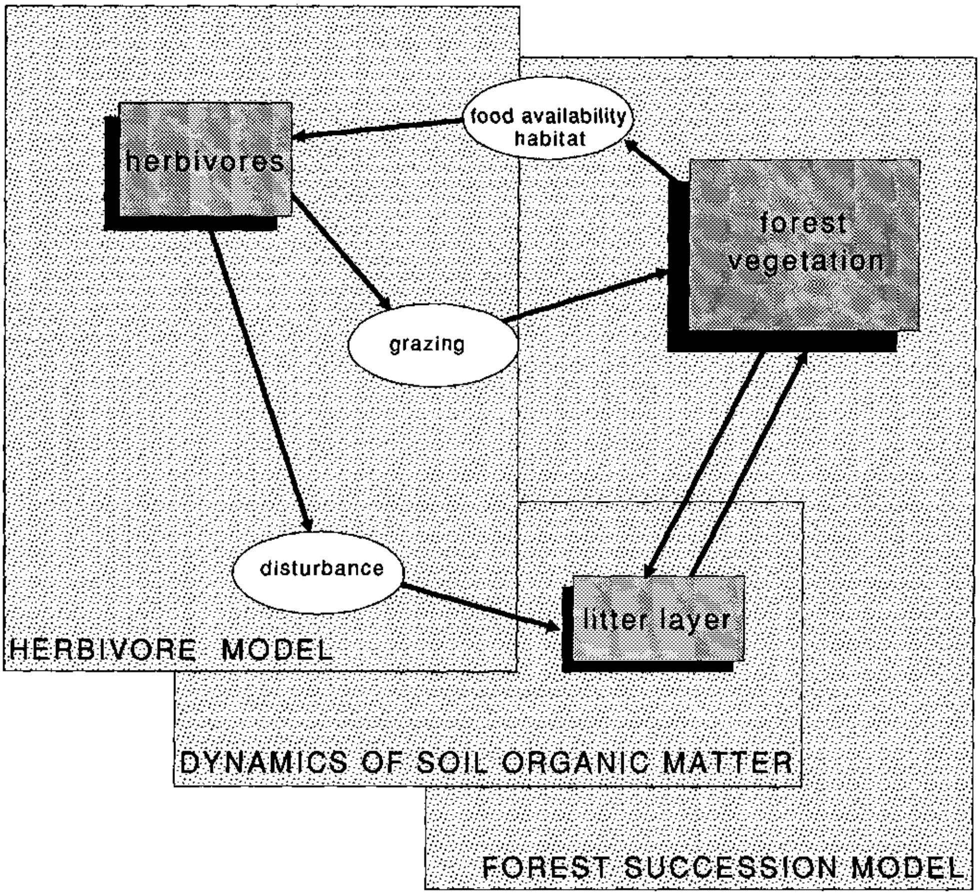

Figure 1. Main interactions between herbivores, the forest and the litter layer, together with the corresponding submodels.

The herbivore model, which is being developed in collaboration with the Wageningen Agricultural University subproject 'Diet choice in large herbivores' describes the diet choice and food intake per herbivore species in various forest ecosystems. The most important interactions between forest succession model and the herbivore model are food consumption in relation to food supply and the effect of grazing on the growth and mortality of the seedlings (see clipping experiment).

The third model describes the dynamics of soil organic matter, which quantifies the effect of trampling by herbivores on the mineralization rate of dead organic matter. The model is being developed jointly with the Winand Staring Centre (SC-DLO). The influence of the changed mineralization rate on growth of the trees forms the interaction between the soil dynamics model and the forest succession model.

The clipping experiment

The effects of grazing on mortality of the regeneration are being quantified by clipping experiments. From 1991 to 1993 more than 2000 seedlings of oak and beech are being defoliated to different degrees at three different light levels. The effects of defoliation on height growth, diameter increment, biomass production and dry matter distribution are being studied. The study aims to describe the cumulative amount of foliage removed and the reduction in growth and in mortality. The results of this experiment will be available in 1994.

Expected results

The simulation model will be used to study forest development under different circumstances. By varying initial forest type, site quality, herbivore species and number of herbivores, the model can be used to shed light on the possible role of herbivores in creating or maintaining open woodlands. The results of this study will be published in 1995.

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An unmanaged forest - research strategy and structure and dynamics

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Keywords: forest reserves, forest ecosystem, methodology, inventory, monitoring and research methods, eco-silvicultural analysis

Introduction

The new Flemish Forest Decree, issued in 1991, enables forest reserves to be established within the present forest area, and emphasizes their scientific function (outdoor laboratories). There are no forest reserves in Flanders. However, a proposal for the establishment of about 30 reserves (potential forest reserves) has been formulated.

A major problem is the lack of a scientifically based, relevant and feasible research methodology that would enable:
- a reconnaissance survey;
- continuous monitoring;
- more thorough research on the future forest reserves.

Our research area, also designated as potential forest reserve, can therefore be regarded as a test-case aiming at an evaluation of a broad spectrum of research techniques (methodological research).

In view of the unusual character of the research area (no management for the last 50 years), the methodological research is linked to an eco-silvicultural analysis of the present forest vegetation, aiming at a more thorough understanding of the self-regulating processes operating in very complex forest structures.

Description of the study area

The research area is situated in the central part of Belgium (Flanders - province of Brabant - Forest of Liedekerke). The sampled forest ecosystem covers 23 ha and varies in elevation between 24 and 36 m a.s.l. It is bordered by the forest of Liedekerke (54 ha) on the west and north and by pasture and farmland on the east and south.

A moderately wet, loamy soil occurs throughout the forest, together with some very wet fragments (brook valley, phenomena produced by reduction). The meso-relief is rather uniform, except for some local depressions.

The forest vegetation is of the coppice-with-standards type and belongs to the Querco-betuletum typico-coryletosum (Quercion). The main tree species are birch, pedunculate oak, northern red oak, aspen, willow, sweet chestnut, yellow locust and black and speckled alder. They are accompanied by secondary species, mainly in the lower tree layer: ash, hazel, hawthorn, buckthorn, black cherry and mountain ash.

The present forest is a remnant of the ancient Carbonaria Sylva (coal forest). Until the middle of this century it was subjected to regular coppicing and was characterized by the occurrence of heath over 40 % of the surface. The most recent human intervention dates back to World War II and consisted of widespread felling by the local population (because firewood was in scarce supply). The ecosystem has remained unmanaged ever since and showed:
- a steady regression of the heath vegetation, culminating in its disappearance in 1970;

- a progression of coppice elements into the higher tree stratum resulting in a standard forest with few coppices.

Research aims

The research strategy has two main aims.

I. An objective and critical evaluation of the research techniques most commonly used as methods for stand diagnosis, paying special attention to criteria such as applicability and relevance in relation to the object being studied (relatively untreated and very complex forest structures).

Three major techniques are being applied and compared:

1. Sampling plots. Variable parameters are the area, shape, pattern and number of plots.
2. Line transect. Variable parameters are the length, orientation and spacing of the lines.
3. Band transects. The same variables are considered as with the line transects, adding the width of the strips as variable parameter.

The most appropriate sampling strategy and/or the ideal combination is searched for, leading to an optimal compromise between accuracy, relevance and feasibility (i.e. labour investment). Secondly, the nature and number of parameters to be recorded are studied within each type of sampling unit. The possible parameters are: coordinates of stem-base, DBH, total tree height, inclination of stem, crown centre, height of crown base, height of maximum crown width, crown projection (number of radii), qualitative tree classification, photographs of the forest canopy taken looking up from the forest floor.

A modified computer software package is being developed to handle the data. It aims to:

- automate the drawing of the horizontal and vertical forest profiles;
- enable a computer-aided simulation of the hemispherical images of the forest canopy.

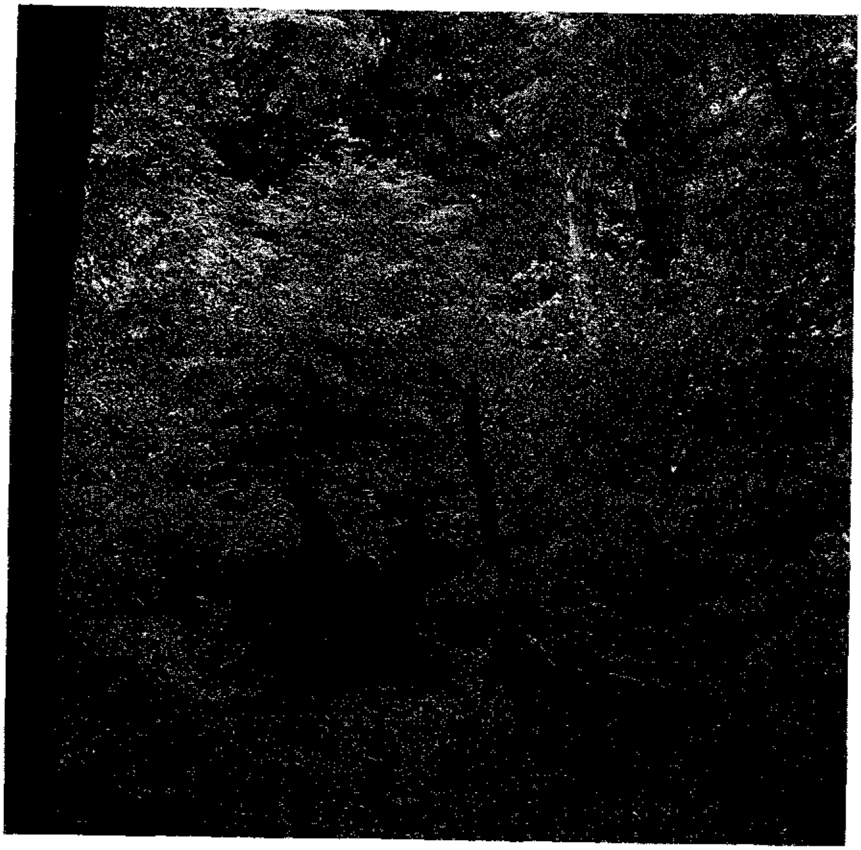
II. Eco-silvicultural analyses of the forest ecosystem. This focuses on:

1. Forest architecture: vertical and horizontal stratification - presence and scale of mosaic structure - repartition of biomass and necromass - grouping of trees in structural cells.
2. Forest dynamics: shifting mosaic structure - occurrence, frequency and scale of forest perturbations - temporal and spatial continuity of forest regeneration - occurrence of regeneration waves - gap dynamics - build-up of biomass and necromass1. build-up.
3. Forest stability: relation with individual tree stability related to the tree's dimensions, age and social position - stabilizing effect of cluster structure.
4. Quantification of competitive stress in the horizontal and vertical planes - relevance of indices - relation to easily measurable stand parameters.
5. Quantification of light climate: control and calibration of crown measurements by means of hemispherical photographs (computer-aided simulation of photographs, based on crown measurements and tree position) - indicative value of easily measurable stand characteristics.
6. Tree physiology: assimilatory efficiency with reference to species and social position.
7. Transferability of research findings to management of forest reserves and non-reserve forest stands.

The above mentioned research forms part of a Ph-D study. Therefore results are not available at this moment. A list of references could be obtained from the author.

Chapter 5

Historical and environmental impacts on forest dynamics



Neuenburg - potentially natural forest.

The Neuenburger forest (Germany) is a forest area of 627 ha. For 100 years the forest has developed practically undisturbed. The forest consists of indigenous tree species. The soil has largely been left undisturbed and has always been under forest. Since the end of the Middle Ages the forest development has been influenced by the selective logging of hornbeam and beech, the planting of oaks, and by fires, the removal of litter, and intensive grazing. In 1870 part of the area was designated as a reserve. In 1947 half of this reserve was felled for firewood in a crisis due to a shortage of coal. In order to restore the character of the old grazed forest as a cultural monument, beeches were felled in 1970 to make space for old oaks, and young oaks were also planted. Though, strictly speaking, this is not natural forest, it comes very close to the potential natural vegetation. Therefore the area is given as an example of the natural forest vegetation of the North-West European climatic zone.

Effects of site history on woodland vegetation

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Summary

An attempt is made to review some of the effects of site history on the composition and diversity of temperate deciduous forests and their communities. An analysis of the dispersal of ancient European woodland species emphasizes the importance of short-distance dispersal. Although they show a unique response to former land use and other variables (e.g. forest area), all ancient woodland species have a slow rate of colonization. The colonization or recolonization of ancient woodland species in recent forests is hampered by surrounding vegetation (e.g. competitive species like *Urtica dioica*) and by the isolation of the forest patches. This is particularly true of forests in agricultural landscapes. Woodland species at the edge of their range tend to favour the largest forests. Former land use largely determines which species are present, but not necessarily their numbers. However, the number of true woodland species differs significantly between ancient and recent forests. Plant communities from ancient and recent forests are very dissimilar and their richness in true woodland species depends not only on soil features but also on former land use. In Flanders the subregional richness in field layer woodland species has deep roots in the past. The current richness correlates significantly with the afforestation rate of the 14th century. The richness in true woodland species in combination with the forest communities observed and the forest area may be used as a key criterion when selecting future forest reserves. In the agricultural landscapes of Western Europe, the management of forests and of forest reserves should be placed in the broader perspective of integrated sustainable management of the landscape.

Keywords: site history, ancient woodland species, plant community, historical ecology

Introduction

Any changes in forest composition and the populations of the constituent plant species, whether they are a consequence of external factors (e.g. global changes in climate, in atmospheric chemistry, in land use) or of internal factors (e.g. changes in management, regeneration, successional changes) will involve and will at least partially depend on the success of dispersal, germination and establishment of species. The latter will also depend on the competition within and between species.

The outcome of these processes may change considerably due to the fragmentation of the forest area in many parts of world. Agriculture, urbanization and industry have strongly intensified and there has been an enormous increase in scale and/or area, particularly in Western Europe (Harms et al., 1987). Two primary effects of fragmentation are an alteration of the physical environment (e.g. microclimate, drainage) within and around the forest remnants and the isolation of each area from other remnant patches. All forest remnants are exposed to these physical and isolational changes to a greater or lesser degree. The effects are modified by the size, shape and position of the individual fragments in the landscape (Saunders et al., 1991).

Because of the longevity of woodland plant species and the long time required for forests to develop, it may take decades before decisive conclusions can be drawn from the direct study of changes in forests. In the meantime climate and other environmental changes may have occurred.

A combined and integrated historical/ecological study of forests and the landscape they are part of may yield valuable information on the spatial and temporal distribution patterns of species, forest communities and the forests (Rackham, 1980; Peterken, 1981; Hermy, 1992). Historical ecology gives an insight into the role and significance of site history for the present forests and their vegetation.

Here an attempt is made to illustrate some of the effects of site history on temperate deciduous forests. Most of the data come from the study of woodlands in Flanders (Hermy and Stieperaere, 1981; Hermy, 1985; Hermy, 1992; Tack et al., (unpubl.)), an intensively used region with a high population density, little forest cover and a complex history.

We will look at examples from four levels: the individual species (e.g. ancient woodland species), the community level, the biodiversity of forests and the regional level. Finally, some conclusions about the selection, development and management of forest reserves are briefly discussed.

The flora of ancient and recent woodlands

Much of Western Europe has been inhabited and extensively cultivated since pre-Roman times (Pounds, 1990). Forest area and its distribution have fluctuated continuously in response to the regional needs for agricultural land, the demand for forest products (fuelwood, timber, litter, acorns, etc.) and industrial needs (e.g. timber for pit props). Because of the importance of forest as a resource, some forest stability in terms of area and position in the landscape is likely. These woodlands under constant forest use are termed primary woodlands (Peterken, 1974; Rackham, 1980). Since evidence of the persistence of woodland on a site is difficult to collect, we prefer the term ancient woodland, suggesting the constant presence of woodland since a threshold date (for Flanders for pragmatic reasons the late 18th century; in England about 1600). Woodlands originating after this date are called recent woodlands; they usually originated from planting.

Ancient woodlands have usually had a long history of treatment as coppice or as coppice-with-standards. The naturalness of ancient woodlands has been reviewed thoroughly by Peterken (1977, 1981). Their field layer has never been planted and a modified original-natural composition has largely survived. Therefore Peterken (1977) called these woodlands past-natural, in contrast to future-natural woods of recent origin but with a spontaneous structure. Nowadays many ancient woodlands have become some form of high forest. Recent woods may have a similar artificial structure; poplars often dominate these woods in Flanders.

In terms of plant strategies (sensu Grime, 1979), temperate deciduous forests as final phases of succession have very many stress-tolerant plant species that are well adapted to a regular light-shade cycle. The traditional management, some form of coppice, favoured species adapted not only to cutting but also to a regular long light phase (rotation cycle) and may be responsible for the impressive displays of spring flowers e.g. *Anemone nemorosa, Hyacinthoides non-scripta, Primula elatior* and the dominance of *Corylus avellana* in the under storey. The regular cutting may be considered a disturbance (sensu Grime, 1979), stimulating more vigorous competitive species (*Vaccinium myrtillus, Pteridium aquilinum*). The flora in recent woods, particularly those of very recent origin, is often different: many more or less ruderal (e.g. *Lapsana communis, Galeopsis tetrahit*) and strongly competitive species *(Urtica dioica, Molinia caerulea, Rubus spp.*) dominate; non-woodland species are conspicuous. They are often favoured by the current, external conditions that cause an input of nitrogen and other "pollutants". Woodland fragmentation enhances the effects of these inputs.

So we expect large floristic differences between ancient and recent woodlands. Plant species with an affinity for ancient woodlands have been described at least from England, Belgium, The Netherlands, Poland and Czecho-Slovakia (Hermy, 1992). A review of that literature yields a list of about 90 woodland species having a strong affinity for ancient woodland (Table 1). This list is not complete since no data seem to be available from a large part of Europe. There is regional variation in the association of plant species and ancient woodland (Peterken, 1974; Rackham, 1980). To overcome the problem of the regional validity, a more general list of true woodland

Table 1. Preliminary review of the ancient woodland species mentioned in the European literature
Wood edge species have been omitted.
$ = Ancient woodland species in Flanders (as derived from Hermy 1985: 640 plots)
Freq.: Frequency of mentions in literature (max. = 10)

$ Species	Dispersal type	Freq.	$ Species	Dispersal type	Freq.
$ Acer campestre	ANE wood	3	Hordelymus europaeus	UNSP	1
Actaea spicata	END	2	$ Hyacinthoides non-scripta	BAR	7
Adoxa moschatellina	END	2	Isopyrum thalictroides	BAR	1
$ Allium ursinum	MYR	2	$ Lamium galeobdolon	MYR	6
$ Anemone nemorosa *	MYR	10	Lathraea squamaria	MYR	2
Anemone ranunculoides	MYR	1	Lathyrus vernus	END	1
Asarum europaeum	MYR	2	Luzula luzuloides *m	MYR	1
Asperula odorata	EPI	4	$ Luzula pilosa	MYR	5
$ Athyrium felix-femina **	ANE	2	Luzula sylvatica	MYR	2
Bromus benekenii	EPI	1	$ Lysimachia nemorum ***	ANE	3
Campanula trachelium	UNSP	5	$ Maianthemum bifolium	END	6
Cardamine glanduligera	BAR	1	Melampyrum nemorosum **	MYR	2
Carex digitata	MYR	3	Melica nutans	MYR	3
Carex laevigata	UNSP	2	$ Melica uniflora	MYR	4
Carex pendula	HYD	2	Melittis melisophyllum **	UNSP	1
Carex pilosa	UNSP	1	$ Mercurialis perennis	MYR	7
Carex remota ***	HYD	4	$ Mespilus germanica	END wood	1
$ Carex strigosa	HYD	3	Milium effusum	ANE	5
$ Carex sylvatica ***	MYR	4	$ Narcissus pseudonarcissus *m	BAR	3
$ Chrysosplenium alternifolium	UNSP	3	Neottia nidus-avis	ANE	4
$ Chrysosplenium oppositifolium	UNSP	2	Orchis mascula	ANE	3
Conopodium majus	MYR	2	$ Oxalis acetosella	AUT	6
$ Convallaria majalis	END	7	$ Paris quadrifolia	END	7
Cornus mas	END wood	1	Phyteuma spicatum *m	ANE	2
$ Cornus sanguinea	END wood	4	Polygonatum multiflorum **	END	6
Corydalis solida	MYR	1	Polystichum aculeatum **	ANE	1
$ Corylus avellana	END wood	5	$ Primula elatior *	ANE	7
$ Crataegus laevigata	END wood	4	Primula vulgaris **	MYR	4
Dactylis polygama **	UNSP	1	$ Pteridium aquilinum	ANE	5
Dactylorhiza fuchsii	ANE	1	Pulmonaria obscura	MYR	1
Daphne mezereum	END	2	Pulmonaria officinalis	MYR	1
Dentaria glandulosa	UNSP	1	Pyrus commune	UNSP wood	1
$ Dryopteris carthusiana	ANE	1	$ Ranunculus auricomus	EPI	5
Dryopteris pseudo-mas	ANE	1	Ranunculus lanuginosus	EPI	2
Elymus caninus	EPI	1	Ruscus aculeatus	END	1
Epipactis purpurata	ANE	1	$ Sanicula europaea	EPI	5
Equisetum sylvaticum	ANE	1	Sorbus torminalis	UNSP wood	4
$ Euonymus europaeus	END wood	4	Symphytum tuberosum	MYR	2
Euphorbia amygdaloides	MYR	3	Tilia cordata	UNSP wood	4
$ Euphorbia dulcis	MYR	1	Tilia platyphyllos	UNSP wood	1
Festuca heterphylla	UNSP	1	Vaccinium myrtillus *	END	2
Gagea lutea *	MYR	1	$ Veronica montana	MYR	3
Geum rivale	EPI	2	$ Vinca minor	MYR	2
Helleborus viridis	UNSP	1	Viola mirabilis	MYR	1
Hepatica nobilis	MYR	2	$ Viola reichenbachiana	MYR	4

Dispersal type:
MYR: dispersal by ants (myrmecochores); END: dispersal by animals and birds via digestion (endo- & ornithochores); ANE: dispersal by wind (anemochores); EPI: disp. by adhesion on animals (epizoochores)
BAR & AUT: passive and active dispersal by plant itself (baro- and autochores)
UNSP: unspecified, uncertain or unknown; HYD: dispersal by water (hydrochores).

Wood: woody species sometimes planted
*: sometimes in old grasslands or heathlands, on former woodland sites
*m: sometimes in grasslands, particularly in the Central Europe
**: sometimes in wood edges
***: often in woodland rides

Source: Hermy (1992)

species for Flanders has been drawn up (see appendix).

In the relatively stable conditions of the forest we may expect that short-distance dispersal is the rule. This should particularly hold for the plant species of the undergrowth. Indeed, some 40% of these European ancient woodland species are dispersed by ants. Although the amount of anemochores is still considerable (about 20%) (Figure 1), the success of wind dispersal for field layer species is probably limited.

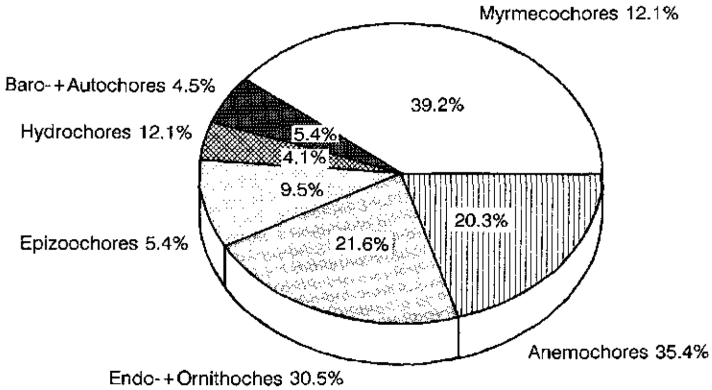

Figure 1. The proportion of the dispersal types in the European list of ancient woodland species (see Table 1). Percentages under the names refer to the proportion of the total plant species composition in forests.

However, dispersal is only one requisite for a successful establishment of a plant species. Germination and growth are strongly affected by the surrounding vegetation. In recent woodlands, often with a dominance of very competitive species (e.g. *Urtica dioica*, *Molinia caerulea*), this is particularly difficult. Fragmentation effects will probably further reduce the establishment success of typical woodland species in recent woodlands. From these considerations we may expect that:

1. Recent woodlands will tend to have smaller populations of ancient woodlands species, if they have them at all; it takes a long time for a population to develop. This is suggested by the distribution of the performance of species like *Hyacinthoides non-scripta*, *Maianthemum bifolium*, *Oxalis acetosella* in recent and ancient woodland plots (Figure 2).
2. Very competitive species may negatively affect ancient woodland species (and their diversity); the more ancient woodlands are invaded by these species, the more the typical woodland plants will decrease in numbers (Figure 3). A very fragmented forest cover and intensive

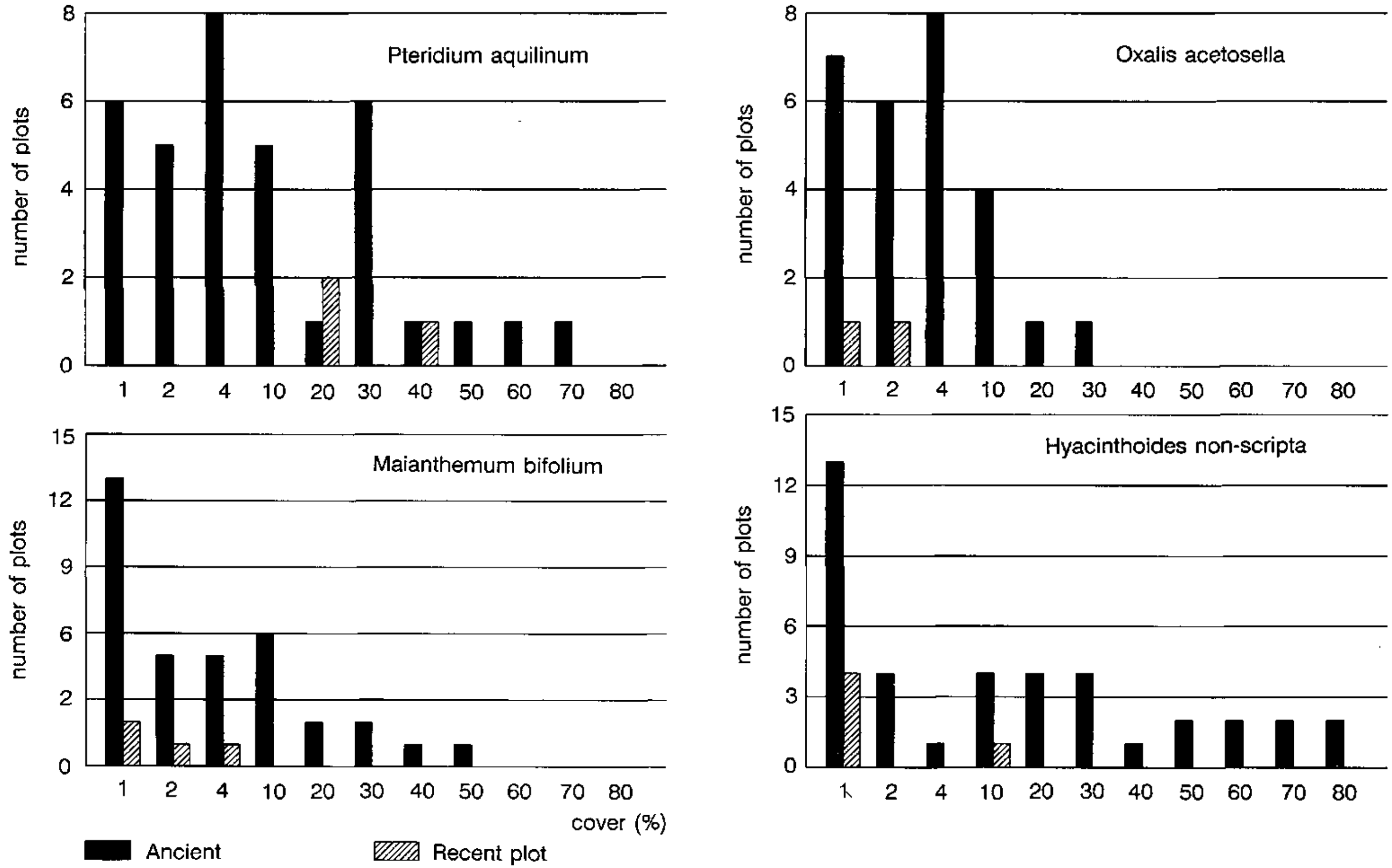

Figure 2. The distribution of the percentage cover (decimal scale) of four common woodland species in 640 plots from ancient and recent forests in the western part of Belgium (Hermy, 1985).

agriculture will accentuate this effect. In field experiments Pigott (1982) found that nitrogen and phosphate reduced the cover of *Anemone nemorosa*; in contrast, the establishment of *Urtica dioica* and other so- called "nitrophilous" species was stimulated by phosphate rather than by nitrogen (Pigott and Taylor, 1964; Pigott, 1971).

