The role of bracken (*Pteridium aquilinum*) in forest dynamics

De rol van adelaarsvaren (*Pteridium aquilinum*) in de bosdynamiek

(met een Nederlandse samenvatting)

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Jan den Ouden

The role of bracken (*Pteridium aquilinum*) in forest dynamics

Proefschrift

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Stellingen

behorende bij het proefschrift getiteld:
"The role of bracken (*Pteridium aquilinum*) in forest dynamics"
van Jan den Ouden,
te verdedigen op 24 oktober 2000.

1. Het voorkomen van adelaarsvaren wordt op de droge zandgronden bepaald door de continue aanwezigheid van een bosvegetatie. De relatie tussen adelaarsvaren en bosgeschiedenis is daarmee historisch bepaald, en niet het gevolg van inherente fysische of chemische eigenschappen van een "oude bosbodem". *(dit proefschrift)*

2. Adelaarsvaren verwerft haar dominantie niet middels allelopathie. *(dit proefschrift)*

3. De bosmuis is in bosvegetaties belangrijker voor de verspreiding van de eik dan de Vlaamse gaai. *(dit proefschrift)*

4. De 'boom van het leven*' kan als metafoor voor de evolutionaire verwantschap tussen organismen beter worden vervangen door het rhizoomstelsel van de adelaarsvaren. * Charles Darwin, *The origin of species*

5. De sterke nadruk op 'positieve resultaten' in onderzoekspublicaties werkt een vals idee van wetenschappelijke vooruitgang in de hand.

6. De nieuwe natuur in Nederland wordt indirect gefinancierd met de vernietiging van oude natuur.

7. Vanwege de eis te promoveren op artikelen is een proefschrift eerder een schrift met proeven dan een proeve van geschrift.

8. Het niet-verlagen van de maximum snelheid op rijkswegen getuigt van politieke lafheid en is oliedom.

9. Aan menig *-isme* gaat de ego vooraf.

10. Vijf natte vingers maken één vuistregel.

11. Spreken is zilver, luisteren is goud.

Voor Barend en Corrie,

door wie ik niet teveel in het koffiedik heb gekeken
want de koffie is altijd bruin.

Abstract

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Bracken fern (*Pteridium aquilinum*) causes stagnation in forest succession in many parts of the world. The mechanisms by which bracken affects the establishment and growth of plant species are studied, focusing on the regeneration of tree species in forest habitats.

Bracken is well adapted to the forest environment. Data show that productivity is maintained under low light levels. When the tree canopy is opened up or removed, above-ground production increases sharply to produce dense swards. Under most tree species (*Pinus*, *Quercus*, *Larix*, *Betula*), the translucent canopies allow for the long term persistence of bracken clones. On the dry sandy soils of The Netherlands, beech (*Fagus sylvatica*) is the only tree species that can completely inhibit bracken growth. The relationship between bracken and ancient forests is mainly historical, and due to the lack of sporal regeneration and low survival of bracken outside the tree canopy cover.

Under favourable conditions, bracken builds a physical structure that strongly reduces light levels available to plants growing under its canopy and smothers plants under collapsing and dead fronds. A field experiment indicated that below-ground competition by bracken is negligible. Species diversity of the forest understorey was negatively correlated with frond biomass.

The slowly decaying litter builds a thick ectorganic soil layer that impedes establishment of light-seeded species. An experiment demonstrated how, besides bulk density and thickness, also the horizontal layering of the organic particles contributes to reduced species establishment on deep ectorganic soil layers. Despite numerous claims that the bracken plant produces substances that are toxic to other plants, experimental evidence did not confirm this allelopathic nature of bracken. A review of the literature suggested that the potential phytotoxicity of bracken is due to the release of compounds that protect the plant against herbivory.

Field experiments showed that voles and mice make preferential use of the protective bracken cover. The increased abundance of rodents resulted in a high seed predation under bracken. The hoarding behaviour of wood mice (*Apodemus sylvaticus*) caused a directed dispersal of seeds towards the bracken structure.

Bracken impinges on all causes of successional change in the vegetation. Tree establishment is blocked unless the clones are physically disturbed. Some implications for forest management are discussed.

Key-words: *allelopathy, bracken, competition, litter,* Pteridium aquilinum, *seed dispersal, seed predation, stagnation, succession.*

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Preface

Bracken fern is often referred to as a lower plant species. 'Lower', however, only concerns the order of appearance of ferns in the evolutionary history of the earth. But there is nothing low about the ecological performance of bracken as it may completely dominate over most higher (but not taller) plants. Unfortunately, cryptogams like bryophytes and pteridophytes receive far less attention in vegetation ecology than is suggested by their presence and abundance in vegetation communities. So, when trying to do ecological research on this group of plants, why not study the most infamous of them all: *Pteridium aquilinum*?

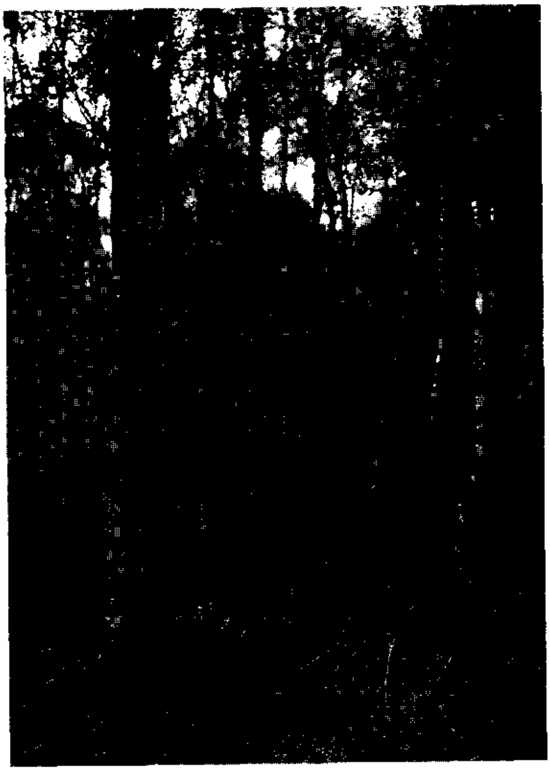
Many studies have already looked into the bracken phenomenon, often initiated by the considerable economical and ecological losses associated with the presence of the species. However, rather than viewing bracken as a problem, I regarded the species as a steppingstone to look in detail at some key ecological processes that occur in plant communities, most notably those that lead to a status quo in forest development. We may learn most of change when there is no change at all.

Trying to grasp the full complexity of ecological interactions between bracken and trees inevitably leads to a multidisciplinary approach. But when taking a broad look, one should always keep an eye on the horizon as not to get dazzled by the multitude of possible pathways that could be followed. Besides, it is very easy to get lost in dense bracken. In this respect I would like to take the opportunity to thank my supervisors, dr. J. Fanta, dr. F. Berendse and dr. F. Bongers, for keeping me on track, the stimulating discussions and their advise during this thesis project.

Parts of this thesis are written in the first person plural because many chapters were prepared in close co-operation with Patrick Hommel, Patrick Jansen, Birgit Janssen, Ruben Smit and Danielle Vogels. I am much indebted by their valuable contributions to this thesis.

Heelsum
5 september 2000

1. Introduction



1.1 Succession

Plant communities are continuously changing. Directional changes in the vegetation are defined as succession. The rate of change greatly depends on the spatial and temporal scale at which one regards the vegetation. On the ecosystem level, changes in overall community structure and composition may remain virtually unchanged over long periods of time. This has given rise to the "climax" community concept of Clements (1916). However, these climax communities are by no means fixed or static entities, but instead will change in both composition and structure due to, for instance, climatic fluctuations, changes in resource availability, colonisation and extinction of species at temporal scales of hundreds to thousands of years (Gleason 1927, Whittaker 1953, Woods & Shanks 1959, Davis 1981).

Viewed on a smaller temporal and spatial scale, however, plant communities are in a constant state of change. Overall, the main driving force behind these changes is the accumulation of biomass and organic matter in the ecosystem. This affects a multitude of system processes, and succession will arise from differential species performance with respect to, for instance, changes in nutrient and water availability (Lawrence 1958, Ovington 1959, Fanta 1982, Tilman 1987, Berendse & Elberse 1990) or overall light availability (Denslow 1980*a*, Brokaw 1987). Also different life history traits of the component species can be an underlying cause of successional change (Gómez-Pompa & Vázquez-Yanes 1981, Botkin 1981, Tilman & Olff 1991, Den Ouden & Alaback 1996), as is differential species availability through seed dispersal and the presence of a seed and seedling bank (Gustafson & Gardner 1996, Van Dorp 1996, Grashof-Bokdam 1997). Finally, herbivory may be an important determinant of successional change (Van der Putten *et al.* 1990, Brown & Gange 1990, Olff *et al.* 1997, Van Wieren *et al.* 1997, Ritchie & Olff 1999).

1.2 Stagnation in succession

Under certain conditions, the vegetation may not change at all for long periods of time. The recruitment of tree species in forests, for instance, may be severely restricted or completely absent, even when light penetration through the canopy is sufficient to sustain plant growth. When the canopy trees die in the absence of recruitment this leads to a treeless stage in forest development. Regeneration failure may be the result of changes in environmental and soil conditions (Walker *et al.* 1981, Bormann & Sidle 1990), herbivory (Smit *et al.* 1998) or interference by other plant species (Eussen 1978, Peters *et al.* 1992). The treeless vegetation that develops due to long term exclusion of regeneration is referred to as stagnant, regressive or retrogressive phases (Clements 1916, Fanta 1982), or plagioclimaxes (Marrs & Hicks 1986, Packham *et al.* 1992) in forest succession.

1.3 Bracken

Bracken fern (*Pteridium aquilinum* [L.] Kuhn) is one of the most intriguing examples of a plant species that can induce stagnation in forest succession (Figure 1.1). Due to its clonal growth, longevity and persistence, bracken can build a dense understory canopy of fronds that may dominate the forest floor vegetation for decades or even centuries (Cody & Crompton 1975, Page 1976, Fanta 1982, Koop & Hilgen 1987, Karjalainen 1989, Ortu a 1999). Such dense bracken may effectively compete for water and nutrients and reduce growth of the canopy trees (Roberts *et al.* 1980, Dutkowski & Boomsma 1990, Richardson 1993). However, the most important consequence for forest dynamics of the presence of a bracken vegetation is its effect on the regeneration of tree species (Fanta 1982, Finegan 1984, Tolhurst & Turvey 1992, Humprey & Swaine 1997).

Figure 1.1: Bracken fern at the edge of an old oak coppice stand at the Valenberg, The Netherlands. The typical tri-pinnate fronds are clearly visible in the foreground. In the background, bracken completely dominates the forest undergrowth.

Under conditions that are favourable for bracken growth, the long term failure of tree regeneration may eventually result in the disappearance of the tree canopy (Fig. 1.2). Such treeless bracken stands occur world wide, for example in Mexico (Ortu a 1999), Italy (Vos & Stortelder 1992), Great Britain (Taylor 1986), North America

(Gliesmann & Muller 1978, Ferguson & Boyd 1988), and Australia (Karjalainen 1989). Often, they have persisted after large scale disturbance events (fire, blow down or anthropogenic forest clearing), as bracken can quickly invade the disturbed sites and prevent new colonisation of trees (Gliesmann 1978, Dolling 1996*a*). Also, bracken may gradually spread from the edges of gaps into the forest, slowly increasing gap size when trees die in the absence of recruitment (H. Koop, unpubl. data).

Figure 1.2: Arial view on a Mexican lowland forest. The light patches are treeless, dense swards of bracken that have established after abandonment of Mayan agricultural fields (see Ortu a 1999: photo taken by F. Bongers).

Under a natural disturbance regime, the shifting mosaic of canopy gaps results in a patchy distribution of bracken in the forest undergrowth. Dominance of bracken on a large scale is often the result of human interference in forest development (Oinonen 1967*b*, Rymer 1976, Taylor 1987, Ortuña 1999). Clear cutting or deforestation often releases bracken from its subdominant position in the forest floor vegetation, and enables it to develop into dense swards. Although bracken is considered a forest species (Page 1976, Rymer 1976), it is well capable to maintain itself outside the forest in many regions. It is usually under such conditions -where bracken can grow unhampered by the forest canopy- that bracken creates problems. Such problems may be related to nature conservation (loss of biodiversity), vegetation management (the loss of certain vegetation types and the failure of tree regeneration) or public health due to the carcinogenic properties of bracken (Evans & Mason 1965, Smith & Taylor 1986, 1995, Thomson & Smith 1990, Pakeman & Marrs 1992*b*).

Due to the lack of efficient control measures, bracken is regarded as one of the world's most troublesome weeds (Oldenkamp *et al.* 1971, Cody & Crompton 1975, Page 1976, Taylor 1986, Karjalainen 1989). It is for this reason that much work has already been done on the biology of bracken, its ecology and control (cf. Smith & Taylor 1986, 1995, Thomson & Smith 1990). The vast majority of this work, however, concerned open habitats. The ecology and role of bracken in forest ecosystems has hardly been assessed (but see e.g. Jones 1947, Roberts *et al.* 1980, Hollinger 1987, Dutkowski & Boomsma 1990, Tolhurst & Turvey 1992, Dolling 1996*a*).

1.4 Aim and outline of this thesis

With this thesis I set out to investigate the role of bracken in the dynamics of forests, in particular how bracken can cause stagnation in forest succession. My main objective is to determine which mechanisms enable bracken to establish complete dominance and block the regeneration of tree species in Dutch forest ecosystems. Further, I want to investigate which factors determine the distribution and local dominance of bracken in The Netherlands, particularly in forests. My second objective is therefore to assess how interactions with the forest canopy affect the presence, growth and productivity of bracken.

I start this thesis with a short introduction on the distribution, biology and ecology of bracken. This chapter 2 is by no means exhaustive, but rather is intended to provide the reader with some relevant background information on this most successful and widespread pteridophyte.

In the next two chapters, I investigate the relationship between bracken and the tree canopy. The productivity and structure of bracken swards under a forest canopy is presented in chapter 3. In this chapter, above ground biomass production of bracken is related to levels of available radiation under different forest canopies.

Additional data are presented from a garden experiment in which bracken was grown under different degrees of shading.

In chapter 4, I investigate the dynamics of bracken stands in relation to forest stand development. I will present data on the dynamics of bracken cover in a managed forest ecosystem using data on bracken distribution in 1958, 1985 and 1996 from the Speulderbos. I will pay special attention to the different modes by which bracken can invade and expand in the forest undergrowth. I hypothesised that, in addition to lateral expansion from the edges of clones, bracken may also expand by means of re-activation of dormant rhizomes.

In the chapters 5-8, I present a number of studies investigating the potential modes of interference of bracken in the regeneration and growth of other plant species. The capacity of bracken to dominate communities and block forest succession has been attributed to a number of mechanisms acting in bracken vegetation. These include shading by the frond canopy (Tolhurst & Turvey 1992, Humphrey & Swaine 1997), physical effects on other plants by decomposing fronds and litter (Frankland 1976, Lowday & Marrs 1992*c*, Humphrey & Swaine 1997), and allelopathy (del Moral & Cates 1971, Gliessman 1976, Horsley 1977, Ferguson & Boyd 1988, Dolling *et al.* 1994). In chapter 5-8, I regard the different modes of bracken interference in the context of forest ecosystems by an analysis of the effects on tree seedlings.

The most prominent mode of interference by bracken is shading by the frond canopy. The frond canopy is supported by an extensive rhizome system. I hypothesised that, in addition to above ground interference, also the below ground parts of bracken affect the growth of other plants. In chapter 5, I present the results of a field experiment investigating the combined effects of above ground and below ground interference by bracken on the performance of tree seedlings.

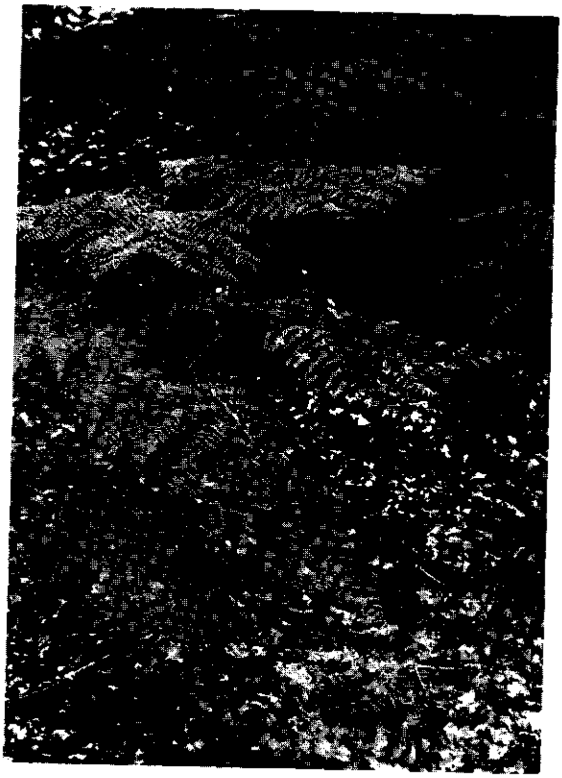
In chapter 6, I investigate the impediment of plant regeneration by the thick ect-organic soil layers that are found under bracken stands. There are numerous studies that have shown that increased thickness and weight of the ectorganic layer result in a decrease in species number and plant biomass. In this chapter I present a study in which I focus on one specific mechanism by which the organic soil horizon interferes with plant growth: the mechanical resistance to root development of newly germinated seedlings. I hypothesised that horizontal layering of the organic particles will result in a smaller effective rooting depth because roots take a route of least resistance. This prolongs the time needed to reach lower soil layers and thus increases susceptibility to desiccation of the seedling.

Allelopathy (chemical interference) has been attributed a dominant role in inhibiting the establishment and survival of plant species in bracken stands (cf. Gliessman 1976). I have conducted a series of experiments to determine whether allelopathy contributes to regeneration failure of tree species in bracken stands. I present the results of a number of these experiments in chapter 7. However, all these experiments failed to demonstrate a negative effect on germination, survival or growth of seedlings due to chemical properties of bracken. I therefore concentrate on the methodologies used in studies into allelopathy, and present the hypothesis that allelopathy is not an active mechanism employed by bracken but rather is a side effect of the chemical defence against herbivory.

Finally, I consider the indirect effects of bracken on tree recruitment through the activity of forest rodents. I hypothesise that the structurally complex bracken vegetation provides habitat to rodents and that bracken presence results in an increased activity and abundance of rodents. In chapter 8, I investigate the possible effects that this higher rodent activity and abundance may have on the regeneration of tree species, mainly concentrating on how bracken influences predation and dispersal of oak (*Quercus robur* L.) by bank voles (*Clethrionomys glareolus* Schreb.) and wood mice (*Apodemus sylvaticus* L.).

In the final chapter 9, I discuss the role of bracken in forest dynamics, and more in particular how bracken can cause stagnation in forest succession. I briefly discuss some aspects of succession theory, and present the hierarchical framework of causes and mechanisms underlying vegetation dynamics as proposed by Pickett *et al.* (1987, 1994). This framework is used to evaluate the role of the different mechanisms of bracken interference, as detailed in the previous chapters, in the recruitment and survival of tree species. Because bracken interference is dependent on the abundance and vigour of bracken, I also discuss the dynamics in bracken stands and the general distribution of bracken in the Netherlands. Finally, I consider some implications for the management of forests where bracken occurs in the understory.

2. Bracken



2.1 General distribution and taxonomy

Bracken is a true cosmopolite, found throughout the world on all continents (except Antarctica) and in almost all climatic zones (Tryon 1941, Page 1976). There is no clear consensus on the taxonomic position of bracken. The genus *Pteridium* has been placed within the Polypodiacaea (Cobb 1963), the Hypolepidaceae (Tutin *et al.* 1964, Page 1976, Heukels & Van der Meijden 1983, Fitter *et al.* 1984) and the Dennstaedtiaceae (Mossberg *et al.* 1992). The genus *Pteridium* is considered to consist of one single, but highly variable species (*Pteridium aquilinum*), divided into 2 subspecies (Tryon 1941): *Pteridium aquilinum* subsp. *aquilinum* and *P. a.* subsp. *caudatum*. The subspecies *aquilinum* occurs in North-America, Eurasia, Africa and Southeast Asia, the subspecies *caudatum* in Southeast Asia, Australia, and South and Central America. Austral bracken (*P. a.* subsp. *caudatum* var. *esculentum*) is often regarded as a different species; *P. esculentum* (Forst. f) Cockayne.

The two subspecies are further divided into several varieties. There is no agreement on the taxonomic position of all the proposed varieties, or whether the varieties should be regarded as subspecies, or even as separate species (cf. Page & Mill 1995). Tryon (1941) distinguished eight varieties within *P. a. aquilinum* and four within *P. a. caudatum*. In Europe, Tryon (1941) distinguished two varieties: *P. a. aquilinum*, and *P. a. latiusculum* (Fig. 2.1).

Figure 2.1: *Pteridium aquilinum latiusculum* in a *Pinus sylvestris - Quercus robur* forest on old river dunes in Eastern Poland. Note the typical horizontal orientation of the lamina.

Recently, Page (1989) and Page & Mill (1995) have proposed the recognition of two more subspecies within *P. aquilinum* in Britain: subsp. *atlanticum* and subsp. *fulvum*. The differences between these subspecies are not at all clear. Due to the large plasticity in frond morphology (see chapter 3), the differences observed may as well reflect environmental differences between habitats, rather than genetic differences between populations of the two proposed varieties (Wolf *et al.* 1995, Dolling 1996*a*). In the Netherlands, to my knowledge, only one variety (*P. a.* subsp. *aquilinum* var. *aquilinum*) occurs. Throughout this thesis, I will not make any distinction between varieties of bracken, and will refer to bracken as *Pteridium aquilinum*. For more information on bracken taxonomy, see Tryon (1941), Page (1976, 1989, 1995), Sheffield *et al.* (1989*b*), Rumsey *et al.* (1991) and Page & Mill (1995).

2.2 The rhizome

Bracken is a rhizomatous fern (Fig. 2.2 and 2.3). The rhizome forms a dense subterraneous network of long shoots that act as storage organs and enable the plant to explore new areas. Attached to the long shoots are the leaf bearing rhizomes or short shoots. The leaf bearing shoots may change into a long shoot and vice versa, giving rise to intermediate rhizomes (Watt 1940, 1976). Occasionally, fronds are also borne directly on the long shoot.

Figure 2.2: The bracken plant, showing fronds, storage rhizomes covered by roots and a short shoot with developing frond. The plant was grown from a piece of rhizome.

Depending on soil conditions, the rhizomes may be found deep (> 50 cm) under the soil surface (Watt 1940, Smith & Lockwood 1990), while the roots may be growing up to one meter deep (Burschel 1953). The rhizome is highly susceptible to anaerobic conditions (Poel 1961), and patterns in soil aeration may greatly determine where bracken can grow (Anderson 1961). Waterlogging of the soil is detrimental to bracken, so it is absent in ecosystems that experience frequent flooding. When soils are wet, or have high ground water tables, bracken may only persist by developing a very shallow rhizome system, with a sparse frond canopy. Heavy soil compaction, for instance under roads, hampers bracken spread and may effectively prevent bracken from crossing roads between forest stands.

At the edges of clones, where new areas are colonised, bracken rhizomes grow deep under the surface (Watt 1940). Frond bearing rhizomes thus start well under the soil surface. Each year a new frond is produced above the old frond. This causes the frond bearing rhizome to slowly grow towards the surface, and ultimately end up in the ectorganic soil layer. In temperate climates, the emergence of the frond tips above the mineral soil makes them susceptible to frost. Locally this may lead to death of parts of the bracken clone, enabling other plant species to invade formerly bracken-dominated areas (Watt 1954, 1955, 1970).

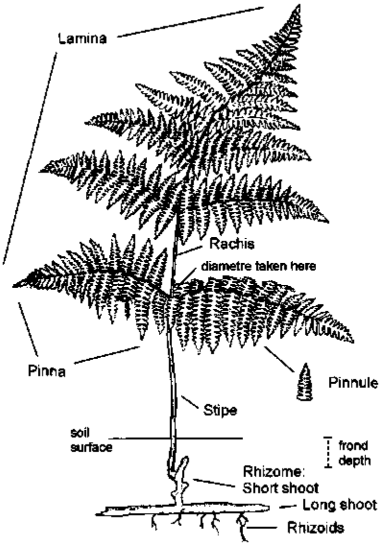


Figure 2.3: The bracken plant: general morphology and used terminology (after Thomson 1990)

The roots are attached to the rhizomes. In well-established plants the root density is notably low, concentrated on the short shoots near the frond base. The plant is highly efficient in re-utilising nutrients, which reduces the need for the plant to invest in structures for capturing soil resources. The roots are often mycorrhizal (Cooper 1976, Jones and Sheffield 1988).

2.3 The fronds

The fronds (leaves) originate from the frond-bearing rhizomes. They are tri-pinnate. In seasonal climates, fronds are deciduous. Leaf shedding may be induced by temperature or by drought at the onset of a dry season (Gliessman & Muller 1978, Dutkowski & Kroemer 1990). In the Netherlands, fronds emerge above the soil surface in late April or early May. Emerging fronds resemble a shepherd s crook (Fig. 2.4), and are appropriately called crosiers. During the unfolding of the frond, the pinnae are formed in pairs along the rachis. It can take several months before the frond has completely developed. The final shape of the lamina is broadly triangular. Fronds are usually between 1-2 meters tall, depending on the developmental stage of the rhizome bearing the frond (Watt 1945, 1969, Marrs & Hicks 1986), resource availability or degree of exposure (Bright 1928). In deep shade the fronds etiolate and when supported by branches of trees and shrubs they can reach 4-6 m in length (Koop & Hilgen 1987).

Figure 2.4: Young emerging frond (crosier).

Figure 2.5: Young sporophyte of bracken, grown from spores on rock wool. Note the strong dissimilarity in leaf-shape from adult fronds.

The spores are born along the edges of the pinnules. Spore production in bracken is highly variable, and related to the energy balance of the plant. High spring and summer temperatures (Kendall *et al.* 1995, Caulton *et al.* 1995) and light availability (Conway 1957, Kendall *et al.* 1995) promote spore production. The spores are very mobile, and may be transported over long distances. After germination, a prothallium develops on which the antheridia and archegonia grow (respectively the male and female reproductive organs). After fertilisation a young sporophyte develops on the prothallium (Fig 2.5). The fronds in this young stage are notably dissimilar to adult leaves. The young sporophyte needs several years to develop into a mature plant. The prothallium and young sporophyte are extremely susceptible to frost and drought. This severely limits the establishment from spores in the Netherlands (see/ 2.5). In humid tropical climates, regeneration from spores appears to be unproblematic (Gliessman 1978, Sheffield *et al.* 1995).

The stipe has special glands are located near the base of the first pair of pinnae. These are called nectaries. Under favourable conditions (high temperature and humidity) the nectaries may excrete a sweet substance that attracts ants. It has been proposed that these glands serve to attract ants that may subsequently attack other insects or arthropods feeding on bracken, thus protecting the plant against herbivory. However, experiments testing this hypothesis have shown that ant activity does not result in lower densities of other insects and arthropods (Heads & Lawton 1984, Rashbrook *et al.* 1992). It has been suggested that this is due to both the relatively low ant density on bracken (Rashbrook *et al.* 1992) and adaptations of bracken-specialised insects to ant predation (Heads & Lawton 1984). In north-western Europe insect herbivory hardly ever leads to extensive defoliation of bracken, which can be related to the extensive chemical defence of the plant (Lawton 1976).

2.4 The growth cycle

The start of the bracken growing season is determined by accumulated degree days above a threshold temperature (Watt 1969, Ader 1990, Pitman & Pitman 1990*a*). The occurrence of frost is lethal to frond tissue, so in temperate climates the growing season for bracken is defined by the period between the last spring frost and the first frost in autumn (Watt 1969, 1976, Ader 1990). In the Netherlands, fronds emergence generally starts in early May. Due to the moderating effect on temperature by the forest canopy, frond emergence starts earlier in forests than in more exposed sites.

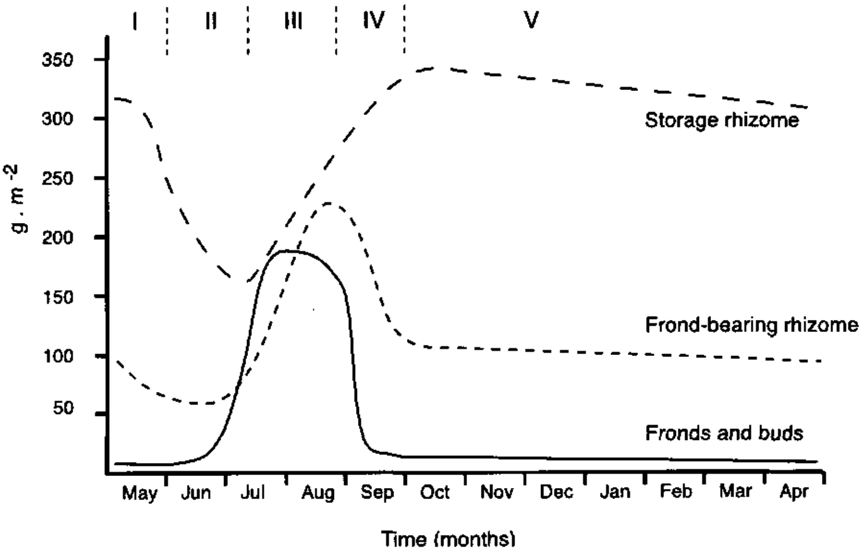


Figure 2.6: The growth cycle of bracken, showing seasonal changes in reserve carbohydrates of the storage rhizome (long shoot), the frond bearing rhizome (short shoot) and fronds and buds (taken from Williams & Foley 1976). Roman numbers indicate the five growth phases distinguished by Williams & Foley (1976).

The large amount of reserve carbohydrates that is stored in the rhizomes enables bracken to quickly build an extensive frond canopy. Stored reserve carbohydrates may represent 25-35% of the dry matter content of the rhizomes (Müller-Stoll & Michael 1949, Williams & Foley 1976). This large energy reserve makes bracken rhizomes an important winter food resource for wild boar (*Sus scrofa* L.) in the Netherlands (Groot Bruinderink *et al.* 1994). The development of the frond canopy and concurrent changes in carbohydrate content of the rhizome and fronds shows a distinct annual cycle.

The annual growth cycle can be separated into several stages (Williams & Foley 1976: see Fig. 2.6). In the early stage (II) of frond development, the expansion of the fronds is supported by the rhizome system, which is accompanied by a sharp drop in carbohydrate reserves of the storage and frond-bearing rhizomes (Fig. 2.6). Approximately 50% of the stored carbohydrates is translocated from rhizomes to the fronds (Müller-Stoll & Michael 1949, Williams & Foley 1976). After the first pairs of pinnae have unfolded (stage II-III), frond expansion is increasingly supported by photosynthates produced by the fronds themselves. During the subsequent period (stage III), the rhizome shifts from acting as a source to function as a sink of carbohydrates, and a net flux of carbohydrates is directed towards the rhizome, replenishing reserves and supporting growth of new tissue (Müller-Stoll & Michael 1949; Williams & Foley 1976). Marrs *et al.* (1993) showed that frond biomass production is approximately linearly related to rhizome biomass. Pitman & Pitman (1990*a*) showed that the rate of frond expansion was directly related to incident irradiation.

2.5 Dispersal and colonisation

In the Netherlands, regeneration from spores is severely limited, most likely due to the frequent occurrence of dry periods and frosts, which are lethal to the prothallium and young sporophyte (Conway 1949, 1953). Reports of new establishments of bracken from spores are extremely rare. Young sporophytes have been reported in only a few instances. In north-western Europe, establishment from spores was reported on the rubbles of bombed houses in Great Britain during the second world war (Braid & Conway 1949; cited in Conway 1953), on stone walls (Conway 1953) and in the damp entrances of rabbit burrows (Farrow 1915).

Fire appears to promote regeneration from spores (Oinonen 1967*a*, Gliessman 1978), but it is not clear what brings about this relationship. The occurrence of fire appears not to be important in terms of providing a sterile substrate. Although the development of the prothallium may be limited by micro-fauna and fungi (Conway 1953), especially on basic soils (Conway & Stephens 1956), experiments showed that the prothallium and young sporophyte are not particularly susceptible to fungal attack (Hutchinson 1976). The short-term release of nutrients and raise of pH may provide good opportunities of prothallial and sporeling development on recently burned areas (Conway 1949, Evans & Conway 1980).

Spore production is highly variable (Conway 1957, Kendall *et al.* 1995), but spore availability is not a limiting factor for regeneration potential (Dyer 1990, Caulton *et al.* 1995). Although Dolling (1996*a*) reported very low viability and germination of bracken spores in Sweden, germination potential of bracken spores is high at lower latitudes (Schwabe 1951, Conway 1953, Hutchinson 1976, Sheffield *et al.* 1993, Sheffield 1994). In The Netherlands this is illustrated by the problems that bracken creates in the greenhouse cultures of roses, where bracken spores easily germinate and grow into adult plants in the continuously moist and nutrient-rich growing substrate. In the greenhouses, bracken may quickly spread and completely overgrow the roses (pers. observ.).

During my research I have looked intensively for young sporophytes, but never encountered them in the field. On the high Pleistocene sandy soils in the Netherlands, on only a very few locations (Hoge Veluwe, Amerongse Berg) I encountered circular bracken clones that must have originated from a recent introduction from spores. The habitats where new establishments frequently occur are found directly along the coast (on dikes or old sand flats: De Zilk, Dintelse Gorzen, Kuinderbos: Bremer 1980) or on dikes in moors. These habitats may be favourable for survival of the prothallium and young sporophyte because of the moderating effects on temperature by large bodies of water, and higher air and soil humidity.

The fact that no young sporelings were found doesn't mean that regeneration from spores never occurs. The failure to find gametophytes in field surveys is a feature that bracken shares with many other fern species (Dyer 1990, Peck *et al.* 1990). There are several reports from the British isles and elsewhere of recently established bracken clones, presumably from sporal regeneration (Dyer 1990). Furthermore, isozyme and DNA-analysis has shown that populations of bracken generally consist of many different genotypes, indicating multiple establishment events from spores (Wolf *et al.* 1988, Parks & Werth 1993).

Because of the very limited extent of sporal regeneration, bracken is mainly dependent on vegetative expansion to colonise new habitats. Lateral expansion by rhizomes differs between habitats and ranges between 0.2 and 1 $m \cdot y^{-1}$ (Watt 1940, Oinonen 1967*a,b*, Marrs & Hicks 1986, Lawrie *et al.* 1992). Under certain conditions, lateral expansion may be much more rapid, for instance when old and decayed rhizomes are present in the soil that have left tunnels through which new rhizomes can penetrate without experiencing mechanical resistance from the soil (Dolling 1996*a*), or growing in low bulk-density substrate (Fletcher & Kirkwood 1979, Lawrie *et al.* 1992). Owing to the persistence and longevity of bracken, individual clones may spread over large areas. Isozyme and DNA analyses have shown that *fronds growing 390 -1015 m apart were from the same genetic individuals* (Sheffield *et al.* 1989*a*, Parks & Werth 1993). Depending on the annual rate of expansion, the maximum age estimates of individual clones range to over a thousand years (Sheffield *et al.* 1989*a*, Parks & Werth 1993). This ranks bracken among the oldest and largest living organisms on earth.

2.6 General ecology and distribution in The Netherlands

Bracken is mostly found on well-aerated, acid soils (Watt 1976, Page 1976). The dominant soil types on which bracken is found comprise brown earths and brown podzolic soils and peaty podzols (Miles 1985, Thompson *et al.* 1986), but it is also found on calcareous soils (Page 1989, Wolf *et al.* 1995). Nutrient requirements are relatively low (Page 1976). Experimental addition of nitrogen hardly increases performance of bracken (Whitehead *et al.* 1995, Dolling 1996*b*, Werkman *et al.* 1996). Bracken productivity appears to be mostly limited by phosphorus: addition of P-fertiliser significantly increases bracken performance (Daniels 1986, Whitehead *et al.* 1995). Bracken is able to mobilise inorganic phosphate, which may raise P-availability in soils underneath bracken (Mitchell 1973). The efficient translocation of nutrients before leaf shedding and rhizome death, and accumulation of nutrients in the rhizome makes bracken well adapted to growth in nutrient deficient soils (Evans *et al.* 1990). Concurrently, leaching of nutrients from the bracken litter and frond canopy greatly contributes to the nutrient cycle in forest, in particular with respect to potassium (Carlisle *et al.* 1967). Its predominant occurrence on acid, podzolised soils is associated with a tolerance to high Al-concentrations in such soils (Koedam *et al.* 1992)

Figure 2.7: The occurrence of bracken in kilometre squares in The Netherlands. The Pleistocene sands and coastal sand dunes are indicated in grey. Source: FLORBASE-2a, Floron, Leiden (bracken distribution), Landschapsecologische Kartering Nederland (soils).

Bracken is a common plant in the Netherlands (Fig. 2.7). It is present in approximately 7% of the kilometre squares that cover the country (Table 2.1). The presence of bracken is mainly concentrated on the Pleistocene sands in the eastern, middle and southern part of the country. Of all kilometre squares were bracken was recorded, 78.5 % had sandy soils as dominant soil type (Table 2.1). It is rare in the western parts, except for a narrow strip of old coastal dunes (Fig. 2.7).

The Pleistocene sands include a large variety of soil types, depending on the origin and nature of the parent material and former land use. The brown podzolic earths represent the most common soil type on which bracken is found (see also Cody & Crompton 1975, Thompson *et al.* 1986). These are acidic, relatively nutrient poor sands with a deep ground water table (> 2m). Such soils are closely related to the long term presence of a forest vegetation. In the Netherlands, bracken is hardly ever found outside the influence of a tree canopy, except on sites with a sufficient water holding capacity like loess deposits (Fig. 2.8), sandy soils with a high loam contents or on peat moors. The close correlation between the presence of bracken and brown podzolic earths has made bracken an indicator species of old forest soils (see 4.4.1), and its associated vegetation types, most notably the Fago-Quercetum (Westhoff & den Held 1969, Stortelder *et al.* 1999).

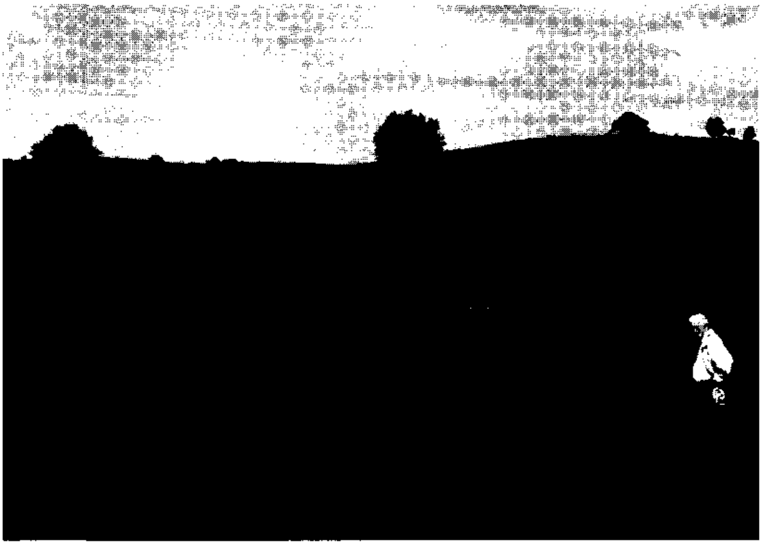


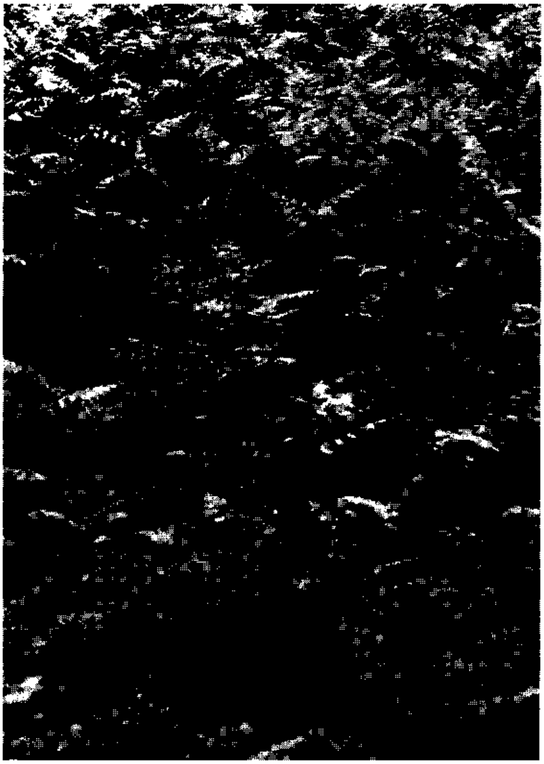
Figure 2.8: A patch of bracken on a local loess deposit in the Posbank (south Veluwe, The Netherlands). This is one of the few areas in The Netherlands where bracken has persisted outside the protection of a tree canopy.

Table 2.1: The distribution of bracken over major soil groups in the Netherlands. Data represent the number of kilometre squares in which a soil group is dominant, and the number of squares in which bracken is present in the flora.

Major soil groups	Kilometre squares		Bracken presence	
	total [1)]	%	total [2)]	%
Pleistocene sands	14961	36.1	2266	78.5
Loess	481	1.2	96	3.3
Old clays and loam	417	1.0	80	2.8
Dune- and marine sands	1286	3.1	75	2.6
Peat	3170	7.6	71	2.5
River clays	2988	7.2	65	2.3
Marine clays	8498	20.5	35	1.2
Open water	6466	15.6	23	0.8
Rest (no soil type defined)	3191	7.7	174	6.0
Total	41458	100.0	2885	100.0

1. Source: Landschapsecologische Kartering Nederland (Bolsius & Eulderink 1994)
2. Source: FLORBASE-2a, Floron, Leiden

3. Productivity of bracken under a forest canopy



This chapter is based on:
den Ouden, J. (in review) Productivity and ecological functioning of bracken (*Pteridium aquilinum*) under a forest canopy. I. The relationship between bracken frond production and canopy shading.

3.1 Introduction

Bracken occurs naturally in forests, or along forest edges (Rymer 1976, Watt 1976), but is equally well able to persist, and even expand, after forest clearance. When the tree canopy is removed, bracken productivity may greatly increase, causing the fern to form dense, single-species stands that cause regeneration failure of most vascular plant species normally occurring on the site. Coupled with the difficulties to control bracken, the blocking of (forest) succession creates serious problems in forest and nature management world-wide (Jones 1947, Fanta 1982, Koop & Hilgen 1987, Pakeman & Marrs 1992*b*). Because bracken creates problems on a large scale (Taylor 1986, 1995), especially when the forest canopy is removed either temporarily or permanently, much research has been focused on the biology and control of bracken (cf. Cody & Crompton 1975, Watt 1976, Karjalainen 1989, Lowday & Marrs 1992*a,b*, Dolling 1996*a*). However, the majority of these studies dealt with bracken growing in open areas, and relatively little attention has been directed towards its behaviour and biology in its natural forest habitat (cf. Roberts *et al.* 1980, Dutkowski & Boomsma 1990, Tolhurst & Turvey 1992, Dolling 1996*a*). In the forest undergrowth, environmental conditions are highly different from open habitats in terms of incident radiation, water availability, temperature, etc. It is therefore likely that interactions with the forest canopy result in different behaviour of the bracken plant, and its subsequent effect on the rest of the forest floor vegetation, with respect to unshaded and more exposed environments.

The tree canopy can have a number of effects on the growth and productivity of bracken. Since frond emergence is correlated with accumulated degree days (Ader 1990, Pitman & Pitman 1990*a*), the moderating effects on temperature by the canopy leads to earlier frond emergence in forests (pers. observ.), effectively prolonging the growing season. The forest canopy may also intercept a significant proportion of the incident rainfall. With tree roots also taking up part of the remaining soil moisture, less water is available for bracken growth. Combined with the high transpiration rates from bracken canopies relative to the tree canopy (Roberts *et al.* 1984), this may lead to soil moisture stress and reduce bracken productivity.

Yet, the most important effect of the forest canopy is the reduction of incident radiation to the forest floor, which will directly reduce net production of bracken in the forest undergrowth. In this chapter, I present a study on the above-ground production of frond biomass of bracken in relation to the presence of a forest canopy. The objective of this study was to determine how the light intensity under a forest canopy affects biomass production and dimensions of bracken fronds. This was done by measuring standing above-ground biomass in a number of stands representing different canopy tree species and light availability, and in a garden experiment in which bracken was grown under different levels of shade. The relationship between light availability and above-ground biomass production will be compared with a previously published simulation model of bracken growth (BRACON; Pakeman *et al.* 1993, 1994, Pakeman & Marrs 1994).

3.2 Methods

3.2.1 Study area and site selection

This study was conducted in the Speulderbos, a forest in the central part of the Netherlands (52°16'N, 5°40'E). The climate is temperate oceanic, with a mean annual temperature of 9.4 °C, and mean annual rainfall of 800 mm (Krijnen & Nellestijn 1992). Soils are all derived from pre-glacial fluvial deposits, tilled during the Saalien ice-age. All soils can be typified as brown podzolic earths, with great variation in texture due to the complex geomorphogenesis of the area (Mekkink *et al.* 1986). See chapter 4 for a more detailed description of the study area.

A total of 13 study sites were selected to represent different tree canopy species. They included 5 stands of Japanese larch (*Larix kaempferi* [Lamb.] Carr.), 4 former oak coppice stands, dominated by English oak (*Quercus robur*) with some interspersed Birch (*Betula pendula* Roth), 3 stands of Scots pine (*Pinus sylvestris* L.), and one site without a tree canopy, in a 12 year old clearing in former oak coppice, and completely dominated by bracken (see Table 3.2).

3.2.2 Biomass sampling

Bracken frond production was sampled in the summer and early autumn of 1995. In each stand, a 10mx20m plot was laid out in an area dominated by bracken. It was not feasible to measure frond biomass production directly from harvesting whole plots because of the large bulk of biomass being produced in the stands and limited access to drying stoves. Therefore, frond biomass of bracken was estimated using a double sampling technique. From each site, 15-20 fronds were collected to be used for the construction of biomass regression equations relating frond dry weight to frond dimensions. Fronds were selected to represent the entire range of frond sizes present on the site. Each frond was pulled out of the ground, so total frond length included the subterraneous part of the stipe between rhizome attachment and soil surface (further referred to as frond depth; see Fig. 2.3). Measurements on each frond included total frond length, length of the stipe, frond depth, and diameter of the rachis, 2 cm above the first pair of pinnae (Fig. 2.3). In an earlier study by Gholz *et al.* (1979), biomass regression equations were developed for bracken using the diameter of the basal part of the stipe, near the soil surface. A pilot study (Den Ouden, unpubl. data) showed that using the basal diameter resulted in less accurate biomass estimates because of the high variability in basal diameters, which was due to thickening of the lower part of the stipe caused by stem boring caterpillars of *Paltodora cystella* Curt. (Lawton 1976). This variation could be avoided by taking the more stable diameter above the first pair of pinnae. A similar approach was used by Tolhurst & Turvey (1992), who developed regression equations on frond biomass and leaf area using the diameter of the stipe just below the bottom pinnae. Each frond was dried for 24 h at 80 °C to determine dry weight.

Additionally 10 fronds per stand were collected in five stands in 1996 to compare regression equations between subsequent years. Plants were separated into structural tissue (stipe and rachis), and leafy tissue (pinnae) to develop regression equations for estimating leaf biomass. Also, one pinna was taken from the middle of each frond and total leaf area was determined using a JVC TK-S310 video camera, connected to a Delta-T Image Analysis System (Eijkelkamp, Giesbeek, the Netherlands). Pinnae were dried for 24 h at 80 °C. Specific leaf area (SLA) was calculated as leaf area per unit dry weight, and combined with pinnae biomass to estimate total leaf area. Leaf Area Ratio (LAR) was calculated as the ratio between total leaf area and total frond biomass. Rhizome and root biomass was not included in this ratio.

Using the developed biomass regression equations, estimates could be made of total frond biomass for all study sites. Per site, 10-28 plots (see Table 3.2) of 1 m^2 were randomly selected in August 1995. Measurements on all living fronds emerging from these plots included total frond length, length of the stipe, rhizome depth, and diameter of the rachis 2 cm above the first pair of pinnae. Estimates of mean frond biomass per site were obtained by applying regression equations to data on individual fronds, pooling all fronds per plot to obtain biomass per 1 m^2, and averaging this per site.

3.2.3 Estimation of available radiation

In order to estimate the percentage of available light under the forest canopy, 15 hemispherical photographs were taken 1.5 m above the soil surface, at random locations in each of the 200 m^2 plots (Fig. 3.1). Photographs were taken in July, at maximum canopy shading. A Canon Ti70 camera, with a Canon 7.5 mm/5.6 Fisheye lens was used. The black and white photographs were digitised, and analysed using Winphot (Ter Steege 1993), with data on percentage of sunshine obtained from 30 year averages from the nearest weather station (Krijnen & Nellestijn 1992). This yielded daily estimates of total percentage of radiation available on the forest floor. These estimates were averaged over the period May-September to obtain mean percentage radiation per sample point, and then the mean over all 15 points was taken as an estimate of total percentage of radiation available on the site (assuming a constant leaf cover).

3.2.4 Garden experiment

I set up a garden experiment to determine the response of bracken to changes in light levels available to the plant under controlled conditions. Blocks of soil containing rhizomes were transplanted to the university gardens. Fronds emerging from these blocks were exposed to different shading treatments.

