The secret life of woody species

A study on woody species establishment, interactions with herbivores and vegetation succession

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Stellingen

1. De kans op vestiging van bomen is groter in vroege dan in late vegetatiesuccessiestadia (dit proefschrift).

2. In het huidige natuurbeheer wordt de invloed van muizen in hoge mate onderschat (dit proefschrift).

3. De grote commotie die is ontstaan over het onderzoek naar de effectiviteit van agrarisch natuurbeheer berust voornamelijk op spraakverwarring.

4. De steeds grotere vraag naar 'bureau-ecologen' brengt het vakgebied van de ecologie op de lange termijn ernstig in gevaar.

5. De in de wetenschap veel gehanteerde uitdrukking 'geen resultaat is ook resultaat' wordt onder de huidige hoge publicatiedruk gelogenstraft.

6. Om een goede generalist te worden dient men als specialist te beginnen.

7. In tegenstelling tot wat veel docenten beweren, bestaan domme vragen wel degelijk.

8. "Alle intellectuele beroepen bestaan uit het continu verrichten van dingen, die apart genomen heel eenvoudig zijn, na een gigantische voorbereiding"(W.F. Hermans, in 'Nooit meer slapen', 1974).

Stellingen
behorende bij het proefschrift getiteld:
"The secret life of woody species. A study on woody species establishment, interactions with herbivores and vegetation succession"
van Ruben Smit,
te verdedigen op 3 mei 2002.

Voor mijn ouders,

aan wie ik zo veel te danken heb.

Abstract

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Woody species are generally known to be among the most successful plant strategist in the world. They play a prominent role in vegetation dynamics because of their size, longevity and ability to survive under stressful conditions. Nevertheless, the establishment stage, involving seed dispersal, germination and seedling survival is very critical. The main objective of this study is to investigate the biotic and abiotic factors that limit woody species establishment. Furthermore, I investigated the role of woody species in plant-animal interactions, i.e. the direct and indirect interactions between woody species and herbivores.
Since woody species do not form seed banks, they strongly depend on the production and dispersal of seeds. During research on secondary succession on abandoned fields, after 30-45 years, woody species became dominant depending on habitat productivity. On rich soils, the colonisation rate of woody species was slower than on poor soils. This difference can be explained by the higher abundance of perennial herbs and grasses on the rich soil type, which inhibited woody species establishment through competition for light, water and nutrients. Establishment chances for late successional 'forest' woody species were found to be higher in early successional communities than in intermediate or late successional communities due to a lower granivory pressure. In early successional communities, abiotic stress was the key factor in woody species establishment of both pioneer as well as mature forest species. During the intermediate and late successional stages, seed predation by small rodents had a negative effect on the establishment of woody species. In the late successional stage, forest species establishment is reduced due to a severe parent tree effect through seedling defoliation by host-specific insects. Grazing exclusion of large herbivores in former, heavily grazed pine woodland resulted in a fast recovery of graze-tolerant shrub species, while grazing introduction in pine forest and oak-beech forest did not have significant effects on the shrub layer. While graze-tolerant woody species were able to recover rapidly following release of grazing, this was not the case for graze-sensitive species like deciduous tree species. Small rodent densities and seed predation intensities were higher in vegetation communities excluded from grazing than in those introduced to grazing. Grazing by large herbivores caused a decrease in small rodent densities. Small rodents depend on vegetation cover for shelter and food. Differences between the effects of

introduction and exclusion of grazing by large herbivores on small rodent communities can be explained by differences in vegetation structure development. The recovery of heavily browsed understory vegetation following release of grazing by large herbivores proceeded faster than the understory degradation due to grazing introduction. Introduction of red deer (*Cervus elaphus* L.) in former roe deer (*Capreolus capreolus* L.) habitats triggered a significant decrease in roe deer performance in these areas. Shifts in habitat use as well as a lower reproduction success of the latter species pointed to competition for woody forage (browse) between red deer, as superior competitor and roe deer as inferior one. Within the context of vegetation dynamics, woody species play a prominent role in important plant-animal interactions. The establishment stage of woody species can be considered as a significant bottleneck in vegetation succession.

Contents

Voorwoord

Voor u een poging waagt dit proefschrift te lezen wil ik u gaarne wijzen op enige achtergrondinformatie bij het tot stand komen van dit werk. Dit proefschrift is min of meer toevalligerwijs tot stand gekomen. Het zat nooit 'echt' in de planning maar deste meer in mijn hoofd. Het doen van ecologisch onderzoek heeft me altijd zeer gegrepen waardoor het me geen moeite kostte om de baan van toegevoegd onderzoeker op het 'Hoge Veluwe project' als pril afgestudeerde ingenieur te accepteren. Ik had net mijn afstudeeronderzoek afgerond bij de toenmalige vakgroep Terrestrische Oecologie en Natuurbeheer (TON) aan de kolonisatiesnelheid van houtigen op verlaten landbouwgronden (zie hoofdstuk 1) en kreeg nu de kans te werken aan de effecten van vergroting van het leefgebied van grote herbivoren op de vegetatie. Ondanks een aanstelling van slechts twee dagen in de week en het feit dat dit onderzoeksproject al enige tijd liep greep ik de kans met beide handen aan. Onder de supervisie van Jan Bokdam en met behulp van vele afstudeerstudenten heb ik dit onderzoek weten uit te voeren en uit te breiden. Veel van dit onderzoek vindt u terug in dit proefschrift aangevuld met een hoofdstuk gebaseerd op mijn afstudeerproject. Met enige weemoed kijk ik nu terug op die tijd waarbij ik gevrijwaard van allerlei onderwijsverplichtingen, het veldwerk kon uitvoeren. Na het afronden van dit onderzoek heb ik veel andere klussen moeten doen om in mijn levensonderhoud te kunnen voorzien. In de tijd die overbleef schreef ik aan wetenschappelijke publicaties die uiteindelijk de hoofdstukken vormen van dit proefschrift. Met veel enthousiasme en in grote vrijheid heb ik aan dit proefschrift geschreven. Dat de hoofdstukken soms zeer uiteenlopend zijn qua invalshoek moet u me maar voor lief nemen. Veel belangrijker vind ik, dat u bij het lezen net als ik, geboeid raakt door het vakgebied.

Voor het realiseren van dit proefschrift zijn veel mensen zeer inspirerend geweest. Zonder het onnavolgbare enthousiasme en de soms geweldige ideeën van Jan Bokdam was ik niet ver gekomen. Frank Berendse heeft me altijd geholpen bij het corrigeren van mijn hoofdstukken en nog belangrijker, hij wist altijd wel betaalde klussen voor me te vinden waardoor ik aan het werk kon blijven. De allereerste lessen in 'wetenschappelijk onderzoek' kreeg ik van mijn goede vriend Jan den Ouden. Dankzij hem ben ik op het spoor van het onderzoek naar plant-dier relaties gekomen. Bij de uitvoering van het veldwerk op de Hoge Veluwe kon ik vertrouwen op een aantal zeer waardevolle afstudeerstudenten. Marcel Schrijvers, Henrike Schot-Opschoor, Erik van Valkengoed, Danielle Babbic, Retze Talsma, Manon Wieringa en Merijn van Steenderen. De directie van het Nationaal Park De Hoge Veluwe was zeer behulpzaam bij het uitvoeren van het onderzoek. Het uitvoeren van de wildtellingen door de diverse opzichters was onmisbaar. Metname de goede relatie met Bart Boers was en is een zeer geschikte voedingsbron van het doen van onderzoek op de Hoge Veluwe. Op de 'vakgroep' ben ik zeer gemotiveerd geraakt door de helaas te vroegtijdig opgeheven werkgroep 'plant-herbivoor-interacties'. Voor de toenmalige trekker en tevens oud afstudeerbegeleider Han Olff heb ik nog altijd een grote bewondering. In perioden van voor- maar vooral ook tegenspoed kon en kan ik altijd bij Maurits Gleichman terecht en voor het vinden van de juiste toets en de, niet onbelangrijk, juiste wetenschappelijke attitude was en is mijn huidige kamergenoot David Kleijn zeer belangrijk. Met Liesbeth Bakker deel ik de grote interesse voor het vakgebied en natuurlijk de vogels en van Fulco Ludwig heb ik nuttige informatie gekregen ten aanzien van de rompslomp rondom de promotie.

Naast deze werkkring zijn vele mensen van onschatbare waarde. Ik doe vermoedelijk iedereen te kort met dit zeer korte stuk tekst maar ook dat moeten jullie me maar vergeven. Bij mijn grote vrienden Bart Wullings en Melchert Meijer zu Schlochtern staat de deur altijd open en samen delen we dezelfde fascinatie voor fotografie. Deze creatieve 'uitlaatklep' staat eveneens centraal in de vriendenclub DeWNF (De Wageningse Natuurfotografen) en geeft naast iets te veel alcolol heel veel postitieve energie. In mijn jonge jaren als natuurliefhebber en fotograaf heb ik onmisbaar veel geleerd van Peter van der Weiden en de relatie met hem heeft mij zeker gebracht waar ik nu sta. De band met mijn directe familie vormt de basis van mijn bestaan. Het is fijn om zo'n stel ouders te hebben die je altijd zullen steunen en een broer en een zus die zo dicht bij je staan. Tja, en niet te vergeten mijn levensmaatje Marisa, wat moet ik nu nog over jou zeggen...? Dat geluk in de liefde veel beter is dan succes op het werk!

Chapter 1

General introduction

1. General introduction

The relevance of the study of woody species

Woody species dominate vegetation succession in many terrestrial biomes. They play a prominent role in vegetation dynamics from the high arctic to the taiga in the North, into the temperate forests and the chaparral southwards to the rain forests and grass-scrubland in the tropics (Begon et al. 1986). Ecological research on the role of woody species in vegetation dynamics started with studies on vegetation succession (Clements 1916, Connel & Slatyer 1977). Much research on vegetation succession in the temperate regions (Bard 1952, Bazzaz 1975, Monk 1983, Pickett 1982, Rankin & Pickett 1989, Osbornova et al. 1990) has reported an increase of woody dominance during vegetation succession, i.e. the directional change of vegetation communities in time (Miles 1979, Grime 1979, Finegan 1984). In many vegetation succession seres, a vegetation community of woody species dominate the final (i.e. the climax) stage, in which long-lived, tall (woody) plants are the best competitors for light (Clements 1916, Watt 1947, Tilman 1987).

According to Grime (2001) the dominance of woody species or any other life form in a vegetation depends on the positive feed-back between (1) the mechanisms whereby the dominant plant achieves a size larger than that of its neighbours and (2) the deleterious effects which tall plants may exert upon the fitness of shorter neighbours due to forms of stress like shading or depletion of nutrients or water. Woody species gain dominance in many vegetation communities because of their size, longevity and ability to survive under stressful conditions like very low light conditions, drought and fire (Grime 2001). Though woody species can be accounted among the most successful plant strategists, it takes a long and difficult pathway to achieve dominance. Differences in growth form, size, allocation pattern, plant tissue, longevity and place of meristems and perennating buds distinguish so called 'woody species' from other life forms (Mueller-Dombois and Ellenberg 1974). Woody species are generally classified as tall species, with long-living woody stems and perennating buds emerging from aerial parts (Raunkaier 1934). Despite the similarities within the woody species as a life form group, great differences among woody species exist. Harper (1977), Grime (2001) and Crawley (1986) separated woody plants in 'trees' and 'shrubs' because of growth form, size and dispersal strategy. In this study, I classified woody species according to several life-history traits and plant attributes divided into 'pioneer trees', 'forest trees' and 'shrubs' (Table 1) (Finegan 1984, 1990). The life history traits characterise plant strategies, which have evolved in plants to survive and play a role in the vegetation dynamics (Grime 2001). In general, pioneer trees are able to establish early in the vegetation succession due to their rapid dispersal and fast juvenile growth while forest trees and shrubs follow later in the vegetation succession due to their slow dispersal rate and slower growth rates.

***Table 1*:** Woody species classification according to life history traits (Finegan 1984)

Life-history traits	*'Pioneer tree'*	*'Forest tree'*	*'Shrub'*
Dispersability	long distance	short distance	short distance
Dispersal mode	wind	rodent/birds	birds
Seed weight	light	heavy	heavy
Longevity	short	long	short
Time to reproduction maturity	short	long	short
Height growth	fast	slow	fast
r-K strategist	r	K	K
Recovery from resource limitation	fast	slow	fast
Shade tolerance	low	high	low

In many nature areas in the Netherlands, woody species play a dominant role in the vegetation dynamics. On the long-term, without human interference, most of the nature areas in the Netherlands are thought to become forests (Clements 1916). In Dutch nature conservation, their presence is either appreciated or despised. In many nature restoration projects, in vulnerable ecosystems woody species are mechanically 'controlled' in order to arrest the vegetation succession towards forest. In 'nature development areas' woody species are appreciated and give rise to 'spontaneous nature'. Recent ideas on nature conservation and management involve the use of large, wild or domesticated herbivores to prevent the development of uniform forests and to induce an increase in species and community diversity by creating more habitat heterogeneity (Vera 1997, Van Wieren et al. 1997). However, within the context of nature conservation, the (re-) introduction of grazing by large herbivores is severely hindered by the lack of ecological knowledge about the effects of large herbivores on woody species on the one hand, and the responses of woody species to herbivory on the other (Bokdam & Gleichman 2000).

The secret life of woody species

According to Harper (1977) a woody species has to master all trades - to be successful in a variety of life stages and to meet the hazards of each layer of the vegetation that it penetrates. Especially in the lower vegetation layers, during the early stages of establishment, woody species are affected by a great range of biotic and abiotic factors. This early stage in the life cycle of woody species establishment comprises different sequential phases; (1) the seed phase, (2) seedling phase and (3) sapling phase. Each phase includes several ecological processes and mechanisms, which may account for many hazards. Before seeds of woody species are able to germinate, they have to colonise new areas from 'outside' since most species do not form seed banks (Burrows 1990, Milberg 1995). During this invasion, many woody species rely on dispersal modes like wind or animals to reach new sites (Table 1) (Wilson 1983). Subsequently, they need a 'safe site' to establish (Harper 1977) involving suitable abiotic and biotic conditions for successful germination. If seeds are still viable, they are extremely vulnerable to desiccation and fungi but also to mammalian and insectivorous seed predators which can kill large numbers of seeds (Pigott 1985, Ostfeld & Canham 1992, Davidson 1993, Myster & Pickett 1993, Ostfeld et al. 1997). After germination, during the seedling (< $\pm$1 year) and sapling phase ($\pm$ 1-5 years), woody seedlings have to cope with several abiotic factors including stress factors like drought and nutrient depletion (Inouye et al. 1994, Berkowitz et al. 1995). In addition, grazing by insectivorous and mammalian herbivores has a major negative impact on the establishment of woody seedlings (De Steven 1991a, 1991b).

Ecological research on the population biology of woody species has focussed on later, mainly pre-mature stages in woody species development while mainly the seed and to a lower extent the seedling phase were rarely taken into account (Crawley 1986, Inouye et al. 1994, Gill & Marks 1991). From a demographic standpoint as well within the context of vegetation succession, the establishment of woody species can be considered as the most limiting stage (DeSteven 1991a). As a general rule, by surviving the first years in their life, the chances of woody species of growing older subsequently increase (Harper 1977). Additionally, the establishment stage of woody species is easily overlooked in the field, which makes it the 'secret' stage in the life cycle of woody species. In this study, I focus on this secret stage in the life of woody species to determine their role in vegetation succession as affected by many biotic and abiotic factors.

Aims & approach

The main objective of this study is to investigate the biotic and abiotic factors that limit woody species establishment. Within the context of vegetation succession, I consider which ecological mechanisms affect the establishment stage of woody species and what the consequences are for the vegetation dynamics. Furthermore, I want to investigate the role of woody species in plant-animal interactions, i.e. the direct and indirect interactions between woody species and herbivores.

The influences of different biotic and abiotic factors on woody species establishment as well as their role in plant-animal interactions can be visualised in a conceptual, theoretical model of multi-species interactions divided into different trophic levels (Fig. 1; adapted from Holt 1979, Connel 1990, Louda et al. 1990, Van Veen 2000). This model originally used to demonstrate the importance of competition in structuring natural communities (Connel 1990), can be used to analyse the woody species interactions at different trophic levels. In figure 1, R represents resources like water, light and nutrients, P1 and Pn represent different woody species (1...n) or in some cases another life form, H and Hn represent different herbivore species and C represents culling or carnivory. At the lowest, physiological level, woody species have to acquire resources like light, nutrients and water. On a higher trophic level, woody species can affect each other directly, via positive or negative relations (Callaway 1992). In some cases, woody species directly interfere with each other ('interference competition') by suppression, direct overgrowth or allelopathy

(Facelli & Pickett 1991). Nevertheless, most of the interactions among woody species are indirect. Indirect, reciprocal relations occur when one of the shared resources is altered by one of the woody species causing a negative effect ('exploitation competition') or a positive effect ('facilitation') on the performance of the other woody species. Competition for light may cause an increase of shade-tolerant woody species in favour of shade-intolerant species (Kobe et al. 1995). Also, shading by canopy trees may positively affect the survival of another woody species by preventing them from desiccation (Menge & Sunderland 1987). Furthermore, herbivores may affect the relation between the various woody species. Herbivory can produce negative reciprocal interactions among woody species by selective, asymmetrical grazing on competing species (Olff & Ritchie 1998). As a result, the non-consumed species can benefit from the low performance of the consumed one ('apparent competition') (Connel 1990). Associational resistance occurs when a woody species may instead of being a competitor, has a net positive effect on another by reducing the herbivory pressure (Callaway 1992, Olff et al. 1999).

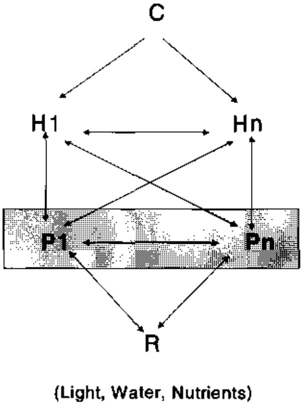

***Figure 1*:** Conceptional model of species interactions on different trophic levels within the framework of establishment of woody species (shaded) . The herbivore population is controlled by culling or carnivory (C). P1 and Pn are woody species; in some cases Pn can be another life form, H1 and Hn represent herbivore species and R represents resources.

Palatable, graze-sensitive, deciduous trees like *Quercus* spec. can be prevented from severe grazing by a protective understory of sticky, thorny plants like *Ilex aquifolium* and *Prunus spinosa* (Morgan 1991, Pott & Hüpe 1993, Vera 1997). The opposite effect may also happen, unpalatable species may be comparatively more grazed when palatable woody species reach higher relative abundances (Olff et al. 1999). In addition, the inverse effect of woody species on herbivore interactions may take place. Direct, exploitative competitive relations or indirect interference relations can exist between herbivores affected by woody species as a shared food resource (Gordon & Ilius 1989, Prins & Van der Jeugd 1993).

Outline of the thesis

This thesis comprises different chapters following the model configuration described in figure 1. I will use a bottom-up approach, starting with the lowest- and ending with the highest trophic level. In each chapter woody species play a central role, either in an active role as main actor or in a more passive role as food resource.

In **chapter two** I start this thesis with a study on the interactions among woody species and other life forms across a successional gradient using old field chronosequences on three different soil types. I examine the time of arrival of woody species during old field succession as well as their colonisation rate as a function of life history traits and habitat productivity.

In **chapter three** the relations between woody species and different herbivore guilds are studied across a successional gradient by measuring the establishment success of different woody species with different life-history traits. Seeds of pioneer woody species as well as mature forest species were sown in exclosures that prohibited access to three different herbivore guilds: a guild including large mammalian herbivores, small rodents and insects, a guild including small rodents and insects and a guild including only insects. These guilds were distinguished to analyse their effect on woody species establishment. In addition, the impact of several abiotic factors on the establishment success was evaluated.

In **chapter four** the botanical changes within the herb layer and shrub layer during seven years of large herbivore grazing are studied across a successional gradient. Effects of introduction of large mammalian herbivores on the vegetation dominated by woody species in former ungrazed pine and oak-beech forests and the effects of grazing release in previously, heavily grazed pine woodlands is examined. Furthermore, the effects of grazing introduction and release on plant species diversity are studied.

In chapter five the interactions between large herbivore and small rodents are studied considering woody species as a food resource and shelter (seeds, shrubs). The indirect effects of large herbivore introduction on the small rodent communities through their impact on the vegetation structure were studied by measuring rodent densities and seed predation inside and outside large herbivore exclosures.

Chapter six considers the interactions among several large herbivore species based on competition for woody species as a main food resource. By making use of a 'natural experiment' I could study the interaction among large herbivores by making use of the enlargement of a former game area. Removal of fences allowed red deer (*Cervus elaphus* L.) and other large herbivore species to enter new forest areas, previously inhabited by only roe deer (*Capreolus capreolus* L.). I aim to get insight in large herbivore interactions and to what extent shifts in resource partitioning reflect the consequences of competition between red deer and roe deer.

Study area

The major part of my study was conducted in The National Park 'De Hoge Veluwe' in the Netherlands (52° 2-8'N; 5° 50-51'E) during September 1994 - December 1996 plus an extra vegetation survey in the summer of 2001 (Fig. 2). The park comprises a typical landscape on sandy soils of glacial and inter-glacial origin. The climate in the area is oceanic with mean annual temperatures of 9.1° C and annual rainfall of 800 mm (Krijnen and Nellestijn 1992). In the Middle Ages, overexploitation of the land by tree cutting and severe sheep grazing altered the landscape in the eastern, Pleistocene part of the Netherlands. As a result, in many, mostly dry areas covered with aeolian soils, severe erosion took place leading to soil degradation. As a result, large parts of the Veluwe area became covered by deposits of drift sand, creating sand dunes and blown-out plains. These new, bare sandy soils became subject to a new vegetation succession, starting in the late 18th and 19th century. In the national park De Hoge Veluwe, a mosaic of vegetation types of different successional stages comprises a vegetation succession gradient (Fanta 1982). The early successional stages are classified as 'heathland'; featuring heather (*Calluna vulgaris* L.) dominated vegetation communities on driftsand and blown-out plains. Heathland is followed by first generation Scots pine with an understory of sand sedge (*Carex arenaria* L.) and wavy hair-grass (*Deschampsia flexuosa* L.) creating 'pine woodland'. Following pine woodland comes 'pine forest', a second generation Scots pine forest with an understory of blue berry (*Vaccinium myrtilis* L.) and a shrub layer of rowan (*Sorbus aucuparia* L.) and silver birch (*Betula* *pendula* Roth.). Late successional species like common oak (*Quercus robur* L.) and beech (*Fagus sylvatica* L.) dominate the deciduous 'oak-beech forests'. In this study I prefer to distinguish 'woodland' and 'forest' based on the density of the tree canopy and the management history. Woodland is classified as a natural established assemblage of trees with an open tree canopy leading to a mixture of grassland and patches of trees. Forest is classified as planted assemblage of trees with a closed tree canopy.

The National Park has a long history of grazing by large herbivores. Since their introduction around 1900 red deer, mouflon (*Ovis ammon musimon* Schreber) and wild boar (*Sus scrofa* L.) occur in varying numbers. Roe deer occurs naturally in the park. The mean annual densities of large herbivores based on spring counts in 1999 are 230 red deer, 230 mouflon, 200 roe deer and 50 wild boar. A strict culling regime was carried out to control these numbers. Until 1993 the populations of red deer, mouflon and wild boar were concentrated in a central, fenced area of 3800 ha. In November 1994, the area available to these populations was expanded to 5000 ha, with two new areas in the northern (Hoenderloo) and southern part (Kemperberg) of the park (Fig.2). These three sub-areas are generally denominated as 'terrain types' (Table 2).

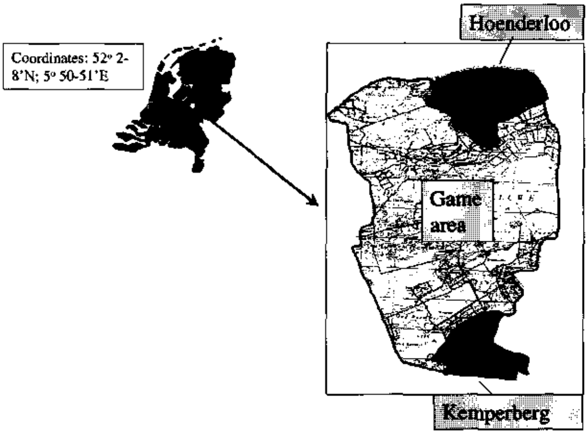

Figure 2: The location and situation of the National Park De Hoge Veluwe. The shaded areas represent the new available terrain types of Hoenderloo and Kemperberg, which were introduced to grazing by red deer, wild boar and mouflon in November 1994

Heathland and first generation pine woodland are mainly situated inside the formerly, heavily grazed game area and have been grazed since 1900 by red deer, roe deer, wild boar and mouflon while pine forest and oak-beech forest became available to red deer, wild boar and mouflon in November 1994 after the inner fences were removed (Table 2, Fig. 2). Among the various chapters I sometimes use different denominations for these vegetation types. In chapter five and six I prefer to use 'habitat types' instead of 'vegetation types' with a slightly different classification based on the same four dominant vegetation types.

Old field succession was reconstructed using chronosequences (outside the national park 'De Hoge Veluwe'). In the summer of 1995, in total 117 old field relevées were used consisting of 80 different old field locations with a known year of abandonment. The relevées were taken in old fields on sandy soils, distributed in the eastern part of the Netherlands. This Pleistocene part of the Netherlands is dominated by dry, poor, aeolian sands and is influenced by a sea climate, based on a mean annual rainfall of 650-700 mm and a mean annual temperature of 9.5-10.0 °C (Krijnen & Nellestijn 1992). Most of these fields were former cornfields (*Zea mays* L.).

***Table 2*:** Description of terrain types in the National Park De Hoge Veluwe

Terrain type	*Size (Ha.)*	*Grazing history*	*Vegetation type (proportion per terrain type)*
Hoenderloo (H)	800	Max. 80-100 roe deer	Oak-beech forest(50%) Pine forest(30%) Pine woodland (10%) Heathland (10%)
Kemperberg (K)	400	Max. 60-80 roe deer	Oak-beech forest(30%) Pine forest(55%) Heathland (15%)
Game area (G)	3800	Max. 275 red deer Max. 50 roe deer Max. 275 mouflon Max. 30-80 wild boar	Oak-beech forest (5%) Pine forest(10%) Pine woodland (20%) Heathland (65%)
Total	5000		

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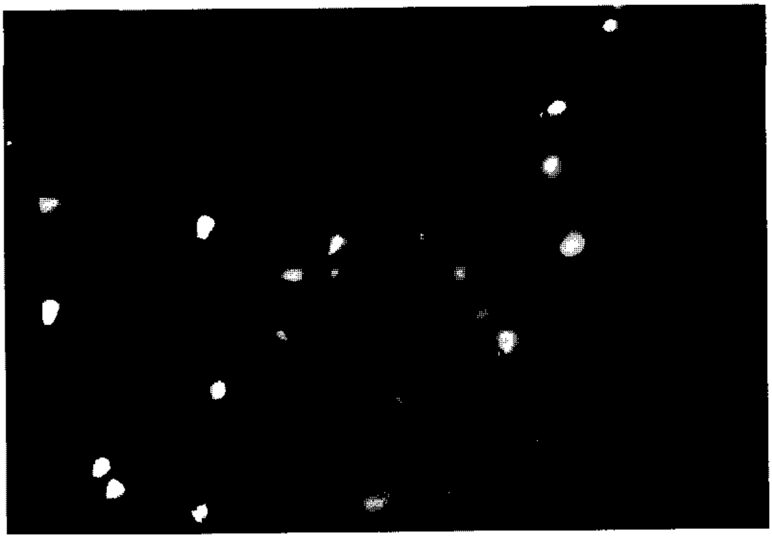
Chapter 2

Woody species colonisation in relation to habitat productivity

R. Smit & H. Olff

Plant Ecology 139: 203-209, 1998.



Keywords: Old fields, Life forms, Life history traits, Dispersal mode, Perennial sward

Abstract

A study was conducted to analyse the effect of habitat productivity on woody species colonisation. Three soil types were distinguished: a relatively poor sandy soil type (1), a somewhat richer sandy type (2) and a relatively rich sandy loamy type (3). Chronosequences were established on these three soil types of 38 (type 1), 20 (type 2) and 54 years (type 3) after abandonment of former agricultural fields. In total 117 vegetation relevées were used to analyse life form change and species responses during old field succession via regression models. On the rich soil type the colonisation rate of woody species was slower than on the poor soil type. This can be explained by higher abundances of perennial species during the first 20 years after abandonment on the rich soil type in contrast to the poor soil type. Perennial species may delay the woody species colonisation. First they close the bare ground which inhibits germination and next they compete with woody seedlings for light, water and nutrients. The effect of habitat productivity on woody species colonisation can only be determined appropriately by taking life history traits into account. Early successional 'pioneer' woody species dispersed by wind have less difficulties colonising old fields than late successional 'forest' species; they colonise old fields prior to the development of a dense perennial sward. Forest species depend on animals to be dispersed which are attracted by vegetation structure. In ± 30 years on the poor soil type and in ± 45 years on the rich soil type woody species become dominant relative to other life forms. Forest species like *Quercus robur* L. invaded relatively early (< 5 years) in contrast to other studies which probably coincides with the distance to seed sources (forest edges).

Introduction

The filtering effect of initial site conditions on seed dispersal and arrival, seedling establishment and subsequent growth and survival of plant species has a major impact on the secondary vegetation succession (Finegan 1996; Miles 1979). Site conditions like habitat productivity (soil richness) affect the colonisation rate of new species indirectly via competition with initial species for light and nutrients (Finegan 1984; Inouye & Tilman 1995). Mainly grass and forb species are experimentally used to test the inhibition hypothesis based on habitat productivity (Reader *et al.* 1994). Tilman (1993) suggests mechanisms of how the species richness dependents on habitat productivity; more productive habitats have more litter accumulation and a lower light penetration inhibiting the establishment of new species.