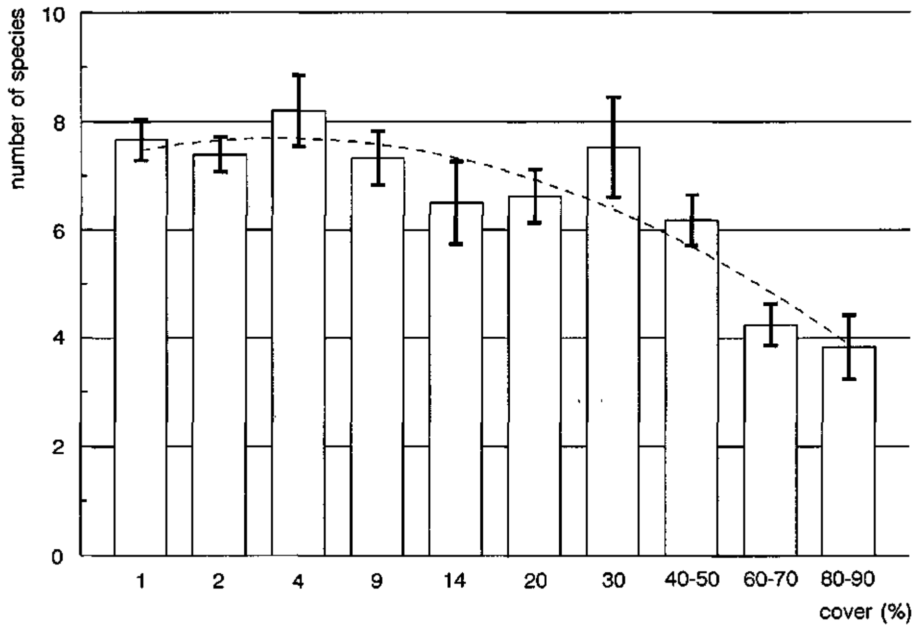

Figure 3. The relation between the mean number of true woodland species per plot (n=308) and the percentage cover of *Urtica dioica*. Error bars (standard errors) are shown and a curve is fitted using a second order polynomial regression. Data come from 640 plots from about 180 woodlands in western Belgium (Hermy, 1985).

For woodland birds Opdam and Schotman (1986) found a clear positive relation between the probability of occurrence and forest area. Larger forests are likely to have a more heterogenous structure and more available food. Opdam (1991) concluded from several studies that the local extinction rate is inversely related to the area of the habitat fragment (which is proportional to the size of the local population). Plants, being less mobile and often considerably long-lived, need much more time before clear responses are evident (usually, the first is regeneration). Yet positive correlations between individual species (particularly the rarer species) and forest area have been found in north-west Germany (Zacharias and Brandes, 1990). In Flanders the probability of occurrence of certain woodland species e.g. *Maianthemum bifolium* and *Luzula pilosa* increases with the size of the woodland and simultaneously with the proportion of the wood that is ancient. Other species, like *Hyacinthoides non-scripta* only showed an effect proportional to the woodland which is ancient (Figure 4). In Flanders, as in north-west Germany, the rarer species tend to occur only in the largest woodlands (Table 2). Usually these are species at the edge of their range in the particular region.

Ancient woodland species all have in common a slow rate of colonization, but all respond differently. For *Hyacinthoides non-scripta* and *Anemone nemorosa*, Pigott (1982) recorded rates of 6 to 10 m and 1 to 2 m in a century. In combination with the absence of persistent seed banks (Brown and Oosterhuis, 1981) this means that elimination by a change to non-woodland conditions (reclamation, even if temporary), to conifers or by competitive exclusion will make it very difficult for them to regain their former population size. However the success of colonization or recolonization may increase if the forests are less isolated. Peterken and Game (1981) found that

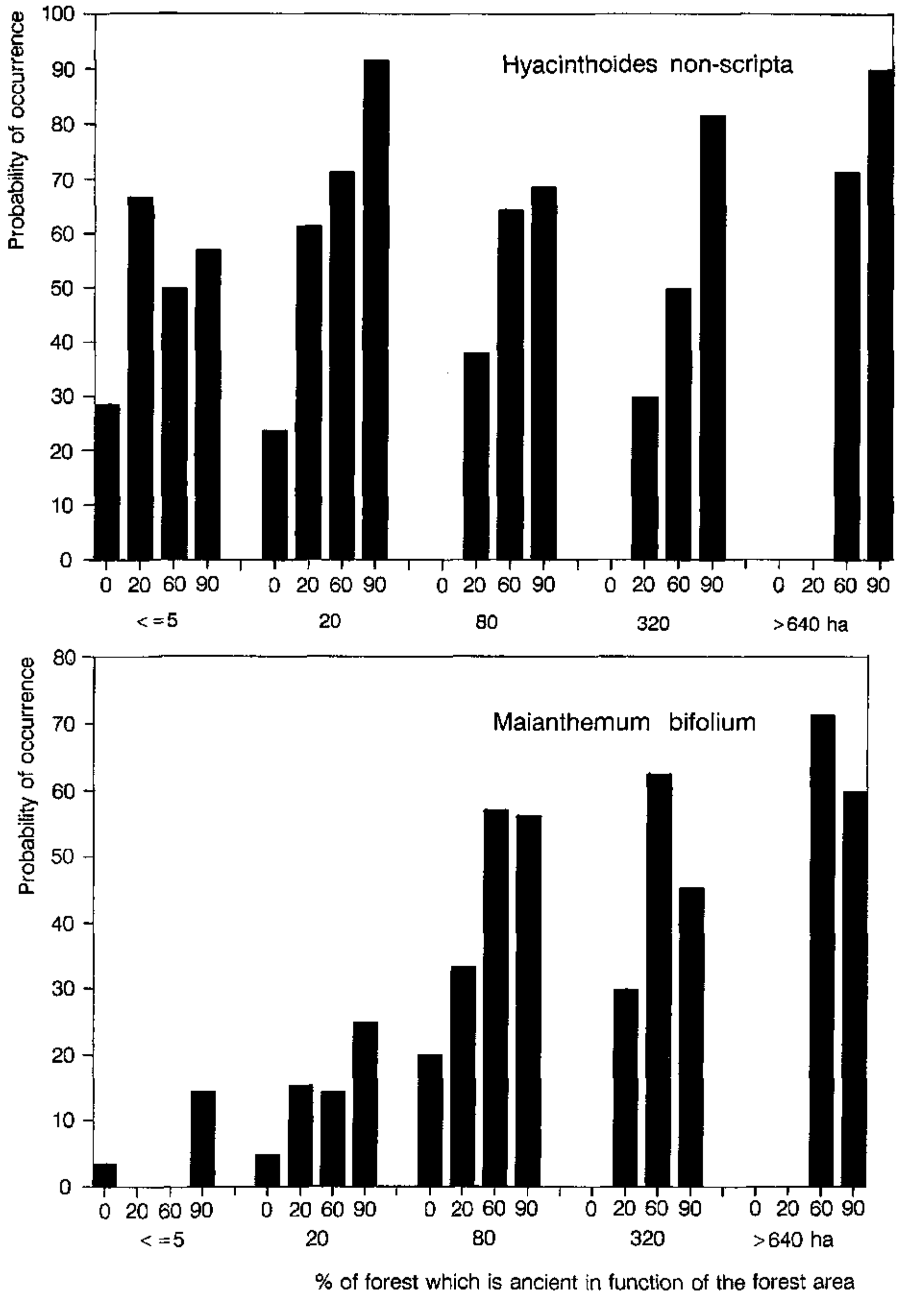

Figure 4. Incidence functions for *Hyacinthoides non-scripta* and *Maianthemum bifolium* on 321 woodland patches in the former county of Flanders. *Hyacinthoides* responds only to the proportion of the woodland which is ancient (site history); the probability of occurrence per area class remains more or less the same. *Maianthemum* responds both to area and site history. Data from an unpublished historical/ecological study of the woodlands in Flanders (Tack et al., unpubl.).

Table 2. Some examples of woodland species having a great affinity for large forests in two regions.

Flanders:	NW Germany:
Corydalis solida	Circaea alpina
Pulmonaria montana	Epipogium aphyllum
Sorbus torminalis	Carex umbrosa
Orchis mascula	Melittis melissophyllum
Neottia nidusavis	Potentilla alba
Euphorbia amygdaloides	Omphalodes scorpiodes

colonization by *Mercurialis perennis* mainly depends on the proximity to refuges in ancient woods and wood-relic hedges. In the eastern part of The Netherlands Van Ruremonde and Kalkhoven (1991) showed that the probability of occurrence of *Lonicera periclymenum* and the density of *Ilex aquifolium* decreased with an increasing isolation of the forest patches. In Bos t'Ename (a woodland in south Flanders) we found that the distribution of *Corylus avellana, Mercurialis perennis* and other typical woodland species was clearly linked to the presence of former non-cleared fringes of woodland vegetation in the 19th century, when the wood was almost entirely reclaimed for agriculture (Figure 5). The subsequent recolonization of the forest area, after the arable land had been abandoned, also showed a clear relation to the slope of the woodlot (colonization proceeded faster downslope than upslope). Sometimes so-called recolonization is merely a consequence of survival under non-woodland conditions (even in arable fields for some geophytes e.g. *Hyacinthoides non-scripta*).

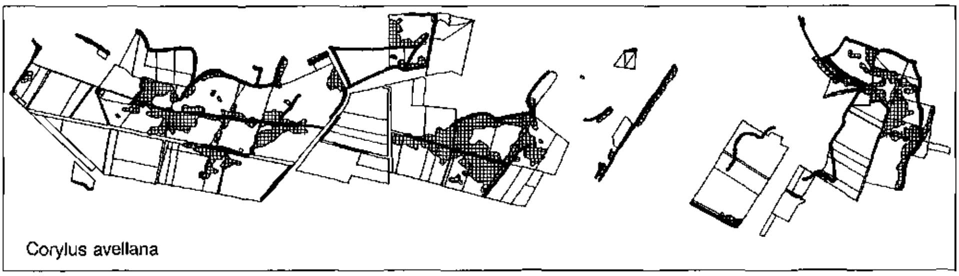

Figure 5. The modern distribution of *Corylus avellana* (hatched pattern) in the woodland of Ename (near Oudenaarde, S. Flanders). This woodland was reclaimed between 1851 and 1896 except for some small lots and many linear elements mostly along rides (thick black lines). Only the elements for which historical evidence is decisive are shown.

Plant communities of recent and ancient forests

Few results are available at the level of forest communities; often, recent forests have not been studied because they are too atypical (Klötzli, 1972).

Since there are floristic differences between ancient and recent forests we may expect that their plant communities will also differ in their relation to site history. Hermy (1985, 1992) found a clear relation between floristically defined communities and the former land use (Figure 6). Additionally there was a marked positive relation between the mean number of true woodland species (see appendix) per community and the proportion of plots from ancient woodland (Figure 7). Total number of plant species was not clearly related to this proportion. In Figure 7 a marked difference in the number of true woodland species in the observed communities is also apparent; Carpinion forest (and also the Fagion) and Alno-Padion forests, i.e. forests on the heavier soils are much richer in ancient woodland species than Quercion forests. We found that the main variation in the forest communities of Flanders was determined by soil factors (texture, moisture), but this depends on the length of the coenocline studied (Hermy, 1987). For example, within the Alno-Padion communities the main cause of variation in composition proved to be former land use.

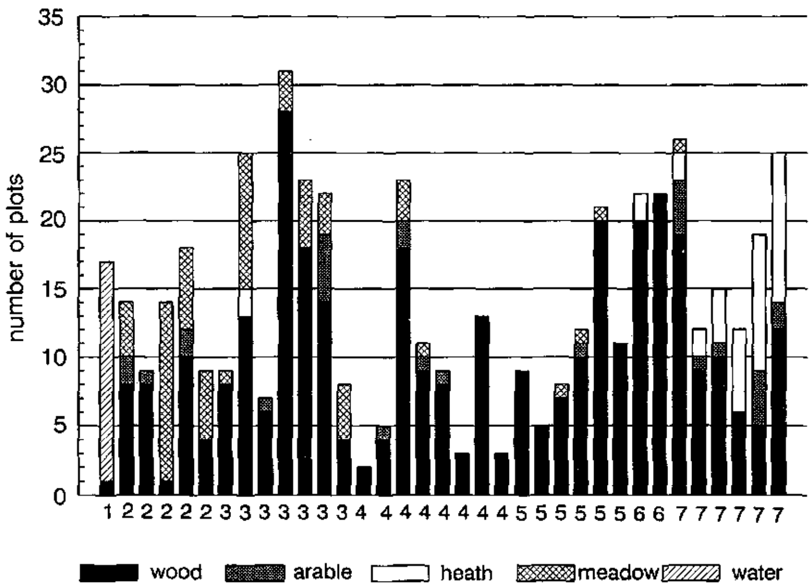

Figure 6. Land use in 1770-1177 in 35 floristically defined (using TWINSPAN) woodland communities in western Belgium (Hermy, 1985).
1: Alnion glutinosae (one community); 2: Basal communities (sensu Kopechy and Hejny 1974) from the Alno-Padion; 3: more or less saturated communities from the Alno-Padion; 4: spring woods; 5: more or less saturated communities from the Carpinion (partially Fagion); 6: fully developed Violo-Quercetum; 7: basal communities belonging to the Quercion.

Plant species richness in ancient and recent woodlands

Peterken and Game (1984) found that ancient woodlands (complete species lists per woodland) had a greater species richness than recent woodlands. Based on plots we found that plant species richness was not statistically significantly different between plots from ancient and recent woodlands. However, the number of true woodland species did differ statistically significantly. The probability of finding a certain number of true woodland species in recent and ancient woodlands was very different (Figure 8). So the number of true woodland species may be used as an indicator of the presence of ancient woodland. Of course, other woodland features e.g. woodland banks, or archaeological and palynological evidence may provide further evidence of the venerability of the woodland (see Rackham, 1980).

It is extremely likely that core species (forest-interior species, e.g. true woodland species) are more affected by former land use and by fragmentation than "edge" species. However, several studies (e.g. Cortenraad and Mulder, 1989; Van den Bremt, (unpubl.)) indicate that typical forest edge species ("Mantel - und Saum Arten") are severely threatened in the agricultural landscapes of Flanders and The Netherlands. Their decline in the last century coincides with the abandonment of traditional management of woodlands and the increasing pressure of agriculture on forest edges, resulting in very sharp boundaries between forest and cultivated land. So, the glade habitat for these species has disappeared at an alarming rate.

A spontaneous development occurring in many forest reserves, particularly those developing

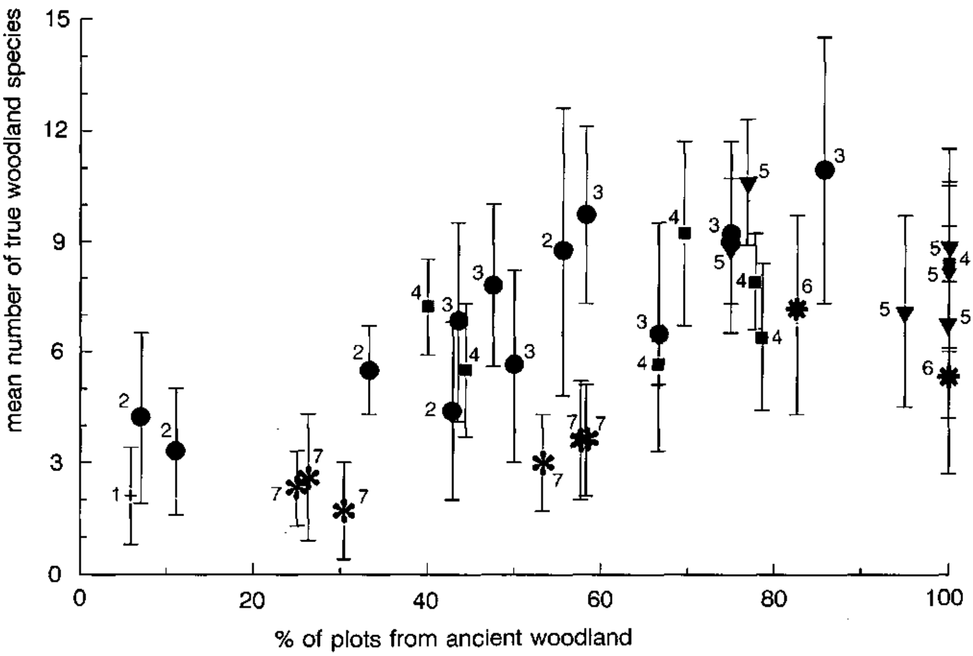

Figure 7. The mean number of true woodland species per plot per vegetation type in relation to the proportion (%) of plots in each vegetation type belonging to an ancient woodland. A positive correlation is observed within the Quercion (*) and the Alno- Padion component (o).
1: Alnion glutinosae (one community); 2: Basal communities (sensu Kopechy and Hejny, 1974) from the Alno-Padion; 3: more or less saturated communities from the Alno-Padion; 4: spring-woods; 5: more or less saturated communities from the Carpinion (partially Fagion); 6: fully developed Violo-Quercetum; 7: basal communities belonging to the Quercion.

from managed forest, will probably result in a further decline of the typical edge species, at least initially. In the long run, when a dynamic mosaic of gaps and more closed areas predominates in the forest, an increase may be expected. However, this will greatly depend on how many populations had survived at the time the mosaic forest structure was established and the potential to colonize (dispersal + establishment) of the edge species. If no populations survive, the re-establishment of forest species will be very disappointing.

Regional differences in forests

Forests differ regionally, usually because the regions vary in topography, soil texture, mesoclimate and many other features (e.g. former land use). In Flanders, where forest area has fluctuated greatly in recent centuries, recent research suggests (Tack et al., (unpubl.)) a strong correlation between the present, total number of field layer woodland species and the ratio of the wooded area ca. 1300 to the area of the subregion (Table 3). Correlation with 19th century afforestation rate is not statistically significant. Although this is not evidence of causal relations, it is an additional argument for the importance of the past to the present vegetation cover. It emphasizes the actual reality of the past, as it is archived in our forests.

Table 3. Spearman Rank Correlation of total number of field layer species from woods in subregions of Flanders and some former area features (n=12). Subregions were defined from the distribution and density of forests at the end of the 18th century.
Total number of true woodland species in the field layer (TOTFIELD); forest area in 1300 (FA1300); forest area at the end of 18th century (FA1800); subregional area (REGAREA); ratio of FA1300 to REGAREA: RAT1300; ratio of FA1800 to REGAREA: RAT1800; ratio of FA1300 to FA1800: RAT1300/1800.

	TOTFIELD	FA1300	FA1800	RAT1300	RAT1800	RAT1300/1800
TOTFIELD	.					
FA1300	0.55*	.				
FA1800	0.48	0.68*	.			
RAT1300	0.75**	0.60*	0.70*	.		
RAT1800	0.39	0.06	0.76**	0.70*	.	
RAT1300/1800	0.66*	0.46	0.15	0.64*	-0.07	.
REGAREA	0.07	0.67*	0.24	-0.02	-0.24	0.37

Partial correlation between TOTFIELD and RAT1300 controlling for forest area in 1800 = 0.72**
Significance: *: $0.01 < P < 0.05$; **: $P < 0.01$

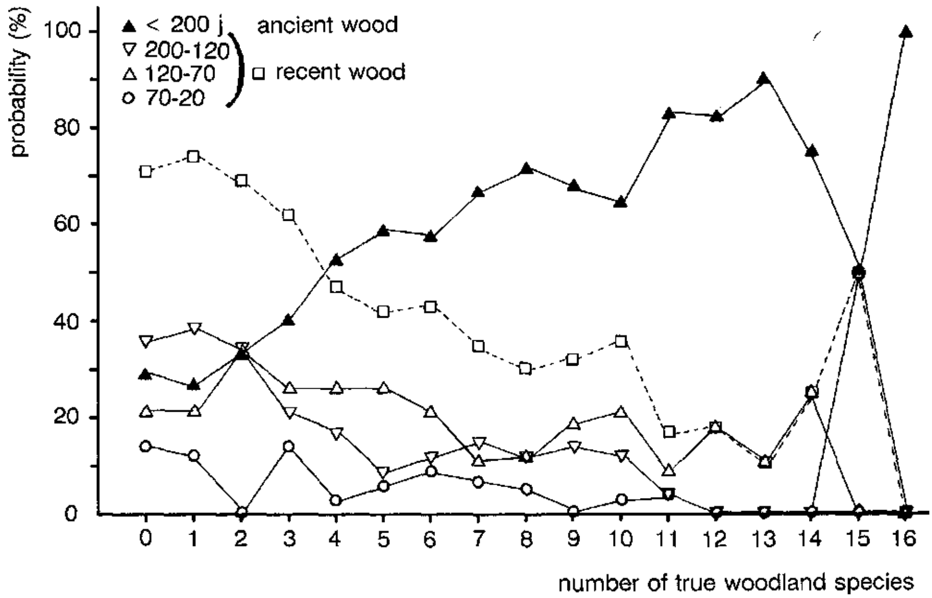

Figure 8. The probability of occurrence of the richness in true woodland species in plots from ancient and recent woodlands in the western part of Belgium. Data are based on 640 plots from 180 woodlands. Recent woodland has been further subdivided depending on the time (in years) of the land use.

Discussion and conclusions

An integrated historical/ecological study of forests and the landscape they are part of may yield an insight into the spatial and temporal distribution patterns of species, forest communities and the forests. Modern forests can be understood only in the light of their history (Rackham, 1980; Tallis, 1991; Hermy, 1992).

Former land use largely determines which woodland species are present, but not necessarily how many (Peterken and Game, 1984). The number of true woodland species (including ancient woodland species) is significantly greater in ancient forests than in recent forests. However, the colonization or recolonization of recent forests proceeds at a slow rate which depends on the presence of relict populations in the neighbourhood. The population of true woodland species in recent forests is very different in size from that in ancient forests. Ancient woodland species may be regarded as extinction-prone (Peterken, 1977), because of their limited colonization capacities and their absence from persistent seed banks. A review of the European ancient woodland species suggests that short-distance dispersal is the rule in ancient woodland species. Short-distance dispersal and more generally any dispersal of plant diaspores is a necessary prequisite for successful establishment, although it is not the only bottleneck. Typical woodland species may decrease or be ousted by vigorous competitive species (which are better adapted to the new environmental disturbances), particularly in small forests in a hostile environment (e.g. on agricultural land).

True woodland species richness in combination with the forest communities present and the forest area may be used as a key criterion when selecting future forest reserves. Such reserves are extremely important for conservation.

Historical ecology will help us understand where we have come from and, to some extent, where we are going. If ancient woodland species are not present, do not expect them soon. It may take centuries. The forest will be more accessible to such species if it is close to or connected with other forests or wood-relic hedges. Isolation may pose strong constraints on the possibilities of colonizing or recolonizing sites. Here, the management of forest or of forest reserves should aim at decreasing the external infuences, even if no internal management is applied. This suggests that we should put forest management in a broader perspective of integrated landscape management. Of course, this raises the issue of sustainable development for the long-term benefit of future generations. But sustainability is another story. It too will call for an interdisciplinary approach.

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Appendix:

True woodland species usually occur in woodlands and their survival depends on the presence of woodland conditions. Tree and shrub species have been excluded, since it was often impossible to distinguish between what is spontaneous and what is planted. The species in the list have been taken from a species data base containing 433 species, created for a general phytosociological study (Hermy, 1985) of woodlands in Western Europe. Species in brackets do not occur in the plots sampled in Flanders.

(Aconitum vulparia)
Adoxa moschatellina
Allium ursinum
Anemone nemorosa
(Anemone ranunculoides)
Arum maculatum
Athyrium filix-femina
Blechnum spicant
(Calamagrostis arundinacea)
Campanula trachelium
Cardamine amara
(Carex brizoides)
Carex elongata
(Carex laevigata)
(Carex ornithopoda)
Carex pendula
Carex remota
Carex strigosa
Carex sylvatica
(Carex tomentosa)
Chrysosplenium alternifolium
Chrysosplenium oppositifolium
Circaea lutetiana
(Conopodium majus)
Convallaria majalis
Corydalis claviculata
Deschampsia flexuosa
Dryopteris carthusiana
Dryopteris dilatata
Dryopteris filix-mas
Elymus caninus
Epilobium montanum
(Equisetum sylvaticum)
(Euphorbia amygdaloides)
(Euphorbia stricta)
Fragaria vesca
Gagea lutea (1)
(Gagea spathacea)
Holcus mollis
Hyacinthoides non-scripta
Impatiens noli-tangere
Lamium galeobdolon
Lathraea clandestina (2)
(Lathraea squamaria)
Listera ovata
Luzula pilosa
(Luzula luzuloides)
(Luzula sylvatica)
Lysimachia nemorum
Maianthemum bifolium
Melampyrum pratense
(Melica nutans)
Melica uniflora
Mercurialis perennis
Milium effusum
Moehringia trinervia
Narcissus pseudonarcissus
(Orhis fuchsii)
(Orchis mascula)
(Orchis purpurea)
Ornithogalum umbellatum (1)
Oxalis acetosella
Paris quadrifolia
(Peucedanicum gallicum)
(Poa chaixii)
Polygonatum multiflorum
(Polygonatum verticillatum)
Polypodium vulgare (s.l.)
Potentilla sterilis
Primula elatior
Primula vulgaris
Pteridium aquilinum
Ranunculus auricomus
Ranunculus ficaria
Ribes nigrum
Ribes rubrum
Ribes uva-crispa
Rubus caesius
Rubus fruticosus coll. (3)
Sanicula europaea
Sedum telephium
(Stellaria nemorum)
(Trientalis europaea)
Vinca minor
(Viola hirta)
Viola odorata
Viola reichenbachiana
Viola riviniana

(1) Ornithogalum umbellatum & Gagea lutea optimally occur on well aerated sandy river banks occasionally outside woodlands.

(2) Lathraea clandestina was strongly associated with poplars too if it occurred outside woodlands.

(3) Rubus fruticosus coll. is considered as a group of species, some of which have frequently been observed in non-woodland habitats. However, as a whole this taxon was generally only abundant on woodland sites and edges.

Recent changes in forest vegetation in North-West and Central Europe and some likely causes

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Summary

Recent European literature on changes in herb layer species composition is reviewed and a Swedish field experiment on forest fertilization is discussed. The species composition of forest undergrowth has changed in several areas of central and western Europe, often indicating increased nitrogen availability and decreased pH. Fertilization with ammonium nitrate simulates the vegetation changes reported and causes pH to decrease.