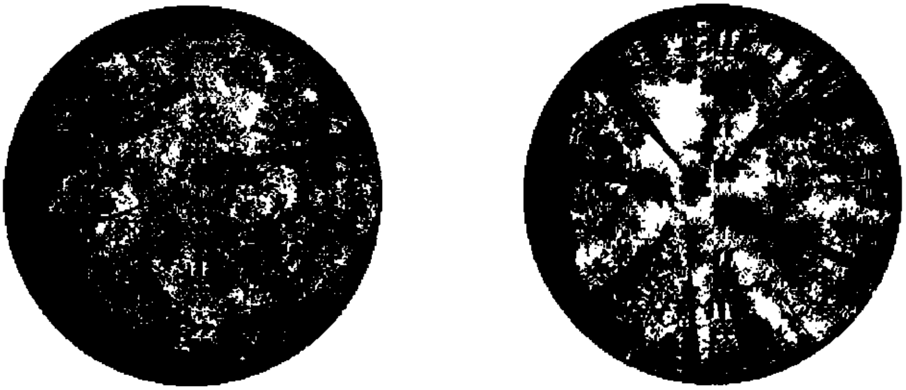


Figure 3.1: Fisheye photographs taken in stands of *Quercus* (left) and *Larix* (right). Percentages of light transmitted through the canopy are 14% and 31% respectively.

In March 1995, 24 soil blocks containing bracken rhizomes were collected from the open site (no forest canopy), two months before the start of the bracken growing season. Blocks of soil, 50cm x 50cm x 20cm, were cut and placed in a wooden frame that secured the sides and bottom of the soil blocks. These blocks, including the wooden frame, were placed in a garden bedding, in three groups of eight blocks, consisting of 2 rows of 4 blocks, with 1 m between blocks. The soil blocks were then surrounded by a 30 cm layer of sandy garden soil, and covered by a 10 cm deep layer of garden peat on top of the blocks (Fig. 3.2).

Shade treatments were established by constructing a 2.5 m high wooden frame that supported shade netting which reduced light levels to 14% and 7% of the total radiation available to the control treatment (no shading). Each of the shade treatments was applied to an entire group of 8 blocks, so this set-up resulted in pseudoreplication with respect to shading. The plants were watered regularly in dry periods during the summer.

Bracken was allowed to grow for three years. In the winter, plots were covered with wheat straw to prevent freezing of the soil. Fronds were cut, and counted, at the end of September of each year, before leaf senescence. In 1995 and 1996, total frond length and above-ground length of the stipe was measured for all fronds. Frond biomass was determined per plot, with fronds separated into leafy biomass (pinnae) and structural biomass (stipe and rachis). In 1997, only total frond biomass was determined. Fronds were dried for 24 h at 80 ¡C prior to weighing. In 1996 and 1997, a pinna from one randomly selected frond per block was collected, and specific leaf area was determined as described above.

Figure 3.2: The garden experiment investigating bracken productivity in controlled shade treatments. In the foreground the 100% light treatment with emerging fronds

3.2.5 Modelling bracken growth

The bracken growth model BRACON (Pakeman *et al.* 1993, 1994, Pakeman & Marrs 1994) was used to estimate the effect of light conditions under a forest canopy on the above ground production of fronds in bracken stands. This mechanistic model calculates daily changes in the amount of stored carbohydrates and tissue biomass of the rhizome. Based on the annual growth cycle of the bracken plant (Williams & Foley 1976; see Fig. 2.6), carbon assimilation and respiration is calculated using a number of physiological and environmental parameters. The build up and senescence of the frond canopy are initiated by changes in temperature. Frond production is calculated from the amount of incident radiation, and rules on partitioning of carbohydrates between rhizome and fronds. Maximum frond biomass is assumed by the model to be linearly related to carbohydrate reserves in the rhizome. The model may be run for any number of years, producing estimates on the yearly cycle of change in the bracken plant, and produces estimates of the equilibrium biomass reached under the given climatic conditions (Pakeman *et al.* 1994).

In order to compare the estimates on biomass production by BRACON with data obtained in this study, a number of climatic parameters were adjusted. Climatic data were obtained from 30-year averages from the nearest weather station (Table 3.1). Sensitivity analyses of the model (Pakeman *et al.* 1994) showed that the values of the light extinction coefficient (K) of the fronds, and the ratio between frond biomass and frond area (z), had a great influence on the estimates of rhizome and frond biomass reached at equilibrium. In this study, K was set to 0.425 (Pakeman *et al.* 1994). The frond biomass/area ratio (z) was calculated as the reciprocal value of LAR (see above), and compared with previous published values of z in Pitman & Pitman (1990*a*). The effects of shading by the forest canopy was studied by running the model under different irradiation levels, expressed as the percentage of available light under the canopy relative to the open. Estimates were compared with actual data on frond biomass.

Table 3.1: Environmental parameters used in BRACON to model bracken productivity, based on data between 1961-1990 from weather station De Bilt.

Parameter	Value	Unit	Reference[1].
January soil temperature at 30 cm	4.3	°C	1
July soil temperature at 30 cm	17.0	°C	1
June Mean daily global irradiation	17.9	$MJ\cdot m^{-2}$	2
December mean global irradiation	1.8	$MJ\cdot m^{-2}$	2
Mean date of last spring frost	130.0	Julian days	2
Mean date of first autumn frost	283.0	Julian days	2
Mean yearly potential transpiration	542.2	mm	2
Mean transpiration August	78.3	mm	2

1. References used:
   1 = Jilderda (data at Royal Dutch Meteorological Institute).
   2 = Krijnen & Nellestijn (1992)

3.2.6 Data analysis

Biomass regression equations were developed with regression analysis using the SPSS (v. 7.0, 1996) statistical package. Biomass data were $\log_{10}$-transformed prior to analysis. Regression models were developed initially with diameter and length as independent variables. Stepwise linear regression with backward elimination was used to determine the best explaining regression model. The effects of sampling year and site on equations were tested using analysis of covariance (ANCOVA) after checking for homogeneity of slopes using linear regression with dummy variables for sampling year or site (Sokal & Rohlf 1995).

Total frond biomass was calculated by applying the biomass regression equations to data of individual fronds, after correcting the intercept of the regression equation for log-bias (Baskerville 1972). Resulting estimates of biomass and leaf area per site (n=13) were regressed against the available percentage of radiation using non-linear regression. Most appropriate regression models were determined using Cademo (v. 3.12, 1997), with minimal residual variance as selection criterion. Final regression parameters were estimated using non-linear regression in SPSS (v. 7.0, 1996).

Data on total frond biomass ($\log_{10}$-transformed), number of fronds, and mean biomass and length per frond from the garden experiment were analysed using a repeated measures model ANOVA, with light treatment as independent factor.

3.3 Results

3.3.1 Biomass regression equations

Stepwise linear regression with backwards elimination showed that the diameter of the rachis was the best explaining variable to predict dry weight of an individual frond, and addition of frond length in the model did not significantly reduce residual variance of the regression model. Also, frond diameter and length were highly correlated ($n = 236$, $r = 0.841$; $P < 0.001$). Including both variables in the model would introduce problems associated with collinearity (cf. Petraitis *et al.* 1996). Therefore, regression models were used with diameter as the only independent variable.

There was a small significant effect of sampling year ($F_{1,128} = 4.19$; $P = 0.043$) on the regression equation for the 5 sites sampled in 1995 and 1996. However, this effect was due to differences in frond weight at the lower range of diameters. When these small fronds (diameter <5 mm) were omitted from the data set, no significant differences were found between regression equations from both years ($F_{1,103} = 0.66$; $P = 0.418$). Such small fronds only formed a minor proportion of fronds encountered in the plots. This means that regression equations may be developed for use over different years.

There were significant differences between regression equations developed for individual sites ($F_{12,222} = 9.76$; $P < 0.001$). Post hoc comparisons showed that most differences occurred between equations derived from different stand types (data not shown). Therefore, data were pooled by stand type, and group equations were developed separately for *Pinus, Larix,* and *Quercus* stands, and the site without tree canopy (Fig. 3.3). The slopes of the regression equations were not affected by stand type, but intercepts were significantly different between stand types ($F_{3,\,231} = 21.65$; $P < 0.001$). The level of the regression lines did not bear any relationship with light levels in the stands, nor were the differences in levels of the regression equations associated with changes in the architecture (ratio length/diameter) of the fronds, although fronds growing in *Pinus* stands showed a significantly ($P = 0.006$) higher ratio in the length/diameter as compared with *Larix* stands. Because no direct functional relationship could be discerned between stand type and regression parameters, and because regression lines were similar in slope, an overall regression equation (EQ. 3.1) was calculated using data from all sites pooled together (n= 236) to estimate frond weight from diameter of the rachis:

$$\text{Log}(W) = -0.177\ (\pm 0.045) + 2.019\ (\pm 0.057) * \text{Log}(D) \qquad R^2 = 0.84 \qquad \textbf{[3.1]}$$

with W = dry weight (g) of a frond, D = diameter (mm) of the rachis 2 cm above the first pair of pinnae, and parameter estimates from linear regression (± 1 se.).

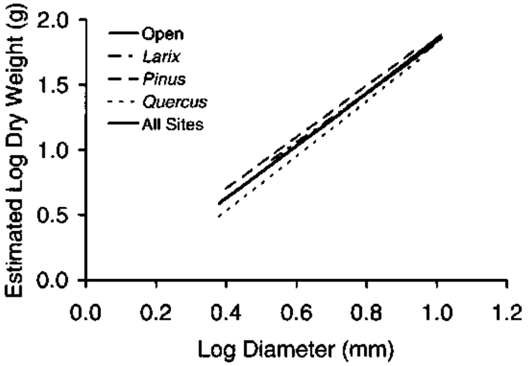


Figure 3.3: ` Regression equations relating rachis diameter to frond biomass, using pooled data per tree canopy species. Data points are not shown for clarity.

3.3.2 Frond production

Total frond biomass was related to the percentage of available radiation on the sites (Fig. 3.4a). There was considerable variation in total biomass between stands at the lower ranges of available light (Fig. 3.4a), which was due to variation in both size and number of fronds produced per m^2 (Table 3.2). Total biomass showed a strong relationship with the number of fronds per m^2 produced on a site, with the exception of one *Pinus* site (Fig. 3.5a). Multiple linear regression showed that mean biomass per frond was positively related to available light on the site (B = partial regression coefficient = 0.697, $t = 11.9$, $P < 0.001$), but negatively related to the number of fronds in the plot ($B = -0.378$, $t = -6.5$, $P < 0.001$), which indicates density dependence of individual frond biomass. Mean frond length was positively correlated with available radiation ($r = 0.608$, $n = 13$, $P = 0.027$).

Table 3.2: Means (± 1 se.) of measured variables in 10m x 20m plots containing bracken in the forest undergrowth. Frond biomass and leaf area were estimated from regression equations (see § 3.3.1).

Canopy species	Stand age (yr)	n	Light (%)	N fronds per m^2	Frond length (cm)	Diameter rachis (mm)	Frond biomass ($g \cdot m^2$)	Leaf area ($m^2 \cdot m^{-2}$)
Open	(-)	10	100	15.4 ± 4.5	245 ± 12	8.2 ± 0.4	731.1 ± 175.8	5.4
Larix	49	19	38	8.1 ± 2.4	241 ± 23	7.4 ± 0.5	313.5 ± 93.4	6.1
Larix	45	20	37	8.5 ± 2.3	216 ± 19	7.3 ± 0.4	316.5 ± 81.9	5.4
Larix	46	23	34	6.1 ± 1.7	203 ± 22	6.9 ± 0.6	207.7 ± 68.5	4.0
Larix	37	24	27	6.2 ± 2.0	193 ± 14	5.7 ± 0.5	136.8 ± 43.7	2.6
Larix	36	25	13	6.4 ± 1.9	165 ± 17	6.2 ± 0.5	175.9 ± 58.9	4.0
Pinus	44	22	23	7.0 ± 2.3	210 ± 13	6.8 ± 0.4	234.2 ± 90.1	6.1
Pinus	30	28	21	3.1 ± 1.4	213 ± 67	6.4 ± 2.0	101.9 ± 56.3	2.6
Pinus	35	20	18	12.9 ± 3.0	129 ± 13	4.4 ± 0.3	177.8 ± 50.0	4.2
Quercus	57	26	8	3.4 ± 2.0	174 ± 56	5.5 ± 1.8	79.4 ± 46.4	2.0
Quercus	49	26	6	3.7 ± 1.6	216 ± 48	6.9 ± 1.5	135.4 ± 67.1	3.1
Quercus	50	21	16	3.9 ± 1.7	176 ± 25	6.1 ± 0.7	104.4 ± 56.3	2.2
Quercus	51	24	12	4.4 ± 1.5	136 ± 33	4.9 ± 1.1	79.7 ± 27.9	1.4

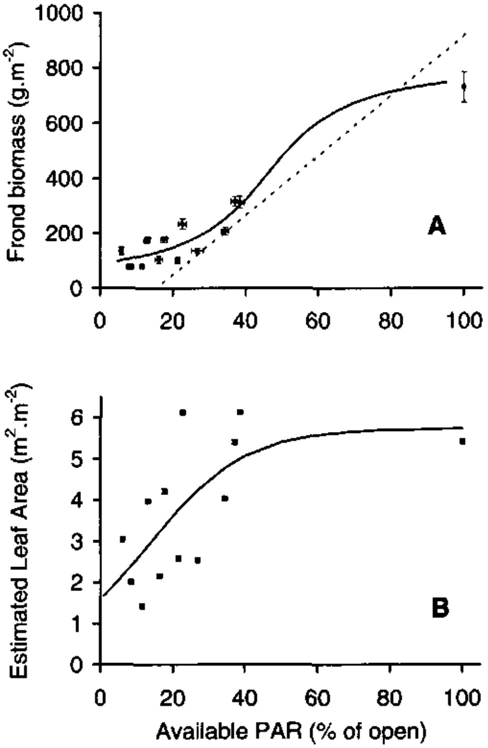


Figure 3.4: Peak frond biomass (A) and total estimated leaf area (B) of bracken in relation to light availability under a forest canopy (as percentage of photosynthetically active radiation (PAR) relative to the open) for the 13 study sites. Solid lines represent non-linear regressions of frond biomass and LAI vs. available radiation. The dashed line in A represents the modelled peak biomass estimates with changes in available radiation from the bracken growth model BRACON. Data points represent means per site. Error bars are 1 standard error.

Used non-linear regression equations were:

A: $W = 833/2 * (1 + 2/\pi * \tan^{-1} (0.062 * (RAD - 45.9)))$ $R^2 = 0.91$
B: $LAI = 5.74 / (1 + 2.58 * e^{-0.074 * RAD})$ $R^2 = 0.45$

with W = total frond biomass in $g{\cdot}m^{-2}$, LAI = Leaf Area Index in $m^2{\cdot}m^{-2}$, and RAD = percentage of available radiation (PAR).

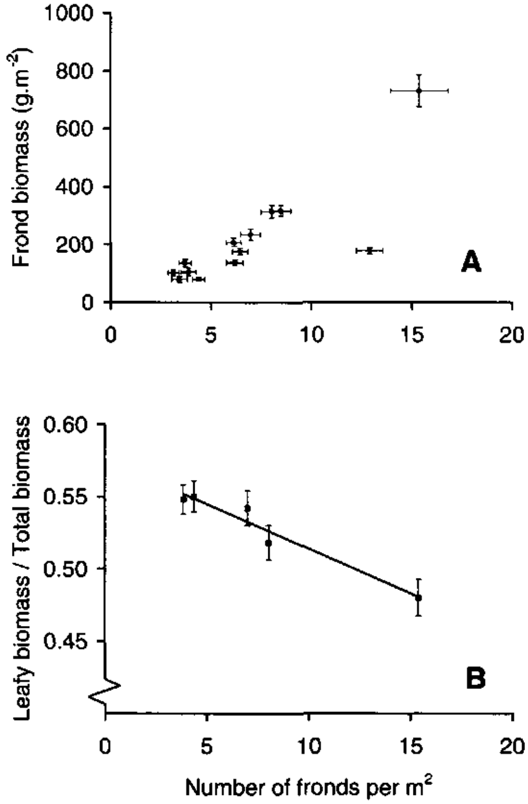


Figure 3.5: Peak frond biomass (A), and the ratio between leafy biomass and total frond biomass (B) in relation to the mean number of fronds in bracken stands under a forest canopy. Error bars represent 1 standard error.
Regression equation in (B):

RATIO = 0.576 - 0.0062 * NFR $R^2 = 0.93$, n = 5

with RATIO = leafy biomass / total biomass, and NFR = mean number of fronds.

To estimate total leaf area, regression equations were constructed relating diameter of the rachis to biomass of leafy tissue (pinnae). It was not possible to determine a straightforward relationship between these two variables, because there were great differences between regression equations from different sites (data not shown). As an alternative, the mean percentage of leafy tissue biomass was calculated relative to total weight of the frond (Fig. 3.5b). This ratio was correlated negatively with frond density, indicating increased self-shading of the lower pinnae at higher frond densities (Fig. 3.5b). Specific leaf area showed a strong decline with increasing light intensities (Fig. 3.6a). SLA of bracken growing in the forest clearing was more than 3 times lower than bracken growing in a stand with 11% light available. The ratio between leafy biomass and total biomass, and SLA, were regarded as site specific, so total leaf area (LA) was calculated as

$$LA = W_t * (L/T) * SLA \qquad \textbf{[3.2]}$$

with W_t = mean total frond biomass per site in $g{\cdot}m^{-2}$, L/T = ratio between Leafy tissue biomass and Total frond biomass in $g{\cdot}g^{-1}$ estimated from regression against frond density (Fig. 3.5b), and SLA = Specific Leaf Area in $m^2{\cdot}g^{-1}$, estimated from regression against available percentage of radiation (Fig. 3.6a).

Total leaf area per m^2 showed a strong increase with increasing light intensity at lower light levels, levelling off at higher light availability (Fig. 3.4b). Maximum leaf area was 6.1 $m^2{\cdot}m^{-2}$.

3.3.3 Garden experiment

Shading reduced the total biomass of fronds produced with respect to the unshaded control (Fig. 3.7a). Initial differences between treatments in 1995 were small, with the fronds receiving 7% of the available radiation producing significantly less biomass ($P < 0.005$) than the 14% and 100% treatments. In subsequent years, the differences in biomass production between treatments became more pronounced, while biomass per treatment gradually increased over time. Total biomass in 1997 was significantly different between all three light levels. By this time, total biomass in the plots receiving full light was 688 ± 50 g per 0.25 m^2 (within-plot mean ± 1 se.). In the biomass sampling of the forest stands in 1995, the open site supported 731±176 $g{\cdot}m^{-2}$ (Table 3.2), which is only 27% of the biomass in the experimental plots. The garden plots were not surrounded by a homogeneous bracken vegetation, and thus did not experience lateral shading. Also, the bracken plants did not encounter water stress in the garden experiment because plots were watered regularly. These factors have contributed to the higher biomass production in the garden experiment. Frond lengths were significantly smaller ($P < 0.001$) when exposed to full radiation (Fig. 3.7c). Mean frond length was not different between the treatments with reduced light availability.

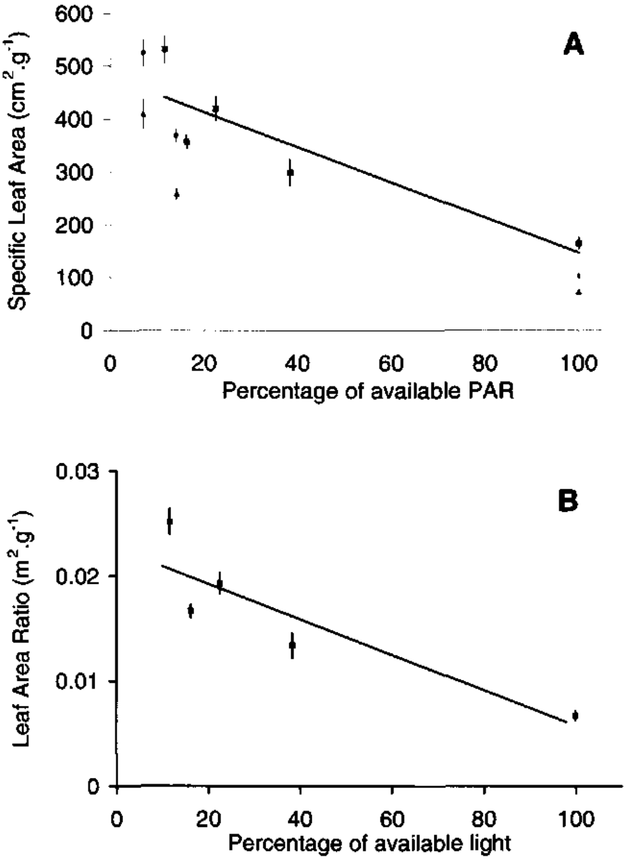


Figure 3.6: Specific Leaf Area (A) and Leaf Area Ratio (B) of bracken fronds in relation to available radiation (PAR) as percentage of the open. Data in A represent SLA for bracken in the field plots (large symbols), and SLA of fronds in the garden experiment (small symbols: triangles = 1996, diamonds = 1997). Error bars are 1 standard error.

Lines represent linear regression equations calculated for bracken growing in the field plots ($n = 5$):

A: $SLA = 480.5 - 3.33 * RAD$ $R^2 = 0.71$
B: $LAR = 226.1 - 1.7 * RAD$ $R^2 = 0.72$

with SLA = Specific Leaf Area in $cm^2 \cdot g^{-1}$, LAR = Leaf Area Ratio in $m^2 \cdot g^{-1}$, and RAD = percentage of available radiation (PAR).

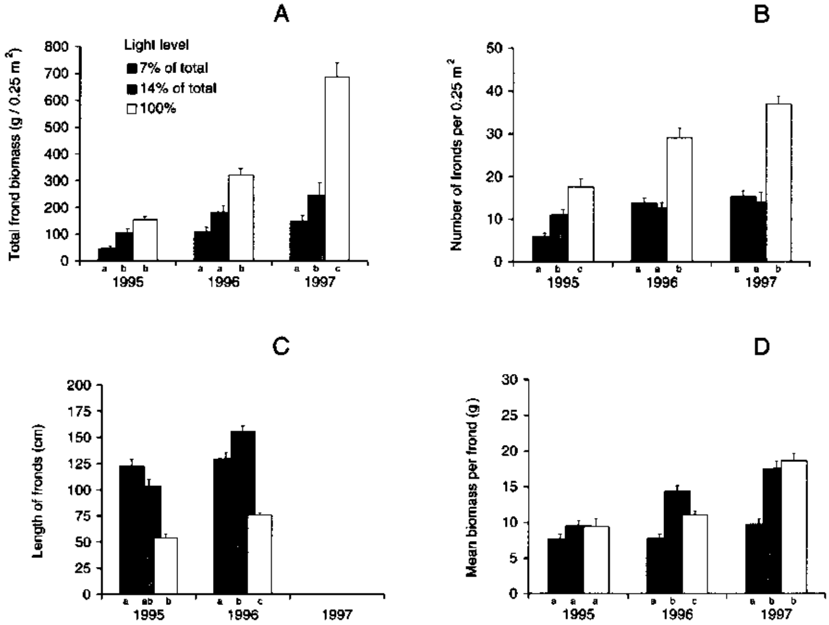


Figure 3.7: Mean total above ground biomass (a), number of fronds (b), mean frond length (c), and mean biomass per frond (d) of bracken grown for three consecutive years in an experimental garden and exposed to different levels of shading. Data represent means of eight 50cm x 50cm plots. Different letters indicate significant ($P < 0.05$) differences between shade treatments within years. Error bars are 1 standard error. [Note that mean and error represent pseudo-replicates since replicates were present under the same shade cloth.]

Experimental shading also had a significant effect on the number of fronds per rhizome block (Fig. 3.7b). In general, shading resulted in the production of less fronds. In 1995, the number of fronds produced was significantly different between all three treatments. In 1995, frond number in the full light treatment (17.6 ± 1.9) was four times higher than the number of fronds in the undisturbed field plots (see Table 3.2). In subsequent years, only the treatment receiving full light resulted in significantly more fronds ($P < 0.001$), while the 7% and 14% treatments produced an equal number of fronds (Fig. 3.7b). There was a close relationship between the number of fronds and total above ground biomass produced in the blocks (Fig. 3.8), which is in accordance with the results from the biomass sampling in the forest stands (Fig. 3.5a). Linear regression of the number of fronds against biomass across light treatments showed that the slope of the regression lines became increasingly steeper over the three sampling years (Fig. 3.8). Regression with dummy variables (Sokal & Rohlf 1995) showed that the slope of the regression line in 1997 was significantly different from those of the previous years (t = 5.875, $P < 0.001$). This implies that the mean weight per frond increased over the course of the experiment (Fig. 3.7d), although the 7% treatment showed no differences in mean frond biomass between years. Fronds from the 14% and 100% treatments became progressively heavier.

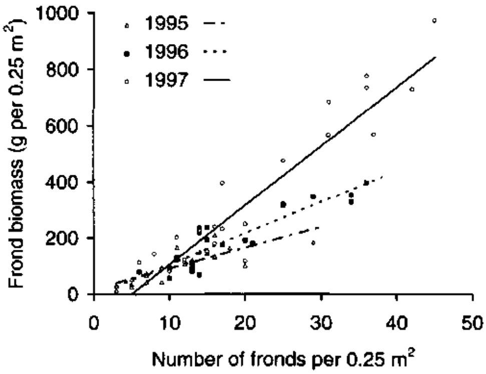


Figure 3.8: Relationship between frond biomass and frond number produced in the garden experiment in 1995, 1996 and 1997. Lines represent linear regression equations.

Specific leaf area of the fronds corresponded well with SLA of plants growing under similar light conditions in the field plots (Fig. 3.6a). In 1996, SLA was lower than in 1997. In both years, the SLA of plants growing under 7% light availability was 5 times higher than SLA of plants in the unshaded treatment. Differences in SLA were accompanied by large differences in morphology of the pinnules (Fig. 3.9). Pinnules from unshaded fronds were stiff and pointed, while pinnules from the shade treatment were very soft and much broader (Fig. 3.9).

3.3.4 Frond biomass estimates from BRACON

When run under the climatic conditions present in the study area, and 100% light availability, BRACON estimated an equilibrium rhizome biomass of 1857 g·m^{-2}, and a peak frond biomass of 918 g·m^{-2} (Fig 3.4a). This is in fair agreement with the measured peak frond biomass of 731 g·m^{-2} at the open site (Table 3.2) in this study.

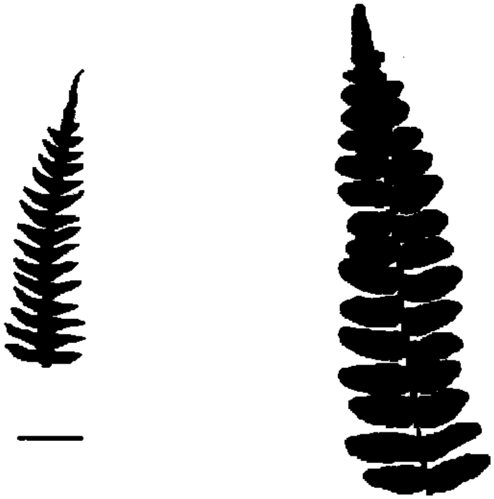


Figure 3.9: Differences in pinnule morphology between bracken growing in full light (left) and when 14% light available (right). Scale bar is 1 cm.

The analysis presented above showed that the leaf area ratio (LAR), and thus biomass of a frond representing 1 m^2 of leaf area (parameter z in the model) was dependent on the percentage of light available under the forest canopy (Fig. 3.6b). The negative relationship of LAR versus light availability is a direct result of changes in SLA over the range in light levels (Fig. 3.6a). This indicates that, under a forest canopy, the cost in terms of carbohydrates allocated to the fronds to produce a fixed leaf area is less than when the frond is growing fully exposed. In full sun, the value of z was 154 – 9.8 g (mean – 1 se.; n = 10), which corresponds well with an earlier published value of 170 g by Pitman & Pitman (1990*a*). Because z was related to light intensity in the stands, and was entered as a constant value (170 g) in the original version, I extended BRACON to account for changes in z over a light gradient using the equation:

$$z = 31.2\ (-\ 3.8) + 1.23\ (-\ 0.08)\ ^{*}\ \mathrm{RAD} \qquad n = 5,\ R^2 = 0.98 \qquad \textbf{[3.3]}$$

with z = biomass (g) of a frond with a leaf area of 1 m^2, and RAD = percentage of available radiation relative to above the canopy.

The estimate of equilibrium biomass at 100% light availability was in fair agreement with the data obtained from the forest clearing (Fig. 3.4a). However, at lower light levels the model did not produce accurate frond biomass estimates. BRACON predicts complete extinction of the bracken rhizome at light levels of approximately 15% of the open. Clearly, the model underestimated bracken productivity at low light levels. BRACON was also used to evaluate the increase in frond production when the forest canopy is removed. The forest clearing used in this study was located within a former oak coppice stand. Bracken frond biomass within this stand was 79.7 ± 27.9 g·m^{-2}. This was taken as initial frond biomass entered into the model. Biomass production was modelled for the first 25 years following canopy removal that resulted in 100% light availability (Fig. 3.10). Equilibrium frond production was reached after 15 years. This corresponds well with the measured frond biomass in the forest clearing that was sampled 12 years after canopy removal (Fig. 3.10).

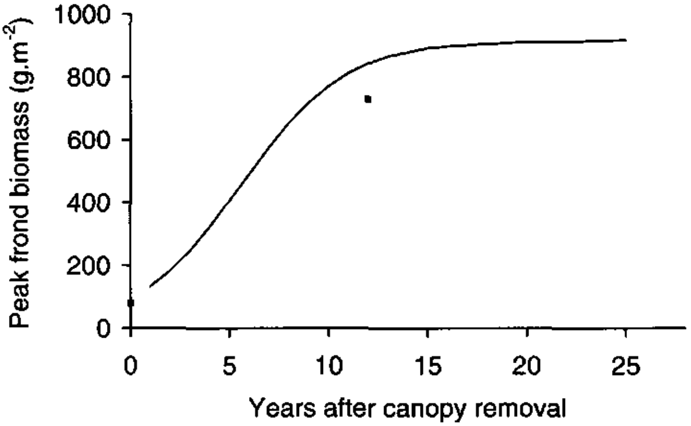


Figure 3.10: Modelled increase in bracken frond biomass production after canopy removal (receiving full light). Data points represent measured frond biomass in a coppiced stand of oak with an intact 30 yr old canopy (at t = 0), and biomass in an area of the same stand in which the canopy had been removed 12 years earlier and is now completely dominated by bracken (the open site).

3.4 Discussion

3.4.1 Bracken growth under a tree canopy

Bracken is well adapted for growth under a forest canopy. It is able to maintain relatively high above ground biomass under low light levels. When light levels are reduced to less than 10% of the total available radiation, above ground biomass is still approximately 15% of the biomass produced in full light (Table 3.2, Fig. 3.4a). During the growing season, the degree of frond expansion and total frond biomass production is linearly related to accumulated incident irradiation (Pitman & Pitman 1990*a*), so increased canopy cover results in lower frond production (Fig. 3.4a). Simultaneously, the bracken plant is able to adjust its morphology to changes in the environment brought about by the forest canopy (cf. Fig. 3.9). A reduction in available radiation leads to an increase in specific leaf area (Fig.3.6a). The reduction of radiation does not result in changes in frond architecture, so a reduction in SLA has a direct effect on the leaf area ratio (LAR), which consequently reduces the amount of resources needed to build a frond with a unit leaf area (parameter *z* in BRACON). This implies that the investment in photosynthetically active tissue is adjusted relative to the light conditions experienced by the frond, while maintaining the same leaf area. Such changes in SLA and LAR are commonly observed in plants growing in shaded habitats, and have been linked with maximisation of canopy photosynthesis (Dijkstra 1989). However, changes in SLA may not only be a result of lowered radiation levels, but also of decreased exposure of the frond (Bright 1928). The changes in SLA are mainly caused by reduced lignification of the fronds under low light conditions (Jones 1983). Concurrent with an optimisation of canopy photosynthesis, this implies a cost in terms of increased susceptibility to pathogens (McElwee & Burge 1990). In the study area, most infection by curl-tip disease, caused by the fungus *Ascochyta pteridis* Bres. (Irvine *et al.* 1991*)*, was found in bracken growing in deep shade (pers. observ.), which is most likely due to the combination of low lignification of the frond tissue, the poor energy status of the plant and high air humidity (Munyaradzi *et al.* 1990). However, bracken may compensate for decreased lignification by increased cyanogenesis to defend against insect attack (Jones 1983).

The length of the fronds only bears a weak relationship to available light. In the field plots, mean frond length was generally higher in stands where more light penetrated through the canopy, but at low light levels, frond length varied considerably (Table 3.2). The length of fronds is the combined result of the energy status of the rhizome, degree of exposure and etiolation when light levels are low. The bracken rhizomes taken from the forest clearing into the garden experiment produced considerably shorter fronds when growing at 100% light than the fronds emerging from rhizomes in the field. This is most likely the result of both reduced rhizome biomass and increased exposure of fronds in the garden plots. In the shade treatments, air humidity was probably higher under the shade cloth, resulting in taller fronds

(Werkman *et al.* 1996). Etiolation occurs when light levels are low. If supported, fronds may grow up to 4 m tall, enabling bracken to overtop low shrubs (Watt 1976, Koop & Hilgen 1987).

3.4.2 Agreement with modelling results

The field observations on the relationship between incident radiation and bracken frond production are not in accordance with model estimates from BRACON, which predicts total elimination of bracken when available radiation drops below 15%. It must be stated that the model was never intended to calculate bracken productivity with such detail. Therefore, the results from this modelling exercise must be regarded with reservation. They do however point towards some aspects that can improve the model.

Several factors may be responsible for the discrepancy between modelling results and field observations. The estimates obtained from BRACON were calculated as equilibrium biomass after running the model for 50 years. Actual biomass production as measured in the field represents bracken clones that are in several stages of development, depending on the thinning, and thus light, history of the site. The sampled stands may also represent different stages in the long-term growth cycle of the plant (Watt 1945, 1976). Furthermore, biomass estimates from BRACON were obtained using long term climatic data, and not actual weather data from the site. The summer of 1995 was relatively dry and warm, which most likely induced higher losses of soil moisture from evapo-transpiration than accounted for by the model. Also, night frosts on the open site occurred until later in the season (end of May), setting back the onset of growth relative to the modelled bracken. The moderating effect of the forest canopy on temperature further results in earlier frond emergence as compared with the open site. The presence of a forest canopy therefore effectively prolongs the bracken growing season, which may partially compensate the reduced productivity due to lower radiation levels and competition for water and nutrients with the canopy trees.

Changes in light levels generally bring about changes in allocation patterns within plants, resulting in lower root/shoot ratios when light levels are reduced. No data are available for changes in this ratio for bracken. However, when BRACON was adjusted to account for different distributions of carbohydrates over rhizome and fronds with changing radiation levels (parameter *j* in the model), model estimates did not substantially improve and still resulted in rapid extinction of the plants under reduced light levels (data not shown).

The value set for *K* (extinction coefficient) was held constant in the model. Pakeman *et al.* (1994) showed that modelling results are very sensitive to changes in this parameter. No measurements were made to determine the value of *K*, but as is the case for the parameter *z* the extinction coefficient will change with specific leaf area. Not taking this into account will result in a further underestimation of bracken productivity in low light levels (Pakeman, pers. comm.).

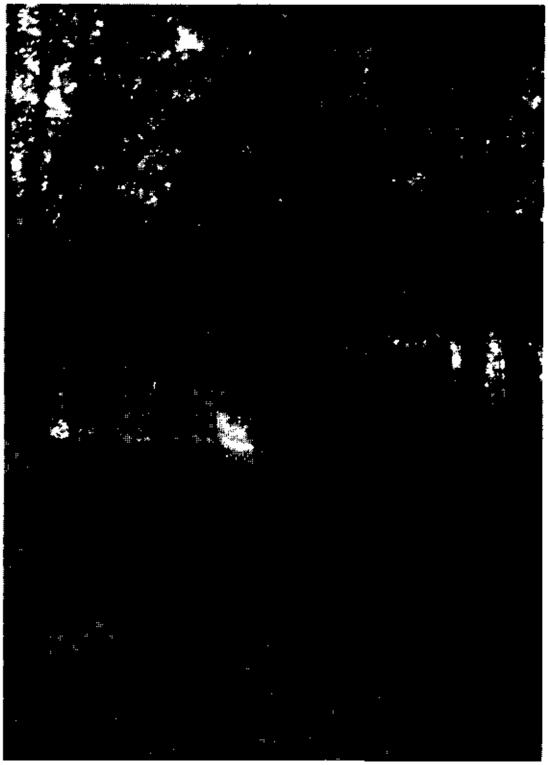
Photosynthetic activity of bracken, and consequently productivity, is greatly reduced under soil water stress (Hollinger 1987). Stomatal conductance is reduced under high specific humidity deficits, but at a much smaller rate than trees in the canopy as for instance *Pinus sylvestris* (Roberts *et al.* 1980), *Pinus radiata* D. Don and *Nothofagus truncata* (Hollinger 1987). This may result in high transpiration rates in bracken relative to the canopy trees, and bracken may significantly contribute to total forest transpiration (Roberts *et al.* 1980). The low responsiveness of stomatal conductance can be seen as an advantage to plants growing in shaded habitats, since it will enable the plant to react more rapidly to the occurrence of sun flecks (Hollinger 1987). Sun flecks could therefore be very important for bracken in maintaining high productivity in shaded conditions, either due to direct responses by increased photosynthesis in individual fronds, or by redistribution of assimilates through the rhizome (Stuefer *et al.* 1994). In this study, the estimates of light levels in the stands were based on hemispherical photos. These average estimates do not directly account for sun fleck distribution and duration. So, the light estimates may have actually underestimated light levels perceived by the bracken plant.

3.4.3 Conclusions

This study has shown that bracken is well adapted to growth in forests by maintaining high levels of productivity even under relatively low light conditions. The high plasticity in frond morphology enables bracken to efficiently exploit all remaining radiation available to the forest undergrowth. When light levels are low, bracken becomes vulnerable to diseases like curl-tip disease, which is probably the combined result of low energy status of the plant, high air humidity and low lignification of the frond tissue.

Although the bracken growth model BRACON is well capable of predicting equilibrium biomass of bracken in open habitats, the introduction of shading in the model results in underestimates of bracken productivity as compared to the field measurements. This may be due to conditions not accounted for by the present model, like the exploitation of sun flecks, changes in the extinction coefficient of the fronds, redistribution of photosynthates through the rhizome, a higher air humidity, or changes in overall allocation patterns to fronds, rhizomes and roots.

4. Bracken dynamics in a managed forest ecosystem



This chapter is based on:
Den Ouden, J. & Hommel, P.W.F.M. (in prep.). Distribution and dynamics of bracken (*Pteridium aquilinum* (L.) Kuhn) in a managed forest ecosystem.

4.1 Introduction

The capacity to grow and persist under relatively deep shade makes bracken a common dominant competitor in many forest ecosystems world-wide (Gliessman & Muller 1978, Dutkowski & Boomsma 1990, Tolhurst & Turvey 1992, Dolling 1996*a*). Because bracken strongly interferes with tree regeneration, its presence can have a significant impact on tree recruitment and subsequent forest development (see chapter 5). Bracken is able to create dense, single-species stands that may persist for decades, even centuries. Because of the potentially long-term presence of bracken, the dynamics of tree species and other species occurring in the forest undergrowth are linked to the dynamics in bracken presence and abundance.

Analogous to canopy dynamics, fluctuations or cycles in bracken dominance may provide transient regeneration niches for tree species. In order to assess the potential role of bracken in successional changes in (forest) ecosystems, it is therefore necessary to get more insight into the short-term changes in bracken presence and abundance. There are many records that show that bracken is able to occupy sites for several hundreds of years (Oinonen 1967*a,b*, Sheffield *et al.* 1989*a*, H. Koop, unpubl. data). Such studies have demonstrated the continuous presence of genetic individuals. However, no information is available on the changes over time in cover and abundance of these clones, especially in forest (cf. Marrs & Hicks 1986).

On a long time scale, bracken can show phasic changes in cover and dominance. Watt (1947, 1955, 1970) extensively described the long term dynamics of bracken clones, and postulated the cyclic nature of changes in bracken vegetation. These are based on autogenic processes in the bracken swards. When colonising a new site, the new fronds emerge from deep short-shoot rhizomes. Each successively produced frond is situated above the old frond attachment, so each new bud is located closer to the soil surface. Concurrently, a thick litter layer will develop under bracken, and given time, the rhizome tips and frond buds will eventually reach this ectorganic layer, making them increasingly susceptible to damage, most notably by frost. This implies that, within time, clones may degenerate which creates opportunities for other species to colonise the patch (Watt 1976). Later, the site may be re-colonised by rhizomes from outside the patch, re-initiating the cycle.
The long term dynamics in bracken presence and dominance, and the postulated phasic interdigitation between bracken and other species (*Calluna* or grass heath), have been re-examined by Marrs & Hicks (1986) on the Lakenheath Warren (UK), one of the important field sites used by Watt (1940, 1945, 1955, 1976). Marrs & Hicks (1986) found that bracken had degenerated over large areas, being replaced by grass heath. Furthermore, in other parts of the site the phasic interdigitation between bracken and *Calluna* described by Watt (cf. 1947, 1955) had mostly broken down. Here, *Calluna* was degenerating while bracken had increased sharply. It was not clear whether *Calluna* degeneration was due to environmental conditions (e.g. frost), attack by heather beetles, physical age of *Calluna* or the result of competition by bracken (Marrs & Hicks 1986).

The study by Marrs & Hicks (1986) pointed out (i) that bracken may degenerate over large areas, even in the absence of any vegetation management (mowing, burning, grazing, etc.), and (ii) that bracken may remain present, albeit in very low densities, in the replacement vegetation following bracken degradation. This has important implications for the assessment of bracken encroachment rates, since re-establishment of bracken on these sites may not represent actual colonisation of new area (true encroachment), but revegetation from rhizomes still present in the soil, or from sparse and undetected clones (Taylor 1980, Marrs & Hicks 1986). This was also observed by Dolling (1996*a*) in a clearcut *Pinus sylvestris* / *Picea abies* forest in Sweden. In a forest where bracken had previously been present, the bracken front expanded almost 15 m within one year after canopy removal, while in a previously unoccupied site the front of the adjacent bracken patch hardly advanced at all.

Apart from autogenic mechanisms, the changes in bracken cover and abundance in forests are also governed by competitive interactions with trees and thus the dynamics of the tree canopy. In managed forest ecosystems, the dominance of bracken is closely connected to stand development (e.g. Ford & Newbould 1977). Bracken increases in cover and productivity in the stages of stand development with high light penetration through the canopy. Canopy closure results in low radiation levels in the forest undergrowth and reduces bracken vigour. Still, bracken is able to maintain a relatively high above ground biomass productivity under low light conditions (see chapter 3). Stand thinning will regularly bring more light to the forest floor, enabling bracken to replenish stored reserves and survive subsequent periods of low light availability after the canopy closes again. This means that bracken dynamics in forest is the result of the superposition of competitive interactions with the understory, autogenic changes in the bracken sward and dynamics of the tree canopy.

In this chapter we investigate the distribution and dynamics of bracken in a managed forest ecosystem in the central part of the Netherlands. We investigated the distribution of bracken at two levels. Firstly, we looked at the general pattern of bracken presence in the forest complex and investigated how the occurrence of bracken was related to site history and soil type. Secondly, we studied the distribution of bracken on a stand level by investigating its relationship with stand type and developmental stage. The patterns in presence of bracken will yield information on the habitat-requirements of bracken.

The establishment of new bracken clones from spores is extremely rare. All changes in the presence of bracken must therefore be related to the colonisation or retreat of rhizomes from already established plants. Our third objective was to assess the modes of bracken colonisation by investigating the importance of lateral expansion of the rhizome into new territory and possible revegetation of formerly held territory.

4.2 Methods

4.2.1 Mapping the Speulderbos

This study was carried out in the Speulderbos, a large forest complex in the central part of the Netherlands. An overview of stand composition of the forest will be presented in the results section (4.3.3). We compared maps of bracken presence made in 1958, 1985 and 1996 on a scale of 1:10,000. The 1958 map was constructed as part of a vegetation survey of the Speulderbos by Leys (1965), in which the presence of bracken in the plant communities was marked separately. In 1985, the vegetation of the entire forest was re-mapped, including the presence of bracken (Mekkink *et al.* 1986). The results were used to study the vegetation changes in relation to environmental factors including soil type, stand types and ages and N-deposition from nearby agricultural areas (Hommel *et al.* 1991). In 1996, a new map of bracken distribution was made and added to the database, and the available map of stand type and age was updated to account for any changes in forest cover due to forest management in the preceding decade. The database further included maps of soil types, stand types and age, and site history (Mekkink *et al.* 1986). All maps were digitised and analysed using the Geographical Information System ARC-INFO.

The following maps of the Speulderbos were used:

Bracken presence
In the surveys of 1958 and 1985, mapping was focused on vegetation communities, and bracken presence was added as a separate legend unit. In 1996, mapping was exclusively focused on the presence of bracken. Bracken stands were mapped at scale 1:5,000, and redrawn at scale 1:10,000. In the field, the density of the bracken stands varied considerably. In general, bracken formed well defined stands with distinct boundaries, and internal frond cover of 75-100% . However, especially in forest stands with low light levels, stands of bracken could be reduced to a few scattered fronds, with frond densities dropping well below 1 per m^2. During the 1985 survey, such sparse bracken stands were mapped separately when overall cover of the fronds was below 50%. Since no such distinction was made in the 1958 survey, we disregarded this distinction in bracken abundance classes in the present study, and indicated bracken cover as either present or absent.

Soils
Original scale 1:10,000 (Mekkink *et al.* 1986). The soils in the study area predominantly consisted of brown podzolic earths (leptic podzols or 'holtpodzolen') and humic podzols ('haarpodzolen'), with the remainder mainly consisting of regosols ('duinvaaggronden') on former drift sands (for used classification and nomenclature of soil types, see De Bakker & Schelling 1989). The brown podzolic earths were subdivided into 4 classes representing differences in loam content and mean

particle size of the soil parent material. A small part of these leptic podzols were turned into arable fields around the turn of the century, resulting in a moderately deep (30-50 cm) dark humic top soil. These 'loopodzolen' were afforested in the first decades of this century.

Site History

Information on former land cover and land use was collected from unpublished maps of the land register of the Putten and Ermelo boroughs from 1832 (scale 1:2,500), and topographic maps of 1871, 1885, 1916, and 1930 (scale 1:25,000). From these maps, site history was represented as the presence of high forest in 1832 (71%), presence of oak coppice in 1832 (17%), reforestation of heath land between 1832-1871 (8%), reforestation of heath land between 1871-1885 (2%), and reforestation of arable fields since 1832 (3%) (see Hommel *et al.* 1991).

Stand type and age

The entire forest area consisted of discrete stands of more or less uniform tree cover. Information on stand types and stand ages in 1958 was obtained from the forest administration. Changes in stand type in 1985 and 1996 were recorded during mapping. Stand ages were aggregated into age classes, with class 0 = 0-4 y, class 1 = 5-14 y, class 2= 15-24 y, etc. Most stands were even-aged monocultures. Stands of *Fagus sylvatica* or *Pseudotsuga menziesii* that were mixed with other species were treated in this study as monocultures of these two species.

4.2.2 Dynamics in bracken cover

There is a large difference in number of years between maps constructed in 1958 and 1985 (27 y) and between 1985 and 1996 (11 y). Changes in the presence of bracken are therefore not directly comparable between these two periods. In this study, we concentrate on the changes between 1985 and 1996.

We investigated the mode of colonisation by bracken by using the information from the 1958 map as baseline data on the area that was covered by bracken prior to 1985. Of course, this does not include areas that have been colonised and then abandoned between 1958 and 1985, or areas abandoned before 1958. We considered this area as potential colonisation sites by means of revegetation. We also determined the area that could potentially be colonised by means of lateral expansion of the rhizome. Maximum lateral expansion was determined by measuring the maximum length of new invasion by advancing bracken fronts in the period 1958-1985-1996 in 22 stands. This resulted in a mean maximum expansion rate of approximately 2 $m \cdot y^{-1}$. Next we took the entire area of bracken in 1985, and let this expand laterally at a rate of 2 $m \cdot y^{-1}$, resulting in a 22 m strip around the 1985 bracken area. When this strip crossed a major road, expansion was not allowed to proceed into the adjacent stand since the high soil compaction blocks vegetative spread across such roads. The final strip represented the total area of potential lateral expansion, and was added as an extra map to the data base.

4.2.3 Data analysis

In order to evaluate the changes in bracken cover in relation to stand type and age, maximum area of potential lateral expansion, soil type and site history we constructed an overlay map that included all combinations of the factors above. The relationship between changes in bracken cover with stand type and age, and the evaluation of colonisation modes were studied in a subset of stands that were larger than 0.5 ha (to reduce edge-effects) and did not change in stand type between 1958 and 1996. Differences in the distribution of bracken cover over the major soil types and areas of different forest history, and bracken colonisation over the areas inside or outside the area of potential lateral expansion and revegetation were analysed using a chi-squared test (Sokal & Rohlf 1995).

4.3 Results

4.3.1 Overall changes in bracken cover

There were large differences in total bracken cover between the three years (Figs. 4.1 and 4.2). Presence of bracken increased from 144 ha to 197 ha between 1958 and 1985, an increase of 36%. However, this net increase was completely nullified by 1996, where total bracken cover had decreased to 147 ha (Figs. 4.1 and 4.2).