Besides grasses and forbs, woody species play an important role during the secondary succession. The vegetation succession on old fields generally proceeds towards forest (Pickett 1982; Monk 1983). Since most temperate woody species do not form seed banks (Burrows 1990; Milberg 1995), they have to colonise old fields by seed rains from 'outside'. Therefore, arable weeds which do form a seed bank are the first to colonise. Thus, before woody species can attain dominance, they have to compete with the initial, herbaceous vegetation. DeSteven (1991b) proved the competition between woody species and the initial vegetation to be a major determinant of woody species growth and survival. The colonisation of woody species can only be analysed appropriately when life history traits are considered. As suggested by Finegan (1984) early successional, 'pioneer' woody species have as compared to late successional woody species ('forest species') different plant attributes such as dispersibility and juvenile growth. Pioneer species are merely wind-dispersed and have fast juvenile growth rates as compared to forest species which are mainly animal-dispersed and have slow juvenile growth rates. In general pioneer species have faster colonisation rates than forest species.

Several theories have been developed to describe forest succession in which habitat productivity is taken into account (Egler 1954; Connel & Slatyer 1977). Occasionally long term old field studies are reported (Pickett 1982; Osbornova *et al.* 1990) but no comparison of how woody species invasion depends on habitat productivity gradient has yet been made. We studied when woody species colonise old fields (1) and how fast they establish as dominant species as influenced by habitat productivity and life history traits (2).

Methods and materials

Study areas and plots

Old field succession was reconstructed using chronosequences. In total 117 old field relevées were used consisting of 80 different old field locations with a known year of abandonment. In large old field complexes more than one relevée was recorded. The relevées were taken in old fields on sandy soils, distributed in the eastern part of the Netherlands. This Pleistocene part of the Netherlands is dominated by dry, poor, coversand soils and is influenced by a sea climate, based on a mean annual rainfall of 650-700 mm and a mean annual temperature of 9.5-10.0 °C (Ormeling 1971). Most of these fields were former corn fields (*Zea mays* L.).

The relevées were recorded using 10*10 m sample plots. This large size of the sample plot obtained a reliable reflection of the old field vegetation, which is frequently heterogeneous. The abundance (% cover) of each species was estimated visually, using subplots (5*5 m) to estimate more accurately. The sample plots were placed in homogeneous vegetation parts and in the centre of the old field; to be representative for the species occurrence and composition of the particular old field vegetation, and to prevent side effects.

Data analysis

Old field succession was reconstructed using chronosequences of three soil types. The classification was based on various discriminating parameters like parent material, depth of organic layer, pH and depth of ground water, using the Dutch soil classification according to Bakker & de Schelling (1976). The soil parameters were sampled in the field using a soil drill and a portable, WTW microprocessor pH meter.

The 117 relevées were subdivided into a poor, podzolic, sandy type (1), a somewhat richer, podzolic, sandy, earthy type (2) and a relatively rich earthy type (3) (Table 1). The chronosequences of the soil types were limited to 38 (type 1), 20 (type 2) and 54 (type 3) years after abandonment. The colonisation of woody species was analysed in two ways: (i) analysis of life form change during old field succession per soil type, and (ii) a species response analysis of the main woody species in comparison to dominant forbs and grasses.

The trends in life form change during old field succession were established using the statistical models of Huisman *et al.* (1993). The dominant species were used to characterise the species responses during the chronosequences.

***Table 1*:** The characteristics of the soil types (de Bakker & Schelling 1976)

age= maximum age of old field, number=number of relevées, HGL=mean highest ground water level, organic layer= depth of organic layer, pH=pH of ground water.

Soil type	*age*	*number*	*parent material*	*HGL*	*organic layer*	*pH*
1	38	88	sand	> 80 cm	< 15 cm	± 5
2	20	17	sand	> 80 cm	15-30 cm	± 5
3	54	12	sand-loam	< 40 cm	> 30 cm	5-6

Besides the woody species that occur in > 25% of the relevées per soil type, the forbs and grasses with a mean abundance > 5% over the whole period of the sequence and occur in >25% of the relevées (per soil type) were selected. Some species of the same genus were added because they showed a similar pattern of occurrence and acted as dominant, perennial competitors with woody species (Table 2). The woody species were subdivided into pioneer and forest species based on the empirically determined plant attributes according to Finegan (1984) (Table 2).

Table 2: The life forms and species used for the regression analysis

Abreviations P=pioneer, F=forest species. Life forms: P= perennial, W= woody, A=annual, B=biennial. *Betula spp= Betula pendula* Roth+*Betula pubescens* Ehrh., *Salix spp= Salix caprea* L.+*Salix aurita* L., *Holcus spp= Holcus mollis* L.+*Holcus lanatus* L., *Agrostis spp=Agrostis tenuis* Sibth.+*Agrostis stolonifera* L.

species	*succession (P, F)*	*life form (P, W, A, B)*
Quercus robur L.	F	W
Betula spp	P	W
Alnus glutinosa (L.) Vill.	P	W
Salix spp	P	W
Prunus serotina Ehrh.	F	W
Holcus spp	-	P
Agrostis spp	-	P
Urtica dioica L.	-	P

Per age the abundance of the life form or species was mediated and arcsine (✓y/100) transformed prior to the analysis, which reduced the heterogeneity of the error variance. Also the regression models of Huisman *et al.* (1993) were used to determine the species responses during old field succession.

Results

Changes in life forms

The life form changes during old field succession were more or less similar on the three soil types (Fig. 1). During the first 20 years after abandonment:

-A relatively high abundance of annual and biennial species during the first 5 years followed by a decrease.

- An increase of perennial species up to a peak abundance (40-100% cover) at 10 years after abandonment followed by a decrease
- An increase of woody species abundance

Table 3: The models of Huisman et al.[1] (1993) fitted on data of life forms during old field succession on soil type I, II and III. Per life form the proportion variance 'explained' (R^2), the degrees of freedom (D.f.) and the model parameters (a, b,c,d) are reported.

Life form	*soil type*	*model*	*R^2*	*D.f.*	*a*	*b*	*c*	*d*
Woody	I	II	0.52	17	5.87	-2.73		
Perennial	I	V	0.14	17	-0.45	-0.2	4.58	0.018
Biennial	I	II	0.21	17	6.88	3.34		
Annual	I	II	0.19	17	5.77	3.43		
Woody	II	II	0.18	8	5.86	-2.37		
Perennial	II	V	0.26	6	4.95	0.96	23.3	-2375.15
Biennial	II	II	0.11	8	7.18	8.76		
Annual	II		0[2]					
Woody	III	II	0.54	7	6.32	-2.64		
Perennial	III	IV	0.81	7	4.07	2.93	-0.13	
Biennial	III	II	0.37	7	6.08	6.72		
Annual	III	II	0.32	7	5.78	3.14		

[1] (I): $y=M/(1+e^{a})$, (II): $y=M/(1+e^{a+bx})$, (III): $y=M/(1+e^{a+bx})* 1/(1+e^{c})$, (IV): $y=M/(1+e^{a+bx})* 1/(1+e^{c-bx})$, (V): $y=M/(1+e^{a+bx})* 1/(1+e^{c+dx})$, where y=% cover, M=upper bound, x=years after abandonment and a, b, c & d are parameters.

[2] A too bad fit to report R^2 values ($R^2<0.1$)

The difference in abundance of perennial species between the soil types is remarkable; a high abundance on soil type 3 relative to soil type 1 and 2 during the first 5 years. The woody species started to dominate the vegetation after ± 30 years on soil type 1 and after ± 45 years on soil type 3. The vegetation succession on soil type 2 is still dominated by perennial species after 20 years of abandonment.

The colonisation of the woody species on the soil types appeared to differ strongly (Fig. 1). On soil type 3, the woody species colonisation started at a lower level of abundance and proceeded slower as compared to soil type 1.

Trends of individual species

On soil type 1, the vegetation was dominated by *Agrostis spp* during the first 5 years (Fig. 2). Than after ± 10 years *Betula spp* starts to become dominant; its abundance rapidly increased from 5% to 30% cover in ±20 years, while the abundance of *Agrostis* spp declined strongly. The 'forest' species *Quercus robur* and *Prunus serotina* slowly increased until an abundance > 10% after 35 years of abandonment. The trend of *Prunus serotina* is still increasing while *Quercus robur* tend to have reached a constant level.

On soil type 2 the abundance of the perennial species *Holcus* spp had a peak occurrence after 5 years of abandonment at ± 10% cover and then strongly declined to zero % cover, while *Agrostis* spp. had a constant level of 2-3% during the first 20 years after abandonment. *Betula* spp strongly increased from 1-3% to ± 15% cover. The forest species *Quercus robur* played a minor role during this period; the abundance increased slowly from 1-4%.

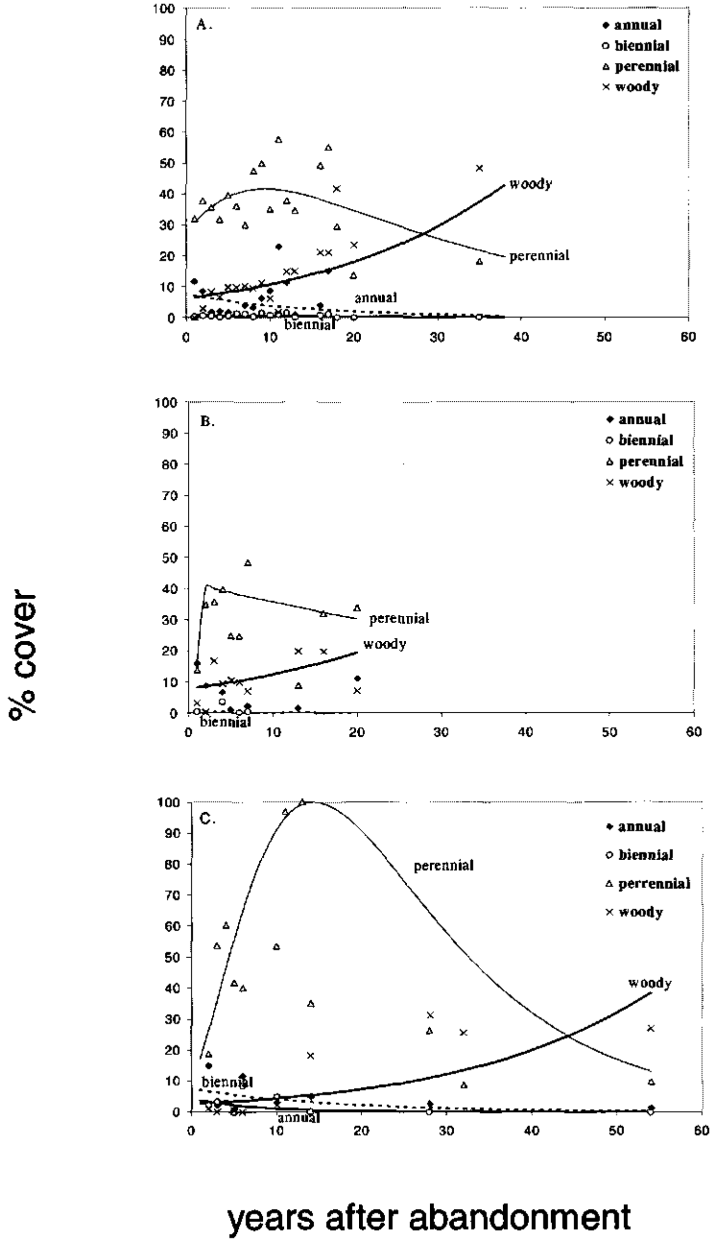


Figure 1: The fitted changes in life forms and observed values during old field succession on A) Soil type 1: poor; podzolic sandy, B) Soil type 2: richer: podzolic, sandy earthy, C) Soil type 3: rich, earthy sandy, using the models of Huisman *et al.* (1993).

On soil type 3 the vegetation was initially dominated by perennial species (Fig. 1c) like *Holcus* spp and *Urtica dioica* (Fig. 2c). The abundance of *Holcus* spp and *Urtica dioica* strongly declined in 30 years from respectively 27% and 7% to < 5% cover. Pioneer woody species like *Alnus glutinosa* and *Salix* spp were present in the first 20 years where *Salix* spp. played a minor role at a level of ± 4% reached after 10 years and remaining constant during the further years. *Alnus glutinosa* started to be dominant after respectively 20 years of abandonment and reaching a level of ± 20% cover after 30 years of abandonment. The occurrence of *Quercus robur* slowly increased to a constant level of ± 10% cover in 30 years of abandonment.

In general, the initial woody species were all pioneers while forest woody species followed the pioneers until an abundance of 10-15% after 38 years on soil type 1, 3% after 20 years on soil type 2 and 10% after 54 years on soil type 3.

***Table 4*:** The best logistic models[1] ($p<0.05$) (Huisman *et al.* 1993) fitted on continuous data of dominant species during old field succession on soil type I, II and III. Per species the proportion of variance 'explained' (R2), the degrees of freedom and the model-parameters (a,b,c) are reported.

Species	*Soil type*	*model*	R^2	*d.f.*	*a*	*b*	*c*
Betula spp.	I	II	0.30	17	6.19	-0.03	
Quercus robur	I	III	0.61	16	1.88	-0.16	5.44
Prunus serotina	I	II	0.41	17	7.10	-0.04	
Agrostis spp.	I	II	0.52	17	5.94	0.08	
Betula spp.	II	IV	0.78	7	-6.14	0.71	10.50
Quercus robur	II	II	0.32	8	7.01	-0.04	
Agrostis spp.	II	II	0.18	8	6.59	-0.04	
Holcus spp.	II	IV	0.26	7	6.51	-0.68	-1.10
Alnus glutinosa	III	III	0.53	6	3.92	-0.22	5.23
Quercus robur	III	III	0.81	4	2.78	-0.21	5.63
Salix spp.	III	III	0.49	6	-6.75	6.31	
Holcus spp.	III	II	0.35	7	5.05	0.04	
Urtica dioica	III	II	0.21	7	5.77	0.02	

[1] See Table 3

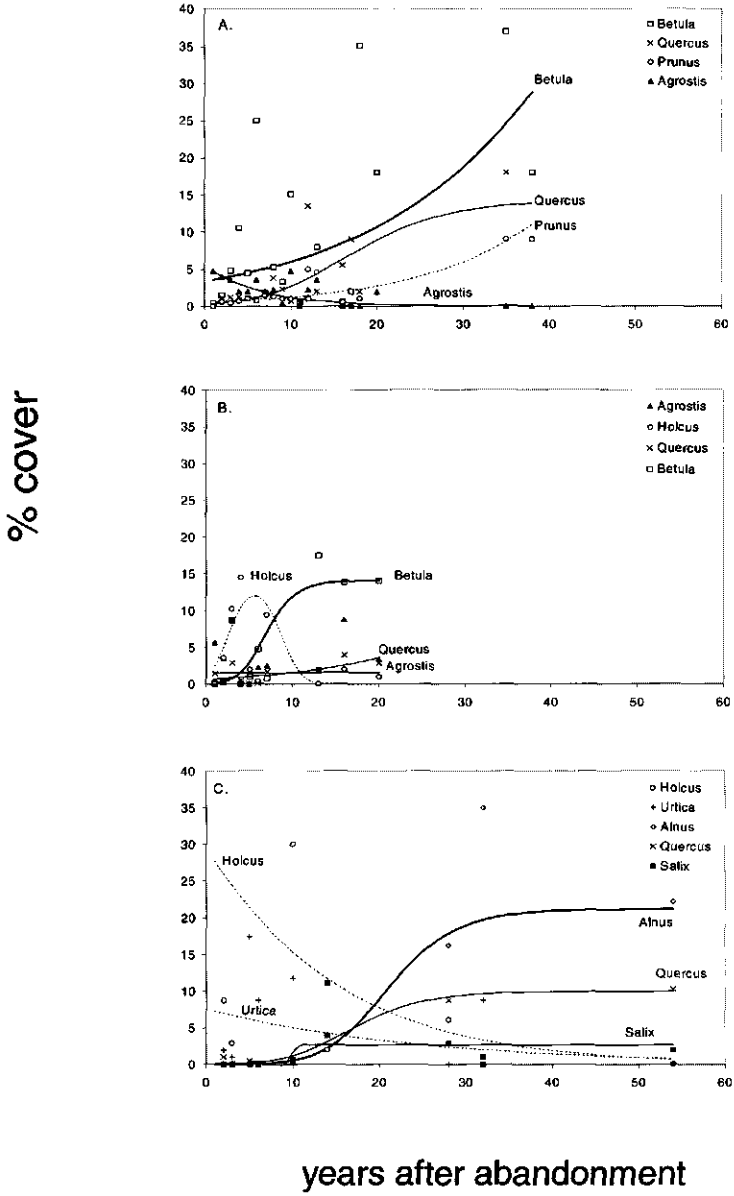


Figure 2: The fitted changes in species abundance and observed values during old field succession on soil types 1 (Fig. 2A), 2 (Fig. 2B) & 3 (Fig. 2C) according to the models of Huisman *et al.* (1993).

Discussion

When analysing the change of life forms during old field succession on the three soil types, a relatively fast establishment of woody species was found (>5% cover in 5 years). This pattern differs from other old field studies woody species remained in lower abundances during the first 10 years was ascertained (Bard 1952; Bazzaz 1975; Pickett 1982; Monk 1983). In this study, probably the proximity of seed sources has affected the colonisation rate of woody species positively. Most of the old fields were located nearby (<100m) seed sources (forest edges.

The general pattern of life form change showed a similar pattern as compared to above-mentioned studies. Concerning the different roles of the perennial species on the soil types, a habitat productivity effect could be seen. A relatively long dominance of perennials on the rich soil type 3 in comparison to a relatively short-time dominance of perennials on the poor soil type 1. In that case, the abundance of perennials which is directly affected by habitat productivity, may cause higher competition intensity with woody species on rich soils as compared to poor soils. This results in a lower colonisation rate of woody species on rich soils in contrast to poor soils. The chronosequence of soil type 2 was limited to 20 years after abandonment where it is probably in an early stage of vegetation succession as compared to soil type 1 and 3.

According to Gill & Marks (1991) the competition with herbs, especially aboveground competition, reduced growth of woody seedlings. The strong competition for light, water and nutrients with dominant perennial species may severely hinder the establishment of woody species. However, dispersal or germination may be even more critical. If woody species have reached old fields via dispersal vectors like wind or animals their germination and thus final establishment depends on the abundance of the initial vegetation dominated by perennials. Seeds of woody species need bare, mineral ground to germinate; wind-dispersed species in particular. The 'perennial window' presumably closes faster on productive soils as compared to less productive soils that prevent further establishment by woody species (Fig. 1a,c). This may declare the even-aged, uniform stands of wind-dispersed pioneers like *Pinus* spp or *Acer* spp on old fields (Rankin & Pickett 1989). These species colonise old fields prior to the development of a dense sward of perennial species. On less productive soils pioneer woody species probably outcompete perennials earlier than on productive soils where especially the competition for light will take longer. In Figure 2a and 2c the shading of woody species may cause the decrease of the abundance of perennial species. Competition for light is the most likely explanation for this pattern.

Until now only the role of pioneer woody species have been discussed. The mature forest species like *Quercus robur* appeared to play a minor role during these stages of old field succession. The role of *Quercus robur* is remarkable; it seems to be present within the early period of secondary succession. Finegan (1984) and McDonnel & Stiles (1983) report an increasing dominance of forest species during old field succession as affected by vegetation structure. In a structural diverse vegetation potential seed dispersers like Jays (*Garrulus glandarius* L.) and Wood mice (*Apodemus sylvaticus* L.) will be attracted and consequently disperse the seeds of forest species into the old fields. Probably the relatively early arrival of *Quercus robur* in this study has been affected by the distance to the seed sources and not by vegetation structure. Probably, when seed sources are close to the old field, relatively heavy seeds of forest species like *Quercus robur* are dispersed by barochory rather than zoochory. Considering *Prunus serotina*, a similar mechanism is at work. Many old fields are colonised by *Prunus serotina* from nearby forest edges because of the foraging behaviour of frugivorous birds like *Turdus* spp (Snow & Snow 1988). In general it clearly emphasises the importance of life history traits (dispersal mode) during old field succession; if nearby seed sources of forest species are not available the invasion of these species may take long (Wilson 1993).

Analysing the application of succession theories considering the woody species colonisation; the tolerance model (Egler 1954) based on the early occurrence of both pioneer and late forest species is only applicable when seed sources of woody species are nearby. Otherwise the establishment of woody species is inhibited by the actual perennial species which is affected by habitat productivity (Connel & Slatyer 1977; Pickett *et al.* 1987). In fact, then especially forest species depend largely on the facilitation of vegetation structure via zoochorous dispersal.

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Chapter 3

Effects of herbivore guilds on woody species establishment across a successional gradient

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Abstract

Herbivory can have a major impact on vegetation succession by the consumption of seeds and seedlings of woody species. We focussed on the establishment success of four woody species with different life history traits and analysed the effects of different herbivore guilds across a successional gradient. We hypothesised that (1) in early stages of vegetation succession, establishment chances of woody seedlings are relatively high due to a lower herbivory pressure and that (2) herbivore guilds have different effects on woody species establishment across the vegetation succession gradient. Four vegetation types covered a successional gradient from heathland through first generation pine woodland to second-generation pine forest and oak-beech forest. We used seeds of both pioneer species: birch (*Betula pendula* Roth.), Scots pine (*Pinus sylvestris* L.); and mature forest species: common oak (*Quercus robur* L.) and beech (*Fagus sylvatica* L.) sown in exclosures with three herbivory treatments comprising different herbivore guilds. We distinguished (1) a guild including all herbivores, (2) a guild including small rodents and insects and (3) a guild including only insects. Establishment chances for woody species are generally higher in early successional communities than in late successional types due to a lower granivory pressure. In these communities abiotic stress is the key factor in woody species establishment. During the intermediate and late successional stages, seed predation by small rodents was found to play a crucial role in woody species establishment. Seed predation inhibits the colonisation of mature forest species. In the late successional stage, mature forest species bear a severe parent tree effect through seedling defoliation by host-specific insects. The results do confirm our initial hypotheses for small rodents and insects only. Large herbivores were not found to play a significant role during woody seedling establishment. Generally, forest succession can easily be arrested or delayed in intermediate and late successional stages. Hence, on the long-term, the different effects of the herbivore guilds on woody species establishment across the successional gradient may cause a shifting mosaic of various successional phases.

Introduction

In the temperate regions woody plants play a dominant role during vegetation succession. Vegetation succession generally proceeds towards forest (Finegan 1984; Picket 1982, Bazzaz 1987). Factors influencing the invasion of woody species (c.f. Inouye et al. 1994) include dispersal characteristics such as seed mass and dispersal mode (De Steven 1991a, Wilson 1993), timing of germination (De Steven 1991a, Morris et al. 1986), behaviour of the dispersers (Myster and Pickett 1992, Jensen and Nielsen 1986, McDonnel and Stiles 1983), competitive or facilitative effects of initial vegetation (De Steven 1991b, Gill & Marks 1991, Myster & Pickett 1992, Smit & Olff 1998) herbivory by mammals and insects (Myster & Pickett 1992, Ostfeld & Canham 1986, Jensen and Nielsen 1986, Smit et al. 2001) and climate (Berkowitz et al. 1995). During succession towards forest (Finegan 1984), as a general rule, wind-dispersed, light-requiring woody species are the first colonists of early successional stages followed by the intermediate and mature shade tolerant forest species dispersed by animals in the later successional stages (Pickett 1982, Monk 1983, Inouye et al. 1987). During forest succession, the establishment phase of woody species is extremely critical and complex affecting the rate of vegetation succession to a great extent (Finegan 1984). Many studies have focussed on a single, isolated mechanism in the establishment phase of woody species in just one vegetation succession stage (Ostfeld & Canham 1993, Gill & Marks 1991). Only few studies have concentrated on woody species establishment across a successional sequence and tried to consider the mechanistic approach (Berkowitz et al. 1995, Smit & Olff 1998).

According to a classical theory in plant ecology, the exploitation ecosystem hypothesis, the physical environment determines the trophic structure through its bottom-up effect on primary productivity (Fretwel 1977, Oksanen 1981). An increase of primary productivity across primary succession may consequently result in an increased herbivore grazing pressure. At low productivity, the available plant biomass is too sparse to support many herbivores. At intermediate productivity, plant biomass is kept at a low level by herbivores and the vegetation is mainly top-down structured by apparent competition (Oksanen et al. 1981, Van de Koppel 1996). At high productivity the herbivore population is controlled by predators or in the absence of predators herbivore grazing may still structure the vegetation. Across a vegetation chronosequence a varying herbivory pressure may affect woody seedling establishment.

Herbivory may retard vegetation succession during the establishment phase of woody species by consuming seeds and seedlings of primarily late-successional species like trees

(Myster & Pickett 1993, Ostfeld & Canham 1986, Davidson 1993, Smit et al, 2001). The diversity in herbivore types resulting in different herbivore assemblages or guilds (Ritchie and Olff 1999) may have different effects on woody species establishment. Browsing of seedlings and saplings of woody species by large and small mammalian herbivores and insects reduces the establishment success of woody species (De Steven 1991, McInnes et al. 1992, Myster and McCarthy 1989, Putman et al. 1989). Also, predation of seeds by large herbivores and small rodents negatively affects the establishment of woody species (Ostfeld et al. 1997, Ostfeld and Canham 1993). The multiple effects of these different herbivore guilds may differ across the stages of vegetation succession.

In later succession stages, vegetation biomass is generally higher as result of biomass accumulation and/or higher soil nutrient mineralization leading to an increase in the number of potential consumers (Janzen 1970, Herrera 1995). We therefore hypothesise that (1) in early stages of vegetation succession, a lower pressure of potential granivores and herbivores may result in higher establishment chances for woody species as compared to later stages of succession, and (2) different herbivore guilds have different effects on woody seedling establishment across the successional stages. In this study we describe and analyse the effects of various herbivore guilds of large herbivores (1), small rodents (2) and insects (3) on woody seedling establishment across a successional gradient. We focus on the establishment success of four woody species with different life history traits and analyse the hierarchy of mechanisms affecting woody seedling establishment.

Materials and methods

Study area

The study was conducted in The National Park 'De Hoge Veluwe' in the Netherlands (52° 2-8'N; 5° 50-51'E) during November 1995- September 1997 (Fig. 1). The climate in the area is Atlantic with mean annual temperatures of 9.1°C and annual rainfall of 800 mm (Krijnen and Nellestijn 1992). The park is characterised by a typical landscape of sandy soils formed in glacial and inter-glacial times. Heavy grazing by domesticated sheep and sod cutting in the late Middle Ages have caused degradation of soil and vegetation. Overexploitation of the land resulted in a vegetation recession from deciduous common oak (*Quercus robur* L.) and beech (*Fagus sylvatica* L.) forest into heathland and even bare sand. In these periods, deposits of aeolian sand covered many parts of the park. In the central parts of the park vegetation communities of open sand plains with species like heather (*Calluna vulgaris* L.) and grey hair-grass (*Corynepherus canescens* L.) still dominate. Nowadays, many parts of the former open plains consist of Scots pine (*Pinus sylvestris* L.) woodlands, which follow the early communities of open sand in the vegetation chronosequence. The understory vegetation of these primary, open woodlands is dominated by wavy hair-grass (*Deschampsia flex*uosa L). During vegetation succession first generation pine woodlands change into more uniform and dense stands of second-generation pine forest with an understory of blue berry (*Vaccinium myrtilis* L.) and a shrub layer of rowan (*Sorbus aucuparia* L.) and silver birch (*Betula pendula* Roth). In the northern and southern parts of the park late successional deciduous common oak (*Quercus robur* L.) and beech (*Fagus sylvatica* L.) forests grow on well-developed, dry podzolic soils on cover sand and fluvio-glacial soils. The mosaic of above described vegetation communities can be used as a vegetation succession gradient (Fig. 2). Analogous to the vegetation succession, soil development starts with an increasing development of the ectorganic layer, including litter-, fermented- and humic horizons. During this soil development the soil fertility is raised due to increasing organic matter contents as well as total N, P and C concentrations, while pH declines (Berendse 1990, Kemmers et al. 1996) (Table 1).

Grazing history

The park has a long history with wild large herbivores. Since the 17th century red deer (*Cervus elaphus* L.) have been known to occur on the Veluwe. Since the reintroduction in 1905, a stable red deer population has occurred in the park. A stable roe deer (*Capreolus capreolus* L.) population has been present since the late 18th century in the park. A fluctuating wild boar (*Sus scrofa scrofa* L.) population has occurred since 1940. Mouflons (*Ovis musimon* Schreber), Corsican mountain sheep, were introduced in the park in 1921. In November 1994, the central game area (3800 ha) was enlarged with the northern and southern deciduous forests of Hoenderloo and Kemperberg (1200 ha) which offered new habitats to red deer, wild boar and mouflon. A stable roe deer population already occurred in these forests (Smit et al. 2001).

Experimental design

Four vegetation types covered a successional gradient from heathland through first generation, second-generation pine woodland and forest to oak-beech forest. We used eight exclosures (replicates) per vegetation type with three 'herbivory' treatments comprising different herbivore guilds. We distinguished; (1) a guild including all herbivores: large herbivores, small rodents and insects (outside exclsoures: treatment 'Deer'), (2) a guild including only small rodents (inside large herbivore exclosures, with a mesh wire of 9 cm^2: treatment 'Rodent') and (3) a guild including only insects ('rodent free cage' with a mesh wire of 0.25 cm^2: treatment 'Insect') (Fig.1).