Keywords: nitrogen deposition, soil acidification, herb layer, forest vegetation

Introduction

Dramatic changes in the species composition of forest undergrowth have been reported from several parts of Europe, especially during recent decades: for example from Sweden (Falkengren-Grerup, 1990), Finland (Lähde, 1987), Germany (Wittig et al., 1985), Czecho-Slovakia (Kubíková, 1989), Poland (Medwecka-Kornás and Gawronski, 1990); Switzerland (Kuhn et al., 1987), and The Netherlands (De Vries, 1982; Hommel et al., 1991).

Some examples

Dalby Söderskog is situated in southern Sweden. It is a mixed deciduous wood of elm (*Ulmus glabra*), ash (*Fraxinus excelsior*), oak (*Quercus robur*), and beech (*Fagus sylvatica*) on heavy, calcareous clay. In 1918 it was designated a national park and has not been subjected to forestry measures since then. Before 1918 it was used for grazing horses. Nowadays it is a popular recreation area. Both Malmer et al. (1978) and Persson (1980) studied the succession, using 74 plots that had already been described in 1935 and in 1969. Between 1916 and 1970 the frequency of elm with > 10 cm dbh had quadruple. This is considered as the major cause of succession of the field layer. Since 1925 the number of vascular plant species in the forest has fallen by 42%. Shade-tolerant species have become more important in the herb layer, as well as the species normally associated with high levels of available nutrients and basic or neutral pH. *Anemone ranunculoides*, *Aegopodium podagraria*, and *Mercurialis perennis* have become more abundant. Persson (1980) summarizes that the succession of the field layer is converging and that a considerable reduction of the McIntosh diversity index of the field layer is evident.

More recently, Falkengren-Grerup and Eriksson (1990) studied changes in soil, vegetation and forest yield between 1947 and 1988 in permanent plots in beech and oak forests in southern Sweden. They analysed both the upper C horizon and the undergrowth in 19 stands. In forty years the exchangeable base and metal cations had decreased by between 20% and 70%. Several species of nitrophilous vascular plants had increased in cover. The authors conclude that the enhanced availability of nitrogen has influenced the undergrowth more than the loss of other macro nutrients. In addition, Rühling and Tyler (1986) hypothesize that the major vegetation gradient in south Swedish oak forests is caused by a gradient in air pollution (both acidification and nitrogen deposition) which is highest in the west (Skane) and lowest in the east (Smaland).

During 1950-1985, Lähde (1987) studied changes in species composition of the herb layer vegetation in stands of Scots pine (*Pinus sylvestris*) in southern Finland. It appeared that species considered to be susceptible to air pollution such as *Vaccinium vitis-idaea, Hylocomium splendens, Pleurozium schreberi* and lichens had decreased significantly. As these species usually grow on acid soils, it is unlikely that soil acidification alone has caused the decrease.

In 1985, Wittig et al. (1985) published a much cited paper about changes in the herb layer of beech forests in the Westphalian Bight (Germany). In 1983 they recorded the herb layer vegetation of 44 sites in millet grass-beech forests (Milio-Fagetum). The plots surveyed were 400-600 m^2. The records were compared with a corresponding set of records made eight years earlier (1976), using Ellenberg's indicator values (Ellenberg, 1979). The authors found an increase in plant species that indicate acid soil conditions. Moreover they found a clear decrease of plant-indicated pH values. The newly established plant species included many nitrogen indicators. The soil within the areas studied had not been ameliorated or otherwise treated. However, in 35 of the 44 stands some logging or removal of individual trees had taken place. In addition it is interesting to note that of the 53 areas that had been recorded in 1976, nine had become useless for study, either because the vegetation had been destroyed or because they had been subjected to major forestry measures. Almost 20% had to be considered as lost; this illustrates that unprotected forest areas are continuously exposed to the hazard of loss of information. Examples like this stress the importance of designating strict forest reserves intended for research and safeguarded from disturbance.

The 'Eilenriede' is a large deciduous woodland near Hannover (Germany) which was surveyed in 1946 and between 1975 and 1980 and is enclosed by urban areas. The vegetation consists of Betulo-Quercetum molinietosum, Fago-Quercetum, and Stellario-Carpinetum. Trepl (1982) reported on the vegetation changes during that period of thirty years. From his results it is clear that true woodland species had decreased in number and that indicator values for nitrogen and pH had increased.

Vegetation changes in Polish fir forests (Pino-Quercetum) have been reported by Medwecka-Kornas and Gawronski (1990). Apart from the dieback of fir (*Picea abies*) they reported a decrease in abundance of acidophilous species such as *Vaccinium myrtillus, Lycopodium anotinum*, and *Pleurozium schreberi* and an increase in nitrophilous species from neutral sites including *Sambucus nigra, S. racemosa* and *Impatiens parviflora*. These changes are undoubtedly caused by air pollution, which is severe in the area. Similar changes in the field layer of spruce (*Abies alba*) forests were reported from the western parts of Czecho-Slovakia (Kubíková, 1989).

In Switzerland, changes in field layer species composition have been reported by Kuhn et al. (1987) who studied ten stands of the Querco-Betuletum helveticum in northern Switzerland, near Zürich and nine stands of Querco-Carpinetum molinietosum near Geneva. The northern stands had been described between 1935 and 1939 and those near Geneva between 1942 and 1947. In all stands the number of species in both herb and shrub layers had decreased dramatically. Application of species indicator values (Ellenberg, 1979) showed an increase of the weighted mean of nitrogen and a decrease of the weighted mean of light, in almost all stands.

De Vries (1982) recorded the species composition of the undergrowth of some young stands of Scots pine (*Pinus sylvestris*) that had been described in detail twenty years before, in 1958 (Bannink et al., 1973). The study area is in the centre of The Netherlands. Her main conclusions were that *Deschampsia flexuosa* and *Ceratocapnos claviculata* had increased considerably and that lichens had disappeared. She attributed these changes to an increase in the atmospheric deposition of nitrogen during the preceding period and by the ageing of the young stand.

In 1988, Hommel et al. (1991) remapped stands of Scots pine in the central part of The Netherlands that had already been mapped in 1958. Their conclusions about succession are based on a comparison of maps using a Geographical Information System (GIS). In thirty years the vegetation types with *Vaccinium vitis-idea, V. myrtillus* and lichens had mostly changed into a Deschampsia-dominated type with *Dryopteris dilatata* or *Ceratocapnos claviculata*. The types with *Rubus 'fruticosus', Lonicera periclymenum*, and *Deschampsia flexuosa* had changed less. The main conclusion is that the vegetation development indicates that during 1958-1988 the whole site had been enriched with plant-available nutrients. On poor soils the enrichment was more obvious than on less poor soils. Hommel et al. (1991) found a clear relation between the enrichment of a site as indicated by the succession and itsdistance from the nearest farm. This relationship indicates that the enrichment could well be caused by local air pollution from farming, as farms are known to emit large quantities of volatile nitrogen compounds.

Summarizing: in several areas of Western and Central Europe recent forest succession has been studied. Forests investigated include beech (*Fagus sylvatica*), Scots pine (*Pinus sylvestris*), spruce (*Picea abies*) fir (*Abies alba*), oak (mostly *Quercus robur*) ash (*Fraxinus excelsior*), and lime (*Tilia cordata*). The changes reported differ. Scots pine and spruce forests tend to share an increase in grasses, *Rubus spp.*, *Dryopteris spp.*, and *Sambucus spp.*, whereas *Cladonia spp.*, *Vaccinium spp.*, *Pyrola spp.* and *Lycopodium spp.* tend to decline. In general, species indicating high nitrogen availability and low pH have increased at the cost of many rare species and those indicating low nitrogen availability and neutral or basic pH. In some cases acidification is also indicated. The changes reported are explained in different ways. In both Germany (Wittig et al., 1985) and Sweden (Falkengren-Grerup, 1990) the observed succession in beech forests has been ascribed to soil acidification caused by air pollution. However, in more recent studies (Kuhn et al., 1987; Hommel et al., 1991; Falkengren-Grerup and Eriksson, 1990) the enhanced levels of plant-available nitrogen are considered to be the main cause of succession. In addition, De Vries (1982) and Fanta (1986) consider the ageing of the forest as a major factor influencing herb layer succession.

Ellenberg junior (1985) published an interesting paper on the changes in the flora of Central Europe in the light of fertilization and air pollution. His first conclusion is that raised levels of plant-available nitrogen are a major threat to the existence of many wild plants, because about 60% of the species threatened can only survive at low levels of nitrogen. Secondly he shows that both endangered species and those that are not endangered are almost equally distributed over the pH values. So acidification as such is probably only a slight threat to plants. Ellenberg's conclusions apply well to forests: in a way they summarize the results of recent forest succession studies in Europe. However, they do not provide evidence to explain the observed vegetation changes.

Swedish field experiments

Introduction

Fertilizing experiments in Scots pine forests in Sweden have been carried out for more than 20 years (Tamm, 1985). The results of these field experiments are worth mentioning here, because they provide evidence that may explain many herb layer changes reported.

Relatively little is known about the effects of fertilization on the floristic composition of the field and bottom layer of the forest ecosystem (Backeus 1980; Persson 1981; Tamm 1985, 1989; Gerhardt and Kellner 1986). Both Backeus and Persson found that experimental application of nitrogen fertilizers had a strong effect on the floristic composition of the herb and moss layers of Scots pine stands. Roughly the same results were obtained by Gerhardt and Kellner and Dirkse and Van Dobben (1989; Dirkse and Martakis, 1992; Van Dobben et al. 1992). Mitka (1987) reported on the increase of *Molinia caerulea* in experimental plots after five years of experimental fertilization with an NPK fertilizer. Tamm and Popovic (1989) have shown that fertilization with nitrogen compounds leads to strong acidification of the soil.

In Sweden four experiments on the optimum nutrition for forests were started in the late 1960s and the early 1970s: at Strasan in 1967 (Tamm et al. 1974b), Lisselbo in 1969 (Tamm et al. 1974a), Norrliden in 1971 (Holmen et al. 1976), and Aseda in 1974 (Tamm 1985). Below the effects to date of the different nutrient regimes in the nitrogen optimization experiment E40 on the vegetation of herb and moss layers in a stand of Scots pine (*Pinus sylvestris* L.) near Lisselbo are discussed (see also Van Dobben et al., 1992).

Site description

Lisselbo (60°28' N, 16°57' E) is in the parish of Hedesunda in the province of Gästrikland, in the lowland of Central Sweden. It is situated about 100 km NNW of Uppsala (Figure 1). The wet deposition of NO_3- and NH_4+ each average about 200 eq/ha/yr (Bjorkdahl and Eriksson 1989).

The Lisselbo region is rather flat, with small rocky hills and low sandy ridges (esker remnants) rising up to about fifteen metres above the shallow depressions, which are usually occupied by peatlands or small lakes. The experimental area is about 80 m above sea level, on glacifluvial sediments (the Gävle esker) which with some interruptions can be followed in the terrain for more than 100 km both north and south of the area (Lundqvist, 1954). There are many eskers in the area, usually several hundreds of metres apart. They were formed during the retreat of the inland ice, which in this area was about 10 000 years ago. At Lisselbo the esker was formed under water, because the weight of the inland ice had depressed much of the lowlands of the Fennoscandian shield below sea level. The subsequent rise of the land meant that the eskers

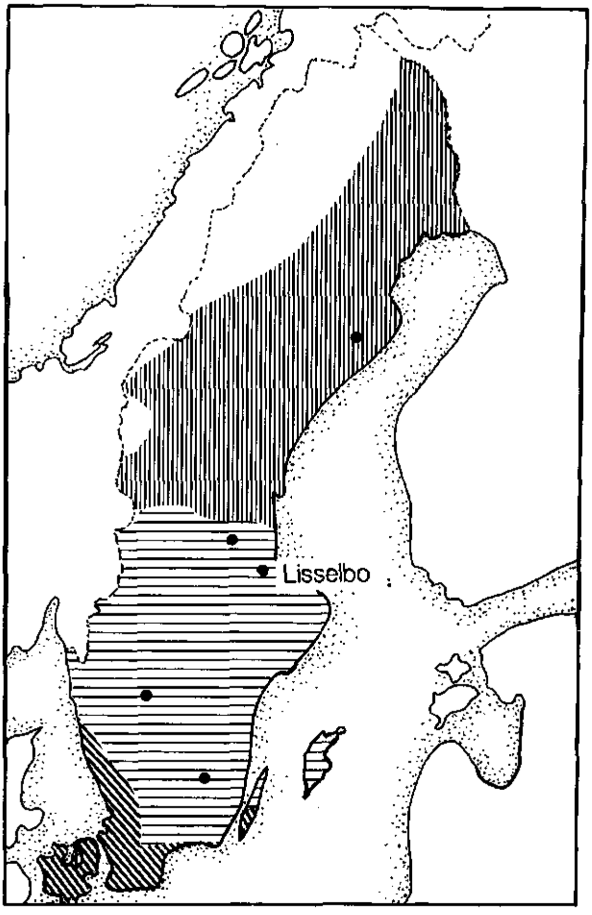

Figure 1. Geographical location of the Lisselbo experiment on optimum forest nutrition. The Swedish forest regions according to Sjörs (1965) are indicated: unshaded: alpine and birchwood region; vertical lines: northern coniferous region; horizontal lines: southern coniferous region; diagonal lines: southern deciduous region.

formed an archipelago, whose islands were exposed to waves removing much of the material from the esker tops, redepositing it on the lower slopes or as sandy outwash plains along the eskers. This erosion by waves accounts for the gradient in soil texture from more stony and gravelly at the top of the esker to medium sand with an admixture of fine sand and some silt on the lower slope (Tamm and Popovic, 1989).

The research site extends from the top of the Gävle esker and along its western slope. It is well drained, even in its lower part. The water table is 3-4 metres below the surface and the sandy soil is very permeable. Sites with sandy soils are generally dry and poorly productive and are dominated by Scots pine, either in an almost pure stand or with an admixture of mostly slow-growing spruce and some hardwoods. The most common hardwood is birch (*Betula pendula*), but as Lisselbo is situated within the northern part of the region where oak (*Quercus robur* and *Q. petraea*) and some other broadleaved species occur on fertile sites (Sjörs, 1965), occasional young specimens of oak and maple (*Acer platanoides*) may also be found.

The experimental stand consists of about 30-year-old Scots pine and some young spruce. The undergrowth is mainly ericaceous (*Calluna vulgaris, Vaccinum myrtillus, V. vitis-idaea*, and *Arctostaphylos uva-ursi*), with bryophytes (*Dicranum scoparium, D. polysetum, D. fuscescens, D. drummondii*, and *Pleurozium schreberi*) and lichens (*Cladina spp.* and *Cladonia spp.*). In 1954, an exceptionally severe storm blew down most of the trees. The remaining trees were removed and in the spring of 1955 the site was scarified and sown. In 1965 some trees were removed in order to regulate the spacing of the young stand, which consisted of both naturally regenerated and sown pines (Tamm et al., 1974a).

Experiment description

The term 'optimum nutrition experiment' indicates that dosages of nutrients are being tested to establish the range between nutrient deficiency and toxicity, in order to be able to specify standards for foliar concentrations of nutrients. The optimum wood yield obtained by supplying an optimum amount of a particular nutrient is found as follows. Nutrients are given annually, starting with high doses which are reduced when foliar concentrations start to level out. Foliage samples have been collected and analysed yearly from the start of the experiments (Tamm et al., 1974a; Tamm, 1985). The final doses which result in more or less steady state foliar concentrations have been maintained for many years (Table 2). Various yield parameters are recorded periodically. At the end of the experiment the highest yield indicates the optimum nutrition dosage.

Table 1. Block design of the optimum nutrition experiment Lisselbo E40. *Plot numbers refer to Figure 2.

Treatment	Blocks I	II	III	IV
Zero	40*	7	28	45
N1	33	17	23	48
N2	39	3	24	44
N3	36	14	32	41
PK	35	20	29	47
N1 + PK	37	11	27	42
N2 + PK	38	5	30	52
N3 + PK	34	9	31	51

The optimum forest fertilization experiment E40 (32 plots) is a dosage experiment, with randomized blocks (Table 1). There are three rates of ammonium nitrate and four replicates. The nitrogen levels are applied with or without a PK treatment. PK is given as Supra PK, a commercial fertilizer containing (by weight) 6.8% P, 13.3% K, 16.0% Ca, 6.0% S, and 13.0% Cl (Tamm and Popovic, 1989). The treatments started in spring 1969. All nutrients are spread by hand. N treatments are repeated yearly in spring, PK every third year, according to the scheme in Table 2. The experiment consists of 32 plots (Figure 2) measuring 30 x 30 m^2. Destructive activities (e.g. soil and biomass sampling) have been restricted to the outer margins (5 m) of the plots. Hence the net plots measure 20 x 20 m^2. The area has been fenced in to keep out moose (*Alces alces*). However, moose has managed to get in on several occasions. For further details on the experimental area and tree development see Tamm et al. (1974a).

Table 2. Fertilizer regimes of optimum nutrition experiment Lisselbo E40. Amounts are in kg of element per ha. N=Ammonium nitrate. P and K are given as Supra PK, a commercial PK fertilizer. B=Boron.

Year	N1	N2	N3	P	K	B
1969	60	120	180	40	76	-
1970	60	120	180	-	-	-
1971	40	80	120	-	-	-
1972	40	80	120	20	38	-
1973	40	80	120	-	-	-
1974	40	80	120	-	-	-
1975	30	60	90	40	78	-
1976	30	60	90	-	-	-
1977	20	40	60	40	78	2.5
1978	20	40	60	-	-	-
1979	20	40	60	-	-	-
1980	20	40	60	40	78	-
1981	20	40	60	-	-	-
1982	20	40	60	-	-	-
1983	20	40	60	40	78	-
1984	20	40	60	-	-	-
1985	20	40	60	-	-	-
1986	20	40	60	40	78	2.5
1987	20	40	60	-	-	-

Fieldwork

The fieldwork was done from August to November 1987. Species composition (phanerogams, bryophytes, and lichens) and abundance were recorded in all net plots. Abundance was estimated as percentage cover in a nine-point scale (Dirkse and Martakis, 1992). Sufficient quantities of all cryptogams were collected from each plot to assure reliable identification.

Data analysis

The records were thoroughly checked and copied onto computer files. All computer processing was done with a Microvax computer. The files were submitted to the programs TWINSPAN (Hill, 1979a), DECORANA (Hill, 1979b), CANOCO (Ter Braak, 1988; Jongman et al., 1987). TWINSPAN is a polythetic divisive method of classification for species as well as samples. The result is a two-way tabular matrix arrangement of samples and species. CANOCO is an extension of DECORANA; it provides several multivariate methods including correspondence analysis (CA), principal components analysis (PCA), and their canonical variants Canonical Correspondence Analysis (CCA) and Redundancy Analysis (RDA). The term canonical means that species abundance data and environmental data are analysed jointly. In canonical techniques regression and ordination are integrated into a multivariate direct gradient analysis, which allows relation-

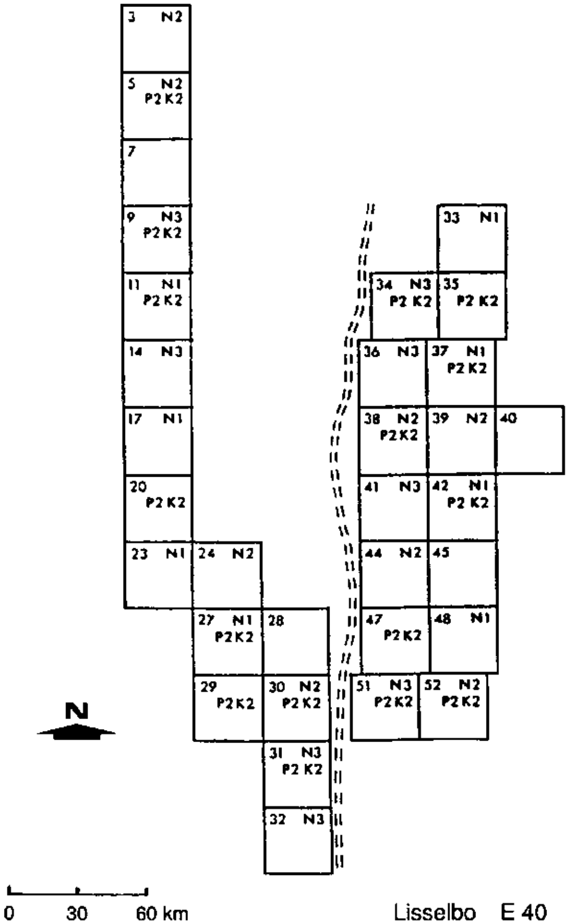

Figure 2. Lay-out of the Lisselbo E40 optimum nutrition experiment (after Tamm et al. 1974a). The plots have been numbered in accordance with a series of experiments. A forest track runs between the sets of blocks (see Table 1).

ships between species and environmental variables to be detected (Ter Braak, 1988). CANOCO also performs analyses in which the effects of particular environmental variables (covariables) are eliminated from the ordination. This is called a partial analysis (see Ter Braak, 1987). The results are usually displayed in a biplot. The biplot is an ordination diagram in which species and sites or environmental variables are jointly displayed. Classes of nominal variables are displayed in the ordination diagrams as centroids of the sites belonging to the classes. In this context, nominal variables are variables that are classes.

TWINSPAN: As a first approximation the data were subjected to TWINSPAN. The program was run with default options and five cut levels: 1 (0-5%), 2 (5-10%), 3 (10-25%), 4 (25-50%), and 5 (50-100%). For more technical information about cut levels, see Hill (1979a). The TWINSPAN result is shown in Table 3. The last three lines must be read vertically and indicate vegetation clusters in a binary way. The first major clusters (eigenvalue: 0.266) are separated by an empty column. Many species (*Rubus idaeus, Brachythecium oedipodium, Polytrichum longisetum, Plagiothecium denticulatum, Dryopteris carthusiana, Trientalis europaea*, and *Plagiothecium laetum*) are restricted to the main left-hand cluster. *Deschampsia flexuosa* is far more abundant (> 50% cover) on the left-hand side than on the right-hand side, where it covers

Table 3. TWINSPAN table of field and bottom layer vegetation of optimum nutrition experiment Lisselbo E40, containing all species recorded. Plot numbers (read vertically) refer to table 1, with the location of the plots given in Figure 2.

	0	2	5	0	1	4	0	3	3	3	3	5	3	3	3	3	4	4	1	1	2	2	2	4	0	2	4	3	3	4	4	2
*	5	4	1	3	4	1	9	4	8	1	6	2	0	2	9	7	2	4	1	7	3	7	0	8	7	8	7	3	5	0	5	9
Anthoxanthum odoratum	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cladonia deformis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Deschampsia cespitosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ptilidium ciliare	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cladonia digitata	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1	-	-	-	-	-	-	-	-	-	-
Hieracium vulgatiformia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-
Frangula alnus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Cladonia macilenta	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Carex canescens	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Festuca ovina	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Lycopodium complanatum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Carex pilulifera	-	1	1	-	1	-	-	-	-	-	-	-	-	-	1	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Brachythecium salebrosum	-	-	-	-	1	-	-	1	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Maianthemum bifolium	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-
Sphagnum capillifolium ·	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Carex ovalis	-	-	1	1	1	-	-	-	1	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ptilium crista castrensis	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Poa pratensis	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cirsium palustre	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Brachythecium velutinum	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tayloria tenuis	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lophocolea bidentata	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Brachythecium starkei	-	-	-	-	1	1	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cladonia bacillaris	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dryopteris expansa	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Leptobryum pyriforme	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Prunus padus	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Drepanocladus uncinatus	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lophocolea heterophylla	-	-	-	1	1	1	1	1	1	1	1	1	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Veronica offocinalis	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Taraxacum officinale	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Senecio sylvaticus	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lepidozia reptans	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Polytrichum formosum	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rubus idaeus	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	-	-	-	1	1	1	-	-	1	-	-	-	-	-	-	-	-
Carex nigra	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Bracgythecium oedipodium	1	1	1	1	2	1	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	-	-	-	-	-	-	-	-
Polytrichum longisetum	1	-	1	-	1	1	1	1	1	-	1	1	-	1	1	-	-	-	1	-	1	-	-	1	-	-	-	-	-	-	-	-
Plagiothecium denticulatum	-	1	-	-	1	-	1	1	-	-	1	1	1	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-
Dryopteris carthusiana	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Trientalis europaea	1	1	1	1	-	-	1	1	1	1	1	1	-	-	-	1	-	-	1	-	1	1	-	-	1	-	-	-	-	-	-	-
Galeopsis tetrahit	-	-	1	-	-	-	1	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Stellaria graminea	-	-	1	-	-	-	-	-	1	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rumex acetosella	1	-	1	-	-	-	-	1	-	1	-	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Brachythecium reflexum	-	1	1	-	1	-	1	1	1	-	1	1	-	-	-	1	1	1	-	-	1	-	-	1	-	-	-	-	-	-	-	-
Deschampsia flexuosa	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	4	5	5	5	5	5	3	3	1	1	1	2	1	1	1	1
Agrostis capillaris	1	-	-	-	-	-	1	-	1	1	-	-	-	1	-	1	-	-	1	1	-	-	-	1	-	-	-	-	-	-	-	-
Plagiothecium laetum	1	1	1	-	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	-	-	-	1	-	-	-	-
Sorbus aucuparia	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	-	-	1	1	-	-	1	1	1	-	1	1	1	1	-	-
Polytrichum commune	-	-	-	1	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-

Table 3. TWINSPAN table of field and bottom layer vegetation of optimum nutrition experiment Lisselbo E40, containing all species recorded. Plot numbers (read vertically) refer to table 1, with the location of the plots given in Figure 2.