In the period 1958-1985, bracken colonised 129.6 ha of new area, and had disappeared from 76.9 ha. In the period between 1985-1996, bracken colonised 61.1 ha, of which 16.5 ha (27%) had already been covered by bracken in 1958. In the same period, bracken had retreated from 110.9 ha (56%). In total 83.6 ha (69%) of this retreat represented area that had been colonised in the previous period. Of the area covered by bracken in 1958, only 40.0 ha (28%) was still covered by bracken in 1996 (Fig. 4.1, also see Fig. 4.9).

The general pattern of bracken distribution over the entire study area is rather fixed. Bracken occurs in large clusters, and the more extensive areas where bracken was absent in 1958 (for instance in the northern part of the forest) remained free of bracken in subsequent sampling years. The increase in bracken cover was mostly confined to areas with previous nearby bracken cover. We found no indications of recently established young clones.

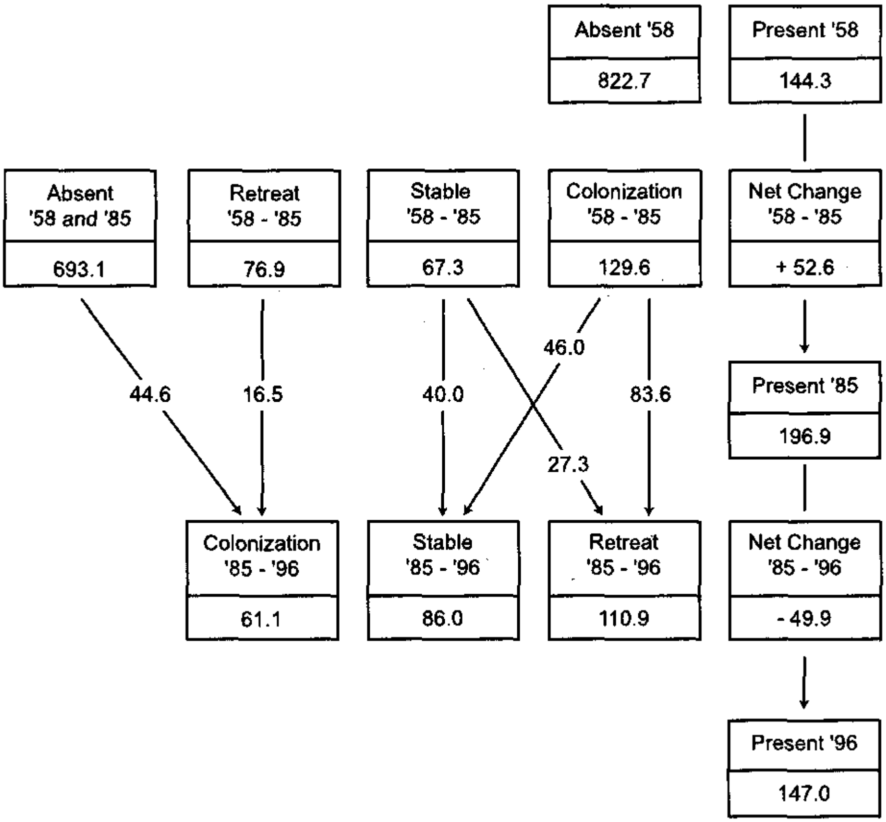
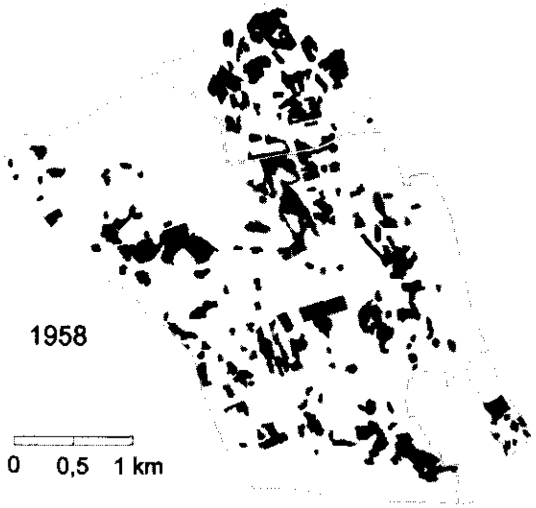


Figure 4.1: Overall dynamics in bracken presence in the Speulderbos between 1958-1985 and 1985-1996. Changes in bracken presence all in ha.

Figure 4.2: (pages 50-51) The distribution of bracken in the Speulderbos in 1958, 1985 and 1996. Also shown is the pattern in bracken dynamics between 1985 and 1996, with black = bracken present in 1958, 1985 and 1996, light grey = bracken colonisation between 1958 and 1985 but retreated by 1996, and dark grey = bracken present in 1996, but absent in 1958 and 1985.


1958
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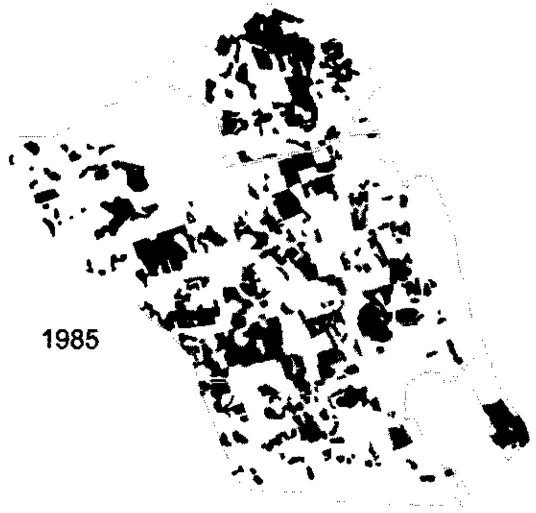
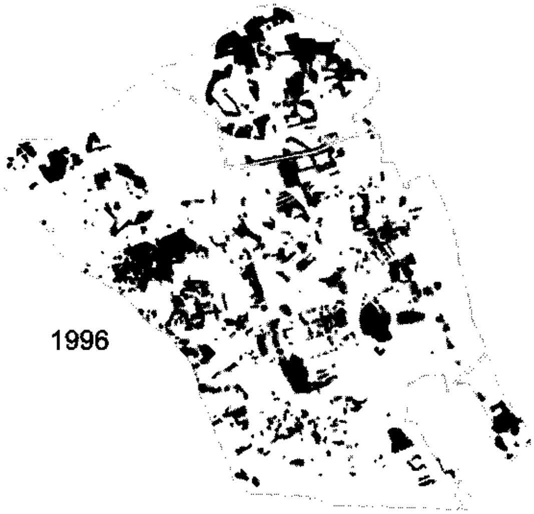
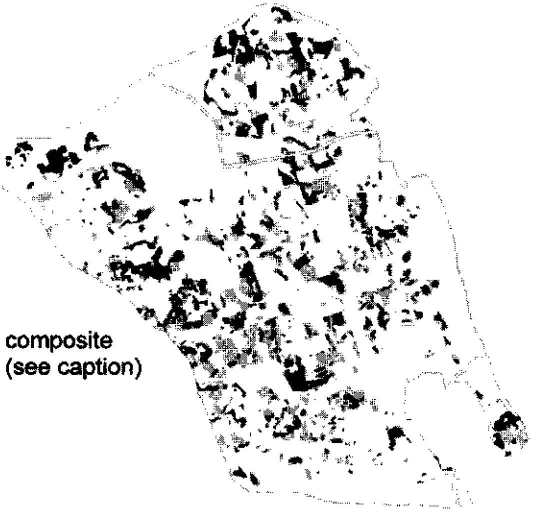

1985


1996


composite
(see caption)

4.3.2 Forest history and soil type

There is a clear relationship between the former land use and the distribution of bracken in the area (Table 4.1). Almost all bracken was found on sites that were covered by forest according to the earliest records available (1832). The higher presence of bracken on long term forested areas is highly significant ($P < 0.001$). The former oak coppice stands contain relatively more bracken than the areas that were covered by high forest. This is due to differences in stand types found on these areas (see 4.3.3). Former heathlands and arable fields had hardly any bracken growing on it in 1958. Since then, bracken has slowly spread into these areas, but total cover remains low (Table 4.1). Forest history, or more specifically the continuous presence of a tree canopy, is therefore a major determinant in the large scale distribution of bracken in this area.

Table 4.1 Bracken presence in relation to forest history in Speulderbos in 1958, 1985 and 1996.

Forest history	Area covered by bracken						Total area	
	1958		1985		1996			
	ha	%	ha	%	ha	%	ha	%
High forest in 1832	107.4	74.5	152.3	77.4	105.5	71.8	667.4	69.0
Oak coppice in 1832	36.7	25.5	43.2	22.0	39.4	26.8	160.9	16.6
Afforested heath 1832-71	0.1	0.1	0.9	0.5	1.5	1.0	74.1	7.7
Afforested heath 1871-85	0.0	0.0	0.0	0.0	0.0	0.0	14.9	1.5
Aff. arable fields after 1832	0.0	0.0	0.4	0.2	0.6	0.4	49.7	5.1
Total	144.3	100.0	196.9	100.0	147.0	100.0	966.9	100.0

The vast majority of the area (88.5%) consisted of brown podzolic soils. On average 98% of the bracken occurred on this soil type (Table 4.2). However, there is a strong correlation between forest history and soil type. The humic podzols, regosols and 'loopodzols' are all located on former heathland and arable fields. Since bracken is slowly colonising former heathlands and arable fields (Table 4.1), the absence of bracken on these soil types is most likely due to former land use rather than differences in inherent soil properties. Within the brown podzolic earths, there were no clear differences in bracken distribution between soils of different texture or loam content.

Table 4.2 Bracken presence on major soil types in the Speulderbos in 1958, 1985 and 1996.

Soil type	Area covered by bracken						Total area	
	1958		1985		1996			
	ha	%	ha	%	ha	%	ha	%
Brown podzolic earth, a [1]	8.4	5.8	9.5	4.8	8.8	6.0	40.4	4.2
Brown podzolic earth, b	24.5	17.0	37.4	19.0	29.7	20.2	177.1	18.3
Brown podzolic earth, c	104.7	72.5	143.1	72.7	103.0	70.1	597.7	61.8
Brown podzolic earth, d	2.2	1.5	3.5	1.8	2.0	1.4	30.7	3.2
Brown podzolic earth with dark top soil ('loopodzol')	0.2	0.2	0.2	0.1	0.3	0.2	13.1	1.4
Humic podzol	2.2.	1.5	2.3	1.2	2.2.	1.5	56.1	5.8
Regosol	1.1	0.8	0.4	0.2	0.4	0.2	21.3	2.2
remaining (buildings, agricultural areas)	0.9	0.6	0.4	0.2	0.5	0.3	30.5	3.2
Total	144.3	100.0	196.9	100.0	147.0	100.0	966.9	100.0

1. Brown podzolic earths are divided according to texture of the parent material:
a = fine sand, high loam content
b = moderately fine sand, high/low loam content
c = moderately coarse sand, high/low loam content
d = coarse sand, low loam content

4.3.3 Stand types and bracken

The area is covered by a large number of different stand types. Since the beginning of this century, large parts of the original forest (mixed, uneven-aged beech/oak high forest and oak-birch coppice woodland) have been converted into more productive coniferous forest, consisting predominantly of *Pinus sylvestris*, *Pseudotsuga menziesii* and *Larix kaempferi*.

Stands of *Fagus sylvatica* represented the most dominant stand type in the area (Table 4.3). These were mostly old uneven-aged mixed stands of *F. sylvatica* and *Quercus robur / Q. petraea* (267 ha in 1958, 253 ha in 1985/1996). These stands have developed for the last century without active management interference, except for some removal of individual trees. In the early 1900s, this stand type consisted of an equal mixture of beech and oak (Sevenster 1995). Due to the lack of management interventions, competition by beech has greatly reduced the proportion of oak. The remainder of the *Fagus* stands (younger age classes) are under regular silvicultural treatment. Between 1958 and 1985, a considerable number of *Pinus* and *Quercus* stands was converted into different stand types. These species were mostly replaced by *Pseudotsuga menziesii*, *Abies grandis* and *Tsuga heterophylla*.

Table 4.3 Major stand types in the Speulderbos in 1958, 1985 and 1996.

Stand type	Area occupied by stand types					
	1958		1985		1996	
	ha	%	ha	%	ha	%
Fagus sylvatica [1,2]	378.2	39.1	375.1	38.8	382.1	39.5
Pseudotsuga menziesii [1]	143.7	14.9	196.0	20.3	188.1	19.5
Pinus sp. [3]	192.5	19.9	109.2	11.3	102.8	10.6
Quercus sp. [4]	104.2	10.8	73.3	7.6	79.9	8.3
Larix kaempferi	64.8	6.7	65.1	6.7	59.3	6.1
other species [5]	54.3	5.6	95.0	9.8	96.6	10.0
no tree cover [6]	29.1	3.0	53.3	5.5	58.1	6.0
Total	966.9	100.0	966.9	100.0	966.9	100.0

1. Including mixtures with other species, predominantly with *Quercus* and *Pseudotsuga*
2. Managed even-aged stands and uneven-aged old high forest
3. Predominantly *P. sylvestris*, with some *P. nigra* and *P. contorta*
4. *Q. robur*, some *Q. rubra*.
5. *Abies grandis, Picea abies, P. sitchensis, Tsuga heterophylla, Thuja plicata, Betula pendula, Populus tremula.*
6. Clearcuts, arable fields, meadows, buildings, nursery.

The age class distribution of the forest has changed considerably between 1958, 1985 and 1996 (Fig. 4.3). In 1958, the forest predominantly consisted of relatively young stands under regular, large-scaled silvicultural treatment. The unmanaged beech/oak forests were all older than 120 years. Between 1958 and 1985, approximately a third of the area was cut or replaced by new stands. The majority of the converted stands included *Pinus* and *Quercus* stands. Also, many *Pseudotsuga* stands were replaced by younger stands after storms in 1972 and 1973 caused major blow down in the area.

In the following period, most stands grew into an older age class. Between 1985 and 1996, only a small fraction of the stands was cut and replanted (Fig. 4.3). During the last decades, forest management has become much more small-scaled, with the use of small regeneration units and the use of natural regeneration. Since many of such changes in forest cover were too small-scaled to be reflected in stand typing of the individual stands, the data probably overestimate the area covered by the older age classes in the study area.

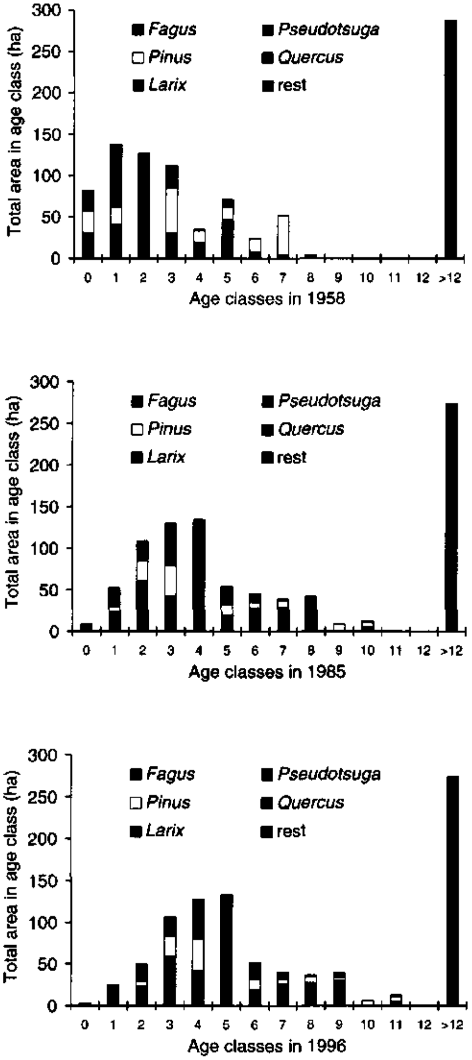


Figure 4.3: Age-class distribution of the major stand types in the Speulderbos in 1958, 1985 and 1996.

Bracken was not evenly present in the different stand types (Fig 4.4). Bracken cover was low in the *Fagus* stands as compared with the other stand types. In the old beech/oak forest, bracken cover was very patchy, mostly consisting of small clones in local areas with low *Fagus* dominance. In almost all cases where bracken was found in this forest type, it was associated with larger canopy gaps and remaining pockets of oak (Fig 4.5). In the managed beech forest, bracken cover was equally low, and mostly concentrated in young stands (Fig. 4.6), or along the edges of stands.

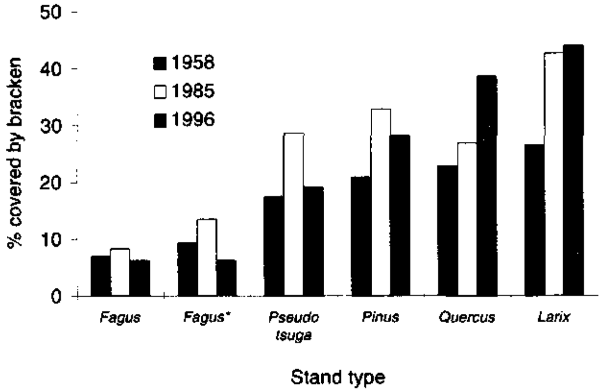


Figure 4.4 Percentage of the total area covered by bracken in 1958, 1985 and 1996 for the five dominant stand types under silvicultural treatment, and the unmanaged high beech/ oak forest (*Fagus**) in the Speulderbos.

The total percentage of bracken cover in stands of *Pseudotsuga* was approximately 18% in 1958 and 1996, but 29% in 1985 (Fig. 4.4). Bracken cover was highest in the young (0-24 y) and old (>65 y) stands, except in 1985 when bracken was also present in the intermediate aged stands (Fig. 4.6). In the period between 1958 and 1985, the storms of 1972 and 1973 had opened up many canopies in these stands. Bracken was most abundant in the *Pinus*, *Larix* and *Quercus* stands, and increased in cover between 1958 and 1996 (Fig. 4.4). Stands of these species have an open canopy structure (see chapter 3). Only stands between 5 and 24 years (thicket- and early pole stages of stand development; Matthews 1989) have sufficiently closed canopies to interfere with bracken growth (Fig. 4.6, 4.7).

Figure 4.5 A patch of bracken in a pocket of *Quercus robur* and *Q. petraea* in the unmanaged high *Fagus* forest. In this forest type, bracken presence was always associated with large canopy gaps or pockets of oak.

Between 1985 and 1996, bracken cover decreased in stands of *Fagus* and *Pseudotsuga*, remained similar in *Pinus* and *Larix* stands and increased in stands of *Quercus*. The net changes in cover by bracken mask the large dynamics present in bracken cover in the stands (Fig. 4.7, Table 4.4). In *Larix* stands for instance, bracken colonised 6.2 ha (= 29% of total 1985 cover) between 1985 and 1996, and retreated from 5.4 ha (= 26 %). The net result is only a 3% increase in bracken cover in *Larix* stands (Fig 4.7).

In *Fagus* stands, bracken retreated across the higher age classes (Fig. 4.7). In *Pinus* stands, bracken retreat was highest in stands between 5-14 years. Bracken cover in *Pseudotsuga* stands highly fluctuated across age classes, and no clear pattern was present (Fig. 4.7). In *Quercus* stands, bracken cover increased with 45%, mainly in the stands of intermediate age (Fig. 4.7).

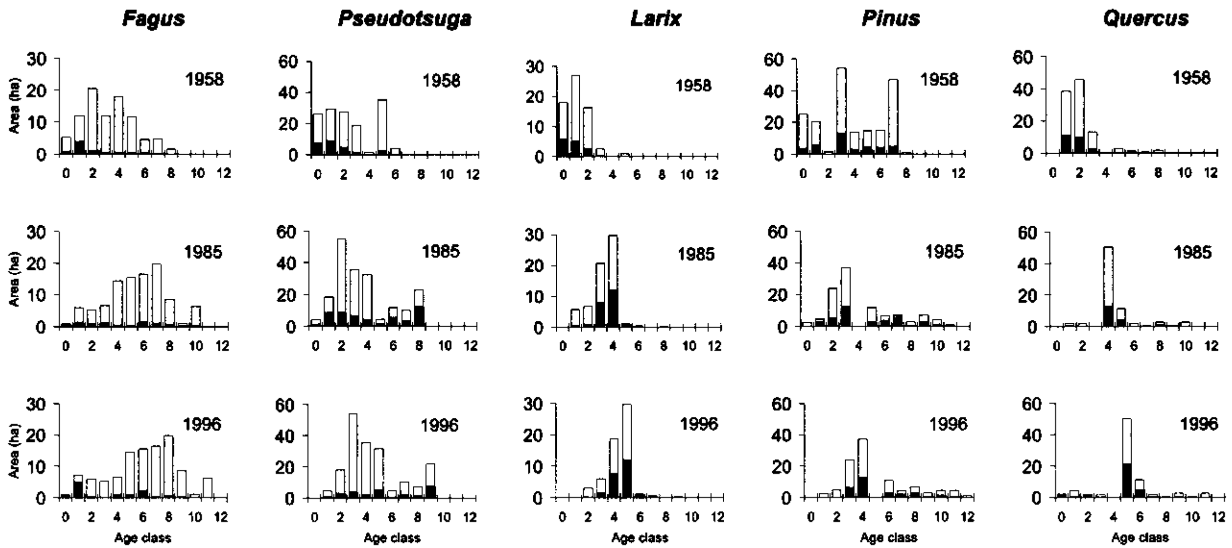


Figure 4.6 Age class distributions of the five stand types under regular forest management in the Speulderbos in 1958, 1985 and 1996. White bars are total area within age classes. Dark bars are the areas covered by bracken within each age class.

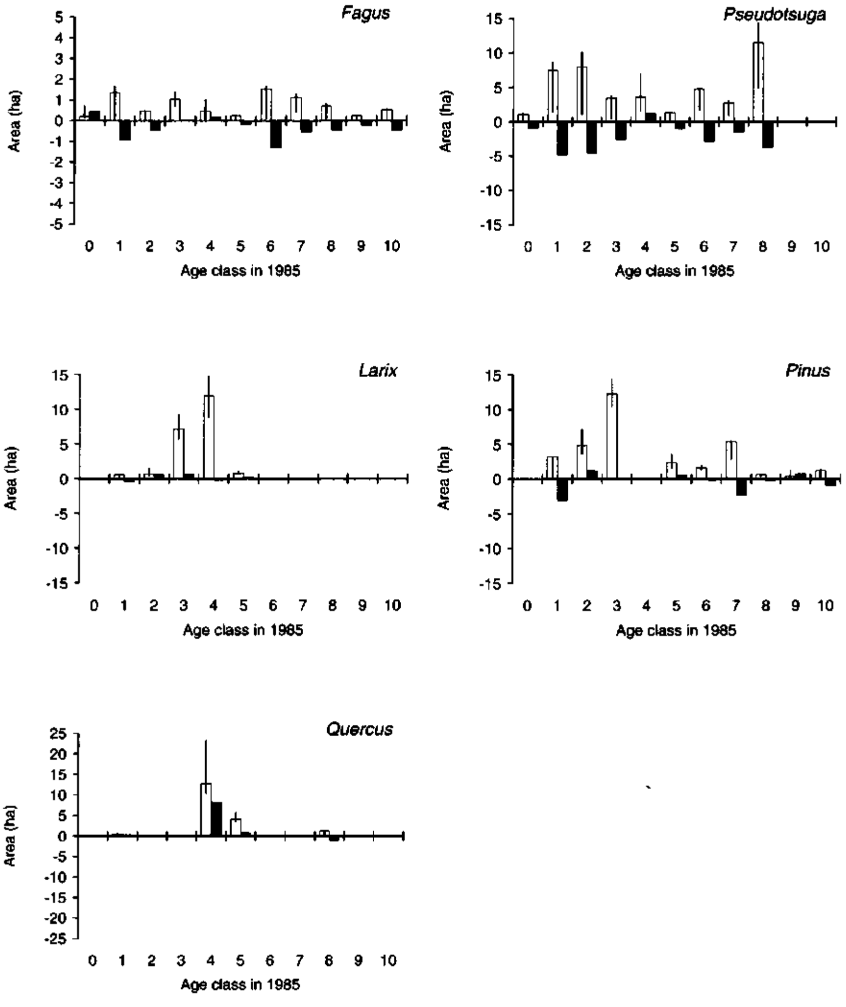


Figure 4.7 Dynamics in bracken cover between 1985 and 1996 by stand type and age class (in 1985). White bars represent the total area covered by bracken in 1985. Dark bars represent net change in cover between 1985 and 1996. Vertical lines are total area colonised (upward) and abandoned (downward) between 1985 and 1996. Only stands >0.5 ha and not converted between 1985 and 1996 were included.

Table 4.4 Total area (ha) colonised and abandoned by bracken between 1985 and 1996 in the major stand types. Only stands > 0.5 ha and not cut or converted between '85 and '96 are included.

Stand type	No. of stands	Cover in 1985 (ha)	Colonised 85-96	Abandoned 85-96	Net change	% change
Fagus, unmanaged	41	33.9	8.6	26.8	-18.2	-54
Fagus, managed	70	10.2	2.8	8.0	-5.2	-51
Pseudotsuga	124	43.8	10.5	31.3	-20.8	-48
Larix	48	21.1	6.2	5.4	+0.7	+3
Pinus	63	31.8	7.0	11.4	-4.4	-14
Quercus	27	18.8	12.8	4.4	+8.5	+45
Total	373	159.6	47.8	87.3	-39.4	-25

4.3.4 Modes of colonisation

Lateral expansion

Between 1985 and 1996, in the stand types under regular silvicultural treatment, bracken colonised a proportionally larger area within the range of potential lateral expansion around the bracken clones present in the stands in 1985. However, differences in areas colonised were not significant when evaluated for each of the individual managed stand types ($P > 0.1$, Table 4.5). On the other hand, in the old and unmanaged high beech/oak forest (*Fagus**) the colonisation of bracken occurred significantly more frequent within the areas of potential lateral expansion ($P = 0.002$, Table 4.5).

When pooling data over all stands, the colonisation was significantly higher in areas of potential lateral expansion ($P < 0.001$). This was not due to the disproportionately (58%) large area represented by the unmanaged high beech/oak forest (Table 4.5). Also the total for only the managed stand types showed a significantly higher proportion of area colonised inside the area of potential lateral expansion ($P = 0.006$, Table 4.5). The data therefore indicate that lateral expansion from the edge of bracken patches accounts for a significant part of the area colonised by bracken between 1985 and 1996.

Table 4.5 Areas colonised by bracken between 1985 and 1996, separated into areas that were inside and outside the range of potential lateral expansion from the bracken present in 1985 (at a rate of 2 $m \cdot y^{-1}$). All data are in ha. Included stands were > 0.5 ha, were not cut or converted between 1958 and 1996, had both an area inside and outside the range of potential lateral expansion, and had bracken colonising between 1985 and 1996.

			Area of potential lateral expansion			Area outside range of lateral expansion				
Stand type	N	Colonised	Total	Colonisation[1]		Total	Colonisation		χ^2	*P*
		'85-'96		obs.	exp.		obs.	exp.		
*Fagus**[2]	34	8.6	49.5	6.0	2.1	154.8	2.6	6.5	9.7	0.002
Fagus	24	1.8	10.0	1.0	0.5	29.8	0.8	1.4	1.0	0.326
Pseudotsuga	33	6.5	10.8	3.7	2.0	23.9	2.8	4.5	2.1	0.152
Larix	23	4.9	7.8	3.8	2.7	6.4	1.2	2.2	0.9	0.353
Pinus	24	3.9	8.1	2.3	1.1	19.3	1.5	2.7	1.8	0.185
Quercus	14	12.2	9.4	5.3	3.7	21.2	6.9	8.5	0.9	0.336
Total	152	37.9	95.6	22.1	10.3	255.4	15.8	27.6	18.5	0.000
Tot. excl. *Fagus**	118	29.3	46.0	16.1	9.2	100.6	13.2	20.1	7.5	0.006

1. obs = observed; exp. = expected (assuming equal chance of colonisation inside or outside the area of potential lateral expansion)
2. uneven-aged, unmanaged high beech/oak forest

Revegetation

We further investigated the distribution of new bracken cover between areas that had previously been covered by bracken, and areas that had no record of bracken growing there in 1958 (Table 4.6). A high proportion of bracken re-appearing in previously covered area would indicate revegetation as a mode of colonisation.

Outside the area potential lateral expansion, we did not find strong evidence for preferential colonisation of formerly occupied areas in all individual stand types (Table 4.6; note that the total areas are small). The proportion of colonised area within the range of potential revegetation tended to be higher than the areas colonised without a previously recorded bracken vegetation. This was only significant when considering all stands together ($P = 0.016$, Table 4.6).

Table 4.6 Areas colonised by bracken between 1985 and 1996 in areas that were covered by bracken in 1958 (potential revegetation), and areas not covered by bracken in 1958. Only areas outside the range of potential lateral expansion were regarded. All data are in ha. Included stands were > 0.5 ha, were not cut or converted between 1958 and 1996, had both an area inside and outside the range of potential revegetation, and had bracken colonising outside the range of potential lateral expansion between 1985 and 1996.

Stand type	N	Area covered by bracken in 1958			Area not covered by bracken in 1958			χ^2	*P*
		Total	Colonisation		Total	Colonisation			
			obs.[1]	exp.		obs.	exp.		
_Fagus_* [2]	21	5.3	0.3	0.1	117.8	1.8	2.0	0.6	0.427
Fagus	10	2.1	0.2	0.1	16.4	0.3	0.5	0.6	0.451
Pseudotsuga	15	5.3	1.0	1.0	8.6	1.7	1.6	0.0	0.952
Larix	8	0.8	0.2	0.2	3.0	0.8	0.8	0.0	0.958
Pinus	13	0.9	0.4	0.1	12.4	0.6	0.9	1.5	0.220
Quercus	10	2.8	1.7	1.1	14.5	4.9	5.6	0.5	0.501
Total	77	17.3	3.8	1.3	172.8	10.1	12.6	5.8	0.016
Total excl. _Fagus_*	56	12.0	3.5	2.1	54.9	8.3	9.7	1.1	0.285

1. obs = observed; exp. = expected (assuming equal chance of colonisation inside or outside areas previously occupied by bracken in 1958, but outside area of potential lateral expansion)
2. uneven-aged, unmanaged high beech/oak forest

4.4 Discussion

4.4.1 Bracken distribution

Despite the large changes in bracken presence in 1958, 1985 and 1996, the general distribution of bracken in the study area remained remarkably constant (Fig. 4.2). New areas colonised by bracken were always in the direct vicinity of existing bracken patches, which implies that the colonisation by bracken occurs only through extension of an existing rhizome system (either by lateral expansion or revegetation from existing rhizomes). New establishments from spores were never recorded, and probably never occurred in the area during the investigated period (see 2.5).

Bracken is considered as an indicator of ancient forest ecosystems (Rackham 1980, Van der Werf 1991, Tack & Hermy 1998, Schoonderwoerd & Nyssen 1999) in North-western Europe. The general distribution of bracken in the Speulderbos clearly demonstrates the relationship with the long-term presence of a forest canopy. Bracken was initially absent from reforested heathlands (Table 4.1). This could not be directly related to soil properties, since 48% of the soils under these former heathlands consisted of brown podzolic earths (data not shown). Over the last decades, bracken is slowly increasing in cover in this previously deforested area (Table 4.1).

In relatively humid climates, or on soils with high moisture availability (but not saturated, see Poel 1961), bracken is able to persist outside the direct protection of a tree canopy (Watt 1976, Taylor 1986, Karjalainen 1989, see Fig. 2.8). On the high sandy soils in the central Netherlands the water holding capacity of the soil substrate is generally low, and desiccation is most likely the major factor resulting in the retreat of bracken once the sheltering forest canopy is removed. Bracken does not regenerate from spores in the area. Once a protective forest canopy is restored, bracken can only slowly colonise this new habitat by lateral expansion of the rhizome. The ecological relationship between bracken and the age of the forest habitat is therefore mainly historical, and not the direct result of an environmental factor associated with an old forest soil.

4.4.2 Dynamics in forest stands

Within the forest habitat, the cover and abundance of bracken is dependent on the canopy characteristics and dynamics that regulate light levels in the stands. The interactions between stand type, the developmental stage of the stand and bracken performance cause large fluctuations in bracken presence in the undergrowth of forest stands. In the period between 1985 and 1996, the overall cover of bracken had decreased considerably after the initially large increase between 1958 and 1985. It is not immediately clear what had caused these large changes in overall bracken presence. Part of the change may have been caused by differences in mapping, for instance in interpretation while recording the presence of small patches or areas with very sparse bracken. This problem is also present in remote sensing studies of landscape dominated by bracken, where sparse bracken may remain undetected (e.g. Taylor 1995). Colonisation recorded at a later census will partly consist of bracken patches growing beyond a threshold density.

Canopy disturbance

The increase in total bracken cover between 1958 and 1985 is likely related to the heavy storms of 1972 and 1973 that caused major blow down of trees in the Speulderbos. For instance, most windthrow had occurred in *Pseudotsuga* stands. Canopy disturbance resulted in light levels rising well above 10% (Bartelink 1997).

This coincides with a relatively high bracken cover in stands of *Pseudotsuga* by 1985 (Fig. 4.4). These transient periods of raised light levels create opportunities for bracken to expand or increase in cover (see chapter 3). Gaps were (partially) replanted, filled by newly established trees, or closed through lateral branch growth. Canopy closure in the dominant tree layer or the regeneration-cohort later reduced light levels again, so 65% of the new areas colonised by bracken between 1958 and 1985 were abandoned again in 1996 (Fig. 4.1).

Stand type and development

Bracken is found in all stand types, but total percentages of bracken cover are different between stand types and depends on the light transmitting properties of the canopy. The total percentage of cover is relatively low in stands of *Fagus*, and high in stands of *Pinus*, *Quercus* and *Larix* (Fig. 4.4). The latter species have transparent canopies, that generally transmit enough radiation to enable bracken growth (see chapter 3). On the other hand, stands of *Fagus* may intercept well over 95% of all radiation (Bartelink 1997) and thus severely restrict bracken growth.
This is also the case for *Pseudotsuga* stands. Light levels are extremely low in closed-canopy stands between 10 and 50 years. Thinning in the canopy can provide bracken a transient foothold until re-closure of the canopy. However, older stands have increasingly transparent crowns, providing suitable but patchy conditions for bracken colonisation.

In young stands of *Pinus*, *Quercus* and *Larix*, light levels are temporarily too low for bracken growth because of the high tree density and low canopy height. When the canopy rises in these stands and following the first thinning (after 15-25 years), light availability increases and gives bracken a permanent foothold in stands of *Pinus*, *Quercus* and *Larix* (Fig. 4.8).

The stability of bracken clones (continuous cover in the three census years) gives insight in the suitability of the different stand types for sustained bracken cover (Fig. 4.9). In the relatively dark stands of *Fagus* and *Pseudotsuga*, only 10-20% of the bracken present in 1958 was still there in 1996 (Fig. 4.9), so bracken is not able to hold territory for longer periods, but is eventually shaded out by the tree canopy. On the other hand, under the transparent canopies of *Pinus* and *Larix*, approximately 60 % of the bracken found in 1958 was still present in the forest undergrowth in 1996. In these stands, canopy shading doesn't pose strong constraints on bracken presence.

Root interference

The availability and distribution of solar radiation under the forest canopy are the dominant factors that can explain the presence and changes of bracken in the forest undergrowth (see also chapter 3). In *Fagus* stand, however, root interference

Figure 4.8: An 18-year old stand of *Larix kaempferi* after the first thinning. The bracken present when this stand was established was shaded out by the larch-thicket, but remained present along the stand edges. After thinning, bracken rapidly re-invaded the stand from the edge.

by the canopy trees represents an additional factor in determining suitable sites for bracken (Lantelm 1963). In the study area, *Fagus* builds a superficial root system with fine roots concentrated in the zone between the ectorganic and mineral soil horizons. This enables *Fagus* to monopolise soil resources (mainly water), and when overall resource levels are low it prevents establishment and growth of other plant species. Trenching experiments in the Speulderbos have shown that when root interference by beech is eliminated, the otherwise bare forest floor is quickly invaded by numerous plant species, including bracken (Oosterbaan, unpubl. data). This indicates that not light levels, but root interference is the dominant factor in the absence of forest undergrowth in *Fagus* stands. Bracken clones that were present in such stands were almost always concentrated near the edges of stands and in canopy gaps, or in remaining pockets of *Quercus* in the unmanaged *Fagus* stands (Fig. 4.5). Even individual *Fagus* trees are able to exclude bracken from underneath their crown projection (=root) areas, even in forests with an otherwise dense bracken vegetation.

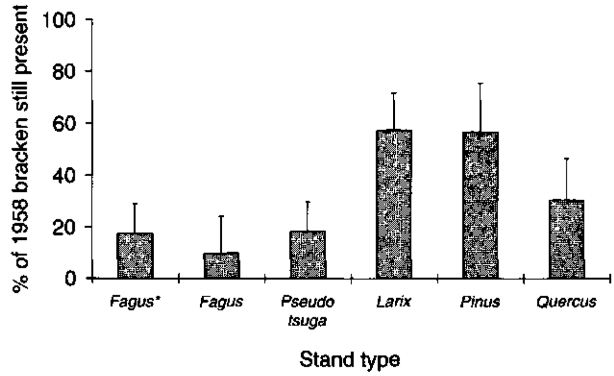


Figure 4.9 Mean percentage of area continuously covered by bracken in 1958, 1985 and 1996 in the six major stand types of the Speulderbos. The percentage is calculated relative to the total bracken cover found in 1958. Error bars represent 95% confidence intervals. Included sites were not cut or converted between 1958 and 1996, and had a bracken cover of at least 10% of the total stand area in 1958.

4.4.3 Modes of colonisation

Lateral expansion

The forest floor is a patchy environment with respect to suitable radiation levels that sustain bracken growth. Since establishment from spores is virtually absent, bracken must colonise new areas by lateral expansion of the rhizome system to escape unsuitable growing conditions. The data show that a significant proportion of the new areas colonised by bracken can be accounted for by invasion through lateral, vegetative spread from the edges of clones. On a spatial scale, this is the case for the area-wide patterns in bracken presence (Fig. 4.2, Table 4.1), as well the patterns within the stands (Table 4.5).

Estimates of the rate of lateral expansion of bracken clones range between 20 $cm \cdot y^{-1}$ in Sweden (Dolling 1996*a*), 20-30 $cm \cdot y^{-1}$ in Finland (Kujala, cited in Watt 1940), 43 $cm \cdot y^{-1}$ in Great Britain (Watt 1954, a 20 year average) and 74 $cm.y^{-1}$ (Watt 1940, a three year average). In this study we deduced a maximum rate of spread of 2 $m.y^{-1}$ from the maps. Fletcher & Kirkwood (1979) report an expansion rate of 2.1 $m \cdot y^{-1}$. This corresponds well with the used rate in this study, but they were growing the plants in a low bulk-density medium in which the growth of the rhizome was not affected by high resistance of soil particles normally present in the field. Therefore, a rate of spread of 2 $m \cdot y^{-1}$ is probably an overestimate, so the proportion of colonised area by bracken accounted for by 'normal' lateral expansion is probably lower that the estimated 58%.

Revegetation

When light levels in the stand decrease, respiratory losses will not be compensated by photosynthesis, and the rhizome system will decrease in size and vigour and reduce frond production. Eventually, the rhizome system will stop producing fronds. The absence of above ground parts (fronds) does not necessarily imply that the subterraneous rhizome is dead or gone. Frond buds of austral bracken (*P. esculentum*) can remain dormant for 10 years (O'Brien 1963). The large amount of dormant buds provide numerous new growth points, making bracken notoriously resilient with respect to mechanical control measures (Marrs *et al.* 1993, Pakeman & Marrs 1994). The relatively large area of bracken appearing in previously unoccupied areas outside the range of lateral expansion does suggest that a change in light availability may induce new frond formation from a suppressed rhizome. Subsequent replenishment of the rhizome system may quickly lead to the formation of a newly established frond canopy.

Bracken is a clonal plant, producing basic constructional unit of two general types: long shoots that are buried deep underground and mostly act as storage rhizome, and short shoots that produce frond buds (Watt 1940). Each rhizome bud is capable of initiating a new subsystem of the rhizome system. The structure that is built by the rhizomes is strongly interconnected, and may show considerable physiological integration. As long as they remain connected the translocation of photosynthates from nearby patches experiencing better conditions (cf. Stuefer *et al.* 1994), may support parts of the rhizome system that are shaded out by a tree canopy, and thus lack fronds.

From Sweden, Dolling (1996*a*) reports of bracken revegetation from an already (or still) present sparse frond canopy after the removal of the *Pinus* / *Picea* canopy. She found a rapid increase in frond density within the first year after clearing, up to 15 m away from the edge of the adjacent bracken front. But does this suggest that the integration of the rhizome system extends over such length, or did the increased frond number arise from smaller, disconnected rhizome systems?
There are often rhizomes present in the soil that precede the advancing front. Generally these are not further than several meters away from the nearest bracken front (Watt 1940, Whitehead & Digby 1995). However, in several stands we found rhizomes that extended over a much greater length, up to 15 m away from the nearest bracken front (Fig. 4.10). Such distantly placed fronds can 'explore' the environment, or escape from a zone with depleted or decreasing resources (Harper 1985). Such rhizomes could be detected because they bore one or a few small fronds placed at irregular intervals along the long shoot. The terminal ends of these long 'spacers' may become nuclei of new colonisation, far beyond the front of the closest bracken clone. It is the ultimate example of a 'guerrilla' strategy (Lovett Doust 1981) in clonal growth forms. On a spatial scale, this mechanism is the same as lateral expansion from existing clones, but it will appear as (re)vegetation of bracken since colonised sites are outside the area of potential lateral expansion.

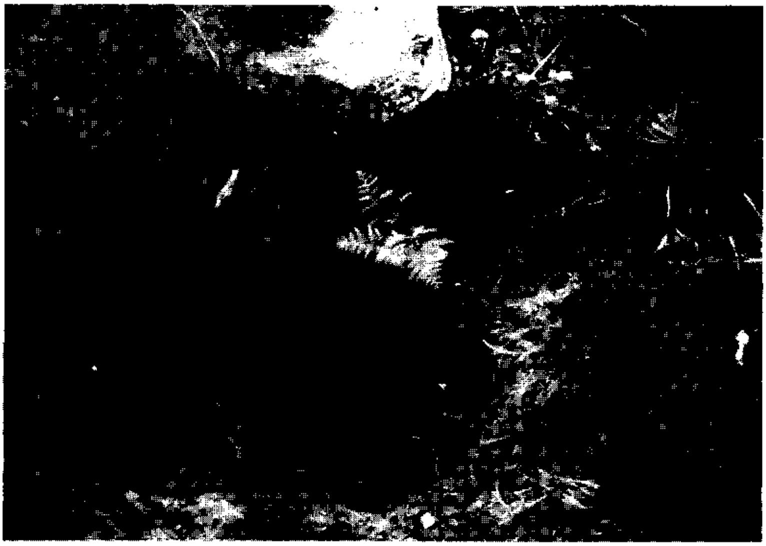


Figure 4.10: A single small bracken frond emerging from the end of a rhizome extending 15 m out of the main bracken front. Such distantly placed fronds and rhizomes can form nuclei of rapid colonisation of new territory well beyond the reach of regular lateral expansion.

However, scattered fronds indicating spacers were very scarce, and can not account for the considerable proportion (42 %) of newly recorded bracken in 1996 that was found outside the range of potential lateral expansion from bracken patches present in 1985 (Table 4.5). At least part of this new cover must have originated from undetected bracken. Allowing for mapping errors, the data indicate that areas with no detectable above-ground presence of bracken may in fact have bracken rhizomes present in a dormant state. It is not known how long such dormant rhizomes may persist. Rhizomes are found well below the soil surface so constant low temperatures reduce respiratory losses and prolong the potential extent of dormancy (i.e. survival of the ramet). Within this time, they can start producing fronds after canopy disturbance, and revegetate the site.

The capacity to form a rhizome bank adds to the persistence of bracken in the changing light environment under the forest canopy. It is analogous to the presence of seed banks in generatively dispersing species (Marks 1974). It also implies that surveys of bracken presence can give no conclusive prediction on short-term colonisation (encroachment) on specific sites without prior knowledge of its distribution in the preceding period.

4.4.4 Conclusions

The lack of sporal regeneration in many areas of north-western Europe restricts the presence of bracken to sites with an extended history of forest cover. Within its forest habitat, the growing conditions for bracken are greatly regulated by the structure and composition of the tree canopy. In single-species stands or pockets of regeneration that are dominated by *Fagus* of *Pseudotsuga*, the dark canopy restricts growth of bracken for several decades of stand development, long enough to completely eliminate bracken presence. Furthermore, root interference by *Fagus* severely restricts bracken growth on soils with low soil water availability. Light levels are sufficient for bracken growth in stands dominated by *Pinus*, *Quercus* and *Larix*, except in young thickets.

The persistence of bracken clones in forests is the result of constant vegetative renewal and lateral spread into favourable patches. Parts of the rhizome located in unfavourable patches may remain supported by parts of the clone that experience sufficiently high light levels to maintain a positive carbon balance. The large proportion of bracken appearing in areas outside the zone of lateral expansion from existing clones suggests that bracken may form a 'rhizome bank' for some time.

In a sense, bracken shows cyclic patterns of change. These patterns are induced by the dynamics of the tree canopy. The cyclic interdigitation described by Watt (1947, 1955) between bracken and other species (in this case *Deschampsia flexuosa*) was not evident. Retreat of bracken was related to changes in light levels, and did not result from interference by grasses.

Bracken dominance of the forest undergrowth greatly reduces, and usually completely blocks, regeneration of tree species. In many cases, this complicates the management of forest stands. Eradication of bracken from forest stands is not feasible by mechanical or chemical means. When bracken poses a problem to forest management, the containment of bracken by planting a fringe of *Fagus* trees in front of advancing clones is the most realistic option. On sites where bracken is already present, its persistence must lead to the acceptance of its presence.

5. Above- and below-ground interference by bracken

This chapter is based on:
Den Ouden, J. (in review) Productivity and ecological functioning of bracken (*Pteridium aquilinum*) under a forest canopy. II. Bracken interference with tree seedlings and the forest undergrowth.

5.1 Introduction

In forests, bracken productivity is directly related to canopy openness, with increased canopy cover resulting in the production of less, and smaller, fronds per m^2, and consequently lower above ground biomass (see chapter 3). Leaf area of bracken rapidly increases with lower canopy cover (Fig. 3.4). Consequently, the light available to the forest undergrowth under bracken canopies may be less than 5% in stands where light interception by the forest canopy is greater than 50% (chapter 3). This implies that bracken effectively reduces available radiation to levels which may hardly sustain other plant growth under the bracken canopy (Tolhurst & Turvey 1992, Humprey & Swaine 1997). Shading is therefore an important mechanism involved in the reduction of plant species abundance and growth in bracken stands.

The negative effects of shading by bracken on the growth of other species appear obvious. The build up of the frond canopy in spring is fully supported by reserves from the rhizome, and fronds rapidly expand to form a dense layer of leaves, overgrowing all other species and casting deep shade. Severely restricted radiation levels subsequently reduce growth and development of sub-canopy species. Simultaneously, however, the frond canopy is supported by an extensive rhizome system (Watt 1940). The resources that are needed to support bracken growth (water, nutrients) have to be extracted from the soil. The uptake of these resources may leave competing species with lower resource levels, and thus restrict growth and development of other species even further. Although root interference is not commonly studied, its importance in plant-plant interactions may be relatively higher than the interference by aboveground plant parts (Wilson 1988).

The main objective of the study presented in this chapter was to determine the effects of above and below ground interference by bracken on the growth of tree saplings. These modes of interference, and their interactions, were studied in a field experiment with tree species of contrasting shade tolerance and rooting strategy. I hypothesised that below ground interference by bracken contributes to the decreased tree seedling growth in bracken stands.
Interference by bracken, regardless of the specific mechanism, will lead to a reduction in presence and abundance of other tree and plant species. In this chapter I will also present results from a study in which I investigated the effects of bracken presence and productivity on the species composition and abundance in the forest undergrowth of stands of different canopy tree species (the same stands that were used in the productivity study of chapter 3). I hypothesised that bracken presence reduces species abundance and changes species composition under the bracken canopy. Since interference by bracken will be related to bracken vigour, I also hypothesised that there is an inverse relationship between bracken standing biomass and number and abundance of forest undergrowth species, including trees.

5.2 Methods

5.2.1 Study sites

This study was conducted in the Speulderbos (for description of the area see 3.2.1 and chapter 4). The experiment studying bracken interference was conducted in two sites between March 1996 and September 1997. One site consisted of a large clearing in a former oak coppice stand, cut in 1983, and since then covered by a dense, uniform vegetation of pure bracken (the open site from chapter 3; Fig. 5.1). The second site was a 42 year old stand of *Pinus sylvestris*, with an understory dominated by bracken, and with interspersed *Dryopteris dilatata* (Hoffm.) A. Gray, *Deschampsia flexuosa* L., *Rubus* sp., and *Vaccinium myrtillus* (Fig. 5.1).