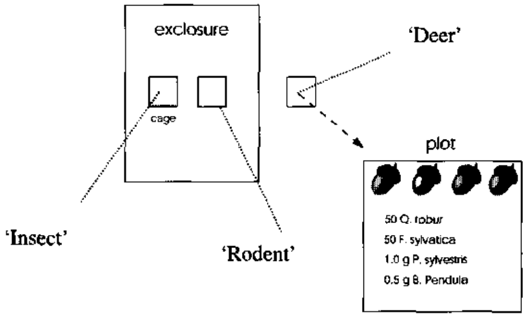

Figure 1: The experimental design. Three seed plots were placed inside and outside large herbivore exclosures representing three different herbivory treatments. (1) available to all herbivores ('Deer'), (2) small rodents and insects ('Rodent'), (3) only insects ('Insect').

We used 4 tree species to study the effects of herbivory. Birch and Scots pine were used as typical pioneer species. Both species have small, wind-dispersed seeds. Oak and beech are both mature forest species with larger seeds depending on animals for dispersal. In respectively November 1995, 50 seeds of beech and oak, and in February 1996 1 g. of Scots pine seeds (around 150 seeds) and 0.5 g. of birch seeds (around 3000 seeds) were sown in seed plots of 1x1 m^2. A random selection of seed size of beech and oak seeds was made to prevent effects of seed size on seedling establishment and survival. Because of the bad establishment success of pine and birch seedlings in 1996, in March 1997 2 g. of birch and 2 g. of Scots pine was additionally sown in the seed plots. Seeds of beech and oak were pushed in a grid pattern in the litter layer of the soil, to prevent desiccation and to simulate natural conditions of hoarded seeds (Van der Wall, Smit et al 2001). During 1996 and 1997 we monitored the number of seedlings established in the seed plots. Each position of the seed or seedling of oak and beech was marked in a grid consisting of 100 different locations of the seeds that allowed recording of the fate of each individual seed. The shoot length of oak and beech seedlings was recorded at the end of the growing season in 1997. The fate of seeds or seedlings of oak and beech was recorded distinguishing evident mortality factors like desiccation, defoliation by insects, browsing by large herbivores or seed predation (granivory). The small size of the seeds of Scots pine and birch hampered the recording of seed- and seedling fate of these species.

Desiccation of seedlings was ascertained by shrivelled conditions of the cotyledon, epicotyle or leaves. Seed predation was identified when seeds were removed completely or consumed on the spot by leaving fragments of seeds (shells). Herbivory effects included clear bite marks of large and small herbivores or insects. The establishment success of woody seedlings was measured as the number of viable seedlings at the end of the two-year experiment, in August 1997. The number of germinated seeds was measured as the maximum number of seeds that showed signs of germination during the study period; i.e. radical elongation to produce a primary taproot, unfolding of cotyledons or production of first shoot and leaves. The seedling fate was calculated relative to the number of seeds as well as to the number of germinated seeds. During the experiment in August 1996 and August 1997, around the 32 large herbivore exclosures the number of pellet groups of the various herbivores including rabbits was assessed to estimate the large herbivore density within the vegetation types. Around each exclosure, five randomly located strips of 100 * 1 m were used in which all individual pellet groups were counted. Individual pellets within a distance of 2 m of each other were classified as one group.

Table 1: Means (± s.e.) of the abiotic factors of the vegetation types representing values inside (in) and outside (out) exclosures sampled from the A_0-and A_m horizon. Abbreviations: O.M.= organic matter, pH = pH (KCL), Ptot= total P concentration, Pe= P extractable, Ntot= total N concentration, light= light in herb layer, litter= litter depth. *No significant differences in abiotic factors were found between inside compared to outside exclosures according to one-way ANOVA.*

Vegetation type	**A_0**	**O.M.** (%)	±	**pH**	±	**Ptot** (mmol)	±	**Pe** (mg)	±	**Ntot** (g)	±	**Litter** (cm)	±	**Light** (PAR)	±
Oak-Beech forest	in	89	0.03	2.98	0.21	16.79	0.63	18.46	1.46	5.53	0.60	6.88	0.45	0.11	0.01
	out	81	0.09	3.13	0.28	17.23	1.67	16.55	1.51	6.13	1.11	7.01	0.60	0.12	0.01
Pine forest	in	84	0.04	3.07	0.35	13.64	0.77	11.86	1.79	5.23	0.61	7.79	0.59	0.16	0.03
	out	99	0.06	3.08	0.35	15.81	0.73	16.06	1.92	12.14	6.66	7.86	0.53	0.17	0.03
Pine woodland	in	79	0.05	2.88	0.04	13.48	0.94	9.97	1.41	4.34	0.42	6.37	0.40	0.22	0.05
	out	84	0.04	2.91	0.10	14.89	0.93	10.36	1.73	6.69	1.61	6.68	0.28	0.40	0.09
Heathland	in	50	0.05	3.35	0.13	10.79	1.53	1.91	0.75	2.72	0.39	3.15	0.39	0.85	0.04
	out	51	0.05	3.36	0.12	11.34	1.26	2.06	0.87	2.18	0.19	2.86	0.39	0.89	0.03
	A_m														
Oak-Beech forest	in	26	0.01	3.31	0.15	4.62	0.56	0.85	0.48	6.57	2.28				
	out	24	0.01	3.35	0.18	4.63	0.87	3.76	2.66	6.08	2.18				
Pine forest	in	20	0.08	3.09	0.11	2.67	0.40	1.47	0.58	3.54	1.19				
	out	20	0.01	3.07	0.08	2.85	0.38	1.69	0.49	1.41	0.97				
Pine woodland	in	17	0.01	3.17	0.06	2.52	0.30	1.40	0.53	1.56	0.79				
	out	17	0.01	3.13	0.04	2.92	0.41	2.42	1.58	1.04	0.70				
Heathland	in	16	0.01	3.51	0.08	3.21	0.48	1.32	1.11	1.89	0.92				
	out	16	0.01	3.58	0.08	3.20	0.40	1.61	1.32	1.11	0.73				

Abiotic factors

Soil samples were collected in early spring 1996 and sifted before use. We took 10 subsamples of soil inside and outside the large herbivore exclosures using an Edelman auger (diameter 7 cm). We sampled from the ectorganic layer (A_o) including litter, fermented horizon and humic horizon and the upper 10 cm of the mineral horizon (A_m). The soil material was transported in plastic bags. We used several abiotic parameters to test their effects on woody species establishment. We measured the depth of the ectorganic (litter) layer (cm), the soil pH (pH KCL), the anount of photosynthetic active radiation (PAR), total N and P contents, P extractable concentrations and the organic matter content (Houba et al. 1986). Organic matter content in the both mineral horizons was measured as loss-on-ignition. The pH was assessed after adding 1 M of KCL to the soil. Total N and P concentrations (spectro-photometrically) in the soil were measured after digestion in H_2SO_4-salicyclic-acid-H_2O_2 and selenium. Extractable N and P in the topsoil were measured after digestion in 0.01 M CaCl2, using a Technicon Auto-analyser (Skalar, Breda, The Netherlands). The amount of photosynthetic active radiation (PAR) available to the seedlings was measured using Licor Quantum-Sensors, connected to Licor LI-1000 data loggers (LI-COR, Inc. Linclon, Nebraska) in the open field. Three sensors were randomly positioned above on the soil surface. Total PAR was measured in 1 minute intervals and integrated over half hour periods. All data on light availability were calculated as daily percentages of light available on the soil surface relative to the open site.

Data analysis

The establishment success, measured as the number of seedlings (x) at the end of the experiment was $^{10}\log(x+1)$ transformed as well as the the number of germinated seeds, also in order to improve the homogeneity of variance. We used a two-way ANOVA with herbivory treatment and vegetation type as fixed factors, exclosure as random factor and with establishment success and number of germinated seeds as dependent variables. One-way ANOVA was used to analyse differences in seed and seedling fate among the vegetation types as well as to analyse differences in abiotic facors inside and outside exclosures. A Tukey HSD test was used as post hoc test to analyse differences between treatments. Stepwise linear regression models were used to analyse the effect of abiotic factors on the seedling establishment inside rodent-free cages. As independent variables, we used the values of mixed soil samples of both soil horizons inside the exclosures. One exclosure was omitted from the data analysis because rodents had entered the rodent-free cage.

Results

Germination

In general, signficant effects of the herbivory treatment on the total number of germinated oak and beech seeds were found ($F_{2,147} = 17.82$, $P < 0.01$). Many oak and beech seeds were found germinating in the seed plots with 'insect' treatment while obviously less germinating seeds were found in seed plots with 'rodent' and 'deer' treatment (Table 2). Also, the number of germinated seeds differed among the woody species as well as among the vegetation types. The number of germinated oak seeds, measured in the seed plots with the 'insect' treatment was significantly higher in oak-beech forest (64-70%) than in heathland and pine woodland (21-52%; Table 2). The number of germinated beech seeds in seed plots with 'insect' treatment did not differ significantly among the vegetation types (42-62%; Table 2). No germinating seeds of Scots pine and birch were found.

Seed fate

In seed plots with 'deer-' as well as 'rodent treatment' seed predation was the major factor limiting oak and beech seedling establishment (64-99%: Table 2). The number of predated seeds of both oak and beech did not differ significantly between the 'deer' and the 'rodent' treatment. Significantly lower numbers of oak and beech seeds (Table 2) were predated in heathland relative to the other vegetation types (Table 2). Significantly higher numbers of oak seeds in heathland, in seed plots with 'insect treatment' were not able to germinate compared to the other vegetation types (respectively 79% and 30-48%; Table 2).

Seedling establishment

In the first year (1996) after the seeds were sown, clear differences in seedling establishment were observed (Fig. 2, Table 3). Combining all species, in 1996 as well as in 1997, a significantly higher number of seedlings was established in seed plots with 'insect treatment' as compared to seed plots with 'rodent' and 'deer treatment' (Table 3).

Table 2: Seed- and seedling fates expressed as % of (i) sown seeds and (ii) germinated seeds (mean % per vegetation type, n=8 †) of oak and beech seeds over the three herbivory treatments: 'Insect', 'Rodent' and 'Deer'.

Abbreviations: dead%= not germinated seeds, pred%=seed predation by small rodents, germ%=germinated seeds, fungi%=seedlings died of fungi, desic%=dessication, insects%=defoliation by insects, herb%=large herbivores, survival%=no. of survived seedlings. Differences among the vegetation communities were tested according to One-Way Anova with Tukey HSD test. Different characters indicate significant differences :*= P<0.05, **=P<0.01 , †= n=7 for Pine forest

	% of sown seeds (n=50)									***% of germinated seeds***					
Insect															
Oak	**Seed fate**			**Seedling fate**						**Seedling fate**					
	pred. %	dead %	germ %	fungi %	desic. %	insects %	pred. %	herb. %	**survival %**	fungi %	desic. %	insects %	pred. %	herb. %	**survival %**
Heathland		79 ^{a}	21 ^{a}	2	4	1 ^{a}			**14 ^{b}**	10	24	6 ^{a}			**60**
Pine woodland		48 ^{a}	52 ^{a}	5	5	3 ^{ab}			**39 ^{a}**	15	14	8 ^{ab}			**63**
Pine forest		36 ^{a}	64 ^{a}	10	5	9 ^{b}			**40 ^{a}**	9	5	11 ^{b}			**75**
Oak-beech forest		30 ^{b}	70 ^{b}	7	4	17 ^{b}			**42 ^{a}**	8	6	18 ^{b}			**67**
		**	**			**			*			**			
Beech															
Heathland		58	42	1	38 ^{a}	1 ^{a}			**2**	2	44 ^{a}	34 ^{a}			**20**
Pine woodland		38	62	3	44 ^{ab}	3 ^{ab}			**12**	3	19 ^{a}	53 ^{ab}			**25**
Pine forest		46	54	1	29 ^{b}	10 ^{ab}			**13**	4	5 ^{b}	71 ^{b}			**20**
Oak-beech forest		51	49	1	17 ^{b}	22 ^{b}			**10**	4	2 ^{b}	90 ^{b}			**5**
					*	*					**	**			
Rodent															
Oak															
Heathland	64	19	18	2	2	3	0	0	**11**	13	9	14	1	0	**63**
Pine woodland	99	1	0	0	0	0	0	0	**0**	0	0	0	0	0	**0**
Pine forest	96	3	1	1	0	0	0	0	**0**	50	0	0	25	0	**25**
Oak-beech forest	81	11	8	0	0	1	6	0	**1**	3	3	9	69	0	**16**

Rodent															
Beech															
Heathland	68^{a}	5	27^{a}	0	25^{a}	1	0^{b}	0	**1**	0	94	4	1	0	**2**
Pine woodland	95^{b}	0	5^{b}	0	4^{b}	0	1^{ab}	0	**0**	0	70	0	25	0	**5**
Pine forest	99^{b}	0	1^{b}	0	0^{b}	0	1^{b}	0	**0**	0	25	0	50	0	**25**
Oak-beech forest	90^{ab}	1	9^{ab}	0	1^{b}	1	5^{a}	0	**2**	3	11	13	55	3	**16**
	*		*		**		*								
Deer															
Oak															
Heathland	74	18	9	1	1	0	0	1	**6^{a}**	6	6	0	3	21	**65**
Pine woodland	95	2	3	2	0	0	0	0	**1^{ab}**	85	0	0	0	0	**15**
Pine forest	93	6	1	0	0	0	0	0	**1^{ab}**	0	0	0	0	0	**100**
Oak-beech forest	86	7	7	0	1	1	4	1	**0^{b}**	0	7	12	71	11	**0**
									*						
Beech															
Heathland	66^{a}	11	23^{a}	0	22^{a}	0	1	0	**0**	0	95^{a}	0	5	0	***0***
Pine woodland	94^{b}	0	6^{ab}	0	3^{b}	1	2	0	**0**	0	48^{b}	16	32	0	**4**
Pine forest	98^{b}	0	2^{b}	0	1^{b}	0	0	0	**1**	0	50^{b}	0	0	0	**50**
Oak-beech forest	91^{b}	1	8^{ab}	0	2^{b}	1	3	0	**2**	3	26^{b}	13	39	0	**19**
	**		*		**						*				

In 1996, a significantly higher (Fig. 2E-H) mean number of respectively 5 seedlings of beech and 17 of oak had established in seed plots with 'insect treatment' as compared to the seed plots with 'rodent and 'deer' treatment (0-2 seedlings). Between 'rodent' and 'deer' effect no significant differences in seedling establishment occurred. Almost in every vegetation type a positive significant effect of the 'insect' treatment on the number of beech and oak seedlings was found (Table 4). Within the seed plots in heathland no significant herbivory effect (in 1996 & 1997, Fig. 2E, F) on the number of oak seedlings occurred. Apparently, only in heathland, seedlings of oak were able to establish themselves in the presence of both small and large herbivores.

Table 3: Two-way ANOVA summary with factors: herbivory treatment, vegetation type, woody species and exclosure with total number of seedlings in 1996 and 1997 as dependent variable. The degrees of freedom (df), Means Square (MS), F-value and significance level (P) of each factor and interaction term are presented for both 1996 and 1997. Between brackets means 'exclosure' is nested within 'vegetation type'.

1996				
Factor	df	MS	F-value	P
Herbivory	2	5.90	116.28	0.00
Woody species	3	4.57	90.09	0.00
Vegetation type	3	0.12	2.10	0.12
Exclosure (Vegetation type)	28	0.05	1.09	0.35
Herbivory x Vegetation type	6	0.44	8.74	0.00
Herbivory x Woody species	6	1.96	38.59	0.00
1997				
Herbivory	2	7.52	59.78	0.00
Woody species	3	4.18	33.23	0.00
Vegetation type	3	1.08	8.54	0.00
Exclosure	28	0.13	1.01	0.46
Herbivory x Vegetation type	6	0.42	3.35	0.00
Herbivory x Woody species	6	1.30	10.35	0.00

The establishment success differed significantly among the species (Table 3). Relative to oak and beech seedlings, low numbers of Scots pine and birch seedlings had established in the seed plots in 1996. In 1997, seedling establishment of Scots pine and birch had increased. In particular Scots pine seedlings showed higher numbers (5-12 ind.) while birch remained low (< 2 ind.) (Fig. 2B, Table 4). In 1997, significantly higher numbers of Scots pine seedlings were found in seed plots with 'insect treatment' in contrast the 'rodent and 'deer' treatment ($F_{2,53}=5.96$, $P<0.01$).

***Table 4*:** Two-way hierachical ANOVA summary with factors:, herbivory treatment, vegetation type and exclosure for respectively the establishment of oak and beech seedlings in 1996 and 1997. Both vegetation type (n=4) and herbivory treatment (n=3) are fixed factors while exclosure (n=8) is a random factor and nested within vegetation type (between brackets). The degrees of freedom (df), Means Square (MS), F-value and significance level (p) with $\alpha=0.05$, of each effect and interaction are presented for each woody species.

Quercus robur 1996	*df*	*MS*	*F-value*	*p*
Factor				
Herbivory	2	9.41	124.59	0.00
Vegetation type	3	0.02	0.14	NS
Exclosure (Vegetation type)	28	0.12	1.62	NS
Vegetation type * Herbivory	6	0.73	9.70	0.00
Quercus robur 1997				
Herbivory	2	7.44	72.1	0.00
Vegetation type	3	0.02	0.13	NS
Exclosure (Vegetation type)	28	0.13	1.29	NS
Vegetation type * Herbivory	6	0.63	6.10	0.00
Fagus sylvatica 1996				
Herbivory	2	2.34	37.15	0.00
Vegetation type	3	0.37	6.87	0.00
Exclosure (Vegetation type)	28	0.05	0.84	NS
Vegetation type * Herbivory	6	0.26	4.06	0.00
Fagus sylvatica 1997				
Herbivory	2	2.72	43.54	0.00
Vegetation type	3	0.19	2.56	NS
Exclosure (Vegetation type)	28	0.07	1.16	NS
Vegetation type * Herbivory	6	0.14	2.22	NS
Pinus sylvestris 1997				
Herbivory	2	0.86	5.04	0.01
Vegetation type	3	3.26	10.34	0.00
Exclosure (Vegetation type)	28	0.32	1.85	0.03
Vegetation type * Herbivory	6	0.11	0.67	NS
Betula pendula 1997				
Herbivory	2	0.02	0.86	NS
Vegetation type	3	0.21	4.16	0.02
Exclosure (Vegetation type)	28	0.05	2.02	0.01
Vegetation type * Herbivory	6	0.02	0.72	NS

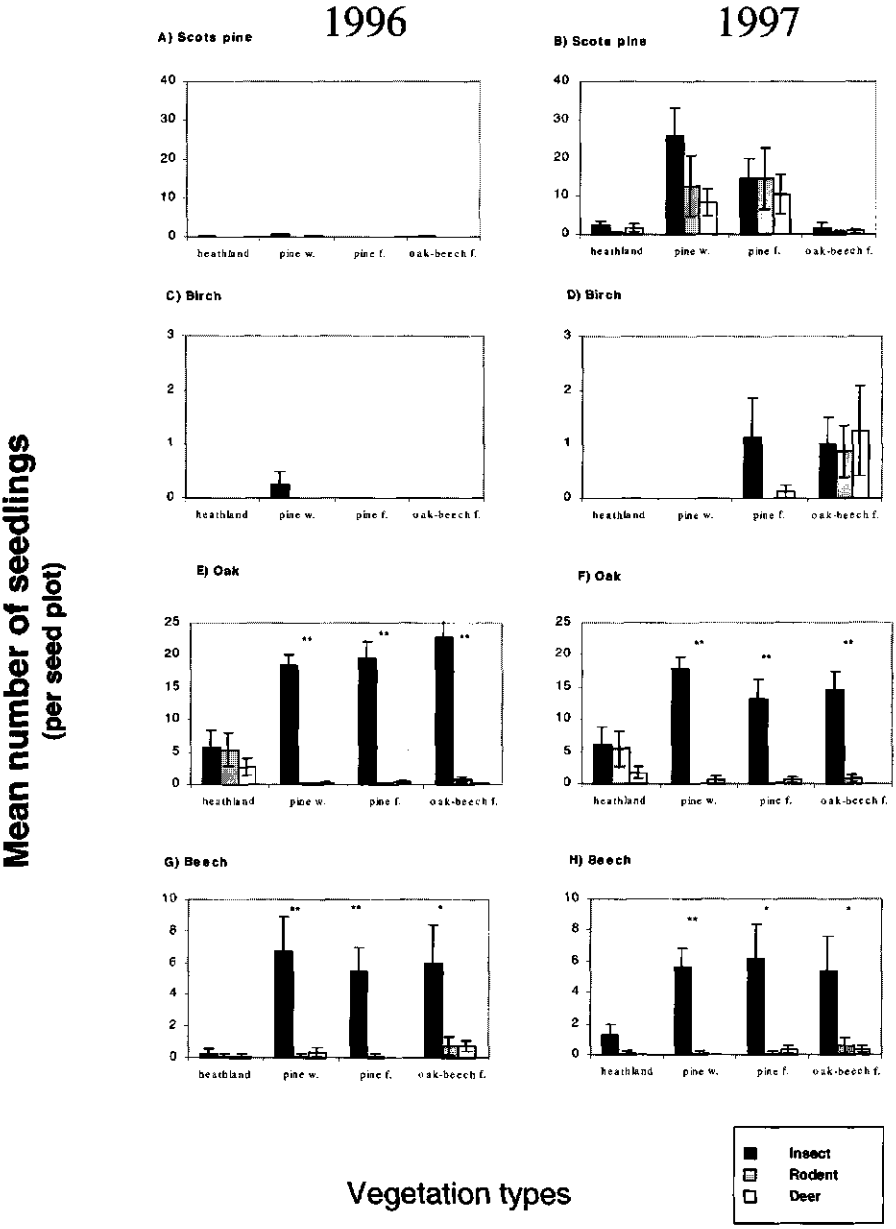

Figure 2: The means (± s.e) of the number of established seedlings of Scots pine, birch, beech and oak per vegetation type in respectively 1996 and 1997 accounted for seed plots outside ('Deer') and inside ('Rodent') exclosures and inside rodent free cage ('Insect'). * P <0.05, ** P <0.01

Among the vegetation types, establishment success of Scots pine differed significantly ($F_{2,31}=8.91$, $P<0.01$, Fig. 2B). Evidently lower numbers of seedlings of oak and beech were found in heathland in contrast to the other vegetation types (Fig 2E-H). Scots pine seedlings were mainly found in pine woodland and pine forest while more birch seedlings were found in oak-beech forest and pine forest (Fig. 2A-D). The establishment of Scots pine and birch seedlings showed a significant variation among the exclosures (Table 4).

Seedling fate

Seedlings of beech and oak were found predated by small rodents in seed plots with the 'rodent treatment', mainly in oak-beech forest relative to the other vegetation types (respectively 6 and 5 ind.;Table 2). Only few seedlings (2 ind.) were found killed by large herbivores. In seed plots with the 'insect treatment' most of the seedlings of beech and oak died of desiccation and defoliation (Table 2) Significantly more beech seedlings died of desiccation in heathland and pine woodland (38-44%) than in pine and oak-beech forest (Table 2). In contrast to beech seedlings, lower numbers of oak seedlings (4-5%) died of desiccation. Most of the beech seedlings were found desiccated during unfolding their cotyledons. The number of oak and beech seedlings that died of defoliation by insect herbivory in seed plots with the 'insect treatment' differed significantly among the vegetation types (Table 2). Especially the relatively high mortality of beech and oak seedlings in oak-beech forest differed significantly from the other vegetation types (Table 2). In general, insect herbivory killed more beech than oak seedlings.

Abiotic factors

The light availability had a significant effect (stepwise multiple regression, Table 5) on the number of beech and oak seedlings in both 1996 and 1997. Also, a slight positive effect of total extractable P on the number of oak seedlings was found. An increasing litter depth had a significant positive effect on the number of Scots pine seedlings, while the organic matter content had a negative effect. No abiotic factor was found to show a significant relation with the number of birch seedlings. Also, the length of both oak and beech seedlings showed a significant negative correlation with increasing light availability.

***Table 5*:** Stepwise multiple regression models (R^2, ß) with the number of seedlings of oak, beech, Scots pine* and birch seedlings* as dependent variables in relation to abiotic factors in seed plots with 'insect' treatment in 1996 and 1997. Only significant models are reported. Also, the significant models with the shoot length of oak and beech seedlings (in 1997) as dependent variable are reported. Abbreviations: Pe= P extractable, Org. matter= Organic matter, Light=Light (PAR) on soil surface * In 1996 to little establishment of Scots pine and birch seedlings was observed

Dep.variable	*Model*		R^2	*ß*	*P*
Oak 96	1)	Pe	0.55	0.38	0.00
	2)	Pe	0.69	0.29	0.00
		Light		-9.43	
Beech 96	1)	Light	0.25	-8.36	0.00
Oak 97	1)	Light	0.30	-21.54	0.00
	2)	Light	0.48	-32.31	0.00
		Ntot		-2.34	
Beech 97	1)	Light	0.18	-10.23	0.02
Scots pine 97	1)	Litter depth	0.18	2.90	0.02
	2)	Litter depth	0.37	3.80	0.00
		Org. matter		-2.54	
Oak shoot	1)	Light	0.50	-19.53	0.00
Beech shoot	1)	Light	0.47	-15.90	0.00

Discussion

Effects of herbivory

The significantly higher numbers of seedlings of oak and beech found in the rodent- free cages relative to the other herbivore treatments were attributed to rodent predation. Even the number of Scots pine seedlings in 1997 showed a significant cage effect. The majority of beech and oak seeds were found to be removed from the seed plot or consumed at the spot. In many cases small fragments of seed shells indicated predation by typical granivorous small rodent species like wood mice (*Apodemus sylvaticus* L.) (Smit et al. 2001). The small size of birch and Scots pine seeds hampered the observation of seed predation of these seeds. Probably, Scots pine and birch seeds have not been predated by small rodents in large numbers because of the low energetic value of the seeds (Vander Wall 1990). In addition to former studies, which concentrated on the effects of seed predation by small rodents in single successional stages only (Ostfeld and Canham 1993, Ostfeld et al. 1997, Myster and Pickett 1993), seed predation was found to play a crucial role in woody species establishment across the successional sequence. The low establishment success of oak and beech seedlings in the presence of large and small herbivores in pine woodland, pine forest and oak beech forest as well as the relative high establishment success in heathland seed plots accessible to herbivores corresponds to the distribution of the densities of the small rodents over the vegetation types. Small rodent densities were established in 1997 (Smit et al. 2001) with highest densities of merely wood mice found in pine forest, woodland and oak-beech forest and significantly lower densities in heathland. The low small rodent density in heathland may have caused the relatively high survival of seeds and as a result the relatively high establishment success of oak. The strong effects of small rodents reduced the apparent effect of large herbivores. No clear effect of browsing by large herbivores outside the exclosures relative to inside the exclosures was found. In only two cases, rooting by wild boars nearby seed plots was observed outside the exclosures. Indirect effects of large herbivores on the small rodent communities may have affected the establishment success of oak and beech seedlings. After two years of grazing exclusion, inside the exclosures in former heavily grazed Scots pine woodlands, a fast recovery of browse- sensitive woody species such as rowan had a significant positive effect on the rodent density (Smit et al. 2001). The development of structural rich understory vegetation may have caused higher small rodent densities and consequently higher seed predation.

Seedling emergence and survival

Despite the prominent seed predation effect, inter- and intraspecific differences in the establishment success occurred across the vegetation succession gradient. These differences could be affected by differences in seedling emergence among the species. All of the beech seeds were found germinating in April 1996 while oak seeds have been observed germinating throughout the season from April until October in 1996. Eventually, oak seeds were still able to germinate in September 1997 (R. Smit, pers. obs.). On the contrary, birch and Scots pine seedlings showed strong year to year differences in germination. The latter two species depend highly on relatively long-term humid and warm conditions and need mineral soil to germinate (Fanta 1982, Dolling 1996). These differences in emergence phenology have important consequences for the seedling survival. The concentrated germination timing of beech seeds in early spring makes it highly vulnerable for abiotic stress factors like spring frost, drought or outbreaks of insects. Despite the high number of germinated beech seeds in early successional communities, many seedlings of beech died of desiccation while unfolding their cotyledons during a long-term dry period in April 1996. Therefore, the establishment of beech seedlings in early successional communities can apparently be severely limited by abiotic stress. Establishment of Scots pine and birch seedlings in pine forests and woodlands took place on pleurocarpous moss carpets growing on deep litter layers, which temporarily improved the moisture conditions of the litter (R. Smit, pers. obs). Nevertheless, survival chances for Scots pine and birch seedlings are low in pine forests and woodlands because they are likely to die of desiccation because their roots never reach mineral layers below the thick litter layer. In early successional communities like heathland woody seedlings have to cope with wide fluctuations in temperature and moisture. Favorable micro-environments for successful germination and establishment are rare. However, only oak seeds were able to cope with this severe abiotic stress. The explanation for these relatively high survival rates must be found in the high contents of stored resources in cotyledons in combination with the long taproot. Brookes (1976) indicated that oaks seedlings depend highly upon cotyledon reserves if grown under conditions of nutrient deficiency. The long taproot enhances the ability to acquire sufficient water. In our study, light availability in the herb layer showed a strong negative relationship with establishment success and the shoot length of oak and beech seedlings. This negative light effect probably implies an indirect desiccation effect across the vegetation succession gradient ranging from low light conditions in oak-beech forest to high light conditions in heathland. At our study sites extreme low ground water tables occur on the aeolic sand deposits. Therefore, moderate shade by canopy trees may facilitate woody species establishment by reducing water stress (Berkowtitz et al. 1995). Especially in early successional communities, seedling establishment is limited by abiotic stress rather than by herbivory or granivory or competition with the present vegetation (Menge & Sunderland 1987). Besides positive effects, canopy trees can have negative effects on woody seedlings. During the spring of 1996, in oak-beech forests many seedlings of beech and to a lower extent of oak died of defoliation inflicted by leaf chewing caterpillars of winter moths (*Optera brumata* L.). Parent trees of oak served as hosts for caterpillars of wintermoths which defoliated the seedlings on their way to the forest soil to pupate (Crawley & Akhteruzzaman 1988). This host-specific predation of woody seedlings by predators from the parent tree is a clear example of a negative parent-tree effect (Janzen 1970, Herrera 1995). For successful establishment, beech and oak seedlings have to escape from their direct parents' neighborhood.