	0	2	5	0	1	4	0	3	3	3	3	5	3	3	3	3	4	4	1	1	2	2	2	4	0	2	4	3	3	4	4	2
*	5	4	1	3	4	1	9	4	8	1	6	2	0	2	9	7	2	4	1	7	3	7	0	8	7	8	7	3	5	0	5	9
Betula pubescens	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	-	1	1	1	1	1	1	-	1	1	1	1	1	1	1	-
Dicranum scoparium	1	1	1	1	1	1	1	1	-	1	1	1	1	1	1	1	1	1	1	1	1	1	-	1	1	-	1	1	1	1	-	1
Dicranum montanum	-	-	-	1	1	1	-	1	-	-	-	-	-	1	1	-	1	-	-	-	-	1	-	-	-	-	-	1	-	1	-	1
Picea abies	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Vaccinium vitisidaea	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1
Pohlia nutans	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Hieracium tridentata	-	-	-	-	-	-	-	1	1	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1
Linnaea borealis	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-	1	-	1	-	-	-	-	-	-	-
Calamagrostis arundinacea	1	-	1	-	1	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	1
Tetraphis pellucida	1	1	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	1	1	-	-	-	-	-	-	-	-
Populus tremula	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1	-	1	-	-	-	-	-	-	-	1
Salix caprea	1	1	-	1	-	-	-	-	-	-	-	-	-	1	-	1	1	1	-	1	1	-	-	-	1	-	-	-	1	-	-	1
Aulacomnium palustre	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-
Luzula pilosa	1	1	-	1	1	1	1	1	-	-	-	-	1	1	-	1	1	1	1	1	1	1	1	1	1	1	1	1	1	-	1	1
Polytrichum juniperinum	-	-	1	1	1	1	-	-	1	1	1	1	1	1	1	1	1	1	1	1	1	-	1	1	1	1	1	1	-	1	1	1
Chamerion angustifolium	1	1	1	-	-	-	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Dicranum polysetum	1	-	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	4	3	1	2	1	1	1	1
Ptilidium pulcherrimum	1	-	-	-	1	1	1	-	-	1	1	-	1	-	-	1	1	-	1	-	-	1	1	1	1	-	1	1	1	1	1	1
Betula pendula	-	-	-	-	1	-	-	1	-	1	1	1	-	1	-	-	-	-	-	-	-	-	1	1	1	1	-	-	-	-	-	-
Cladonia crispata	-	-	-	-	-	-	-	-	-	-	1	-	1	1	1	1	1	-	-	1	1	1	1	-	1	1	1	-	1	-	1	1
Pleurozium schreberi	1	1	1	2	2	1	1	2	2	2	2	2	3	3	4	3	3	3	4	2	4	4	4	4	4	5	5	5	5	5	4	4
Cladina arbuscula	-	-	-	-	-	1	-	-	-	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Cladonia cornuta	-	-	-	-	-	-	-	-	-	1	1	1	1	1	1	1	1	-	1	1	-	1	1	1	1	1	1	1	1	1	1	1
Cladonia chlorophaea	-	-	-	-	1	-	-	-	-	1	-	-	-	1	1	1	-	1	1	1	1	-	-	1	1	-	-	1	1	1	1	1
Cephaloziella spec.	-	-	-	-	-	1	-	-	-	1	1	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	1	1	-	-	1	-
Melampyrum pratense	1	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1	1	1	1	1	2	2	1	1	1	1	1	-
Cladina anomaea	-	-	-	-	-	-	-	-	-	1	-	-	1	1	1	1	1	1	-	1	1	1	1	1	1	1	1	1	1	1	1	1
Cladonia sulphurina	-	-	-	-	-	-	-	-	-	1	1	1	1	1	1	-	1	1	-	1	1	-	1	1	1	1	1	1	1	1	1	1
Hylocomium splendens	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	1	1	1	1	1	1	1	1	-	-	-	1	-
Vaccinium myrtillus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	4	1	1	3	1	2	1	2	1	3	3	3	3	5	3	4	2	2
Cladina rangiferina	-	-	-	-	-	-	-	-	-	-	1	1	1	1	1	1	1	-	-	-	1	-	1	1	1	1	1	1	1	1	1	1
Cladonia cenotea	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	1	1	1	-	1	-	-	1	1	1	1	1
Cetraria islandica	-	-	-	-	-	-	-	-	-	1	1	1	1	1	1	1	1	1	-	-	-	1	-	1	1	1	1	1	1	1	1	2
Calluna vulgaris	-	-	-	-	-	-	-	1	-	1	1	1	1	1	1	1	1	1	-	-	-	1	1	1	1	2	1	2	4	3	2	2
Empetrum nigrum	-	-	-	-	-	-	-	-	-	1	1	-	-	-	1	-	-	1	-	-	-	-	-	1	-	1	1	1	1	1	1	1
Dicranum spurium	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	1	1	-	-	-	-	-	-	-	-	1	1	1	-	1	1
Solidago virgaurea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1
Cynodontium strumiferum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Pinus sylvestris (pl.)	-	-	-	1	-	-	1	1	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-	1	1	1	1	1	1	1	1	-
Dicranum fuscescens	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	1	-	-	-	-	-	1	1	1	-	1	1	1	1	1	-
Lecidea granulosa	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	1	-	-	-
Cladonia coccifera	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1
Cladonia mitis	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Cladonia botrytis	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1
Arctostaphylos uvaursi	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1	1	-	1	1
Juniperus communis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	1	-	-	-
Cladina stellaris	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-
Buxbaumia aphylla	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Cladonia gracilis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Dicranum drummondii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1
	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1	1	1
	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	1	1	1		0	0	0	1	1	1	1	1	

less than 25%. This cluster represents all N2, N3, and NPK plots, and half of the N1 plots. The main right-hand cluster consists of 10 records, representing all the zero and PK-treated plots, and half of the N1 treated plots. This cluster is characterized by *Cladonia spp.*, *Dicranum fuscescens*, and high abundances of *Dicranum polysetum*, *Vaccinium myrtillus*, *Calluna vulgaris*, and *Pleurozium schreberi*. Further divisions, indicated at the bottom of Table 3, do not reflect treatments and therefore do not merit further comment. Nevertheless the TWINSPAN result shows that ammonium nitrate has a much greater effect than Supra PK.

CANOCO: In the CANOCO analysis N supply was treated as a quantitative variable, whereas PK addition was treated as a nominal variable. Before the analysis the data were corrected for block effects; technically this turns the RDA into a partial RDA (see Ter Braak, 1987). Only species with an N2 value of 5 or more were included in the analysis. The N2 value is Hill's second diversity number, it represents the effective number of occurrences of a species (Ter Braak, 1987). Species and treatment scores have been combined into a biplot (Figure 3) in which both ammonium nitrate (N) and PK have been indicated by arrows. Species arrows are fictitious. The biplot can be interpreted by the rules of a PCA biplot. The longer the arrow the greater the change. The angle between arrows roughly reflects correlation between species. Species whose arrows are perpendicular to each other show no correlation, whereas arrows pointing in the same direction indicate highly correlated species. Only species with an N2 value > 5 are represented in the biplot.

Almost all the information is extracted by the first RDA axis with an eigenvalue of 0.389, accounting for 93% of the variance in species abundance explained by the diagram (41%). This axis is correlated with N addition, describing a gradient from unfertilized plots to N3 treated plots. A Monte Carlo test (Ter Braak, 1988) showed the N effect to be very significant ($p < 0.01$). The second axis contributes negligibly (eigenvalue 0.025) to the information. Higher axes have been discarded because there were only two environmental variables.

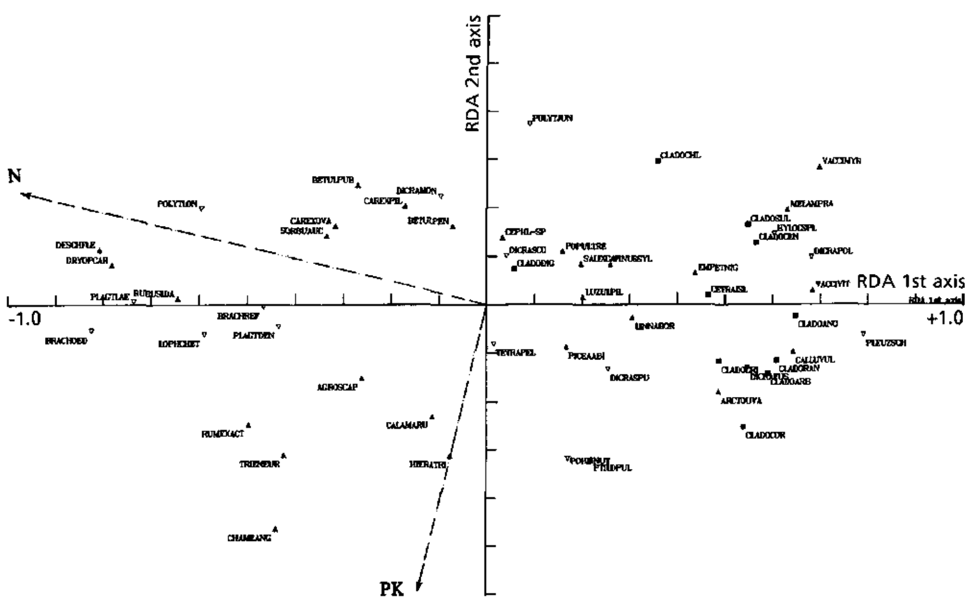

Figure 3. RDA ordination diagram of the Lisselbo E40 data, after removing of block effects, showing species codes and treatments. Species codes refer to Table 3. Black triangles: phanerogams; open triangles: bryophytes; black squares: lichens. Both N supply and PK are represented by dotted lines (arrows).

Brachythecium oedipodium, Deschampsia flexuosa, Dryopteris carthusiana, Plagiothecium laetum, Rubus idaeus, Polytrichum longisetum, and *Lophocolea heterophylla* show the highest negative scores on the first axis, indicating that high doses of ammonium nitrate (N2, N3) have a strong positive effect on these species. Moreover, all species on the left-hand part of the diagram are more or less positively influenced by N supply.

Pleurozium schreberi, Vaccinium myrtillus, Vaccinium vitis-idaea, Dicranum polysetum, Calluna vulgaris, Cladonia anomea, Calluna vulgaris, and *Melampyrum pratense* behave in the opposite way. These species decrease with increasing N supply. Some species, such as *Betula pendula, Carex pilulifera,* and *C. ovalis* tend to benefit from a low N gift (N1), but suffer if the gift is larger.

Chamerion angustifolium, Rumex acetosella and *Trientalis europaea* react positively to the addition of PK. The species in the upper right-hand part of Figure 3, including *Vaccinium myrtillus, Melampyrum pratense* and *Dicranum polysetum,* respond negatively to additional supply of PK. The effect of PK addition alone has a significance level of 2%. The combined effect of N and PK was not significant ($P = 0.17$). Therefore it was discarded. It may affect some individual species, but not the species composition as a whole.

From Figure 4 it may be inferred that the Shannon's diversity index is almost negligibly lowered by the addition of ammonium nitrate.

Some other experimental evidence (Gerhardt and Kellner, 1986; Dirkse and Van Dobben, 1989; Van Dobben et al., 1992) indicates that acidification and eutrophication have different effects. In Sweden there is an interesting twofold field experiment (Tamm et al., 1974a; Van Dobben et al., 1992) in which pH manipulation is tested against N supply. The pH is lowered by spraying diluted sulphuric acid and raised by adding lime. Nitrogen is added as a compound (ammonium nitrate) at a rate of 40 kg N/ha/yr, with or without the addition of PK. The treatments started in 1968 and were repeated every year until 1976. There were 18 plots measuring 30 x 30 m^2 each.

The results show that the fertilization with ammonium nitrate is the most important factor in explaining the succession from *Calluna vulgaris, Vaccinium vitis-idaea* and *Cetraria islandica* to *Deschampsia flexuosa* and *Brachythecium spp.* This shift is slightly modified by pH manipulation. Acidification alone destroys most phanerogams, leading to vegetationless areas which are soon invaded by one single moss species, the common *Pohlia nutans.* The application of sulphuric acid was stopped in 1976, because then it had completely burnt away both the herb and moss layers.

Discussion

The effects of ammonium nitrate upon the species composition of moss and herb layers of pine forest are indisputable, yet the crude scale for estimating species abundance, and the fertilization effects merit discussion.

The rather rough nine-point scale used to estimate species cover did not blur the effects of the fertilization regimes. This crude estimate of cover was chosen to give a quick overview of the effects. However, a more detailed estimation of cover or abundance might have been desirable, especially in the light of further statistical analysis of the response of individual species to the treatments.

The results of a multivariate analysis of the floristic data leave little doubt that inorganic N is a key factor in the species composition of the undergrowth of pine forests. *Vaccinium vitis-idaea, Calluna vulgaris, Cetraria islandica,* and *Dicranum polysetum* react adversely to any addition of N. A small dose of N benefited (N1: 20 kg N/ha/yr) *Vaccinium myrtillus, Pleurozium schreberi* and *Dicranum scoparium,* but these species reacted adversely to larger doses. Large doses of N (N2-N3: 40-60 kg N/ha/yr) benefited *Rubus idaeus, Dryopteris carthusiana, Deschampsia flexuosa, Brachythecium oedipodium,* and *Plagiothecium laetum.*

Persson (1981) and Gerhardt and Kellner (1986) are among the researchers who have studied the effects of N fertilizers on undergrowth vegetation. Persson studied the effect of ammonium

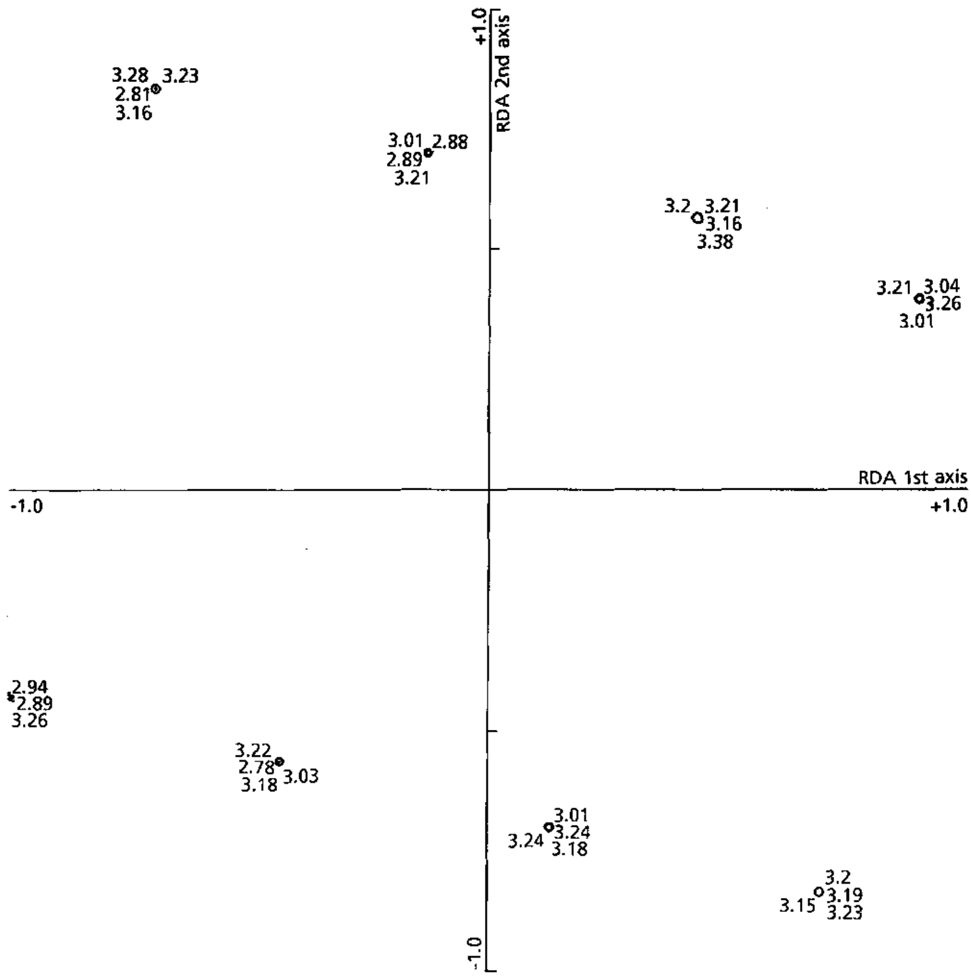

Figure 4. RDA ordination diagram of the Lisselbo E40 blocks and their corresponding Shannon's index of diversity (S): S=-SUM(P_i*ln(P_i)) P_i=abundance of species i.

nitrate on species composition in permanent plots (1973-1980) in a young stand of Scots pine at Ivantjärnsheden, ca. 60 km N of Lisselbo. Annual fertilization strongly benefited *Chamerion angustifolium* and *Rubus idaeus*, whereas lichens (*Cladonia spp.*) disappeared. Gerhardt and Kellner made a comparative study of species composition in plots with different fertilizer treatments and non-fertilized plots in stands of Scots pine and Norway spruce at four sites in Sweden. Repeated fertilization caused negative responses of *Cladina rangiferina, Pleurozium schreberi* and *Hylocomium splendens*. The grass *Deschampsia flexuosa* increased significantly in the plots given large amounts of nitrogen (as urea or ammonium nitrate). Mosses growing on litter (including *Brachythecium spp.* and *Plagiothecium spp.*) increased in the fertilized plots. Tamm (1974) gives some quantitative data on how dwarf shrubs are being ousted by raspberry in a Swedish spruce stand. These results agree well with the results of the Lisselbo experiments, stressing the major importance of plant-available nitrogen as a factor for plant growth and species composition. According to Burgtorf (1981), Holmen et al. (1976), and Tamm (1974) the same holds for the effects of N on the growth of Scots pine (*Pinus sylvestris*) and spruce (*Picea abies*).

Conclusions

1. In recent decades the species composition of forest undergrowth has changed in several areas of Europe, often indicating an increased availability of nitrogen and a decrease of pH.
2. Experimental evidence consistently proves that the effects of nitrogen fertilization can to some extent simulate the vegetation changes reported. The nitrogen effects override those of other nutrients.
3. Nitrogen fertilization causes pH to decrease.
4. The aim that forest reserves should develop undisturbed is unrealistic in many parts of Western and Eastern Europe.

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Ectomycorrhizal succession in Scots pine forests: the role of Deschampsia flexuosa

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Summary

It was investigated whether components in shoots and roots of the grass *Deschampsia flexuosa* inhibit ectomycorrhizal fungi. The growth rate of *Laccaria proxima, Rhizopogon luteolus* and *Paxillus involutus* appeared to be strongly inhibited by extracts of the shoots. Extracts of the roots inhibited the growth of these fungi only slightly. *Laccaria bicolor* was only inhibited by the strong concentrations of root extracts. The shoot extracts contained 3-5 times more high molecular weight components, aliphatic acids and phenolics than the root extracts. The role of *D. flexuosa* in ectomycorrhizal succession and its implications for successional processes in forest reserves are discussed.

Keywords: ectomycorrhizal fungi, phytotoxicity, succession

Introduction

In recent decades the grass *Deschampsia flexuosa* (L.) Trin. has spread enormously in Scots pine forests in The Netherlands. Some investigators (e.g. Mettivier Meyer et al., 1986) consider this increase to be part of normal succession, others (Tamm, 1991; Van der Werf, 1991) believe it is a consequence of increased nitrogen availability. At the same time ectomycorrhizal fungi characteristic of late stages of succession of Scots pine forests have become rare (Termorshuizen and Schaffers, 1991). *Deschampsia flexuosa* might play a causal role in this change, for instance by a phytotoxic effect on the growth of ectomycorrhizal fungi and/or on the formation of fruiting bodies. Hardly any fruiting bodies of ectomycorrhizal fungi occur in grass-rich pine forests (Veerkamp and Kuyper, 1992). Under controlled conditions Timbal et al. (1990) found that the grass *Molinia caerulea* (L.) Moench depressed the numbers of ectomycorrhizae formed by *Laccaria bicolor* (Maire) P.D. Orton, and inferred an indirect allelopathic effect. Such allelopathic effects might hamper the establishment and survival of ectomycorrhizal fungi in grassy pine forest. At present this is the most common forest type in The Netherlands and many forest reserves are represented by this forest type. This suggests there may be serious implications for the future development of tree species composition. It was therefore investigated whether components in shoots and roots of *D. flexuosa* have an inhibitory effect on mycorrhizal fungi.

Material and methods

Fungal growth

In the north-east of The Netherlands mycorrhizal fungi were isolated from carpophores in the autumn of 1990. *Laccaria proxima* (Boud.) Pat., an early successional species, was collected in a young Scots pine stand (3 years), *L. bicolor* in an old stand (65 years) and *Paxillus involutus* (Batsch: Fr.) Fr., both indifferent species in a middle-aged stand (27 years). All three stands were secondary. *Rhizopogon luteolus* Fr., an early successional fungus, was obtained from a primary middle-aged stand (15-20 years). These fungi were isolated on modified Melin-Norkrans agar medium. Extracts were made from the shoots and roots of the grass *Deschampsia flexuosa*. The grass originated from a 65-year-old Scots pine forest in The Netherlands and was sampled in the autumn of 1991. The shoots and roots were separated and dried (50°C, 24 h). To 475 ml distilled water 100 g dry matter of shoots or roots was added. Extracts of shoots and roots were made by shaking (22°C, 24 h). The extracts were autoclaved for 20 min. (0.5 atm, 110°C) and added to modified Melin-Norkrans agar medium in two concentrations: 1.6 and 7.9% (w/v). For inoculation mycelial plugs 6 mm diameter were cut from the edge of fungal colonies on MMN agar medium and transferred to media with the extracts and control media (no extract added). Each treatment was replicated four times. The agar plates were incubated at 22°C. The radial growth was determined by measuring the colony diameter every three days during the time the growth of the controls was linear. The periods during which colony diameter was measured lasted 17 days for *L. bicolor*, 44 days for *L. proxima*, 21 days for *P. involutus* and 12 days for *R. luteolus*.

Analysis of extracts

The concentration of water-soluble phenolics (polyphenols and simple phenolics) of shoot and root extracts was measured spectrophotometrically, using the Folin-Ciocalteus reagent. Tannic acid was used as a standard and the concentration of water-soluble phenolics in the litters was expressed as mg TAE (tannic acid equivalent) g^{-1} dry matter (Kuiters, 1987). Total C and N were determined by a Carlo Erba element analyser.

Autoclaved extracts used in this experiment and untreated extracts were analysed, to investigate the possible effects of autoclaving. Prior to analysis, samples were membrane filtered (0.45 μm). To ascertain the abundance and nature of organic compounds in the extracts, litter solutions were subjected to gel permeation chromatography using Sephadex G-25, with a separation range from 100 to 5000 dalton for dextrans. A column of 20 * 1.6 cm i.d. was used. Of each sample, 0.5 ml was brought on the column, eluted with a 0.01 M sodium acetate solution of pH 5.5 and the effluent was monitored for UV absorbance at 280 nm. This method allows the dissolved components to be fractionated into a high and a low molecular weight fraction; the latter consists of low molecular weight phenolic compounds.

Statistical analysis

The growth rates of the fungi were analysed for homogeneity by Bartlett's test. Normally distributed data were analysed by analysis of variance (MANOVA). Differences among means were evaluated with the LSD test ($p < 0.05$) (Sokal and Rohlf, 1981). Data not normally distributed were tested with the Kruskal-Wallis and Mann Whitney U-test (Siegel, 1956).

Results

Fungal growth

The growth rates of *L. proxima, R. luteolus* and *P. involutus* were strongly inhibited by the extracts of the shoots. The strong concentration of the shoot extract totally inhibited the growth of *L. proxima* and *R. luteolus*. The weak concentration of the root extracts had a significantly negative effect on the growth of *L. proxima*. Both concentrations of the root extracts reduced the growth of *P.involutus* significantly. *Laccaria bicolor* was not affected by the extracts, except by the strong concentration of the root extracts, which inhibited growth.

Composition of extracts

The extracts of the shoots contained about 7 times more total C and about 3-6 times more total nitrogen than the extracts of the roots (Table 1). More phenolics were found in the shoot extracts than in the root extracts (Figure 2).

Separation on Sephadex G-25 showed that the shoot extracts contained about 3 times more high molecular weight components and about 5 times more aliphatic acids and phenolics than the root extracts (Figure 3). The autoclaved extracts contained less of these components than the untreated extracts (Figure 3).

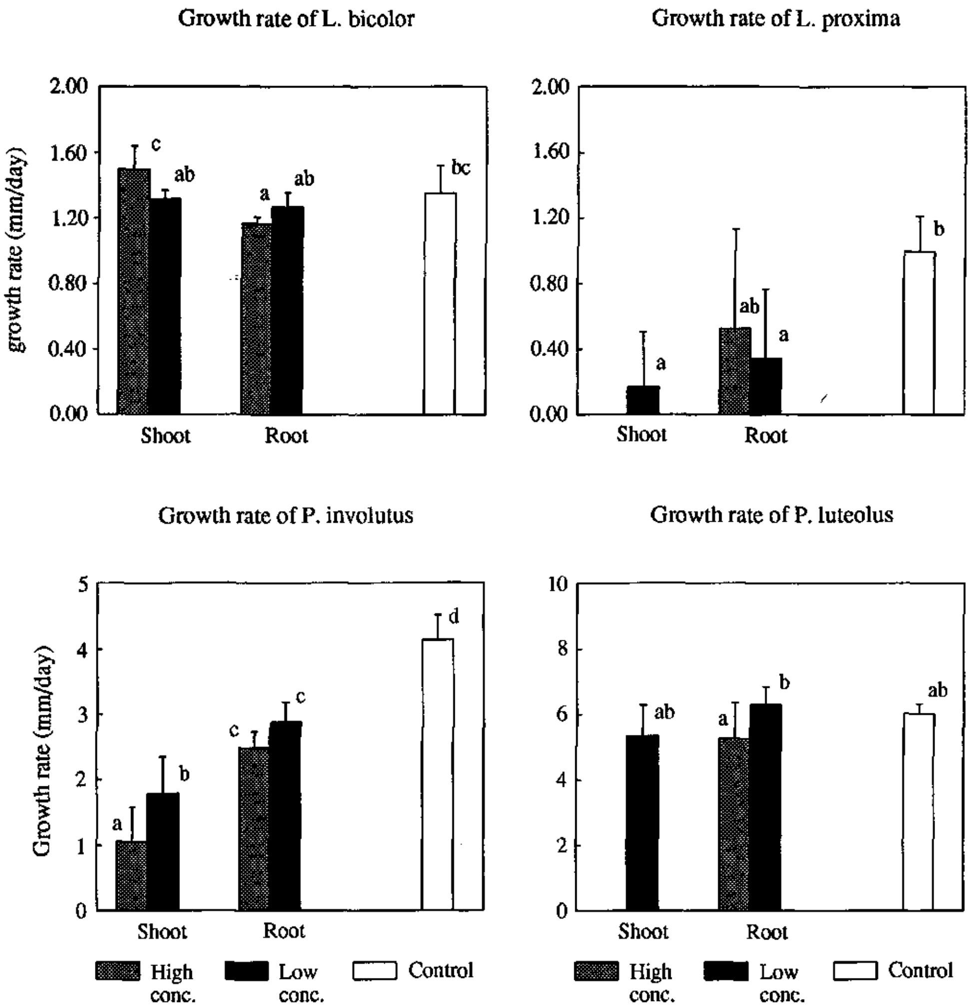

Figure 1. Average growth of L. bicolor (a), L. proxima (b), P. involutus (c) and R. luteolus (d) on agar with grass extracts in two concentrations (1.6% and 7.9% (w/v). Pairwise comparisons (LSD and Mann Whitney U-tests) between growth rates with a bar that are followed by completely different letters are significantly ($p < 0.05$) different.

Discussion

The growth of all species except of *L. bicolor* was negatively affected by the extracts of *D. flexuosa*. This indicates that *D. flexuosa* may negatively influence the development of ectomycorrhizal fungi under field conditions. Autoclaving caused an underestimation of the amount of

Table 1. Total C and N of the autoclaved and untreated extracts of the shoots and the roots of D. flexuosa in mg/l.

Extracts	Autoclaved mg/l	Total C mg/l	Total N
Root	+	637	72
Root	-	788	45
Shoot	+	4535	250
Shoot	-	5663	280

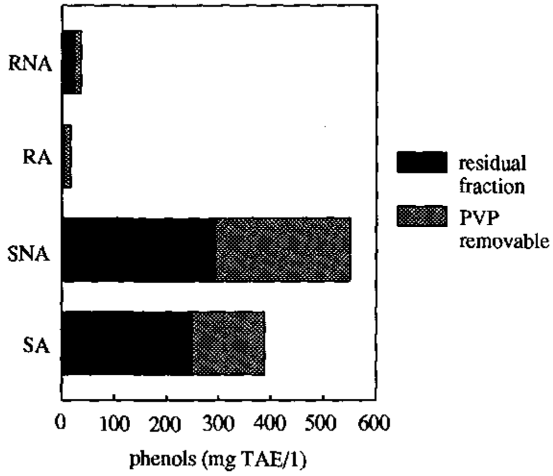

Figure 2. The amount of phenols in root and shoot extracts in mg TAE/l. RA = autoclaved root extract, RNA = untreated root extract, SA = autoclaved shoot extract and SNA = untreated shoot extract.