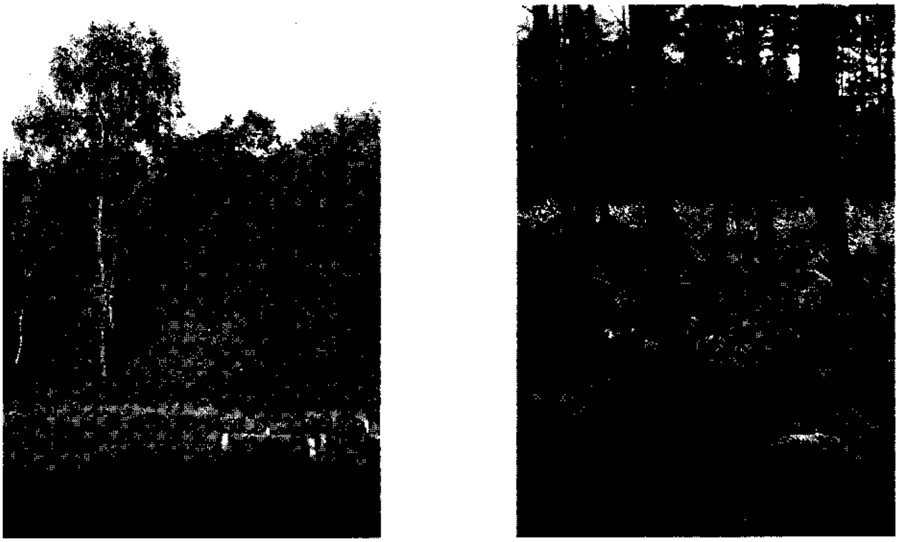


Figure 5.1: The two sites used in the interference experiment. Left: the open site in the clearing. Right: the site in a 43 yr old Scots pine forest.

In the summer and early autumn of 1995, the 12 stands of 3 different tree species of the bracken productivity study (chapter 3) were selected. These included 5 stands of Japanese larch (*Larix kaempferi*), 4 former oak coppice stands, dominated by English oak (*Quercus robur*) with some interspersed Birch (*Betula pendula*), and 3 stands of Scots pine (*Pinus sylvestris*). In each stand, one plot of 10m x 20m was placed in an area dominated by bracken, and another plot in an adjacent area without bracken present in the forest undergrowth. This way, a comparison could be made between plots with equal site history and tree canopies, only differing in the presence of bracken. In each plot, the composition and abundance of the forest floor vegetation was recorded, depth of the organic soil layer was sampled, and number and condition of tree seedlings was determined. Total frond biomass production of the bracken stands and light availability under the forest canopy have been described in chapter 3.

5.2.2 Bracken interference with tree sapling growth

In the spring of 1994, in both the open site and the pine stand an area of 20mx50m was enclosed by a 2 m high fence to exclude deer, wild boar, hares and rabbits from the experiment. Blocks were defined within these exclosures, as strips of 10mx 20 m resulting in 5 blocks in the open site. In the pine stand, 4 blocks were established. Blocks were split in two 10m x 10m sections. In the centre of each section, an experimental area was defined of 5m x 4m (Fig. 5.2). The remaining area was used as buffer zone in which the bracken vegetation was left undisturbed. Two treatments were established in a factorial design, investigating the effects of shading by bracken and the effects of below ground interference by bracken roots and rhizomes on the growth of beech (*Fagus sylvatica*) and Scots pine (*Pinus sylvestris*) saplings. *Fagus* is a shade tolerant, deciduous broad-leaved tree, with a predominantly lateral rooting system. *Pinus* is a less shade-tolerant conifer, and produces a tap root.

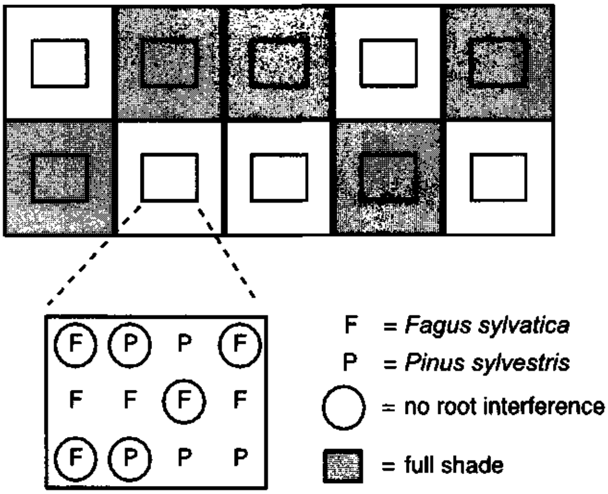


Figure 5.2: Design of the field experiment investigating above- and below ground interference by bracken on the growth of tree saplings.

The shading treatments were randomly assigned to entire sections within blocks (main plots). In one section, bracken fronds were allowed to grow undisturbed, while in the other section bracken fronds were clipped just below the second pair of pinnae. This way, the fronds remained alive, but shading was reduced to a fraction of the light interception by intact fronds. I assumed that in this way the rhizome system was not disrupted as severely as when the entire fronds were removed because fronds remained photosynthetically active. This is relevant because the experiment was set up to study interactions between shading and below ground interference. Less disruptive methods to reduce shading (for instance by bending the fronds) were not feasible because of the large bulk of frond biomass produced on the sites (Table 3.1). During the course of the experiment, newly emerging fronds were clipped each 2-3 weeks.

The effects of below-ground interference were evaluated by excluding bracken roots and rhizomes using PVC tubes driven into the soil at six random positions within each main plot. The tubes were 30 cm long, with a diameter of 15 cm. At locations where saplings were planted without PVC tubes, a square area was cut with a spade of approximately the same size and depth as occupied by the tubes. This way, the treatment with below-ground interference present also contained dead roots and rhizomes that resulted from inserting the tubes.

In the plots, 1-year old saplings of *Fagus sylvatica*, and 2-year old saplings of *Pinus sylvestris* were planted in March 1996, divided equally over the treatments. Saplings were planted in 3 rows of 4 plants, with 1 m between saplings. Saplings were obtained from a commercial nursery, and were of homogenous size and provenance.

In summary, the experiment was set up as a split-plot design, with the shading treatment replicated 5 (or 4) times, the below ground interference treatment replicated 3 times per species within each main plot, resulting in a total of 60 (or 48) saplings per site of each species (Fig. 5.2).

The amount of photosynthetic active radiation (PAR) available to the saplings was measured in 1997 using Licor Quantum-sensors, connected to Licor LI-1000 data loggers (LI-COR, Inc., Lincoln, Nebraska). Per site and shading treatment, three sensors were randomly positioned at 20 cm above the soil surface. Per site, two additional sensors were mounted on 2 m poles to determine light available above the frond canopy. In the open site, this represented total radiation. In the pine forest, this represented radiation transmitted through the tree canopy. Light availability was determined in 4 periods between May and September. 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 above the frond canopy in the open site, between 9.00 AM and 17.00 PM (± 4 hours around solar noon).

After planting the saplings in March 1996, initial height and diameter of the root collar was measured for all saplings. Before planting, 20 saplings of each species were randomly selected. These were dried at 80 °C for 48 hours, and weighed. Weight of stems and branches was regressed against diameter to be able to estimate initial above-ground biomass for the planted saplings from initial diameter.

Total length, length of the leader shoot, and diameter of the saplings were recorded in September 1996 and 1997. At harvest in September 1997, *Fagus* saplings were divided into leaves, 1-yr old branches, and older branches and stems. *Pinus* saplings were divided into 1-yr old needles, 2-yr old needles, 1-yr old branches, and older branches and stems. All plant components were dried at 80 °C for 24 h, except stems which were dried for 48 h. At harvest, samples of 25 leaves or needles from 10 randomly selected individuals of each species were collected from each shading treatment from the two sites. Leaf area was measured using a Licor 1300 Leaf Area Meter, and specific leaf area (SLA) was calculated from dry weight after drying for 24 h at 80 °C. Total leaf area per plant was calculated by multiplying leaf biomass with SLA.

5.2.3 Sampling vegetation, tree regeneration and organic soil depth

For each of the two 10m x 20 m plots in the 12 forest stands, the total percentage of cover was recorded for the canopy tree species, and all vascular plant species and trees smaller than 2 m occurring in the forest undergrowth. Mosses were sampled as a group. Percentage cover was estimated to the nearest unit for cover <10%, and to the nearest 5% for cover > 10%. For each plot the Shannon index of species diversity was calculated for the forest undergrowth. In the plots containing bracken, the cover of bracken was not included in the calculation of species diversity.

Within each plot, 10 circular 5 m^2 subplots were randomly placed on the forest floor, and all tree seedlings and saplings present were counted by species. Plants that had germinated in the spring of the sampling year were recorded separately. For each individual, the amount of damage due to herbivory was assessed using three damage classes, with 0 = no signs of herbivory, 1 = minor damage (less than 50% of the plant damaged), and 2 = major damage (more than half of the plant browsed by herbivores). Major herbivores occurring in the study area include roe deer (*Capreolus capreolus* L.) and red deer (*Cervus elaphus* L.).

Within each subplot, the organic soil layer was sampled on 3 randomly selected locations. The organic soil layer was defined by the ectorganic soil (O) horizons, subdivided into a litter and upper fermentation (LF1) layer, the lower fermentation (F2) layer, and humus (H) layer, and the upper (A) horizon of the mineral soil compartment (Green *et al.* 1993, Emmer 1995). The 3 samples were averaged to obtain organic soil depth per subplot.

5.2.4 Data analysis

The effects of above- and below-ground interference by bracken were analysed using a split-plot design with the factor shading by bracken entered as main effect, and the factor below ground interference was tested within the subplots (Snedecor & Cochran 1989). All biomass data were $\log_{10}$-transformed prior to analysis.

Differences in ectorganic soil layers between stand types were tested nonparametrically using the Kolgomorov-Smirnov test (SPSS 1996). Data on tree regeneration were pooled over the ten $5m^2$ subplots to obtain total number of seedlings (< 1 year old) and saplings (>1 year old), representing 50 m^2. Data were square-root transformed prior to analysis (Sokal & Rohlf 1995). The effect of canopy tree species and presence of bracken on total number of seedlings was tested using ANOVA (n = 24). Post hoc comparisons were made using Tukey's HSD-test.

Effects of bracken presence on browsing damage to saplings were evaluated using a test for Goodness of fit, with Williams' correction for small sample size (Sokal & Rohlf 1995).

5.3 Results

5.3.1 Interference experiment

Initially, frond clipping resulted in the emergence of significantly more fronds in the clearing as compared with the treatments were bracken fronds were left intact (Table 5.1). This is common reaction of bracken to cutting (Lowday *et al.* 1983). During the course of the experiment, the bracken growing within the experimental areas on both sites suffered a reduction in number of fronds in all treatments. This was most likely the result of trampling while visiting the plots over several years. Consequently, the shading by bracken was less than could normally be observed in bracken stands (chapter 3, Humphrey & Swaine 1997).

Table 5.1. Mean number of fronds per m^2 (± 1 se.) in the experimental areas of the field experiment in 1994 (first year after site preparation) and 1997 (at the end of the experiment). Means are averages of three samples per plot, with n = 5 per shading treatment in the site without tree canopy, and n = 4 in the pine forest.

Year:	1994		1997	
Shade treatment:	no canopy	pine forest	no canopy	pine forest
fronds left intact	33.1 ± 4.1	18.7 ± 2.2	13.2 ± 1.3	6.6 ± 0.8
fronds clipped	52.8 ± 4.5	14.5 ± 1.2	8.9 ± 0.6	4.8 ± 0.4

Light availability was reduced by bracken only well into the growing season (Fig. 5.3). In the clearing, light availability was not different between treatments until the beginning of June. In August, when frond biomass peaked, the light availability in plots without heavy bracken shading was 60% of the total light available. In the plots with intact fronds, light levels had dropped to 20% relative to the open (Fig. 5.3). In the pine stand, the canopy reduced total available radiation to 35% of the light above the canopy. Additional light reduction due to bracken shading was relatively low, and did not differ between light treatments (Fig. 5.3). Note that in summer the total light availability was similar between the forest plot and the intact bracken frond plots in the clearing. During the autumn and winter of 1996-1997, all *Pinus* saplings in the pine stand died after infestation by fungi, mostly *Lophodermium*, *Sclerophoma* and *Sphaeropsis*, and were thus not included in the analysis.

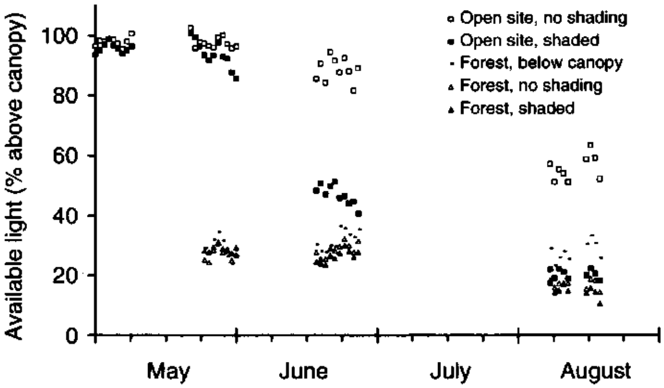


Figure 5.3: Mean daily percentages of photosynthetically active radiation (PAR) in the second year of the field experiment, relative to total available PAR above the canopy in the two study sites, in plots with or without shading by bracken. Each point represents the mean of integrated half hour readings between 9.00 and 17.00 h.

In the site without a forest canopy, sapling performance of both tree species was significantly affected by bracken shading (Fig. 5.4, Table 5.2). For *Fagus*, reduction of shading by bracken resulted in significantly larger diameters ($F_{1,8} = 31.1$, $P < 0.001$), greater plant heights ($F_{1,8} = 8.7$, $P = 0.018$) and higher total above ground biomass ($F_{1,8} = 9.6$, $P = 0.015$). Leader length was not different between shading treatments (Table 5.2). Specific leaf area of *Fagus* saplings did not differ between shading treatments, so the overall mean SLA was used (186 ± 9 $cm^2 \cdot g^{-1}$; mean ± 1 se.) to calculate total leaf area. Leaf area was significantly lower ($F_{1,8} = 7.1$, $P = 0.028$) in the plots with heavy shading by bracken (Table 5.2).

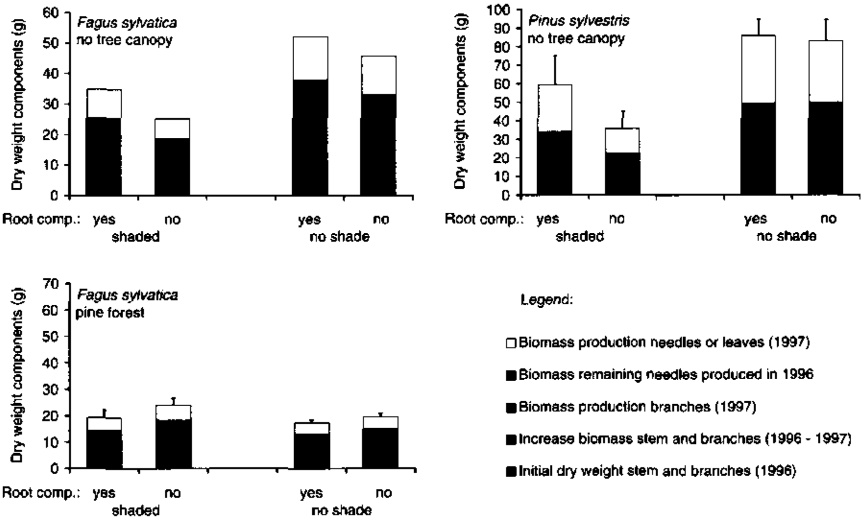


Figure 5.4: Above-ground biomass of *Fagus sylvatica* (top) and *Pinus sylvestris* (bottom) saplings in a site without tree canopy (left) or in a Scots pine forest (right). Saplings were subject to treatments with or without root competition, and with full or reduced shading by bracken fronds. Final biomass was divided into different plant components. Initial dry weight of stem and branches was estimated from regressions of biomass against diameter. Error bars represent 1 standard error of total biomass.

Pinus saplings were significantly higher ($F_{1,8}$ = 11.3, P = 0.008), had longer leader shoots ($F_{1,8}$ = 7.7, P = 0.022), larger diameters ($F_{1,8}$ = 12.0, P = 0.008) and higher total above-ground biomass ($F_{1,8}$ = 15.5, P = 0.004) when experiencing reduced shading by bracken in the open site (Table 5.2). Specific leaf area was significantly higher (t = 2.36, df = 18, P = 0.015) in the shaded plots (53.0 ± 3.2 $cm^2 \cdot g^{-1}$) as compared with the plot with reduced bracken shading (44.8 ± 1.5 $cm^2 \cdot g^{-1}$). Total leaf area was not significantly different between shading treatments for *Pinus*, although total needle biomass produced in the second year was significantly higher ($F_{1,8}$ = 13.0, P = 0.006) in plots with reduced shading (Table 5.2, Fig. 5.4).

Table 5.2: Effects of above- and below-ground interference by bracken on final plant size and above ground biomass of 3 year old *Fagus sylvatica*, and 4 year old *Pinus sylvestris* saplings, after two growing seasons in a pine forest and a large forest clearing (no tree canopy). Numbers indicate treatment means, with standard error in brackets. Within rows, different letters indicate significant differences ($P < 0.05$) between means.

Light treatment	Shaded by bracken				Light shade from bracken			
Root interference	yes		no		yes		no	
Fagus sylvatica in pine forest								
Diameter (mm)	9*a*	(0)	10*a*	(0)	9*a*	(0)	10*a*	(0)
Plant height (cm)	73*a*	(6)	81*a*	(6)	71*a*	(5)	79*a*	(3)
Leader Length (cm)	26*a*	(5)	33*a*	(5)	29*a*	(4)	28*a*	(2)
Aboveground biomass (g)	19*a*	(3)	24*b*	(3)	17*a*	(1)	20*a*	(1)
Leaf area (dm^2)	13*a*	(2)	15*a*	(2)	11*a*	(1)	12*a*	(1)
Fagus sylvatica, no tree canopy								
Diameter (mm)	11*a*	(1)	10*a*	(0)	13*b*	(1)	13*b*	(0)
Plant height (cm)	79*a*	(7)	78*a*	(5)	95*b*	(5)	87*b*	(4)
Leader Length (cm)	32*a*	(5)	35*a*	(4)	42*a*	(4)	42*a*	(3)
Aboveground biomass (g)	35*a*	(8)	25*a*	(3)	52*b*	(8)	46*b*	(5)
Needle area (dm^2)	17*a*	(4)	12*a*	(1)	26*b*	(4)	24*b*	(2)
Pinus sylvestris, no tree canopy								
Diameter (mm)	15*a*	(2)	12*a*	(1)	18*a*	(1)	18*a*	(1)
Plant height (cm)	54*a*	(6)	51*a*	(5)	63*a*	(4)	64*a*	(3)
Leader Length (cm)	21*a*	(3)	17*a*	(3)	23*b*	(2)	25*b*	(2)
Aboveground biomass (g)	59*a*	(16)	36*a*	(9)	86*b*	(9)	83*b*	(11)
Needle area (dm^2)	13*a*	(4)	7*a*	(2)	16*a*	(2)	15*a*	(2)

For *Fagus*, the results from the pine stand were in contrast to the open site. Shading by bracken had no effects on diameter, plant height, leader length or total above-ground biomass (Table 5.2). Specific leaf area was also not different between shading treatments, but overall SLA (267 ± 5 $cm^2 \cdot g^{-1}$) was significantly higher ($t = 8.0$, $P < 0.001$) as compared with SLA from the open site.

The exclusion of interference by bracken roots and rhizomes had no significant effects on any of the measured variables for both species in the site without a forest canopy (Fig. 5.4, Table 5.2). In the pine stand, however, *Fagus* saplings growing in the tubes had produced significantly higher above ground biomass ($F_{1,35} = 4.4$, $P = 0.044$) as compared to saplings that were exposed to below-ground interference by bracken and by canopy trees (Fig. 5.4).

5.3.2 Forest undergrowth

In the 12 studied forest stands, the vegetation composition and abundance was strikingly similar among the three different canopy tree species in the 10x20 m plots without a bracken canopy (Table 5.3). The forest undergrowth in all stands was dominated by *Deschampsia flexuosa* and *Vaccinium myrtillus*, the most common forest grass and dwarf shrub species occurring in Dutch forest stands on well drained sandy substrates. Other relatively abundant species occurring evenly over all stand types were *Dryopteris dilatata*, *D. carthusiana* (Vill.) H.P. Fuchs, and *Rubus* sp. The only well represented annual *Ceratocapnos claviculata* (L.) Lidén, and *Galium saxatile* L., were found only in *Larix* and *Pinus* stands. *Lonicera periclymenum* L. was abundant only in the *Quercus* stands (Table 5.3).

The presence of bracken caused a strong reduction in abundance and number of species in the forest undergrowth (Table 5.3). The dominance of *D. flexuosa* and *V. myrtillus* was considerably less in the bracken stand, and cover of all other species was reduced likewise. The only exception was *L. periclymenum*, which was found in approximately the same abundance in plots with or without bracken in the *Quercus* stands. Total moss cover was also similar between the plot pairs in the stands (Table 5.3). Consequently, the presence of bracken had a marked effect on species diversity in the forest undergrowth. Total number of species present in the 200 m^2 plots dropped from 13.7 ± 1.2 (mean ± se.; n = 12) in plots without bracken to 7.8 ± 0.9 in plots dominated by bracken (Table 5.3). The Shannon index of species diversity was significantly lower in the presence of a bracken canopy ($F_{1,18} = 40.6$, $P < 0.001$), but was not affected by canopy tree species (Fig. 5.5a). The difference in species diversity between bracken and non-bracken plots was greater in *Larix* and *Pinus* stands than in the *Quercus* sites (Fig. 5.5a). Species diversity was negatively correlated with the total amount of frond biomass in the plot (r = -0.666, n = 12, $P = 0.018$; Fig. 5.6).

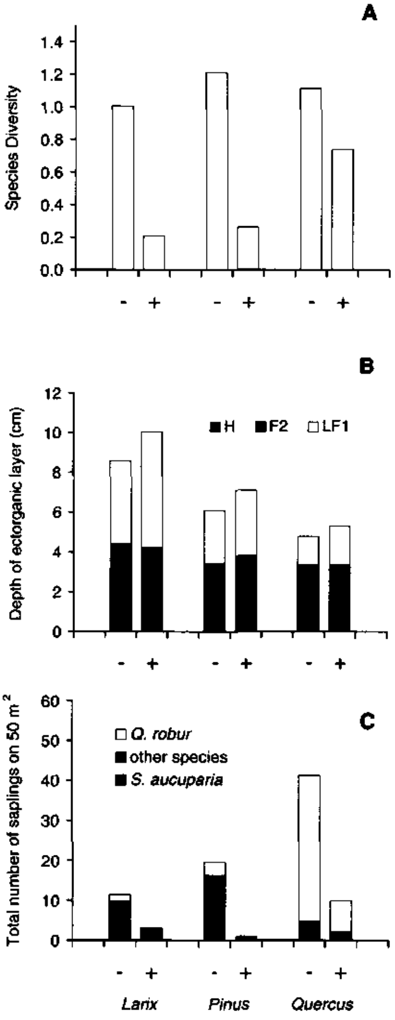


Figure 5.5: Means of the Shannon index of species diversity (A), depth of organic soil layers (B), and total number of saplings on 50 m^2 (C) in plots with (+) or without (-) bracken in the forest undergrowth, separated by canopy tree species. Error bars represent 1 standard error. Ectorganic soil layers were separated into litter and upper fermentation layer (LF1), lower fermentation layer (F2) and humus (H) layer.

5.3.3 Ectorganic soil profiles

Both the canopy tree species and the presence of bracken in the undergrowth had an impact on the total depth of the ectorganic soil layer (Fig. 5.5b). Stands of *Larix* and *Pinus* had the deepest ectorganic soil layers, with particularly thick LF1 layers. Stands of *Quercus* had the shallowest ectorganic layer, approximately half as deep as under *Larix*. Between stand types, differences in the total depth of the ectorganic soil layer were all significant ($P < 0.01$). Concurrently, the humus (H) horizon was significantly more developed under *Quercus* than under the two coniferous species ($P < 0.03$, Fig. 5.5b). Within the 12 sites, the total depth of the ectorganic soil layer was significantly higher under the bracken stands as compared to the undergrowth without bracken (Wilcoxon's Z = -2.09, N = 12; $P = 0.036$). There were no interactions between bracken presence and canopy type on humus type or depth.

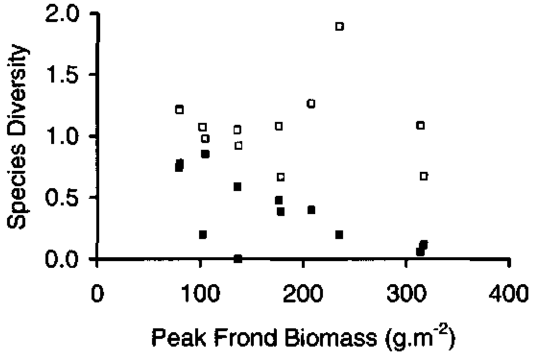


Figure 5.6: Shannon- indices of species diversity in 200 m^2 plots inside (solid markers) bracken stands, in relation to peak frond biomass. Species diversity of adjacent plots without bracken are indicated by open markers.

Table 5.3: All vascular plant species occurring in 200 m^2 plots inside and outside bracken stands in the 12 study sites. Data represent percentages of cover: + : only one or few individuals present; ++: percentage cover = 0.5; *na* = data not available

	No bracken in undergrowth												Bracken present in undergrowth											
Stand type:	*Pinus*			*Larix*					*Quercus*				*Pinus*			*Larix*					*Quercus*			
Canopy trees																								
Pinus sylvestris	55	30	70										55	30	70									
Larix kaempferi	5			60	40	*na*	40	60					5			60	40	*na*	40	60				
Quercus robur									75	90	90	90									70	80	70	90
Betula pendula									5			3									10	5	20	2
Quercus rubra																						5		
Shrubs, tree seedlings, herbs and grasses																								
Pteridium aquilinum													85	95	75	95	90	96	95	90	75	70	60	60
Deschampsia flexuosa	15	20	80	30	40	25	70	75	10	60	40	70	10		3	5	5		++		10	5	4	5
Vaccinium myrtillus	1	20	2	40	30	1	20	++	50	5	40	30		++	++	5	5	++	++		15	10	10	10
Lonicera periclymenum		1	1						15	5	2	++		++			++				5	10	6	
Carex pilulifera		++	++		++	++		++		++	++							+			++	++	++	++
Dryopteris dilatata	++	15	5				1	1	2		1	++	++										++	++
Sorbus aucuparia	++	1	1	1	2	++	++	1	++	++	1				+	++	++				++	2	1	
Rubus fruticosus	++	1	1	++	1		1	2			++	++		+	++			++			+	+		
Quercus robur		10	1	2	1		++	1	3	3	3	4		2			+				++	++	++	1
Fagus sylvatica		2	+	++			1	++	+	3	3	8	++			++			+		+		++	3
Dryopteris carthusiana		1	1	2	1	1	1	1		++	1	++		++	++	++								
Ceratocapnos claviculata	1	1	1	1		++	1	1	++	++			++		+	++								
Rhamnus frangula		2	1	++	++		++	2	++					+										
Galium saxatile		5	3		5		5							++		1	++						++	
Molinia caerulea		1	2		1				1								+							

continued on next page

Table 5.3: *continued*

	No bracken in undergrowth												Bracken present in undergrowth											
	Pinus			*Larix*					*Quercus*				*Pinus*			*Larix*					*Quercus*			
Pinus sylvestris	++		++					+					++											
Picea abies	++	++				+																		
Pseudotsuga menziesii	++	++	+			++	++	+																
Larix kaempferi			+			1		+					++				+	++						
Betula pubescens			++			1		++								++		++						
Quercus rubra			+					+		++												++	+	
Prunus serotina			1				++	++	++	++											+	2	++	
Betula pendula		1			++			++			+		++											
Ilex aquifolium	++								+												+			
Luzula multiflora		++	+					2																
Tsuga heterophylla	++																							
Holcus lanatus	++																							
Agrostis capillaris	++				1																			
Amelanchier lamarckii				++																				
Chamenaerion angustifolium						++																		
Rumex acetosella	++							++																
Sambucus nigra								++																
Galeopsis tetrahit										++														
Hedera helix																					+			
Castanea sativa										+														
Mosses	2	30	90	85	80	70	80	90	1	2	2	3	20	40	50	95	75	60	90	90	2	1	2	1
Bare litter	80	10	5	2	2	10	2	3	75	40	60	30	60	60	40	3	20	40	10	10	90	95	95	95
No. Species	14	18	21	10	12	11	13	21	12	13	11	8	8	8	7	9	9	6	4	1	12	10	12	7
Diversity[1]	0.7	1.9	1.1	1.1	1.3	0.7	1.1	0.9	1.2	1.0	1.2	1.0	0.4	0.2	0.2	0.5	0.4	0.1	0.1	0.0	0.8	0.9	0.7	0.6

1. Shannon index of diversity ($-p_i{*}\ln(p_i)$). Diversity is calculated excluding bracken cover.

5.3.4 Tree regeneration

In total 12 different tree species were found in the plots as saplings >1 year old. Total tree regeneration was significantly lower in the plots dominated by bracken ($F_{1,11} = 19.4$; $P = 0.001$; Fig. 5.5c). There were no significant effects of canopy tree species on the total number of saplings. Saplings of *Pinus sylvestris* were completely absent in the sample plots, and only a few individuals occurred in the Scots pine sites (Table 5.3). This was in contrast with the relatively high number of *Pinus* seedlings (<1 year old) found in pine stands. Within pine stands, the number of *P. sylvestris* seedlings was higher in plots without bracken (155 ± 166 ; mean ± sd., n = 3) as compared to the bracken plots (30 ± 49). This difference was not significant but indicates, however, that germination conditions are affected by bracken as well as growing conditions for the established saplings.

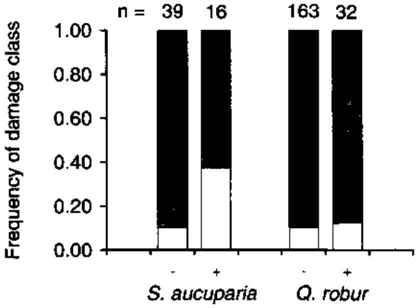


Figure 5.7: Frequency distributions of damage from herbivory to saplings of *Sorbus aucuparia* and *Quercus robur* in plots without (-) or with (+) bracken in the forest undergrowth. Herbivory damage classes represent no damage (white bars), slight damage (hatched bars), and heavy damage (black bars). Data are pooled over 12 study sites. N indicates total number of seedlings.

Most frequently found sapling species were *Sorbus aucuparia* and *Quercus robur*. Saplings of *S. aucuparia* were fairly evenly distributed over the stand types and plot pairs, while *Q. robur* was mostly restricted to the oak stands (Fig. 5.5c). Together, these two species made up about half of all tree regeneration in the *Larix* and *Pinus* stands. Both *S. aucuparia* and *Q. robur* saplings showed considerable damage by browsing. To analyse possible effects of the presence of bracken in the undergrowth on browsing damage, data on browsing were pooled over all sites for each species (Fig. 5.7). The proportion of heavily damaged plants was smaller in the plots with bracken in both species. For *S. aucuparia*, the distributions of damage classes were significantly different between the plots with and without bracken (G_{adj} = 26.7, df = 2, $P < 0.001$). The distributions of damage classes for *Q. robur* were not significantly different (G_{adj} = 4.82; P = 0.09; Fig. 5.7), but the same trend was present as in *S. aucuparia*.

5.4 Discussion

5.4.1 Interference by bracken

This study demonstrates the dominant role of light interception by the frond canopy in preventing tree species from establishment and survival in bracken stands (Watt 1919, Tolhurst & Turvey 1992, Humphrey & Swaine 1997). When shading by bracken was reduced, performance of the saplings greatly increased for both *Fagus* and *Pinus*, despite the relatively low density of bracken fronds at the end of the experiment (Table 5.1). The negative effect of bracken shading on the growth of tree regeneration will even be more pronounced in undisturbed bracken stands. Productivity of bracken is largely determined by light availability under the forest canopy, and morphological plasticity of the bracken fronds enables the fern to maintain a high total leaf area, even under relatively low light conditions (chapter 3). The remaining light that is transmitted through the tree canopy is thus effectively intercepted by bracken and reduced to levels that severely restrict the growth of other plants.

The results from this study indicate that below-ground interference by bracken is negligible. However, the methodology used poses some constraints on the conclusions that can be drawn from the data. Planting seedlings inside tubes not only excluded roots and rhizomes of bracken, but also confined the available rooting space for the saplings. It appears that this confinement caused a reduction of growth in both *Fagus* and *Pinus* saplings, especially when plants were shaded by bracken in the open site (Fig. 5.4). This negative effect was stronger than the potentially positive effect of excluding the below ground interference by bracken. Frequently clipping the fronds probably caused increased root growth to support the renewal of frond biomass, which could induce increased root interference by bracken and mask the negative influence of root confinement in the unshaded treatments.

On the other hand, however, *Fagus* saplings in the pine stand produced significantly more above ground biomass when growing inside the tubes as compared with the saplings growing without tubes. Part of this result may be explained by reduced root production in the low light conditions under the tree canopy (a low root/shoot ratio). The soil volume needed to accommodate the root system was probably lower for *Fagus* in the pine stand, reducing the differences between treatments due to root confinement. Furthermore, the roots of the canopy trees were excluded by tubes as well. I suggest that root interference by the Scots pine stand is the most probable cause of the difference in *Fagus* sapling growth between plots in treatments with or without below-ground interference present. The reduction of growth (Fig. 5.4) and abundance (5.5a) of tree saplings in bracken stands is therefore not attributable to below ground interference by bracken. This is in line with the low amount of roots that are attached to bracken rhizomes (Whitehead *et al.* 1995, pers. observ.).

5.4.2 Bracken and forest undergrowth composition

The presence of bracken has a pronounced effect on the species abundance and tree seedling density in the forest undergrowth (Table 5.3, Fig. 5.5c). Only saplings of *Sorbus aucuparia* and *Quercus robur* were encountered in greater numbers. These represent tree species with relatively large seeds and are dispersed by birds or small rodents within the forest. Their young seedlings have initial reserves to sustain growth under the low light conditions in bracken stands. Larger saplings (>1 m) of these species, however, are not present. Concurrently, bracken strongly reduces the number and abundance of plant species present on the forest floor. This depends on tree canopy openness. When light availability under the tree canopy is reduced, bracken frond production and subsequent shading is also lower. This results in a decreased impact of bracken on composition and abundance of the forest undergrowth (Table 5.3, Fig. 5.6).

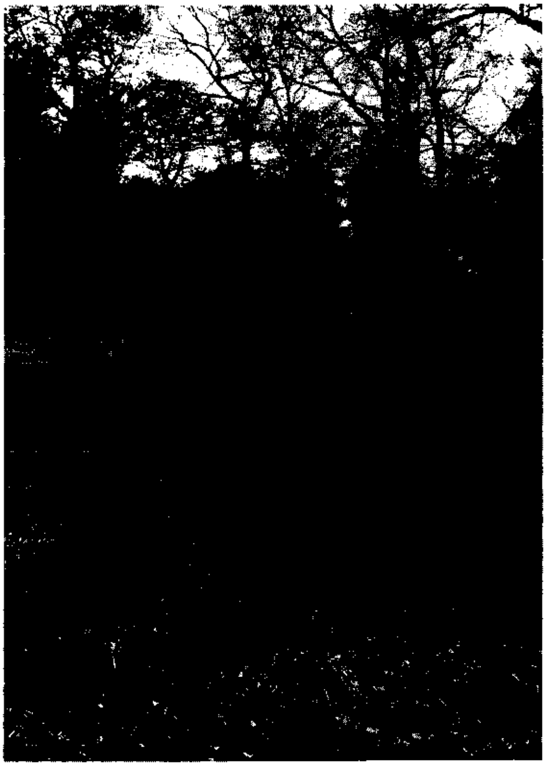
The net effect of shading by bracken is related to the phenology of bracken and co-occurring species. In the study area, fronds emerge early May, and are only fully grown by the end of July (Fig. 5.3). Most tree species in north-western Europe flush at the end of April or the beginning of May (Kramer 1996), so the interference by a fully expanded bracken canopy is present only well into the growing season (Humprey & Swaine 1997). Saplings of evergreen coniferous tree species are able to start photosynthesis when temperatures start to rise in early spring (Ledig & Botkin 1974), well before bracken fronds emerge. This implies that coniferous tree species will be able to grow without direct shading by the bracken canopy for about 4 months in the study area, greatly reducing the light interference by bracken on growth of these species. In the field experiment, the reduction in biomass of *Fagus* and *Pinus* saplings in the shade treatments were approximately the same (61% and 56% respectively, relative to unshaded treatments, see Table 5.2). This similarity is in contrast with the differences in shade tolerance of the two species. Therefore, the capacity of photosynthesis in late winter and early spring probably gives an advantage to conifers in bracken swards (cf. Marrs & Hicks 1986). Winter photosynthesis can also explain the similarity in cover of mosses between plots with or without bracken (Table 5.3).

5.4.3 Conclusions

Direct shading by the bracken canopy greatly reduces growth and development of tree saplings. The relative growth reduction is larger when bracken can grow unchecked by the tree canopy. The rhizomes and roots play an insignificant role in the interference of bracken with other species. Under a tree canopy, interference by tree roots is probably much more important. However, methodological constraints prevent a definitive conclusion, since the use of inserted tubes confines the root system of the tree saplings.

The presence of bracken in the forest undergrowth greatly reduces presence and abundance of other vascular plant species, including trees. Species diversity and cover are relatively less affected when bracken productivity is reduced by tree canopy shading. When more than 30% of light is available for bracken, the frond canopy effectively blocks all other plant growth. Differences in phenology with bracken enable a number of species to remain present in the vegetation, despite heavy shading by the bracken canopy later in the season. Well established tree saplings appear to be less affected by large herbivore browsing in bracken stands.

6. Bracken litter and tree establishment



This chapter is based on:
den Ouden, J. & Vogels, D. (1997) Mechanical resistance by an ectorganic soil layer on root development of seedling *Pinus sylvestris*. *Plant and Soil* 197: 209-217.

6.1 Introduction

Litter input and the subsequent build-up of an ectorganic soil profile can have a strong influence on species composition and abundance in plant communities (Sydes & Grime 1981*a*, Molofsky & Augspurger 1992). Numerous studies have shown a negative relationship between the presence of an organic soil layer and plant performance, which could generally be attributed to germination failure (Marshall & Jain 1970, Hamrick & Lee 1987), chemical interference by toxic substances (Nilsson & Zackrisson 1992), or physical hindrance of emerging shoots from below ground meristems (Koroleff 1954, Sydes & Grime 1981*b*). However, the majority of these studies have only regarded the effects of the freshly fallen litter layer, and have not explicitly considered the lower ectorganic soil layers.

When decomposition is slow, annual litter input will result in the build-up of an ectorganic soil profile. This is established by the increase in depth of the fermentation (F) and the humus (H) layers (Klinka *et al.* 1981, Emmer 1995). These layers are considerably different from the litter (L) layer, which only represents the youngest, physically and chemically unaltered, input of fallen organic material on top of the soil surface. From a physical point of view, the fermentation and humus layer have a higher bulk density (Emmer 1995), contain much smaller particles (Bisdom *et al.* 1996), and create more favourable moisture conditions when compared to the litter layer.

The fermentation and humus layer of the ectorganic soil profile create a physical and chemical barrier for seeds and seedlings after they have germinated in the upper layers and try to reach the "safe" mineral soil (Martin & Sparke 1982, Klein *et al.* 1991). Similar to emerging seedlings (Winn 1985, Molofsky & Augspurger 1992), or leaves and shoots from subterraneous meristems (Sydes & Grime 1981*b*), the descending root of a seedling may be mechanically impeded by the ectorganic soil layers. Mechanical forces acting on the root tip have a strong impact on root development (Hettiaratchi 1990, Bengough & MacKenzie 1994), so mechanical properties of the ectorganic layer can be expected to have a potentially strong influence on the establishment of seedlings that have germinated on top of the ectorganic soil profile.

The presence and thickness of an ectorganic soil layer in bracken stands has a pronounced negative effect on the diversity and biomass of associated plant species (Pakeman & Marrs 1992*a*). Bracken can produce a massive amount of litter each year (Fig. 6.1). Annual production of frond biomass may be as high as 10-14 $Mg \cdot ha^{-1} \cdot yr^{-1}$ (Pearsall & Gorham 1956, Al-Mufti *et al.* 1977), resulting in low light conditions under the frond canopy during the growing season (Pitman 1995), and in a large annual litter input to the soil surface. Because bracken litter is highly resistant to decomposition (Frankland 1976), dominance of bracken usually results in an increased depth of the ectorganic soil layer (Watt 1976; see 5.3.3).

Figure 6.1: Decaying fronds in a dense bracken sward.

In this chapter we set out to investigate the effect of the physical resistance by the ectorganic soil profile on the downward extension of roots to the mineral soil. In a mineral soil environment, a higher penetration resistance (generally characterised by increased bulk density) of the substrate results in reduced root length, and increased diameter of the root (Blom 1978, Bengough & Young 1993). The forces generated by the granular particles may be assumed to be equal from all directions (Hettiaratchi 1990). This is in contrast with an ectorganic soil, where humus particles are packed in more or less horizontal layers. This will result in a higher penetration resistance in a vertical direction, and smaller resistance between the particles in a horizontal direction.

We hypothesised that roots growing through a humus layer will tend to grow around the organic particles, taking a route of least resistance by following the air pore structure, rather than grow straight through the particles. Because of the differential penetration resistance, this may result in a horizontal component in the direction in root elongation, and thus reduce the depth reached by the root relative to total root length. Disturbance of the ectorganic soil layers will lead to a less pronounced horizontal layering of humus particles, and could therefore enhance root growth through the ectorganic layers.

Figure 6.2: Detail of the sampled ectorganic soil layer in a dense bracken sward in the Weenderbos (study site). The tip of the pen is located at the top of the mineral soil, and directly above the tip of a young developing frond bud.

The objectives of this study were to determine the responses in root growth of tree seedlings to differences in bulk density of the ectorganic layer from a bracken stand. We also investigated whether disturbance (mixing) of the fermentation and humus layers has an impact on root growth, as compared with an undisturbed ectorganic soil profile of equal bulk density.

6.2 Methods

We grew Scots pine (*Pinus sylvestris*) seedlings in pots using three treatments containing the ectorganic soil substrate from a bracken stand, representing two bulk densities of mixed substrate, and an intact soil profile. Two extra treatments with similar bulk densities were set up using commercial garden peat. The peat treatments were included to account for the influence of differences in organic substrate type, and possible allelopathic effects of the bracken substrate (Gliessman 1976). Furthermore, half of all organic treatments received continuous watering, while the other half was allowed to dry out, which enabled us to assess the effect of desiccation of the substrates on root development. Finally, we prepared a series of pots containing a sandy medium with three different bulk densities to be able to compare the responses of roots to changes in bulk density between organic and mineral substrates.

6.2.1 Preparation of treatments

We collected the ectorganic soil substrate from a dense bracken stand in the Weenderbos, a nature reserve in the north of the Netherlands (Nat. Grid Ref. 271-558). This stand occupies an open area, surrounded by forest, and is completely dominated by bracken. The open area was already present on a 1852 map, and has probably been continuously covered by a bracken vegetation to the present day (H. Koop, unpubl. data). In the centre of this stand, a relatively deep (10-20 cm) ectorganic layer has developed, on top of loamy sand (Fig. 6.2).
We randomly located 10 plots of 1 m^2, within an area of approximately 200 m^2. From each plot we collected the entire soil organic layer, but excluding the fresh litter, from an area of approximately 0.25 m^2. This material was put in a bag, thoroughly mixed, and transported to the greenhouse to be used for the mixed bracken treatments. From each plot, we further took three soil cores by pressing a PVC tube (10 cm long, 10 cm diameter) vertically through the ectorganic layers until the mineral soil was reached. Total height of the ectorganic profile in the tubes was 8 cm on average. The bottom of the tubes was closed by 5 mm mesh polyethylene netting to secure the soil profile in the tube. From this set, 12 randomly selected tubes were used in the experiment as the 'intact' treatment.

We determined the bulk density of the organic profile in the field at each sample point (n = 30) by taking a fixed volume (70 cm^3), drying this for 24 hours at 70 °C, and dividing the dry weight by the known volume (Table 6.1). Four sets of 12 PVC tubes were then filled with 8 cm of garden peat, or the mixed organic material collected in the field. The bulk densities of the material in these tubes were predetermined to be the same ('loose' treatment), and twice ('compact' treatment) the bulk density of the bracken substrate in the 'intact' treatment. Therefore, experimental treatments included two types of substrate (bracken organic soil and peat), each of two 'mixed' bulk densities, and an intact profile (bracken soil only) (Table 6.2).
For each treatment, we used 4 extra pots to check the bulk density (Table 6.1). Also, we determined total pore volume in the substrates using a picnometer (Russel 1949). The percentage of pore volume containing air was calculated to check whether the increased compactness of the substrates could potentially cause anaerobic conditions in the treatments. This was not the case (Table 6.1; see Bengough & Young 1993).

Table 6.1: Pore volumes filled with water and air (as % of total), and bulk densities of the substrates used in the experiments (n = 4).

Substrate	Compactness	Pore-volume (%)		Bulk Density
		Water	Air	(g·cm^{-3})
Bracken	Intact	30.1	62.1	0.09
	Loose	20.8	70.9	0.07
	Compact	49.3	38.7	0.15
Peat	Loose	10.9	79.6	0.09
	Compact	30.5	55.3	0.17
Sand	Loose	20.7	60.9	0.37
	Intermediate	28.9	46.7	0.52
	Compact	35.1	32.7	0.67

To study root growth in sand, 3 x 3 pots (1 l) were filled with a 1:1:1 mixture of sand, potting soil and sphagnum peat. Three levels of compactness were obtained by filling the pots with 8 cm of different quantities of the sandy mixture, resulting in bulk densities of 0.37, 0.52, and 0.67 g·cm^{-3} (Table 6.1).

6.2.2 Experimental procedure

The experiments were conducted in a greenhouse during May 1995. Temperatures were held constant at 20 °C, with 50% relative air humidity. The pots were dug randomly into a greenhouse bedding containing peat, with the top of the substrate in the pots level with the bedding surface. In each pot we planted 5 pre-germinated *Pinus sylvestris* seeds, obtained from a commercial seed orchard (provenance: Grubbenvorst). The plants were grown under ambient light.

All treatments containing an organic substrate were further divided into two groups. One group of pots was watered regularly (every 3-4 days) during the experiment. The other group was watered for one week to help the transplanted seeds to establish, but did not receive any water during the remainder of the experiment. This treatment was used to assess the possible consequences to root development of desiccation of the organic substrate. The pots containing sandy substrate were watered regularly. See Table 6.2 for an overview of the experimental design concerning the organic substrates.

Table 6.2: Experimental design and treatments included in the analyses of variance for evaluation of root growth in mixed organic substrate (Anova1), or in bracken substrate only, including an undisturbed, intact profile (Anova2).

		Factors:		Treatments included in:	
Harvest time	Watering	Substrate	Compactness	Anova1	Anova2
2,3,4 weeks	continuous	bracken	intact	-	x
		bracken	loose	x	x
		bracken	compact	x	x
		peat	loose	x	-
		peat	compact	x	-
	first week only	bracken	intact	-	x
		bracken	loose	x	x
		bracken	compact	x	x
		peat	loose	x	-
		peat	compact	x	-
n[1] = 3	2	2	2 (3)	48	36

[1] Total number of levels of factors included in the experimental design, and total number of observations in the two Anova's (using 2 replicates).

After 2, 3, and 4 weeks, two random pots (n = 2) were selected per treatment containing an organic medium. Plants growing in the sandy medium were all harvested after 3 weeks (n = 3 pots). We measured water content in each pot from weight loss after drying for 24 h at 70 °C to determine desiccation of the substrate over time. Plants were harvested after carefully removing the substrate until roots were exposed. For each surviving seedling we measured total root length and the total rooting depth of the plant in the pot (Fig. 6.3) using a ruler, with length and depth recorded to the nearest mm. The ratio between root length and rooting depth can be considered as a measure of the amount of twist in the root. We defined the variable 'twist' as the following percentage:

Twist = (Total root length - Rooting depth) / Total root length * 100

So, the larger the difference between total root length and the total depth reached by this root, the larger the amount of twist in the root.

Finally, we measured root diameter 5 mm behind the root tip, using the projection of the microscopic image of the root in fresh condition.

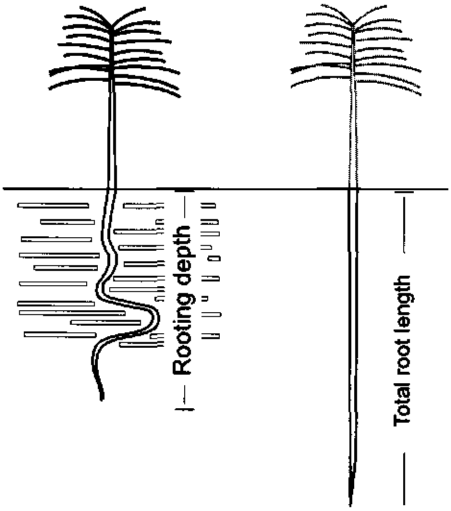


Figure 6.3: Rooting depth and Total root length of the *Pinus* seedlings, used to calculate the amount of twist in the roots.