Herbivore guilds

We hypothesized that (1) in early stages of vegetation succession, establishment chances of woody seedlings are relatively high due to a lower herbivory pressure and that (2) herbivore guilds have different effects on woody species establishment across the vegetation succession gradient. The results of our study do confirm the first hypothesis for small rodents and insects only. In fact, the grazing pressure by large herbivores was high in early successional vegetation types compared to the later successional vegetation types but did not have significant negative effects (see Chapter 6). Relative to oak-beech and pine forest, red deer but also mouflon were observed to use heathland and pine woodland as their primary habitat. In early or intermediate successional communities, typical grazers and intermediate feeders (Hofmann 1989) like, respectively mouflon and red deer but also rabbits, have a relatively high foraging efficiency (Van der Koppel et al. 1996). In these communities grazing 'lawns' of species like *Deschampsia flexuosa*, create ideal forage for these herbivores. Despite the relatively high densities of large herbivores, seedlings of oak were able to survive. For that reason, the low densities of small rodents in early successional communities is probably more important in woody seedling establishment than the high number of large herbivores. In general, large herbivores play a more prominent role within the life of woody species during the sapling stage rather than during the seed or seedling stage (Inouye et al. 1994, McInnes et al. 1992, Anderson and Katz 1993, Putman 1986).

First, grazing on relatively small woody seedlings is very inefficient and second other small, selective herbivores like rodents and insects have consumed the seeds or seedlings before large herbivores had the chance to do so. As a consequence, our second hypothesis has been confirmed by our results. Small rodents played an important role in the establishment of late successional woody species like oak and beech during the intermediate and late successional stages while insects were an important factor during the late successional stages. On the other hand, pioneer woody species like birch and Scots pine were not found to be severely affected by any group of herbivores during the establishment stage. Furthermore, the palatability of the woody species to herbivores plays a very important role in the establishment success and consequently the vegetation succession (Anderson and Katz 1993, Olff et al. 1999, Van Hees et al. 1996, Pigott 1985). Palatable oak and beech seedlings suffered from a higher grazing pressure by rodents and insects than Scots pine seedlings leading to higher establishment chances of the latter species. The combination of a relatively low palatability and a high dispersability (wind-dispersed diaspores) makes Scots pine a very successful woody species in a heavily grazed area.

Forest succession

As a result of this study, we are able to evaluate the consequences of the effects of the different herbivore guilds on woody seedling establishment for forest succession. If we assume seed dispersal to be no limiting factor we understand the final effects on forest succession on the basis of the interactions between biotic (herbivory-granivory) and abiotic factors (abiotic stress). Establishment chances for woody species are generally higher in early successional communities than in late successional types due to a lower granivory pressure. In these communities, abiotic stress is the key factor in woody species establishment. As a result, the establishment chances for mature woody species like beech are very low. During the intermediate successional stages, high granivory intensity inhibits the colonization of mature forest species. Pioneer woody species like birch and Scots pine undergo a continuous water stress due to interference with present vegetation (a dense grass sward). In the late successional stage, mature forest species will bear a severe parent tree effect via herbivory by insects and granivory by small rodents. Forest succession can easily be arrested or delayed in intermediate successional stages due to the low establishment chances for mature woody species. Hence, on the long-term, the various effects of the herbivore guilds on woody species establishment may cause a shifting mosaic of various successional phases (Olff et al. 1999).

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Chapter 4

Botanical changes during 7 years after large herbivore introduction and exclusion across a woodland-forest gradient

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Abstract

We used the enlargement of the habitat of a wild large herbivore population in the National Park De Hoge Veluwe to study the botanical changes during seven year after grazing introduction and exclusion across a woodland - forest gradient. We hypothesised that grazing introduction in pine forest and oak-beech forest would suppress graze-sensitive, palatable species leading to an increase of graze-tolerant species because of competitive release. Grazing exclusion in former, heavily grazed pine woodland was hypothesised to induce a recovery of palatable graze-tolerant and -sensitive species. Neither exclusion nor introduction of grazing significantly affected the composition of the herb layer in either of the three vegetation types. The most significant effects of introduction of large herbivores took place within the shrub layer. Grazing exclusion resulted in a fast recovery of graze-tolerant shrub species, while grazing introduction did not have significant effects on the shrub layer. Inside the exclosures of the new forest areas, the shrub layer could develop undisturbedly without the former interference of roe deer. The recovery of a dense shrub layer negatively affected the cover of the perennial grass layer mediated by competition for light leading to an increase of litter cover. Neither the introduction nor the exclusion of grazing significantly affected the vascular species richness. The impacts of grazing introduction and grazing exclusion do not reflect reversible ecological processes. The time required for recovery of the understory vegetation following release from grazing is not proportional to the time the understory is degraded by grazing introduction. While graze-tolerant species were able to recover rapidly following release of grazing, this was not the case for graze-sensitive species like deciduous tree species. From the nature conservation point of view, we conclude that grazing introduction of deer in forests may not be a successful tool in maintaining or creating a higher species or community diversity.

Introduction

During the last decade, grazing by large herbivores has been a favourite tool in nature management and conservation (Bakker 1989). Herbivores are generally thought to enhance species diversity by consumption of competitively dominant plant species and indirect effects on plant competition (Olff & Ritchie 1998). Grazing by large herbivores is assumed to cause an increase of the heterogeneity of the vegetation structure through the selectivity of the herbivores on the one hand and the response of the vegetation to herbivory on the other (Adler et al. 2001). Consequently, grazing by large herbivores results in an increase in species and community diversity (Fletcher et al. 2001). Despite of the fact that discussion on the effect of grazing by large herbivores on plant diversity has not yet led to an overall consensus (Oba et al. 2001), many natural areas in North-western Europe have become subject to grazing by domesticated or wild large herbivores. The (re-)introduction of grazing by large herbivores is hindered by the lack of knowledge about the effects of large herbivores on the vegetation on the one hand, and the vegetational responses to herbivory on the other (Bokdam & Gleichman 2000).

Botanical changes following the relief of grazing in contrast to the introduction of grazing are essential to understand the mechanistic pathway of the plant-herbivore interactions. The insight into the ability of plant species to recover following removal of long-term large herbivore pressure has been a research theme in only a few studies (Anderson & Katz 1993, Putman et al. 1989). These studies focussed on a single environment or vegetation type, but did not take into account the different effects of grazing introduction and exclusion across a successional sequence of vegetation types. Understanding how plant recovery from herbivory interacts with the successional stage and consequently habitat productivity is necessary to predict under what resource conditions plants are most affected by herbivory, and ultimately how herbivory impacts plant population dynamics (Hawkes & Sullivan 2001). Plants have different strategies to cope with herbivory (Grime 1979). They either avoid or tolerate herbivory (Olff et al. 1999). Plants can resist or prevent grazing damage by using mechanical or chemical defence strategies (Fineblum & Rausher 1995) or by allocating their biomass out of reach (Crawley 1983). Generally, graze-tolerant plants show a rapid regrowth capacity after being grazed or have a physiological adaptation to grazing (Anderson & Katz 1993, Olff et al. 1999). Graze-sensitive species are commonly less flexible to grazing showing a slow regrowth capacity or even mortality after being grazed (Grime 1979). Severe and long time grazing by large herbivores in the New Forest area resulted in clear differences in species composition in the herb and shrub layer leading to higher abundances of species resistant to grazing and an absence of many graze-sensitive species (Putman et al. 1989). Some plant species directly depend on the presence of herbivores such as typical ruderal species growing on excretion or dung patches and treading places (Olff & Ritchie 1998, Bokdam & Gleichman 2000).

In our study we used the enlargement of the habitat of wild large herbivore populations in the National Park De Hoge Veluwe to study the effects of introduction as well as exclusion of large herbivores on the botanical composition of the herb and shrub layer across a woodland - forest gradient. We placed 24 large herbivore exclosures to study the effects of respectively herbivore introduction and exclusion encompassing a former heavily grazed pine woodland with a long grazing history and both previously ungrazed pine forest and oak-beech forest. These vegetation types comprise a vegetation succession gradient. We hypothesised that grazing introduction would suppress graze-sensitive species leading to an increase of graze-tolerant or graze-resistant species because of competitive release. Grazing exclusion was hypothesised to induce a recovery of palatable graze-tolerant and -sensitive species. Overall, grazing introduction was assumed to increase species richness as compared to exclusion (i) due to the colonisation of typical ruderal species rather than the extinction of graze-sensitive species in the introduction area and (ii) the extinction of ruderal species in the exclusion area.

Methods

Study area

The study was conducted in The National Park 'De Hoge Veluwe' in the eastern part of the Netherlands (52° 2-8'N; 5° 50-51'E) (Fig. 1) during four consecutive years from July 1994-August 1997 plus an extra survey during the summer of 2001. The climate in the area is Atlantic with the mean annual temperatures being 9.1° C and annual rainfall of 800 mm (Krijnen & Nellestijn 1992). The park is characterised by a typical landscape of sandy soils of glacial and inter-glacial origin. Heavy grazing by domesticated sheep and sod cutting in the late Middle Ages have caused soil degradation resulted in a vegetation recession from deciduous common oak (*Quercus robur* L.) and beech (*Fagus sylvatica* L.) forest into heathland and even bare sand. Aeolian sands have covered mainly the central parts of the park creating sand dunes and blown-out plains.

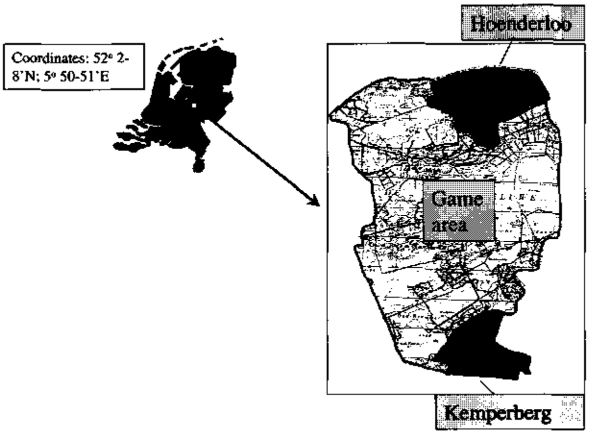

Figure 1: The location of the National Park De Hoge Veluwe in the Netherlands divided into the new forest areas introduced to grazing (shaded) and the former, central game area that was grazed before 1995. The introduction areas represent mainly pine forest and oak-beech forest and the exclusion area represents pine woodland and short vegetations like heathland and grassland. In our study we only used pine woodland, pine forest and oak-beech forest.

Nowadays, many parts of the former open plains consist of Scots pine (*Pinus sylvestris* L.) woodlands, which follow the early successional communities of open sand dominated by lichens (*Cladonia* spec.), grey hair-grass (*Corynepherus canescens* L) and heather (*Calluna vulgaris* L.). Wavy hair-grass (*Deschampsia flexuosa* L) and sand sedge (*Carex arenaria* L.) dominate the understory vegetation of these primary, open pine woodlands (Table 1). During vegetation succession first generation pine woodlands change into more uniform and dense stands of second-generation pine forest with an understory of blue berry (*Vaccinium myrtilis* L) and a shrub layer of rowan (*Sorbus aucuparia* L) (Table 1). In the northern and southern parts of the park late successional communities dominated by common oak (*Quercus robur* L.) and beech (*Fagus sylvatica* L.) grow on well-developed, dry podzolic soils on cover sand and fluvio-glacial soils. The above-described mosaic of woodland and forest comprise different communities that we consider being part of a successional sequence.

Table 1: Description of the vegetation types divided into grazing treatment (large herbivore introduction or exclusion), grazing history (large herbivores species before and after 1995) area (total number of hectares in the park), pH (of the litter layer) and dominant vegetation (T=tree, S=shrub, H=herb and B=bryophyte).

Vegetation type	*grazing treatment*	*grazing history*	*Area*	*pH (KCL)*	*Dom. vegetation*
Oak-beech forest	Introduction	< 1995: roe deer > 1995: all large herbivores	300	3.0	Quercus robur (T) Fagus sylvatica (T) Deschampsia flexuosa (H) Vaccinium myrtilis (H) Polytrichum formosum (B)
Pine forest	Introduction	< 1995:roe deer > 1995: all large herbivores	600	3.1	Pinus sylvestris (T) Sorbus aucuparia (S) Deschampsia flexuosa (H) Vaccinium myrtillus (H) Pleurozium schreberii (B)
Pine woodland	Exclusion	< 1995: all large herbivores > 1995: all large herbivores	2000	2.9	Pinus sylvestris (T) Deschampsia flexuosa (H) Carex arenaria (H) Hypnum cuppressiforme (B)

Grazing history

Since the reintroduction in 1905, a stable red deer (*Cervus elaphus* L.) population has occurred of 200-250 animals in the national park 'De Hoge Veluwe'. A stable roe deer (*Capreolus capreolus* L.) population (150-200 animals) has been present since the late 18th century in the park. A fluctuating wild boar (*Sus scrofa scrofa* L.) population has occurred since 1940 (30-80 animals). Mouflons (*Ovis musimon* Schreber), Corsican mountain sheep, were introduced in the park in 1921. During the last decades, the population has grown to approximately 250 animals.

In November 1994, the central game area (3800 ha) was enlarged with two new forest areas in the northern and southern part of the park by fence removal. These new areas (1200 ha.) offered new habitats to red deer, wild boar and mouflon (Fig. 1), but they had already a stable roe deer population (100-150 animals). The large herbivore population was controlled by a relatively constant culling regime (Smit et al. 2001).

Experimental design

Three vegetation types covered a successional gradient from first generation Scots pine woodland (1) to second-generation pine forest (2) to oak-beech forest (3). In 1994, 24 exclosures of 15 x 25 m excluding all large herbivores including rabbits were placed to monitor changes in vegetation composition with and without large herbivore grazing. We placed eight exclosures both in the previously ungrazed pine forest and oak-beech forest (introduction areas) and eight in the formerly, heavily grazed pine woodland (exclusion area). The exclosures were constructed using wire netting with a height of 200 cm and a mesh width of 5x5 cm. The mesh width allowed small rodents to enter the exclosures. To study the effects of introduction and exclusion of large herbivores on the vegetation composition we used permanent quadrates of 10 x 10 m inside and outside the large herbivore exclosures. We surveyed the vegetation composition of the herb layer (< 50 cm) by using the line intercept method (Kent & Cooker1994). In each quadrat four lines of 10 m length directed to the north, were laid out. Within 10 x 10 cm subplots on 50 permanent positions along each line the dominant and subdominant vascular plant species (including litter, bryophytes, lichens, bare sand, stems, algae, dung) were recorded. The dominant species was characterised by the largest (external) cover of aboveground parts within the subplot while the subdominant species had the second largest cover with a minimal cover of 5%. If the subdominant species covered less than 5% the dominant species was ranked as subdominant as well. In total, 200 permanent subplots per quadrat were used to survey the vegetation composition of the herb layer inside and outside the large herbivore exclosures. In addition to the described method, in 1994 and in 2001 all vascular plant species were counted in the permanent quadrats inside and outside exclosures as well to determine the species richness.

To survey the shrub layer (50-500 cm) we counted the number of shrub and tree individuals within the quadrates divided into three height classes; 0-50 cm (1), 50-200 cm (2) and 200-500 cm (3). We used the central stem base of the shrub or tree species to distinguish individual trees and shrubs. Individual shoots located further away than 10 cm from the stem base were counted as individuals. No distinct changes within the tree layer canopy (500-2500 cm) were noticed during the study period.

Data analysis

We analysed changes within the composition of the herb layer for each vegetation type, by using the total number of dominant and subdominant 'hits' per permanent quadrat of grouped species in the herb layer. We distinguished five life form groups; perennial grasses, sedges, dwarf shrubs, nitrophilous herbs (Ellenberg nitrogen indicator value, $I_N \geq 6$, Ellenberg 1979) and herbs (Table 2). We also used the number of hits of bryophytes and bare litter to describe changes in the herb layer. We analysed changes within the herb layer relative to the initial cover (in 1994). For each quadrat during the study period we used the difference in the number of hits between the initial cover (in 1994) and the cover in the following years.

For the analysis of botanical trends within the herb layer of each vegetation type, we only used life forms that had a mean, minimum number of dominant or subdominant hits over the study period ≥ 10. We categorised the shrub layer in three groups, shrubs, deciduous trees and coniferous trees (Table 3). Analysis of variance for repeated measurements with Hotelling's Trace (type III, GLM, SPSS release 8.0) (Norušis 1993) was performed to determine between effects of grazing, year and interactions on botanical trends within the herb layer, shrub layer and species richness for each vegetation type. As dependent variables we used the number of dominant as well as subdominant hits, the number of individuals per height class and the number of species. Levene's test was used to test the homogeneity of variance for each dependent variable across all level combinations of the between-subjects factors. In 1997 and 2001, one exclosure in pine woodland was omitted from the data set because the vegetation outside the exclosure was seriously damaged by forestry activities.

Table 2: The species in the herb layer (<0.50 m), grouped as perennial grasses, sedges, dwarf shrubs, nitrophilous herbs (according to nitrogen indication value of Ellenberg (1979), I-N≥ 6) and herbs.

Perennial grasses	*Sedges*	*Dwarf shrubs*
Deschampsia flexuosa	Carex areneria	Calluna vulgaris
Agrostis capillaris	Carex pilulifera	Erica tetralix
Molinia caerulea		Vaccinium myrtillus
Festuca ovina		Rubus fructicosus
Nitrophilous herbs	*Herbs*	
Ceratocapnos claviculata	Rumex acetosella	
Galeopsis tetrahit	Galium saxatile	
Stellaria media	Melampyrum pratense	
Chamenerion angustifolium	Senecio sylvaticus	
Cerastium fontanum	Lonicera perclymenum	
	Dryopteris dilatata	

Table 3: The species in the shrub layer (0.5 – 5 m), classified as shrub, deciduous tree and coniferous trees

Shrubs	*Deciduous trees*	*Coniferous trees*
Sorbus aucuparia	Quercus robur	Pinus sylvestris
Amelanchier lamarckii	Quercus rubra	Larix kaempferi
Rhamnus frangula	Betula pendula	Pseudotsuga menziesii
Prunus serotina	Betula pubescens	
	Fagus sylvatica	

Results

Herb layer

Pine woodland (exclusion)

In pine woodland, changes within the composition of the herb layer did not show a significant effect of grazing exclusion (Fig. 2). Both inside as well as outside the exclosures, comparable trends in life form groups could be observed. The cover of perennial grasses, dominated by *Deschampsia flexuosa*, showed a strong decline in 1995 both inside and outside the exclosures (From 120 to 70 dominant hits; Fig. 2A, B). The cover of herb species, dominated by *Rumex acetosella* and *Galium saxatile*, showed a stronger decrease inside exclosures than outside exclosures (From 28 to 10 dominant hits inside and from 22 to 12 dominant hits outside; Fig. 2C, D). The cover of nitrophilous herbs, dominated by *Ceratocapnos claviculata*, decreased strongly initially both inside and outside the exclosures followed by a recovery in 2001 inside the exclosures (From 12 to 1 subdominant hits in 1997 to 10 in 2001; Fig. 2E, F). The cover of bryophytes, dominated by pleurocarpous mosses like *Hypnum cuppressiforme* changed significantly (Table 4) both inside and outside the exclosures during the study period. Inside the exclosures, the number of dominant hits increased during the first 3 years showing a decrease in 2001 (From 20 to 50 dominant hits in 1997 to 35 in 2001; Fig. 2G). In contrast, the moss cover outside the exclosures showed a decrease during the whole study period (From 60 to 15 subdominant hits; Fig. 2H). Additionally, the cover of litter changed significantly during the study period (Table 4). Inside the exclosures, the litter cover increased strongly, with a temporal decrease in 1997 (From 10 to 70 dominant hits; Fig. 2I). Outside the exclosures, the litter cover increased strongly after one year of grazing and than fluctuated during the rest of the period (Fig. 2J).

Pine forest (introduction)

Within the herb layer of pine forest, no significant effect of grazing introduction could be observed (Fig. 3). Most life form groups showed similar trends inside as well as outside the exclosures. The cover of perennial grasses, dominated by *Deschampsia flexuosa*, decreased inside the exclosures (from 75 to 30 dominant hits, Fig. 3A) while outside the exclosures the cover decreased as well, but recovered in 2001 (Fig. 3B).

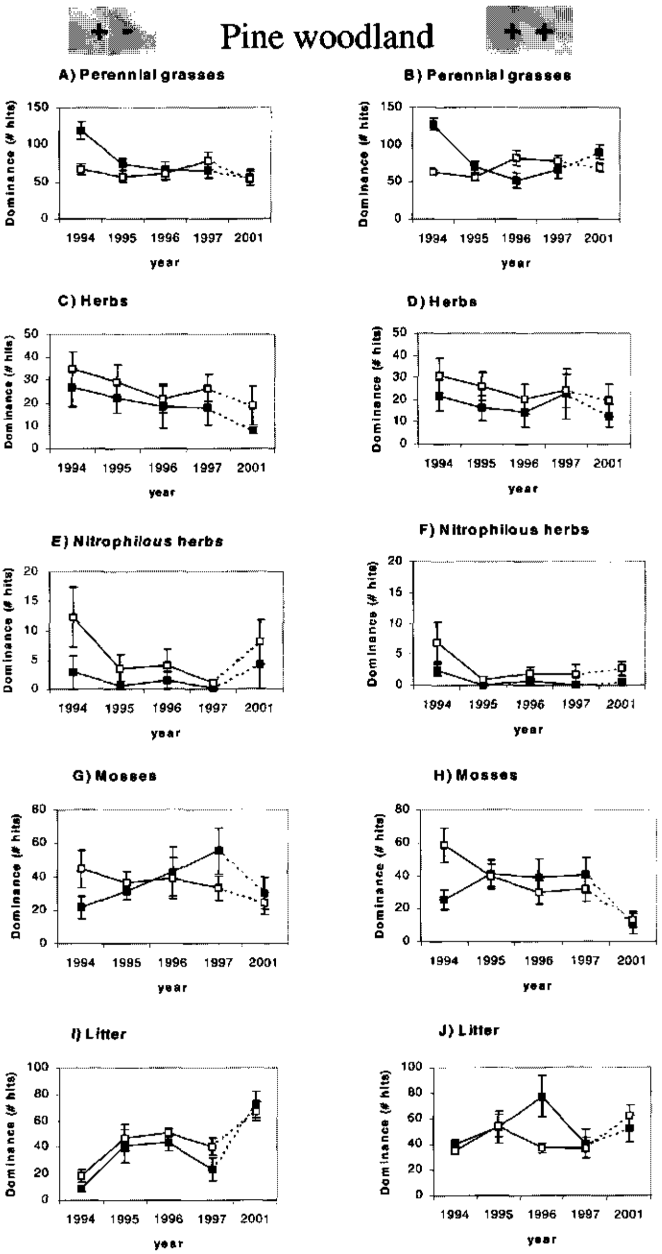

Figure 2: Changes in life form trends of mean number of dominant (closed squares) and subdominant (open squares) hits (± s.e.) in pine woodland 1994-2001 ivided into perennial grasses (A, B), herbs (C, D), nitrophilous herbs (E, F), mosses (G, H) and litter (I, J). The symbols '–' and '+' correspond to the effect of large herbivores (+ = 'with', - ='without'), the first symbol represents the situation before 1995 and the second the situation after 1995 (until 2001). The dashed line represents the gap in measurement between 1997 and 2001.

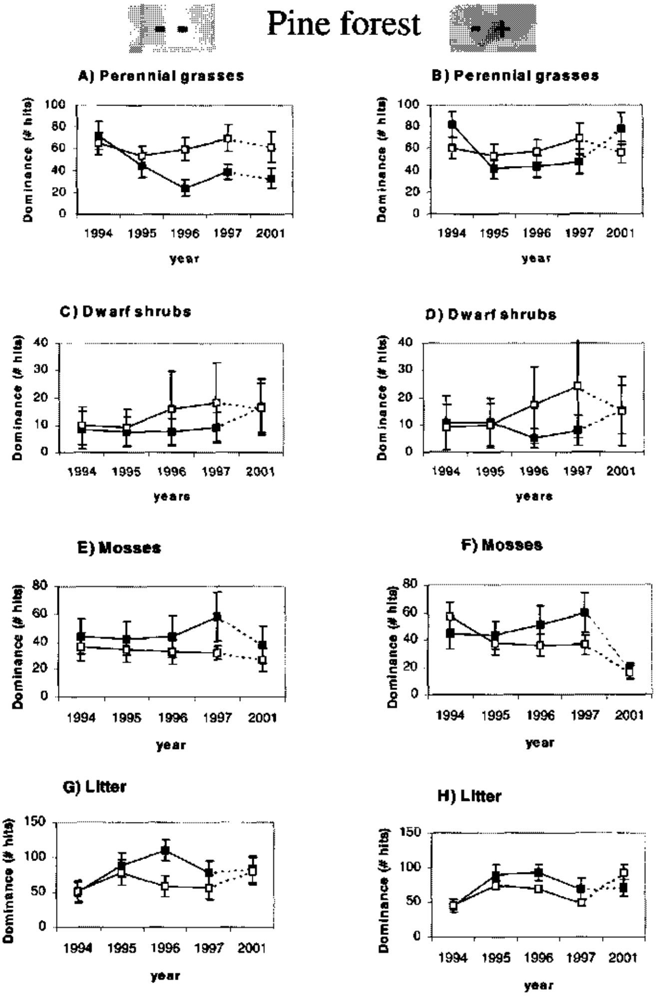

***Figure 3*:** Changes in life form trends of mean number of dominant (closed squares) and subdominant (open squares) hits (± s.e.) in pine forest 1994-2001 divided into perennial grasses (A, B), dwarf shrubs (C, D), mosses (E, F), and litter (G, H). The symbols '–' and '+' correspond to the effect of large herbivores (+ = 'with', - ='without'), the first symbol represents the situation before 1995 and the second the situation after 1995 (until 2001). The dashed line represents the gap in measurement between 1997 and 2001.

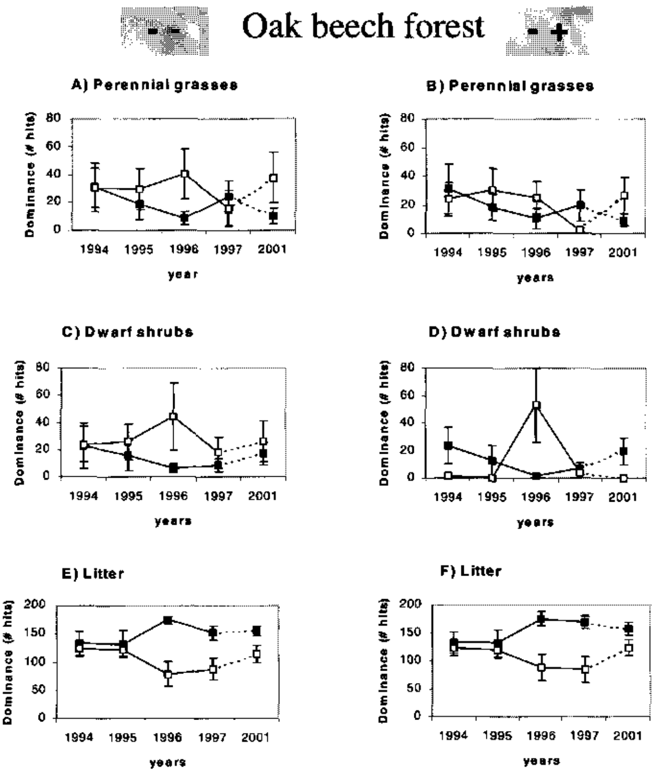

Figure 4: Changes in life form trends of mean number of dominant (closed squares) and subdominant (open squares) hits (± s.e.) in oak-beech forest 1994-2001 divided into perennial grasses (A, B), dwarf shrubs (C, D) and litter (E, F). The symbols '–' and '+' correspond to the effect of large herbivores (+ = 'with', - ='without'), the first symbol represents the situation before 1995 and the second the situation after 1995 (until 2001). The dashed line represents the gap in measurement between 1997 and 2001.

The cover of dwarf shrubs, dominated by *Vaccinium myrtillus*, showed a small increase inside as well as outside exclosures (From 10 to 15 dominant hits inside and outside, Fig. 3C, D). The moss cover, dominated by pleurocarpous mosses like *Pleurozium schreberii* showed a significant decrease in subdominance (Table 5) mainly outside the exclosures (from 60 to 20 subdominant hits, Fig. 3F). The cover of bare litter increased significantly (Table 5) both inside as well as outside the exclosures (from 50 to 70 dominant hits, both inside as well as outside, Fig. 3G, H).

***Table 4*:** Test results of ANOVA for repeated measurements according to Hotelling's Trace with 'year' and 'year x grazing' effects, analyzing trends in life forms (number of dominant hits (D) and subdominant hits (S)) in pine woodland. * = significant ($\alpha<0.05$).