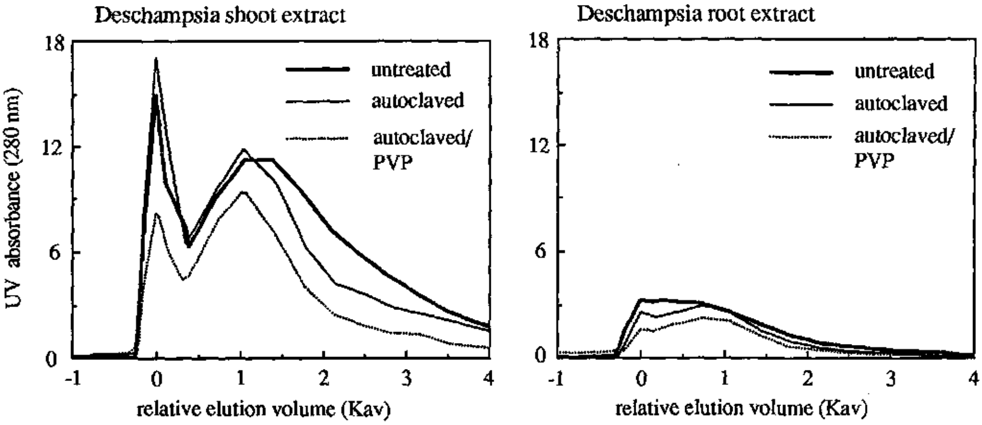

Figure 3. Elution profile of the components of root and shoot extracts after separation on Sephadex G-25 for molecular size.

phenolics. It is unknown how strong the effects are in the field, because the concentrations of the extracts are not translatable to field conditions.

It is still unclear which organic components are responsible for the negative effects caused by the grass extracts. Investigations by Coté and Thibault (1988) and Timbal et al. (1990) suggest that phenolics might play an important role. In our experiment the shoot extracts which caused the largest reduction of the growth contained much more phenolics and high molecular weight components than the root extracts.

Phytotoxicity of extracts of *D. flexuosa* may be only one of the causes of the decline of ectomycorrhizal fungi. Phytotoxity of Scots pine needles might also play a role. *Laccaria proxima* and *R. luteolus*, both early successional species, were found to be sensitive to needle extracts as well. *Paxillus involutus* which occurs in stands of different ages, seems to be more sensitive to grass extracts than to needle extracts (Baar et al., 1992). Neither can the absence of *L. bicolor* in grassy stands of *P. sylvestris* be attributed to phytotoxicity of Scots pine needles; *L. bicolor* was even stimulated by needle extracts (Baar et al., 1992). The absence of *L. bicolor* may be explained by the grass mat of *D. flexuosa* mechanically impeding the formation of fruiting bodies. Such a grass mat may impede not only the formation of carpophores but also the establishment of spores. The latter may hold for other ectomycorrhizal fungi too.

It therefore seems likely that the dense cover of *D. flexuosa* in several forest reserves affects successional processes by favouring facultatively ectomycorrhizal trees (e.g. birch) or tree species that can also form vesicular arbuscular mycorrhizae (e.g. rowan tree). It will accelerate developmemt towards deciduous forests. Mycological observations in grassy pine forests compared with pine forests in the coastal area tend to support this hypothesis (Veerkamp and Kuyper, this volume).

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Water management as a factor in forest development

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Summary

Watermanagement is an important factor in forest development because of the influence of water on biological, physical and chemical processes as well as the financial aspects of watermanagement.

Special attention must be paid to the specific water balance of a tree. Tree species show different mean total interception and transpiration. At the same time minor geographical variation can be calculated due to climatic effects, like wind velocity, temperature and radiation.
The relation between soil water content and growth-parameters of trees is given. Calculations show that some species, such as Corsican pine, can cope better with drought than other species like beech and ash.

The relation of atmospheric deposition on forest stand stucture is explained. A recent study showed high correlations between acidifying components and parameters reflecting the aerodynamic roughness of a stand. Parameters related to the surface area of the canopy, such as LAI and crown volume, also correlate with net throughfall fluxes of SO_4, NO_3 and NH_4.

Keywords: watermanagement, waterbalance, deposition, tree growth

Introduction

The Dutch have a special interest in water management of forests for several reasons. First, in the Netherlands there is a tradition of controlling the environment, and in particular the hydrological situation, to a great degree. This is because of the country's geography (the low-lying delta of the rivers Rhine and Meuse, with a precipitation excess). Dutch scenery testifies to this control in urban and in rural regions. Table 1 illustrates the importance of water in The Netherlands: the areas under forest and nature areas, 0.3 mln and 0.2 mln ha respectively, together comprise ca. 12% of The Netherlands; of this, half is wet/waterlogged. Nearly 200 000 hectares (4.5%) is under the aegis of the Dutch State Forest Service.

Table 1. Statistics on forest areas in The Netherlands.

	area (ha.)	%
The Netherlands	> 3.5 mln	100
Forest/nature areas	0.50 mln	12
Wet/waterlogged forest/nature areas	0.25 mln	6
State Forest Service	0.19 mln	4.5

The second reason for the State Forest Service's interest in water management is financial. About 15 mln guilders per year is spent on water management. This not only represents direct investments; almost two-thirds of the total amount consists of taxes paid to district water boards.

Altogether a quarter of the budget is free to be spent on various kinds of water management measures for the benefit of nature and forest, such as:

- isolating areas from the inflow and outflow of surface waters by building dams and weirs;
- diverting water because of water quality problems;
- guiding water through helophyte-marshes in order to improve the waterquality;
- restoring original hydrological conditions, e.g. by exfiltration by raising the piezomatric surface.

Water balance of a tree

The main factors affecting the growth of trees are the water table and the physical and chemical conditions of the soil. The latter includes the wetness of the soil and factors like penetration resistance and dimensions of soil particles. The two latter factors are especially important for the growth and development of roots.

Altogether, the relations between ground water level, soil water conditions and growth of trees are rather complex. There are different feedback reactions as is illustrated by the following: in a well-growing forest evaporation steadily increaeses because of the growth of the vegetation. This increasing evaporation causes the water table to fall, which results in lack of water in the soil, which in turn causes growth to decrease and the water table to rise again, and so on.

Conversely, in a situation of equilibrium, under optimal groundwater level and maximal growth, a rise in the phreatic head will cause growth to decrease. Consequently, water use will decrease and the groundwater level will rise again, and so on.

The water balance of a tree takes a central place in the complex relation between water management - site - growth of trees (Van Beusekom et al., 1990). Figure 1 shows several components of the water balance.

Very simplified, the net groundwater discharge may be considered to be a result of gross precipitation, interception and transpiration. Various characteristic situations may be considered, as is shown in Figure 2: summer and winter; situations with or without capillary rise.

Several components may be measured, directly or indirectly, or may be calculated with computer models. Dutch research institutes recently studied this. The findings are described below.

In	: gross precipitation	= N
	stem flow	= N_s
	through fall	= N_d
	capillary rise	= Gaa_1
	intake by roots	= Gaa_2
Out	: transpiration	= T
	interception	= I
	soil eva poration	= E_{bd}
	percolation	= Gaf_1
Rest	: Net Groundwater discharge	= Gaf_2

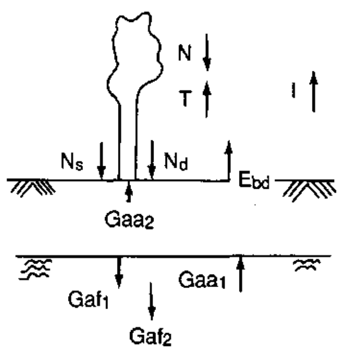

Figure 1. Diagram of the water balance of a tree and its main components.

Water use and discharge

During the last decade research has been done on the evaporation from forests. Computer models have been developed to simulate relevant processes. However, in The Netherlands these models cannot be used without modifications, because certain conditions (especially the climatic conditions

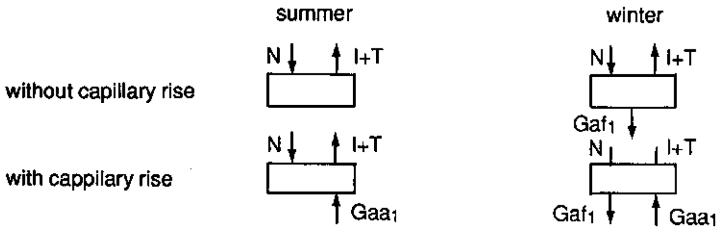

Figure 2. Schematic diagram of four characteristic situations of the water balance of a tree. See Figure 1 for abbreviations.

and stand characteristics) are different. Therefore, researchers in the Department of Physical Geography of Groningen University have adapted these models to Dutch conditions (Nonhebel, 1988). The Gash model (Gash, 1979) was used for interception, a model based on the Stewart model (Stewart, 1988) was used for transpiration, in combination with the Penman equation (Van Roestel, 1984). After this first adaption the models were tested and run for several specific situations, such as geographical variation, different soils and different stands. Table 2 shows the geographical variation calculated which is attributable to climatic effects, such as wind speed, temperature and radiation.

Table 2. Geographical variation in the yearly means of gross precipitation (mm) and water use (mm and percentage) per land use/tree species determined over the period 1974 - 1978 on sandy soils in five areas.

Area	Kooy	Vliss.		Eelde		Bilt		Z.Limb.		National Mean			
Gross precipitation		682		681		696		721		707		697	
Water use (in mm & %)													
Arable	323	(46)	312	(46)	328	(47)							
Grassland	445	(64)	456	(63)	450	(55)							
Dark conifers													
Norway spruce		587	(86)	635	(92)	629	(90)	656	(91)	660	(92)	633	(90)
Douglas-fir		547	(80)	593	(87)	576	(83)	571	(80)	584	(82)	574	(82)
Mean	567	(83)	614	(89)	603	(86)	613	(85)	622	(87)	603	(86)	
Light conifers and deciduous forest													
Scots pine		382	(56)	410	(60)	383	(55)	376	(52)	384	(54)	387	(56)
Japanese larch		351	(51)	404	(58)	361	(52)	340	(49)	349	(50)	361	(52)
European oak		374	(55)	430	(62)	417	(59)	388	(55)	431	(61)	408	(59)
Beech	330	(48)	388	(56)	339	(49)	315	(45)	333	(47)	341	(49)	
Poplar	375	(55)	447	(64)	405	(54)	349	(56)	401	(56)	395	(57)	
Birch	354	(52)	416	(60)	385	(55)	362	(50)	387	(54)	381	(55)	
Mean	361	(53)	416	(60)	381	(54)	356	(49)	381	(54)	379	(54)	

The results show that on the south-western site (Vlissingen) the total water use (transpiration plus interception) exceeds the totals of other sites.

Table 3 shows that total water use varies between the species, with a remarkable difference between the dark conifer forest (spruce and Douglas- fir) and the other species (light conifer forest and deciduous forest).

In recent years the Winand Staring Centre in Wageningen has worked on a soil water balance

Table 3. Yearly means of gross precipitation (mm) and total water use (percentage) of various land uses on sandy soils.

	1974	1975	1976	1977	1978	AVERAGE
Gross precipitation (mm)	907	698	530	741	641	704
Total water use (%)						
Arable land	44	49	49	51	46	48
Grassland	58	69	65	62	66	64
Spruce (Norway)	83	97	105	94	100	90
Douglas-fir	70	80	91	77	82	82
Oak	50	60	67	54	61	59
Poplar	48	57	64	51	57	57
Scots pine	45	54	64	52	55	56
Birch	43	52	60	46	54	55
Larch	43	51	58	46	51	52
Beech	41	48	55	43	48	49

Discharge can be calculated: gross precipitation minus total water use

Table 4. Mean variation of monthly total use of water (mm) for various land use.

	OAK	FIR	GRASSLAND	ARABLE LAND
SUMMER	30-110	30-65	25-95	5-120
WINTER	5-30	10-45	5-40	5-15

model SWATRE/SWACROP (Hendriks, 1990). This dynamic model enables the the water balance to be simulated. The following parameters are input in the model:

- net radiation, temperature, air humidity, wind speed, precipitation;
- physical charateristics of the soil;
- species, height of trees, density of the stand, leaf area index, and root length.

In the meantime the evaporation of a northern red oak stand was measured. Two methods were used: the energy balance (Bowen-Ratio) method and the water balance method. In the first method the energy balance is found by measuring several components above the forest. The main component is the net radiation. The available energy that is determined may be divided over two heat fluxes: palpable and latent. The latent flux is used to calculate the evaporation. Preliminary results of these investigations clearly showed that both the methods yielded only small differences in the evaporation.

Moisture, growth and production

The relation between soil water content and the growth parameters of trees may be very relevant in practice. It enables the effect of changes in the moisture conditions on production to be predicted. The main processes to be dealt with are the transpiration of the superficial parts of the tree and the water use by the roots. The transpiration process depends on the groundwater level and some physical and chemical properties of the soil. The hydrological environment determines the potential rate of transpiration.

The water use depends on the soil moisture content and on whether the soil water is accessible to the roots. Therefore, apart from the mere occurrence of soil water, the mechanical properties of the various layers are important, as these influence root penetration.

Too shallow ground water levels cause lack of oxygen and toxicity. As a consequence, growth will decrease. In contrast, a very deep groundwater level may cause a decrease of water use and transpiration and hence reduce growth. Stand age is also important. As trees age they become less adaptable.

Table 5 gives the relationships between the relative growth of some tree species and the available soil water (Van den Burg, 1987). Under optimal conditions of soil water content the growth is assumed to be maximal (100%). If there is less soil water content, growth per tree species declines. Unfortunately no observations were done on sites with less than 50 mm available soil water. It is clear that some species such as Scots pine and Corsican pine can cope with drought better than, for example, beech and ash.

Table 5. Average relative growth of some tree species, belonging to various ranges of avialable soil water (capillary rise included).

Available soil water	Scots pine	Corsican pine	Douglas fir	Japanese larch	Norway spruce	European oak
1 200 mm	100	100	100	100	100	100
2 150-200 mm	100	98	98	96	83	94
3 100-150 mm	93	84	84	77	59	88
4 50-100 mm	70	60	54	49	40	67
5 50 mm	-	-	-	-	-	-

Available soil water	Aspen	Sessile oak	Northern red oak	Beech	Black poplar	Ash
1 200 mm	100	100	100	100	100	100
2 150-200 mm	97	83	80	85	90	87
3 100-150 mm	89	66	62	64	74	54
4 50-100 mm	58	50	49	38	21	14
5 50 mm	-	-	-	-	-	-

Water quality

Water quality may be relevant in two ways: atmospheric deposition, net throughfall fluxes and infiltration on one hand, and soil water quality and growth of trees on the other hand. The latter is not dealt with in this context.

Recently, research the Department of Physical Geography, Utrecht University has done research on atmospheric deposition in relation to forest stand structure. The aim was to elucidate the processes involved, to improve deposition models and to evaluate forest structure adjustments, in order to reduce the rate of atmospheric deposition to forests.

During one year the wet and dry deposition in thirty forest stands was estimated by monitoring bulk precipitation and throughfall. As well as the atmospheric input, forest structure was also characterized for each forest stand. It was found that statistically significant differences in net throughfall fluxes occur between forest stands and between tree species. Figure 3 shows the differences of yearly mean net throughfall fluxes per tree species (Douglas-fir, Scots pine and oak).

Several good relationships were found between net throughfall fluxes and forest structure characteristics. Especially strong correlations were found between acidifying components and parameters reflecting the aerodynamic roughness of a stand. Parameters reflecting the collecting surface area of the canopy parameters, such as LAI, crown projection and crown volume, also correlate significantly (although to a lesser extend) with net throughfall fluxes of SO_4, NO_3 and NH_4. From the study it was concluded that in general, thinning of forest stands causes a reduction in the canopy collecting surface area as well as a reduction of the aerodynamic roughness (Van Ek and Draaijers, 1991). As a consequence the atmospheric deposition of the stand will be reduced. However, for forests with a very dense canopy the occurrence of gaps may enhance the aerodynamic roughness. A decrease or increase of atmospheric deposition in such forests will ultimately be determined by the net effect of the change in aerodynamic roughness and canopy collecting surface area.

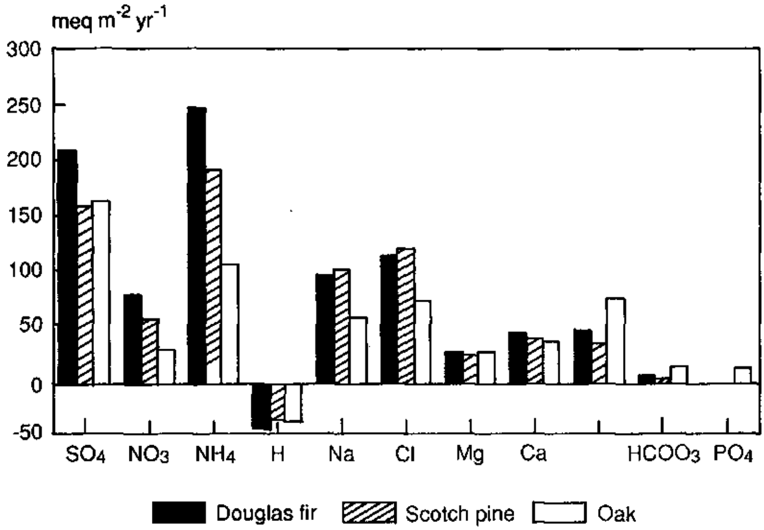

Figure 3. Yearly mean net throughfall fluxes (meg m^2 yr^1) per tree species.

Examples in practice

Many forests in The Netherlands were planted on moist or wet sites several decades ago. In those days the areas were artificially drained by trenches, ditches and drains. Until now, these ditches have been maintained each year. The cost of this is enormous. But hydrological and forestry conditions have changed. For various reasons many sites now suffer from drought. On the other hand, there is a trend towards multifunctional forest objectives. In many cases the situation needs to be reassessed. Therefore in the areas of Hooghalen, Leende, Mastbos and Flevoland integrated studies were carried out in order to optimize the relation between production function and the costs of water management, taking into account other functions if necessary. In general, the research was involved four steps:

- First the present hydrological situation and the management streategy were described.
- Next, the hydrological conditions needed for optimal growth of the present tree species were created.
- Then these two situations were compared.
- Finally various scenarios were postulated, with various combinations of forestry and hydrology and including necessary mutual adjustments and, of course, the costs involved (investment and exploitation).

These studies were done jointly by a hydrologist and a forester and resulted in recommendations for management:

- For instance it was recommended to focus on a more extensive maintenance of forests on wet sites, in combination with maintaining the hydrological situation. This might enable a more "natural" forest to develop.
- In other cases it was recommended not to cut trees in large areas, in order to avoid a rise in groundwater levels.
- On wet sites it was thought to be wise to achieve a good vertical structure in the forest. This would protect against wind effects and allow shallow-rooted trees to grow.

Recently, the local forest managers drew up their management plans taking these recommendations into consideration. This may result in the forests fitting more closely with natural hydrological conditions and spontaneous processes.

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Dutch alder and birch carrs

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Keywords: forest ecosystem classification, vegetation types, site factors

Introduction

In the project "Classification of Dutch Forest Ecosystems" Dutch forests are described as a series of related ecosystems. These relationships are depicted in schemes intended to assist in the management, conservation and development of forests and woodlands. The approach aims at integrating vegetation types, site characteristics and management practices. The project focuses on present-day ecosystems, including recently planted forests. Alder and birch carrs are distinct group of forest ecosystems in The Netherlands. They occur on bogs (birch), fens (alder and birch), and in brook valleys (mainly alder).

Forest ecosystem classification

The ecosystem classification starts by clustering a large number of vegetation samples (relevés) on the basis of the floristic assemblage. A site typology is then drawn up, based on the primary site factors that prove to be relevant for different developments in vegetation. At an abstract level of classification, geomorphological and hydrological features are used to distinguish three main land systems: brook valley systems, bogs and fens. A further subdivision into site types is elaborated using the criteria: water level, water dynamics, water quality, thickness of the peat layer and occurrence of loamy layers in the topsoil. On each site type, one or more forest ecosystem types may occur, defined as combinations of site types and vegetation types (Figure 1).

In addition to the morphological soil features, the chemical characteristics of each site are studied. Striking differences in water quality (in terms of ionic ratio and electrical conductivity) have been found between site types (Figure 2).

In addition to the floristic composition the vegetation, the structure of the forest types is systematically described. On 10 x 30 metre plots the canopy height and cover are recorded and depicted. Special attention is paid to the structural variation within the herb layer.

Forest development

Various plant communities may occur on the same site type, because of the different impact of spontaneous developments as well as the former or actual land use practices. The ecosystem types occurring on a similar site type have been arranged in schemes in which the dynamic relationship between the plant communities is indicated (Figure 3). These schemes may be used in order to predict spontaneous forest development and the impact of different forest management practices or environmental impacts (e.g. water extraction, lowering of ground water level, water pollution).

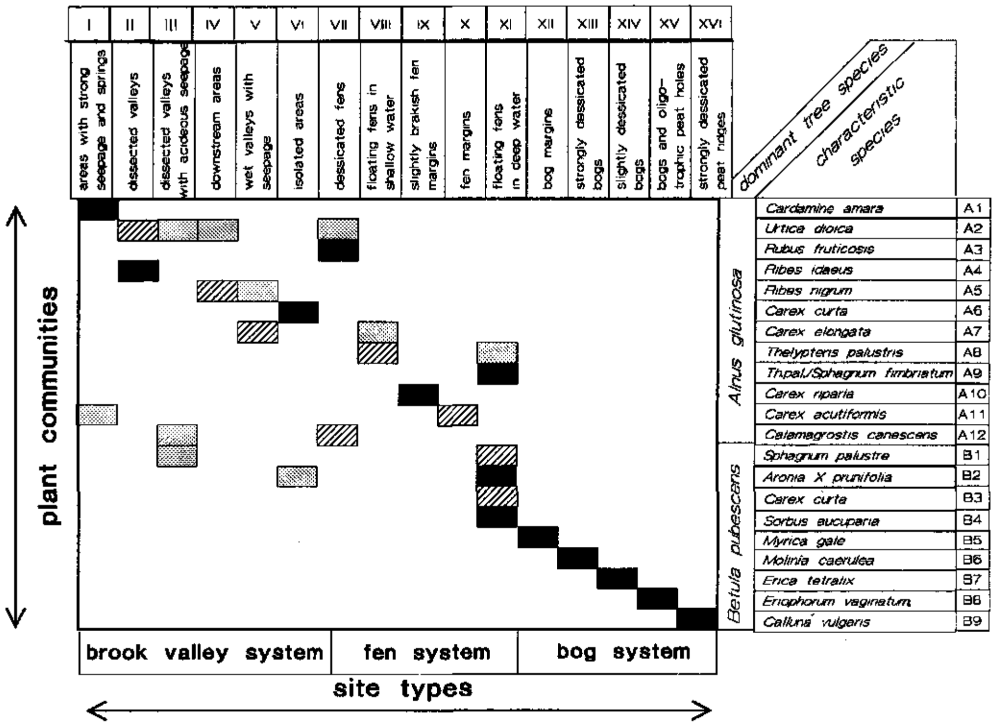

Figure 1. Ecosystems are defined as unique combinations of plant communities and site types. For a description of the plant communities and the site types, see Stortelder et al. (in prep).

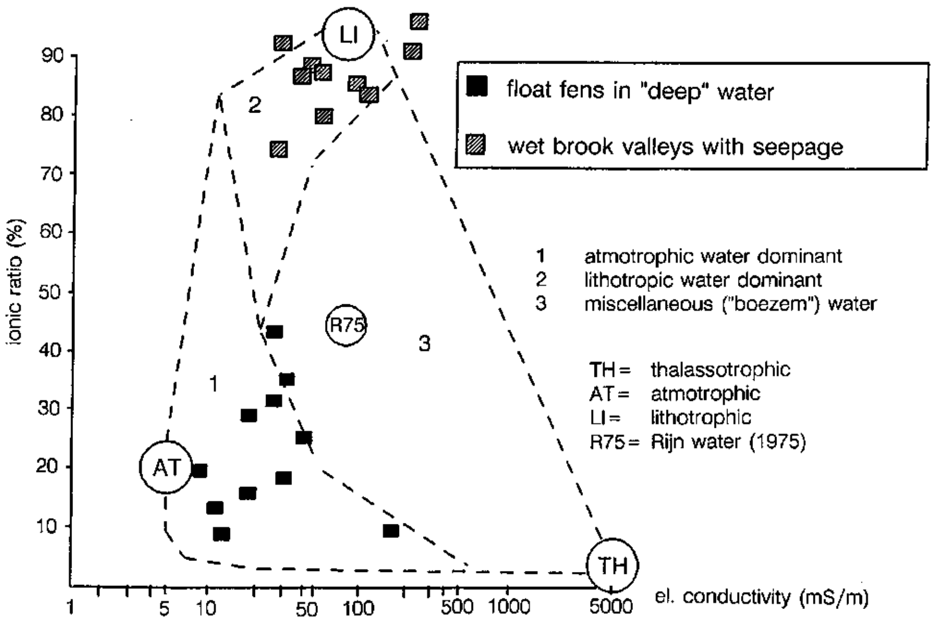

Figure 2. Example of two site types differing greatly in water quality; diagram of ionic ration ($Ca^{2+}/Ca^{2+}+Cl^{-}$) and electrical conductivity after Van Wirdum (1991).

An example

Alder carrs may develop fast and over large areas. Figure 4 shows the spontaneous development of alder carrs during the period 1932-1982 on former reed lands in the Weerribben area is shown.Abandonment of land and extensivation of reed cultivation and grazing clearly affect landscape development by enabling spontaneous forest development.

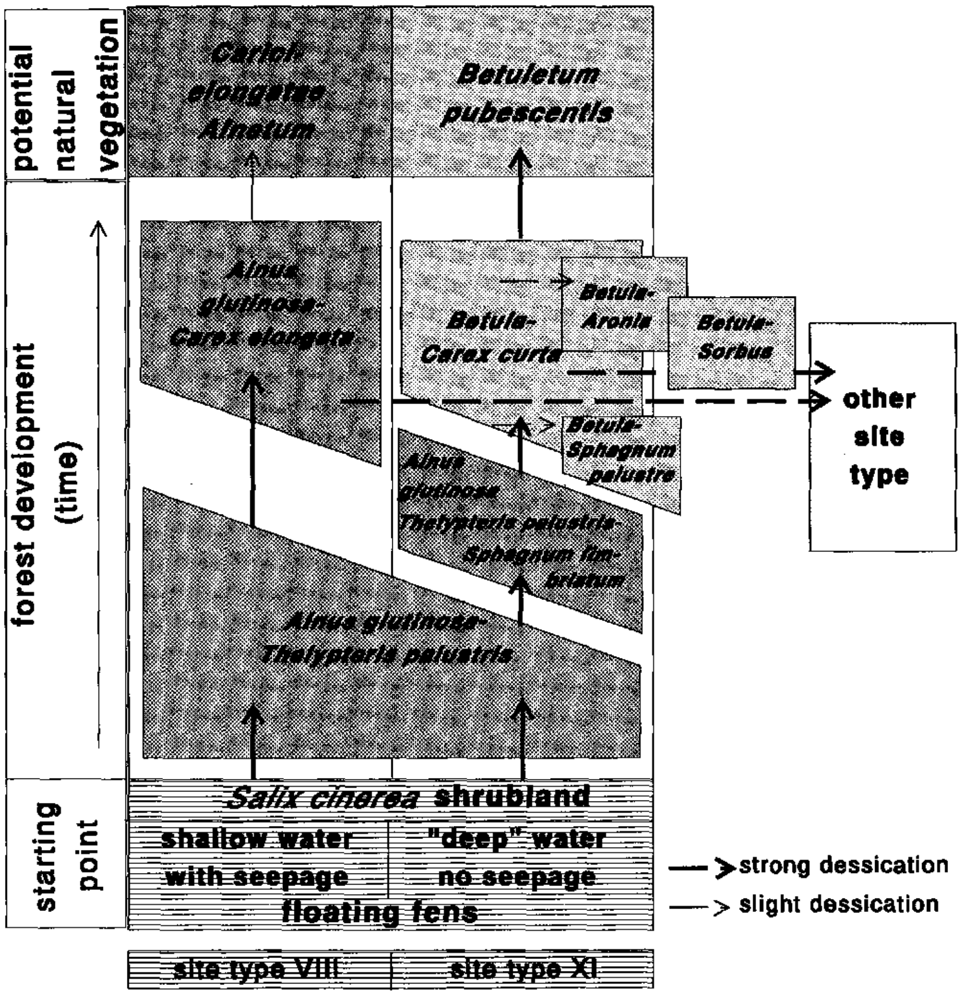

Figure 3. Forest development on two ecologically related site types. Severe "drying up" (a fall in the water table) leads to a transition towards a new, ecologically aberrant site type.