6.2.3 Data analysis

Effects of substrate type, watering, compactness and harvest time on the measured variables was analysed using a Model I Anova (Sokal & Rohlf 1995). Data on individual roots were averaged per pot to avoid pseudo-replication (Hurlbert 1984). Data on total root length and rooting depth were log-transformed to normalise the heteroscedastic distribution of these variables. The amount of twist was arcsine-square root transformed prior to analysis (Sokal & Rohlf 1995). The effect of treatments on the survival of plants was investigated using a hierarchical log-linear model (SPSS 1996).

The inclusion of the intact treatment was restricted to the bracken substrate only. This treatment was only represented in a single (low) bulk density. To avoid non-orthogonality of comparisons, separate analyses of variance were conducted (Table 6.2). When analysing the effects of substrate type (bracken or peat), only the data of the mixed treatments were included. For the comparison within substrate type 'bracken', the intact treatment was included as a third level of the factor compactness. Therefore, the effect of horizontal layering could not be tested directly, but had to be inferred from post hoc comparisons within the factor compactness, using Tukey's HSD test.

6.3 Results

6.3.1 Root growth in sand

When growing in a sandy medium, root length and diameter of *Pinus* seedlings were both affected by the bulk density of the substrate. Total root length differed significantly ($F_{2,6} = 63.6$; $P < 0.001$) among the three bulk densities, with reduced root length in substrate of higher bulk density (Fig. 6.4). The diameter of the root tip increased with bulk density (Fig. 6.4). This trend was not significant ($F_{2,6} = 4.8$; $P = 0.058$), probably due to the low replication (n = 3) of the treatments in this study.
The amount of twist in the root did not show any significant differences between treatments (Fig. 6.4). The overall mean twist across treatments was 4.8 ± 0.1% (mean ± se; n = 9), indicating that the total depth reached by the roots was only slightly less than the total root length. Roots therefore grew practically straight down into the sand, regardless of bulk density.

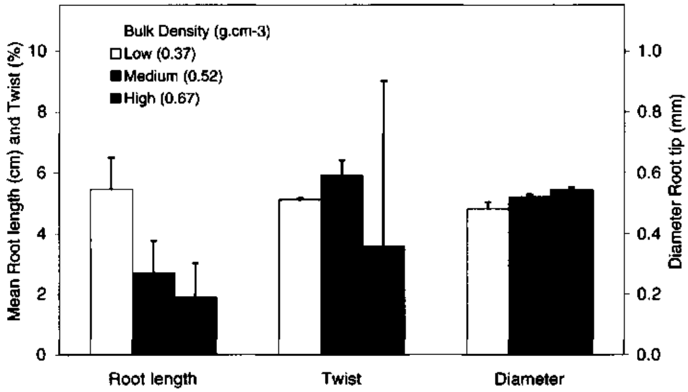


Figure 6.4: The effect of bulk density in a sandy medium on total root length, twist, and diameter of the root tip in *Pinus sylvestris* seedlings after 3 weeks of post germination growth. Error bars represent 1 se. (n=3). Data represent back-transformed averages per treatment (see Methods). Only the root lengths are significantly different ($P < 0.001$) between treatments.

6.3.2 Root growth in mixed organic substrate: effect of bulk density

When growing in a mixed organic medium (Anova1; Table 6.2), root length and twist were both affected by the bulk density of the substrate (Fig. 6.5a,b). Total root length was significantly ($F_{1,23} = 39.4$; $P < 0.001$) higher in substrate with a low bulk density, regardless of harvest time and watering. There were no differences between plants growing in the organic substrate from the bracken stand, and plants growing in peat (Fig. 6.5). Plants growing in a substrate with low bulk density continued root growth until the second harvest (3 weeks), while root length in the substrates of high bulk density hardly increased after the first harvest (2 weeks).
The amount of twist in the roots was only significantly affected ($F_{1,23} = 18.1$; $P < 0.001$) by the compactness of the substrates (Fig. 6.5b). Watering, harvest time and substrate type had no effect on twist. Across all other treatments, the doubling of the bulk density resulted in a twofold increase in twist from 6.7 ± 0.02% (mean ± se, n = 24) in the loose treatment, to 12.8 ± 0.02% in the compact treatment.
The diameter of the root tip was not affected by the bulk density, watering, or substrate type. There was a significant effect of harvest time ($F_{2,23} = 4.9$; $P = 0.016$), with the diameter being significantly lower in the second harvest compared to the first harvest (Tukey's HSD; $P = 0.014$).

6.3.3 Root growth in bracken substrate: effect of horizontal layering

If only the treatments with the ectorganic substrate from the bracken stand are considered, we are able to assess the role of the natural horizontal layering of the organic particles by including the intact treatments (bulk density = 0.09 $g{\cdot}cm^{-3}$) in the analysis (Anova2; Table 6.2), and comparing the responses in root growth with the treatments containing mixed substrate of similar (0.07 $g{\cdot}cm^{-3}$) and twice (0.015 $g{\cdot}cm^{-3}$) the bulk density.

Total root length was significantly ($F_{2,18} = 7.5$; $P = 0.004$) affected by compactness of the substrate (Fig. 6.5a). Plants growing in the mixed treatment with low bulk density had significantly longer roots than plants growing in the high bulk density ($P = 0.005$), or the intact treatment ($P = 0.024$), even though root lengths in the first harvest were similar across treatments (Fig. 6.5a). There was no difference in root length between the mixed high bulk density treatment, and the undisturbed, intact, substrate of lower bulk density (Fig. 6.5a).
Including the intact treatment in the analysis resulted in the absence of any significant differences in the amount of twist between treatments. Compactness had no significant effect on twist ($F_{2,18} = 2.5$; $P = 0.113$), which was mainly due to the high variability in twist in the intact treatment (Fig. 6.5b). The overall mean twist in the intact treatments in the bracken substrate was 11.4 ± 2.4% (mean ± se, n = 12), which is closer to the twist in root from the high bulk density treatment (12.7 ± 1.7%) than the twist in the mixed substrate of similar bulk density (7.4 ± 1.0%).

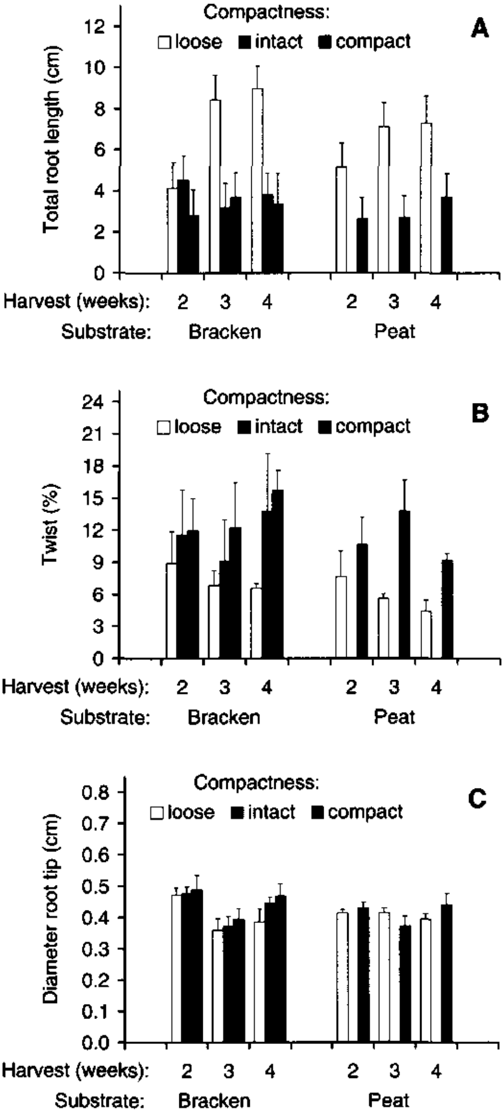


Figure 6.5: The effects of bulk density and mixing of bracken ectorganic soil and peat on (A) total root length, (B) the amount of twist in the roots, and on (C) diameter of the root tip of *Pinus* seedlings, at three different harvest times. Desiccation of the substrate did not significantly affect the roots, so data from watered and unwatered pots are pooled. There are no differences between substrate types.

Root diameter was again not affected by compactness. Like in the comparison of the mixed treatments only, the same effect of harvest time on root diameter emerged when including the intact treatment in the analysis ($F_{2,18} = 8.0$; $P = 0.003$).

6.3.4 Desiccation of the organic substrate and seedling survival

The water content in the pots receiving continuous watering was not significantly different between harvest time, compactness, or substrate type, with an overall mean moisture content of 74.4 ± 1.2% (mean ± se.; n = 30). However, the pots in which watering was discontinued after 1 week, showed a significant decrease in moisture content for all treatment combinations at the time of harvest (Fig. 6.6). Pots filled with peat dried out at a faster rate than pots with the bracken substrate (harvest x substrate: $F_{2,12} = 28.2$; $P < 0.001$). Also, pots with low bulk density dried out faster than pots with a high bulk density (harvest x compactness: $F_{2,12} = 26.1$; $P < 0.001$). Despite the strong desiccation in certain treatments, watering had no effect on root length, twist, or diameter.
Seedling survival was only significantly affected by watering (Likelihood Ratio χ^2 = 9.76, df = 22, $P = 0.988$). The percentage of seedlings surviving prior to harvesting was 78% in the watered pots, versus 49% in the pots not receiving water. All other factors and interactions did not significantly affect survival.

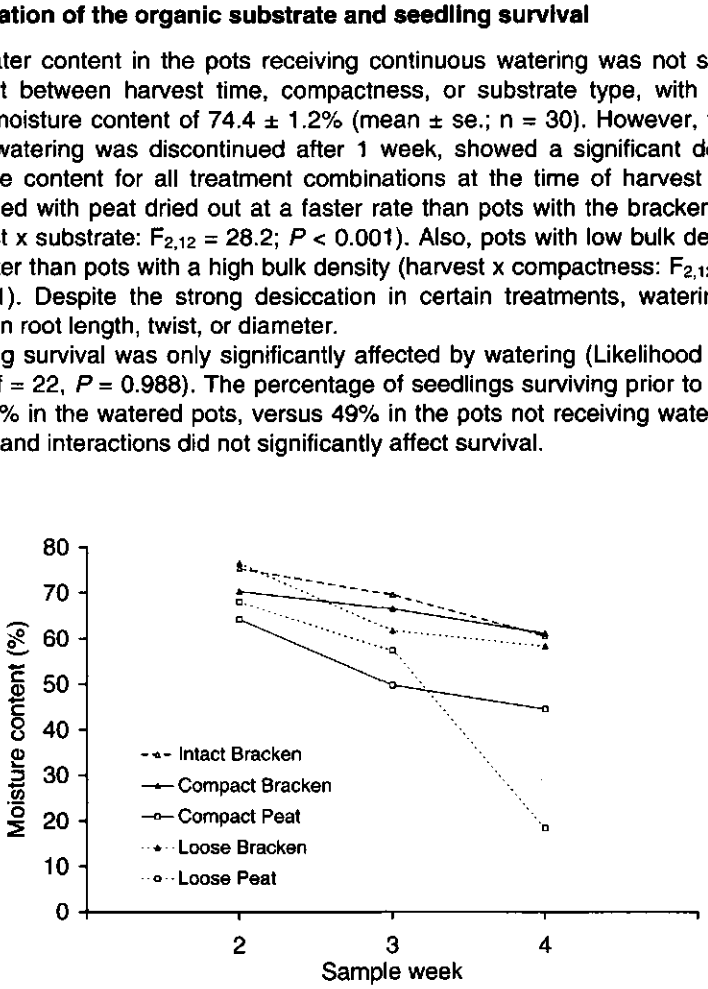


Figure 6.6: Desiccation of the organic substrates after watering was stopped after 1 week. Water retention was greatly influenced by the bulk density of the substrate. Peat dried out faster than bracken substrate.

6.4 Discussion

Compactness of the ectorganic substrate had a marked influence on the development of seedling *Pinus* roots. Higher compactness of mixed (ect)organic material resulted in a reduced root length growth (Fig. 6.5), but had no direct effect on root diameter. Root length growth in the undisturbed bracken ectorganic soil was comparable with mixed substrate of higher bulk density, but was significantly lower in the mixed substrate of similar bulk density (Fig. 6.5). Disturbance of the soil layers may have led to higher mineralisation rates in the mixed substrate as compared with the intact profile, which complicates the interpretation of treatment effects. However, we think that this possible increase in nutrient availability is only marginal, because root growth responses in the nutrient-poor peat were identical to responses in the mixed bracken treatments (Fig. 6.5). The lack of differences between the peat and bracken treatments also confirms the absence, in north-western Europe, of any allelopathic potential of bracken humus to affect root development (den Ouden 1995; see also Sydes & Grime 1981*b* and chapter 7). The results indicate that, in addition to bulk density, the natural layering of the humus particles poses an extra mechanical constraint on root growth in an ectorganic bracken soil profile.

6.4.1 Bulk density and root growth

After two weeks of growth in the bracken substrate, root lengths in the loose treatments were just slightly higher than in the compact or intact treatments (Fig. 6.5a). However, in later harvests, root growth continued only in the loose substrate. This suggests that both doubling the compactness and preserving horizontal layering of the organic substrate impose equivalent resistance on the extending root. It is remarkable that after 3 weeks of growth the total root length reached by the seedlings in the compact and intact organic treatments was in the same range as root length in the medium bulk density sand treatment (Figs. 6.4 and 6.5), despite the large difference in bulk densities between the organic and sandy substrates (Table 6.1). This result raises the point that bulk density in general is not a good measure of the mechanical resistance imposed on the root. Differences between mineral granules and organic particles in specific weight, size, and orientation, together with contrasting pore structure, create highly different physical environments for the extending root tip when comparing organic and mineral substrates.

Yet, even within mineral substrates, the use of bulk density as a measure of mechanical impedance is not straightforward, because linear increase in bulk density leads to a curvilinear rise of penetration resistance by the substrate (Bengough & Young 1993). Furthermore, direct measurement of the penetration resistance by the substrate is problematical. Penetrometers have been used to quantify the forces needed by a root tip to penetrate mineral substrates (sand, loam, glass beads), but their use tends to overestimate actual forces experienced by the root (Bengough & Mullins 1990, Hettiaratchi 1990). Because of the highly variable pore sizes and horizontal orientation of organic particles (Bisdom *et al.* 1996), we did not attempt to use penetrometers to characterise penetration resistance in the organic treatments.

In sand, *Pinus sylvestris* seedlings show a clear response in root length and root diameter to bulk density of the substrate. In this study, the increase in diameter with higher bulk density (Fig. 6.4) was not significant ($P = 0.058$), which is probably due to the low replication of treatments ($n = 3$). Nevertheless, the trend is consistent with earlier studies that have shown an increase of root diameter, and reduction of root length growth, when plants are grown in mineral substrates of increasing bulk densities (Blom 1978, Moss *et al.* 1988, Bengough & Mullins 1990, Hettiaratchi 1990).

Increasing the bulk density of mineral soils leads to a reduction of pore sizes (Table 6.1), and stronger packing of the granular particles (Bengough & Young 1993). Penetrating roots that encounter pores which can't accommodate the root tip must overcome the axial pressures acting on the root tip. This is accomplished by an increase in radial growth of cells just behind the root tip, causing local radial displacement of soil particles and thereby reducing axial pressures acting on the root tip (Hettiaratchi 1990). In response to increased bulk density of the granular substrate, roots grow thicker at the expense of root length. The amount of twist, however, was not affected by increased bulk density of sand (Fig. 6.4). This can be expected, because the granular particles in a homogeneous sandy soil can be assumed to exert equal force from all directions (Hettiratchi 1990). Therefore, the positive geotropy of the root could dominate the growth direction in the well mixed sandy substrate, resulting in a straight course down into the substrate.

In contrast to responses in the sandy medium, root diameter was not affected by bulk density of the organic substrates (Fig. 6.5c), while the amount of twist increased significantly in mixed substrate of higher bulk density (Fig. 6.5b). The bulk densities of the organic substrates used in this study were similar to the bulk densities of the humus layers under *Pinus sylvestris* stands on poor sandy soils (Emmer 1995), but considerably lower than bulk densities of sand (Table 6.1). The low bulk densities of organic substrates are the product of the smaller specific weight of organic particles, and the larger pore volume in organic material as compared with mineral substrates (Table 6.1). Overall penetration resistance in organic substrates may not have been high enough to induce radial growth of the root tip. Because increased bulk density did affect root length, we argue that the different responses in root diameter and twist between sand and organic substrate was caused by the different sizes and arrangement of the organic particles. When the root tip encounters a pore that can't accommodate the growing root, the organic substrate may be more easily displaced by the root tip because the particles are not uniformly packed as in sand. Furthermore, roots that encounter an organic particle, and thus increased resistance, have the alternative to follow the pore structure in the organic substrate until the vertical resistance is low enough to continue growth downward, without the necessity to increase the diameter. This will result in twisting of the roots, as a consequence of the root taking a route of least resistance.

6.4.2 Horizontal layering and root growth

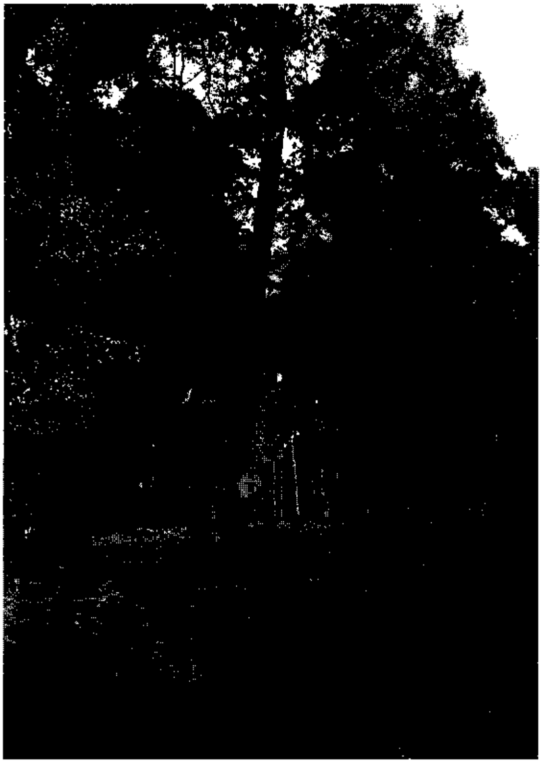
The horizontal layering of organic particles appears to be an important determinant of root growth, additional to bulk density. This is illustrated by the different responses between the intact and loose bracken treatments. Even though these two treatments have a similar bulk density, responses in root length and twist are clearly different (Fig. 6.5b), albeit that the differences in twist between intact and mixed substrate were not significant. Mixing the substrate disturbs the natural layering of the particles, causing a less pronounced horizontal pore direction. When considering the mixed treatments only, we argue that the significantly increased twist in the roots in the compact treatments is caused by a partial restoration of the horizontal layering of the humus particles after compression of the substrate. In the loose treatment, the low compression applied when preparing the treatment has prevented this rearrangement, so horizontal pore directions were less pronounced. Roots could thus follow a straighter path down. This search for the route of least resistance has also been demonstrated with roots growing along cracks in mineral soils (Scholefield & Hall 1985, Dexter 1986). This behaviour implies that, if the surface area of the organic particles is increased, roots of species which can't generate the forces needed to grow through the particles will reach smaller depths per unit total root length. This is analogous to the findings of Sydes & Grime (1981*b*), who found that total surface area of litter ($m^2 \cdot m^{-2}$) is more important than total weight ($g \cdot m^{-2}$) of the litter in determining the effects on the yield of grass species growing upwards through a litter layer.

6.4.3 Conclusions

This study has demonstrated that natural layering of organic particles in the ectorganic soil profile creates an extra mechanical constraint on root development of *Pinus* seedlings. The forces that can be generated by the extending root depend on the size of the root (Bengough & Mullins 1990), so large seeded species may have a greater potential to penetrate the ectorganic soil layers and successfully establish in sites with accumulated organic material. Several studies have demonstrated differentiation in seedling establishment potential between species growing through ectorganic soils of increasing depths (Martin & Sparke 1981, Klein *et al.* 1991), or from different sources (Jarvis 1964). However, these studies have used mixed substrate instead of intact ectorganic soil profiles. The differences between species found in these studies do therefore not directly represent differences in the potential to grow through a horizontally packed ectorganic layer. Instead, they probably reflect differences in the relatively unimpeded elongation of the primary root after germination.

Soil disturbance is an effective management tool for curbing the negative effects that deep ectorganic soil layers have on species establishment. In north-western Europe, bracken stands on acid soils with a well developed raw humus layer mostly contain only a few other, mostly clonal or long-living, plant species (Marrs *et al.* 1986), and the presence of 'litter' greatly reduces establishment of plant species regenerating from seed (Pakeman & Marrs 1992*a*). Management practices involving disturbance of the organic soil (litter) layers result in higher species richness and biomass production of other plant species in such stands (Lowday & Marrs 1992*b*). The increased establishment of species after disturbance is the result of a number of processes, like transportation of seeds from the seed bank to the surface, or initially higher nutrient availability due to increased mineralisation rates. This study has shown that it is likely that, after disturbance of the ectorganic layer, the alteration of the physical structure of organic substrate will probably also relieve the mechanical barriers on root development of seedlings that germinated in the ectorganic soil layer.

7. The allelopathic nature of bracken



This chapter combines two papers prepared on the subject:
den Ouden, J. 1995. (see references)
den Ouden, J. & Janssen, B. (in review) Allelopathy in bracken: fact or artefact?

7.1 Introduction

7.1.1 Allelopathy

Plants continuously produce compounds that are released from their tissue, either actively or passively. Production and excretion of these compounds may have a variety of causes or functions. They may simply be the by-products of photosynthesis or other biochemical processes (for instance the release of oxygen), produced as repellent against herbivores or protection against diseases (for instance cyanogenesis), attract parasitic insects to reduce damage by herbivorous insects (Mattiacci & Dicke 1995), serve as exchange molecules for nutrient uptake (Harborne 1997) or have no directly known function and/or accidentally leach from the plant tissue. Compounds that are released by the plant may have an effect on the growth of other plant species. Molisch (1937) was one of the first researchers to link the release of chemical compounds by one plant to the growth of another plant. He observed that beech (*Fagus sylvatica*) seedlings showed reduced growth when exposed to ethylene released from rotting apples. He introduced the term allelopathy, composed from the Greek words *allelon* (from each other) and *pathos* (to suffer) to indicate the chemical interactions between plants.

The most commonly used definition of allelopathy was phrased by Rice (1984); *Allelopathy is any direct or indirect influence, positive as well as negative, that one plant (including micro-organisms) has on the other through the production of chemical compounds that are released into the environment.* Unfortunately, this definition includes all possible effects that such compounds may have on other species. This complicates the discussion around allelopathy, especially if we wish to consider it as a functional mechanism employed by plants to interfere with potential competitors (cf. Harper 1977, Crawley 1997). In a number of cases, however, plants were demonstrated to actively release compounds that have a strong inhibitory effect on the growth or performance of other species (cf. Rice 1984, Thompson 1985, Rizvi & Rizvi 1992). In some cases, as in *Empetrum hermaphroditicum*, these compounds were positively identifiable and produced in special glands, making a clear case for allelopathy as a functional mechanism in plant-plant interactions (Nilsson & Zackrisson 1992).

7.1.2 Allelopathy and bracken

A number of studies has invoked allelopathy as an important mechanism by which bracken interferes with the establishment and growth of other plant species (Gliessman & Muller 1972, Gliessman 1976, Dolling *et al.* 1994). A large variety of experimental approaches has been applied to demonstrate the potential chemical interference of bracken with other plant species. However, results from such experiments have often been contradictory, with test species responding differently to treatments, with the occurrence of inhibitive effects varying with experimental approach, and with treatment effects varying with the origin (climatic zones) and nature (green, senescing or dead fronds) of the bracken material applied in the experiments (Table 7.1). Gliessman (1976) has attempted to resolve the problem of the high variability in phytotoxic potential of bracken between studies by postulating a mechanism in which the release of toxins from bracken is tuned to the period of germination of co-occurring plant species. In studying the allelopathic potential of bracken between three different climates he found that, going from the subtropics (Costa Rica), through a Mediterranean climate (California, USA) to the temperate zone (Washington State, USA), release of toxic compounds from bracken shifts from the green leaves, through senescent leaves, to litter. This way, allelopathic interference should be active throughout the year in the (sub)tropics, at the onset of autumn rains in Mediterranean climates, or in early spring in temperate regions (Gliessman 1976).

7.1.3 The body of evidence

Studies that evaluated the allelopathic potential of bracken mainly focused on three plant developmental processes: germination, elongation of the radice after germination, and growth of the seedling (Table 7.1). Test species were exposed to media that were derived from different parts of the bracken plant by extraction in water, or by collecting leachates from them. Germination appeared hardly affected, despite a large range in species tested (Table 7.1). Most inhibitive effects were found for radicle elongation in extracts or leachates, especially in warmer climates (Table 7.1). Green or dead bracken material mixed within soil inhibited seedling growth in several cases (Table 7.1). In temperate climates, germination of plant seeds occurs predominantly in spring. Any inhibition of radicle elongation in germinating seeds must therefore act through litter, since the frond canopy does not develop until late spring. Earlier experiments in Dutch bracken failed to find evidence of chemical interference by green fronds, senescing fronds, or litter (Den Ouden 1995, presented in this chapter). This was in compliance with results from Scotland (Martin & Sparke 1982, Sparke 1982). Yet, Dolling *et al.* (1994) reported phytotoxic effects from green fronds in two Swedish bracken populations.

The presence of high amounts of phenolic compounds in the litter, and accumulation of a range of potentially toxic phenolics in bracken soil (Whitehead 1964) has led to the hypothesis that allelopathic interference by bracken is the result of the release of phenolic compounds into the environment (Bohm & Tryon 1967, Glass & Bohm 1969, Gliessman & Muller 1972, 1978). The release of phenolic compounds by bracken litter is a common feature shared with many late-successional species (cf. Feeny 1970, Lodhi 1976). Kuiters *et al.* (1986) reported high phenolic contents in litter from beech (*Fagus sylvatica*) and oak (*Quercus robur*), two of the dominant tree species in the habitats where bracken is found naturally. Mixing litter of these species with soil strongly reduced seedling growth in a range of species. However, Kuiters (1987) reported significantly less inhibition when litter with a relatively high N content was added to his treatments. This led to the hypothesis that, when incorporating litter into the soil, reduction in growth could also have been caused by immobilisation of nitrogen by decomposers confronted with easily accessible carbon, but with a high C/N ratio.

7.1.4 Objectives

The experiments presented in this chapter were designed to investigate whether bracken, and more specifically, its litter, produces phytotoxic effects that could potentially reduce establishment or growth of tree species that are commonly associated with bracken in north-western Europe. The data represent only a small fraction of all the experiments conducted in relation to allelopathy and bracken. Other experiments included growth of *Fagus sylvatica* and *Betula pendula* seedlings in bracken soil, germination and radicle elongation of *Pinus sylvestris*, *Geum urbanum*, *Holcus mollis*, *Betula pubescens* Ehrh. and *Stellaria media* L. in bracken litter extracts, the effect of growing temperature on phytotoxic potential of bracken fronds, and the activity of anaerobic bacteria in green frond extracts. All these experiments yielded no indication whatsoever that bracken chemically interferes in the germination, radicle elongation or growth of the species used in the experiments. Therefore, in this chapter we will focus on some methodological aspects of the test procedures involved in studying allelopathy in bracken. We argued that the variation in test results found in previous studies (Table 7.1) may depend more on specific experimental methods employed, rather than inherent variation in phytotoxic potential of the bracken plant.

Our objectives were to investigate whether phytotoxic effects by bracken litter were related to the nature of the substrate by assessing phytotoxic potential of fresh litter versus litter that was allowed to leach over winter, thus reducing the total phenolic content of the substrate. We also investigated whether extraction of litter yields different phytotoxic potential of test solutions as compared to the soil solution in bracken humus *in situ*, and whether increasing the extraction time used to prepare water extracts of the litter, and consequently the phenolic content of the test solutions, would result in stronger inhibition of radicle elongation of the test species. Furthermore, we investigated whether phytotoxic effects on seedling growth due to exposure to the litter mixed into soil could be due to N-immobilisation. Finally, we studied radicle elongation and seedling performance in treatments containing substrates from oak and beech, in order to compare the presumed allelopathic potential of bracken with that of other late successional species from the same habitat.

Table 7.1: Overview of results obtained in studies investigating phytotoxic potential of bracken from temperate and Mediterranean or subtropical climates. Results are divided into different processes (germination, radicle elongation, and seedling growth), the test media in which the seeds or seedlings were exposed to bracken substrate (extracts or leachates of plant material, and bracken substrate mixed into soil), and the different components of the bracken plant that were used in the experiments (green and senescent fronds, and dead fronds or litter). Experimental results are presented as percentage of individual tests that showed significant ($P < 0.05$) inhibition of plant performance with respect to the controls used. Total number of individual tests are given between brackets.

		Plant developmental process								
Test medium	Bracken component	Germination		Radicle elongation		Seedling growth		Total		Ref[1]
		%	(n)	%	(n)	%	(n)	%	(n)	
				Temperate climates						
extract	green fronds	60	(5)	60	(5)	33	(3)	54	(13)	1,2,3,4,9
	dead / litter	0	(8)	56	(9)	-	-	29	(17)	2,3,4,8, 12
leachate	green fronds	0	(3)	0	(3)	-	-	0	(6)	10
	dead / litter	0	(3)	0	(3)	-	-	0	(6)	10
mixed in soil	green fronds	-	-	-	-	-	-	-	-	
	dead / litter	-	-	-	-	20	(5)	33	(3)	12
Total Temperate		16	(19)	40	(20)	25	(8)	29	(45)	
				Mediterranean and subtropical climates						
extract	green fronds	0	(13)	14	(14)	-	-	7	(27)	6,8,11,14
	senescent	-	-	0	(2)	-	-	0	(2)	5,6
	dead / litter	-	-	75	(4)	-	-	75	(4)	5,6
leachate	green fronds	-	-	63	(8)	-	-	63	(8)	13
	senescent	-	-	100	(2)	-	-	100	(2)	13
	dead / litter	-	-	71	(7)	-	-	71	(7)	6,7
mixed in soil	green fronds	14	(7)	0	(7)	100	(4)	28	(18)	11
	senescent	-	-	-	-	-	-	-	-	
	dead / litter	-	-	-	-	100	(1)	100	(1)	6
Total Medit. + Subtropics		5	(20)	39	(44)	100	(5)	33	(69)	

[1] References: 1= Brown 1967, 2 = del Moral & Cates 1971, 3 = den Ouden 1995, 4 = Dolling *et al.* 1994, 5 = Everson & Breen 1983, 6 = Gliessman & Muller 1972, 7 = Gliessman & Muller 1978, 8 = Gliessman 1976, 9 = Horsley 1977, 10 = Martin & Sparke 1982, 11 = Nava *et al.* 1987, 12 = Stewart 1975, 13 = Taylor & Thomson 1990, 14 = Tolhurst & Turvey 1992.

7.2 Methods

7.2.1 Phytotoxicity of extracts and *in situ* soil solutions

The phytotoxic potential of bracken litter extracts and *in situ* soil solutions was tested by means of bioassays, using seeds of *Pinus sylvestris*, *Betula pendula* Roth. and *Ceratocapnos claviculata* (L.) Lidén. These species are commonly found in woodlands with bracken in the Netherlands. Seeds of *Pinus* and *Betula* were collected in a seed orchard. *Ceratocapnos* seeds were collected in a forest near Wageningen. All seeds were exposed to extracts and/or centrifuge solutions that were derived from dead standing bracken fronds, as well as from the combined litter and upper humus layer from a dense bracken stand.

Extracts were made by adding 1000 ml of distilled water to 100 g of fresh substrate and left soaking at room temperature for 24 hours. The substrate consisted of the combined litter and upper fermentation layer from a pure bracken stand, collected December 3, 1993. Another extract was made of the yellow and brown standing dead fronds collected on the same date using the same procedure. Since there are many problems associated with the use of extracts in bioassays (cf. Harper 1977), a centrifuge was used to directly sling the moisture out of the samples. Centrifuge solutions were made of the combined litter and upper fermentation layer at three different times (December 3, 1993, February 11, and March 23, 1994). Samples were centrifuged for 20 min at 7500 RPM immediately after collection. All solutions were paper filtered to remove solids and were kept frozen before use.

In a pilot experiment (den Ouden, unpubl. data) the germination of *Stellaria media* and *Betula pubescens* was significantly higher in a centrifuge solution of the litter layer than in an extract. The pH of these solutions was respectively 3.8 and 6.8, and a follow-up experiment suggested that the low pH of the centrifuge solution had stimulated germination in *Stellaria*. To avoid such an effect, the pH of the extracts used in this study was adjusted to the same level as the centrifuge solutions (pH 5.0) using 0.001 M H_3PO_4.

For each species, batches of 50 seeds were placed in petri dishes on filter paper moistened by 5 ml of the test solutions. Distilled water was used as a control. Each treatment was replicated three times, except for the control ($n = 4$). Seeds were left germinating in an incubator, at alternating temperatures of 20/27 °C in alternating 12 h of dark/light. The number of germinated seeds was recorded approximately every 2 days, until no additional seeds germinated for 3-4 days. Length of the radicle was recorded for each seed after 2 days for *Pinus* and *Ceratocapnos*, and after 4 days for *Betula* following germination.

In a second bioassay, the phytotoxic potential of green fronds was investigated using seeds of *Pinus sylvestris*. Green bracken fronds were collected June 21, 1994 and 300 g of fresh frond material was extracted in 3000 ml of distilled water for 3 hours at 55 °C. This extraction procedure was chosen to yield a potentially large concentration of phytotoxic water soluble compounds (Field 1989). Distilled water was used as a control. The same experimental procedures were followed as described above, except that both treatments were replicated 4 times. Petri dishes were sealed, and germination and radicle elongation recorded once after 8 days (approximately T_{50}, see Fig. 7.1).

7.2.2 Phytotoxicity of fresh and leached litter of bracken, beech, and oak.

We collected freshly fallen leaf litter of bracken, beech and oak in late October, 1995. Bracken and oak litter was collected in an oak coppice stand the Speulderbos (52°16'N, 5°40'E), and beech litter collected from a beech stand in Wageningen (52°58'N, 5°40'E). Litter samples were divided in two, with one half air dried and stored frozen at -18 °C immediately after collection. The other half was placed in wooden trays (50cm x 100cm x 15cm), closed at the top and bottom with 5 mm mesh metal wire netting to secure the litter, and left outdoors in the university gardens to allow natural leaching of the substrate over winter. In April 1996, the leached litter was collected, air dried and frozen before use. Part of the litter was used to make water extracts to test for potential phytotoxic effects on radicle elongation of germinating seeds of *Pinus sylvestris*, *Picea abies* and *Betula pendula* in a bioassay. The remainder of the substrates (excluding oak) was used in a pot experiment assessing the potential phytotoxicity of the different substrates when mixed with soil by evaluating early growth and nutrient acquisition in *Pinus* and *Picea* seedlings.

Bioassays with water extracts

The dried fronds and leaves were fragmented to pass through a 5 mm mesh screen, and extracted using 50 g of dry matter in 1 l demineralised water. The material was held in Erlenmeyer flasks, and flushed with N_2 for 1 minute to prevent oxidation of the substrate during extraction. Flasks were sealed, and shaken continuously for 24, 48 and 96 h at 20 °C. The solutions were then passed through a paper filter (Schleicher & Schnell, No. 589[1], Dassel, Germany), and resulting extracts were used in the bioassays. The pH of the extracts was measured using a Schott GG840 (Tiel, The Netherlands). Total phenolic content of the extracts was measured colorometrically according to methods described by Scalbert *et al.* (1989) using a spectrophotometer (Hitachi U-2000). Phenolic content was calculated as mg gallic acid equivalents per liter.

One layer of filter paper was placed on the bottom of petri-dishes (10 cm diameter), and soaked with 5 ml of the different extracts. Demineralised water was used as control. Per petri-dish, 10 pre-germinated seeds of *Pinus sylvestris*, *Picea abies*, or *Betula pendula* were placed on the filter paper. Petri-dishes were sealed with parafilm. Each treatment was prepared in duplo, except for the control (n = 5). This resulted in 54 treatment combinations (3 litter species, 2 litter types, 3 extraction times, 3 test species). All petri dishes were placed in a growing chamber at 20 °C, with 12 hours of daily illumination. After 3 days, radicle elongation was measured for all seeds, and averaged per petri dish. All data were expressed as percentage of the control.

Pot experiment

We filled plastic 1 l pots with 1000 g of a 3:1 v/v mixture of sand and leaf mould, which had been composted for at least 3 years. To this soil, 10 g of fresh or leached bracken and beech litter was added. In half of the treatments, the organic material was placed on top of the soil; in the other half the material was mixed into the soil. As a control, commercial garden peat was used in the same manner. The widespread use of garden peat as a growing medium in nurseries and gardening has already demonstrated the absence of phytotoxic potential in this substrate. Using peat instead of a treatment with no additional organic matter would control for the physical alteration of the growing medium when mixing organic matter into the soil.

In each pot, 5 pre-germinated *Pinus* or *Picea* seeds were planted and allowed to grow for 11 weeks. Pots were randomly placed in a greenhouse that was kept at a constant temperature of 18 °C, with 70 % relative air humidity. Seedlings were illuminated with 400 Watt full-spectrum growth lamps, during 12 h each day. All pots were watered regularly. One set of treatments received additional nutrients as 0.5 ml of a full strength nutrient solution (Steiner 1961), representing a weekly nitrogen gift of 10 mg per pot. The other half of the treatments received distilled water only. This treatment was added to control for potential N-immobilisation in the pots. The set up resulted in the following treatments: 5 litter substrates (peat, and fresh or leached litter of bracken and beech), 2 litter positions (on top of soil or mixed), 2 levels of nutrients (no nutrients or 10 mg N per week), and 2 seedling species. Each treatment combination was replicated 3 times, resulting in a total of 120 pots.

At harvest, after 11 weeks, all surviving seedlings were counted and length of shoot, primary root and lateral roots was recorded for each individual. Plants were separated into shoot, root, and needles, dried at 70 °C for 24 h, and weighed. Nutrient content of the seedlings was determined in bulk samples representing all plants growing within a treatment. Samples were oxidised by sulphuric acid and salicylic acid. Total N and P were measured using segmented flow analysis (Skalar Analytical, Breda, The Netherlands), Na, K, and Ca using a flame photospectrometer (ELEX 6361, Eppendorf, Hamburg, Germany), and Mg with atomic absorption (SpectrAA 300, Varian, Australia). C/N ratio was determined using an element analyser (EA 1108 CHNS-O, Fisons Instruments).

7.2.3 Data analysis

Effects of treatments on germination percentages and radicle elongation in the comparison between extracts and centrifuge solutions were determined using analysis of variance. All germination percentages were arcsine-square root transformed prior to analysis. Individual treatments were compared using Tukey's HSD multiple comparison test.

Effects of the extracts on radicle elongation were tested in a general linear model, with the factors species (*Pinus*, *Picea*, *Betula*), substrate nested within species (bracken, beech or oak), substrate type nested within species and substrate (fresh or leached), and extraction time (1,2, or 4 days) nested within all forgoing. The same design was also used to test for differences within the three species separately (N = 36).

The pot experiment was analysed using analysis of variance, with factors substrate (5), position (2), and nutrients (2). Differences between treatments were evaluated using Tukey's HSD. Data were represented as means per pot (measures of length or dry weight), or as single values per treatment (nutrient concentrations). Data on dry weight and length were log-transformed prior to analysis. All calculations were performed using SPSS (1996).

7.3 Results

7.3.1 Toxicity of extracts and soil solutions

There were no significant differences between extracts and soil solutions in final germination percentage and radicle elongation for all three species. Overall germination percentage was highest for *Pinus sylvestris* (around 90%), while less than 50% of *Betula pendula* and *Ceratocapnos claviculata* seeds germinated (Table 7.2). *Betula* showed the highest germination rate with most seeds germinating within 4 days (Fig. 7.1). Seed germination was slow in *Ceratocapnos* (Fig. 7.1). In this species, the germination rate was highest in the control and slowest in the litter extract (Fig. 7.1), but the difference in number of germinated seeds was just significant after 18 days only ($P = 0.04$).

In the extract of green fronds, germination percentage after 8 days for *Pinus* was higher than in the control (Table 7.3), but this difference was not significant. Radicle elongation was similar in both treatments (Table 7.3).

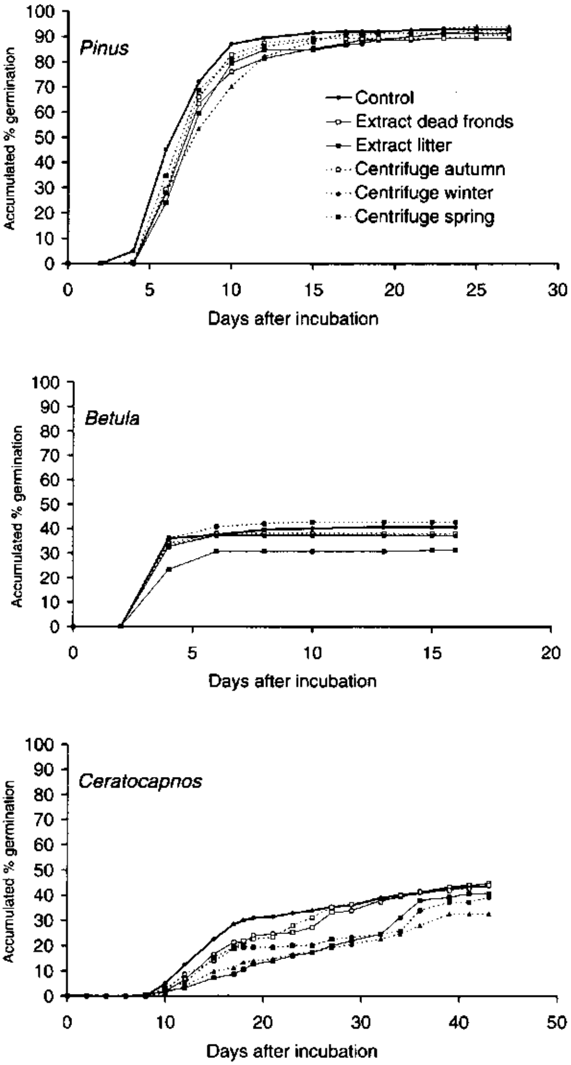


Figure 7.1: Accumulated germination percentages of seeds of *Pinus sylvestris*, *Betula pendula* and *Ceratocapnos claviculata* in extracts of dead fronds and litter, and centrifuge solutions of soil underneath bracken collected at three dates. Demineralised water was used as control.

Table 7.2: Germination and radicle elongation in extracts of dead bracken fronds, extracts of the upper organic soil layer, and centrifuge solutions from bracken humus sampled in three different seasons.

Treatment	Species		
	Pinus sylvestris	*Betula pendula*	*Ceratocapnos claviculata*
		Germination (%)	
control	93.0 ± 3.8 [1]	40.5 ± 6.3	43.6 ± 1.7
centrifuge (autumn)	90.7 ± 0.7	38.0 ± 5.3	44.0 ± 3.1
centrifuge (winter)	94.0 ± 2.3	37.3 ± 5.9	32.6 ± 4.7
centrifuge (spring)	92.7 ± 3.7	42.7 ± 5.5	39.4 ± 0.7
extract dead fronds	91.3 ± 5.7	37.3 ± 1.8	44.6 ± 4.1
extract litter and humus	89.3 ± 2.4	31.3 ± 1.3	40.6 ± 2.4
		Radicle elongation (mm)	
control	15.7 ± 0.4	4.7 ± 0.1	9.3 ± 0.9
centrifuge (autumn)	14.4 ± 0.8	5.5 ± 0.2	9.1 ± 1.2
centrifuge (winter)	14.5 ± 0.4	5.6 ± 0.2	9.1 ± 0.7
centrifuge (spring)	14.8 ± 0.4	5.2 ± 0.4	10.9 ± 0.4
extract dead fronds	13.9 ± 0.7	4.6 ± 0.4	7.5 ± 0.7
extract litter and humus	16.3 ± 0.2	4.8 ± 0.1	8.7 ± 3.1

1. Numbers represent means per treatment ± standard error (n = 3, control: n = 4)

Table 7.3: Germination and radicle elongation of *Pinus sylvestris* in an extract of green bracken fronds.

Treatment	Germination (%)	Radicle elongation (mm)
control	54.1 ± 10.4 [1]	6.6 ± 1.1
extract	73.0 ± 1.3	8.5 ± 0.8

1. Numbers are means per treatment ± standard error (n = 4)

7.3.2 Toxicity of bracken, beech and oak litter

Chemical composition of the substrates

The extracts made from the three different substrates showed large differences in phenolic content (Fig. 7.2). The oak litter yielded the highest concentrations of phenolic compounds, while extracts from bracken litter showed a comparatively low phenolic content. Leaching of the substrate greatly reduced the amount of phenolic compounds. A longer extraction times resulted in a higher phenolic content of the extracts from fresh substrates, especially in the oak litter. However, leached substrate did not yield more phenolic compounds when extraction time was prolonged (Fig. 7.2). The pH of the solutions varied between 4.7 and 6.8 (data not shown).

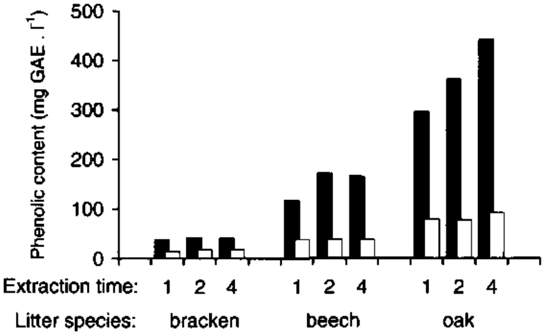


Figure 7.2: Total phenolic content, expressed in gallic acid equivalents (GAE) for fresh litter (black bars), and litter that was allowed to leach over winter (white bars), in water extracts of three different litter species and extracted during 1,2, and 4 days.

The nitrogen and phosphorous content of the litter was higher in bracken litter as compared with beech litter. Leaching hardly changed initial N- and P-concentrations of the bracken litter (Table 7.4). However, leaching of the litter over winter resulted in a considerable decrease in potassium-content in both bracken and beech litter (Table 7.4). The C/N ratios of the bracken substrates were considerably lower than in the beech substrates. The initially high C/N ratio in beech leaves was reduced considerably after leaching and partial decomposition during winter (Table 7.4).

Table 7.4: Nutrient content (mg/g) and C/N ratio of the substrates used in the pot experiment. Samples were analysed in duplo.

Substrate	N	P	K	Ca	Mg	C/N
Bracken, fresh	14.5	1.3	3.7	5.3	1.9	28
Bracken, leached	15.4	1.3	1.6	6.3	2.0	30
Beech, fresh	8.4	0.9	3.9	13.5	1.3	53
Beech, leached	10.9	1.1	1.5	13.8	1.1	40
Peat	7.6	0.8	0.9	9.6	1.3	46

Bioassays

There was no correlation between phenolic content of the test solutions and radicle elongation in the bioassay (r = -0.004, P = 0.980, n = 54; Fig. 7.3). In general, the extracts did not reduce radical elongation in the three species (Fig. 7.4). There were no significant effects of substrate, or whether this was fresh or leached (Table 7.5). Only in *Pinus*, radicle elongation was significantly lower (P = 0.049) in extracts made of fresh substrate. This was due to slightly lower radicle growth in fresh bracken substrate (Fig. 7.4). Extraction time did have a significant effect on the radicle elongation of *Pinus* (P = 0.002) and *Betula* (P < 0.001)(Table 7.5). *Betula* showed strongly reduced radicle elongation in extracts from fresh bracken litter made over 4 days (Fig. 7.4).

Table 7.5: Nested analyses of variance, testing the effect of water extracts of bracken, beech, or oak litter (Substrate), either fresh or leached throughout the winter (Type), and extracted during 1, 2, or 4 days (ExTime), on the radicle elongation of three tree species (as percentage of the demineralised water control).

		Pinus sylvestris		*Picea abies*		*Betula pendula*	
Source of variation	df	F	*P*	F	*P*	F	*P*
Substrate	2	2.02	0.086	0.89	0.574	0.39	0.951
Type(Substrate)	3	2.36	0.049	0.44	0.924	0.57	0.836
ExTime(Type(Substrate))	12	4.48	0.002	1.76	0.134	8.80	0.000
Error	18						

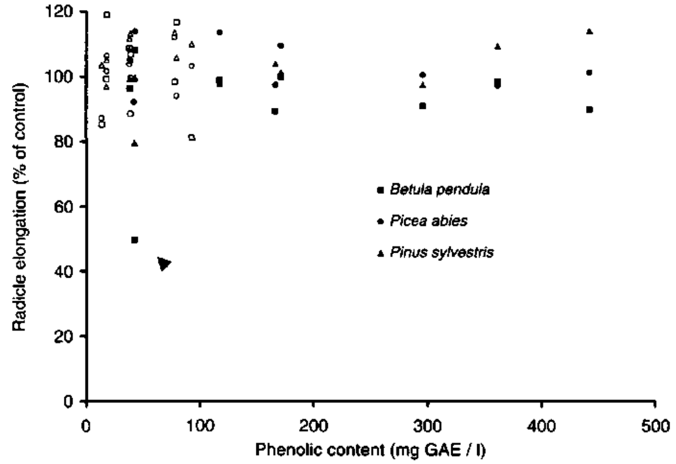


Figure 7.3: Radicle elongation (as percentage of the demineralised water control) as a function of the total phenolic content of extracts from fresh (open symbols) or leached (filled symbols) litter of bracken, beech, and oak. The arrow points toward the only significant treatment effect (*Betula pendula* in 4 day extracts of fresh bracken litter).