Life form	*Dominant/ Subdominant*	*Effect*	*df (hypothesis, error)*	*F*	*P*
Perennial grasses	D	year	3,12	1.77	0.21
	D	year x graze	3,12	0.97	0.44
Perennial grasses	S	year	3,12	2.14	0.15
	S	year x graze	3,12	1.61	0.24
Herbs	D	year	3,12	2.54	0.11
	D	year x graze	3,12	1.04	0.41
Herbs	S	year	3,12	1.59	0.25
	S	year x graze	3,12	1.54	0.26
Nitrophilous herbs	D	year	3,12	2.03	0.16
	D	year x graze	3,12	1.58	0.25
Nitrophilous herbs	S	year	3,12	1.59	0.24
	S	year x graze	3,12	1.44	0.28
Mosses	D	year	3,12	3.01	0.07
	D	year x graze	3,12	1.47	0.27
Mosses	S	year	3,12	3.59	0.05
	S	year x graze	3,12	0.52	0.68
Litter	D	year	3,12	5.98	0.01*
	D	year x graze	3,12	2.09	0.16
Litter	S	year	3,12	2.47	0.11
	S	year x graze	3,12	0.93	0.46

Oak-beech forest (introduction)

The changes within the herb layer of oak-beech forest did not show a significant effect of grazing introduction. All studied life form groups showed comparable trends inside as well as outside exclosures. Perennial grasses, dominated by *Deschampsia flexuosa* showed a decrease in cover both inside as well as outside exclosures (From 30 to 10 dominant hits, Fig. 4A, B). Dwarf shrubs, dominated by *Vaccinium myrtillus* showed a relatively constant level of approximately 5- 20 dominant hits both inside and outside exclosures with a shift from dominant to more subdominant hits only in 1996 (Fig. 4C, D). Litter showed a significant decrease (Table 6) in subdominance (From 120 to 100, both inside and outside, Fig. 4E, F). Analogous to the decrease in subdominance, the number of dominant hits increased inside exclosures (From 120 to 150, Fig. 4E).

Table 5: Test results of ANOVA for repeated measurements according to Hotelling's Trace with 'year' and 'year x grazing' effects, analyzing trends in life forms (number of dominant hits (D) and subdominant hits (S)) in pine forest. * = significant ($\alpha<0.05$).

Life form	*Dominant/ Subdominant*	*Effect*	*df (hypothesis, error)*	*F*	*P*
Perennial grasses	D	year	3, 12	1.61	0.24
	D	year x graze	3,12	1.78	0.21
Perennial grasses	S	year	3,12	0.50	0.69
	S	year x graze	3,12	0.14	0.94
Dwarf shrubs	D	year	3,12	2.13	0.15
	D	year x graze	3,12	0.56	0.65
Dwarf shrubs	S	year	3,12	2.83	0.08
	S	year x graze	3,12	0.30	0.83
Mosses	D	year	3,12	1.97	0.17
	D	year x graze	3,12	0.40	0.76
Mosses	S	year	3,12	3.48	0.05*
	S	year x graze	3,12	0.56	0.65
Litter	D	year	3,12	3.11	0.07
	D	year x graze	3,12	0.33	0.80
Litter	S	year	3,12	8.09	<0.01*
	S	year x graze	3,12	0.49	0.70

Shrub layer

Pine woodland (exclusion)

In pine woodland inside the exclosures the number of shrubs, dominated by *Sorbus aucuparia* rapidly recovered after grazing relief. Within the seven year study period the shortest class (0-50 cm) grew into the middle (50-200 cm) and tallest class (200-500 cm) with the largest mean proportion (> 80%) occurring in the tallest class in 2001 (Fig. 5A). Outside the exclosures, the number of shrubs remained in the shortest class during the whole study period (Fig. 5B). The number of deciduous trees inside the exclosures dominated by *Quercus robur* also showed an increase of the proportion of individuals in the tallest class (Fig. 5C) while outside the exclosures almost all trees remained in the shortest or in the middle class (Fig. 5D).

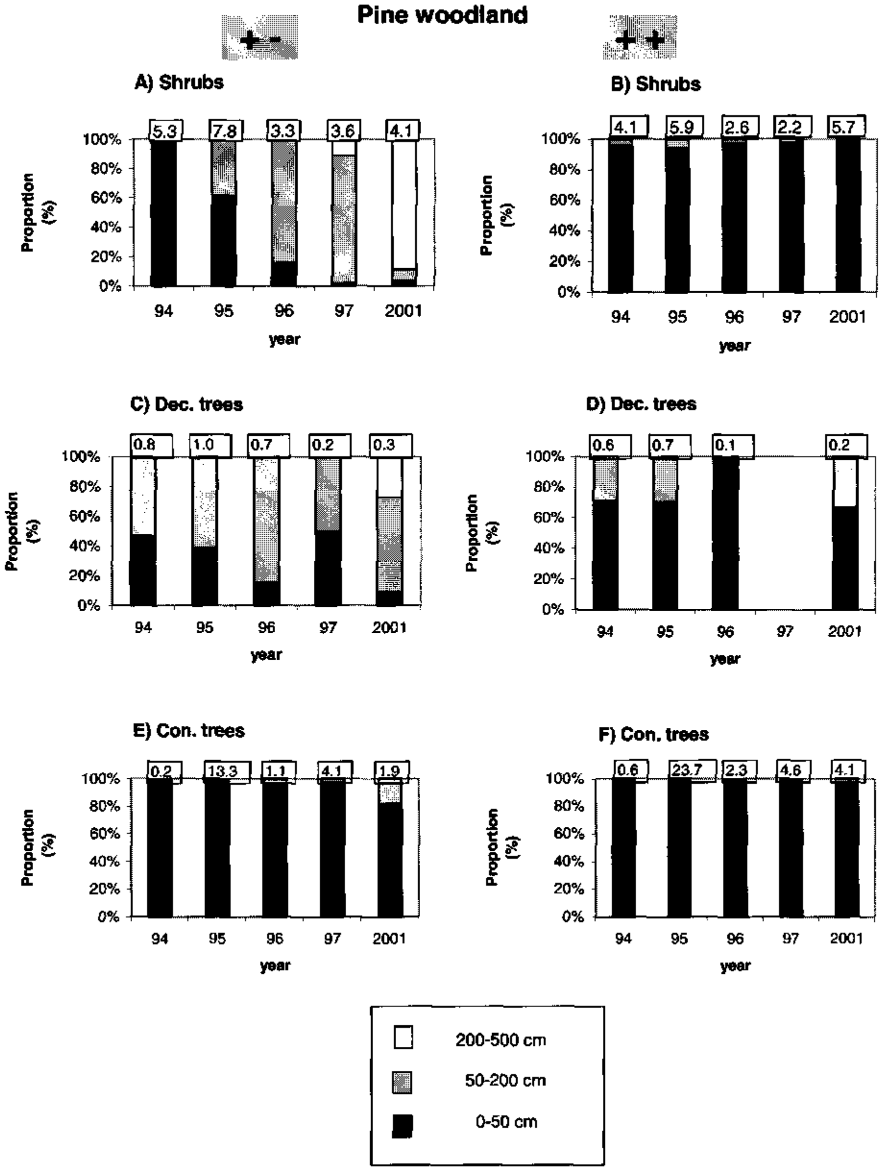

Figure 5: Changes in mean number of shrubs (A, B), deciduous trees (C, D) and coniferous trees (E, F) per height class (0-50 cm, 50-200 cm, 200-500 cm) during 1994-2001 in pine woodland reported as the proportion (%) per height class. The symbols '–' *and '+' correspond to the effect of* large *herbivores, the first symbol represents the situation* before 1995 and the second the situation after 1995 (until 2001). Numbers on top of the bar represent the mean absolute numbers of all individuals.

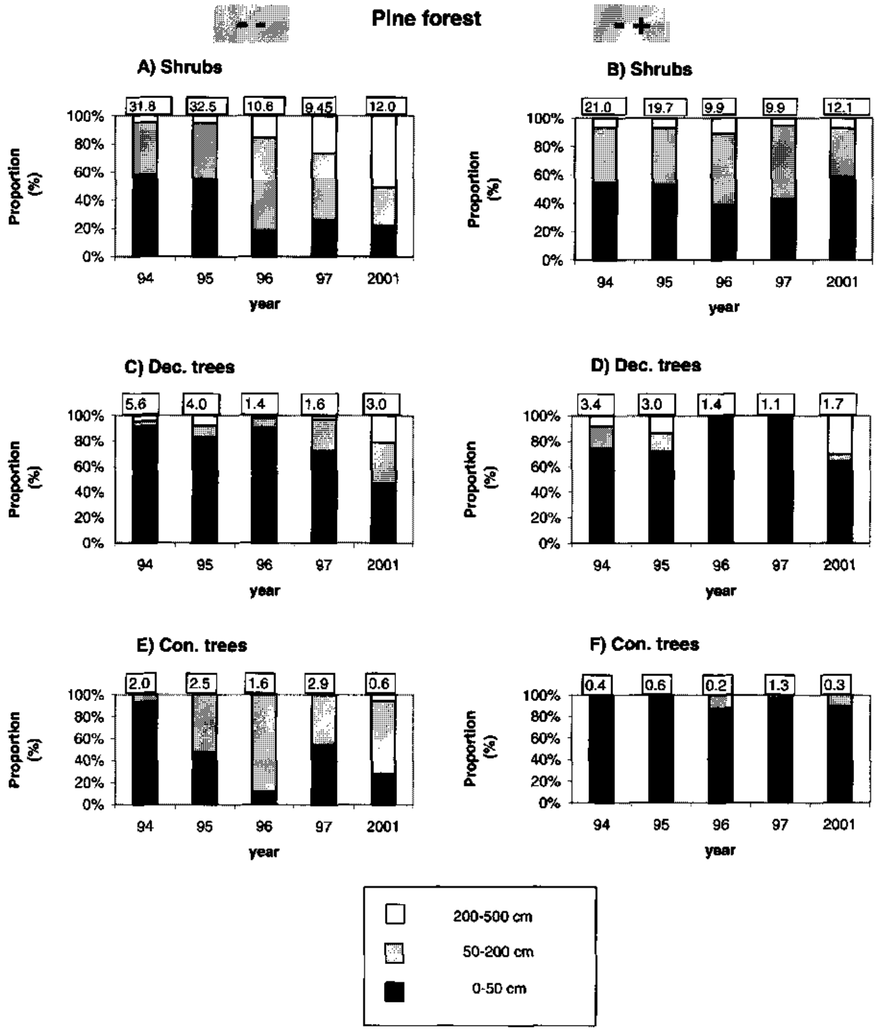

Figure 6: Changes in mean number of shrubs (A, B), deciduous trees (C, D) and coniferous trees (E, F) per height class (0-50 cm, 50-200 cm, 200-500 cm) during 1994-2001 in pine forest reported as the proportion (%) per height class. The symbols '–' and '+' correspond to the effect of large herbivores, the first symbol represents the situation before 1995 and the second the situation after 1995 (until 2001). Numbers on top of the bar represent the mean absolute numbers of all individuals.

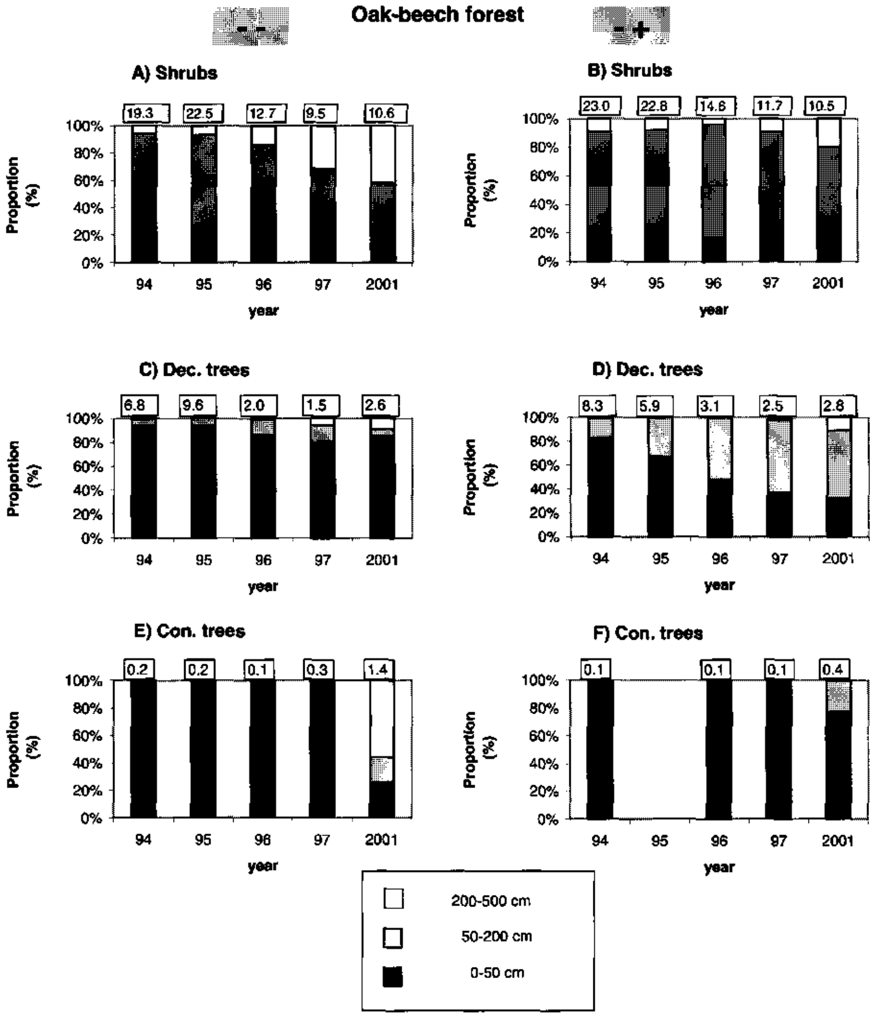

***Figure 7*:** Changes in mean number of shrubs (A, B), deciduous trees (C, D) and coniferous trees (E, F) per height class (0-50 cm, 50-200 cm, 200-500 cm) during 1994-2001 in oak beech forest reported as the proportion (%) per height class. The symbols '–' and '+' correspond to the effect of large herbivores, the first symbol represents the situation before 1995 and the second the situation after 1995 (until 2001). Numbers on top of the bar represent the mean absolute numbers of all individuals.

The number of coniferous trees, dominated by *Pinus sylvestris*, strongly fluctuated throughout the study period inside (Fig. 5E) as well as outside (Fig. 5F) the exclosures, but all remained in the shortest class.

Table 6: Test results of ANOVA for repeated measurements according to Hotelling's Trace with 'year' and 'year x grazing' effects, analyzing trends in life forms (number of dominant hits (D) and subdominant hits (S)) in oak-beech forest. * = significant ($\alpha<0.05$).

Life form	*Dominant/ Subdominant*	*Effect*	*df (hypothesis, error)*	*F*	*P*
Perennial grasses	D	year	3, 12	2.37	0.12
	D	year x graze	3,12	0.67	0.59
Perennial grasses	S	year	3,12	1.70	0.22
	S	year x graze	3,12	0.72	0.56
Dwarf shrubs	D	year	3,12	2.19	0.14
	D	year x graze	3,12	0.21	0.89
Dwarf shrubs	S	year	3,12	1.91	0.18
	S	year x graze	3,12	0.53	0.67
Litter	D	year	3,12	1.76	0.21
	D	year x graze	3,12	0.51	0.68
Litter	S	year	3,12	9.13	<0.01*
	S	year x graze	3,12	0.61	0.62

Pine forest (introduction)

The number of shrubs dominated in pine forest dominated by *Sorbus aucuparia* and *Amelanchier lamarckii* showed a significant effect of grazing on the number of shrubs in the tallest class during the study period ($F_{4,10}=3.30$, $P=0.05$). Inside the exclosures, the number of shrubs steadily grew from the shortest class into respectively the middle and tallest class (Fig. 6A). Both inside and outside the exclosures, the number of shrubs within the shortest class and the middle class fluctuated strongly throughout the study period. Outside the exclosures the number of shrubs remained mainly in the shortest and middle class (respectively 50% and 40%) (Fig. 6B). Inside the exclosures, the number of deciduous trees showed an increase in the middle and the tallest class (Fig. 6C), while outside the exclosures the number of deciduous trees fluctuated among the classes (Fig. 6D). The number of coniferous trees inside the exclosures increased in the middle and tallest class

(Fig. 6E) while outside the exclosures the majority of the coniferous trees remained in the shortest class (> 90%) (Fig. 6F).

Oak-beech forest (introduction)

In oak-beech forest, inside as well as outside exclsoures, the number of shrubs increased in the tallest class relative to the middle and shortest class (Fig. 7A, B). The majority of deciduous trees remained in shortest class inside the exclosures (Fig. 7C) while outside the exclosures (Fig. 7D) the number of trees in the middle and outside class increased relative to the number in the shortest class. In general, the mean number of coniferous trees in oak-beech forest was very low in contrast to those in the other vegetation types (Fig. 7E, F). However, the number of coniferous trees inside exclosures increased mainly in the tallest class relative to the middle and shortest class only in 2001 (Fig. 7E). Outside the exclosures, the number of coniferous trees remained mainly in the shortest class (Fig. 7F).

Species richness

The species richness did not show an overall grazing effect (Fig. 8) between 1994 and 2001. Combining all vegetation types inside as well as outside exclosures, a significant decrease in species richness was found during the seven years of this study ($F_{2,40}=4.01$, $P=0.03$) from on average two species. In pine woodland, both inside as well as outside exclosures the mean species richness decreased from on average 12 to 10 species. Species that disappeared from this vegetation type inside exclosures include typical nitrophilous species such as *Cerastium fontanum* and *Stellaria medea*, which grow on dung patches and species that benefit from an open understory vegetation like *Agrostis capillaris*, *Senecio sylvatica* and *Rumex acetosella*. Outside the exclosures mainly typical graze-sensitive tree species disappeared like *Quercus robur*. However, in pine forest and oak-beech forest some of the nitrophilous species like *Stellaria media* and *Senecio sylvatica* were able to colonise outside the exclosures while typical graze -sensitive tree and shrub species like *Betula pendula, Quercus robur* and *Rubus ideas* disappeared. Furthermore, some herb species (e.g. *Melampyrum pratense*, *Dryopteris dilatata*) were able to colonise pine forest and pine woodland inside and in some quadrats also outside exclosures.

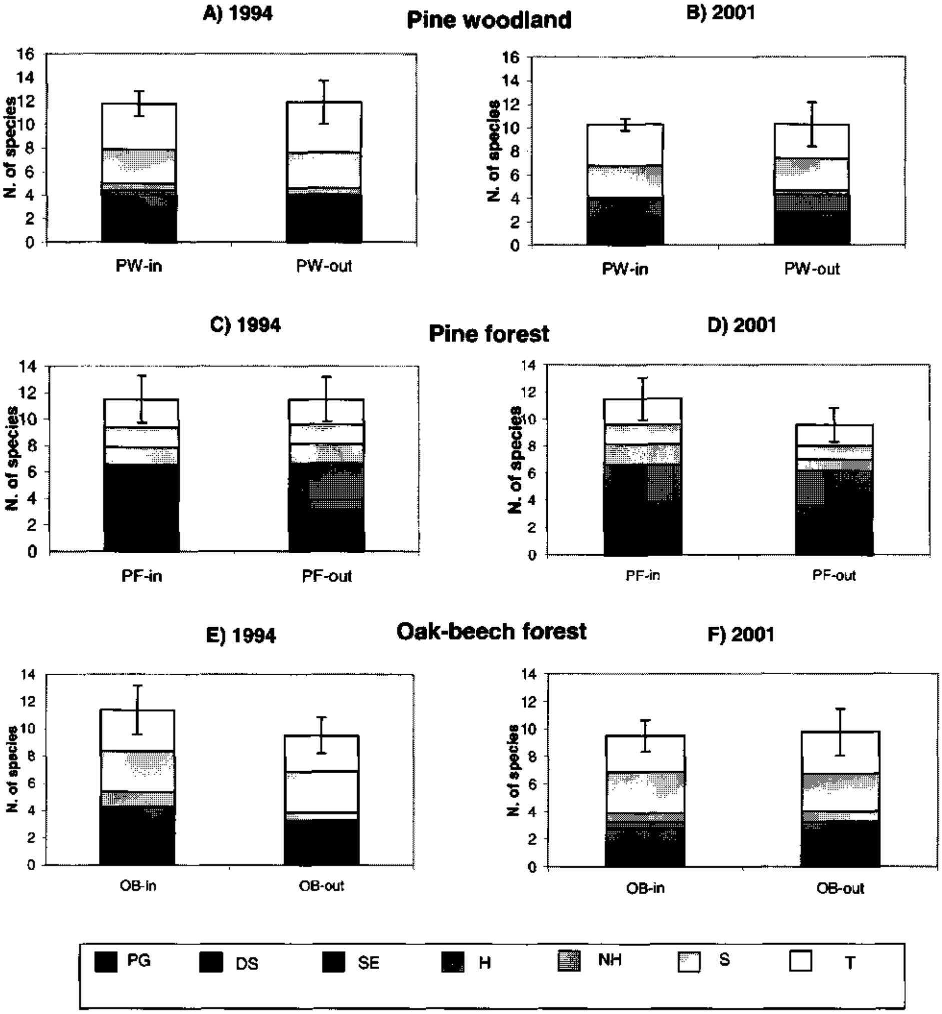

***Figure 8*:** The mean species richness (number of vascular plants) (± s.e) in pine woodland (A, B), pine forest (C, D) and oak-beech forest (E, F) inside and outside exclosures in 1994 and 2001 divided into different life-form groups. Species abbreviations: T=trees, S=shrubs, NH=nitrophilous herbs, H=herbs, SE=sedges, DS=dwarf shrubs, PG=perennial grasses.

Discussion

Introduction and exclusion effects

Neither exclusion nor introduction of grazing significantly affected the composition of the herb layer in either of the three vegetation types. Trends in life forms showed comparable patterns inside as well as outside exclosures referring to the importance of fluctuations in environmental conditions rather than to grazing effects. However, minor changes in botanical composition occurred especially within the herb layer. The increase in litter cover in former heavily grazed pine woodland may correspond to the botanical changes in the shrub layer as a result of grazing exclusion. In pine woodland the shrub layer was able to recover rapidly after the grazing relief. Like in other studies (Putman et al 1989, Anderson & Katz 1993) a rapid regeneration of the shrub layer took place immediately after exclusion. Small heavily grazed individuals of *Sorbus aucuparia* were able to grow rapidly into the taller height classes. Analogous to the increase of graze-tolerant shrub species within the shrub layer, a decrease of graze-tolerant perennial grasses took place. Within the herb layer in pine woodland the perennial grass cover dominated by *Deschampsia flexuosa* decreased after exclusion. The recovery of a dense shrub layer negatively affected the perennial grass layer due to competition for light. As a result, the dense shrub layer indirectly caused an increase of the litter cover due to the decrease in cover of *Deschampsia flexuosa* (Putman 1989). No significant effects of grazing introduction on the shrub layer in pine forest and oak-beech forest were found. Nevertheless, in a few quadrats in pine forest and in oak-beech forest we observed clear effects of grazing by red deer on palatable deciduous trees and shrubs in the shrub layer. Permanent settlement of male red deer herds in the new forest areas as well as daily migration from the central game area (R. Smit pers. obs.) caused an immediate pressure on the shrub layer in these new forest areas (Smit et al. 2001). In some cases, saplings of deciduous tree species like *Quercus robur* were killed by red deer or were set back from the tallest class to the middle and shortest height class. Among other factors, this red deer invasion may be explained by the relatively high browse supply in the introduction area (Smit et al. 1997, Homolka 1993). Species like *Sorbus aucuparia* and *Quercus robur* provide highly nutritious food for red deer containing relatively high contents of important minerals like calcium, magnesium and phosphorous (Hearney & Jennings 1983, Van Wieren et al. 1997). On the other hand, inside the exclosures of the new forest areas, the shrub layer could develop undisturbedly, without the former interference of roe deer, leading to a further development of the shrub and tree layer. In general, during the previous years large herbivores had been able to retard the vegetation succession in the central, former game area while in the new forest areas the vegetation succession from coniferous forest to deciduous forest could proceed. After the exclusion of large herbivores, the vegetation succession rapidly resumed while in the introduction area grazing hindered the vegetation succession.

The introduction of grazing did not cause a significant increase of graze tolerant or ruderal species in the herb layer. Probably the dense tree canopy in pine forest and in particular in oak-beech forest hampered the establishment of perennial grass species and herbs. In some cases, in the new forest areas deer-mediated dispersal of typical nitrophilous species like *Stellaria media* growing on old dung patches was found. However, the species richness was not increased following the introduction of grazing. The net effect of extinction of typical ruderal species in the former central game area overruled the effect of colonisation of these species in the new areas. Typical graze-induced, nitrophilous species could not survive in the exclusion area without the direct interference of large herbivores. They were negatively affected by outshading due to the development of a dense shrub layer.

In our study the availability of palatable, nutritious plant species, e.g. the shrub species *Sorbus aucuparia* and deciduous tree species *Quercus robur*, affected the impact of herbivory rather than differences in habitat productivity (soil fertility) (Hawkes & Sullivan 2001, Proulx & Mazumder 1998). Nevertheless, the availability of a well-developed shrub layer indirectly reflected better light conditions which facilitate the presence of light requiring shrub species. According to our results, the availability of palatable species as a functional group can be regarded as a key variable that determines the effects of grazing on vegetation development (Davidson 1993).

Management implications

Overall, the introduction of red deer did not increase the species richness. In fact, in both pine woodland as well as in pine forest the species richness decreased after the enlargement of the herbivore habitat. In general, forests or woodlands with a long grazing history show a higher species richness as compared to ungrazed or recently grazed forests and woodlands due to the long-term success of different species adapted to grazing (Putman et al. 1989, Ritchie & Olff 1999). The arrival and establishment of 'new species' requires a long grazing history by different herbivore types leading to heavily grazed environments with 'open conditions' favouring a wide-range of light demanding grassland species (Putman et al. 1989, Olff et al. 1999). However, in our study area, the actual period of seven years is too short and the herbivore assemblage too narrow to expect these consequences. In many other studies severe grazing by deer only, reduced species diversity (Putman 1989, 1996, McInnes et al. 1992, Pettit et al. 1995, Fletcher et al. 2001). Direct effects of selective grazing by deer on graze-sensitive plant species generally result in dramatic changes in the composition and relative abundance of these species within the woodland understory vegetation. Additionally, the potential net change in species richness depends largely on the total species pool of the environment (Proulx & Mazumder 1998). As compared to other grazed forests and woodlands (Buckely et al. 1997, Putman et al. 1989) the species richness of our woodlands and forests is relatively low, which is probably responsible for a low chance of significant changes in species richness.

Overall, the observed impacts of grazing introduction in the new forest areas and grazing exclusion in former, heavily grazed areas do not reflect reversible ecological processes. In contrast to other studies (Anderson & Katz 1993) we found that the time required for recovery of the understory vegetation following release from grazing is not proportional to the time the understory is degraded by grazing introduction. The recovery of graze-tolerant shrub species proceeded faster than the understory degradation. Graze-tolerant species like *Sorbus aucuparia* are able to produce long apical shoots directly after exclusion. While graze-tolerant species were able to recover rapidly following release, this was not the case for graze-sensitive species like deciduous, late successional tree species. Only a few individuals of *Quercus robur* were able to establish inside the exclosures of pine woodland. Long-term grazing in the New Forest area caused almost complete extinction of graze-sensitive species (Putman 1989 et al.). As a result, the restoration of former heavily grazed woodlands through a regenerative recolonisation of graze-sensitive tree species will require a long time period. Dispersal of seeds depends strongly on the availability of nearby seed sources as well as on the dispersal behaviour of jays (Bossema 1979) and small rodents (Jensen & Nielsen 1986). From a nature conservation point of view, this study has shown that after seven year of grazing introduction by red deer, little or no effects on habitat heterogeneity and consequently species diversity occur. We may therefore conclude that grazing introduction of deer in forests is not a successful tool in maintaining or creating a higher species or community diversity.

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Chapter 5

Effects of introduction and exclusion of large herbivores on small rodent communities

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Abstract

In this study we analysed the effects of large herbivores on small rodent communities in different habitats using large herbivore exclosures. We studied the effects of three year grazing introduction by red deer (*Cervus elaphus* L.) in previously ungrazed pine and oak-beech forest and the exclusion of grazing by red deer, roe deer (*Capreolus capreolus* L.) and mouflon *(Ovis ammon musimon* Schreber) in formerly, heavily grazed pine woodland and heathland. At eight exclosure sites within each habitat type, small rodents were captured with live traps using trapping grids. At each trapping grid, seed plots of beechnuts (*Fagus sylvatica* L.) and acorns (*Quercus robur* L.) were placed to measure seed predation by rodents.

Exclusion of grazing by large herbivores in formerly, heavily grazed habitats had a significant effect on small rodent communities. Inside exclosures higher densities of mainly wood mice (*Apodemus sylvaticus* L.) and field voles (*Microtus agrestis* L.) were captured. Introduction of grazing by red deer appeared to have no significant negative effects on small rodent communities. The seed predation intensity of beechnuts and acorns by small rodents was significantly higher in ungrazed situations, particularly in habitats that were excluded from grazing. The differences between grazing introduction and exclusion effects on small rodent communities can be explained by differences in vegetation structure development. The recovery of heavily grazed understory vegetation after large herbivore grazing exclusion proceeded faster than the understory degradation due to grazing introduction. Small rodents depend on structural rich vegetations mainly for shelter. We conclude that large herbivores can have significant effects on vegetation dynamics not only via direct plant consumption but also through indirect effects by reducing the habitat quality of small rodent habitats.

Introduction

The direct effects of large mammalian herbivores on the vegetation composition and dynamics have been widely studied. Herbivores affect the vegetation through biomass removal (Pacala and Crawley 1992; McInnes 1992; Harper 1977) but also modify vegetation structure through physical disturbance. The effects of herbivory on vegetation structure depend on habitat type, herbivore species and grazing pressure (Olff and Ritchie 1998). In heathlands, a heavy grazing pressure of red deer and sheep can induce a decrease in plant height and architecture of heather which may result in a short vegetation of graminoids and forbs (Welch and Scott 1995). Severe browsing by red deer (*Cervus elaphus* L.) and moose (*Alces alces* L.) in woodlands may eventually eliminate the shrub layer and prevent tree regeneration (Putman *et al.* 1989; McInnes *et al.* 1992).