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B. 1962

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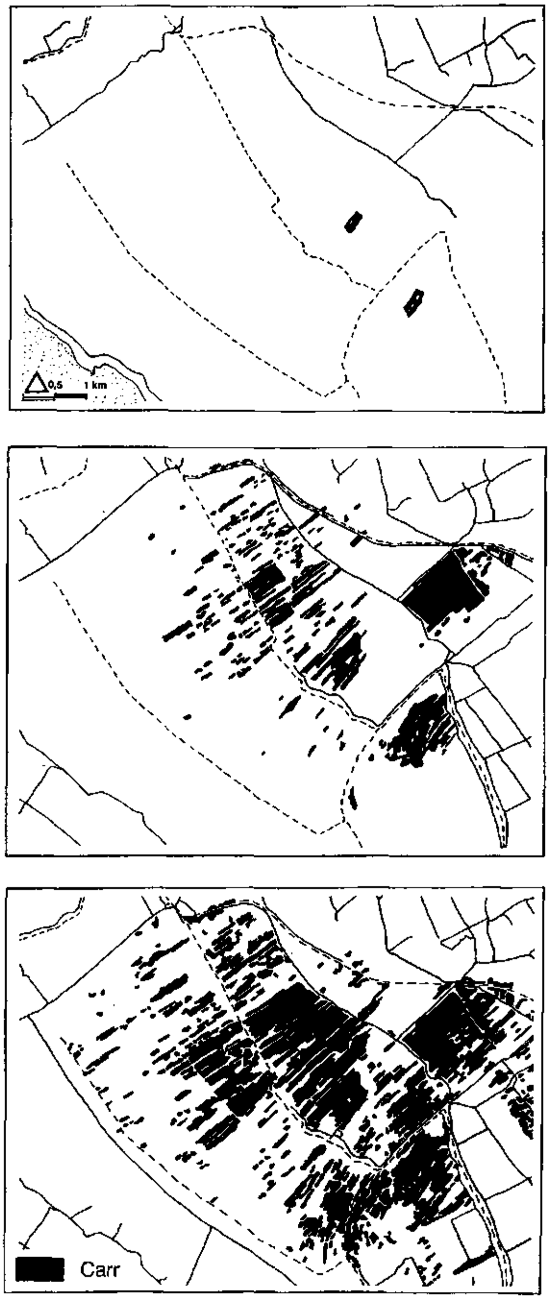

Figure 4. *Forest development in the Weerribben area, province of Overijssel, The Netherlands (after Wolf, 1991).*

Application of forest dynamics research in landscape planning and management.

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Summary

Forest research in Scandinavia includes both the more traditional investigations of forest dynamics at the population and community level as well as the use of computer simulation models. Both approaches are complementary and can be used in planning and management. Historical evidence and extrapolations to the future indicate that communities are by no means spatially or temporally fixed. Natural and anthropogenic changes operate continuously. present research which examines changes in the distributions of some of the major tree species such as Picea abies in the last 4000 years, is described. Evidence from pollen and charcoal indicates that these changes are under the overall control of climate though disturbances are extremely important in changing a landscape, once critical climatic thresholds have been crossed. We also look to the future, examining possible effects of climate change on landscapes. We describe results from different approaches including the correlative approach, the static shell approach and dynamic modelling methods using examples from Sweden and Italy. Finally we try to place this research in a landscape perspective and look to possible options available for landscape management in periods of rapid change.

Keywords: forest dynamics research, modelling, climate change, landscape management

Introduction

In this contribution some of the research on forest dynamics that is being undertaken in Scandinavia is examined, with particular emphasis on the uses of it for landscape planning and management. It is natural that much of the research that directly relates to landscape management is concentrated on the effects of the environment on forest dynamics. We think in particular of the possible effects of global warming on forests and the likely responses which will be required from landscape managers in order to cope with these changes.

Changes in the world's climate are predicted to happen in the next 50 to 200 years as a direct effect of increasing concentrations of greenhouse gases (Bolin et al., 1986; Houghton et al., 1990). Several experiments with General Circulation Models (GCMs) (Harrison, 1990) have been performed and the output from the models suggest that such changes are likely to occur. However, model predictions disagree on the degree of change. But there is general agreement on one aspect; the greatest degree of warming is likely to occur in high latitudes (Schlesinger and Mitchell, 1987; Hansen et al., 1988) with changes of a lesser magnitude elsewhere. This area of greatest warming includes the Fenno-Scandian region and it is here that there is much research under way into possible effects on forest as well as other ecosystems, such as the possible changes in the famous limestone grasslands on the island of Öland which are of particular interest to us (Krahulec et al., 1986; Peet et al., 1990; Van der Maarel and Sykes, 1993).

Forest dynamics, meaning the changes in structure and species composition occurring in forests, are ultimately under the control of climate. Indeed, changes predicted to occur along with regular disturbances that have occurred in the past, indicate major consequences for Scandinavian forests. We examine first research into past forest communities and then look into the future.

However, we should first distinguish between some different forms of forest dynamics, that is:
- secular succession: long-term changes under the influence of changing climatic conditions;
- primary succession: natural development from virginal substrates;
- secondary succession: forest development after agricultural use;
- regeneration succession: development after disturbance, storm, fire.
This paper will focus on secular and regeneration succession.

An historical perspective

According to recent findings Scandinavian forests have had only rare periods of stability in the last 10 000 years (Bradshaw and Zachrisson, 1990; Bradshaw and Hannon, 1992). For example, if we examine one of the major species in Scandinavia - *Picea abies* - we find that throughout the Holocene there has been a steady movement westward so that spruce entered Sweden 4000 years ago (Huntley, 1988), moving steadily throughout Scandinavia to its present position today where it is found almost everywhere except in the far south of Sweden and in the extreme west, in coastal Norway.

Bradshaw and Hannon (1992) have studied the dynamics involved with this on a local scale, using pollen and charcoal analysis from tiny bogs within the forest of Fiby near Uppsala. They found that there were three different dynamic periods:

1. A mixed deciduous forest period occurring 4000 to 2200 yr BP which was dominated by *Betula* and *Pinus* pollen, though *Alnus, Corylus, Quercus, Tilia* and *Ulmus* were also present. There were many charcoal fragments indicating repeated burnings in the area, which were likely to be natural before 2000 yr BP. Abrupt changes in pollen occurred around 2500 yr BP caused by some disturbance event such as severe late frosts. *Quercus, Alnus, Tilia* and *Corylus* all decrease and *Betula, Pinus*, grasses and *Calluna* increase. *Picea* occurs for the first time in this period. Its immigration into the area has been attributed by Huntley (1988) to colder winters, increased precipitation and storms. A further disturbance occurred around 2200 years ago affecting other canopy tree species and allowed the *Picea* population to increase in size.
2. A small *Picea abies* population was present during a period of relative stability 2200 to 200 yr BP. The tree canopy was composed mainly of *Quercus, Alnus, Pinus, Betula* and *Corylus*. *Picea* was still subordinate during this phase. *Calluna* was again common and fires which were frequent were possibly now human influenced.
3. A *Picea abies* dominant-phase started about 200 yr BP lasting to the present. A dramatic change occurs in composition and structure of the forest during this phase. *Picea* rises to dominate the forest and the canopy closes over. Burning and grazing ceased, this change in the disturbance regime resulted in a greatly modified forest. The information gathered by Bradshaw and Hannon (1992) contributes to the argument concerning Hesselman (1935) and Sernander (1918, 1936) and the role of a particularly severe storm about 200 years ago. Sernander suggested that the open forest conditions resulting from the storm released suppressed *Picea* trees, allowing them to attain dominance. The data of Bradshaw and Hannon (1992), however, support the Hesselman (1935) view that human disturbance and grazing had kept the forest open long before the storm occurred and it was the termination of these activities perhaps combined with the storm effects which led to the *Picea* dominated forest of today.

The forest dynamics at Fiby over the last 4000 years show a movement from a nemoral to boreal forest. Liu Qinhong and Hytteborn (1991) have shown that disturbance at the stand level is important in the forest while Bradshaw and Hannon (1992) point out that disturbance also has an important role in aiding climatically-induced shifts in vegetation type. They show that at the landscape scale changes in vegetation over long-period may seem to be gradual (Huntley and Birks, 1983) but at the local level can occur much more quickly. Disturbances at 2500 and 2200 yr BP were decisive in the change from a nemoral to boreal forest. They suggest that disturbances, after critical climatic thresholds have been crossed, are extremely important -

possibly causing major changes in forest composition. This notion has important consequences for us as we go through a period of rapid climate change.

At a larger scale the role of *Picea* in southern Scandinavia is also of interest, particularly with regard to landscapes and climate change effects. Its range is thought to be climatically controlled, along with that of *Fagus sylvatica* (Huntley et al., 1989; Dahl, 1990). In Sweden these two species meet in an area in southern Sweden where they are likely to be in some sort of competitive interaction, at least as far as when they occur on the same soil type - *Fagus* is found without *Picea* on rich soils and *Picea* without *Fagus* on poor soils (R. Bradshaw pers.comm.). Both are potential dominants and slight variations in the controls on their competitive abilities could greatly affect the forest composition of the area. It is this area that is predicted to be affected, maybe to a large extent, by changes in climate.

Thus historical research tells us that both on a local and a landscape scale the dynamics in Scandinavian forests are under the over-riding control of climate, but disturbance in the form of fire or by some other anthropogenic influence can be extremely important.

Looking to the future

Much research in Scandinavia is at present concentrating on the climate change problem and attempting to predict how this will affect the landscape. This follows a number of lines, three of which we describe: the correlative approach, an approach assessing the sensitivity of individual species, and the use of simulation modelling of forest dynamics in climate change experiments

A correlative approach

The correlative approach of Dahl (1990) and Holten (1986, 1990) has been used to predict plant distributions both in Norway and in Europe. This approach has one advantage in that no eco-physiological explanation is required to predict species distribution patterns. Essentially these authors use correlation with some climate parameter or parameters to explain distributions. This enables future distributions of individual species to be predicted from predicted climate changes. For example, Dahl (1990) has produced new distribution maps for *Picea abies* and *Fagus sylvatica* using the correlative approach under expected climate changes. They are then compared with current distributions. He predicts an expansion of *Fagus* in eastern Europe and further movement into Scandinavia using an increase in winter temperature of 4° C. In contrast, with a similar increase *Picea*, whose present distribution is correlated with the -2.0°C isotherm, is likely to retreat from much of south-eastern Europe and southern Scandinavia.

A species sensitivity approach

An approach being developed in our group (Sykes and Prentice, in prep.) is intermediate between the correlative approach and a full dynamic simulation approach and estimates species sensitivity to climate changes. It is intended to give high resolution information at the landscape scale. This approach involves interpolating climate station data of mean monthly temperature, precipitation and sunshine (Leemans and Cramer, 1990) down to a grid of 0.5° cells over the whole of northern Europe. Species distributions are then described according to present-day climate and a quantitative measure of the relative performance of individual species in that climate is calculated. A number of future climate scenarios can then be used to assess species sensitivities to these changes at the resolution of individual 0.5° grid squares.

Dynamic forest modelling approach

A Swedish example: A fully dynamic approach to future climate change involves simulation modelling of forest dynamics. Forest gap modelling has been shown to successfully simulate small-scale forest dynamics in Sweden and elsewhere e.g. FORSKA 1 in Fiby, Uppsala (Leemans and Prentice, 1990). But from the point of view of landscape management and effects of climate change the updated version FORSKA 2 is required (Prentice et al., 1992). This allows simulation of a generalized landscape, where the landscape is treated as an array of independent patches. A disturbance regime is available which can be set to allow an increasing likelihood of disturbance with age of the patch, so that a mosaic of different-aged patches is produced over the landscape. Climate is allowed to affect the establishment and growth of individual species, this includes the effects of minimum growing degree days, maximum and minimum temperatures of the coldest month, minimum temperature of warmest month and a drought index based on the Priestly-Taylor coefficient.

Prentice et al. (1991) allowed the model to select from more than twenty available tree species, and with a likely disturbance rate of once a 100 years showed that they can predict dominance of tree species in the Swedish landscape as well as the approximate biomass of these species in today's climate. They then used output from a doubling of CO_2 GCM applied over 100 years to predict the likely transient responses and eventual forest composition that would occur. In central Sweden for example this would lead to a shift from a forest dominated by *Picea abies* to a mixed forest of *Fagus sylvatica*, *Quercus robur*, *Q. petraea* and *Pinus sylvestris* with no *Picea*. They predict the changes may take place over 150 to 200 years, with a substantial time lag in the reaction of subsequent ecological processes.

Much of what has been described both from research considering the Holocene and predicted into the future has stressed the over-riding importance of climate. But as has been shown, both from the pollen analysis and simulation modelling, changes in the forest landscape are actually initiated by some sort of disturbance which allows species more compatible with the new climate to rise to dominance. Major disturbances that affect forests include fire, storms, late frosts, drought, insect attack, grazing and human interference. It is likely that some of these disturbances may increase in the future; for example, Suffling (1992) suggests that with climatic warming forest fire frequency may well increase in boreal forests.

An Italian example: Human disturbance and pressure in and on forests is likely to continue or increase into the future. There is already a long history of disturbance in Europe dating back to climatic phases which were different from today. For example, in the sub-mediterranean forests of peninsular Italy the lack of relatively undisturbed forests makes it difficult to know what sort of forests may have been there in climatic phases different to today's and the influence this has on today's forests of the region. Spada and Sykes (1992) have attempted to model possible effects of disturbance in sub-mediterranean forests in peninsular Italy using the forest dynamics model FORSKA 2. They included all the major tree species of central west Italy and the climate of Rome in 500-year simulations of undisturbed and disturbed forests. Preliminary results indicate that forests predominantly evergreen early in the succession do not persist into the late successional stages under no or little disturbance, suggesting a "mixed" character of the potential vegetation, as the deciduous *Quercus pubescens* comes to dominate, within the present-day Mediterranean, evergreen vegetation belt. The predominantly evergreen character of the potential vegetation is only maintained by a disturbance rate of 100 years or greater which accords with real man-made disturbances by fire, clear-felling and grazing.

Some landscape-ecological perspectives

In the examples discussed several factors, such as fire and clear-felling may have a local extension. If we consider the landscape as a larger entity, such disturbances will only affect parts of the landscape, either in some sort of regular pattern, or randomly. Most probably the same type of disturbance will affect other parts of the landscape mosaic at some later point.

Our general expectation is that if we take a time perspective long enough the forest landscape may show various elements in a mosaic, each of them representing some phase in the regeneration cycle. If we consider the landscape as a whole, each landscape element will occur with a certain frequency and the frequency values will not change much over time. Clearly we need an idea of the relation between temporal scale of the disturbances and the spatial scale of the landscape.

When global or regional climatic changes are operating as a sort of basic vector of change, the elements of the disturbance mosaic will still be there, but dominant woody species playing their roles in the play of pattern and process will change.

Conclusions

1. Both historical evidence and extrapolations to the future (by a number of methods) indicate that communities are by no means fixed in time or space. Both natural and anthropogenic changes operate continuously, both on shorter and longer time scales. The pessimistic conclusion here is that predictions of forest development in relation to global changes are very uncertain.
2. It seems to be overridingly important to maintain a high diversity of species within a landscape so that many species are available which can respond to the climate or to climatically induced changes.
3. There may be delay in species migration into a new potentially suitable area because corridors and stepping stones for movement become fewer. On the other hand, unusual events may often cause irregular, but rapid migration for some species. For instance, during extreme wind storms diaspores and even whole plants and animals may be transported over hundreds of km.
4. One could consider the possibility of introducing species outside their distribution area in order to cope with the migration problems. This may be risky, even at short distance from the present distribution area. It has been shown that if *Picea abies* is planted outside its normal range e.g. in Denmark it has problems consistent with stress imposed by growing in unsuitable climates, such as increased susceptibility to insect attack (Larsen, 1991).
   Despite such negative experiences with planting or sowing species, particularly tree species outside their present distribution area, there seems to be potential for introducing species with a too slow migration into new areas where the environmental conditions seem to have changed so that certain species will be able to establish there.
5. There is no doubt that forest reserves should be as large as possible to allow for this diversity and to maintain species pools from which movement outwards can occur. This is also of the utmost importance for allowing cycles and mosaics of different development stages to co-exist in the same area - in fact a prerequisite for maintaining a high diversity.
6. An important role of landscape planning could be the planning and creation of new forests on places where they have disappeared. It may take 100 years or more before a forest soil develops and the first woodland species immigrate spontaneously, but planting and sowing could encourage the immigration. The active alteration of species' distribution areas has always been criticized heavily within plant geography and ecology. There is room for an alternative philosophy now; such activities are only marginal compared to the enormous changes in abiotic conditions man has created and is creating in ever-growing intensity. Moreover, earlier civilizations probably contributed much to the distribution of plants and animals, consciously or unconsciously. So, active extension of species distribution areas on a landscape-ecological basis seems justified.

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A process-based growth model (FORGRO) for analysing forest dynamics in relation to environmental factors

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Summary

A general, dynamic simulation model of forest growth is being developed as part of an interdisciplinairy study of forest ecosystem dynamics in relation to environmental factors. The model is based on a carbon balance for the whole forest stand, using a top-down approach to forest primary production, implying that production situations of increasing complexity are considered. Weather conditions such as temperature and radiation, together with tree physiology determine potential growth, which is further limited by incomplete canopy closure and water and nutrient availability. An additional model extension includes direct effects of air pollutants. At present, the model is limited to even-aged stands, and includes thinning. Thus, the model outcome can be validated against permanent field plot data from growth and yield research. The model operates with time steps of one day, and requires daily input values for radiation, minimum and maximum temperature, air humidity, wind speed and precipitation. Simulations can cover periods up to 100 years. The model is primarily aimed at understanding tree growth in relation to species, site, and stand characteristics. So far, the model has been applied in coniferous forest stands (mainly Douglas-fir); for application in deciduous stands the model is being extended with a detailed submodel of the annual cycle that accounts for bud burst and cessation of growth in autumn. In the near future, the model will be used to calibrate basic growth functions for use in management-oriented growth and yield prediction systems, and for use in models of forest succession.

Keywords: forest growth, modelling, primary production, coniferous forest stands

Introduction

Forest growth is determined by a range of species, stand and site conditions. Because of the size and longevity of its main constituents, the trees, a forest ecosystem is not very suitable for experimentation under controlled conditions. However, deterministic simulation models can be used as a framework to study the complex interactions in a forest ecosystem. In such models the influence of various environmental conditions such as weather variables on basic processes such as photosynthesis rates, respiration, and dry matter distribution are quantified individually and in combination. The separated processes are subsequently integrated at a higher level of organization, to simulate ecosystem processes at the level of the forest stand. This modelling approach is deterministic, based on eco-physiology and environmental physics. Essentially, primary production in vegetation canopies is modelled in a top-down approach, in which relatively simple production situations are considered first, and more detail is added to account for additional growth-limiting or growth-reducing factors (Table 1, Rabbinge and De Wit, 1989; Mohren and Rabbinge, 1990). Optimal growth, not limited by water or nutrient availability but determined by climate and plant physiology only, is considered to be the first, most elementary growing situation that has to be dealt with. Next, water and nutrient limitations are taken into account, as well as incomplete canopy closure.

The approach was developed for agricultural crops during the sixties and seventies by de Wit and co-workers from the Department of Theoretical Production Ecology of Wageningen

Table 1. Production situations on the basis of growth-determining and growth-limiting factors, assuming a completely closed canopy and absence of pests, diseases, weeds, or other growth-reducing factors (from Mohren and Rabbinge, 1990).

1. Potential growth of a closed canopy with abundant water, nitrogen and minerals; growth determined by weather variables (radiation and temperature) and tree physiology only
2. Growth limited by the availability of soil moisture during part of the growing season
3. Growth limited by the availability of water and nitrogen or phosphorus during at least part of the growing season
4. Growth limited by the availability of water, nitrogen and/or phosphorus, and other minerals during at least part of the growing season

Agricultural University. Recent overviews of the development of this approach were published by Van Keulen and Wolf (1986) and Rabbinge et al. (1989). In recent years the modelling approach has been applied in coniferous forest stands as well (Mohren, 1987); it is now being extended to include deciduous species as well, by incorporating a submodel for the annual cycle of phenological development (Kramer and Mohren, this volume). Additional aspects of primary production in forest stands can be incorporated in the present model when their effects on process rates or on state variables can be quantified. Examples are disturbances of growth through air pollution and soil acidification (Mohren et al., 1992) and effects of pests and diseases (see Table 2, for an overview).

Table 2. Growth reductions and growth disturbances that may be superimposed on the production situations outlined in Table 1 (from Mohren and Rabbinge, 1990).

- Direct effects of e.g. air pollutants on process rates such as photosynthesis and respiration
- Changes in forcing functions or driving variables that affect soil conditions for tree growth, such as effects of soil acidification on availability of nutrients
- Delayed or long-term response to continuous disturbing agents such as changes in assimilate allocation and ageing of tissue
- Irregular canopy damage through injury or reduction of living, functional tissue such as through frost, wind, insect attack, or diseases

In the model, the biomass of the forest stand is represented by the total dry weights of foliage, branches, stems and roots. The foliage biomass is separated into a number of individual age classes (up to five). Total stem dry weight is separated into sapwood and heartwood. Root biomass is separated into fine roots and coarse roots. Principally the model calculates stand characteristics, as amounts per unit of area. Additional structural properties of the forest are derived from the dry weight of each biomass component. Leaf area index (LAI) is calculated from total foliage dry weight. The lifetime of foliage of conifers usually exceeds one growing season; hence the distribution of the foliage over several age classes is modelled by distinguishing up to 10 age classes of needles. Growth is calculated in a carbon balance approach, using canopy assimilation of carbon dioxide, respiration requirements, assimilate allocation, and conversion of assimilation products (sugars) to structural dry matter. Figure 1 gives an elementary relational diagram of the basic carbon balance approach underlying the simulation model. Canopy assimilation is estimated from the photosynthesis rate of individual leaf layers inside the canopy. For a given temperature, the relationship between photosynthesis rate per unit of leaf surface and the amount of photosynthetically active radiation absorbed can be described by a photosynthesis-light response curve such as the negative exponential equation:

$$P_i = P_{max} \cdot \{ 1 - \exp(- \varepsilon \cdot I_{abs,i} / P_{max}) \} - R_i$$

with
- P_i net photosynthesis rate of layer i (kg CO_2 $ha^{-1}h^{-1}$)
- P_{max} maximum gross photosynthesis rate at light saturation (kg CO_2 $ha^{-1}h^{-1}$)
- ε initial light use efficiency at low light (kg CO_2 $ha^{-1}h^{-1}J^{-1}m^2s$ or kg CO_2J^{-1})
- $I_{abs,i}$ photosynthetically active radiation absorbed per unit of leaf surface (Wm^{-2})
- R_i carbon dioxide production due to maintenance respiration (kg CO_2 $ha^{-1}h^{-1}$).

In the FORGRO model the above equation is used to calculate gross photosynthesis rates for different leaf layers in the canopy, in relation to light climate and absorption of photosynthetically active radiation by the foliage. For this, gross photosynthesis ($P_{g,i}$) is defined as $P_i + R_i$. The physiological parameters P_{max} and ε are taken from experimental work on CO_2 exchange in relation to light interception and temperature.

Light conditions above the canopy, total leaf area and leaf area distribution together with the radiative properties of the foliage determine the amount of photosynthetically active radiation that is intercepted. To calculate canopy assimilation the assimilation rates per leaf layer have to be integrated the leaf layers in the canopy (LAI); integration over the day length subsequently yields total daily gross canopy assimilation. Integrations over daylength and over LAI are both done by a Gaussian integration scheme (Goudriaan, 1986), thereby accounting for sunlit and shaded foliage, and for clustering of foliage in shoots and around branches. Daily gross assimilation is calculated by integration of the instantaneous assimilation rates over the day. For this the 3-point Gaussian integration is used; at the Gaussian distances, subroutines are called to specify radiation conditions and the resulting photosynthesis rates. The procedure according to Goudriaan (1986) is used, whereby the day is considered to be symmetrical about noon, and the integration is carried out over the second half of the day. The result of these calculations is the daily total gross canopy assimilation at any one day of the year, expressed as kg CO_2 $ha^{-1}d^{-1}$.

In order to calculate net dry matter increment from gross photosynthesis, growth and maintenance respiration have to be taken into account. In the model, growth respiration is determined by the Penning de Vries method, which considers growth to consist of three biosynthetic processes: conversion of glucose into organic components, translocation of the glucose from the source to the growing site and the cost of nitrogen reduction (Penning de Vries et al, 1989). The conversion efficiency from assimilates to structural dry matter can be calculated, once the biochemical composition of the structural biomass is known. In general, increment for each biomass component is estimated according to:

$$G_j = c_j \cdot a_j (\Sigma P_{g,i} - \Sigma R_j) - L_j$$

with
- G_j net dry weight increment of biomass component j (in kg $ha^{-1}d^{-1}$)
- c_j dry weight conversion efficiency of component j (in kg dry weight per kg carbohydrates $(CH_2O)_n$)
- a_j dimensionless distribution coefficient for the assimilates available for growth
- $\Sigma P_{g,i}$ gross photosynthesis, summed over the foliage layers i (in kg $(CH_2O)_n$ $ha^{-1}d^{-1}$)
- ΣR_j total maintenance requirements for all living tissue (in kg $(CH_2O)_n$ $ha^{-1}d^{-1}$)
- L_j rate of litter loss or biomass turnover for component j (in kg $ha^{-1}d^{-1}$)

The dry weight of the stem component is converted into total stem volume, using an average measure of basic wood density. Using a genuine volume equation or taper function, diameter increment is calculated from height and volume increment. Phloem and bark are incorporated in the estimate of stem dry weight. The model is distance-independent; individual trees are not explicitly taken into account, instead an average tree is calculated from stocking density and total stand characteristics.