Pot experiment

The growth of seedlings in treatments with bracken litter did not differ from the treatments with the peat control in the pot experiment (Fig. 7.5). The total length of lateral roots produced by *Pinus* and *Picea* was significantly lower in pots containing leached beech litter than in the other treatments (Table 7.6; data not shown). Primary root length was only significantly reduced by leached beech litter in *Picea* (Table 7.6, Fig. 7.5). Dry weights of all the different plant components were also significantly reduced in treatments with leached beech litter, except for shoot biomass in *Pinus* (Table 7.6). Especially in *Picea*, the weight reduction in leached beech litter was stronger in treatments with litter incorporated into the soil as compared with litter placed on top (Fig. 7.5), resulting in significant interactions between substrate and position (Table 7.6).

The addition of nutrients had no significant effects on the length or biomass of the two test species (Table 7.6). In *Picea* seedlings, only length and dry weight of the root was significantly influenced by nutrient addition. This effect was due to a higher root length (13.8 ± 0.3 cm; mean ± 1 se., n = 15) and dry weight (18.1 ± 1.3 mg) of seedlings in pots receiving nutrients where litter was mixed into the soil, as compared with pots with litter placed on top (10.7 ± 0.5 cm and 11.4 ± 0.8 mg respectively). The root/shoot ratio was also significantly affected by nutrient addition (Table 7.6), with supplemental nutrition resulting in a higher root/shoot ratio in *Picea* (data not shown).

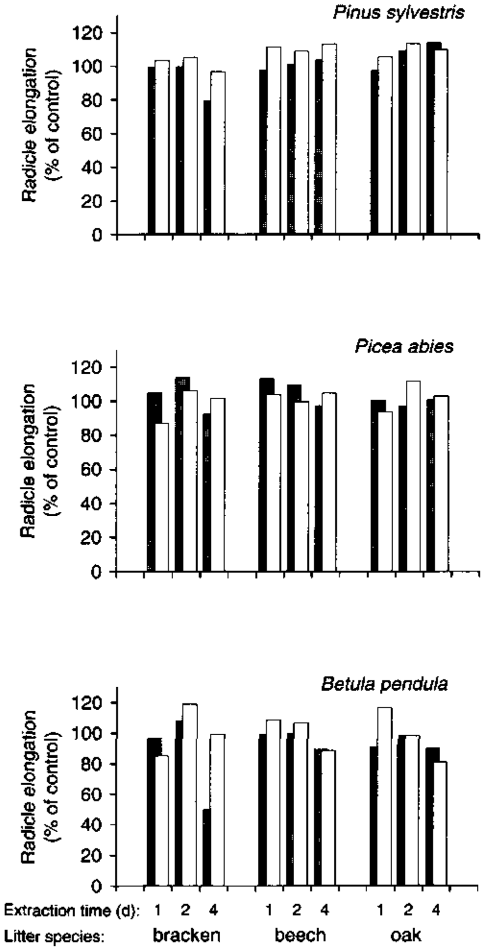


Figure 7.4: Radicle elongation (as percentage of the control) of seeds of *Pinus sylvestris* (top), *Picea abies* (middle) and *Betula pendula* (bottom), in extracts of fresh (shaded bars) and leached (white bars) litter of bracken, beech and oak, and extracted during 1, 2, and 4 days. Data are duplo means of average values of 10 seeds per petri-dish.

Position of the litter had a pronounced effect on root and shoot lengths, and dry weights of the different plant components for the two seedling species (Table 7.6, Fig. 7.5). Roots of *Pinus* and *Picea* were significantly longer, and had higher dry weights, in treatments with the substrate mixed into the soil. On the other hand, shoot length and biomass were significantly higher in the treatments with substrate placed on top of the soil. Total dry weight of the seedlings was only significantly affected by position in *Picea*, which could be totally attributed to differences in root weight (Fig. 7.5). The large differences in root weight resulted in the highly significant differences in root/shoot ratios between different litter positions (Table 7.6).

The nutrient concentrations (N, P, K) in the two seedling species were not affected by the addition of supplemental nutrients. Therefore, nutrient concentrations were investigated across nutrient treatments for substrate and position only. There were differences between seedling species in their final nutrient concentrations within treatments. In *Pinus*, nitrogen concentrations were significantly lower in treatments containing beech litter ($P < 0.01$), and in *Picea* N-concentration was significantly higher in treatments with bracken litter ($P < 0.05$; Fig. 7.5). In both species, N-concentration was significantly lower in treatments when the litter substrates were mixed into the soil (Fig. 7.5).
Phosphorous-concentrations were significantly different between treatments in *Pinus* (Anova, $F_{4,10} = 6.6$, $P = 0.007$). In *Picea*, substrates did not influence P-concentration, but mixing litter into the soil significantly reduced P-concentrations in the seedlings. Concentrations of potassium were also affected by substrate and position in both seedling species. In *Pinus*, K-concentrations were lowest in treatments with beech litter ($P < 0.05$), and highest when bracken litter was added ($P < 0.05$). Mixing litter resulted in significantly reduced K-concentrations in both *Pinus* ($F_{1,10} = 44.7$, $P < 0.001$) and *Picea* ($F_{1,10} = 10.8$, $P = 0.008$).

In *Pinus*, total weight of the seedlings was positively correlated with N- ($r = 0.58$, $P = 0.07$) and K- concentrations ($r = 0.50$, $P = 0.026$). In *Picea*, however, total dry weight of the seedlings was negatively correlated with N- ($r = -0.55$, $P = 0.013$), P- ($r = -0.47$, $P = 0.038$), and K- concentrations ($r = -0.45$, $P = 0.048$). Dry weight production in stems and roots was similar between species, but in *Pinus* considerably more needle biomass was produced as compared to *Picea* (Fig. 7.5). This was due to developmental differences in the seedlings of the two species, with *Pinus* having produced considerably more needles during post-cotyledonary growth. This suggests that differences in nutrient concentrations are more indicative for possible toxic interference in the treatments for *Pinus*, whereas in *Picea* differences in nutrient concentrations may in part be a result of dilution of initially present nutrients in the endosperm over the extending seedling.

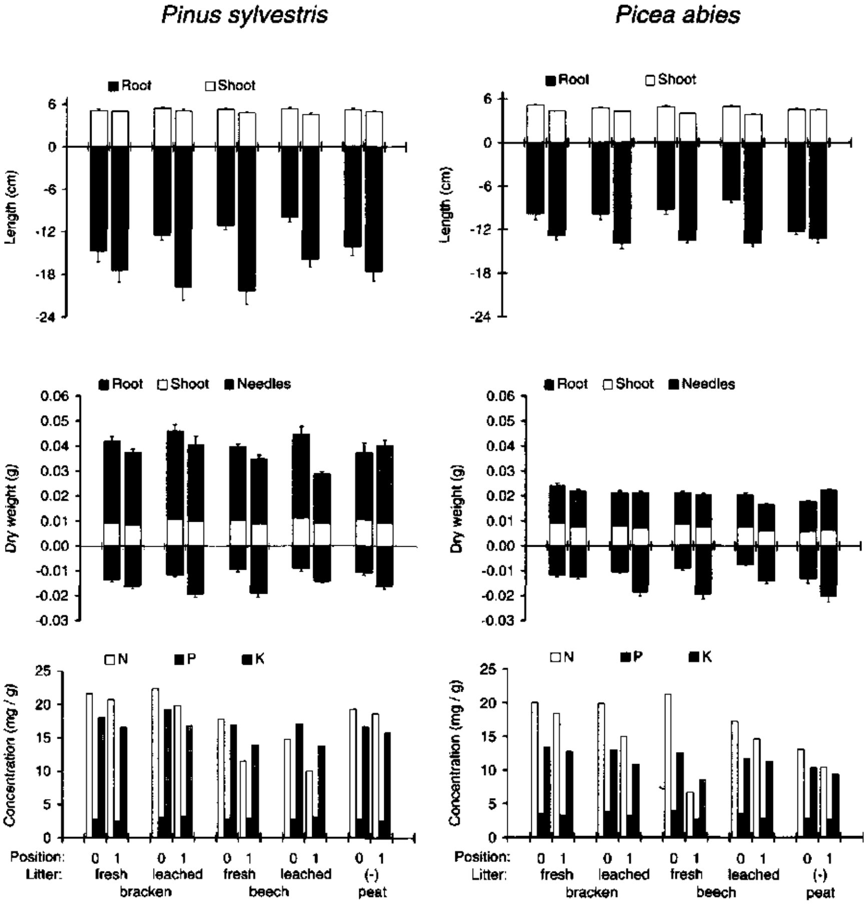


Figure 7.5: Mean lengths of shoot and primary root (top), dry weights of root, shoot, and needles (middle), and nutrient concentrations of seedling *Pinus sylvestris* and *Picea abies*, growing in sand with different organic substrates placed on top (position = 0) or mixed within pots (position = 1). Error bars represent 1 standard error of mean root and shoot length (top) and mean above and below ground dry weight (middle). Data on length and dry weight are means per pot (n=6), data on nutrient concentrations are means per treatment (n=2).

Table 7.6: F-statistics from the ANOVAs of the treatment effects of substrate (fresh and leached bracken and beech litter, and peat), position of litter (on top, or mixed into the soil), and the addition of nutrients on a number of plant properties in seedling *Pinus sylvestris* and *Picea abies*. Plants were harvested after 11 weeks. All data (except the root-shoot (R/S) ratio) were log-transformed prior to analysis. Levels of significance are indicated by superscripts: 1 = $P < 0.5$, 2 = $P < 0.01$, 3 = $P < 0.001$. Non-significant effects are not shown.

		Length			Dry weight				
Source of Variation	df	Shoot	Primary Root	Lateral Roots	Shoot	Needles	Root	Total	R/S-ratio
				Pinus sylvestris					
Substrate	4			5.4^{2}		3.7^{1}	4.2^{2}	3.0^{1}	
Position	1	12.8^{2}	47.2^{3}	14.4^{3}	11.0^{2}	9.7^{2}	69.2^{3}		202.8^{3}
Nutrients	1								
Subs x Pos	4			3.6^{1}		4.7^{2}			7.3^{3}
Subs x Nutr	4								
Pos x Nutr	1								
Subs x Pos x Nutr	4								
Error	40								
				Picea abies					
Substrate	4		3.9^{2}	10.5^{3}	12.3^{3}	9.9^{3}	6.0^{2}	7.2^{3}	5.3^{2}
Position	1	91.1^{3}	109.5^{3}	5.8^{1}	12.6^{2}		65.0^{3}	29.6^{3}	66.0^{3}
Nutrients	1		11.7^{2}				5.3^{1}		8.4^{2}
Subs x Pos	4	6.3^{3}	6.7^{3}		3.6^{1}	7.5^{3}	4.4^{2}	4.3^{2}	5.1^{2}
Subs x Nutr	4								
Pos x Nutr	1		4.7^{1}			6.7^{1}			
Subs x Pos x Nutr	4								
Error	40								

7.4 Discussion

The subject of allelopathy is highly controversial, and many claims of allelopathic interference can be, and have been, dismissed in favour of other plant-plant or plant-animal interactions (Bartholomew 1970, Harper 1977, Crawley 1997). Definite proof of allelopathy is difficult to obtain, not in the least because it is extremely problematical to separate the process of chemical interference from other mechanisms of interference among plants, especially under field conditions (Harper 1977, Fuerst & Putnam 1983).

7.4.1 Bioassays with plant extracts

The applied methodology to demonstrate phytotoxic potential of plant substances also raises problems in inferring allelopathy, especially from laboratory studies using extracts of plant material. For bracken this is demonstrated by the variation in results from bioassays using test solutions that were produced using different extraction times. In the present study we only found significant effects on radicle elongation for seeds exposed to solutions that had been extracted from bracken litter for 96 hours. The same long extraction time was needed by Dolling *et al.* (1994) to demonstrate phytotoxic effects in extracts from green bracken fronds in Sweden. Litter extracts made over 24 hours never inhibited radicle elongation in this study, or other studies dealing with European bracken (Martin & Sparke 1982, Den Ouden 1995, Dolling, pers. comm.). Apparently, raising the extraction time results in an increase of some toxic compound(s), possibly from decomposition during extraction. Dolling *et al.* (1994) suggest for instance that the reduced germination and radicle elongation they found could have been the result of increased levels of cyanide released by the fronds during the 4-day extraction. This clearly illustrates the point made by Harper (1977, p. 369), who states that *"Almost all species can, by appropriate digestion, extraction and concentration, be persuaded to yield a product that is toxic to one species or another"*. The few cases in which inhibition of radicle elongation in bracken extracts was demonstrated in European bracken all occurred after prolonged extraction of the bracken material. We believe that such extracts do not provide a relevant model for the chemical environment encountered by seeds in the field.

In this study we accounted for the problems involving the use of extracts by taking the soil solution directly out of the humus layer underneath bracken using a soil centrifuge. Solutions obtained from a centrifuge give a good representation of the actual composition and concentration of (in)organic compounds present in the humus layer (Zabowski & Ugolini 1990). However, also the soil moisture present in bracken litter *in situ* showed no phytotoxic potential (Fig. 7.1). The few cases in which phytotoxicity was demonstrated in bracken extracts (Dolling *et al.* 1994, this study) must therefore be seen as an artefact of prolonged extraction. In conclusion we argue that, based on studies of bracken litter extracts (Table 7.1), there is no case for the chemical interference with germination or radicle elongation by bracken in north-western Europe.

7.4.2 Mixtures of litter and soil

Seedlings exposed to bracken litter mixed into the soil, or placed on top of the soil, showed no inhibition in growth with respect to the peat control. When litter was mixed with soil, root length and biomass were significantly higher than in treatments where litter was placed on top of the soil (Fig. 7.5). This may be explained by better aeration, or by the lower bulk density in the mixed treatments, which reduces physical impedance by the substrate to the developing root (Den Ouden & Vogels

1997; chapter 6). N-concentrations (*Picea*) and K-concentrations (*Pinus*) were significantly higher in plants growing in treatments containing bracken litter (Fig. 7.5). Therefore, also this experiment failed to demonstrate any phytotoxic potential of bracken litter, although this may have been masked by the relatively low relative growth rates of the two seedling species used in this study (cf. Stewart 1975).

When exposed to beech litter, the seedlings showed a reduction in primary (*Picea*) and lateral (*Pinus* and *Picea*) root length, and reduced biomass of most plant components in both species. In *Pinus*, the significantly lower concentrations of N and K in treatments containing beech litter confirm the potential of beech litter to inhibit nutrient uptake and consequently growth of seedlings (Kuiters 1987). However, does reduction of seedling biomass indicate the action of toxins in soils when litter is incorporated? When Kuiters (1987) added *Acer* litter to his treatments, the growth reduction that was previously found disappeared completely. Litter of *Acer* had a considerably higher N-content and lower C/N ratio than did the litter of the other tree species used in his treatments. In the present study we tested the hypothesis that a high C/N ratio of litter, when mixed in the soil, causes immobilisation of nutrients by soil-organisms so less nutrients are available for uptake.

The C/N ratio of fresh and leached bracken was approximately 30 (Table 7.4), and nutrient addition had no effects on plant growth or nutrient concentrations in plants growing on bracken substrate. However, fresh and leached beech litter had a high C/N ratio of respectively 53 and 40, which made the beech treatments prone to N-immobilisation (Staaf 1980).

Mixing beech litter into the soil significantly reduced dry weights of *Picea* seedlings, and nutrient concentrations in both *Pinus* and *Picea*. Addition of nutrients did result in higher root biomass of *Picea* seedlings, which indicates that immobilisation of nutrients may have occurred in the pots. Addition of nutrients did, however, not have a direct effect on total seedling growth or nutrient acquisition. The negative effects on growth and lower nutrient concentrations in plants growing in treatments with beech litter could therefore not entirely be attributed to immobilisation of nutrients by soil-organisms, but instead could be a result of toxic compounds released from beech litter.

7.4.3 Phytotoxicity of phenolic compounds

The identification of potential phytotoxins in bracken has mainly been focused on phenolic compounds released from the plant (Bohm & Tryon 1967, Glass & Bohm 1969, Gliessman & Muller 1978), or accumulated in the soil underneath (Whitehead 1964, Glass 1976). However, the total amount of extractable phenolics from the litter substrates used in this study bore no relationship at all with radicle elongation or growth of the seedlings (Figs. 7.2 and 7.3, Kuiters 1987). It may be argued, however, that not the total quantity of phenolic compounds, but rather the concentration of specific compounds in the litter or soil, is relevant in causing phytotoxicity. Most notably monomeric phenols like benzoic and cinnamic acids and their derivatives, have a distinct toxic effect on plant growth, even in low concentrations (Wang *et al.* 1967, Glass 1976, Einhellig & Rasmussen 1978). Whitehead (1964), who had identified relatively high amounts of specific monomeric phenolic acids in soils under bracken, later concluded that the concentrations of these compounds were too low to exert a direct toxic influence on plant growth (Whitehead *et al.* 1982). Even if released in large quantities, these compounds may be quickly detoxified after binding to soil particles, microbial decomposition, or polymerisation to humic acids (Wang *et al.* 1971, Turner & Rice 1975).

The release of phenolic compounds into the environment is a common phenomenon in late successional vegetation types (Lodhi 1976, Kuiters & Sarink 1986), where individual species must meet the biochemical requirements for longevity through the production of herbivore repellents or decay-resistant wood (cf. Feeny 1970). It should be noted that, compared to beech and oak, the litter of bracken contains only a modest quantity of extractable phenolics (Table 7.4), so consequently the contribution of bracken to total soil phenolics in its natural habitat will be comparatively low. Furthermore, the inhibition of plant growth due to phenolics does not in itself provide an argument in favour of an evolved functional mechanism in the species that are the source of these compounds (but see for instance Nilsson & Zackrisson (1992) for the clear allelopathic strategy of *Empetrum hermaphroditicum*). Instead, we argue that in general the presence of phenolic compounds in the soil must be seen as an environmental condition inherent to vegetation in late successional stages, and not as an adaptive strategy of the component species to exclude other species from the habitat through chemical interference.

7.4.4 The origin of bracken toxicity

The bracken plant produces a large variety of secondary organic compounds, like lignins, tannins, terpenoids, flavonoids, ecdysones, and cyanogenic compounds (Cooper-Driver 1976). This production shows large seasonal or ontogenetic (Cooper-Driver *et al.* 1977, Jones 1983, , San Francisco & Cooper-Driver 1984, Alonso-Amelot *et al.* 1992) and spatial (Cooper-Driver *et al.* 1977, Hadfield & Dyer 1986) variation. As several authors (Gliessman 1976, Sparke 1982) already speculated, the negative results of this study may be caused by a lower toxin concentration in the variety of bracken (*P. aquilinum* subsp. *aquilinum* var. *aquilinum*) considered here, as compared to bracken varieties found elsewhere. However, in a review on flavonoid and phenolic acid content, Cooper-Driver (1976) found no clear distinctions in the composition of these important groups of phytotoxic compounds between bracken varieties. There is therefore no direct evidence to support the hypothesis that differences in toxicity are based on genetic differences in the production of secondary compounds between bracken varieties.

Many of the identified compounds found in bracken can be related to a chemical defence mechanism against herbivory and microbial attack (Carlisle & Ellis 1968, Feeny 1970, Lawton 1976, Cooper-Driver *et al.* 1977, San Francisco & Cooper-Driver 1984, Scalbert & Haslam 1987). Some have proven toxic to large herbivores, including humans (Evans & Mason 1965, Potter & Pitman 1995). Cyanogenesis in bracken fronds was evident in this study (pers. observ.), and that of Dolling *et al.* (1994). In warm climates, other types of secondary compounds may be metabolised in excess, and washed from the fronds in the first rain after a period of accumulation (Taylor & Thomson 1989).

It remains problematical, however, to determine to what extent the production of secondary compounds plays a functional role in the defence against herbivory (Crawley 1997), or in allelopathy for that matter. Cyanogenesis is highest in shady habitats, while tannins, lignins and other phenolic compounds are produced in habitats which receive more light and are more exposed (Jones 1983, Schreiner *et al.* 1984). Ecologically, this means that there is an inverse relationship between N-based chemical defence through cyanogenesis and carbon based defence against herbivores and physical protection against the environment (Jones 1983, Coley 1983). This suggests that the presence of phytotoxic potential in bracken is directly determined by the carbon balance of the plants. It appears that the toxic effects on plants are a by-product of this chemical balance. The inhibition in germination or establishment of other plants that was found in a minority of the published experiments (Table 7.1) may as well be regarded as collateral damage, and not a direct result of an allelopathic mechanism. We argue that there is no direct reason for an evolutionary interpretation of the variation in toxic potential in bracken as was put forward by Gliessman (1976), who proposed that *"... bracken has evolved a system of toxin release that concentrates the input of inhibitors so as to coincide with the (...) germination of associated plants".*

7.4.5 Conclusions

The experiments that were presented in this chapter, combined with a large number of additional (but unpublished) data from other experiments, gave no indication whatsoever that bracken releases -either actively or passively- chemical compounds that have an allelopathic effect on other plant species. A review of the literature also showed that there is little direct evidence that allelopathy is a general active mechanism by which bracken interferes with the germination, establishment or growth of other plant species. There are many mechanisms by which bracken gains, and holds, dominance over other pant species: shading and smothering (Watt 1919; Humphrey & Swaine 1997, chapter 5), or the build up of a thick litter layer (Sydes & Grime 1981*a*; Lowday & Marrs 1992*b*, den Ouden & Vogels 1997; chapter 6). Lack of firm evidence must lead to the conclusion that allelopathy is of little relevance among them.

8. Seed predation and dispersal by rodents

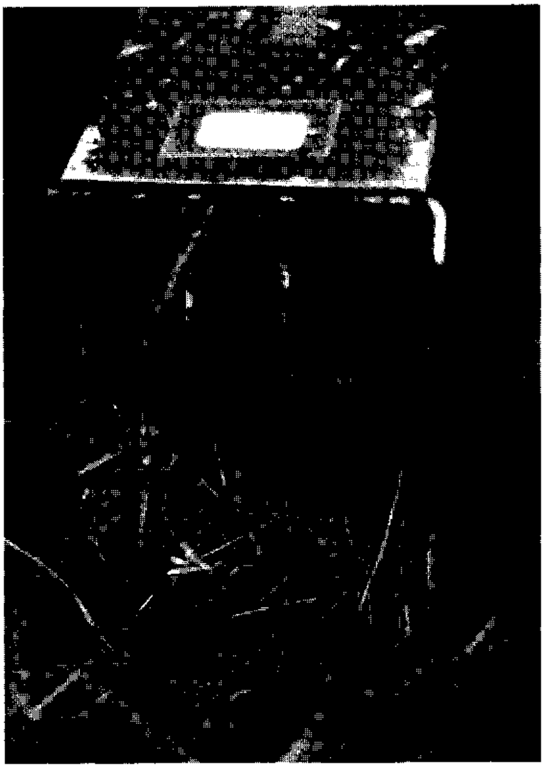


Photo by R. Smit

This chapter is based on:
den Ouden, J. & Smit, R. (in review) The effect of vegetation structure on seed removal and dispersal by forest rodents.
den Ouden, J. & Smit, R. (1996) Seed removal and dispersal by forest rodents: Effects of vegetation structure. *Acta Bot. Neerl.* 46: 327.

8.1 Introduction

8.1.1 The effects of small rodents on forest ecosystems

Small rodents are abundant in many forest ecosystems, but, by virtue of their size and elusive activity patterns, their presence usually remains inconspicuous. The direct influence of rodents on the vegetation can be detrimental in years of population outbreaks (Larsson & Hansson 1977, Rousi 1988), but in general the long term quantitative effects are small, with an average of 3% of the net primary production being consumed by small mammals in temperate ecosystems (Golley *et al.* 1975). However, in a qualitative sense, small forest mammals can have a significant effect on ecosystem functioning by redistributing consumed plant biomass through faeces (Turcek 1959), improving soil moisture conditions and creating favourable sites for germination by burrowing activity (reviewed in Golley *et al.* 1975), or through dispersal of mycorrhizal fungi (Maser *et al.* 1978, Johnson 1996). Furthermore, selective feeding on seedlings (Pigott 1985, Ostfeld & Canham 1993), and predation of preferred seeds by granivorous rodents (Turcek 1959, Jensen 1985) may have a significant impact on the demography of tree species. In this chapter we will focus of the role of small forest rodents in the dispersal and fate of tree seeds, and how this could be influenced by the presence of a bracken vegetation.

8.1.2 Rodent habitat

Within a given ecosystem, overall species composition of the rodent community is influenced by productivity and composition of the vegetation (cf. Aulak 1970). However, the spatial patterning in densities and species composition of rodent populations is dependent on the structural characteristics of the habitat (Kikkawa 1964, Brown 1969, De Jonge & Dienske 1979, Van Apeldoorn *et al.* 1992). Factors such as vegetation cover, presence of dead wood or litter depth greatly determine local habitat suitability for most rodent species, but there may be large differences among rodent species in local habitat utilisation (Hansson 1978, Foster & Gaines 1991). For instance, among European forest rodents a number of vole species (*Clethrionomys, Microtus*) are mostly confined to habitats that provide sufficient cover, while wood mice (*Apodemus*) can also be found in structurally less complex habitats (Hansson 1978, De Jonge & Dienske 1979, Van Apeldoorn *et al.* 1992). The dependence on cover also has consequences for the mobility of species. Small rodents avoid large open areas, and activity outside the protection of cover is usually restricted to short exploratory excursions (Wolton 1985). In Dutch woodlands and forests the most common rodent species are the bank vole (*Clethrionomys glareolus* Schreb.: Fig. 8.1) and wood mouse (*Apodemus sylvaticus* L.: Fig. 8.2). Burrows of bank voles are mainly found in patches providing sufficient cover, whereas wood mice appear less discriminate with regards to nest site location (Kikkawa 1964, Wolton 1985).

Figure 8.1: Bank vole (*Clethrionomys glareolus*) Photo by R. Smit.

8.1.3 Seed dispersal

Both wood mice and bank voles actively forage on large seeds, and may completely remove seed crops of *Fagus sylvatica* and *Quercus* sp. from the forest floor (Watt 1923, Jensen 1985), even in years of heavy masting (Baumler & Hohenadl 1980). However, a large fraction of the removed seeds will not be consumed immediately, but cached for later use (Jensen 1985, Jensen & Nielsen 1986, Vander Wall 1990). Wood mice especially rely heavily on stored seeds during the winter season, and take food from caches through spring (Watts 1968). Seeds cached by wood mice are usually found in shallow depressions dug in the forest floor, containing only one or a few seeds (scatterhoarding), or in the walls of subterranean runways (Jensen 1985). Bank voles, on the other hand, are not known to scatterhoard seeds. Instead, they collect seeds and transport them directly into their burrows, establishing caches with many seeds together (larderhoarding). Scatterhoarding is assumed to be beneficial for both the hoarding animal and the plant. Dispersion of buried seeds over a large area reduces the chance that the food reserves stored by one animal are taken by a competing animal all at once (spreading of risks), especially when the hoarding species is not able to defend the stored food. For the plant, dispersal and burial of the seed means temporary escape from direct predation by non-hoarding seed consumers like for instance wild boar, deer and pigeons. Also, transport away from the parent tree reduces density- and distance-dependent mortality of the seed or developing seedling from pathogens and predators associated with the parent tree (see Vander Wall (1990) for an excellent review on this subject).

Figure 8.2: Juvenile wood mouse (*Apodemus glareolus*) Photo by R. Smit.

8.1.4 Objectives

We set out to investigate whether bracken stands provide a suitable habitat for forest rodents, creating locally higher population densities as compared to areas adjacent to bracken stands with a structurally less complex vegetation. Differences in rodent density and activity will influence the regeneration pattern of tree species, especially for the large-seeded genera like *Quercus* and *Fagus*, through a complex of effects on seed survival (Jensen 1982, 1985, Wada 1993, Herrera 1995), seed abundance (Baumler & Hohenadl 1980), germination and establishment (Shaw 1968), and herbivory on seedlings (Pigott 1985, Ostfeld & Canham 1993). The possible spatial structuring of rodent populations by bracken could therefore have an effect on the fate of seeds and seedlings inside and outside the bracken stands (cf. Price & Waser 1985, Wada 1993). Furthermore, we investigated whether a possible higher rodent density under bracken may also result in dispersal of seeds in the direction, or into, the bracken patches.

We focus this chapter on the removal, predation, and dispersal of acorns of *Quercus robur* by small forest rodents, and tested the following hypotheses:

1. Small forest rodents preferentially use bracken stands compared to adjacent areas without bracken that show less structural complexity.
2. Higher rodent abundance and activity results in higher seed removal rates.
3. Structurally suitable habitat patches are focal points for directed seed dispersal by rodents.

8.2 Methods

This study was conducted in the Speulderbos (see chapter 4). Throughout the forest, scattered fragments of former oak coppice stands occur that have often been invaded by bracken, creating structurally complex microhabitat patches, often with sharp edges, in the forest undergrowth (Fig. 8.3). We conducted two experiments, determining rodent abundance and seed removal (experiment 1: / 8.2.1) and seed dispersal (experiment 2: / 8.2.2) in relation to microhabitats with or without a bracken vegetation.

Figure 8.3: Former oak coppice woodland with partial cover of the forest floor by bracken. Note the distinct edge of the bracken patch.

8.2.1 Seed removal and rodent abundance (experiment 1)

Study sites

We selected five former oak coppice stands with an understory vegetation that was partially dominated by bracken. The understory vegetation in all stands could be typified as representative of the Fago-Quercetum (Westhoff & Den Held 1969), with those areas not yet invaded by bracken dominated by *Vaccinium myrtillus*, *Deschampsia flexuosa*, and *Lonicera periclymenum*, with scattered tussocks of *Molinia caerulea* and *Carex pilulifera* (Table 8.1). Bracken had invaded parts of all sites, and formed relatively sparse stands with frond densities of 3-5 fronds per m^2, and standing above-ground biomass of approximately 100 $g \cdot m^{-2}$ (see chapter 3). The moss layer was poorly developed, mainly consisting of small patches of *Hypnum cupressiforme* Hedw. (mostly around stem bases and old stumps), *Dicranum scoparium* Hedw., and *Polytrichum formosum* Hedw. All stands were last coppiced between 30-40 years ago, which has resulted in a mono-layered canopy of *Quercus robur* with some interspersed *Betula pendula*.

In each of the five stands we established two plots of 20m x 20m. One plot was located inside the bracken stand, the other one in the adjacent vegetation without bracken. The plots were separated by a 15 m wide buffer strip that included the edge of the bracken stand. In each plot, a 5 x 5 grid was established, resulting in a total of 25 intersection points, with 5 m between points (Fig. 8.4). In a 5 m^2 circle, centred around each grid point, we measured a number of structural habitat variables that could potentially affect rodent density (Hansson 1978, Dueser & Shugart 1978, Van Apeldoorn *et al.* 1992), including the percentage cover of shrubs (2-5 m), dead wood, old stumps, and dominant understory species. We also counted the total number of tree seedlings and saplings (<2 m in height) per species within the 5 m^2 circle. The depth of the ectorganic soil layer (further referred to as the litter layer) was measured at three random locations within the circle and averaged per grid point.

Rodent trapping

We determined small rodent population densities in each stand during 4-day trapping sessions in September and October, 1994. Rodent traps were located at each of the 25 grid points in the two grids established per stand. The two grids were sampled simultaneously using one Longworth livetrap per grid point. Traps were filled with hay, baited with carrot and rolled oats, and put in the field on Fridays. The traps were set on Monday mornings, and checked twice a day at sunrise and sunset until Friday morning. All captured rodents were individually marked by fur clipping to allow identification of recaptured animals. For each animal we determined species, sex, and maturity (adult or juvenile). The five sites were sampled successively within a 5-week period. Rodent abundance will be represented as the minimum number of rodents known to be alive at the end of the trapping sessions (MNA).

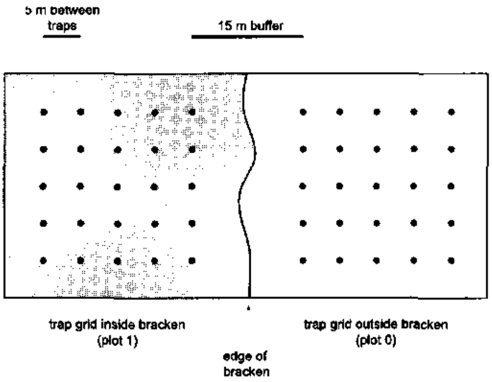


Figure 8.4: Layout of the 2 x 25 trap stations used for rodent trapping inside and outside bracken stands (experiment 1).

Seed removal

In the week following trapping, we used the same plots to determine the effect of the presence of the bracken vegetation on seed removal rates by small forest rodents. We used seeds of *Quercus robur*, collected from a single stand, and obtained from a certified commercial seed company. To determine seed removal rates, we established a 20 m base line through the centre of each grid (Fig. 8.5). At 2 m intervals, 10 m lines were laid down perpendicular to the base line, alternately to the left and right. This resulted in 5 lines to the left, and 5 lines to the right of the base line (Fig. 8.5). We placed single acorns among the ground litter at 50 cm intervals along each line, and marked each position with a small wooden toothpick. So, 200 acorns covering an area of 400 m^2 were presented to seed dispersers on each of the two grids in the five stands. The grids were checked daily until all acorns had been removed. During the sampling period, the natural seed crop was negligible in all stands. Since we determined seed removal rate in the week directly following the trapping sessions, we could relate seed removal rates to rodent abundance on each site.

8.2.2 Seed dispersal and rodent abundance (experiment 2)

We investigated the effect of habitat structure, represented by the presence/ absence of bracken vegetation, on the dispersal pattern of *Quercus robur* acorns by small mammals using a method similar to that of Iida (1994). Small magnets inserted in the acorns allowed dispersed acorns to be retrieved using a magnetometer (Fisher, model FX-3). The magnets were inserted through a 4 mm hole, drilled in the base of the acorn, on the side opposite the embryo. We used neodymium magnets, measuring 5 mm in diameter and 3 mm thick, with a magnetic field density of approximately 1500 Gs. The hole was plugged with grafting wax to prevent rot. Tagged acorns did not differ in weight (5.01 – 0.15 g ; mean – 1 se.; n = 40) from untagged acorns (4.95 – 0.14 g). All magnets were colour coded with paint to identify the original source area from which they were removed.

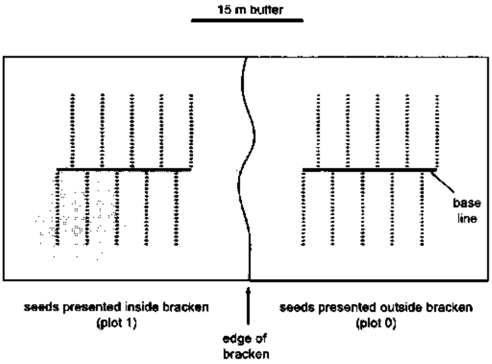


Figure 8.5: Layout of the 2 x 200 acorns presented to rodents for studying seed removal rates from inside and outside bracken stands (experiment 1).

Study sites

We selected two sites for the seed dispersal experiment. Site A was the same site as site 1 of the seed removal experiment. In this site, we determined dispersal patterns in two consecutive winters. In the winter of 94-95 (hereafter referred to as the 1995 experiment), a pilot study was done to evaluate the use of magnets in determining seed dispersal patterns. Since the method proved valuable, and because of contrasting results with the experiment in the winter of 95-96 (the 1996 experiment), we present the results of the pilot experiment of 1995 as part of this study. In the winter of the 1995 experiment, there was no background seed crop present on site A. By 1996, the trees had produced an abundant mast of acorns.

In the 1996 experiment, an additional site was selected in a beech-oak forest. Site B (Fig. 8.6) was dominated by *Fagus sylvatica*, with some interspersed *Quercus robur* and *Q. petraea*. Dominant trees were 20-25 m high, and formed an irregular canopy with some large gaps due to windthrow and previous selective logging. This second site was selected because of a high contrast in understory structure with site A. The beech-oak forest was almost completely void of understory vegetation, except for a large patch of bracken, and some scattered thickets of holly (*Ilex aquifolium*), bramble (*Rubus* sp.), planted *Q. petraea*, and naturally regenerated *F. sylvatica*. Both beech and oak had produced an abundant seed crop on the site.

Seed dispersal

In each site, groups of tagged acorns were presented in two source areas: one located well within the bracken stand, and the other 10-15 m into an open area outside the bracken stand. In site A, the same source area was used inside the bracken stand in the two years, but for the plot outside the bracken a different source area was chosen in 1996 to create more distance to the edge of the bracken stand. Within sites, the distances between source areas ranged between 30 m and 42 m (for exact layout, see Fig. 8.10). Hereafter, we will refer to the two different source areas in relation to the presence or absence of bracken as the cover plot and the open plot, respectively.

The 1995 experiment began November 28, 1994. In each plot, 200 tagged, and 100 untagged acorns were presented as one group, and covered by a 1 x 1 m wooden frame with 5 mm mesh polyethylene netting that allowed access to the source areas by small rodents only, thus preventing seed removal by larger mammals and birds present in the area. The untagged acorns were used to determine whether the insertion of a magnet had an effect on the removal rate of the acorns. Frequent checks on the remaining acorns indicated that this was not the case. The source areas were checked regularly until all acorns had been removed from both plots. We started searching for dispersed acorns one month after the onset of the experiment.

The 1996 experiment was initiated October 31, 1995, and conducted as described above except that in this experiment 150 tagged acorns were presented at each source area. In contrast to the 1995 experiment, dispersed acorns were retrieved after 5 months, thus allowing the assessment of survival of cached acorns until early spring (April 1996).

For each recovered magnet, with or without acorn, we determined the exact position (direction and distance from the source), condition (eaten, intact), burial depth in cm (only for intact acorns), and proximity (<30 cm) to tree stems or stumps. We spent at least 40 h searching per source area. The area within a 30 m circle around the source areas was searched exhaustively. In the 1995 experiment, we also searched 16 transects, extending between 30 and 55 m outward from the plot centre. The number of acorns in the transects (distance-class > 6) was corrected for the proportion of area represented by the transects traversing the circular strips using the formula $N_{corr,i} = N_i \cdot \pi \cdot (K_i + 2.5) / 48$ where $N_{corr,i}$ is the corrected number of acorns in the i-th distance class, N_i is the actual number of acorns found in the i-th distance-class in the transects, with K_i the lower class limit in m.

We decided not to leave intact acorns on the site to study rehoarding or cache robbery (cf. Iida 1994, Sone & Kohno 1996), since digging around while retrieving magnets or tagged acorns greatly disturbed the cache context.

Figure 8.6: The beech-oak forest site used in experiment 2.

Rodent abundance

In order to assess rodent abundance and local habitat preferences on sites A and B, a grid was laid out in the two sites in late summer preceding the 1996 dispersal experiment. Rodent traps were placed 10 m apart (for exact arrangement of traps, see Fig. 8.8). We conducted trapping sessions in the late summer, early and late fall, and in the week prior to the search for dispersed acorns in the spring of 1996. Trapping procedures were the same as in the seed removal experiment, except that individual rodents were toe-clipped for identification. The spring census included three trap days, instead of four as in all previous censuses.

8.2.3 Data analysis

In experiment 1, differences in structural habitat variables between sites and plots with or without bracken were tested using ANOVA with only the main factors entered in the model. Data were used as means per grid (n = 10). Differences in rodent abundance between grids inside and outside the bracken stands were tested non-parametrically using a sign test.

In order to determine habitat preferences of rodents in experiment 2, trap stations were divided into three groups: traps under cover, traps in the open, and traps located within 5 m of the edge of the bracken stand or other structurally complex microhabitat patches. To correct for different sample size, we calculated the relative number of captures per habitat type by multiplying the proportion of captures of a species in one of the three habitat types (open, edge, cover) by N_{tot}/N_i, with N_{tot} representing total number of traps in a site, and N_i the number of traps in the i-th habitat type. Differences in structural habitat preference of rodents were tested by analysing the frequencies of rodent captures in traps located in the open, along the edges, or under cover, using tests for goodness of fit, with Williams' correction for small sample size (Sokal & Rohlf 1995).

Seed removal rates and mean survival times were estimated for each grid (n = 200), and for the two grids combined (n = 400) using the Kaplan-Meier survival analysis (SPSS 1996). Differences in mean survival time of the acorns between grids inside and outside bracken were tested using a log-rank test (Pyke & Thompson 1986). Within a grid the spatial pattern of acorn removal was clustered, especially within rows. This indicates that the chance of an individual acorn being found and removed is dependent on the probability that its neighbour is detected (cf. Stapanian and Smith 1984). However, removal rates are estimated for an entire grid, and survival probabilities are calculated over the entire cluster being removed during a given day. Assuming that the size of the removed clusters is only dependent on the activity of the rodents we feel that the use of the Kaplan-Meier survival analysis is justified, despite the spatial interdependency of individual removal chances. Mean survival times calculated this way correspond with the half-life of acorns derived from non-linear regression models (using the Weibull-function) fit on the accumulated number of acorns removed (data not shown).

For each plot in the seed dispersal experiment, the overall directionality of dispersal was determined by constructing a 95%-confidence ellipse around the "centre of gravity", which was calculated as the mean of the (x_i,y_i) coordinates of all retrieved magnets and acorns relative to the source area $(x_0,y_0 = 0,0)$, using the methods described by Batchelet (1981). These mean coordinates represent the end points of the vector of mean dispersal direction and distance. Deviations from the origin of the mean vector, indicating directionality of dispersal, were tested using Hotelling's one-sample test (Batchelet 1981). For the 1995 experiment, only data from within the 30 m circle were included in the analysis.

Differences in the distribution of caches or of individual acorns as a function of distance from the source between the open and covered plots on a site were tested non-parametrically using a Kolgomorov-Smirnov test. For site A, 1995, only data from within the 30 m circle were used.

8.3 Results

8.3.1 Seed removal and rodent abundance (experiment 1)

Structural habitat variables

The five selected sites showed only minor differences with respect to the measured structural habitat variables (Table 8.1). Overall, the data indicate that the presence of a bracken stand creates the sole major difference in structural habitat between plots on the sites, as was intended in this study. The amount of dead wood and percentage shrub cover was significantly different (ANOVA, $F_{4,4}$ = 16.2 and 7.2 respectively; $P < 0.05$) between sites, but there were no differences in these variables between plots inside and outside the bracken stand. The area covered by stumps was variable between and within sites, but no systematic differences were present. In the grids inside the bracken stands, percentages of bracken cover varied between 22 and 33 % (Table 8.1).

Table 8.1: Structural habitat variables and seedling counts in sites and plots used for the seed removal experiments. Within sites, plots are without (0) or with (1) a bracken canopy. All values are means from 5 m^2 circular plots around the trap stations (n = 25). Dominant species of the forest undergrowth are *Vaccinium myrtillus* (*Va.my.*) and *Deschampsia flexuosa* (*De.fl.*)

		Structural elements (% cover)				Litter		Dominant species (%)		Tree seedlings		
site	plot	bracken	shrub	stump	dead wood	cover	depth	*Va. my.*	*De. fl.*	Total ($N/5m^2$)	oak (%)	beech (%)
1	0	0	3.2	2.6	0.5	70	1.5	37.0	23.0	2.3	95	0
1	1	28	0.6	3.4	2.0	81	2.0	8.4	7.0	0.6	88	13
2	0	0	2.4	2.4	3.1	53	1.3	28.6	23.4	1.8	67	24
2	1	32	0.0	7.0	4.9	84	2.6	17.0	1.4	0.5	67	25
3	0	4	13.4	7.2	1.4	74	1.8	9.9	9.0	1.3	73	24
3	1	24	3.0	3.5	4.6	76	2.0	9.8	15.0	1.8	89	9
4	0	0	5.0	3.6	8.0	79	1.6	15.6	15.4	2.9	99	1
4	1	22	1.8	1.0	9.3	86	1.9	6.2	0.2	0.4	78	11
5	0	0	14.0	2.2	2.5	64	1.6	19.6	26.2	1.8	87	11
5	1	33	12.2	3.2	1.7	88	2.3	3.6	2.8	1.2	97	3

Plots inside bracken stands had significantly deeper litter layers ($F_{1,4}$ = 10.3; P = 0.033), had a larger percentage litter cover on the ground, and lower percent cover of *Vaccinium myrtillus* and *Deschampsia flexuosa* than plots without bracken. Both *Vaccinium* and *Deschampsia* were the only two dominant plant species outside the bracken stands; yet most of the forest floor remained covered by bare litter (Table 8.1). The number of seedlings was generally lower inside the bracken stands. This trend was not significant ($F_{1,4}$ = 4.8; P = 0.052), due to the higher number of seedlings inside the bracken stand of site 3 (Table 8.1).

Rodent species and abundance

Both wood mice (*Apodemus sylvaticus*) and bank voles (*Clethrionomys glareolus*) were common on the sites. In site 1, one individual house mouse (*Mus domesticus* L.) was captured, but this was probably a stray animal from a nearby farm. The total number of animals caught varied greatly between sites and between grids within sites, as did the minimal number of animals known to be alive (MNA) on the site after trapping was completed (Table 8.2). Within sites, the total number of rodents captured was significantly less (sign test, P = 0.032) in the grids outside the bracken stands than grids inside bracken. However, there were large differences between the two species. *A. sylvaticus* was caught more or less evenly between the two grids, with several individuals caught in traps on both grids. In contrast, *C. glareolus* was caught exclusively on the grids inside the bracken stands (Table 8.2).

Seed removal

Seeds disappeared rapidly from the plots (Fig. 8.7). On numerous occasions we found seed shell fragments, indicating that acorns were consumed on the spot. When pooled over the plot-pairs, mean survival times (MST) of the acorns ranged from 2.1 d in site 3 to 12.4 d in site 5 (Table 8.2). Except for site 1, MST's of the acorns were significantly different between the two plots per site (Logrank test for sites 2-5, df = 1, $P < 0.001$). In sites 3, 4 and 5, the acorns were removed at a faster rate from the plots inside the bracken stands, as indicated by lower MST's (Fig. 8.7, Table 8.2). However, in site 2 this pattern was reversed, with significantly faster removal of acorns from the plot outside bracken (Fig. 8.7, Table 8.2). Pooled over the two grids, the mean survival times (n = 400) of the acorns were negatively correlated with MNA of adult individuals (r = -0.85, P = 0.033).

The large MST for site 5 was due to the fact that acorns were not discovered until the fifth day after onset of the experiment. Indeed, no rodents were known to be present at this site when we laid out the acorns (Table 8.2). The only animal present during the previous week was a female bank vole, who was found dead in her trap after the fourth time she was captured. Apparently, this site was invaded on the fifth day by one or more rodents that removed 75% of the acorns from the bracken plot in the first night after discovery. Subsequent seed removal in the nearby plot without bracken was considerably slower (Fig. 8.7).

Table 8.2: Total number of captured wood mice (*Apodemus sylvaticus*) and bank voles (*Clethrionomys glareolus*) in 20m x 20m grids (25 traps) inside and outside bracken stands, and minimal number of individuals alive (MNA) after 4-day trapping sessions in 5 former oak coppice stands. Mean survival times (MST) of 200 acorns per plot, or 400 when pooled per site, were calculated using the Kaplan Meier Survival Analysis (see Methods). Small survival times indicate rapid seed removal rates.

Site	Plot	Total number of captures		MNA[1] in site		MST
		A. sylvaticus	*C. glareolus*	*A. sylvaticus*	*C. glareolus*	(d)
1	outside	5 (1)	0 (0)			6.3
	combined			5 (1)	0 (0)	6.4
	inside	7 (3)	0 (0)			6.4
2	outside	3 (0)	0 (0)			2.2
	combined			4 (0)	5 (2)	2.9
	inside	5 (0)	10 (6)			3.5
3	outside	2 (0)	0 (0)			2.2
	combined			2 (0)	4 (0)	2.1
	inside	3 (0)	10 (0)			1.9
4	outside	0 (2)	0 (0)			7.1
	combined			2 (1)	1 (0)	5.0
	inside	2 (0)	4 (0)			2.9
5	outside	0 (0)	0 (0)			17.3
	combined			0 (0)	0 (0)	12.4
	inside	0 (0)	4 (0)			7.4

1. Numbers represent adults and (juveniles)

8.3.2 Seed dispersal and rodent abundance (experiment 2)

Rodent abundance

The trapping results from the two sites of the seed dispersal experiment showed essentially the same patterns in rodent species composition and habitat use as in the seed removal experiments, with *A. sylvaticus* and *C. glareolus* as the two dominant rodent species. The only other mammalian species captured was the common shrew (*Sorex araneus* L.), a predominantly insectivorous species that will not be considered further.