The indirect effect of herbivory on vegetation structure, is an underestimated phenomenon. By modifying the vegetation structure large herbivores may indirectly affect small herbivores such as small rodents and their predators (Putman 1986). Small rodents occur at high densities in structurally complex habitats with high cover of ferns (den Ouden and Smit 1997), bramble (van Apeldoorn et al. 1990), grasses (Foster and Gaines 1991) or juvenile trees (Hazebroek et al. 1995). Small rodents depend on the shelter in these habitats which provides protection against predators (Miller and Getz 1976; Hanson 1978), suitable microclimates and profitable food resources (Keesing 1998).

Small rodents can have significant effects on vegetation dynamics. Especially via seed predation and dispersal of tree seeds, small rodents can have a major impact on the establishment of tree species and thus on vegetation succession (Vander Wall 1990; Jensen 1982). We hypothesise that grazing by large herbivores will induce a decrease in small rodent densities due to a decrease in structural complexity of the vegetation. Consequently, large herbivores will induce lower seed predation due to reduced small rodent densities. In this study we try to determine the effects of large herbivores on small rodent communities and seed predation in a spatial mosaic of habitat types in different stages of vegetation succession and with a different grazing history. We studied the indirect effects of grazing by (i) measuring rodent densities and (ii) predation of tree seeds, within and outside large herbivore exclosures.

Methods and materials

Study area

The study was conducted in The National Park 'De Hoge Veluwe' in the Netherlands (52° 2-8'N; 5° 50-51'E) during October - December 1996 (Fig. 1). The park comprises a typical landscape on sandy soils of glacial and inter-glacial origin. The climate in the area is oceanic with mean annual temperatures of 9.1°C and annual rainfall of 800 mm (Krijnen and Nellestijn 1992). The National Park has a long history of grazing by large herbivores. Since their introduction around 1900 red deer, mouflon (*Ovis ammon musimon* Schreber) and wild boar (*Sus scrofa* L.) occur in varying numbers. Roe deer (*Capreolus capreolus* L.) occurs naturally in the park. The mean annual densities of large herbivores based on spring counts in 1999 are 230 red deer, 230 mouflon, 200 roe deer and 50 wild boar. Hunting controls these numbers. Until 1993 the populations of red deer, mouflon and wild boar were concentrated in a central, enclosed area of 3800 ha. In November 1994, the area available to these populations was expanded to 5000 ha.

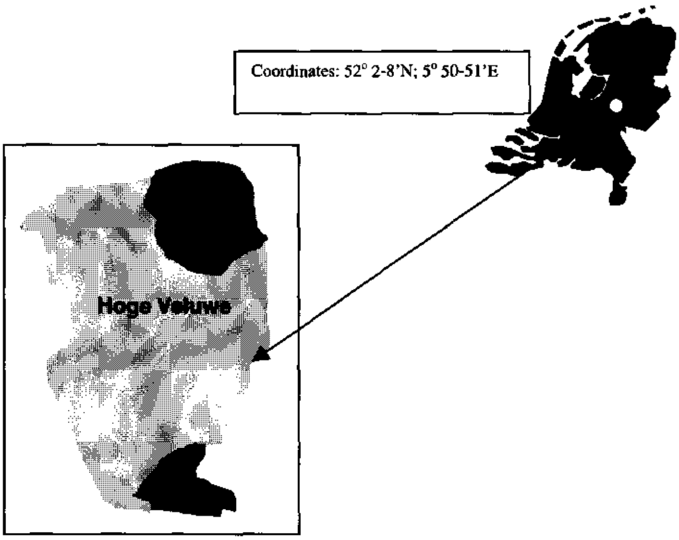


***Figure 1*:** The location of the National Park 'The Hoge Veluwe' in the Netherlands and the spatial position of the exclusion area (light grey) consisting of heathlands and first generation pine woodlands and the introduction area (dark grey) recently available to large herbivores, consisting of second generation pine and oak-beech forests.

The major habitat types in the area are assumed to be part of a successional sequence (Fanta 1982) (Table 1). Early successional stages feature heather (*Calluna vulgaris* L.) dominated vegetation communities on driftsand and blown-out plains with grey hair-grass (*Corynepherus canescens* L.) and sheep's fescue (*Festuca filiformis* Pourr.) followed by first generation Scots pine dominated vegetation with an understory (< 50 cm) of sand sedge (*Carex arenaria* L.) and wavy hair-grass (*Deschampsia flexuosa* L.). Following these stages comes second generation Scots pine with an understory of blue berry (*Vaccinium myrtilis* L.) and a shrub layer of rowan (*Sorbus aucuparia* L.) and silver birch (*Betula pendula* Roth.). Late successional species like common oak (*Quercus robur* L.) and beech (*Fagus sylvatica* L.) dominate the deciduous woodlands. Heathland and first generation pine woodland are situated inside the formerly, heavily grazed game area and have been grazed since 1900 by red deer, roe deer and mouflon while second generation pine forest and oak-beech forest became available to red deer and mouflon in November 1994 (Fig. 1, Table 1).

***Table 1*:** Habitat type description based on grazing history, grazing exclusion or introduction, dominant vegetation and size of the habitat type

Habitat type	*Grazing history*	*Exclusion(E) Introduction (I)*	*Vegetation*	*No. hectares in the park*
Heathland	> 1900	E	Calluna vulgaris Corynepherus canescens Festuca filiformis	1300
Pine woodland (I)	> 1900	E	Pinus sylvestris Carex arenaria Deschampsia flexuosa	2000
Pine forest (II)	> 1994*	I	Pinus sylvestris Vaccinium myrtilis Sorbus aucuparia Betula pendula	600
Oak-beech forest	> 1994*	I	Quercus robur Fagus sylvatica	300

* Before 1994 only with roe deer

Experimental design

In 1994, 32 exclosures of 15x25 m excluding all large herbivores including rabbits, were placed to monitor changes in vegetation composition with and without grazing. We placed 16 exclosures both in the previously ungrazed habitats and in the formerly, heavily grazed game area. In both areas, 8 exclosures were located in each of the four habitat types (Fig. 2) consisting of heathland and first generation pine woodland in the formerly, heavily grazed game area and oak-beech forest and second generation pine forest in the previously ungrazed area. The exclosures were constructed using wire netting with a height of 200 cm and a mesh width of 5x5 cm. The mesh width allowed small rodents to enter the exclosures.

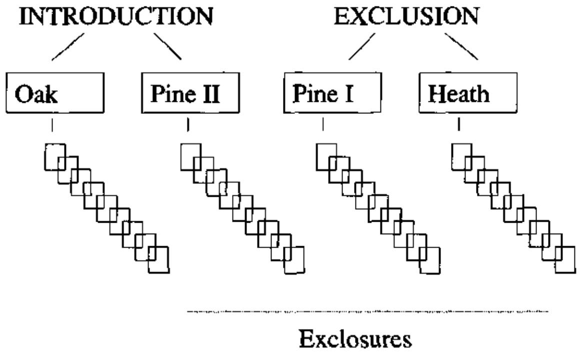


Figure 2: Experimental design divided into an introduction and exclusion area comprising respectively oak and second generation pine woodland and first generation pine woodland and heathland habitats. Each habitat encompasses eight exclosures.

To sample rodent densities we used trapping grids of 15 Longworth live traps placed in grids of 5x3 traps with a distance of 5 m between the traps. The traps were filled with hay and baited with rolled oats, apple and carrot. Per exclosure, three similar trapping grids were used, one inside, one outside at a short distance from the fence (10m) and one outside at a larger distance (75m). The distance between the two outside grids was large enough to assess independent rodent populations according to home ranges of dominant rodent species like wood mouse (*Apodemus sylvaticus* L.) and bank vole (*Cletrionomys glareolus* Schreber) (Kikkawa 1964). The rodents were captured during 5 days with a prebait period of two days. Each captured and released rodent was marked by cutting a bit of skin, so that it could be individually recognised after recapture.

Habitat features

We distinguished 7 habitat features at each trapping grid that are considered to be important for small rodents (Miller and Getz 1977; Hazebroek *et al.* 1995; Hanson 1978). We measured the height of the understory (grasses, forbs and dwarf shrubs < 50 cm tall), the understory cover (% cover) and the number of (living) small tree stems with a diameter <10 cm. Furthermore, we recorded the litter depth (cm), the number of (living) big tree stems (tall trees: diameter > 10 cm), the number of stumps/trunks and dead wood cover (% cover).

Each feature was recorded inside the trapping grids enlarged with 2.5 m in length and width. In each grid the values of the features were based on 10 random samples. Understory height was measured with a foam disc (diameter 10 cm; weight 7.5 g) with a hole in the middle that drops along a wooden stick until stopping on top of a plant. The number of stems was counted and the percentage cover of the understory and dead wood cover was estimated.

Seed predation

During the week preceding the small rodent trapping a seed predation experiment was conducted. In each rodent trapping grid a seed plot was laid in the centre of the capture grid. The grid was sized 5x5 m containing 25 acorns and beechnuts. All seeds were laid down on the litter layer, wearing gloves to prevent human odours. All seed pairs were marked with wooden tooth sticks. All seeds were checked daily, and inspected for signs of rodent activity. Seeds were either consumed on the spot (leaving remnants like shells) or were removed completely. Seed predation was measured during one week. In addition, six random exclosures were monitored twice daily to check for possible effects of other, diurnal active seed predators besides the nocturnal small rodents that we studied (Kikkawa 1964).

Data analysis

To test for differences in effects of large herbivores on small rodent communities in exclusion and introduction areas first rodent densities and second seed predation were analysed. The number of individual rodents trapped (Minimum Number Alive; Krebs 1980) and the total numbers of captures were used as a measure for rodent density per trapping grid. Differences in rodent densities and interactions between grid and habitat type were tested using a hierarchical three-level, type III ANOVA with habitat type, exclosure and trapping grid as factors. The eight exclosures were nested within each of the four habitat types. For analysing respectively *introduction* and *exclusion* effects of grazing, the ANOVA was used separately for rodent densities in introduction (previously ungrazed habitats) and exclusion (formerly, heavily grazed) areas. Differences in grazing effects between the introduction and exclusion area could not be analysed because of the different habitat types occurring in these areas. The ANOVA was followed by Tukey HSD tests for pairwise comparison of the trapping grids (Sokal and Rohlf 1981). Rodent densities were $^{10}\log_{x+1}$ transformed prior to the analysis in order to improve the homogeneity of the data. Prior to the ANOVA, data were checked for normality (Kolmogorov Smirnov test) and homogeneity (Levene test). Differences in habitat features were tested between grids, using one way ANOVA followed by Tukey HSD tests. Bivariate correlation analysis (Pearson: two-tailed) was used to find out relations between rodent density and habitat features. We only selected habitat features for this analysis that showed significant differences between grazed and ungrazed situations using One Way Anova with Tukey HSD test. Seed predation was measured as the time (number of days) where after seed predation took place, which is reported as the 'survival time' of a seed. Seed survival of acorns and beechnuts was analysed for each seed plot using the Kaplan-Meier survival analysis (Kaplan and Meier 1958: SPSS v 6.0 1994). Significant differences in seed survival were compared between seed grids (inside, next to, outside)and species (acorns, beechnuts) for both introduction and exclusion areas using the Log-Rank Mantel-Cox test (Pyke and Thompson 1986). Seeds that were not predated at the end of the experiment were treated as seeds with survival time equal to the duration of the experiment (seven days).

Results

Rodent density

Overall, only in the exclusion area analysis of variance showed significant differences in rodent density between the trapping grids ($F_{2,28}=3.96$, $P=0.031$). A significant higher rodent density inside exclosures as compared to outside and next to trapping grids was measured (Table 2). The rodent densities (total number of individuals & captures) in the introduction area did not differ significantly between the trapping grids. In the exclusion area, the rodent density varied greatly over the habitat types (total number of individuals: $F_{1,28}=8.71$, $P=0.01$; total number of captures: $F_{1,28}=7.81$, $P=0.01$) with higher rodent densities in pine woodland as compared with heathland. Within the habitat types no significant differences in rodent densities between the trapping grids were found.

Rodent species

In general, wood mouse was the dominant rodent species (Table 2), whereas field voles *(Microtis agrestis* L.) and bank voles were present in lower numbers. Wood mice were caught in all habitat types (Fig. 3) while field voles were more common in heathland and first generation pine woodland and bank voles in second generation pine forest and oak-beech forest. The wood mice density (total number of individuals) in the exclusion area differed significantly between the trapping grids ($F_{2,28}=3.81$, $P=0.03$; Table 2) and habitat types ($F_{1,28}=9.82$, $P=0.007$). Also, the field vole density (total number of captures) in the exclusion area was significantly higher inside exclosures as compared to outside exclosures ($F_{2,28}=3.41$, $P=0.04$; Table 2).

***Table 2*:** Averages and standard errors of the mean of rodent densities (n=16) per trapping grid, per grazing area (*Introduction* and *Exclusion* area).

Significantly different at $\alpha=0.05$ according to Tukey HSD test. ^{a}= significantly different between inside – outside, ^{b}= significantly different between inside – outside & inside – next to.

	INTRODUCTION						EXCLUSION					
Species	inside	s.e	next to	s.e	outside	s.e	inside	s.e	next to	s.e	outside	s.e
Total individuals	6.63	0.92	5.75	0.93	7.06	1.00	5.56^{a}	0.96	4.56	0.98	3.38	0.83
Total captures	15.13	2.47	11.25	2.34	15.38	2.54	12.25^{b}	2.16	8.25	2.02	7.25	1.76
Total individuals *Apodemus Sylvaticus*	5.31	0.66	5.06	0.71	6.00	0.75	5.06^{a}	0.90	4.19	0.92	3.25	0.82
Total captures *Apodemus Sylvaticus*	10.69	1.49	8.63	1.26	12.56	1.88	10.25	2.07	7.38	1.71	7.13	1.76
Total individuals *Microtis agrestis*	0.13	0.13	0.00	0.00	0.06	0.06	0.50	0.22	0.38	0.18	0.13	0.09
Total captures *Microtis agrestis*	0.69	0.69	0.00	0.00	0.06	0.06	2.00^{a}	1.00	0.88	0.54	0.13	0.09
Total individuals *Clethrionomys glareolus*	1.19	0.57	0.88	0.44	1.00	0.41	0.00	0.00	0.00	0.00	0.00	0.00
Total captures *Clethrionomys glareolus*	3.75	1.94	2.63	1.47	2.75	1.26	0.00	0.00	0.00	0.00	0.00	0.00

Habitat features

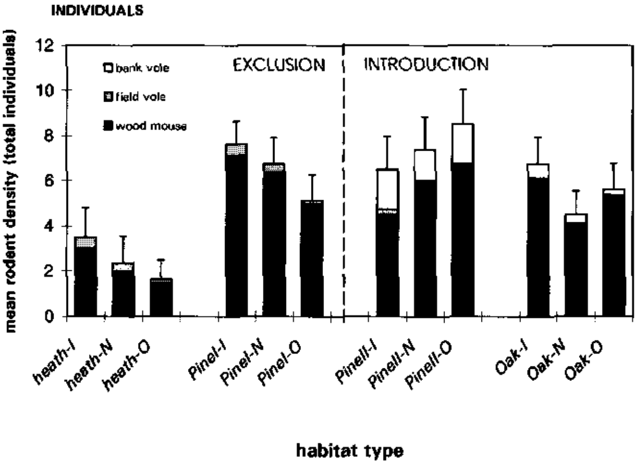
There were no significant differences in habitat features between the trapping grids when all 32 exclosures were taken into account (Table 3). When the formerly, heavily grazed exclosures were considered separately, we found a significant higher understory height inside than outside exclosures (Tukey HSD: $F_{2,47}=3.28$, $P=0.047$).

We selected understory height as main habitat variable influenced by grazing to be correlated with rodent density. The difference in understory height between inside and outside grids showed a significantly positive correlation with the difference in total small rodent individuals ($p=0.40$, $n=36$, $P<0.05$) for all exclosures.

Seed predation

At the end of the measurement period 80.8% of all beechnuts and acorns was predated. The vast majority of the seeds were removed (78.8%). Only 2% was gnawed or consumed at the spot. The remaining 19.2% remained untouched. We did not find significant differences in the percentage of these types of seed predation between the seed grids (inside, next to, outside), seed species (beechnuts and acorns) or habitat types. In respectively 91% and 89% of the beechnuts and acorns seed predation took place by night. The seed survival pattern differed significantly among grazed and ungrazed seed grids for beechnuts as well as acorns in both introduction and exclusion areas(Fig. 3). According to the Log rank test, the seed survival times of beechnuts and acorns were significantly higher in the grids outside the exclosures as compared to the grids inside and next to the

A)



B)

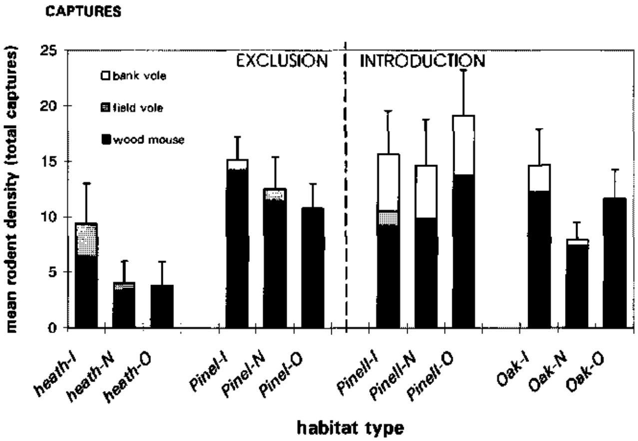


***Figure 3*:** Mean rodent density per species per habitat type inside (i), next to (n) and outside (o) exclosures. A) Total of captured individuals, B) Total number of captures. Vertical lines represent standard errors of the mean.

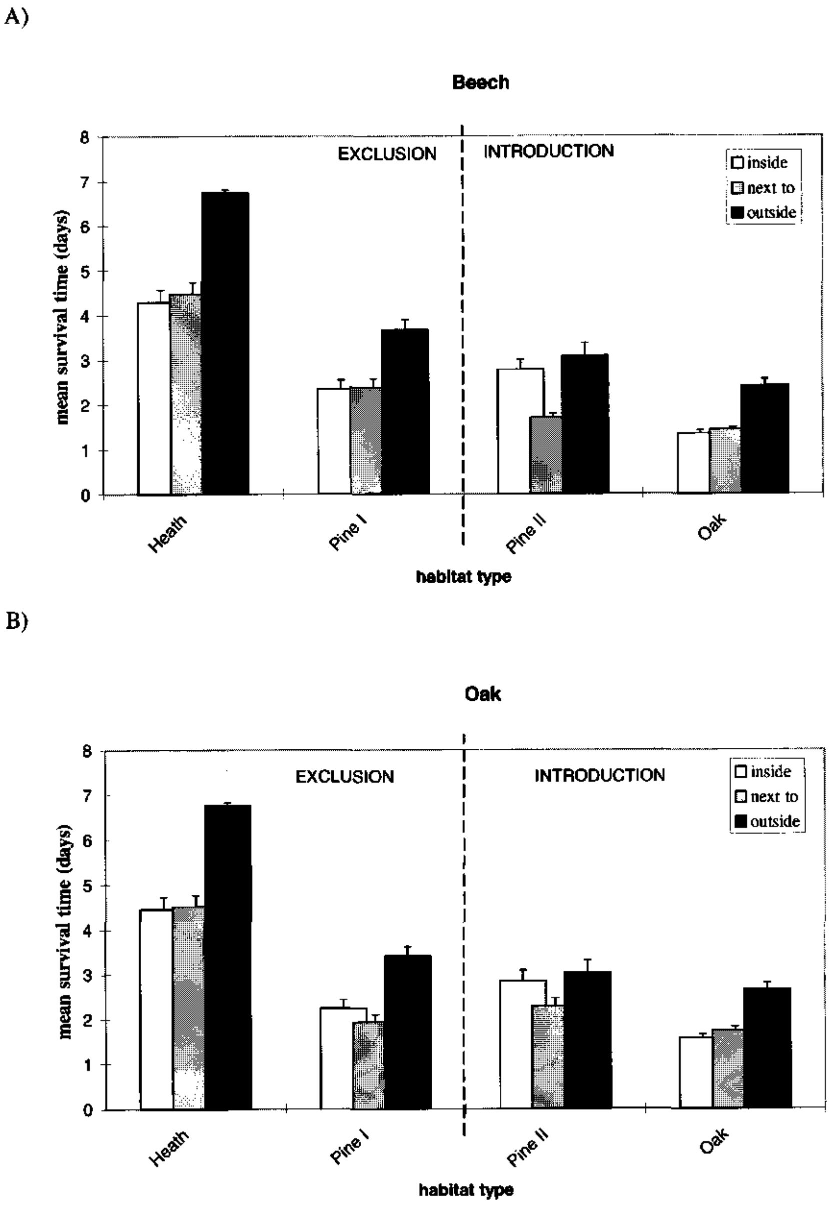


***Figure 4*:** Mean survival times per habitat type inside, next to and outside exclosures for beechnuts (A) and acorns (B)

exclosures (beechnuts: Log Rank statistic (LR): inside=120.7, outside=126.5: $P<0.000$; acorns: LR inside=89.51, outside=90.59: $P<0.000$). Differences in seed survival between the seed species and between the grids inside and next to the exclosures between the exclusion and introduction area were not significant. In heathland, the surival times were significantly higher than in the other habitat types (LR 50.4: $P<0.000$). Approximately 60% of beechnuts and acorns in the grids next to and inside exclosures survived from predation as compared to approximately 80% in the grids outside exclosures.

Rodent density and seed survival

A negative lineair relation was found between wood mice density and the mean survival time of seeds (Fig. 5, for acorns: $R^2=0.31$, $P<0.01$, $n=64$) for grids inside and outside exclosures. A higher wood mice density resulted in a lower mean survival time of acorns and beechnuts.

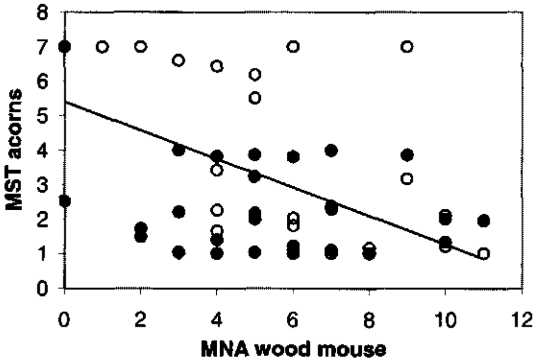


Figure 5: Linear relation between wood mice density (total number of individuals) and mean survival time of acorns for grids inside and outside exclosures in exclusion (open circles) and introduction area (closed circles). $y=-0.42x + 5.4$ $R^2=0.31$, $n=64$, $P<0.01$

Discussion

Both our trapping experiment as well as our seed predation experiment pointed out the negative effects of grazing by large herbivores on small rodent communities. First, on the whole rodent densities appeared to be lower outside large herbivore exclosures than inside. Second, rodent densities appeared to be significantly higher inside large herbivore exclosures. However, the effects of respectively exclusion and introduction of large herbivores on small rodent communities differed severely. Large herbivore exclusion in heavily grazed habitats had a clear, positive impact on rodent density, while in the presence of large herbivores the rodent density was low. These results confirm the general hypothesis that large herbivores reduce the habitat quality of small rodents and thereby cause a decrease in small rodent density (Geier and Best 1980; Putman 1986, Keesing 1998). Large herbivore exclosures 'create' ideal habitat patches for small rodents in a short, heavily grazed vegetation. Inside exclosures in habitats with a long grazing history a well-developed herb- and shrub layer can recover which provides an appropriate habitat for rodents (Dueser and Shugart 1978; Den Ouden and Smit 1997). In our study the vegetation height appeared to correlate significantly with rodent density; a higher vegetation height may imply a better habitat for rodents. Small rodents benefit from a closed understory canopy inside exclosures through a lower apparent predation risk (Kotler 1984; Kotler and Blaustein 1995). Furthermore, the increase of vegetative biomass may also cause an increase in quantity and quality of food availability (Keesing 1998). The recovery of browse-sensitive plant species inside large herbivore exclosures appeared to be fast. We found a fast recovery of mainly rowan in pine woodland, where after three years of grazing release from mainly red deer, approximately 80% of individuals of rowan moved from the smaller (< 50 cm) into the higher (200-500 cm) height classes (Smit, unpub. data). Anderson and Ketz (1993) found an apparent recovery of browse-sensitive trees like hemlock (*Tsuga canadensis* L.) after twelve years of white-tailed deer (*Odocoileus viriginianus* Zimmerman) exclusion, while Putman *et al.* (1989) found a rapid regeneration of birch, beech, oak and holly (*Ilex aquifolium* L.) after 6 years of exclusion of red, roe and fallow deer (*Dama dama* L.) and domestic stock.

In fact, exclosures for large herbivores in heavily grazed vegetations become enclosures for small rodents.

The effects of the introduction of large herbivores on rodent communities were not significant. Probably, the actual 3 years of grazing by mainly red deer (Smit *et al.* 1998) is too short to cause a degradation of the understory and thereby causing a decline in rodent density. Putman *et al.* (1989) found clear differences in rodent density between large herbivore grazed and ungrazed woodlands after 22 years of grazing, as a result of changes in many habitat features. In general, degradation of vegetation structure by introducing large herbivores may take longer than the recovery of vegetation structure after excluding large herbivores. The selective foraging by large herbivores on the one hand, and the strong recovery capacity of browse-sensitive plants on the other, causes severe differences in vegetation structure development among habitat types which are respectively introduced to and excluded from large herbivores.

In general, large herbivores significantly affect the seed predation by small rodents. Outside the large herbivore exclosures the survival time of acorns and beechnuts appeared to be higher than inside exclosures. Similar to the differences between rodent densities, seed survival differed more distinctly in the exclusion area as compared to the introduction area. Wood mouse, as the dominant small rodent species in our study area and typical granivore species (Watts 1968) appeared to be the main seed predator. A higher wood mouse density caused a lower seed survival. Besides a lower predation risk inside exclosures, small rodents may suffer from a higher exploitation (direct) competition with other seed predators like deer and wild boars (Herrera 1995). In our study area large herbivores and small rodents are sharing food resources. Exclusion of one species (large herbivores) resulted in an increase of the abundance of the other (small rodents) which may refer to direct competition (Schoener 1983; Heske & Brown 1994).

The consequences for vegetation dynamics of the relationship between large herbivores and small rodents are yet unclear. A change in small rodent density can have significant effects on seed dispersal, seed - and seedling survival of woody plants (Ostfeld and Canham 1993). The establishment of seedlings and saplings of oak and beech trees depends on the dual relationship with small rodents. Not all seeds predated by small rodents have to be 'killed' (Price and Jenkins 1986); small rodents can act as dispersal agents. Undiscovered seed caches of small rodents can be recruitment foci of seedlings (Vander Wall 1990; Herrera 1995). The dispersal of heavy seeds of late successional tree species like common oak and beech by wood mice is an important mechanism in forest succession (Jensen and Nielsen 1986; Finegan 1984). According to Janzen (1970) seeds of oak and beech have the best perspectives to escape from seed predators far away from the parent trees. First, seeds have to be hoarded by rodents to reach 'safe sites' (Harper 1977) and second, seeds need a temporary low small rodent density to ensure seed survival and subsequent seedling establishment.

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Chapter 6

Shifts in resource partitioning between large herbivore species in response to interspecific competition.

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Submitted in revised form to Wildlife Biology

***Keywords:** interspecific competition, resource partitioning, large herbivores, red deer, roe deer*

Abstract

Interactions among roe deer, red deer, mouflon and wild boar were studied in the National Park De Hoge Veluwe (NPHV) in the Netherlands by making use of the enlargement of a former Game area. We aimed to get insight in large herbivore interactions and to what extent shifts in resource partitioning reflect a potential for one-sided competition between red deer and roe deer. Before the enlargement, fences around the Game area within the NPHV acted as a barrier for the various herbivore species. The removal of the fences allowed the herbivore species to enter two new forest areas, which were until then, exclusively inhabited by roe deer. Red deer and to a smaller extent wild boar, colonized the new areas soon after they came available while mouflon remained in the former Game area. The mean density as well as the performance of the roe deer population in the red deer invaded forests declined significantly while the performance of red deer increased. The habitat use of roe deer in the park shifted from deciduous and coniferous forests to pine woodland and heathland. Both results point to one-sided competition between red deer and roe deer but mechanisms behind this interspecific relationship are still hypothetical. Competition between roe deer and red deer seemed to be mediated by exploitation competition for woody forage (browse) including twigs, buds and leaves of mainly deciduous species. Red deer browsing decreased the woody understory, which may have caused a reduction of the quality of preferred roe deer habitats. This study indicated how resource competition could lead to shifts in resource partitioning in limited environments.

Introduction

Understanding the precise nature of interspecific interactions among herbivores is difficult due to the variety of processes playing important roles within herbivore guilds including social relations (Bartos et al. 1996, Putman 1986), facilitation (Damman 1989, Van der Wal et al 2000), direct or indirect competition (Schoener 1983, Belovsky 1984, Ritchie & Tilman 1992) and predation (Sinclair 1985, Jędrezejweski et al. 1992, Klein & Bay 1994). Nevertheless, the coexistence of herbivore species is mainly explained by the theory of resource partitioning. Resource partitioning may be defined as the differential use by organisms of resources such as food and space (Begon et al. 1990). Competition is considered to be a major selective force causing the differential use of resources and the consequent morphological and behavioural differences among species (Cody 1974, Schoener 1983, Pianka 1983, Gordon & Ilius 1989). Basically, three criteria are recognisable in different definitions of interspecific competition (Wiens 1989, Tokeshi 1999, Grime 1979, Keddy 1991); (1) different species share the same resources, (2) shared resources are in short supply and (3) resource depletion has a negative reciprocal effect on the fitness of species in the guild.