The model runs with time steps of one day and numerical integration is carried out over growth rates expressed per day. Figure 2 gives examples of model output on canopy assimilation and respiration during the year. Diurnal cycles are to some extent included in the model, as

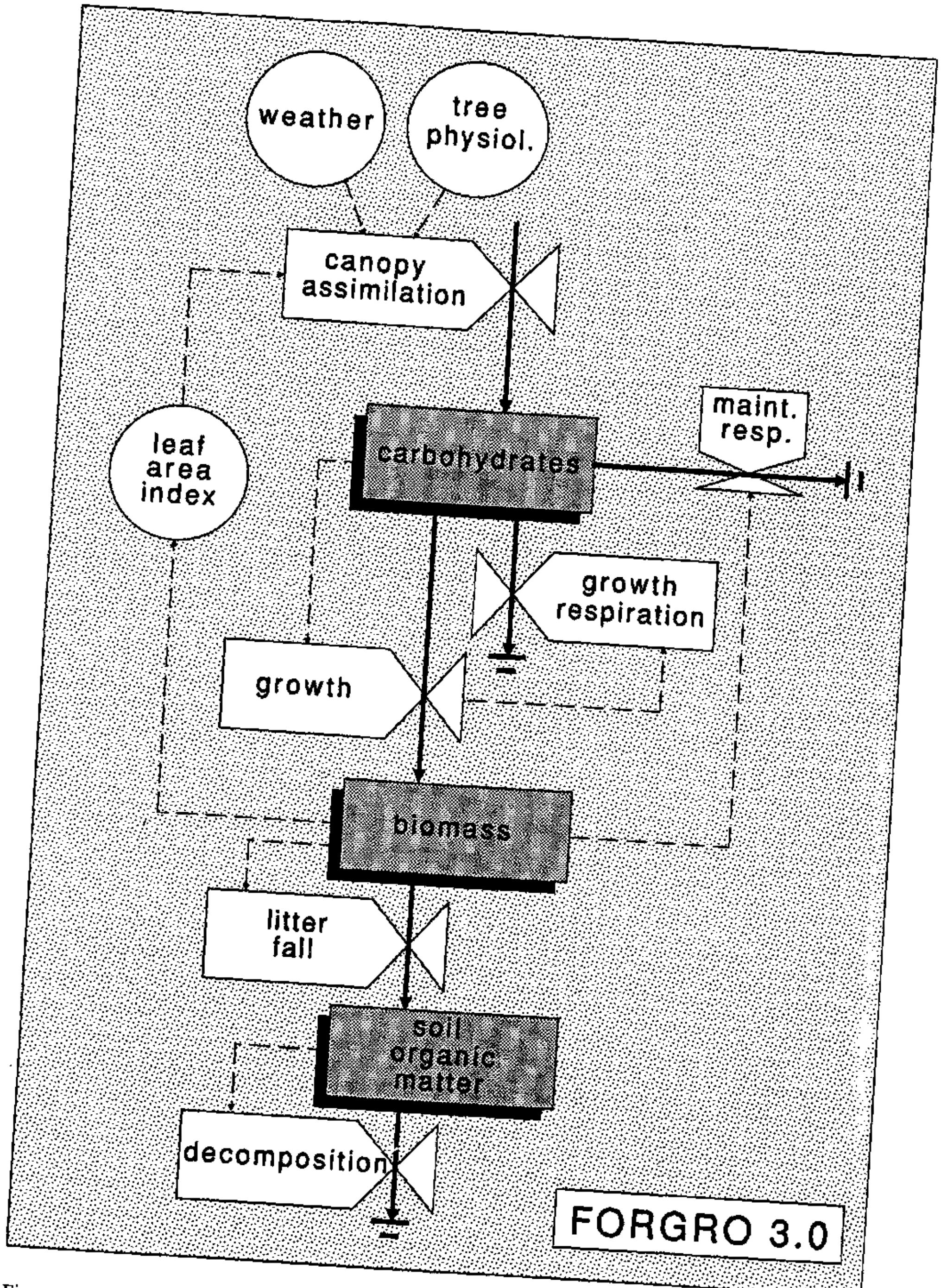

Figure 1. Elementary diagram illustrating the carbon balance approach underlying the simulation model. Boxes: state variables; valves: rate variables; arrows: flows of carbon (drawn lines) or information (dotted lines).

daytime and nighttime are separated, and a sinusoidal variation of radiation during the day is included in the calculation of canopy assimilation (essentially, however, the time step for integration remains one day). At the beginning of each time step, daily average values for environmental conditions independent of the simulated system are determined. Next, daily growth rates are calculated in terms of dry matter per day and per unit of soil surface. The model may include thinning at the end of the year, in which a prescribed amount of stem volume and a certain number of trees are removed from the stand. In the case of thinning, the biomass components other than stem biomass are adjusted according to the fraction of stem volume removed. The total period for the simulation may cover up to 100 years, but in the present version has to start after the canopy has closed, which usually means that initial tree age cannot be less than 15-20 years.

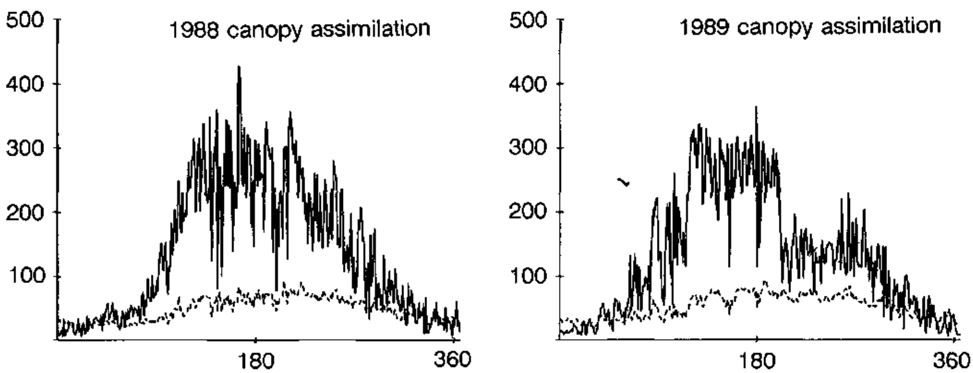

Figure 2. Example of simulated canopy assimilation and maintenance respiration in 1988 and 1989 for the ACIFORN monitoring site "Kootwijk" (values in kg $(CH_2O)_n$ per day). Solid lines: gross daily canopy assimilation; dotted lines: daily canopy maintenance respiration.

State of model development, extensions

To date, the model has been applied in even-aged coniferous forest stands. It has been extensively applied in Douglas-fir stands, among others to quantify direct effects of air pollutants against the background of genuine growth-limiting factors (Jorritsma et al., 1992; Mohren and Bartelink, 1990; Mohren et al., 1992; see also Van de Veen et al., this volume). For Douglas-fir, the model has been validated against measurement series from permanent field plots (Mohren, 1987). As part of an ongoing collaboration within the Forest Ecosystem Research Network (FERN) of the European Science Foundation, the model is being applied in Scots pine stands and compared with other carbon balance models.

As regards the production situations outlined in Table 1, the model has so far dealt only with potential production and with water-limited production situations. Concerning water relations, the effects of rooting densities on transpiration and thus on total canopy assimilation in relation to soil water conditions have been studied in some detail (Florax et al., 1990; Olsthoorn and Florax, 1990). At present, the growth model is being combined with a ganeral model of soil chemistry, enabling the model to be extended to production situations 3 and 4 (see Van de Veen et al., this volume).

In order to be able to derive a summary approach to forest growth from the detailed model as described above, emphasis is being placed on calibrating the overall efficiency of dry matter production in relation to absorbtion of photosynthetically active radiation by the foliage for various species and site conditions. This is being done with the aim of feeding the results of this more detailed physiological model into models of forest dynamics that contain more detail on ecosystem structure and composition, and less detail on basic ecophysiological relationships. In this way, detailed information on physiological properties of tree species, combined with the main site features that determine growth and development, is used to derive a mechanistic modelling approach of competition and population dynamics in uneven-aged, mixed stands. Such models are being developed to study forest succession (see e.g. Jorritsma et al., this volume, and Mohren et al., 1991), and to study primary production and stand dynamics in mixed stands.

Coupling a primary model to a forest succession model with more emphasis on regeneration, competition, mortality, and population dynamics, enables the analysis of forest development under changing site conditions, e.g. through air pollution, climate change, or site development such as that resulting from accumulation of soil organic material.

As part of the analysis of production ecology of forest stands, the current model is being extended to include other tree species such as Norway spruce, oak, beech, and poplar. To be able to apply the model to deciduous trees the basic growth model FORGRO is being extended to include an elementary description of the annual cycle of growth and phenological development in relation to weather conditions. This extended version of the model is being used to evaluate the effects of selected climate change scenarios on primary production and risk of frost damage for the main Dutch forest tree species (see Kramer and Mohren, this volume.

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Simulation of integrated effects of air pollution and soil acidification on forest ecosystems

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Summary

Dynamic simulation models of soil acidification and of forest growth are being combined into a comprehensive, integrated model that can be used to study both direct and indirect effects as well as their interactions in relation to site conditions. Direct effects are quantified through uptake of air pollutants through the stomata and the physiological effects of pollutant metabolites within the living tissue. Indirect effects mainly relate to soil chemistry such as nutrient availability and physico-chemical conditions for root growth. Indirect effects determine the nutrient status of the trees, which in turn influences the susceptibility to direct effects of gaseous air pollutants. With the combined models, an analysis of long-term effects of air pollution and soil acidification becomes feasible, thereby using up-to-date information on short-term effects at the level of physiological and geochemical processes. On the basis of such integrated analyses, elementary dose-response relationships can be calibrated, for use in strategic regional studies such as those required for analysing pollution abatement policies.

Keywords: forest growth, soil acidification, modelling, atmospheric deposition

Introduction

In recent acidification research, extensive data have been collected on effects of air pollution and soil acidification on selected aspects of forest ecosystems, such as physiological processes and biogeochemical nutrient cycling. However, a quantitative assessment of direct and indirect effects of air pollution and soil acidification on forest growth remains difficult. Such an integration of experimental results against the background of traditional growth- determining and growth-limiting factors (inherent to tree physiology as well as weather and soil conditions) may be achieved using a deterministic models of forest growth (Mohren and Rabbinge, 1990). In addition to this, dynamic simulation models enable the analysis of long-term processes such as gradual effects of soil acidification on nutrient availability, or the dynamic response of forest ecosystems to nitrogen saturation or changing levels of pollution.

During the first and second phases of the Dutch Priority Programme on Acidification the direct and indirect effects of both air pollution and soil acidification were studied experimentally and in the field (see Mohren, 1991, for a list of projects). In addition, various models of forest growth and of soil acidification were developed in order to evaluate these experimental results against the background of genuine site factors such as water and nutrient limitations (e.g. De Vries and Kros, 1991; Mohren, 1991). So far, the models have been applied mainly to quantify direct effects on forest growth (Mohren et al., 1992), to study particular ecosystem processes in detail (e.g. Gijsman, 1990; 1991), and to quantify soil chemical changes and associated critical loads, both in detail (De Vries et al., 1990; De Vries and Kros, 1991) and in a general regional analysis (e.g. Tiktak et al., 1992; De Vries et al., 1992).

In order to arrive at an integrated approach in which the combined effects of both direct and indirect disturbances are assessed, available models of forest stand growth and of soil acidification have to be combined. In this way, direct aboveground effects may be quantified in relation to tree nutrient status, which in turn is determined by soil acidification and soil nutrient status. Using such a combined model the long-term effects of air pollutants may be analysed, more meaningful criteria may be derived for use in calculations of critical loads, and elementary dose-effect relationships may be traced for use in regional studies and policy scenario analysis.

The modelling approach

To arrive at an integrated assessment of the direct and indirect effects for different types of forest ecosystems as described above, the FORGRO stand growth model (developed by Mohren and co-workers at IBN-DLO) and the SAM detailed soil chemistry model (developed by De Vries and co-workers at SC-DLO) have been combined, so that the water, carbon and nutrient cycles can be quantified in relation to species physiology, soil chemistry, and site conditions such as weather and atmospheric inputs. The integrated stand growth model does account for direct effects of SO_2, O_3 and NO_x, and includes uptake and cycling of major tree nutrients such as nitrogen, magnesium, phosphorus, and potassium, accounting for canopy exchange processes, litter fall, decomposition of soil organic matter, weathering, uptake, accumulation in biomass, and leaching.

The forest growth model and soil acidification models are essentially mechanistic, dynamic simulation models based on the main underlying physical, physiological and chemical ecosystems processes, and aim at clarifying ecosystem processes. The forest growth model is based on the carbon balance of an entire forest stand, and calculates growth from intercepted radiation, canopy photosynthesis, maintenance requirements, and allocation of available assimilates to growing tissues. The model operates with time steps of one day, and may cover simulation periods of several decades up to 100 years. The approach to growth modelling may be considered top-down, starting with optimal primary production determined by radiation, temperature and species physiology only. Next, water and nutrient limitations are considered, by keeping track of soil moisture and stand hydrology, and by analysis of nutrient demand and supply. As regards nutrients, the growth model is mainly used to estimate the nutrient demands of a growing forest, but so far cannot be used to estimate nutrient availability at a particular site. The direct effects of air pollutants are considered as additional growth-reducing factors that are incorporated in the model by quantifying their effects on physiological processes such as photosynthesis and respiration (Mohren and Rabbinge, 1990; Mohren et al., 1992).

Most existing soil acidification models simulate ion concentrations in the bulk soil solution for the major elements involved in soil acidification, accounting for deposition, weathering, buffering and exchange of protons, cations and aluminium at the exchange complex, root uptake of cations and anions (and possible proton excretion associated with this), leaching, etc. In general, soil acidification leads to increased leaching of cations, increase of Al/Ca ratios, decreased root growth, and hampered nutrient uptake; long-term soil acidification leads to depletion of the various buffering systems in the soil, and causes a pH decrease associated with the transition from one buffering system to another (such as from an aluminium to an iron buffered system). Present soil acidification models may be used to study the dynamic response of selected soil characteristics, such as the ratio between the concentrations of aluminium and calcium, to various deposition scenarios. However, the dynamic response of tree and forest growth to these soil characteristics remains uncertain, as only limited feedback between forest and soil is taken into account, and root uptake of nutrients in relation to soil conditions is not modelled explicitly.

Using recently developed models of water and nutrient uptake in which demand (by the growing plant) and supply of nutrients (in the bulk solution) are balanced through uptake per unit of fine root length, it becomes feasible to combine a soil acidification model that simulates the nutrient supply in terms of the concentration in the bulk solution, with a growth model that estimates nutrient demand. Such root uptake models (e.g. De Willigen, 1989; Gijsman, 1990, 1991; Gijsman and De Willigen, 1991) take into account aspects of rooting density and root architecture, and can be applied when detailed information is available on the root system, such as root mass and periodicity of root growth. Such data are increasingly being generated by detailed ecosystem monitoring studies (see e.g. Olsthoorn and Tiktak, 1991).

The performance of the coupled model (FORSAM) will be evaluated using long-term monitoring data from a number of selected field sites in the Netherlands and abroad (e.g. the ACIFORN field sites). In addition to the analysis of the dynamic response of forest ecosystems to pollution and deposition scenarios, the simulation models will also be used when calibrating elementary dose-response relationship for use in regional scenario analysis carried out within the Dutch Acidification System (DAS).

Preliminary conclusions

Under Dutch conditions, the short-term direct effects of the main gaseous air pollutants (SO_2 and NO_x) are of minor importance. The short-term direct effects of O_3 can be potentially harmful during episodes of high concentrations (> 200μg m^{-3}). Long-term effects of exposure to gaseous air pollutants are expected to have an effect through increased ageing of foliage, especially in stands with low LAI such as Scots pine (Mohren et al., 1992). Most forest soils in The Netherlands appear to be in the aluminium buffering range. Depletion of this aluminium buffering capacity with ongoing soil acidification at the present rate of acid deposition is expected to occur 30-200 years from now, depending on the type of soil. In such cases there will be a transition from the aluminium to the iron buffering range, which is likely to have drastic consequences for tree growth.

Overall, it was concluded (Mohren, 1991) that nitrogen is the key factor in explaining current changes in Dutch forest ecosystems; nitrogen deposition contributes to soil acidification, and leads to nutrient imbalances, changes in root growth and nutrient uptake patterns, and increased susceptibility to drought. In addition, it is expected that nitrogen deposition and increased cation leaching lead to increased susceptibility to direct effects of gaseous air pollutants. Figure 1 indicates the most likely causal pathways involved in integrated effects of air pollution and soil acidification in forest ecosystems in The Netherlands.

Table 1. Calculated growth rates as % of potential growth, accounting for water shortage and short-term effects of SO_2 and O_3 for the two ACIFORN sites "Speuld" and "Kootwijk" in the Netherlands (Douglas-fir, potential growth equal to 24-25 Mg $ha^{-1}yr^{-1}$). Two-year average concentrations for SO_2 and O_3 were 10 μg m^{-3} and 50 μg m^{-3} respectively (see also Mohren, 1991, and Mohren et al., 1992, for more details on stand conditions).

	Speuld		*Kootwijk*	
	1988	1989	1988	1989
water shortage	94	85	91	72
short-term effects	99	99	99	99
water+short-t. eff.	94	84	91	72

Ongoing research

At present, the FORGRO and SAM models are being coupled to arrive at the FORSAM combined model described above. This integrated model will be used to quantify nutrient cycling during forest stand development and to study in detail the effects of root characteristics on nutrient uptake in relation to soil acidification. Also, soil criteria for calculating static critical load will be re-examined, and selected scenario analysis will be carried out.

The integrated model will be parameterized for Douglas-fir and Scots pine, using data from recently completed and ongoing experimental work. Additional work has been started to apply the integrated model to oak (*Quercus robur*) and Norway spruce (*Picea abies*) as well. The model will be evaluated and calibrated using data from selected monitoring sites. The final integrated model

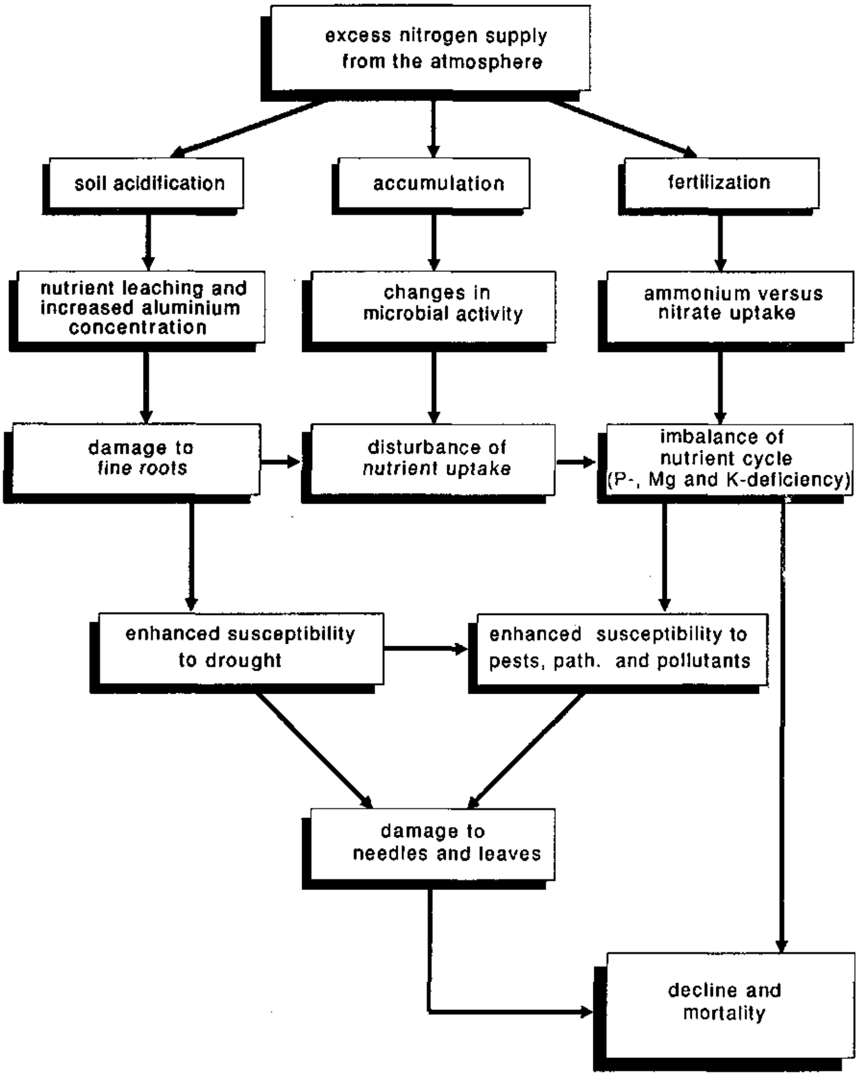

Figure 1. Simplified overview of major disturbances leading to forest decline in The Netherlands (taken from Mohren, 1991).

will be used in the calibration of regional effect modules with the Dutch Acidification System (DAS), such as the model SOILVEG. In collaboration with two Dutch research institutes (SC-DLO and RIVM) the models will be used to analyse long-term effects for different species and different site conditions, using common pollution abatement scenarios as input.

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Monitoring atmospheric input in natural forest reserves of South West Germany

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Keywords: atmospheric input, litter restoration, forest ecosystems, soil acidification

Introduction

The recent increase of atmospheric input into ecosystems is thought to change element balances and to promote acidification of soils. Changes in vegetation are expected. Natural Forest Reserves may be of use in the monitoring of processes and subsequent vegetational changes of forest ecosystems.

Sampling plots an[illegible] [illegible]udy areas

In south-west Germany (State of Baden-Württemberg) (Figure 1, Table 1) several Natural Forest Reserves (Bannwälder) were observed from 1986 through 1991, in order to estimate the magnitude of external (atmospheric) input (bulk deposition) and of litter restoration of elements. (For methods, see: Bücking and Steinle, 1991; Hochstein and Hildebrand, 1992.)

Table 1. Research plots in natural forest reserves.

Natural forest reserve	Growth area of Baden-Württemberg	mNN	Annual precipitation mm.	Geology/ soiltype
Napf (spruce, mountain maple)	Black forest	1350	~2340	Gneiss/ podzolic brown earth
Brunnenholzried (spruce, beech)	Foothills of the Alps	577	~990	young moraine/ brown earth
Grubenhau (beech)	Swabian Alb	540	~820	silty loam over juranic limestone/ argillic brown earth

Results

Atmospheric deposition

Atmospheric deposition in the open increases with the amount of precipitation or the altitude of the sampling point above sea level. Figure 2 shows this for nitrate. Bulk deposition in stands is also determined by crown processes (additional dry deposition), in most cases leading to greater deposition rates than in the open (spruce > beech). Regional annual deposition rates of some elements into ecosystems amount to 10 - 20 kg N per hectare in the open, 10 - 20 kg N/ha in deciduous stands, 15 - 35 kg N/ha in spruce stands (Figure 3) and 30 - 50 kg SO_4/ha in the open, 40 - 60 kg SO_4/ha in deciduous stands, 80 - 100 kg SO_4/ha in spruce stands (Figure 4). Total acid input (calculated as H^+ + NH_4^+) amounts to at least 0.5 - 1.5 kmol proton equivalents/ha/year in the open, to about 1 - 1.5 kmol in deciduous stands and 1.5 - 2 kmol in spruce stands (Figure 5). In the high montane region (atlantic climate with annual precipitation > 2000 mm) H^+ input predominates; in the eastern submontane regions (continental climate with annual precipitation < 1000 mm) acid input by ammonium prevails. In the Napf plots the bulk ammonium deposition in the stands is lesser than in the open, because of NH_4^+ absorption in the crown (the calculated difference between NH_{4+} deposition in the open and in the stands is marked as "diff. NH4+" in Figure 5). This NH_4^+ difference is counted as acid input.

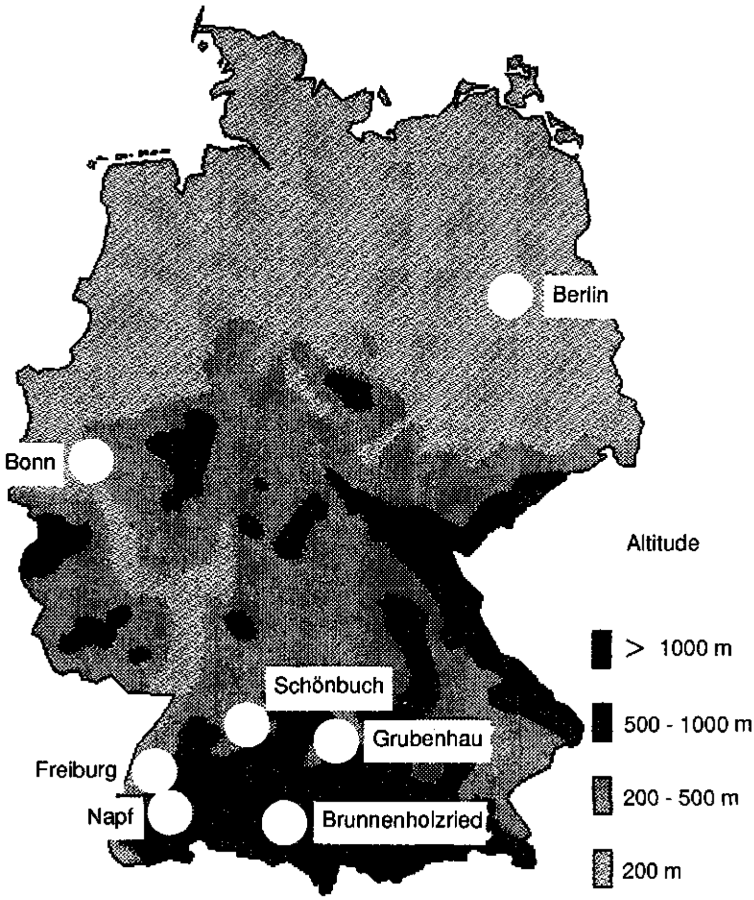

Figure 1. Location of study plots in south-west Germany

Atmospheric deposition and litter input

Total element input (atmospheric + litter; Table 2) varies only slightly for potassium and phosphorus. Calcium and magnesium input are smaller in ecosystems on silicate bedrock (Napf plots in comparison to Grubenhau and Brunnenholzried plots on calcareous bedrock). Total nitrogen input varies visibly in the different deposition landscapes. In low deposition regions the relation between atmospheric input and litter is < 0.5 (for spruce), in elevated deposition regions it is > 0.5 (Table 3).

Table 2. Atmospheric deposition and litter input in Natural Forest Reserves.

Sampling plot	Input	Precipitation open (mm/year)	Precipitation stand (mm/year)	Litter Dry matter t/(ha.a)	N kg/(ha.a)	P kg/(ha.a)	K kg/(ha.a)	Ca kg/(ha.a)	Mg kg/(ha.a)
NAPF									
Spruce	Bulk deposition[1]	2238	2038	-	14.0	0.1	19.9	14.7	2.6
	Litter[1]	-	-	3.1	33.3	2.0	5.3	13.3	1.1
					47.3	2.1	25.2	28.0	3.6
Mountain maple	Bulk deposition[1]	2338	1873	-	11.0	0.2	22.1	10.5	2.1
	Litter[1]	-	-	3.1	31.5	1.8	5.6	15.6	1.6
					42.5	2.0	27.7	26.1	3.7
BRUNNENHOLZRIED									
Spruce	Bulk deposition[2]	990	517	-	34.8	0.1	14.8	16.4	3.0
	Litter[2]	-	-	4.4	55.1	2.2	4.0	46.4	3.4
					89.9	2.3	18.8	62.8	6.4
Beech	Bulk deposition[2]	990	654	5.8	21.5	0.1	17.9	10.5	2.0
	Litter[2]				62.3	2.6	8.7	51.2	3.7
					83.8	2.7	26.6	61.7	5.7
GRUBENHAU									
Beech	Bulk deposition[3]	823	558	-	17.0	1.0	20.0	10.5	2.4
	Litter[3]	-	-	6.6	90.1	4.9	11.3	67.9	6.1
					107.1	5.9	31.3	78.4	8.5

[1] Period 1986-1989
[2] Period 1986-1991
[3] Period 1986-1990

Table 3. Ratios Bulk Deposition in the stand / litter input.