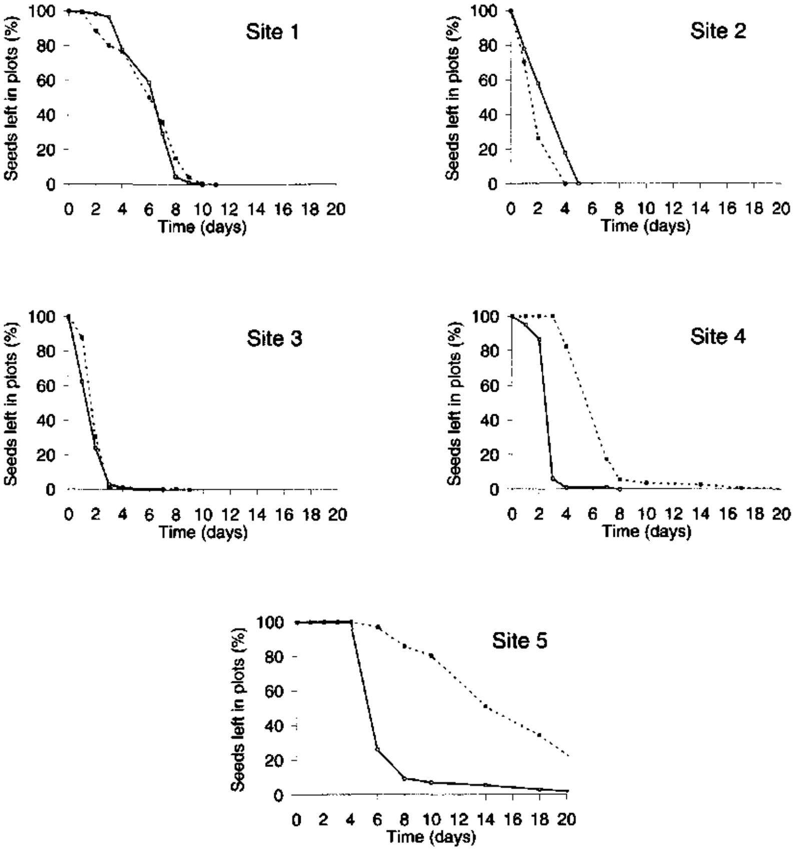


Figure 8.7: Seed removal from plots inside (solid lines) and outside (dashed lines) bracken stands in five former oak coppice woodlands. In site 5, seed removal from plots inside and outside bracken was 100% after 32 and 39 days, respectively.

There were considerable fluctuations in the number of rodents present on the two sites over the four trapping sessions (Table 8.3). There was a decline in the activity for both species in site A from late summer through autumn 1995, but the number of animals present changed only marginally during this period (Table 8.3).

Table 8.3: Total number of rodents captured, and mean number of animals alive at the end of the trapping sessions (MNA) in 4 censuses at the two sites of the seed dispersal experiments. The number of individuals recaptured represents animals that were found on the site in a following census. Rodent MNA of the Sept '94 census has been added for illustration.

		Apodemus sylvaticus				*Clethrionomys glareolus*			
Census	Trap days	Total capt.	MNA ad	MNA juv.	Ind. re-capt.	Total capt	MNA ad	MNA juv	Ind. re-capt.
site A: oak coppice wood;land[2]									
Sep '94[1]	*4*		*5*	*1*	-		*0*	*0*	-
Aug '95	4	21	4	1	-	37	10	7	-
Sep '95	4	17	1	2	3	17	3	1	4
Oct '95	4	5	0	3	0	8	3	3	2
Apr '96	3	38	24	3	0	19	10	2	0
site B: beech-oak forest[3]									
Aug '95	4	6	1	1	-	2	1	0	-
Sep '95	4	3	2	1	1	16	3	3	1
Oct '95	4	9	6	2	0	3	3	0	1
Apr '96	3	36	18	5	0	7	4	2	0

1. MNA from site 1 of the seed removal experiment, based on captures from an area 3.6 times smaller (1500 m^2) than the grid used in the seed dispersal experiment.
2. Total number of traps: 54; total trapping area: 5400 m^2.
3. Total number of traps: 42; total trapping area: 4200 m^2.

On site B, there was an increase in the number of wood mice in October, 1995. Numbers of individual bank voles were variable, as was the number of captures on the site, with highest activity in September 1995 (Table 8.3). By April, 1996, the number of wood mice increased on both sites compared to the previous census in October, 1995. The number of bank voles only increased in site A. In contrast, vole numbers remained more or less constant in site B (Table 8.3). There was a high turnover of individual rodents. No animals that had been captured in the previous autumn were recaptured on the sites in the spring of 1996. In particular wood mice in site A were rarely recaptured in the successive 1995 censuses (Table 8.3). Given seasonal and sexual differences in trappability (Jensen 1975), the results from these censuses indicate that rodent populations were highly dynamic on both sites.

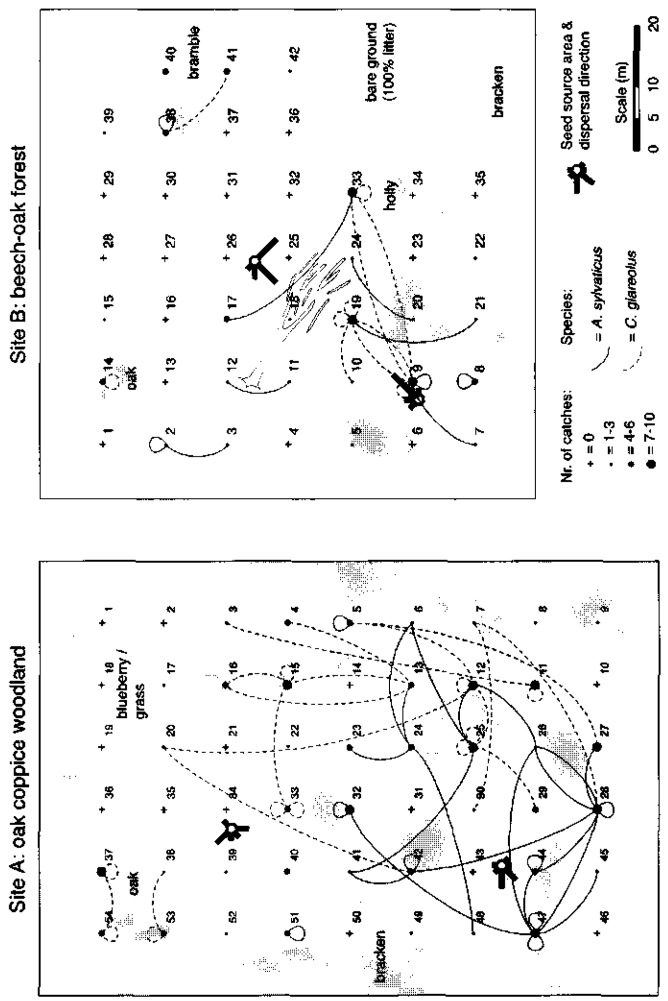


Figure 8.8: Total number of captured rodents per trap station and recorded movements of individual rodents in the two study sites. The presence of structurally complex habitat patches is indicated by shading. Movements are indicated by lines connecting trap stations where individuals were caught on consecutive events within a census period. The directionality of acorn dispersal is represented by the relative number of acorns found in each of eight directions, each representing a 45 degree section of the area around the source areas.

Habitat use and mobility

Wood mice and bank voles showed similar habitat preferences as in the seed removal experiment (Table 8.2; Figs. 8.8 and 8.9). The number of animals caught at a given trap station was clearly dependent on micro-habitat type, and activity of both species was mainly concentrated in the areas that provide cover (Fig. 8.8). Also, movements of recaptured individuals were mainly restricted between traps in the areas with cover, or in the edges with the open areas. Only a few movements were recorded towards traps in the open areas (Fig. 8.8). Such patterns were also observed in rodent mobility studies (Kikkawa 1964, Brown 1969), where movements into open areas can be interpreted as excursions (Wolton 1985) or foraging bouts (Longland & Price 1991) out of the more protected home range.

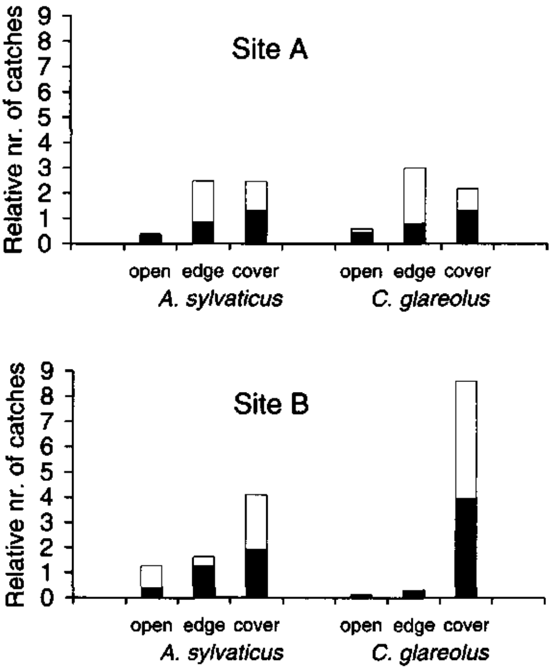


Figure 8.9: The influence of structural habitat, provided by a bracken stand and scattered scrub, in a former oak coppice woodland (Site A) and a mixed beech-oak forest (Site B) on the relative number of trapped adults (solid bars) and juveniles (open bars) of wood mice (*Apodemus sylvaticus*) and bank voles (*Clethrionomys glareolus*). Data were pooled over 4 censuses between July 1995 and April 1996. For calculation of relative number of captures, see Methods.

Both *A. sylvaticus* and *C. glareolus* were predominantly caught in traps under cover or near the edges (Fig. 8.9). Open areas were avoided. This pattern was strongest in the beech-oak forest, where no vegetation was present on the forest floor, as opposed to the oak coppice site where there was still some cover by *Vaccinium*, *Deschampsia,* and *Lonicera* outside the bracken stand (Table 8.1). Both species, in both sites, were captured significantly more often in traps in the edges or under cover ($G_{adj} > 15.0$; df = 2; $P < 0.001$). The only exception to this pattern is shown by juvenile wood mice in site B (Fig. 8.9), who were not trapped significantly more frequently in covered areas ($G_{adj} = 5.5$; $P = 0.06$). The high relative number of juveniles caught in the open area was caused by a single female in the April 1996 census, probably on an excursion from a nearby burrow located just outside the trapping area.

Seed removal and recovery

In the 1995 experiment on site A, all seeds disappeared from the source within 10 days. In 1996, seeds were removed within 3 weeks from the cover plot, and within 6 weeks from the open plot. On site B, seeds were completely removed from the cover plots only after 2.5 months, while in the open plot of site B, 128 (= 85%) acorns still remained on the source area by April 1996. Of these remaining 128 acorns, 19 were partially consumed on the spot, showing rodent teeth marks. The other 109 acorns were left untouched.

The percentages of retrieved tagged acorns and magnets varied between 28-89 % (Table 8.4). Magnet recovery was lowest in 1995. Magnets and acorns not recovered were probably either located outside the searched area (or located between the transects beyond the 30 m circle in site A, 1995), or buried too deep (for instance inside the nests) to be detected by the magnetometer. Earlier tests showed that the detection limit was at least 15 cm, so acorns missed on the searched area were probably buried at depths that present unfavourable conditions for seedling establishment (Watt 1923, Iida 1995).

Dispersal distance

In site A, the dispersal patterns showed large differences between years. Dispersal distances were largest in 1995, with a mean dispersal distance of 18.5 and 22.1 m from the source areas inside and outside bracken respectively (Table 8.4, Figs. 8.10 and 8.11). The maximum distance recorded was 62.9 m for an acorn removed from the open plot (this was an accidental find outside the search area, and is therefore not included in the analyses). In the following year, the acorns were dispersed over much smaller distances (10.5 and 8.1 m, respectively). This coincided with abundant acorn production on the site in 1996. Caches originating from the cover plot in 1995 were more or less uniformly distributed over the distance classes, while there was a peak in dispersal distance between 20-25 m away from the open source area (Fig. 8.11). The recovered magnets, representing consumed acorns, were more concentrated around the open source area (Fig. 8.10), whereas the intact caches still remaining after one month were located significantly farther away from the source (Mann-Whitney U = 656; $P = 0.027$). The few remaining intact acorns in 1996 (Table 8.4) were all located less than 10 m from the source area (Figs. 8.10 and 8.11).

In the 1996 experiment, the distribution of caches as a function of distance from the source differed between plots inside and outside bracken for both site A ($Z = 1.525$; $P = 0.019$) and site B ($Z = 1.673$; $P = 0.007$). In site A the number of dispersed acorns in the open plot decreased rapidly with distance from the source area. In contrast, the acorns dispersed from the open plot in site B were transported a greater distance away from the source than acorns in the cover plot, where the mean dispersal distance was confined by the edges of the bracken stand (Fig. 8.10). However, only 22 seeds were taken from the open source area in site B. Of the retrieved magnets, 86% were found in structurally complex microhabitat patches, or under tree stems (Fig. 8.10).

Cache spacing and location

The nearest neighbour distances of located caches did not differ between plots on site A in both years (Mann Whitney U-tests, both $P > 0.05$). The nearest neighbour distances were much smaller in 1996 than in 1995 (Table 8.4), which follows directly from the differences in mean dispersal distance of the acorns between the two years (Figs. 8.10 and 8.11). In site B, the greater nearest neighbour distances in the open plot are a direct consequence of the low number of retrieved magnets. For site A, 1995, the nearest neighbour distances between intact acorns only were 4.6 ± 0.1 m (mean ± 1 se) for both plots.

Nearest neighbour distances were significantly correlated with distance from the source, except in the plot outside bracken in site A, 1995 (Table 8.4). This indicates that cache spacing increases with distance from the source. Correlations in site A, 1995, were calculated using data of caches found only < 30 m from the source, since no precise nearest neighbour distances could be calculated from the caches located in the transects between 30 and 55 m.

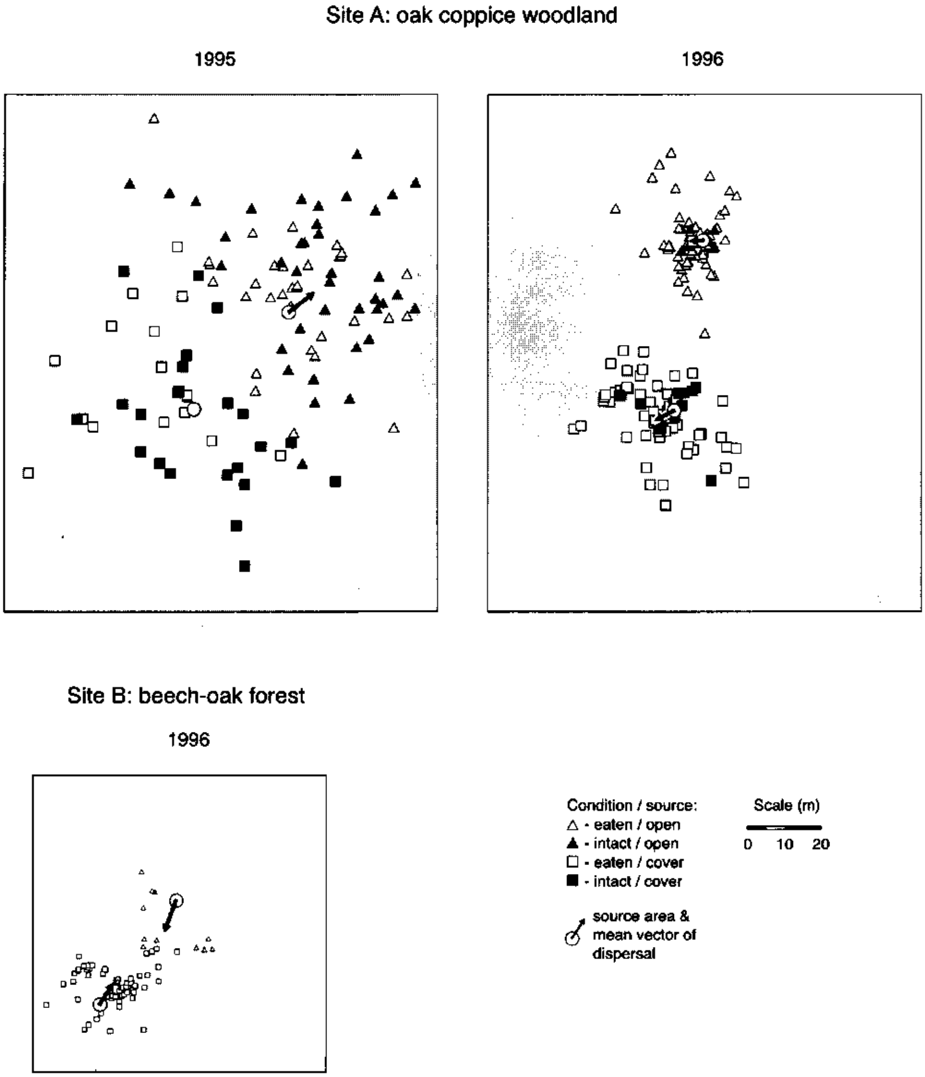


Figure 8.10: Seed dispersal patterns in the study sites in 1995 (site A only) and 1996 (both sites). Arrows represent the mean vector of dispersal direction and distance. Tagged acorns were retrieved after 1 month (1995) or after 5 months (1996). Shaded area represents structurally complex habitat.

Table 8.4: Summary statistics for the seed dispersal experiment. Acorns were tagged with small magnets, and retrieved 1 month (1995) or 5 months (1996) after onset of the experiment. There was no acorn crop in 1995, while both oak and beech had abundant masts in 1996.

Site	A: oak-birch woodland				B: beech-oak forest	
Year	1995		1996		1996	
Plot	cover	open	cover	open	cover	open
N offered	200	200	150	150	150	150
Time until complete removal (wk)	1.5	1.5	3	6	10	>25
N not removed from source	0	0	3	36	13	128
N retrieved	55	84	122	134	106	14
% retrieved [1]	28	42	81	89	71	64
Intact acorns						
Nr. Intact acorns	28	47	16	9	0	2
% intact	50.9	56.0	13.1	6.7	0.0	14.3
Mean dispersal distance (m)	20.4	24.1	6.8	3.2	(-)	6.4
Nr. Intact caches	23	39	11	8	0	1
Mean nr. Acorns per cache	1.2	1.2	1.5	1.1	(-)	2.0
Mean cache depth (cm)	2.7	3.0	3.4	2.5	(-)	2.0
All retrieved magnets & acorns						
Total nr. Caches	40	73	76	67	59	12
Mean cache size	1.4	1.2	1.6	2.0	1.8	1.2
Mean cache distance from source (m)	22.1	22.5	11.1	8.0	9.9	13.4
Mean dispersal distance all tagged (m)	18.5	22.1	10.5	8.1	10.2	13.0
Mean Near. Neighbour distance.(m)[2]	4.3	3.3	1.9	1.8	1.6	3.4
Correlation cache distance x NN	*0.43* ^{1}	*0.25*	*0.53* ^{3}	*0.80* ^{3}	*0.33* ^{1}	*0.74* ^{2}
Mean vector length (m) [3]	1.7	7.9	4.5	2.2	6.4	8.0
Hotelling's T [4]	0.8	31.7 ^{3}	47.5 ^{3}	19.1 ^{3}	134.2 ^{3}	15.8 ^{1}

1. For site B, plot outside bracken, the percentage of retrieved magnets is calculated over the fraction of acorns removed, so excluding the 128 acorns left on the source area.
2. For 1995, nearest neighbours were calculated for caches <30 m from the source area only.
3. Mean vector length represents the distance between the source area, and the "centre of gravity" of dispersal distance and direction (see Methods) of all retrieved magnets (<30 m).
4. Significance levels are indicated by superscripts: 1 = $P < 0.05$, 2 = $P < 0.01$, 3 = $P < 0.001$.

Dispersal directions

The two-dimensional pattern of cache direction and distance away from the source can be reduced to a single resultant vector, which points towards the "centre of gravity" of dispersal (Batchelet 1981). Except for the plot inside bracken in site A, 1995, this centre of gravity was significantly different (Hotelling's T^2, df = 1, $P < 0.01$) from the origin (source area) for all plots, indicating that dispersal patterns were not random around the origin, but instead show a significant directionality (Table 8.4). However, the resultant dispersal directions for the entire cache populations did not clearly relate to the position of nearby cover (Fig. 8.10). The directionality of dispersal becomes apparent when we compare the distributions of caches over eight 45-degrees sections around the source areas (Fig. 8.8): the major dispersal directions point towards centres of rodent activity.

Table 8.5: Conditions (eaten or intact), and position related to vicinity of stems and stumps, of all retrieved acorns on site A, in 1995 (retrieved after 1 month) and 1996 (retrieved after 5 months).

Distance from	1995			1996		
stems & stumps	eaten	intact	total	eaten	intact	total
< 30 cm	40	16	56	149	11	160
> 30 cm	24	59	83	43	14	57
Total	64	75	139	192	25	217

Most consumed acorns (only magnets retrieved) were found near tree stems and stumps (Table 8.5). In site A, 1995 the majority of the acorns was still intact 1 month after the start of the experiment. A significantly ($G_{adj} = 26.0$, df = 1; $P < 0.001$) higher proportion of these intact acorns was located >30 cm away from stumps and stem bases. In the 1996 experiment, 87-100% of the retrieved acorns were consumed, leaving only the magnets (Table 8.4). These magnets were found significantly more frequently ($G_{adj} = 31.0$, df = 1; $P < 0.001$) close to stem bases and stumps (Table 8.5). Loglinear analysis showed that there is a highly significant interaction ($P < 0.001$) between condition of the retrieved acorn (eaten or intact) and proximity to stem bases and stumps. This suggests that the positions of the magnets represent the spots where the acorns were eaten after being taken from a cache, or directly from the source area. Therefore, locations of magnets do not represent actual cache sites of the acorns.

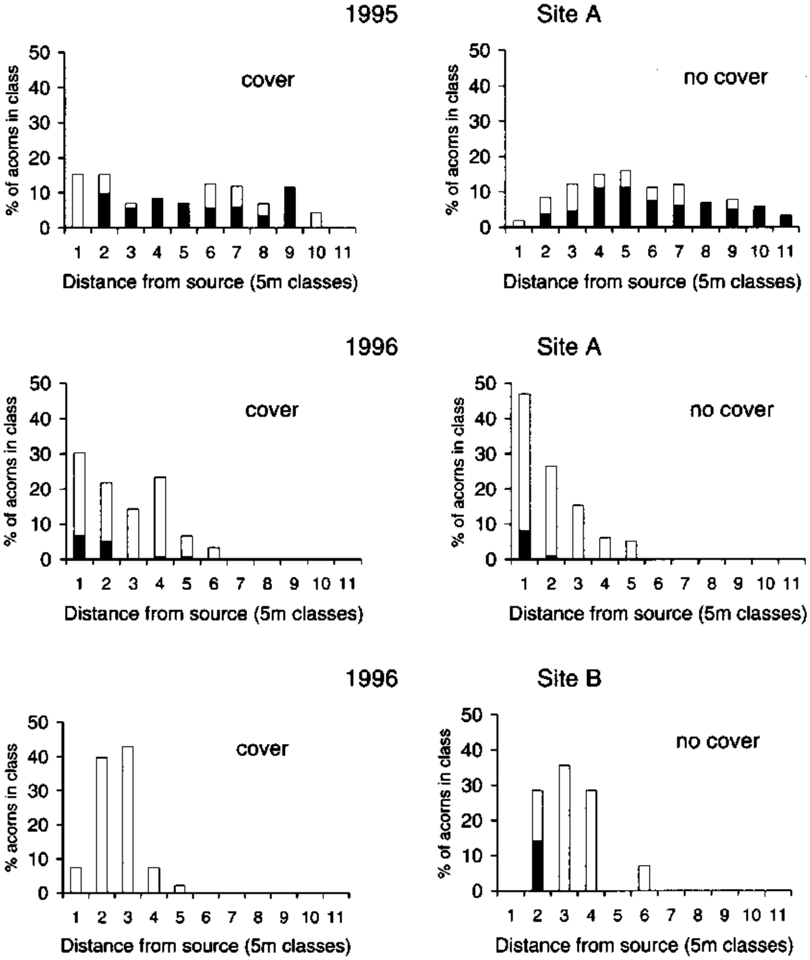


Figure 8.11: Distributions of retrieved intact acorns (solid bars) and consumed acorns (open bars) over distance from a single seed source, located inside (cover) or outside (no cover) a bracken stand in a former oak coppice woodland (Site A), and a mixed beech-oak forest (Site B), and for two consecutive years (Site A only). Retrieved acorns and magnets were grouped in circular strips, 5 m wide. The number of acorns in the transects (distance-class > 6) of the 1995 experiment was corrected as described in methods. In 1995 and 1996, acorns were retrieved after 1 and 5 months respectively.

Surviving caches

In April, 1996, only 2 intact acorns remained outside both source areas of site B, representing 1.7% of all retrieved acorns on the site (Table 8.4). On site A, 7-13% of the retrieved acorns were intact after 5 months. Of these acorns, 17 out of 25 had started to germinate, indicating that insertion of magnets may not have a large negative influence on germination. When including the data from 1995, characteristics of caches containing intact acorns in site A were not different between years or plots (Table 8.4, Fig. 8.12). Mean overall cache size varied between 1.1 and 1.5 seeds per cache. Average burial depth was approximately 3 cm, which positions the acorns in the lower parts of the ectorganic soil layer, near the mineral soil surface (Fig. 8.13). There were no differences in burial depth between plots, or years. The frequency distributions of cache depths were also similar among years and plots in site A (Fig. 8.12).

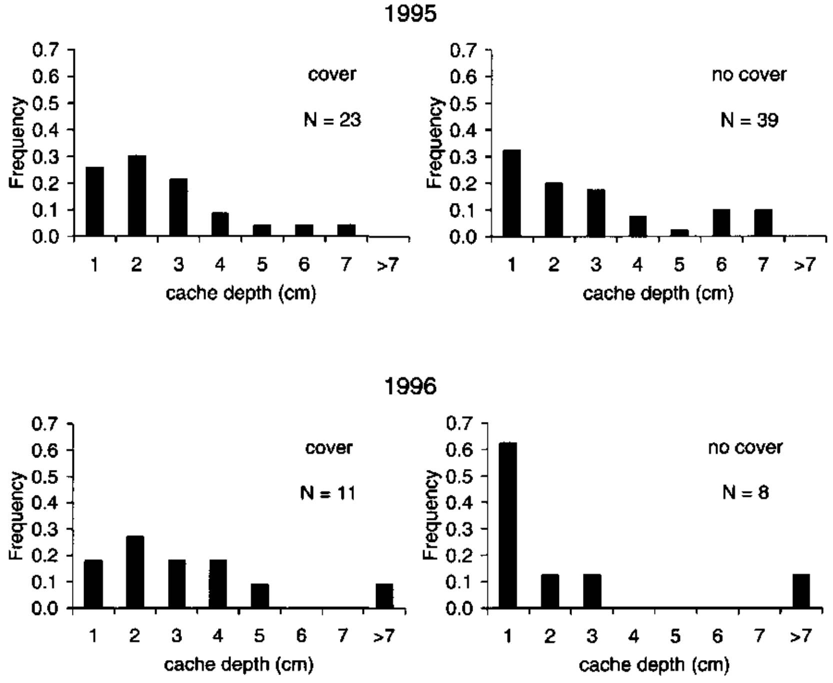


Figure 8.12: Depths of caches containing one or more intact acorns for the two experiments in site A, a former oak coppice woodland in 1995 and 1996. Acorns were cached by rodents, and taken from plots inside (cover) and outside (no cover) a bracken stand. N denotes total number of retrieved intact caches.

8.4 Discussion

8.4.1 Rodents and seed dispersal

Rodents have a considerable impact on the demography of large seeded tree species by strongly reducing the number of seeds available for germination through seed predation. In the period during seed fall, many rodent species preferentially forage on large seeds, and are able to destroy a substantial proportion of the local seed pool. However, most seeds will escape immediate predation because they are cached by the rodents for later use (Sork 1983, Jensen 1985, Jensen & Nielsen 1986, Stapanian 1986, Vander Wall 1994, this study). Consequently, it is impossible to use seed removal rates as such to directly infer the effects of rodents on plant population dynamics. Instead, removal rates of seeds are indicative only of rodent activity or abundance, and their ability to harvest seeds (cf. Hoch & Adler 1997).

Seed caching by scatterhoarding rodents like *A. sylvaticus* can be regarded as beneficial to tree species like *Quercus* or *Fagus*, since it increases short term survival of the seeds by hiding them from other seed predators and thus prevent immediate predation (Herrera 1995), and by placing them in sites where germination is more likely to be successful (Watt 1923, Jarvis 1964, Jensen 1985, Herrera 1995). Seed caching will further result in dispersal of the seeds away from the parent tree. This potentially increases the chances that seeds end up in habitat patches that are more favourable to the plant for establishment and growth (Howe & Smallwood 1982, Nilsson 1985, Venable & Brown 1993), and may reduce distance-dependent seed or seedling mortality due to herbivores or pathogens associated with the parent tree (Janzen 1971, Augspurger 1984).

8.4.2 Dispersal distance

In general, the maximum distance covered by small forest rodents while dispersing seeds lies within a range of 13-45 m (Sork 1984, Jensen 1985, Iida 1994, Sone & Kohne 1996). In this study, dispersal distances up to 63 m were found, which corresponds well with the activity range of wood mice when on exploratory excursions (Kikkawa 1964, Bergstedt 1966, Wolton 1985). The final dispersal distances may even be larger when seeds are retrieved and subsequently rehoarded elsewhere (Vander Wall 1990).

On site A, the seed dispersal patterns were strikingly different between the 1995 and 1996 experiments (Figs. 8.10 and 8.11). The strong reduction of mean dispersal distance in the 1996 experiment coincided with an abundant seed crop, and thus a higher background density of cached seeds already present on the site. Masting has been shown to cause a decrease in seed removal rates from artificial

Figure 8.13: A surviving cache containing 6 acorns.

seed caches of varying density (Stapanian & Smith 1984, O Dowd & Gill 1984, Nilsson 1985) or of seeds fallen directly from the parent tree (Sork 1983), but we know of no previous studies showing a relationship between dispersal distance and seed abundance. Such a relationship could have important implications for the dispersal pattern of seeds from individuals or species that fruit either at the same time (short dispersal distances), or out of synch (long dispersal distance) with others in the same habitat (cf. Snow 1965).

8.4.3 Directed seed dispersal

The data from this study (Figs. 8.9 and 8.10) suggest that differential rodent activity, mediated by structural habitat characteristics, induces a redistribution of the local seed population. The presence of structurally complex microhabitat patches may therefore act as focal points for directed seed dispersal by rodents. Directed seed dispersal has been demonstrated for a number of bird- (Vander Wall & Balda 1977, Krijger *et al.* 1997) and ant-dispersed species (Handel 1978, Culver & Beattie 1980, Hanzawa *et al.* 1988). Ants carried seeds towards their nests, where the seedlings showed significantly higher establishment rates or survivorship when compared to nonant-dispersed seeds. In principal, directed dispersal refers to the non-random deposition of seeds. Used in an evolutionary context, the term has further been restricted to refer to dispersal towards specific habitat patches where seeds or plants experience higher survivorship or fecundity (Howe & Smallwood 1982, Venable & Brown 1993). In an ecological context this means that seeds must be dispersed to a safe site.

In this study, dispersal patterns of acorns by small rodents were clearly not random, with dominant dispersal directions pointing towards centres of rodent activity. The consequences for long-term survival of the seeds and seedlings will depend on both the specific characteristics of the structurally complex patches, and the presence and activity of the rodents, or other herbivores and granivores, within these patches. Dispersal into a bracken vegetation will reduce survival chances of the seedlings because of the strong interference by bracken (see previous chapters). Yet, when structural habitat is built by other species, survival may be enhanced when interference from the plant species providing the structure is relatively low, and seedlings remain protected from grazing, as has been observed inside crowns of windthrown trees and in patches of *Prunus spinosa* L., *Rubus* sp., or *Ilex aquifolium* (Morgan 1991, Vera 1997).

8.4.4 Seed and seedling survival

Long term seed survival will depend on the presence and activity of rodents in structural habitat patches during the winter and spring following seed caching. Dietary studies show that wood mice feed on acorns through the end of May (Watts 1968). They will either feed on seeds taken directly from caches, or on the cotyledons that are removed from young seedlings (Sonesson 1994). Seeds are thus able to germinate only when they are not retrieved (or robbed by a competitor) from the cache by spring.

In general, population densities of rodents show large yearly fluctuations, with lowest numbers in spring. In spatially heterogeneous habitats, rodent population structure can be considered as a complex of meta-populations, and small isolated patches will frequently show extinction of the resident rodent population (Van Apeldoorn *et al.* 1992). Such local extinction could result in increased seedling establishment from non-recovered caches, much as seedling establishment in ant-dispersed seeds may be enhanced when an ant colony moves to build another nest (Culver & Beattie 1978). We therefore suggest that, within the disperser system of small forest rodents and large seeded tree species, long term effects on seed survival and seedling establishment are determined by the interaction between the spatial distribution of structurally complex habitat patches and temporal patterns in rodent population density and composition.

Differential rodent activity and directed dispersal have consequences for local seed abundance in spatially diverse habitats. Further long-term studies are needed to investigate the net effects of seed production, dispersal and predation on establishment and survival of seedlings. The potential benefits to large-seeded tree species of dispersal by rodents (either in evolutionary or ecological time) can therefore not be concluded from short term studies that only take a snap shot of a process that involves a large number of concurrent mechanisms operating in a structurally complex environment. This study does indicate, however, that we may have to reconsider the use of continuous, distance-dependent dispersal functions of rodent-dispersed tree species in spatially explicit models of forest dynamics (i.e. Pacala *et al.* 1996).

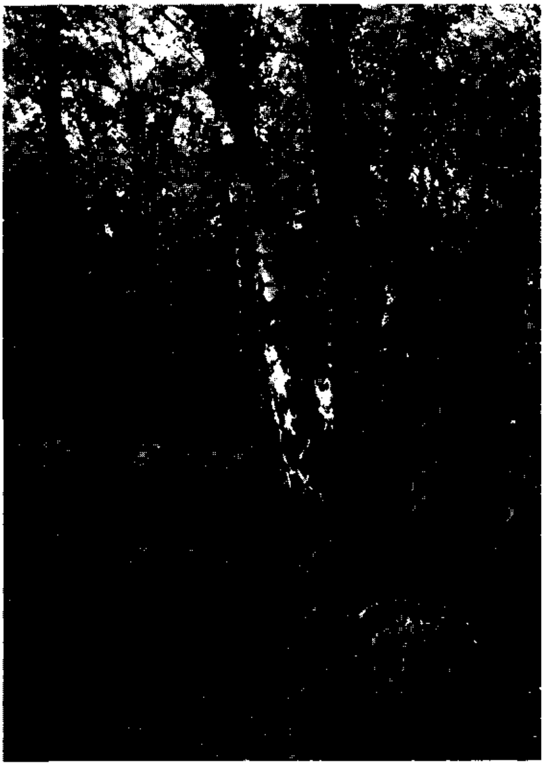
8.4.5 Conclusions

Rodents are omnipresent in forest ecosystems and can have a significant impact on seed abundance and seedling survival. Local population densities and activity are strongly differentiated with respect to structural characteristics of the habitat (Dueser & Shugart 1978, Foster & Gaines 1991, Van Apeldoorn *et al.* 1992, Bowers & Dooley 1993). Our study indicates that differential rodent activity and directed seed dispersal may result in a redistribution of seed within the system, causing spatial differentiation in seed abundance that is mediated by habitat structure.

It is extremely difficult to quantify the net effects of rodents on the regeneration of tree species under natural conditions. Population dynamics of rodent species show large fluctuations both in time and space, as do seed production and environmental conditions determining possibilities for germination and establishment of the tree species. Furthermore, population dynamics and habitat use of small forest rodents may be controlled by the social and behavioural characteristics of the different species (Hansson 1982, Wiger 1982), greatly complicating the incorporation of plant and animal population interactions into models of ecosystem development.

The role of forest rodents in the establishment of tree seedlings in bracken vegetation can not be quantified from this study. The positive effects of scatterhoarding by wood mice may alleviate some of the negative effects of bracken interference with tree seedling establishment and growth. On the other hand, bracken also provides habitat for more herbivorous species like bank voles that may damage disproportionate numbers of seedlings in bracken stands as compared to areas outside bracken stands. The interactions between rodent abundance and activity, seed dispersal and habitat structure do, however, require closer investigation, especially in systems where the structural complex habitat patches may also provide a safe site for the developing seedling.

9. The role of bracken in forest dynamics



9.1 Introduction

Bracken is a fierce competitor in forest ecosystems. It has the capacity to build up an extensive network of rhizomes and a dense frond canopy, and its persistence often enables it to maintain complete dominance during long periods. When bracken is present in the vegetation, it can easily invade and occupy favourable habitats. In a dense sward of bracken, hardly any other plant species can coexist. Gaps in the forest canopy or open canopy forests that are occupied by bracken may see a lack of tree regeneration for many decades, or even centuries. During such a period, the vegetation appears static, lacking any change. Succession grinds to a halt.

What causes this stagnation of forest succession in bracken vegetation? Examples of plant species that induce stagnation of succession can be found world-wide. These include various species of bamboo in *Fagus* forests in southeast Asia (Tanaka 1988, Peters & Ohkubo 1990, Peters 1992) and *Nothofagus* forests in south America (Veblen 1982), *Calamagrostis villosa* in central European forests (Fanta 1997), *Imperata cylindrica* (Eussen 1978) and lianas (Hommel 1987) in tropical forests. Together with bracken, these species share a number of characteristics. They generally are a minor component of the undergrowth of the relatively undisturbed closed forest. Their clonal growth form and high relative growth rate enables them to rapidly proliferate and dominate the vegetation after canopy removal. These species are very persistent, and the combined employment of various modes of interference impedes regeneration, establishment and growth of tree species.

In the previous chapters I have presented a number of studies into the different modes of interference between bracken and tree seedlings and the dynamics of bracken vegetation. In this final chapter I will bring these together and discuss how they contribute to the long term absence of tree recruitment in bracken vegetation. Before getting into details on the effects of bracken on forest dynamics I will first pay attention to the general distribution of bracken in The Netherlands. Next, I focus on the ecology of bracken in forests, mainly concentrating on the interactions between bracken and the tree canopy. This sets the stage for a discussion on the role of bracken in forest dynamics and the possible successional pathways leading to the restoration of a forest canopy. Finally, I discuss some implications for forest management.

9.2 Distribution of bracken

Bracken is a cosmopolite. It is present on all continents (except Antarctica) and in all climates of sufficiently high temperature and humidity (Tryon 1941, Page 1976). It has a long evolutionary history; *Pteridium*-like species are reported from as early as the Jurassic epoch (Zhen & Zhang 1983). In northern Europe, bracken was absent during the major glaciations, so it had to re-colonise the region along with all other plant species. This re-colonisation of Europe started in the early Holocene, and bracken had reached its northern limit by 7000 BP (Huntley & Birks 1983).

9.2.1 Bracken and land use history

Pollen records from all over Europe show sharp increases in bracken spores during the Holocene. The timing varies, but the increase is strongly correlated with periods of human settlement and subsequent forest clearing. For instance, pollen of cereals and ruderals usually increase along with bracken spores. This suggests that bracken invasion has been facilitated by the opening up and cultivation of the landscape (Rymer 1976, Taylor 1987, Van Smeerdijk 1989, Ortuña 1999). But does an increase in spore counts reflect an actual increase in bracken? Sporulation of bracken is highly variable and positively influenced by temperature and light intensity (Conway 1957, Caulton *et al.* 1995, Kendall *et al.* 1995). When the forest canopy is removed, bracken abundance may increase. Yet, more light and higher temperatures may as well have stimulated spore production in the bracken already present. Increased spore counts therefore do not necessarily reflect a general increase in bracken distribution.

In its natural forest habitat, the tree canopy has a twofold influence on bracken. On the one hand, the canopy reduces light levels and thus checks bracken growth. On the other hand, the canopy raises air humidity and reduces frosting and direct exposure to solar radiation and wind (Barkman & Stoutjesdijk 1987). When the canopy is removed, bracken can temporarily increase in biomass, but it is totally depending on the right climatic and soil conditions for its long term survival outside the influence of a tree canopy. On dry sandy soil, bracken appears to be unable to maintain itself outside the protective cover of a tree canopy in the central Netherlands (Fig. 9.1). Only loamy soils, or soils with a high organic content, provide a sufficient water holding capacity to continuously support a bracken vegetation outside the influence of a tree canopy (Fig. 2.8). Therefore, when the forest canopy is removed, the habitat will become inhospitable for bracken growth in most areas in The Netherlands, which will eventually lead to local extinction of bracken.

In many other regions with high levels of soil moisture and air humidity, and low incidence of frosting, bracken is able to survive in open habitats. Here, the bracken vegetation replaces the original forest community, facilitated by human disturbance (Taylor 1986, Pott 1992). In fact, such bracken communities may have the same woodland species (vernals like *Viola*, *Anemone*, *Scylla*, or mosses) as the former forest undergrowth (Rodwell 1991).

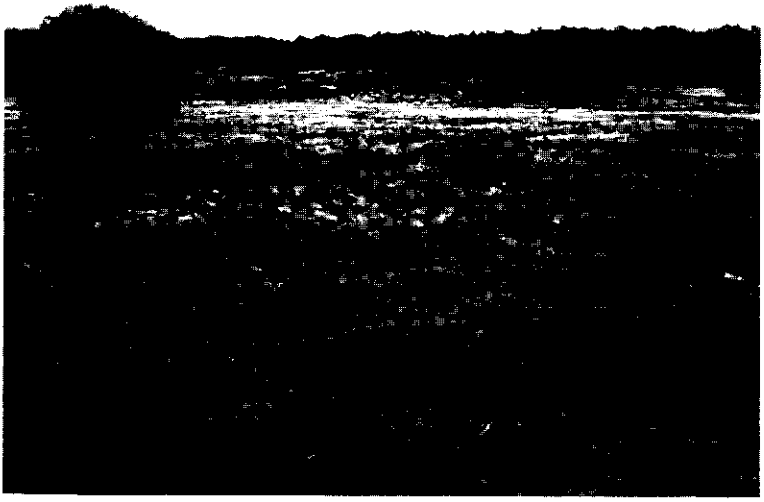


Figure 9.1: Remnants of a bracken vegetation, formerly present in an old forest complex but now slowly decreasing in vigour after the removal of the canopy in the nature reserve Planken Wambuis, The Netherlands.

9.2.2 Current bracken distribution

During the previous millennia, most forests in The Netherlands were cut and converted into heathlands or arable fields and meadows. Bracken present in the original forest undergrowth was unable to persist in the exposed habitats, and combined with the negative effects of grazing and trampling by livestock, mowing and other agricultural practices (Taylor 1986, Lee *et al.* 1986), bracken was eventually eliminated from deforested areas. By the turn of the century, a reforestation program was started to convert the unproductive heaths into more productive forests. This created new opportunities for bracken to increase its range of distribution.

The reforestation of The Netherlands has, however, not lead to a larger range of bracken. This must be seen as the direct result of the failure of bracken to colonise new habitats by sporal regeneration. This is not caused by a lack in germination potential (Schwabe 1951, Sheffield *et al.* 1993, see 2.5). Rather, the prothallial and young sporeling stage in bracken ontogeny seems to form the bottleneck in bracken reproduction (Conway 1957, Hutchinson 1976). New establishments from spores remain extremely rare in Dutch forests, so virtually all bracken invasion must be the result of vegetative regeneration of existing rhizome systems (see chapter 4). In almost all cases where I found bracken growing in reforested areas in The Netherlands, I found its occurrence related to either the presence of ancient forests, wooded banks or old hedgerows that provided refugia for bracken (pers. obs., Taylor 1986, Figs. 9.2 and 9.3).

Figure 9.2: A hedgerow in central Wales (UK) with bracken, bramble and honeysuckle. Bracken can survive in these hedgerows, and recolonise the bordering fields once agriculture stops.

Large scale deforestation and cultivation, the incapacity of bracken to survive outside the forest canopy and the extreme rarity of sporal regeneration have produced the current pattern of bracken distribution in Dutch forests. Here, bracken presence is almost completely restricted to ancient forest (Rackham 1980, Schoonderwoerd & Nyssen 1999). This is why bracken is used as an indicator species of old forest habitat. It shares this characteristic with a range of woodland species that have a restricted capacity to disperse from their current forest habitat and regenerate in potentially suitable new areas (Grashof-Bokdam 1997, Tack & Hermy 1998).

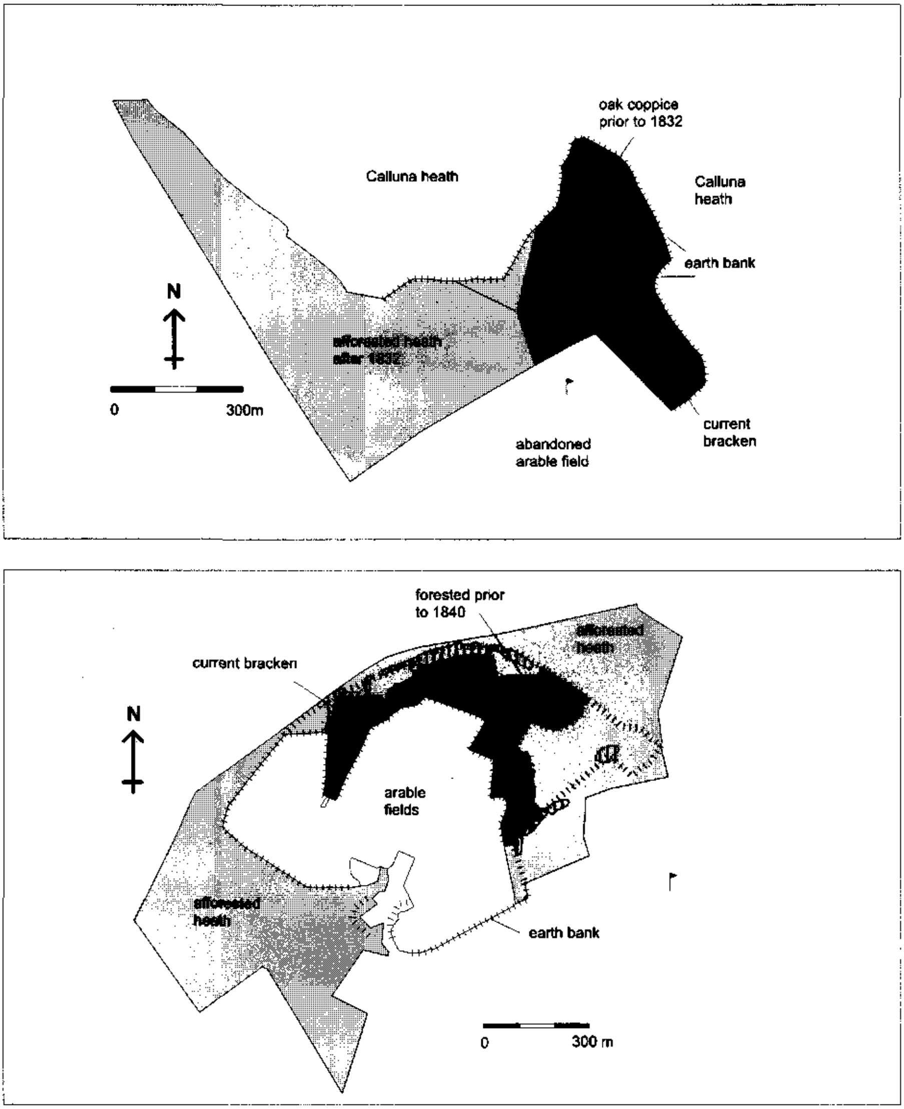


Figure 9.3: Current distribution of bracken (hatched) in two oak woodlands in relation to forest history. Top: Valenberg, bottom: Klein Boeschoten, both in the Veluwe region. Flags indicate Nat. Grid Ref. coordinates 180,453 and 175,470 respectively.

From chronosequences of forest understory successions, Stortelder & Hommel (1990) postulated that bracken enters the forest floor vegetation on sites that have been under continuous forest cover for at least 90-150 (200) years, depending on soil conditions and forest type. It is not clear which property of the qualification "old forest soil" should underlie this pattern in bracken distribution. In fact, the periods mentioned relate only to the earliest release of topographic maps from which forest history could be reconstructed.

In conclusion, on the dry sandy soils of The Netherlands, bracken is restricted to refugia that escaped long term deforestation. Most bracken represents individuals that have established hundreds to thousands of years ago. The relationship between bracken distribution and Dutch ancient forests is the result of the superposition of bracken biology and land use history. The almost exclusive presence of bracken on old forest soils is not the result of inherent physical and chemical properties of such soils, but forced upon by cultural history.

9.3 Bracken in forest

In forests, bracken proves to be as versatile as in the open. It shows a large ecological amplitude with respect to light requirements and soil resources. In forested ecosystems, bracken is able to maintain itself even under dark canopies. The growth of bracken is directly related to light that passes through the canopy. This links bracken dynamics to canopy dynamics. Interference by most other species in the forest undergrowth is negligible. For instance, the interfaces between bracken and *Deschampsia* that I have inspected under tree canopies usually have old grass tussocks underneath bracken litter, suggesting that the higher shade tolerance of bracken enables it to outcompete the less tolerant grass. Because bracken does not spread by spores, its presence and abundance is the result of vegetative reproduction only.

9.3.1 Plasticity

Bracken shows a high morphological plasticity that enables it to cope with a changing environment. In deep shade, fronds can etiolate and extend 4-6 meter to escape shading from small shrubs. When the fronds grow under sparse canopies, they are leathery and thick. In deep shade the fronds are slender and soft. This results in a higher specific leaf area (area per gram of leaf tissue) when light levels are low (Figs. 3.6 & 3.9). This way, the costs for leaf display are lower when light resources are low as well. This higher efficiency in exploiting light resources, however, makes the fronds susceptible to herbivores and pathogens. Bracken can compensate in part by chemical defence (e.g. cyanogenesis, Jones 1983; see 3.4.1).