Classical field studies with removal and introduction experiments have documented the presence of interspecific competition among closely related species within many taxa (Cody 1974, Connell 1961, Hairston 1980, Ritchie & Tilman 1992; Tilman 1986). The effects of interspecific competition can result in changes in reproduction, survivorship and growth. Nevertheless, competition among different herbivore species is hard to demonstrate (Schoener 1983). Resource partitioning of herbivore species studied in existing, stable multi-species assemblages of herbivores (Prins & Douglas-Hamilton 1990; Prins & Olff 1998) may either be the result of actual competition or 'the ghost of competition past' (Connell 1980, Tokeshi 1999).

In the temperate grazing ecosystem of the Netherlands two different wild herbivore species, roe deer (*Capreolus capreolus* L.) and red deer (*Cervus elaphus* L.) occur. Roe deer are relatively small herbivores (15-30 kg) and select materials of high nutritious values (Homolka 1993, Gill et al 1996; Putman 1996) and show a more territorial behaviour than red deer do (Andersen et al. 1998). According to the large herbivore classification of Hofmann (1989) roe deer can be classified as browsers. In general, roe deer prefer forested areas with dense understory vegetations in openings and young forest stands (Hearney & Jennings 1981, Henry 1981, Homolka 1996, Andersen 1998). Red deer is a much bigger (80-150 kg) and versatile herbivore species able to use a broader range of habitats (Van de

Veen 1979, Putman 1989, Homolka 1996) and food items. Red deer can be classified as intermediate feeders (Hofmann 1989).

We studied the effects of removing the fences within a national park area, which had previously isolated the various herbivore species, on the resource partitioning between the large herbivore species. The removal of the fences allowed, amongst others, red deer to enter two new forest areas, which were until then, exclusively used by roe deer. By comparing the situation before and after the introduction of red deer in former roe deer habitats, we sought to analyse the changes in resource partitioning between roe deer and red deer based on spatial distribution, habitat use and its effect on roe deer performance. We aim to get insight in large herbivore interactions and to what extent shifts in resource partitioning after fence removal reflect a potential for interspecific competition between red deer and roe. We assumed asymmetrical, one-sided competition between the superior red deer and the inferior roe deer (Schoener 1983, Begon et al. 1990, Tokeshi 1999). We therefore tested the following hypotheses. In response to fence removal we predicted (1) spatial segregation between red and roe deer(2) differentiation in habitat use between red and roe deer and (3) a decline in performance of roe deer in former roe deer habitats.

Methods and materials

Study area

The study was conducted in the National Park 'De Hoge Veluwe' (5000 ha) in the eastern part of the Netherlands (52^0 2-8'N; 5^0 50-51'E) (Fig. 1, table 1). The park comprises a typical landscape on poor, aeolian sandy soils of the Veluwe area shaped in glacial and interglacial times.

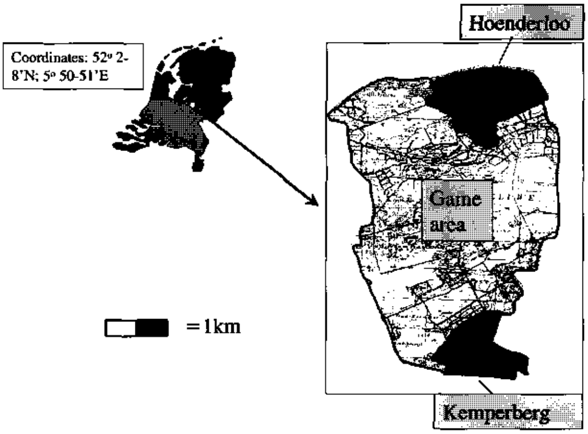


Figure 1: Location and situation of the study area before the removal of the fences. The shades areas represent the new available areas of Hoenderloo and Kemperberg, which were until1995, exclusively used by roe deer.

The landscape is an erosion landscape formed by heavy sheep grazing in the middle ages. It is characterised by open vegetation types dominated by *Corynepherus canescens* L. or *Calluna vulgaris.*L growing on sand dunes and blownout areas. Pine woodlands follow the lichen communities in the vegetation succession; large parts of the park are covered by first and second generation Scots pine (*Pinus sylvestris* L.). Deciduous forests of common oak (*Quercus robur* L.), birch (*Betula pendula* Roth) and beech (*Fagus sylvatica* L.) occur as well as coniferous forests with Scots pine, rowan (*Sorbus aucuparia* L.) and Douglas fir (*Pseudotsuga menziesi* L.) (Table 2).

The park has a long history of wild herbivores. Since the 17th century red deer (*Cervus elaphus* L.) have been known to occur on the 'Veluwe'. A stable population of red deer has been present in the park after its reintroduction in 1905. Mouflon (*Ovis musimon* Schreber), Corsican mountain sheep, were introduced in the park in 1921 (Broekhuizen et al. 1992). Roe deer were already present in the middle ages but went almost extinct in the late 18th century due to heavy culling regimes and the degeneration of the forests into heathland and drift sand. Roe deer clearly benefited from the reforestation of the Veluwe area (Broekhuizen *et al.* 1992). Wild boar (*Sus scrofa scrofa* L.) populations of 30-150 animals have occurred since 1940, with a rather stable population of 40-60 animals during 1985-1999. Fences prevent emigration or immigration of wild herbivores from the park.

Table 1: Area type description. * Between brackets: in phenological season 2 & 3. The habitat type description is reported in table 2.

Terrain type	*Size (ha.)*	*Visible area (ha)**	*Grazing history*	*Habitat type (proportion per terrain type)*
Hoenderloo (H)	800	142 (124)	max. 80-100 roe deer	• Deciduous forest(50%) • Coniferous forest(30%) • Heathland (10%) • Pine woodland (10%)
Kemperberg (K)	400	174	max. 60-80 roe deer	• Deciduous forest(30%) • Coniferous forest(55%) • Heathland (15%)
Game area (G)	3800	2168	max. 275 red deer max. 50 roe deer max. 275 mouflon	• Deciduous forest(5%) • Coniferous forest(10%) • Heathland (65%) • Pine woodland (20%)
total	5000			

Until January 1995 the herbivore populations of red deer, mouflon and wild boar were enclosed in the central part of the park, which consists of 3800 ha of pine woodland and heathland. This former Game area (G) was expanded in January 1995 to 5000 ha, by removing the inner fences (Fig. 1). New areas became available for red deer, mouflon and wild boar populations, existing of mainly deciduous and coniferous forests in the northern (Hoenderloo) and southern part (Kemperberg) of the park grown on more productive soils. Before 1995, when the other herbivores were 'introduced', Hoenderloo and Kemperberg had a stable roe deer population (Table 1). Each year a constant culling regime is carried out from September to March to control the wild herbivore populations. Annually, on average 20 roe deer, 85 red deer, 75 mouflon and 50 wild boar have been culled.

***Table 2*:** Dominant plant species in the habitat types (after Smit et al. 1998)

Habitat type	***Dominant plant species***
Heathland	*Calluna vulgaris, Erica tetralix, Cladonia spp, Corynepherus canescens, Molinia cuerulea, Festuca ovina*
Pine woodland	*Pinus sylvestris, Betula pendula, Carex arenaria, Deschampsia flexuosa*
Coniferous forests	*Pinus sylvestris, Pseudotsuga menziesie, Sorbus aucuparia, Betula pendula, Vaccimium myrtilis, Deschampsia flexuosa*
Deciduous forests	*Quercus robur, Fagus sylvatica, Quercus rubra, Vaccinium myrtilis, Deschampsia flexuosa,*

Wild herbivore monitoring

From January 1995 till July 1997, the spatial distribution of the herbivore species was monitored using five permanent road transects, equally distributed within the park. Approximately once a week at sunset wild herbivores were counted from the car along the transects. We measured the distribution of the herbivore populations over the three areas; Hoenderloo (H), Kemperberg (K) and the former Game area (G) (Table 1). In addition to the data on the distribution of red and roe deer populations data on spatial distribution of the mouflon and wild boar populations were also recorded.

The habitat use of all herbivore species was analysed by using counts of faecal pellet groups. Each year from 1994-1997, at 32 permanent plots the number of pellet groups of the various herbivores was assessed. Five main habitat types were distinguished in the park: heathland, pine woodland, deciduous forests and coniferous forests (Table 2). Eight plots were located in Hoenderloo and eight plots in Kemperberg in the dominant vegetation, respectively four in coniferous and four in deciduous forests. In the Game area eight plots were located in pine woodland and heathland. In each plot, five randomly located strips of 100 x 1 m were used in which all individual pellets were counted. Individual pellets within a distance of 2 m of each other were classified as one group. From 1994 until 1997, pellet groups were counted in August or September. From 1995 to 1999 during spring counts, park managers estimated roe deer populations in each area (in Hoenderloo; from 1991 to 1999). The calf/doe ratio of one-year-old roe deer calves were used to indicate reproductive success. Additionally, culling provided data on weights of one-year-old red deer calves. Consequently these data were used as a performance (fitness) measure (Conradt et al 1999, Coulson et al. 1997).

Data analysis

The herbivore observations were grouped into biological (phenological) seasons: winter (December - February), spring (March - May), summer (June- August) and autumn (September - November) based on the quality and quantity of the available food (Putman 1996; van de Veen 1979). The numbers of herbivores were averaged per count per season for each species and phenological season. Because visibility varied among the habitat types, the effective width of the transects varied in the calculations of animals per unit area (Prins & Van der Jeugd 1993). The visible area was estimated in summer (March - August) and winter season (September - February) because of differences in visibility due to changes in forest canopies.

Habitat overlap among all herbivore species was calculated according to Pianka's overlap formula (Pianka 1973: equation 1) where, O_{jk} is the habitat overlap (varying from 0) based on mean pellet group densities per transect per habitat type during the period 1994-1997, U_{ij} is the relative use of habitat i by herbivore j, and U_{ik} is the relative use of habitat i by herbivore k and n is the number of habitats

equation 1:
$$O_{jk} = \frac{\sum_{i=1}^{n} U_{ij} x U_{ik}}{\sqrt{\sum_{i=1} U_{ij}^{2} x U_{ik}^{2}}}$$

In order to analyze temporal trends in spatial distribution of red deer and roe deer densities we used two-way ANOVA (type III, GLM, Repeated Measurements, SPSS release 8.0) (Norušis 1993). Trends were tested as interactions among phenological season and year effects within each area. A two-way hierarchical ANOVA design (Sokal & Rohlf 1980), with year and habitat type as fixed factors and site as random factor nested within habitat type, was used to analyze shifts in habitat use based on changes in pellet group densities. A residual analysis was used to detect the type of transformation. Large herbivore densities as well as pellet group densities were $^{10}\log_{x+1}$ transformed prior to the analysis in order to improve the homogeneity of variance. A paired samples T-test was used to analyze changes in roe deer and red deer performance and roe deer density before and after fence removal.

***Table 3*:** Mean (absolute) number of herbivores per count per terrain type (H=Hoenderloo, K=Kemperberg, G=Game area) for the phenological seasons (1995-1997) ± s.e

	Roe deer						**Red deer**					
Phen. Season	**H**		**K**		**G**		**H**		**K**		**G**	
95-1	14.6	*±2.0*	4.7	*±1.2*	6.3	*±2.0*					23.2	*±3.4*
95-2	10.8	*±1.9*	3.4	*±1.4*	5.1	*±0.8*	5.1	*±1.3*			23.8	*±3.7*
95-3	5.3	*±0.9*	2.3	*±0.6*	4.2	*±0.6*	7.6	*±1.9*	3.0	*±0.4*	21.2	*±3.5*
95-4	3.7	*±1.0*	3.1	*±0.8*	3.5	*±0.6*	5.8	*±2.3*	3.7	*±1.2*	13.2	*±1.8*
96-1	7.7	*±1.1*	7.0	*±1.0*	4.7	*±0.8*	4.0	*±1.5*	10.0	*±2.0*	16.1	*±2.0*
96-2	7.3	*±0.9*	6.2	*±1.2*	5.4	*±0.8*	7.6	*±1.3*	9.8	*±2.5*	20.4	*±2.1*
96-3	5.5	*±0.7*	4.7	*±1.5*	3.1	*±0.4*	5.6	*±1.3*	6.7	*±1.5*	21.8	*±4.1*
96-4	3.4	*±1.0*	1.9	*±0.3*	3.1	*±0.5*	7.5	*±1.5*	5.8	*±2.4*	14.7	*±2.5*
97-1	4.3	*±1.0*	3.8	*±1.0*	8.9	*±1.6*	8.2	*±2.4*	5.6	*±1.1*	20.7	*±3.9*
97-2	4.9	*±0.9*	3.2	*±0.6*	4.3	*±0.6*	11.7	*±4.0*	7.8	*±1.5*	18.3	*±2.7*

	Mouflon						**Wild boar**					
Phen. Season	**H**		**K**		**G**		**H**		**K**		**G**	
95-1					38.4	*±13.0*						
95-2					46.1	*±22.5*	2.00	*±1.0*	4.0	*±0.0*	5.0	*±3.1*
95-3					54.1	*±19.8*	8.75	*±4.3*	1.5	*±0.5*	3.9	*±1.9*
95-4					32.6	*±10.7*					2.0	*±1.0*
96-1					20.7	*±4.8*					16.0	*±0.0*
96-2					29.4	*±8.4*	9.75	*±3.4*	9.5	*±8.5*	6.1	*±2.5*
96-3					66.4	*±22.1*	14.17	*±4.3*	15.0	*±7.2*	6.4	*±1.7*
96-4			200.0	*±114.9*	14.8	*±4.7*	3.00	*±0.0*			7.4	*±3.6*
97-1					23.3	*±8.8*			1.0	*±0.0*		
97-2					39.9	*±12.5*			1.5	*±0.3*	3.9	*±1.2*

Results

Spatial distribution

In general, densities of counted large herbivore species fluctuated widely among seasons during the study period (Fig. 2,Table 4). Significant lower red deer and roe deer densities were counted in autumn and winter season than in spring and summer (Table 4). Lower densities correspond to the culling season. The culling activity in autumn and winter seasons negatively affects the visibility of the wild herbivore species (B. Boers, pers. obs).

The roe deer population in Hoenderloo (H) declined significantly ($t=2.86$, $P_{\text{1-tailed}}=0.032$, $n=4$) after the fences were removed while the density in Kemperberg (K) and the Game area (G) remained relatively constant (Fig 2A, 4A). Overall roe deer densities were relatively high in H (3-10 deer/100 ha), lower in K (2-5 deer/100 ha) and lowest in G (<1 deer/100 ha).

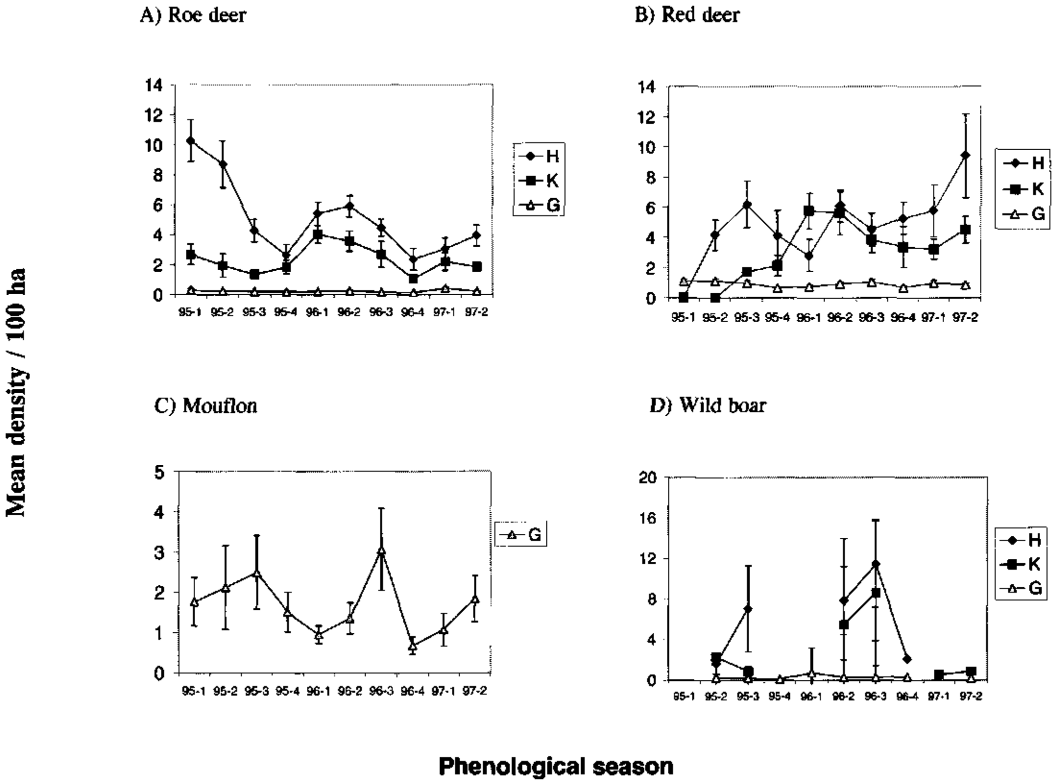
The red deer population colonised H and K relatively soon after removal of the fences (Fig. 2B, Table 3). First H was colonised in spring of 1995 followed by K in the summer season of 1995. As soon as H and K were colonised the density of red deer increased significantly from 4-6 deer/100 ha to 6-10 deer/100 ha in H (Table 4) and from 2-3 deer/100 ha to 4-6 deer/100 ha in K. In G the density remained continuously low (<2 deer/100 ha).

The mouflon population from G did not colonise H and K (Fig. 2C, Table 3). In G, a relatively constant density of 2 mouflons/100 ha was found.

The population of wild boar from G colonised H and K in spring of 1995 (Fig. 2D, Table 3) and showed strong fluctuating densities; from 0-10 wild boars/100 ha in H and from 0-8 wild boars/100 ha in K while in G the density remained low (< 1 wild boar/100 ha).

Habitat use

The habitat use of roe deer shifted significantly during the study period (Fig. 3A & Table 5). In 1994 still 75% of the pellet groups was found in deciduous forests while in 1996 and 1997 only 10-20% was found in this habitat type. The decrease in the utilisation of deciduous forests coincided with an increase in the use of coniferous forest (from 20% in 1994 to 25-70% in 1995-1997) and heathland (from < 5% in 1994 to 10-20% in 1996-1997).



A) Roe deer

B) Red deer

C) Mouflon

D) Wild boar

***Figure 2*:** The mean density ± s.e. (number of animals per 100 ha) of respectively roe deer (A), red deer (B), mouflon (C) and wild boar (D) per phenological period (1=winter, 2=spring, 3=summer, 4=autumn) per terrain type (H=Hoenderloo (diamonds), K=Kemperberg (squares), G=Game area (triangles) during January 1995 untill June 1997

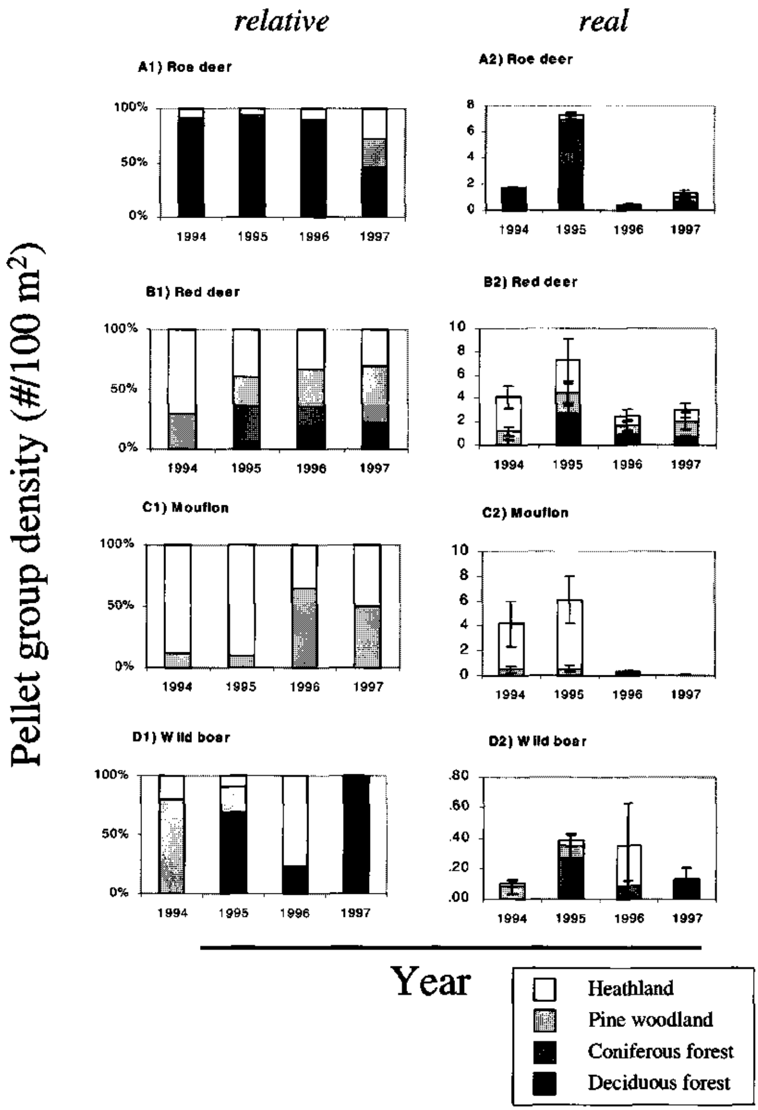


***Figure 3*:** Changes in habitat use of roe deer (A), red deer (B) and mouflon (C) reported as the relative (1) as well as the real (2) (± s.e.) mean density of pellet groups per habitat type during 1994-1997.

***Table 4*:** Two-way ANOVA GLM Repeated Measurements with dependent variable red and roe deer herbivore density for each phenological season tested on between year effects. The degrees of freedom (df), F-value (according to Hotelling's Trace) and significance level (p) of each effect and interaction are presented for each area with α=0.05.

Roe deer		***df***	***F-value***	***p***
H	season	3	8.30	0.004
	season x year	3	2.32	NS
K	season	3	6.88	NS
	season x year	3	3.11	NS
G	season	3	3.57	0.024
	season x year	3	0.38	NS
Red deer		***df***	***F-value***	***p***
H	season	3	37.97	0.000
	season x year	3	11.29	0.001
K	season	3	6.11	NS
	season x year	3	3.04	NS
G	season	3	5.07	0.004
	season x year	3	0.22	NS

Also, the habitat use of red deer changed significantly during the study period (Fig. 3B, Table 5). The use of heathland and pine woodland in 1994 shifted into the use of a mix of these two habitat types with coniferous and deciduous forests. Especially heathland utilisation (75% in 1994; 25% in 1997) tended to be replaced by the utilisation of coniferous and deciduous forests (25% in 1996-1997) and pine woodland (25% in 1994, 30-50% in 1996-1997).

The habitat use of mouflon changed too during the study period (Fig. 3C). In 1994 and 1995 habitat use was concentrated in heathland (> 75%), in 1996 and 1997 the use of pine woodland significantly increased (Table 5) (<25% in 1994 and 1995; 50% in 1996 and 1997).

Before the fences were removed (in 1994; Fig. 3D), the habitat use of wild boar was concentrated in pine woodland (>75%) and heathland (<25%). After 1994, wild boar appeared to use coniferous and deciduous forests as well. In 1997, pellet groups of wild boar were exclusively found in coniferous and deciduous forest.

***Table 5*:** Two-way hierachical Anova summary of pellet group density with factors: habitat type, year and transect. Both habitat type (n=4) and year (n=4) are fixed factors while transect (n=8) is a random factor and nested within habitat type. The degrees of freedom (df), Means Square (MS), F-value and significance level (p) of each effect and interaction are presented for each herbivore species with α=0.05.

Roe deer

Factor	***df***	***MS***	***F-value***	***p***
Habitat type	3	9.92	5.11	0.006
Year	3	19.83	15.68	0.000
Transect	28	1.94	1.54	NS
Habitat type * Year	9	5.58	4.41	0.000

Red deer

Factor	***df***	***MS***	***F-value***	***p***
Habitat type	3	14.57	1.68	NS
Year	3	9.27	4.95	0.003
Transect	28	8.70	4.65	0.000
Habitat type * Year	9	3.88	2.07	0.041

Mouflon

Factor	***df***	***MS***	***F-value***	***p***
Habitat type	3	40.36	6.53	0.002
Year	3	17.47	6.82	0.000
Transect	28	6.18	2.41	0.001
Habitat type * Year	9	14.05	5.49	0.000

Wild boar

Factor	***df***	***MS***	***F-value***	***p***
Habitat type	3	4.26.10-2	0.58	NS
Year	3	4.37.10-2	1.01	NS
Transect	28	7.40.10-2	1.71	0.03
Habitat type * Year	9	6.11.10-2	1.40	NS

***Table 6*:** Results of spring counts by park managers of the roe deer population in the areas Hoenderloo, Kemperberg and the former Game devided into sex (male, female), age (adult, juvenile: < 1 year), unidentified sex or age, total population, density and reproductive succes ($\frac{\sum_{calves}}{\sum_{ad.female}}$).

For Hoenderloo: *=$p<0.01$ (one-tailed) according to paired-samples T-test, NS=not significant with $\alpha=0.05$

year	*male ad.*	*female ad.*	*male calf*	*female calf*	*unid. adult*	*unid. calf*	*total calves*	*total pop*	*density (#/100 ha)*	*reproductive succes* ($\frac{\sum_{calves}}{\sum_{ad.female}}$)
Hoenderloo										
1991	21	26	8	6		1	15	62	7.75	0.58
1992	24	36	9	6	2		15	77	9.63	0.42
1994	23	21	3	7	3		10	58	7.25	0.48
1995	33	23	4	7	3		11	70	8.75	0.48
1996	18	23	3	2			5	46	5.75	0.22
1997	24	28	4	5			9	61	7.63	0.32
1998	23	25	3	5			8	56	7.00	0.32
1999	18	20	2	1			3	41	5.13	0.15
	NS	NS	*	*			*	*	*	*
Kemperberg										
1995	17	21	7	6			13	51	12.75	0.62
1996	26	17	4	4	2	2	10	55	13.75	0.59
1997	28	18	1	2			3	49	12.25	0.17
1998	20	16	5	7			12	48	12.00	0.75
1999	24	25	1	6	2		7	58	14.50	0.28
Game area										
1995	61	45	10	8			19	125	3.29	0.50
1996	45	49	8	8			18	112	2.95	0.47
1997	43	44	5	6			11	98	2.58	0.29
1998	41	37	3	14	1	1	18	97	2.55	0.47
1999	38	41	3	7	2		10	91	2.40	0.26

Changes in roe and red deer performance

The roe deer calf/doe ratio declined significantly in H after the fence removal (Fig. 4B; $t=3.64$, $p_{\text{1-tailed}}=0.018$) marked by a sudden step down from 1995 to 1996. Before the removal of the fences the calf/doe ratio was 0.4-0.6 and after the removal of the fences the declined to 0.2 - 0.3 (Table 6). Both the number of male and female calves appeared to decrease significantly after fence removal (Table 6). The calf/doe ratio showed relatively wide fluctuations with peaks in 1998 in K and G. In 1999 all terrain types showed a low calf/doe ratio (0.2-0.3). The red deer calf weights significantly increased after fence removal ($t=3.57$, $p_{\text{1-tailed}}=0.02$, Fig. 5) from 35-36 kg to 36-42 kg.

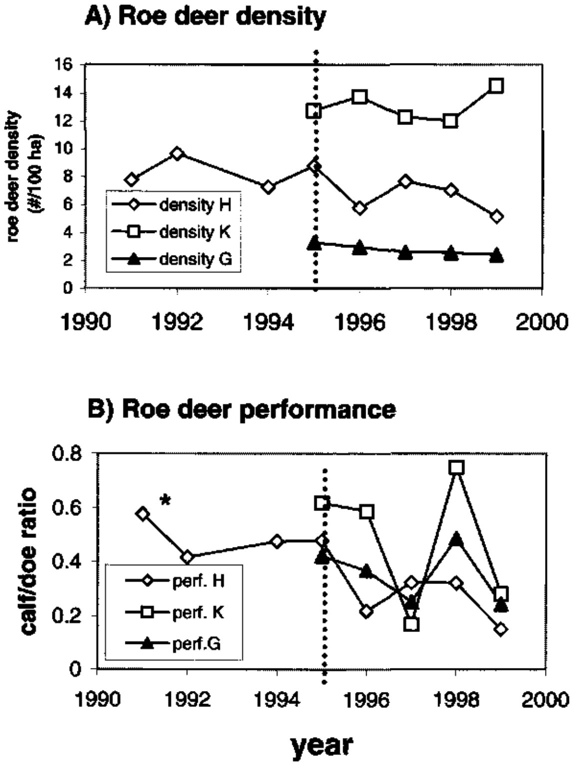


Figure 4: Changes in A) density and (B) performance of roe deer populations in Hoenderloo (H), Kemperberg (K) and Game area (G) during 1995 - 1999 (H: 1991-1999) measured as the survival of calves after their first winter as proportion of the adult female population. The dashed line respresents the time of fence removal.

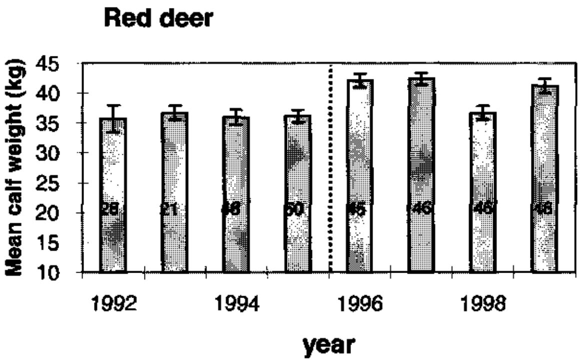


Figure 5: Changes in red deer calf weights (± s.e) in the whole park during 1995-1999. The bars represent the mean calf weight (kg). The numbers within the bars represent the number of individual calves used for the analysis. The dashed line respresents the time of fence removal.