	N	P	K	Ca	Mg
Spruce					
Napf	0.4	0.1	3.8	1.1	2.3
Schönbuch*	0.3	< 0.1	3.3	0.4	1.1
Brunnenholzried	0.6	0.1	3.7	0.4	0.9
Managed Forests*	0.8	0.4	4.0	0.5	1.3
Brunnenholzried					
Grubenhau	0.7	0.1	3.2	0.4	1.0
Beech					
Brunnenholzried	0.4	< 0.1	2.1	0.2	0.5
Grubenhau	0.2	0.2	1.8	0.2	0.4
Schönbuch*	0.2	0.4	0.9	0.2	0.5
Mountain Maple					
Napf	0.3	0.1	4.1	0.7	1.3

* Managed Forests, from Bücking & Steinle 1991.

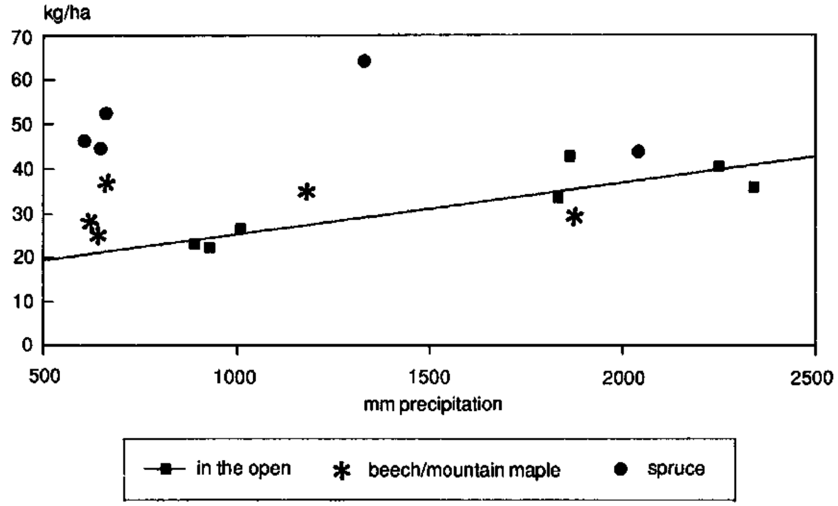

Figure 2. Nitrate deposition in the open and in stands in relation to precipitation (from Bücking and Steinle, 1991) Freiland: in the open; Buche/Bergahorn: beech/mountain maple; Fichte: spruce.

Composition of seepage water

The composition of seepage water in the ecosystems studied extends from Al predominance throughout the profile, over Al predominance in the upper soil, to calcium predominance throughout the profile, whereas the most important anion is nitrate (Figure 6). Acidification of systems will continue as acid input is greater than annual buffer rate (ca. 0.5 kmol/(ha/yr); Ulrich 1986).

Vegetation

Changes of vegetation were not yet evident as long as stand structure was closed. Gaps and storm damage induce clearing vegetation with regional floristic and sociological characteristics; an increase in nitrophytes is probable, but has not yet been proved in the cases studied.

Conclusion

The atmospheric input of various elements to forest stands will continue to be an important site factor influencing all forests. Observation of biological and structural succession in natural forest reserves (which is often the predominant aim of these reserves) should be accompanied by monitoring of atmospheric input and element turnover in order to explain the ongoing processes.

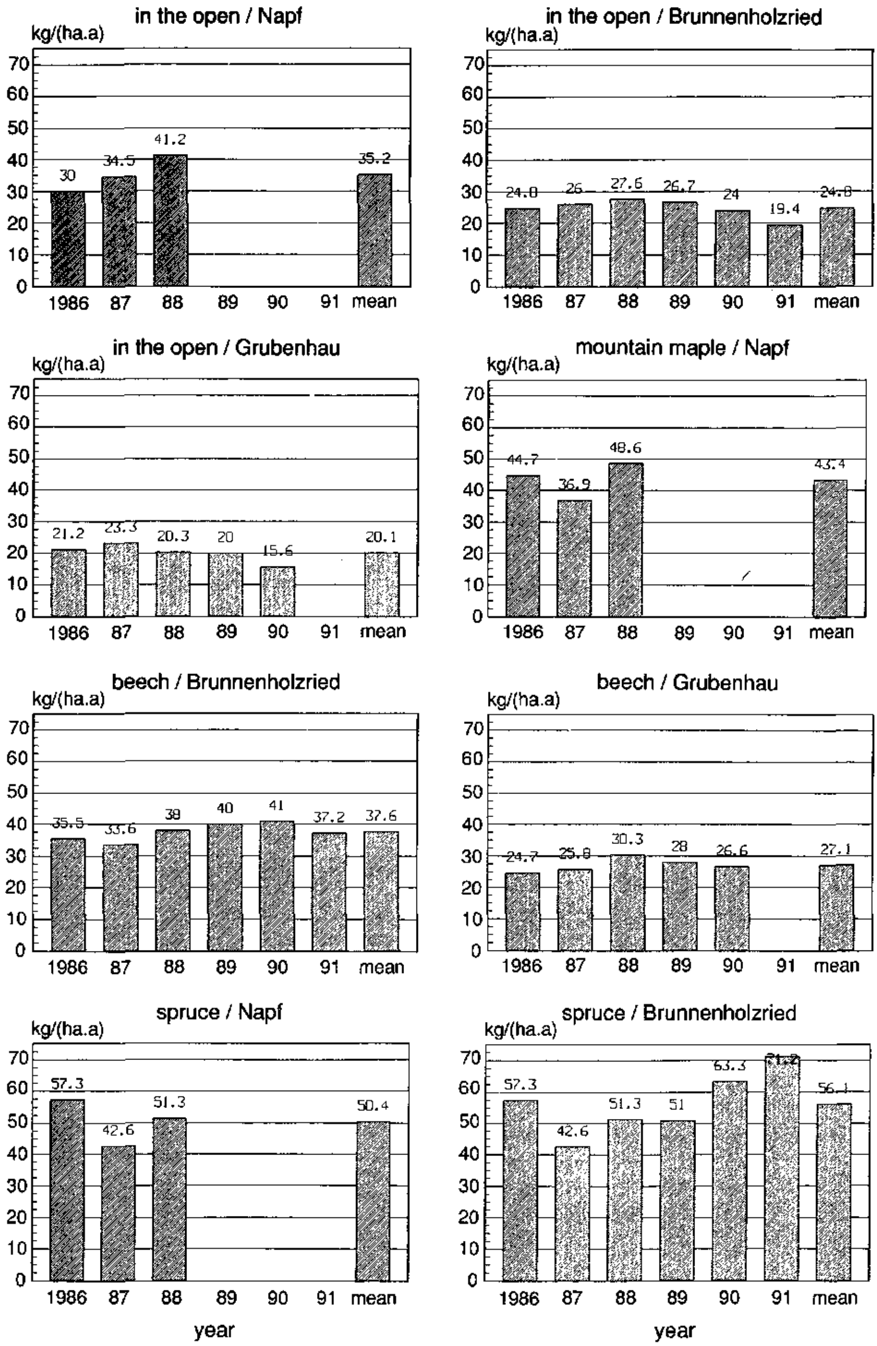

Figure 3a. Nitrate (NO_3^-) deposition.

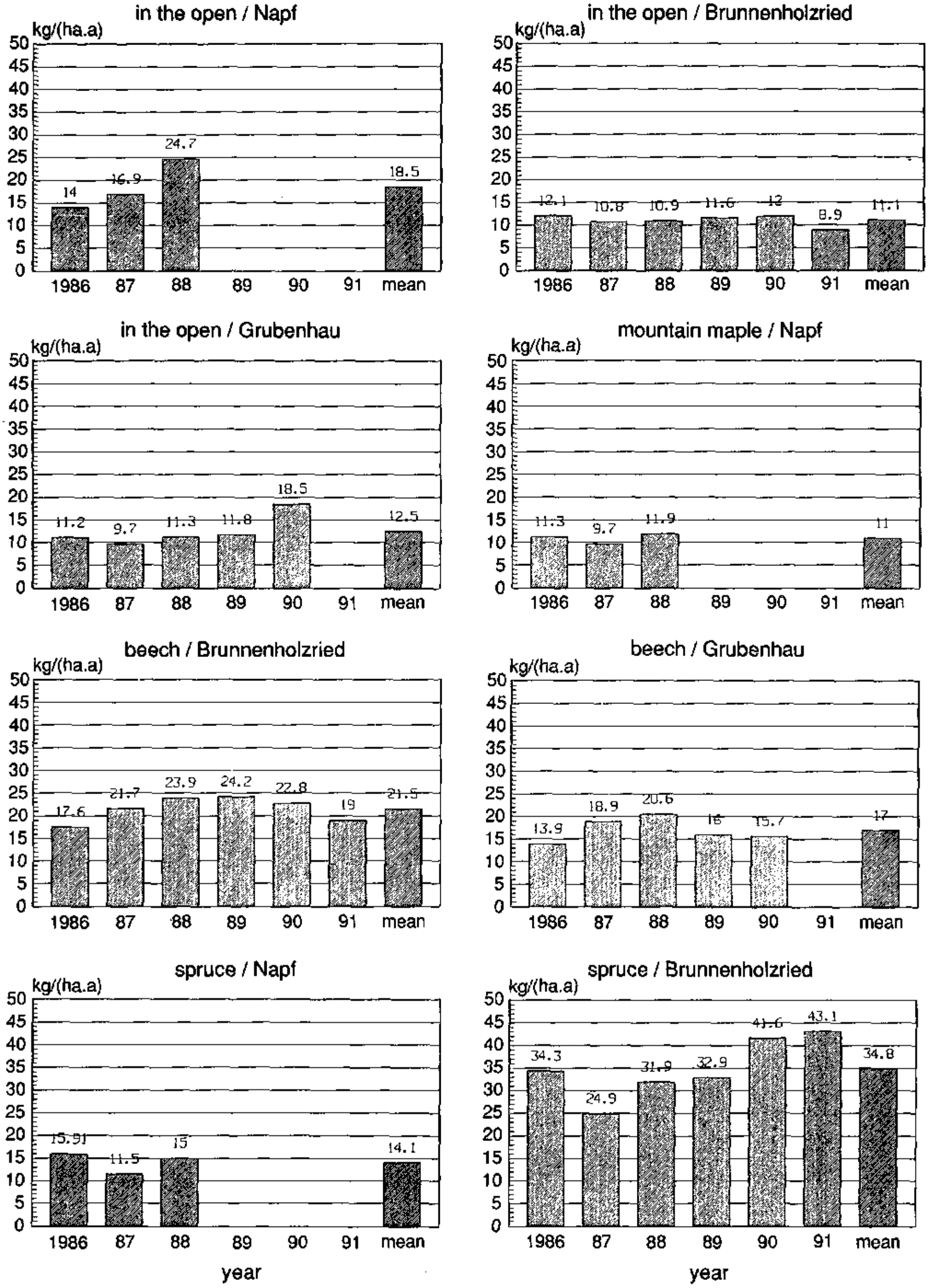

Figure 3b. Nitrogen (NO_3-N + NH_4^+-N) deposition.

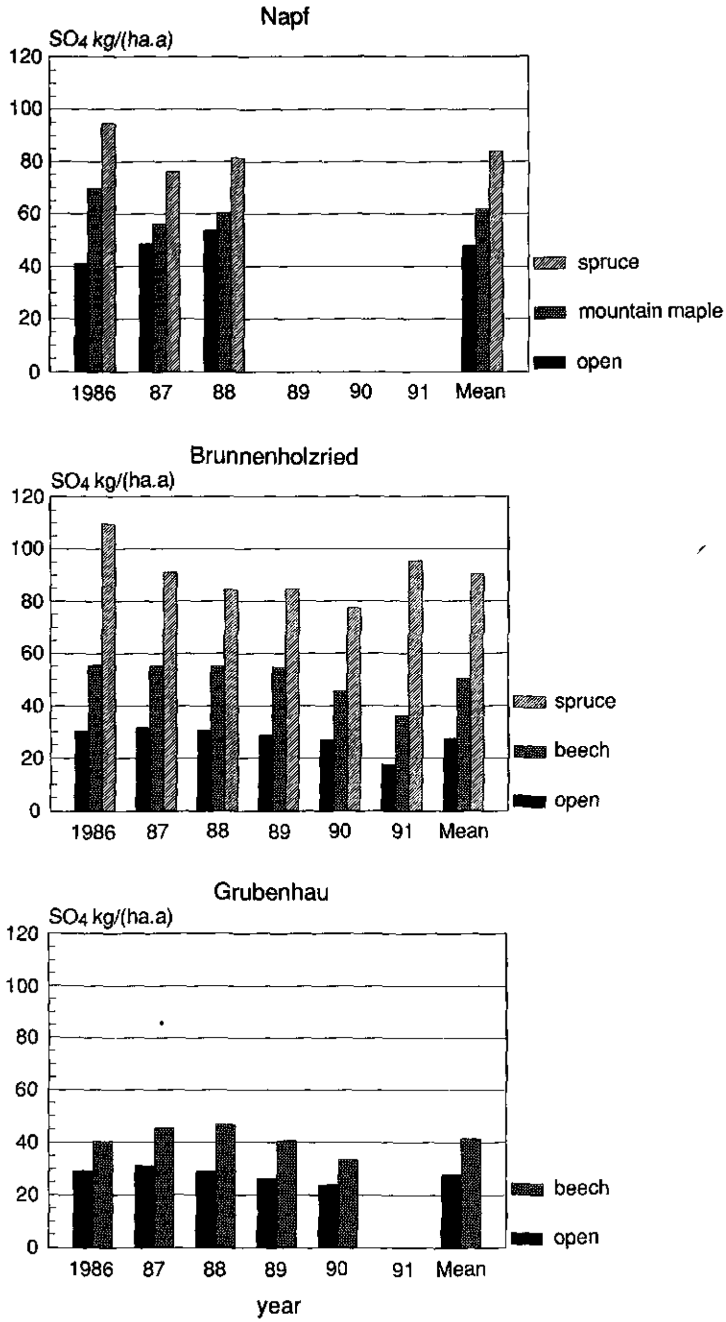

Figure 4. SO_4 deposition.

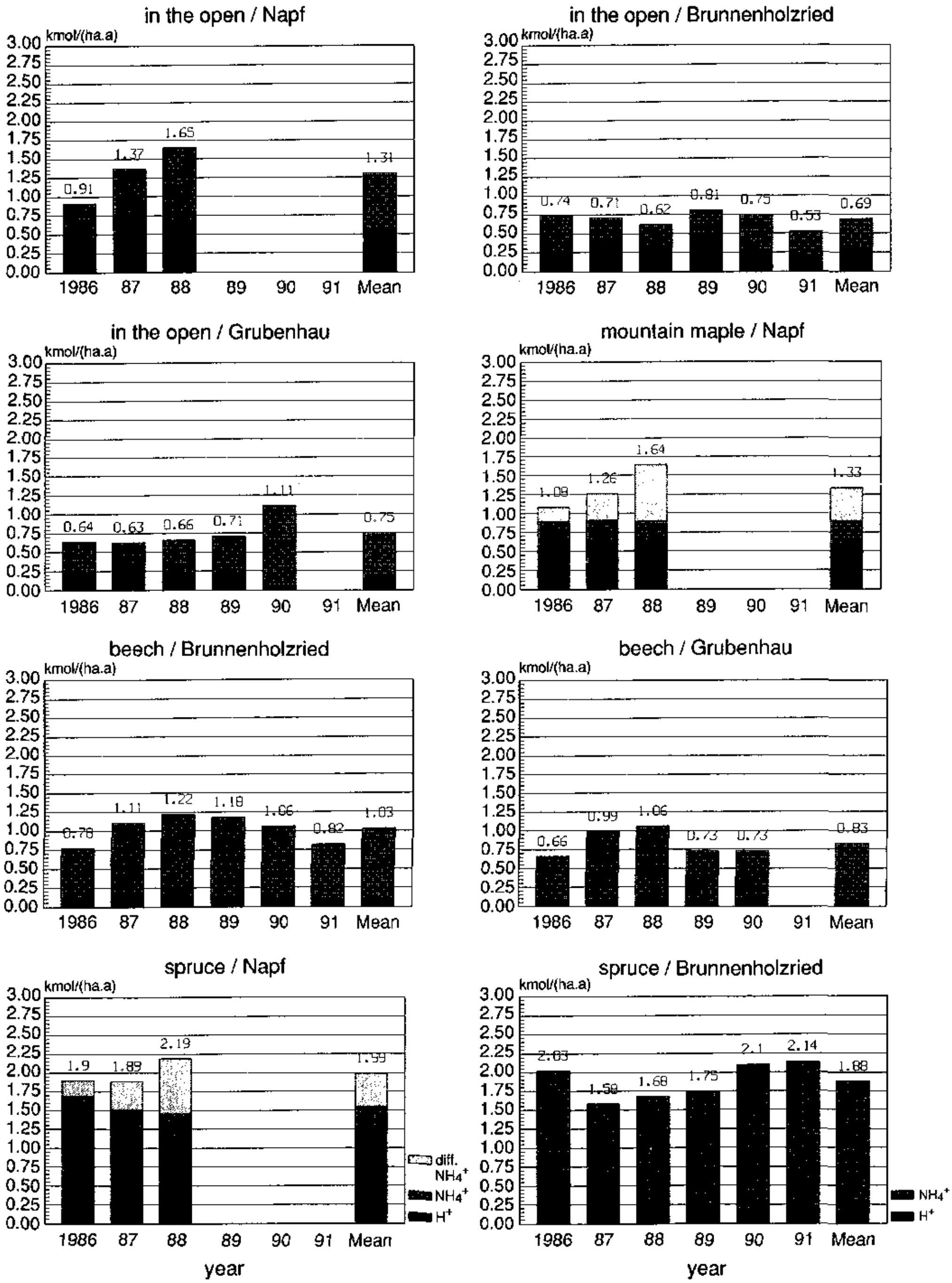

Figure 5. Acid deposition (H^+ + NH_4^+, proton equivalents)

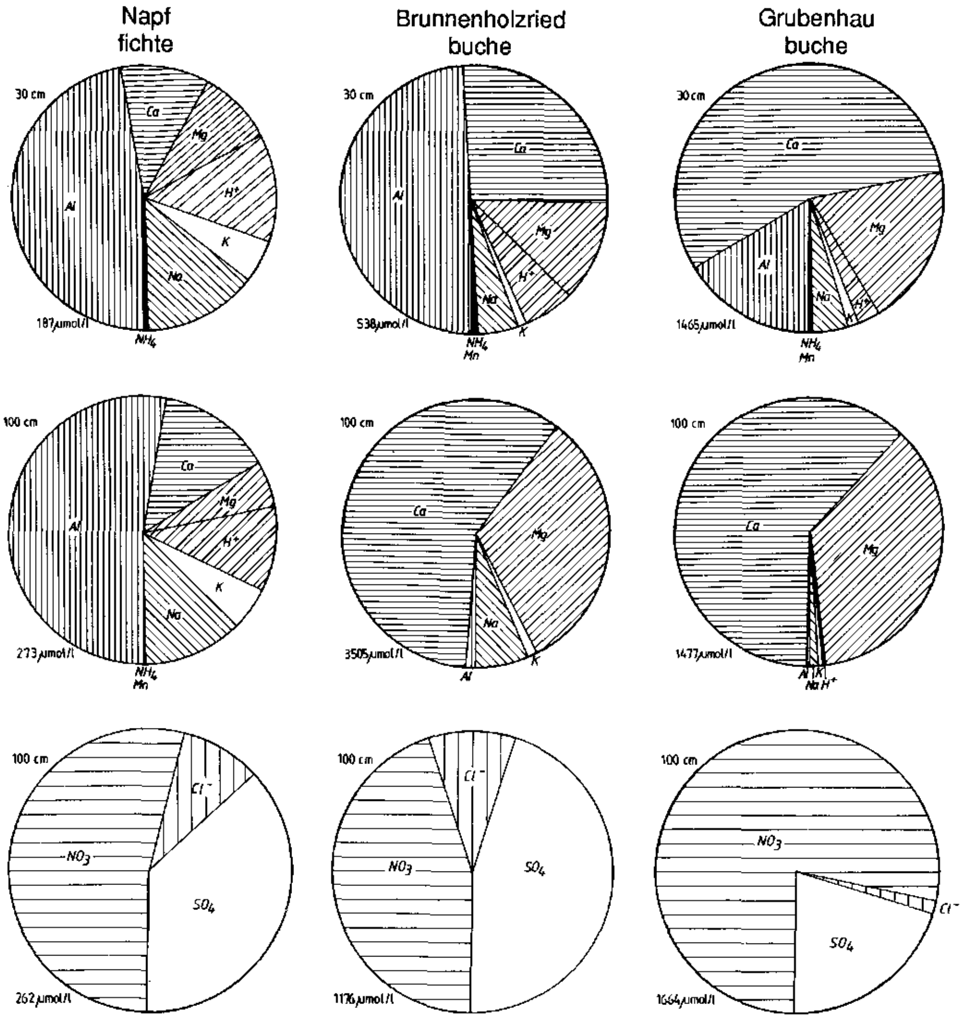

Figure 6. Chemical composition of seepage water (examples from Napf, Brunnenholzried, Grubenhau plots; cation composition from 30 and 100 cm soil depth; anion composition from 100 cm soil depth). Buche:beech; Fichte:spruce.

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Reactions of Fagus sylvatica to climate change; a modelling approach

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Keywords: climate change, phenology, modelling

Introduction

A study was recently started, aiming to (i) develop a simulation model for the annual cycle of *Fagus sylvatica* in relation to climatic factors and physiological processes, and (ii) to evaluate the impacts of climate change on phenology, primary production and competitive relations. Two working hypotheses on the possible impacts of climate warming on beech were formulated:

1. The onset of growth is delayed due to lack of chilling. Consequently, the risk of spring frost damage decreases, and so does the duration of the growing period.
2. The onset of growth is brought forward, because of faster rates of development, provided that the chilling requirement is met at increased winter temperature. Consequently, the risk of spring frost damage increases, depending on how much earlier budburst occurs, and the duration of the growing period increases.

If co-occuring species respond differently to climate warming, their competitiveness relative to the other species may change. This will eventually lead to an altered species composition.

Methodology

Three methods are being applied. The first is the analysis of existent phenological models, using long-term historical observations of phenological events, provenance experiments, etc. in combination with weather variables. The second is the modification of an existent mechanistic model of forest growth (FORGRO), by incorporating a selected model of phenological development. This combined model will then be used to evaluate climate change scenarios of primary production and growth, risk of frost damage, and competitiveness.

Preliminary conclusions and ongoing research

Three conclusions have been drawn so far:

- a phenological model with strict separation of attainment of chilling and forcing requirements performs best;
- the onset of growth of beech occurs earlier when winter temperature rises, but not to such a degree that the risk of spring frost damage will increase;
- temperature sum is not a reliable tool for evaluating the effects of climatic warming for species requiring chilling (see Figures 1 and 2).

Topics for further study are the application of the model to other tree species (oak, pine, spruce, etc.), the use of the model with data from existent International Phenological Gardens (about 60 European stations, with phenological observations of clones of different species from 1963 until now), and the analysis of weather variables in order to generate consistent climate change scenarios on a daily basis.

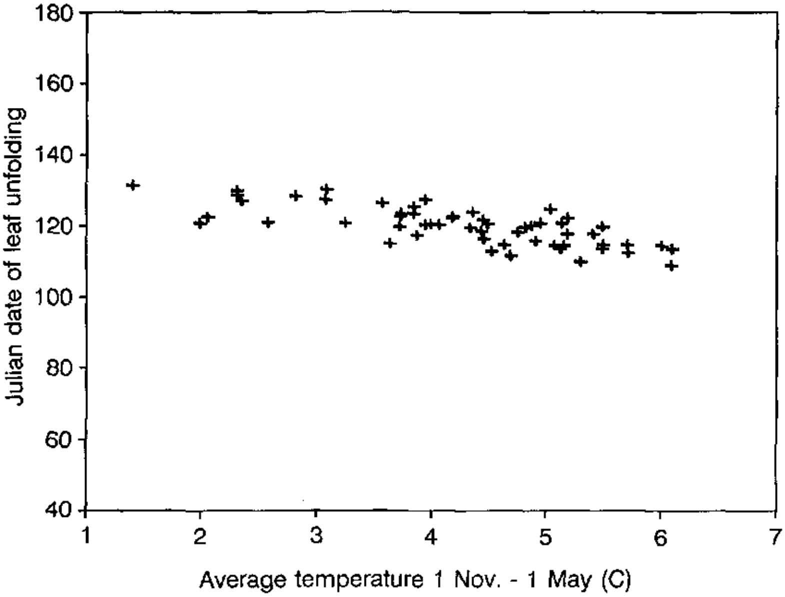

Figure 1. Observed relation between average winter temperature and average date of leaf unfolding.

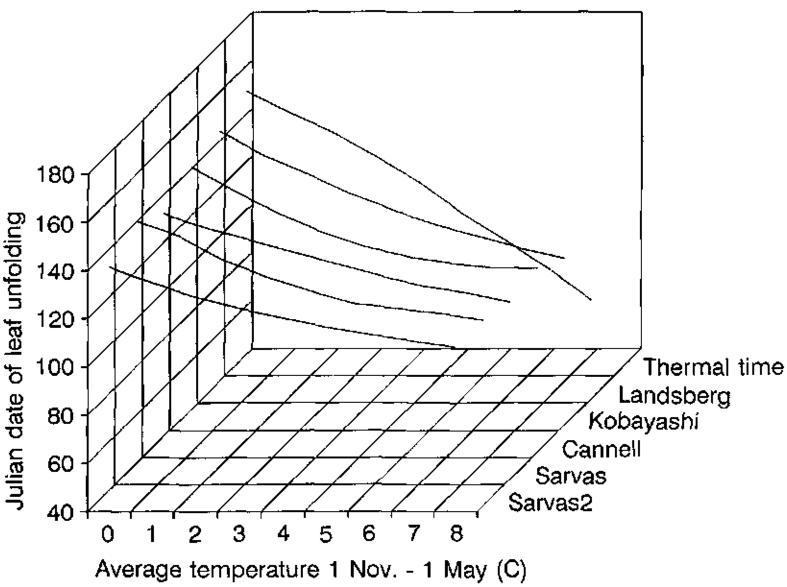

Figure 2. Calculated relation between average winter temperature and date of leaf unfolding using different models.

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Recommendation of the European Forest Reserves Workshop

Participants of the European Forest Reserve Workshop held at Wageningen on 6 - 8 May 1991,

Recognising:

1. That (unmanaged) Forest Reserves have value (i) for the study of natural processes (in the environment), (ii) as reference points to study the effects of forestry and other land uses on ecosystem processes, biodiversity and sustainability and (iii) as locations for monitoring large-scale environmental change (at a European scale) free of local active impacts.

2. That unmanaged Forest Reserves (as large as possible) may have high value for the conservation of in situ native species and genetic diversity;

3. That resources for recording, analysing and interpreting processes and changes on such reserves are severely limited;

4. That many European countries have national programs for Forest Reserves and recording, whilst others are developing and modifying such programs;

5. That the significance of woodlands and forests for the European countryside is growing in importance;

Resolves:

1. That a network of unmanaged Forest Reserves should be established in a representative range of forest types throughout Europe;

2. That these should be located in close geographical association with managed forests and other landuses with wich they may be compared;

3. That interdisciplinary studies should be established in these reserves and maintained in a long-term basis;

4. That the core of the record in these Forest Reserves concerns stand dynamics, structure and composition in order to understand the functioning of the ecosystem;

5. That records should reach a minimum standard for the measurement of change;

6. That a certain degree of standardisation is necessary to enable adequate communication between countries and comparisons between sites;

7. That it is necessary to build up resources for human and financial research.

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