Habitat overlap

The habitat use of roe deer and red deer overlapped little before the fences were removed (0.12; Table 7) but increased considerably after fence removal (0.5- 0.9; Table 7). The habitat overlap between red deer and mouflon was high (0.8 - 0.9) during the whole study period. Between roe deer and mouflon overlap in habitat use was low at the beginning but ended high in 1997. On the contrary, the overlap in habitat use between red deer and wild boar decreased strongly in 1997 compared to the years before. The habitat overlap between mouflon and wild boar and wild boar and roe deer fluctuated among the years.

Table 7: Habitat overlap among the herbivore species according to Pianka (1973)

	1994	**1995**	**1996**	**1997**
Red*Roe	0.12	0.54	0.48	0.88
Red*Mouflon	0.97	0.75	0.83	0.94
Red*Wild boar	0.60	0.76	0.72	0.18
Roe*Mouflon	0.12	0.09	0.07	0.74
Roe*Wild boar	0.05	0.76	0.38	0.43
Mouflon*Wild boar	0.37	0.18	0.47	0.00

Discussion

The main criteria that allow interspecific competition to take place should be analysed first before we discuss the results regarding our hypotheses. These criteria are: resource limitation (I), dietary (II) and habitat overlap (III) between the herbivore species (De Boer & Prins 1990, Mysterud 2000). First of all (I), the main limiting forage for red and roe deer in our study area is 'browse'; forage material like twigs, bark, buds and leaves of woody species (Smit et al. 1998). In our study area the intensive browsing of *Sorbus aucuparia* L., *Quercus robur* L. and *Vaccinium myrtilis* L. confirm that these species are preferred by both red and roe deer (Van Wieren et al. 1997). These plants provide a highly nutritious food for red and roe deer containing relatively high contents of important minerals like calcium, magnesium and phosphorus (Hearney & Jennings 1983, Van de Veen 1979, Wilmshurst & Fryxell 1995). Despite differences in herbivore types (Hofmann 1989), roe and red deer both highly depend on browse as very important forage species (Hazebroek & Groot Bruinderink 1995, Homolka 1993; Van Wieren et al. 1997). In the new forest areas of Hoenderloo and Kemperberg the browse supply was much higher than in the former Game area, where the browse supply was depleted by the red deer population of over 200 animals (Smit et al. 1998). Fence removal triggered a 'run for browse' by red deer from the browse depleted Game area into the browse-rich deciduous and coniferous forests in Hoenderloo and Kemperberg leading to a sgnificant increase of performance.

In response to the colonisation of deciduous and coniferous forests in Hoenderloo and Kemperberg by red deer and wild boar, roe deer as well as mouflon appeared to adjust their habitat use (II). Roe deer showed a significant shift in the use of red deer invaded deciduous and coniferous forests to heathland and pine woodland. Mouflon appeared to take over the former, abandoned habitats of red deer (pine woodland) in the former Game area. Mouflon as a typical grazer species (Hofmann 1989) is better adapted to the grass-dominated habitat types like heathland and pine woodland (Homolka 1996). The mouflon population had no need to migrate and took the benefits of the emigration by red deer. The wild boar population clearly exchanged the pine woodland and heathland for the coniferous and deciduous forests in the newly available areas. The higher food supplies in these habitats mainly consisting of seeds of oak and beech trees (mast) but also roots, berries and grass (Van Wieren et al. 1997) might have caused the shifts in terrain and habitat use of the wild boar population. Colonising wild boars in the forests of Hoenderloo and Kemperberg may have also affected the local roe deer population through predation of young (< 2 months) roe deer calves (Fig. 6, arrow 3). However, we have no direct evidence of this.

The habitat overlap (III) between red and roe deer increased obviously after fence removal, which may indicate interspecific competition. Though, many studies on habitat overlap derive different ecological interpretations from the term (Schoener 1983, De Boer & Prins 1990). A high degree of overlap may equally well indicate an absence of competition permitting a sharing of resources (Gordon & Illius 1989, Mysterud 2000). In this study, the increase in habitat overlap was caused by the shifts in habitat use of both red deer and roe deer. On the one hand, red deer invaded former roe deer habitats and the other hand roe deer invaded typical, unexploited red deer habitats within the new areas. Despite the decline in density, the roe deer population did not move from the forests in Hoenderloo. The sudden stress after the arrival of red deer may have caused an increase of the natural mortality (B.Boers, pers. obs.). Additionally, the roe deer population in Hoenderloo adapted their habitat use from purely coniferous and deciduous forests to more heathland and pine woodland. The arrival of red deer forced roe deer to find new habitats within the previous area. The increase in habitat overlap related to the shifts in habitat use as well as the patterns in spatial use and the decline in roe deer performance after fence indicated interspecific competition between red and roe deer.

As in most other studies (Leuthold 1978, Loft et al. 1991, Voeten & Prins 1999, Mysterud 2000), the mechanisms behind the observed competitive interactions between herbivore species remain hypothetical. First, interference competition for browse in Hoenderloo may have caused a decline of the performance of the smaller more selective herbivore (roe deer) in favour of the larger, more versatile herbivore species (red deer) (Fig.6, arrow 1). Mainly in Hoenderloo, roe deer density and performance significantly declined. Red deer preferred the forests of Hoenderloo because of the higher productivity compared to Kemperberg. For that reason, the understory vegetation in Hoenderloo is generally richer of typical browse species than in Kemperberg (Smit et al. 1998) leading to a greater impact of red deer on roe deer in Hoenderloo than in Kemperberg.

We observed no direct interference (Begon et al. 1990) between red deer and roe, however social antipathy can not be excluded (Batcheler 1960). Second, 'exploitation competition' (Begon et al. 1990) on browse between red deer and roe deer may have caused a decline in roe deer performance through the reduction of the browse supply due to red deer foraging (Fig. 6, arrow 2). As soon as red deer colonised Hoenderloo and Kemperberg the shrub layer and understory was destroyed. A well- developed shrub layer of mainly *Sorbus aucuparia* and *Rhamnus frangula* was reduced 2.5 meters in height by red deer in two years time (Smit et al. 1998). Roe deer are highly territorial and prefer dense forest understories for food and shelter (Henry 1981, Gill et al. 1996, Putman 1986, Andersen 1998). By modifying these habitats, red deer probably reduced the quality of roe deer habitat (Schoener 1983).

Competitive hierarchy and functional traits

The competitive superiority of red deer over roe deer might be based on several morphological and behavioural traits. First, red deer are more generalist feeders than roe deer and relies on a broader menu of food items than roe deer does (Hofmann 1989, Homolka 1996, Van Wieren et al. 1997). Roe deer, as a typical specialist browser, depends more on quality than on quantity of the food items (Homolka 1993). Roe deer will probably be out competed by red deer as soon as the browse supply in the new forests was depleted quantitatively and qualitatively. Second, red deer are larger than roe deer, which may allow red deer to win direct physical conflicts. An additional explanative trait for the dominance of red deer over roe deer can be the territoriality of the species. Roe deer is a territorial species and will try to monopolise the best available habitats (Anderson 1998). In contrast to roe deer, generally red deer is a non-territorial species that does not have to defend habitats (Clutton-Brock et al. 1982). As a result, better habitats could attract larger numbers of individuals of red deer, which could deplete available resources to a lower level than roe deer are capable of (Conradt et al. 1999).

Evidence for interspecific competition

The clear shift in habitat use of both roe deer and red deer, the observed changes in spatial distribution and the decline in performance of the roe deer population after the colonisation of red deer provide evidence for one-sided interspecific competition (Gordon & Ilius 1989, De Boer & Prins 1990). The reduction of the niche of roe deer in presence of the superior competitor (red deer) can be seen as an example of competitive exclusion (Begon et al. 1990, Abramski & Sellah 1982). This study indicated how resource competition could lead to shifts in resource partitioning in limited environments.

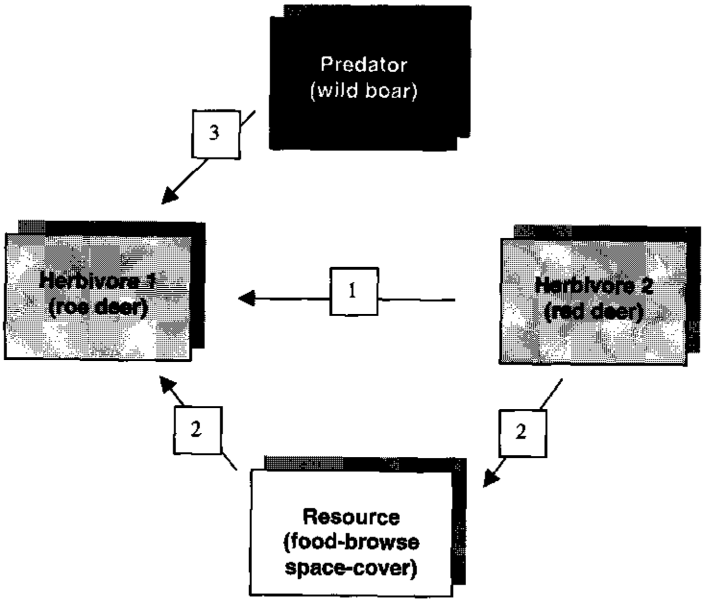


***Figure 6*:** . Interspecific relations between herbivore species.
Arrow 1: Interference competition. Arrow 2: Exploitative competition on browse or indirect competition via reduction in habitat quality. Arrow 3: Predation of roe deer calves by wild boar

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Summary / samenvatting

Summary

In many vegetation succession seres, woody species dominate the final (i.e. climax) stage, because long-lived, tall plants are the best competitors for light. Though woody species can be accounted among the most successful plant strategists, they need to follow a long and difficult pathway to gain dominance. Especially the establishment stage including the 'seed', seedling' and 'sapling' phase is very critical in the population biology of woody species. By surviving the first years in their life, the chances of woody species of growing older subsequently increase. Ecological research on woody species has primarily focussed on later stages in their life while the establishment stage was rarely taken into account. In addition, this stage is easily overlooked in the field, which makes it the 'secret' stage in the life cycle of woody species. This 'secret stage' involves many hazards like dispersal problems, pathogens, abiotic stress, competition with the present vegetation for light, water and nutrients, seed predation and herbivory. In many nature areas in the Netherlands, woody species play a dominant role in the vegetation dynamics. Recent ideas on nature conservation and management involve the use of large, wild or domesticated herbivores to prevent the development of uniform forests and to induce an increase in species and community diversity. However, within the context of nature conservation, the (re-) introduction of grazing by large herbivores is severely hindered by the lack of ecological knowledge about the effects of large herbivores on woody species on the one hand, and the responses of woody species to herbivory on the other.

In this study, I investigated the biotic and abiotic factors that limit woody species establishment. Within the context of vegetation succession, I consider which ecological mechanisms affect the establishment stage of woody species and what the consequences are for the vegetation succession. Furthermore, I investigated the direct and indirect interactions between woody species and herbivores.

The results presented in chapter 2 demonstrate that the colonisation rate of woody species is affected by habitat productivity. On three different soil types comprising a relatively poor sandy, a somewhat richer sandy and a relatively rich sandy loamy type, the colonisation rate of woody species was studied during old field succession. Chronosequences were established on these soil types on former fields in the Eastern and Southern part of the Netherlands. On the rich soil type, the colonisation rate of woody species was slower than on the poor soil type. The high abundance of perennial herbaceous species during the first 20 years of abandonment on the rich type may have delayed the woody species colonisation. First the herbaceous species cover the bare ground, which inhibits germination, and next

they compete with woody seedlings for light, water and nutrients. In ± 30 years on the poor soil type and in ± 45 years on the rich soil type woody species became dominant relative to other life forms. In contrast to other studies, typical 'forest' species like *Quercus robur* L. invaded relatively early (< 5 years) which coincides with the relatively close distance to the nearest seed sources.

In chapter 3, I focussed on the effects of herbivory on the establishment success of four woody species with different life history traits across a successional gradient. In the national park De Hoge Veluwe, a gradient from early (heathland) through intermediate (pine woodland) to late successional vegetation communities (pine forest and oak-beech forest) was used to study woody species establishment with different life history traits. Seeds of pioneer species like birch (*Betula pendula* Roth.), Scots pine (*Pinus sylvestris* L.) and mature forest species like common oak (*Quercus robur* L.) and beech (*Fagus sylvatica* L.) were sown in exclosures with three herbivory treatments comprising different herbivore guilds. Three different guilds of herbivores were distinguished: a guild including all herbivores (1), a guild including small rodents and insects (2) and a guild including only insects (3). In contrast to the intermediate and late successional types, a higher number of seedlings was found in early successional vegetation communities in presence of all herbivores. Establishment chances for woody species were generally higher in early successional vegetation communities than in late successional types due to lower seed predation (granivory) intensity by small rodents. In the early successional stage, abiotic stress is the key factor in woody species establishment. In the intermediate and late successional stage, seed predation as well as insect herbivory inhibited the colonisation of forest species. As a result, forest succession can easily be arrested or delayed in intermediate and late successional stages.

In chapter 4, I studied the botanical changes across a woodland-forest gradient during seven years after grazing introduction and exclusion of large herbivores. The botanical composition of the herb and the shrub layer was studied in permanent quadrats, inside and outside large herbivore exclosures. Introduction of red deer (*Cervus elaphus* L.) in pine forest and oak-beech forest did not have significant effects on the composition of the herb and the shrub layer, while grazing exclusion in former, heavily grazed pine woodland resulted in a fast recovery of graze-tolerant shrubs like *Sorbus aucuparia* L. The recovery of a dense shrub layer negatively affected the cover of the perennial grass layer mediated by competition for light leading to an increase of litter cover. Neither the introduction nor the exclusion of grazing significantly affected the vascular plant species richness. The impacts of grazing introduction and grazing exclusion did not reflect reversible ecological processes.

The time required for recovery of the understory vegetation following release from grazing appeared to be much shorter than the time needed for the degradation after grazing introduction. While graze-tolerant species were able to recover rapidly following release of grazing, this was not the case for graze-sensitive species like deciduous tree species. From the nature conservation point of view, grazing introduction of red deer in forests may not be a successful tool in maintaining or creating a higher species or community diversity.

In chapter five, the interactions between large and small herbivores were studied by analysing the effects of introduction and exclusion of large herbivores on small rodents communities. The small rodent density as well as the seed predation intensity on oak and beech seeds were measured inside and outside large herbivore exclosures in former, heavily grazed pine woodland and heathland and previously ungrazed pine and oak beech forest. Exclusion of grazing by large herbivores had a significant positive effect on the small rodent density. In the former, heavily grazed heathland and pine woodland, inside large herbivore exclosures a higher density of mainly wood mouse (*Apodemus sylvaticus* L.) as well as a higher seed predation intensity was found as compared to outside the exclosures. Introduction of red deer did not have significant effects on small rodent communities. The differences between grazing introduction and exclusion effects correspond to differences in vegetation structure development. The recovery of heavily grazed understory vegetation after large herbivore exclusion proceeded faster than the understory degradation due to grazing introduction. Small rodents depend on structural rich vegetations mainly for shelter. As a result, grazing exclusion positively affected the small rodent density due to the development of more favourable habitats for small rodents inside the exclosures.

In chapter 6, the interactions among roe deer (*Capreolus capreolus* L.), red deer, mouflon (*Ovis musimon* Schreber) and wild boar (*Sus scrofa scrofa* L.) were analysed in the national park De Hoge Veluwe by studying the effects of the enlargement of the area available to red deer, wild boar and mouflon. Before the enlargement, fences around this area acted as a barrier for the various large herbivore species. The removal of the fences allowed the herbivore species to enter new forest areas, which were until then, exclusively inhabited by roe deer. After the colonisation of these new areas by red deer and wild boar, the mean density as well as the performance of the local roe deer population significantly decreased. On the contrary, the red deer performance increased after the colonisation of the new areas. In addition, the habitat use of roe deer shifted from deciduous and coniferous forests to pine woodland and heathland. Both results point to competition for woody forage (browse). Furthermore, red deer browsing decreased the woody understory, which may have caused a reduction of the quality of preferred habitats based on shelter. I conclude that, the establishment stage of woody species is a significant bottleneck in the population biology of woody species as well as within the vegetation succession. In addition, woody species play a prominent role in the interactions between herbivores and vegetation development.

Samenvatting

Houtige planten (bomen en struiken) spelen een dominante rol in de vegetatiedynamiek. Tijdens de climaxfase blijken langlevende, hoge planten de beste concurrenten om licht. Hoewel houtige planten gerekend kunnen worden tot de meest succesvolle strategen onder de planten, is de weg naar uiteindelijke dominantie lang en moeilijk. Vooral de vestigingsfase van houtige planten, betreffende de verandering van zaad via kiemplant tot juveniele plant, is een uitermate kritische fase in de levenscyclus van houtige planten. Door dit stadium te overleven worden de kansen aanzienlijk groter zich te vestigen als een volwassen plant. Ecologisch onderzoek naar houtige planten heeft in het verleden weinig aandacht besteed aan deze vestigingsfase. Omdat de vestigingsfase in ecologisch veldonderzoek gemakkelijk over het hoofd wordt gezien beschouw ik deze als geheime fase in de levenscyclus van houtige planten. In deze fase zijn er veel potentiële gevaren als een beperkte dispersie, pathogenen, abiotische stress, competitie met aanwezige vegetatie om licht, water en nutriënten, zaadpredatie en herbivorie.

In veel natuurgebieden in Nederland spelen houtige planten een dominante rol in de vegetatiedynamiek. Recente ideeën op het gebied van natuurbescherming en beheer hebben betrekking op het gebruik van grote, wilde of gedomesticeerde herbivoren als beheersinstrument om de vorming van uniforme bossen in natuurgebieden te voorkomen en de soortenrijkdom van zowel flora als fauna te laten toenemen. De inzet van grote herbivoren in het Nederlandse natuurbeheer wordt beperkt door gebrekkige wetenschappelijk kennis van de effecten van grote herbivoren op houtige planten enerzijds en de respons van houtige planten op herbivorie anderzijds.

In deze studie onderzocht ik welke en in welke mate diverse biotische en abiotische factoren de vestiging van houtige planten beïnvloeden. Binnen het kader van vegetatiesuccessie bestudeerde ik welke ecologische mechanismen de vestigingsfase beïnvloeden en wat de consequenties zijn voor de vegetatiesuccessie. Tevens onderzocht ik de directe en indirecte interacties tussen houtige planten en herbivoren.

In hoofdstuk 2 blijkt dat de kolonisatiesnelheid van houtige planten wordt beïnvloed door de bodemrijkdom. Op drie verschillende bodemtypen met verschillende bodemvruchtbaarheid werd de kolonisatiesnelheid van houtige planten bestudeerd gedurende de vegetatiesuccessie op verlaten landbouwgronden ('oldfield succession'). Chronosequenties werden bestudeerd op bodemtypen op zandgronden in Oost- en Zuid-Nederland. Op het rijkste bodemtype bleek de kolonisatiesnelheid aanmerkelijk trager te zijn dan op de armere typen. Met name de hoge abundantie van overblijvende grassen en kruiden op vooral het rijke type heeft een negatief effect op de kolonisatiesnelheid. Ten eerste sluiten ze het kiemvenster van houtige planten en ten tweede concurreren ze met houtige planten om licht, water en nutriënten. Houtige planten begonnen de vegetatiesuccessie te domineren na ca. 30 jaar op het arme en na ca. 45 jaar op het rijke bodemtype. Met name de snelle invasie van typische late successiesoorten als zomereik (*Quercus robur* L.) was opmerkelijk en hield verband met de nabije aanwezigheid van zaadbronnen.

In hoofdstuk 3 bestudeerde ik de effecten van herbivorie op de vestigingsfase van vier verschillende soorten houtige planten over een vegetatiesuccessiegradiënt. In het Nationaal Park De Hoge Veluwe werd een successiegradiënt van heide naar eerste en tweede generatie grovedennenbos tot eiken-beukenbos gebruikt om het vestigingssucces van ruwe berk (*Betual pendula* Roth.), grove den (*Pinus sylvestris* L.), zomereik en beuk (*Fagus sylvatica* L.) te bestuderen onder invloed van herbivorie. Zaden van bovengenoemde soorten werden ingezaaid in exclosures die onder invloed stonden van een verschillende groep herbivoren; (1) een groep bestaande uit alle soorten herbivoren (dus inclusief grote herbivoren als herten), (2) een groep bestaande uit muizen en insecten en (3) een groep bestaande uit slechts insecten. In vergelijking met grove dennenbos en eiken-beukenbos werden er in heide naar verhouding meer zaailingen in aanwezigheid van alle herbivoren gevonden. In het algemeen bleken de vestigingskansen van houtige planten groter te zijn in vroege successiestadia dan in late vanwege een geringere zaadpredatiedruk door muizen. In vroege successiestadia was abiotische stress een belangrijke factor tijdens de vestigingsfase van houtige planten terwijl in de latere successiestadia zaadpredatie door muizen en intensieve vraat aan zaailingen door insecten de voornaamste factor waren. Bossuccessie bleek zowel in de middellate en late vegetatiesuccessiestadia volledig te worden geremd door diverse groepen herbivoren.

De botanische veranderingen ten gevolge van de introductie van grote herbivoren in grove dennenbos en eiken-beukenbos werden bestudeerd in hoofdstuk 4. De effecten van begrazing door grote herbivoren op de compositie van de kruid- en struiklaag werden bestudeerd met behulp van permanente quadraten. Het introduceren van edelherten (*Cervus elaphus* L.) in grove dennenbos en eiken-beukenbos had geen significant effect op de compositie van de kruid- en struiklaag, terwijl het stoppen van begrazing in de voormalige, zwaar begraasde wildbaan resulteerde in een snel herstel van begrazings-tolerante struiksoorten als de lijsterbes (*Sorbus aucuparia* L.). Dit herstel had een negatief effect op de bedekking van de overblijvende grassen ten gevolge van de concurrentie om licht. Noch het introduceren van begrazing, noch het stoppen van begrazing door grote herbivoren had enig effect op soortenrijkdom van de hogere planten. De impact van het introduceren enerzijds en het stoppen van begrazing anderzijds, heeft geen omkeerbare ecologische processen tot gevolg. Het proces van het herstel van een zwaar begraasde vegetatie verloopt naar verhouding sneller dan de degradatie van de vegetatie door het introduceren van begrazing. Terwijl begrazings-tolerante soorten snel herstelden, bleef het herstel van begrazings-gevoelige soorten als loofboomsoorten zoals de zomereik, uit. Vanuit het perspectief van natuurbeheer biedt het introduceren van edelherten in bossen geen garantie voor het verhogen van de soortsdiversiteit van hogere planten.

In hoofdstuk 5 werden de interacties tussen grote en kleine herbivoren bestudeerd aan de hand van de effecten van het introduceren en stopzetten van begrazing door grote herbivoren op de populaties van verschillende soorten muizen. De muisdichtheid alsmede de zaadpredatiedruk op zaden van eik en beuk werden bestudeerd in exclosures voor grote herbivoren in gebieden waarin begrazing door grote herbivoren werd geintroduceerd en waarin begrazing door grote herbivoren werd stopgezet. In voormalige zwaar begraasde heiden en grove dennenbossen werd binnen de exclosures een hogere dichtheid aan muizen aangetroffen, van voornamelijk bosmuis (*Apodemus sylvaticus* L.), dan buiten de exclosures. Tevens werd een hogere zaadpredatiedruk vastgesteld binnen deze exclosures dan daar buiten. De introductie van grote herbivoren, voornamelijk van edelhert, had geen significant effect op de muisdichtheid en de zaadpredatiedruk. Het verschil tussen de effecten van het introduceren en stopzetten van begrazing door grote herbivoren correspondeert met de verschillen in ontwikkeling van vegetatiestructuur. Door het snelle herstel van de vegetatie in de voormalige wildbaan ontstond er een groter verschil in vegetatiestructuur tussen binnen en buiten de exclosures dan in de bossen waar begrazing werd geintroduceerd. Muizen hebben baat bij een structuurrijke vegetatie vanwege de dekking tegen predatoren maar ook door de aanwezigheid van voedselplanten. Het stopzetten van begrazing had een positief effect op de muizendichtheid door het ontstaan van een geschikter muizenhabitat.

In hoofdstuk 6 werden de interacties tussen edelhert, ree (*Capreolus capreolus* L.), moeflon (*Ovis musimon* Schreber) en wild zwijn (*Sus scrofa scrofa* L.) bestudeerd door de effecten van vergroting van het leefgebied in het nationaal park De Hoge Veluwe te analyseren. Na verwijdering van de tussenrasters konden grote herbivoren gebruik maken van nieuwe, relatief voedselrijke bossen in het noorden en zuiden van het park, die voor verwijdering van de tussenrasters het leefgebied waren van reeën. De kolonisatie van deze nieuwe bossen door met name edelhert en wild zwijn had een significant negatief effect op de dichtheid en de reproductie van de lokale populatie reeën. In tegenstelling tot reeën, nam de reproductie van de edelherten toe na de kolonisatie van nieuwe gebieden. Tevens verschoof het habitatgebruik van ree van rijk loof- en naaldbos naar arm grove dennenbos en heide. Beide resultaten wijzen op voedselconcurrentie tussen edelhert en ree gebaseerd op een gemeenschappelijke voedselbron bestaande uit 'browse' (takken, knoppen, bast van houtige planten). Door het plaatselijk afbreken van de struiklaag had de introductie van edelherten een negatief effect op de habitatkwaliteit van reeën.

Uit mijn onderzoek kan ik concluderen dat de vestigingsfase van houtige planten een significante 'bottleneck' is, zowel in de populatiebiologie van houtige planten als in de vegetatiesuccessie. Tevens spelen houtige planten een prominente rol in de interacties tussen herbivoren en vegetatieontwikkeling.

Curriculum vitae

Als oudste zoon van Nico Smit en Mariëls Verplaalen werd Ruben Smit geboren op 31 oktober 1971, te Hillegom. Zijn jonge jaren bracht hij door in Heemstede. Geheel tegen het advies in van het schoolhoofd van de lagere school begon hij aan zijn HAVO opleiding aan het Triniteits Lyceum te Haarlem. Als een der laatste 'Trinitariërs sloot hij zijn carrière aan de middelbare school af met het behalen van zijn VWO diploma om in Wageningen Bosbouw te gaan studeren. Reeds gedurende zijn middelbare schooltijd koesterde hij een grote belangstelling voor de natuur. In 1986 begon hij als 15-jarige aan ecologisch veldonderzoek naar de effecten van begrazing door runderen op de broedvogelpopulatie op 'Het eiland van Rolvers' in de Amsterdamse Waterleidingduinen. Zonder het toen zelf goed te beseffen legde hij daar de basis voor zijn latere werk.

In september 1991 begon hij aan de opleiding Bosbouw waarbij al snel duidelijk werd dat ecologie en natuurbeheer zijn interessegebieden waren zonder dat daar in die tijd tijdens de studie overigens veel aandacht aan werd besteed. In zijn tweede jaar werd een ludieke actie waarbij het vakgroepsbord van de vakgroep Bosbouw uit de tuin van Hinkeloord naar de toenmalige vakgroep Ecologische landbouw werd verplaatst, hem bijna fataal. De actie, om aandacht te vragen bij het vakgroepsbestuur voor de onduidelijke situatie waarin de studenten verkeerden na het vertrek van hun laatste hoogleraar, viel bepaald niet in goede aarde. Gelukkig kon hij door allerlei baantjes als studentassistent bij vele onderwijselementen zijn draai weer vinden wat resulteerde in een zeer vruchtbare samenwerking met de toenmalige AIO, Jan den Ouden (huidige UD Bosecologie & Beheer). Het afstudeervak naar de invloed van adelaarsvaren op de zaadpredatie door muizen wakkerde zijn interesse voor veldecologisch onderzoek verder aan. Op de toenmalige vakgroep TON deed hij een afstudeervak naar de kolonisatie van houtigen op voormalige landbouwgronden onder begeleiding van Ab Masselink en Han Ollf (het eerste hoofdstuk in dit proefschrift). Nog voor zijn afstuderen in augustus 1996 kon hij aan de slag als toegevoegd onderzoeker bij de vakgroep TON om het onderzoek naar de 'effecten van verwijdering van tussenrasters op de vegetatie in het Nationaal park De Hoge Veluwe' onder supervisie van Jan Bokdam te voltooien. Zijn tijdelijke aanstelling van twee dagen in de week weerhield hem er niet van veel extra onderzoek te doen met behulp van de inzet van vele afstudeervakkers. Deze dataset legde de basis voor het voor u liggende proefschrift. Na een korte periode als onderzoeker bij buro Silve en als tijdelijke kracht bij de Vlinderstichting kwam hij wederom in dienst bij de vakgroep TON aan de toenmalige Landbouw Universiteit. Vanaf dat moment heeft hij meegewerkt aan allerlei onderwijselementen als assistent maar ook als hoofddocent en coördinator, onder andere bij de huidige leerstoelgroep Natuurbeheer in de Tropen en Ecologie van Vertebraten. Als toegevoegd onderzoeker zette hij in het vroege voorjaar van 2000 het onderzoek naar 'De effectiviteit van agrarische natuurbeheer' op poten en voerde hij in teamverband het veldwerk van het weidevogelonderzoek uit. Vanaf januari 2001 maakt hij deel uit van het Opleidings Uitvoerings Team (OUT) als opleidingsvoorlichter voor de opleiding Bos en Natuurbeheer. In de tijd die overbleef schreef hij aan wetenschappelijke artikelen dat resulteerde in een proefschrift in maart 2002.

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