9.3.2 Interactions with canopy dynamics

Under translucent canopies (for instance *Pinus, Larix, Betula, Quercus*), the light levels are sufficiently high to let bracken persist as dominant for many decades (chapter 4). Bracken is a toxic plant and a food source for just a few species that hardly ever do serious damage to the fronds. There may be periods of low vigour or senescence, but even as sparse vegetation or as scattered individuals, bracken may persist for many centuries on a site. Bracken is not able to survive the long periods of dense shade under large thickets of young trees. Shade-casting species (*Fagus, Picea, Pseudotsuga, Abies*) exclude bracken as long as their canopies remain closed. When the trees reach maturity, their canopies open up and bracken can re-invade. On dry soils, root competition excludes bracken altogether from *Fagus* stands or around individual trees.

As is the case in open habitat, area-wide abundance of bracken in forests is related to large scale (stand level) human intervention in the system dynamics of forests. Uniform stand-level forest management has created uniform swards of bracken. Coppicing, thinning and clearcutting all benefit bracken. Coppicing has been the main silvicultural system until the twentieth century in The Netherlands (Buis 1985). The coppice cycle allows bracken to increase in biomass in the periods directly after cutting. The following period of dense thickets is sufficiently short to help maintain bracken in the undergrowth, allowing it to re-build a frond canopy after the next cut (Ford & Newbould 1977). Thinning has a similar effect. Clearcutting stands releases bracken and provides it with opportunities to increase in vigour and size until the canopy of the new stand closes. Cultivation of forests has therefore been an important contributor to the dominance of bracken, mainly by resetting successional changes in the forest, permanently keeping it in a young (pioneer) stage.

In natural forest, bracken clones occur much more scattered. Variation in canopy density, gap formation and tree species composition create variable conditions for bracken growth. Natural disturbance (windthrow, fire) is irregular in time and space. Without intervention and in the absence of catastrophic disturbance, succession generally leads to dominance of shade-casting species (most notably *Fagus*). This leads to a decrease in bracken presence and dominance. For instance in the Speulderbos, succession in the mixed oak beech forest (Fago-Quercetum) resulted in dominance of *Fagus* (Sevenster 1995). Bracken clones in this forest type are very scattered and only present in pockets of *Quercus* or along stand edges (Fig 4.5). The ever-changing light conditions under the canopy require bracken to move about the forest floor, exploiting favourable patches and abandoning unfavourable ones. Its clonal growth form provides bracken with the means to do so.

9.3.3 Bracken dynamics

Under the soil surface, bracken builds an extensive rhizome system (see chapter 2). The long shoots are buried deep in the soil, and allow bracken to spread laterally to explore new patches. The long shoots act as storage organ and produce short shoots that grow vertically and carry the fronds. Each year, one or several fronds are produced on the short shoot. When the fronds are positioned in a favourable patch, the short shoots may continue to produce fronds for several decades allowing bracken to completely exploit the patch (Watt 1940). When growing conditions change, it can activate dormant buds to increase or restore frond numbers. With its long shoots, it can escape adverse conditions and explore new areas. This clonal growth form is appropriately called a guerrilla strategy (Lovett Doust 1981). It provides flexibility in a changing environment, and allows persistence when encountering favourable conditions.

Rhizomes are highly efficient storage organs. Water is stored to survive periods of drought. Indeed, root mass is remarkably low relative to the mass of fronds and rhizomes. Resorption of nutrients from the senescing fronds reduces nutrient losses. Since bracken generally impedes growth of other species in the undergrowth, it has exclusive access to soil resources that are not taken up by the trees. The connected rhizomes also form integrated networks. Rhizome sections in favourable patches may support parts of the clone that experience low resource levels. This can, for example, be of great importance in the efficient utilisation of sun flecks. In a varied light environment, a high level of integration may further increase productivity (cf. Stuefer *et al.* 1994).

During clonal life-time, parts of the rhizome system become detached. This disintegration can be the result of natural death of rhizome parts, mortality due to local resource depletion and deep canopy shade, or disturbance by rooting animals like wild boar. A bracken sward usually consists of numerous sub-systems of bracken clones (and different genetic individuals). Each of these subsystems has the potential to expand and build new, larger networks. For example, a 20 cm piece of rhizome can produce up to 26 m of new rhizomes within a year under non-competitive conditions (Lawrie *et al.* 1992).

Under dark canopies, bracken clones can completely disintegrate, with only a few scattered fronds revealing their presence. Eventually, all frond production may stop. Our research on bracken dynamics in the Speulderbos (chapter 4) strongly suggests that the absence of fronds in the undergrowth does not necessarily imply absence of rhizomes. When the canopy opens up (after gap formation or thinning), 'dormant' rhizomes may, as an analogue to seed banks, start producing fronds and quickly re-invade the undergrowth when environmental conditions improve (cf. Lowday & Marrs 1992*a* ,Dolling 1996*a*). This adds to the flexibility of bracken and its survival in transient periods of adverse growing conditions. This also has important consequences for the management of bracken-infested forests (see 9.5).

9.4 Bracken and forest dynamics

Successional changes in the vegetation may follow a predictable pathway, or, in other words, show a certain directionality. This directionality has played an important role in succession theory, and has often been part of the definition of succession (Clements 1916, Finegan 1984, Burrows 1990). Especially in primary succession (the development of vegetation on a substrate with no prior vegetation), changes in the vegetation are directional because of the overriding dominance of soil development in the establishment and growth of species (Lawrence 1958, Walker *et al.* 1981, Fanta 1982). The species entering the vegetation follow a well predictable sequence. However, this directionality mainly concerns the large scale pattern in community structure and composition, and only holds in the first stages of succession. During later stages of succession, the rate of change in soil development slows down, and the dynamics of the community are increasingly governed by the properties of the community itself (*reaction* in Clements' (1916) terms). Changes in the vegetation may then appear highly variable and not predictable at all (cf. Drury & Nisbet 1973).

The characteristics and dynamics of the canopy have an overriding influence on the changes in species abundance and composition in forest vegetation (Doyle 1981, Van der Meer 1995). Maintenance of a dark, closed canopy will effectively block any regeneration of tree species for as long as canopy disturbance stays out. This is apparent, for example, in beech forests that may remain void of any undergrowth for extended periods of time. Regeneration of tree species occurs in cohorts that reflect timing and severity of disturbance events (Koop & Hilgen 1987, Peters 1992). Such long periods of tree regeneration failure are commonplace in bracken vegetation. As long as bracken can maintain a dense frond canopy, no significant changes occur in the structure and composition of the community. But what causes this stagnation in succession? And is it possible to predict what happens as soon as bracken dominance is broken?

9.4.1 Succession

The theory on succession is one of the oldest and most prominent topics in the ecological literature (Peters 1991). The terminology in use now often dates from the early contributions to the debate, most notably Clements (1916). Although the terms have persisted, their meaning may have changed considerably. In this section I will first discuss the terminology regarding the treeless stages in ecosystem development. Next, I will consider the question on how we may predict successional changes.

The course of succession: regression and stagnation

Stages in forest development where tree recruitment is suppressed are sometimes referred to as regressive phases (i.e. Clements 1916). This term is rather unfortunate, because regression is the antonym of progression. This is the legacy of Clements that spawned many of the controversy in the debate on succession. He viewed plant communities essentially as organisms, and successional changes necessarily led to the final stage, the climax. Departure of the community from this climax, "regression", was not possible: "*Succession is inherently and inevitably progressive (...) and regressive development is impossible and regressive succession does not occur*" (Clements 1916: p. 147,148).
However, as many studies have pointed out since, plant communities appointed as climax can divert dramatically from this ("steady") state, even without great climatic changes. This is the case, for instance, during the successional development in the *Picea/Tsuga* forests that develop after glacial retreat in Southeast Alaska (Lawrence 1956). Ugolini & Mann (1979) showed that in the later stages of succession, podzolisation leads to the formation of an iron hardpan in the soil (paludification). The stagnating water and great acidity of the soil increasingly inhibit tree growth, and finally a *Sphagnum*-dominated bog may remain. This must be seen as a normal successional pathway (Zach 1950) rather than a regressive phase in community development. Regression or retrogression implies inherent progression towards the climax, which premise is analogous to the notion that evolution inevitably must lead to the rise of mankind (cf. Gould 1977). In order to avoid this teleological pitfall, I have preferred to denote treeless stages in forest succession as stagnant phases.

The term regression has also been used in relation to successional pathways after forest destruction and subsequent ecosystem degradation (Fanta 1982, Pott 1992). In north-western Europe, this mostly comprises heathlands and drift sands. However, in the case of bracken there are no indications that its dominance leads to degradation of the soil, as opposed to, for instance, the invasive and persistent grass *Imperata cylindrica* (Eussen 1978). In fact, nutrients like phosphorus are mobilised by litter, concentrations of other soil nutrients are maintained, and old rhizome tunnels increase aeration of the soil (Mitchel 1973, Miles 1985, Ortuña 1999).

The significance of the stagnation of succession in bracken swards is not the divertissement from a 'normal' successional pathway. Rather, it is the specific combination of biological characteristics and ecological relationships enabling bracken to dominate and persist that warrants our attention. Unfortunately, viewing succession as the mere result of interacting causes and mechanisms greatly complicates predictability. Models incorporating all relevant mechanisms must deal with all relevant levels of interaction at the appropriate spatial and temporal scales (Pickett *et al.* 1994).

Predicting successional change

Different scales of observation (in time or place) have been an underlying cause for many of the disagreeing viewpoints in succession theory (cf. McIntosh 1981). The debates have been hampered by the intermingling of pattern with process (Pickett *et al.* 1994). Clements (1916) viewed each change in the community in the grand pattern of progressive development towards a climax. Gleason (1918) saw the changes in species composition of a meadow, and regarded it as the outcome of a myriad of processes, devoid of purpose or predetermined end. This view now dominates ecology.

The complexity of ecosystem and population interactions has prompted several theories of underlying causes and mechanisms of successional change. Clements (1916) regarded facilitation as the major mechanism leading to the formation of the climax. However, this was beset with many critical problems, and prompted for a more detailed approach to successional mechanisms. For instance, Connel & Slatyer (1977) constructed a framework in which succession was viewed as the outcome of several mechanisms which they termed inhibition, tolerance and facilitation. Although appealing in simplicity, their model has proven problematic since the assignment of one of these mechanisms to interacting organisms or populations is largely dependent on the perspective one chooses when describing the successional interactions between them (cf. Pickett *et al.* 1987, 1994, Burrows 1990).

In order to overcome these problems, Pickett *et al.* (1987, 1994) have taken an hierarchical approach. They proposed a conceptual framework that allows for the complex nature of ecosystem and community interactions, and recognises the numerous different processes that define the nature of change in plant communities. They distinguish three general causes of successional change (Fig. 9.4). For any change to take place, there must first be sites available where plants have the potential to establish and survive. When this is the case, the ability of species to reach such sites and the composition of the local species pool determines the initial composition of the new patch. Once established, the differential ability of species to grow and survive in the local chemical, physical and biological environment will determine the subsequent development and composition of the new vegetation. Bracken encroaches upon all three of these general causes of successional change. In the following sections, I will discuss the way bracken affects succession with respect to these three causes, focusing on the Dutch forest ecosystems.

General causes of succession:	***Site availability***	***Differential species availability***	***Differential species performance***
Contributing processes or conditions and some *Defining factors*	**Disturbance** *size* *severity* *timing* *dispersion*	**Dispersal** *agents* *landscape configuration* **Propagule pool** *dispersal agents* *(former) land use* *seed predation*	**Resource availability** *soil* *microclimate* **Ecophysiology** *germination* *growth rate* **Life history** *allocation* *reproductive traits* **Competition** *presence and identity of competitors* *resource base* **Allelopathy** *soil properties* *neighbouring plants* **Herbivory** *plant defences* *community structure and composition*

Figure 9.4: The hierarchical framework of a theory on causes, processes and some defining factors in successional change or plant community dynamics (modified after Pickett *et al.* 1987, 1994)

9.4.2 Site availability

The clonal growth form and longevity of the bracken plant results in the creation of distinct patches that form a structural contrast with the surrounding vegetation. During the growing season, bracken develops a dense canopy of fronds, up to 2.5 m high, that efficiently intercepts the major part of the available radiation (Pitman & Pitman 1990). Because of mechanical limitations in the supporting tissues in the stipe, tall fronds usually collapse under the weight of the leaf blade, even before total expansion of the frond (Watt 1976). Such fronds remain alive and, together with the senescing fronds in autumn, smother the vegetation and seedlings present underneath (Watt 1919, Humphrey & Swaine 1997, Fig. 9.5). At the onset of winter the dead fronds form a substantial input to the fresh litter layer, and their resistance to decomposition (Frankland 1976) leads to an increase in depth of the ectorganic soil layer. From Mexico, Ortu a (1999) reports ectorganic soil layers under bracken of several metres deep! This alteration of the physical habitat structure by bracken is the main contributor to the monopolisation of its habitat. As long as bracken maintains a dense canopy, the site is effectively unavailable to species requiring for instance light for germination and growth or the proximity of mineral soil for post germination survival.

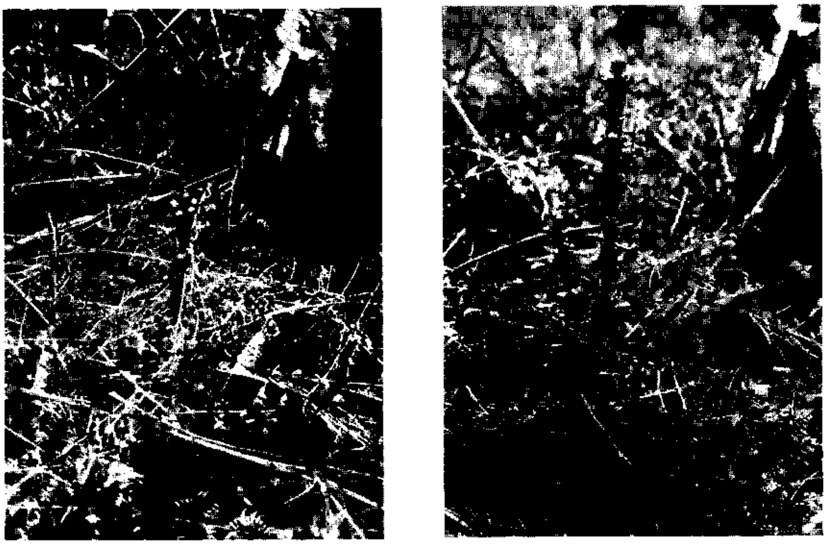


Figure 9.5: A sapling of Norway spruce (*Picea abies*) smothered by bracken litter in the Reichswald, Germany. On the left: the sapling covered by dead bracken fronds; on the right: the sapling after removal of the litter.

Litter under bracken

There is a close relationship between the thickness of the litter layer and the diversity and biomass production of many life forms, including vascular plants (Sydes & Grime 1981*a,b*, Molofsky & Augspurger 1992), mosses (Den Ouden & Alaback 1996), and fungi (Baar 1995). A thick litter layer causes germination failure by trapping seeds before they reach the mineral soil (Hamrick & Lee 1987), or by covering seeds that are depending on light for their germination (Black & Wareing 1955; Marshall & Jain 1970). The thick ectorganic soil layer physically hampers root extension towards the mineral soil (Den Ouden & Vogels 1997). This makes the soil under bracken effectively unsuitable for the colonisation of light seeded species like *Pinus* and *Betula*. Disturbance of the ectorganic soil layer strongly enhances colonisation (Lowday & Marrs 1992*b*).

On the other hand, a litter layer may improve germination conditions by hiding seeds from predators (Jarvis 1964, see 9.4.3), and by reducing evaporation from the underlying substrate (Evans & Young 1970; Hamrick & Lee 1987). The germination of large seeded species like *Fagus, Quercus* and *Sorbus* is not restricted by bracken litter.

Reduction of bracken dominance

Bracken clones are not always dense. Under dark canopies, the sparse bracken vegetation has many other species growing between the fronds. In dense bracken, animals like wild boar (*Sus scrofa*) cause local disturbance and expose the mineral soil over large areas. Heavy spring frosts can dramatically reduce frond cover for several years. Sparse bracken vegetation makes the site available to a large range of species (Table 5.3, Marrs & Hicks 1986). Yet, tree seedlings are rare, even in sparse bracken, and these rarely grow beyond the bracken canopy. Either their seeds can't get there in time to take advantage of the (transient) opportunity to enter the community, or the established seedling can't survive in the bracken environment.

9.4.3 Differential species availability

Once an opening in the bracken canopy or litter layer is created, tree seedlings can only establish after their seeds have reached the site. Seeds can be already present in the soil and wait for favourable conditions. However, tree species in The Netherlands do not make persistent soil banks. Therefore, colonisation must mainly take place directly from seeds dispersed from the parent tree. Once the seeds have arrived, seed mortality by predation or infestation may reduce or eliminate the seed pool.

Tree species in The Netherlands show two major modes of dispersal. *Betula* and conifers like *Pinus*, *Larix*, *Picea* and *Pseudotsuga* all have wind dispersed seeds. The quantity and composition of the seed rain of wind-dispersed species into bracken swards is directly related to the distance and direction from parent trees in the local species pool.

Species that produce larger seeds or fruits are usually dispersed by animals; *Sorbus* and *Ilex* mainly by birds, *Fagus* en *Quercus* by birds and rodents. Of the latter species, seed production is concentrated in mast years and thus seed availability is variable in time. These species also have spatially variable distributions of viable seeds around the parent tree . The seed distribution pattern depends on the dispersal of the seeds away from the parent tree and pre-germination mortality. Without dispersal, seeds remain concentrated on the forest floor under the parent tree, and are extremely vulnerable to predation by mammals and birds, freezing and desiccation (Watt 1919, 1923, Jarvis 1964). Seeds can escape density dependent mortality near the parent tree (mainly predation) by dispersal. Jays (*Garullus glandarius*) take acorns mainly from the canopy and store them along forest edges and in open vegetation (Bossema 1979, pers. obs.). Under a forest canopy, however, oak and beech are predominantly dispersed by rodents, in particular by wood mice.

Population densities and activities of wood mice (*Apodemus sylvaticus*) and bank voles (*Cletrionomys glareolus*) are higher under structurally complex stands of bracken as compared to adjacent areas without the protective cover of fronds and litter (chapter 8, Brown 1986). Seeds falling into this structure are rapidly sequestered by wood mice and stored in part for later use. They do this by burying the seeds several centimetres deep under the litter layer, in groups of one to several seeds (scatterhoarding). Later, the hoarded seeds are retrieved for consumption or reburial elsewhere. A higher activity of rodents results in a higher seed predation (see next section) inside bracken swards. Yet, because of the scatterhoarding of large seeds by wood mice, the influence of bracken on seed dispersal extends well beyond the borders of its actual presence.

While collecting seeds, wood mice may transport these over distances greater than 60 metres. When doing so there is a net transport of seeds towards the centres of their home ranges, in this case the structurally more complex bracken stands. At the interface of bracken with structurally less complex patches, this directed dispersal initially results in increased seed densities inside, and directly adjacent to, bracken stands. Seeds benefit from this hoarding behaviour because burial conceals them from (other) predators and protects them from frost and desiccation.

However, the higher rodent density and activity in bracken stands strongly reduces seed availability because of higher mortality of large seeds reaching the bracken stands (chapter 8). Of the hoarded seeds, only a small fraction will escape predation by cache retrieval or cache robbery by competitors like wild boar and squirrels that also preferentially feed on large seeded species. Yet, despite the high predation pressure on seeds, the net effect of the presence of a scatterhoarding disperser like the wood mouse is an increases pre-germination survival of large seeds (Hererra 1995).

Because of their efficient dispersal and relatively lower loss to predation, wind dispersed tree species dominate the tree seed pool in bracken swards (Lowday & Marrs 1992*b*).

The seeds that do survive are facing a whole new problem: how to survive as a seedling?

9.4.4 Differential species performance

Post-germination growth and survival of tree seedlings depends on the species' capacity to cope with the alteration of the physical, biological and chemical environment in bracken stands. The reduction of resource availability (light, water, nutrients) has a direct effect on growth and survival of tree species. Also, it has been suggested that the chemical composition of bracken and its litter suppresses germination and growth of plant species (allelopathy; cf. Gliessman 1976). Finally, susceptibility to herbivory may have a strong influence on the survival of species in bracken stands.

Resource availability

The depletion of nutrients by bracken is probably not a limiting factor with respect to tree seedling development. In my experiments (chapter 5), rhizome and root presence did not affect seedling growth. This suggests that bracken does not limit tree seedlings in their nutrient and water uptake by active resource depletion. In fact, phosphorus availability may be higher in bracken (Mitchell 1973, Marrs *et al.* 1992). Also, species colonising bracken stands indicate a high nitrogen availability (Lowday & Marrs 1992*b*). In heathland communities, soil fertility is maintained or even improved in the presence of bracken (Mitchel 1973, Miles 1985; Marrs *et al* 1992, see also Ortuña 1999). In the sites of the Speulderbos, there were no differences in soil nutrients between bracken plots and adjacent vegetation (data not shown). The nutrient availability to tree seedlings is therefore more dependent on soil type rather than the presence or absence of bracken.

In the dry sandy soils of The Netherlands, water is the dominant limiting factor in tree growth (Van den Burg 1999). The direct uptake of water by roots probably only has a small effect on soil moisture reduction (see chapter 5). More importantly, however, the frond canopy and litter layer may intercept a large proportion of the incident precipitation and lower soil moisture in bracken swards, especially during the growing season (Pitman & Pitman 1990*b*, Smith & Lockwood 1990). The water holding capacity of the soil will determine whether this effect promotes species that can better resist or avoid water stress, like *Pinus* and *Betula*. Also, the ectorganic soil layer physically hampers root development of seedlings, increasing mortality due to desiccation (Den Ouden & Vogels 1997). Large-seeded species (*Quercus*, *Fagus*) are well able to rapidly penetrate the bracken litter into the mineral soil and reduce the risk of desiccation.

In the recruitment phase, shading by the fronds is the main direct mode of bracken interference with tree seedlings. Bracken fronds have one of the highest relative growth rates measured for plants in the temperate zone (Al-Mufti *et al.* 1977), even though full extension of the fronds takes several months. Increased tree canopy cover reduces bracken frond biomass, but the bracken canopy remains closed even under relatively heavy shade (Fig 3.4). Unless the bracken canopy opens up (after disturbance, in senescing patches or due to interference by other species), light conditions under bracken are inhospitable to most species (Fig. 9.6). Only shade tolerant species like *Fagus* have a chance on survival.

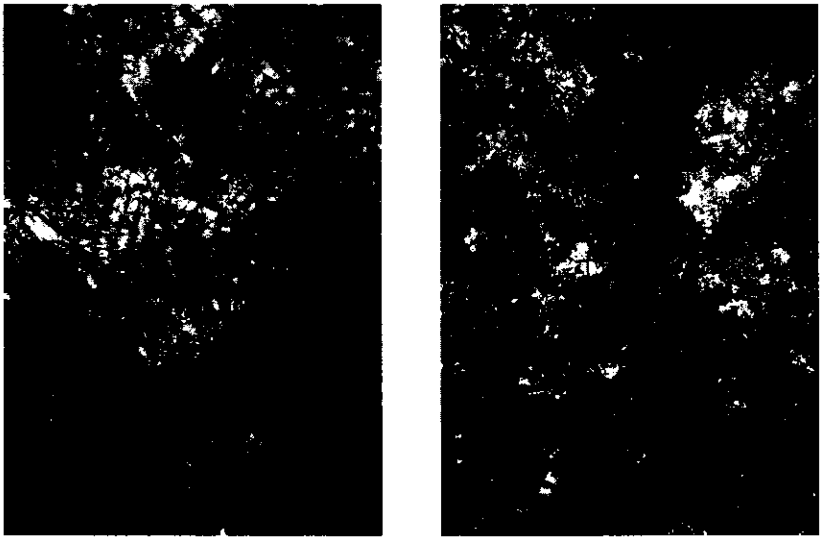


Figure 9.6: The canopy of a dense bracken sward (left) and a mature beech forest (right). Both canopies reduce light availability to well below 1% relative to the open.

Vernal species can coexist with bracken because they start development in early spring, well before bracken emerges. They hereby avoid shading by bracken (or the tree canopy), and complete their life cycle before the bracken canopy casts deep shade. Evergreen tree species may have a comparable advantage as compared with deciduous species. Conifers like *Pinus*, *Picea* and *Pseudotsuga* can avoid part of the shading by starting photosynthesis early in the season.

The structure of the canopy not only reduces light levels reaching seedlings; it also causes seedling mortality when snapped or senescing frond collapse on the seedlings and smother them (Watt 1976, Humphrey & Swaine 1997). The litter buries seeds, causing germination failure in species that require light for germination. The higher air humidity under the fronds promote fungal diseases. Especially *Pinus* and *Quercus* seedlings suffer high mortality rates due to fungal infestation (Chapter 5, pers. observ.).

Bracken is one of the strongest competitors in the Northwest-European flora (Grime 1979). It does so by maintaining a dense frond canopy that severely reduces light levels underneath. Nutrient availability is not negatively influenced, but soil moisture is reduced through interception of rain by canopy and litter.

Allelopathy

Bracken produces a great diversity of biochemical compounds in its tissues (Cooper Driver 1976). It has been suggested that a number of these compounds, in particular phenolics, suppress the germination and growth of plant species growing in bracken stands. There is, however, no firm proof that allelopathy is an active mechanism in bracken in Northwest Europe. I argue that chemical interference by bracken has no direct effect on the forest community (chapter 7). Decomposition of the litter is slow, but it releases far less phenolics than the litter of most tree species (Fig. 7.2, Kuiters & Sarink 1986). Young seedlings grow as well in bracken litter as in garden peat (Fig. 7.5). The evolution of a defence system against herbivory is a more likely cause for the chemical richness and complexity of bracken and the presence of potentially phytotoxic compounds. Allelopathic effects on other plant species that are occasionally found (mainly in warmer climates) may thus be seen as collateral damage from defence against herbivory.

Herbivory

The high number of small rodents under bracken puts a strong predation pressure on seeds and emerging seedlings. Under the protection of the physical structure built by bracken, rodents can forage relatively free of predation pressure. Wood mice are mainly granivorous. Damage to seedlings only occurs directly after germination when they remove the cotyledons from emerging oak seedlings. Jays and wild boar also use such emerging seedlings as flags, and remove the cotyledons. As long as the seedling is not pulled out of the ground, this does not negatively *affect survival and growth of oak seedlings* (Sonesson 1994, *unpubl. data*).

Bank voles are predominantly herbivorous. Seedlings, especially those of broad-leaved species, are an important food source and can be completely decimated by bank voles (Pigott 1985). For instance, in my field experiment (chapter 5) bank voles destroyed the entire population of oak end beech seedlings within a week after planting. Herbivory by rodents therefore plays an important role in the reduction of seedling populations in bracken stands. More research is needed to elucidate the quantitative effect of rodents on tree recruitment. Our studies have shown that effects of rodents largely account for the reduction of seeds and seedlings in bracken stands, and that they may have a large quantitative and qualitative effect on composition of the seedling bank in structurally complex habitat (chapter 8, Pigott 1985). Interestingly, this is the same conclusion that Bartholomew (1970) drew when investigating the lack of recruitment in Californian shrub and grass communities. Instead of allelopathy (the earlier hypothesis), granivory and herbivory could account almost completely for the reduced recruitment of plant species in bracken stands (see also Gliessman & Muller 1978, Fig. 9.7).

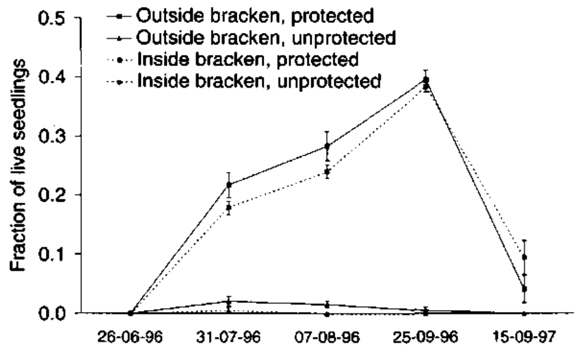


Figure 9.7: The fate of seeds and emerging seedlings planted in small cages protecting them from small and large mammals inside and outside bracken in a former oak coppice woodland in the Speulderbos. Data represent means (n = 8) of groups of 50 acorns per treatment. Seedlings initially survive on reserves stored in the cotyledons, but later suffer high mortality due to insect defoliation and fungal attack (mainly by mildew).

Conversely, bracken stands moderate the effects of browsing and grazing by large herbivores. Saplings of *Quercus* and *Sorbus* inside bracken stands show less damage by deer browsing than saplings growing outside the bracken stand (Fig. 5.7). Shelter provided by bracken stands, like in tree thickets or crowns of windblown trees, appears to provide protection from grazing by large herbivores (cf. Morgan 1991).

9.4.5 Successional pathways

The most prominent feature of bracken vegetation is the lack of tree recruitment during long periods. The main successional pathway in bracken vegetation is the status quo: stagnation. Eventually, however, a tree canopy may be restored. In this section I will evaluate which successional pathways may lead to this new phase in forest development.

Stagnation

The stagnation in succession is prolonged for as long as bracken can maintain a closed canopy. Site pre-emption by bracken blocks any change in the vegetation. The thick ectorganic layers under bracken impedes germination and establishment of small-seeded species. Seed and seedling predation by rodents further depletes the seed pool in bracken swards. Seedlings that do establish have to cope with heavy shading and smothering. The combination of these three processes results in complete elimination of tree recruitment. Unless bracken dominance is broken, there are no opportunities for tree species to establish in bracken stands and grow above its canopy.

Bracken clones are persistent and may live for thousands of years. This does, however, not mean that they exert a continuous strong influence on their environment. Autogenic dynamics result in fluctuating densities (Watt 1970). Interference by other species leads to shifting mosaics or local disappearance of bracken (chapters 3 & 4, Watt 1947, Marrs & Hicks 1986). The lack of change is probably only apparent on the (small) human time-scale. Eventually, even bracken dominance may break down. This creates opportunities for species to invade bracken and rebuild a tree canopy.

Restoration of a tree canopy

Successional patterns in forests can be linked to the frequency and intensity of canopy disturbance (Denslow 1980*b*, Foster & Zebryck 1993, Van der Meer 1995, Peters 1998). Canopy disturbance can be seen as a reset of the succession, restarting a new sequence in the created gap. Which species enter this new (secondary) succession depends on the size and nature of the disturbance, and the composition of the local species pool. Recurrence of disturbances may then produce a cyclic successional pattern (Watt 1947, 1955, Fanta 1982: see Fig. 9.8.).

The main successional pathways on Dutch sandy soils have been described by Fanta (1982). On moderpodzols and brown earths (the major soil types on which bracken is found), succession generally leads to the dominance of *Fagus sylvatica* (or codominance with *Ilex aquifolium*, see Smit (1999)). *Fagus* is a shade tolerant species and either replaces itself or regenerates and later dominates in earlier successional stages with *Betula* and *Quercus* (Fig. 9.8). The replacement of tree species and regeneration of the forest stagnates in the presence of bracken. In his representation, Fanta (1982) recognises only one pathway leading to restoration of the tree canopy: regeneration of *Fagus* in bracken stands (Fig 9.8).

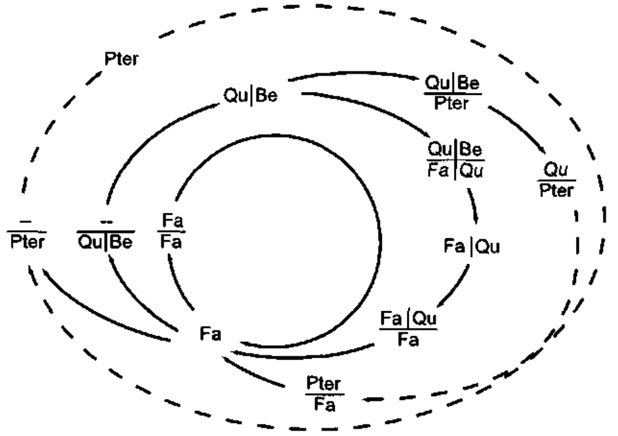


Figure 9.8: Schematic representation of the cyclic successional pathways in Dutch Fago-Quercetum forest ecosystems (from Fanta 1982). Solid lines represent replacements in the forest canopy (above the horizontal lines) and regeneration (below the horizontal lines). The dashed lines represent treeless stages. Essentially, this is a species-by-species replacement model. Note that in this model only *Fagus* is able to regenerate under bracken. Species codes: Fa=*Fagus sylvatica*, Qu=*Quercus robur* and *Q. petraea*, Be=*Betula pendula*, Pter=*Pteridium aquilinum*.

In bracken stands, opportunities for regeneration only exist when the bracken canopy is not closed, so light penetration is sufficiently high to sustain plant growth. A tree canopy reduces bracken vigour, but the remaining light levels on the forest floor under bracken remain too low to support seedling growth. Canopy disturbance is then a prerequisite for successful recruitment from the seedling pool present at the time of disturbance. Seedlings must be able to attain sufficient height before the bracken canopy closes again in response to the increased light levels under the tree canopy. The only tree species that have the potential to maintain a transient seedling bank are *Quercus* and *Fagus*. The high shade tolerance and lower susceptibility to herbivory gives *Fagus* a competitive advantage over *Quercus*. However, potential recruitment of these species requires the proximity of parent trees. After tree canopy disturbance, wind dispersed species like *Betula* and *Pinus* may regenerate on the exposed mineral substrates of windthrow mounds or pits. Which species is able to regenerate in a bracken-dominated forest undergrowth is therefore strongly dependent on the size and nature of tree canopy disturbance, the proximity of seed sources and presence of herbivores. On an individual basis, *Fagus* appears to have the highest likelihood of recruitment. Yet, the composition of the local species pool will ultimately determine which species may regenerate.

When tree regeneration is continuously blocked by bracken, the tree canopy will gradually break down and eventually a treeless stage in forest development may develop. The time required for the development of such a treeless stage depends on the species composition of the tree canopy. Maximum life span of species ranges from 150 (*Betula*) to over 400 years (*Quercus*). The larger these treeless patches are, the higher the relative importance of wind dispersed species in the seed pool. Again, recruitment of these species is only possible if the bracken canopy opens up and the litter layer is disturbed. This can take place after degeneration of the clone, climatic fluctuation (frost, drought), competitive interactions with other vegetation and animal disturbance.

The invasion of tree species into treeless bracken stands may result in the restoration of a forest canopy, but as long as this canopy remains sparse, or consists of species with translucent crowns, bracken may continue to dominate the undergrowth. The species composition and structure of the forest then is determined by the cohorts that were able to establish at the moment bracken dominance was reduced. This is analogous to the effects of tree canopy dynamics on forest composition and structure. Restoration of the canopy is not only restricted to *Fagus*, as proposed by Fanta (1982). However, this appears to be the only tree species that is able to eliminate bracken from the vegetation. Bracken may therefore dominate the dynamics of forests for many centuries, until *Fagus* is able to enter the vegetation and dominate the canopy.

9.5 Bracken and forest management

Bracken is considered a troublesome weed world-wide. Great efforts are put in research on ways to eradicate, or at least control, bracken. Again, most of this work has focused on bracken in open habitat, where large-scaled bracken dominance leads to a variety of problems such as the loss of biodiversity, loss of certain vegetation types, reduction of grazing area for livestock, loss of landscape values, and even public health risks (cf. Smith & Taylor 1986, 1995). Fortunately, bracken is not considered all bad, and numerous beneficial aspects of bracken have been recognised (Pakeman & Marrs 1992*b*, Thomas 1995). In principle, this also holds for bracken in forested ecosystems.

The problematic nature of bracken is fully dependent on the objectives and goals of forest management. When nature conservation is the primary objective, bracken must be regarded as a natural component of the forest undergrowth. Its presence itself indicates special natural values (ancient forest habitat). The structure of bracken vegetation provides cover and habitat for many animal species. Traditionally, however, forest management has concentrated on tree or meat yields, either as game (hunting), seeds (pig herding) or wood. Here, regeneration of trees is an important objective which can be seriously frustrated by bracken.

Dealing with bracken

The negative effect of bracken on tree regeneration confronts forest management with a dilemma: tree regeneration is only possible when tree canopy shading is reduced. Concurrently, this will release bracken. Furthermore, when bracken has been known to be present in a stand prior to canopy closure, its later absence may be deceptive. Although a bracken canopy may sometimes favour germination conditions of tree species by providing a relatively humid micro-environment (Jones 1947, Stewart 1975), subsequent shading and smothering will make natural regeneration of trees virtually impossible (Tolhurst & Turvey 1992, Humphrey & Swaine 1997).
When tree stands are converted artificially, this problem can easily be circumvented by planting and a few years of aftercare by mowing bracken. In vigorous bracken stands, mowing twice a year and planting large nursery stock do, however, add to high costs. This is inevitable if high stocking rates are needed.

It is extremely difficult, and costly, to eradicate bracken in open habitats (Robinson 1995). Mowing or application of herbicides may have to be continued for decades to ensure total extermination of bracken (Lowday & Marrs 1992*a*). In forest management, such control measures are not feasible, unless they are part of a long-term strategy of outshading bracken by species that continuously cast deep shade for several decades (like *Fagus, Picea, Pseudotsuga*). However, this strategy depends on the maintenance of homogenous, dark stands and a large bracken-free buffer zone to avoid re-colonisation from lateral expansion of adjacent clones. It is unlikely that such drastic methods can be justified in terms of dealing with a bracken problem only.

On relatively dry soils (sandy soils with deep ground water tables) it is well possible to contain bracken and prevent further expansion into new areas. This can be achieved by planting beech just outside the area with bracken. Shading and root interference by beech will prevent further lateral expansion of bracken into the forest behind the beeches. Such a bracken fence can stand for hundreds of years.

Accepting bracken

An old Welsh saying states: *famine under heather, silver under gorse, gold under bracken* (Smith & Taylor 1995). Rather than fighting it, forest managers should count their blessings for having bracken present in the undergrowth. Bracken indicates the presence of special natural values in The Netherlands. Where bracken grows, the site generally has specific characteristics associated with a long forest history such as the presence of other ancient forest species and soils that are not degraded by other forms of land use.

Bracken provides important habitat for many species. As a replacement community, bracken provides opportunities for the survival of some woodland herbs without the presence of an actual tree canopy, and thus maintain species diversity (Rodwell 1991). Bracken also provides valuable habitat for a number of animal species (*cf.* Pakeman & Marrs 1992, Thomas 1995). Stands with bracken provide cover for deer and wild boar. For the latter species, bracken is an important winter food source (Groot Bruinderink *et al.* 1994). Badgers (*Meles meles*) prefer dense bracken to locate their burrows. Small rodents maintain higher population densities under the shelter of bracken fronds and litter. Finally, bracken litter creates a suitable environment for hibernating reptiles like the common lizard (*Lacerta agilis;* Fig. 9.9) and the slow worm (*Anguis fragilis*).

Figure 9.9: Male common lizard *(Lacerta agilis)*, basking in the spring sun after hibernating in bracken litter.

9.6 Conclusions

Stagnation of succession is a natural and common phenomenon in bracken vegetation. As one of the strongest competitors in the European flora, bracken blocks the regeneration of tree species through a combination of shading, smothering, the build up of a deep ectorganic soil layer and the support of a high density of herbivorous and granivorous rodents. The claim that allelopathy is an important mechanism in suppressing regeneration by bracken cannot be supported. Potential phytotoxicity in bracken is more likely a side-effect of its chemical defence against herbivores.

The persistent nature of bracken clones and the capability to endure heavy shading by the canopy results in long-term impediment of tree regeneration. This may result in a treeless replacement community which may persist for very long periods. On the dry sandy soils of The Netherlands, *Fagus sylvatica* appears to be the only major tree species that is able to completely eliminate bracken.

Large scale bracken dominance is brought on by prior deforestation or forestry practices. Bracken dominance in open habitats is rare in The Netherlands. Over-exploitation, degradation and the relative poverty and low moisture content of the sandy soils eliminate bracken from sites outside the protection of a forest canopy. Since regeneration from spores is practically absent, bracken presence is restricted to sites that have had a continuous presence of a tree canopy. Bracken that is found in these refugia may represent individuals that have established several thousands of years ago.

Summary / Samenvatting

Summary

Bracken fern (*Pteridium aquilinum*) is one of the world's most widespread plant species. It occurs on all continents (except Antarctica) and in many climates. When bracken meets favourable growing conditions it is able to completely dominate the vegetation, suppressing the establishment and growth of other plant species. In bracken dominated habitat, tree regeneration may fail for centuries. It is this capacity to stagnate forest succession that has given bracken its reputation as a troublesome weed in many regions in the world.

Bracken is a species that, like most other ferns, is associated with the presence of a tree canopy. In its natural forest habitat, bracken rarely reaches high densities. It is when the tree canopy is removed that bracken can proliferate and create dense swards. The problems associated with bracken are therefore particularly manifest in open areas like clearcuts or previously forested heaths. The vast majority of the studies that have looked into the bracken 'problem' are not surprisingly done in such open vegetation. This thesis deals with the biology and ecology of bracken in its natural forest habitat in order to find out how, and under which circumstances, bracken can cause long term tree regeneration failure and thus create stagnant phases in forest succession.

In this thesis I address two main questions. Firstly, which mechanisms enable bracken to establish complete dominance and block the regeneration of tree species? Secondly, which factors determine the distribution and local dominance of bracken in forest? After a brief introduction on the biology and ecology of bracken (chapter 2), I present data on the productivity and dynamics of bracken in forest in chapters 3 and 4. In the next four chapters, several mechanisms are studied that contribute to the dominance of bracken over other plant species with special attention to tree seedlings. In the final chapter the role of bracken in the dynamics of the forest is assessed using an hierarchical framework of forest succession theory.

Bracken productivity

Bracken productivity in forests was investigated by relating the above ground biomass production of bracken to light availability under the tree canopy. I applied a double sampling technique by constructing biomass regression equations relating individual frond biomass to frond dimensions, and applying these equations to measurements on bracken fronds in 1 m^2 plots.

Total frond production depends on light availability under the forest canopy, and ranged from >700 $g{\cdot}m^{-2}$ in a large forest clearing (100% light available) to 100 $g{\cdot}m^2$ in a stand with only 5% of light available. Bracken showed high plasticity in specific leaf area (SLA) in reaction to changing light levels. Between light levels of 100%

and 11.5%, SLA ranged between 165 and 533 $cm^2 \cdot g^{-1}$. Differences were mainly due to reduced lignification of the pinnae in shady conditions. The relationship between light availability and bracken frond production was also compared with estimates form a previously published model of bracken growth. In full light, model estimates were in fair agreement with measured frond biomass. However, the model underestimated bracken productivity at the low range of light intensities.

Bracken dynamics in forests

The dynamics of bracken under a forest canopy were studied by comparing the distribution of bracken in 1958, 1985 and 1996 in the Speulderbos. Bracken presence and changes thereof were related to soil conditions and forest history, age and composition.

The general pattern in presence of bracken was clearly related to the long-term presence of a forest canopy. Areas that had been deforested and later replanted had no bracken growing there, except for colonisation from the edges.
In the forest, the distribution and vigour of bracken is related to the composition and structure of the tree canopy. In forests dominated by pine (*Pinus*), larch (*Larix*) and oak (*Quercus*), bracken can persist under the translucent canopies. In young stands of douglas fir (*Pseudotsuga menziesii)*, bracken is completely eliminated and can only re-colonise when the pole stage of stand development has passed and the canopy opens up. Beech (*Fagus sylvatica*) stands can permanently inhibit the growth of bracken. This is most likely caused by intensive root competition of beech, especially on the relatively dry sandy soils of the study area.

Colonisation of bracken is totally dependent on vegetative reproduction by rhizomes. The data indicate that besides this lateral expansion, bracken is able to reestablish from dormant rhizomes. Since these dormant rhizomes have ceased frond production, the absence of bracken can thus not be concluded from the lack of fronds without knowledge of prior presence of bracken on the site.

Above- and below ground interference

The importance of above, and below ground interference by bracken was studied in a field experiment. Saplings of beech and Scots pine (*Pinus sylvestris*) were grown in a Scots pine stand and a large forest clearing. Reduction of shading from bracken resulted in increased growth in both species in the clearing. The exclusion of below ground interference had no effect on the growth of beech in the clearing. Seedling growth of beech was significantly lower when root interference was present in the pine forest. This was attributed to root competition from the canopy trees. It is concluded that reduced sapling growth in bracken stands does not arise from below ground interference by bracken.

The presence of bracken greatly reduced the number and abundance of plant species in the forest undergrowth and the number of juvenile trees. The negative effect of bracken presence on species diversity in the forest undergrowth was correlated with frond biomass. The late emergence of bracken enables coexistence of forest plants with bracken, especially vernal plant species. The dense vegetation structure within bracken patches appears to provide protection to saplings from damage by larger herbivores.

Effects of bracken litter

Bracken produces a large amount of litter each year. This litter decays slowly, and tends to accumulate into a thick ectorganic soil layer. The literature shows a strong negative relationship between the thickness and bulk density of the litter layer and the establishment and growth of other plant species. We investigated another potential physical constraint to plant establishment: the natural horizontal layering of particles in the ectorganic soil layer.

Responses in early root development of Scots pine seedlings to two levels of bulk density (0.07 and 0.15 $g{\cdot}cm^{-3}$) in mixed bracken substrate were compared with effects in peat of similar bulk densities, and in sand of three different bulk densities (0.37, 0.52, and 0.67 $g{\cdot}cm^{-3}$). The effect on root growth of the natural horizontal layering of the organic particles was examined by comparing intact with mixed ectorganic bracken soil profiles of similar bulk densities.

Root length growth was significantly reduced in the organic and sandy substrates of high bulk density. Root diameter was not affected by bulk density in the organic substrate, but increased with higher bulk density in sand. Preservation of horizontal layering in the intact ectorganic profile significantly reduced root length compared with mixed substrate of similar bulk density.

Roots growing in high bulk density, and intact, organic substrate showed increased twisting, which resulted in a smaller depth reached by the root relative to total root length produced. In sand, root twisting did not change with increased bulk density. This suggests that roots growing through organic substrate follow a path of least resistance and implies that organic particle size and orientation are more important in determining root development than bulk density alone. Disturbance of the ectorganic soil layer may therefore enhance establishment of seedlings by reducing the mechanical resistance to developing seedling roots.

Allelopathy

Several studies investigating the potential phytotoxicity of bracken to other plant species concluded that allelopathy is an important mechanism responsible for the exclusion of plant species from sites dominated by bracken. Often phenolic acids were implicated in the inhibition of germination, radicle elongation or growth of young seedlings when exposed to bracken substrate.

We investigated the potential phytotoxicity of bracken by exposing germinated seeds of Scots pine, Norway spruce (*Picea abies*) and silver birch (*Betula pendula*) to extracts derived from bracken fronds, and compared this with exposure to extracts from litter of beech and oak (*Quercus robur*). Extracts were made during 1, 2, or 4 days, from fresh litter or litter that was allowed to leach naturally during the winter season. Extracts showed a large variation in total phenolic content, but did not influence radicle elongation in all tested species. Only litter from bracken that was extracted for 4 days significantly reduced radicle elongation in birch seeds. We also compared the potential phytotoxicity of bracken litter extracts with the soil solution collected *in situ*. No differences in germination or radicle elongation were found for seeds of Scots pine, Norway spruce and climbing corydalis (*Ceratocapnos claviculata*).

In another experiment, fresh and leached litter of bracken and beech was mixed into soil and growth of planted Scots pine and Norway spruce seedlings was monitored during 11 weeks. Bracken litter had no negative effects on seedling growth. Beech litter caused reduced dry weight production in both species. The hypothesis that reduction in seedling growth -when they are exposed to mixed litter/soil substrates of bracken- may be the result of nutrient immobilisation, could not be confirmed.

Based on the results of this study, and many other reports investigating the potential phytotoxicity of bracken, there is no reason to assume that allelopathy is an important mechanism employed by bracken in preventing regeneration and establishment of other plant species.

Rodent habitat and seed availability

Bracken stands offer protection to mice and voles. The presence of these rodents may have strong effects on seed availability through dispersal and predation. We investigated the effect of the structural habitat created by bracken on removal rate and dispersal pattern of *Quercus robur* acorns by wood mice (*Apodemus sylvaticus*) and bank voles (*Clethrionomys glareolus*).

Rodent activity was significantly higher in bracken stands as compared to vegetation directly adjacent to the bracken stands. *C. glareolus* was found almost exclusively inside bracken stands, but *A. sylvaticus* was frequently caught outside the protection of vegetation cover. Seed removal rates were generally higher inside bracken stands, and were correlated with the abundance of rodents on the site. The seeds that disappeared were either consumed or stored for later use.

Dispersal direction of acorns from outside the bracken stands was directed towards centres of rodent activity inside the bracken stands, or towards other structurally complex microhabitats. Dispersal distances were related to seed crop production. In a year with no acorn crop produced on the site, mean dispersal distance of experimentally introduced acorns was twice (20-25 m) the distance than in a masting year with an abundant crop (10-15 m).

This study indicates that vegetation structure may have an indirect influence on local seed availability through the directed dispersal of seeds by rodents towards patches of high structural complexity. Also, mice and voles greatly reduce seed and seedling abundance through heavy predation.

The role of bracken in forest dynamics

Bracken is well adapted to the environmental conditions under a forest canopy, but appears to be unable to survive outside the protection of the forest on the dry sandy soils of the Netherlands. Since regeneration from spores is virtually absent, the dynamics in bracken populations emerge from death or vegetative renewal of existing rhizomes. The relationship between bracken and ancient forest is therefore mainly historical, rather than based on current soil properties of such sites.

Its 'guerrilla' growth form enables bracken to explore new area and completely exploit a suitable patch. Under favourable conditions the fronds may grow up to 2.5 m tall and forms a dense canopy. At the end of the growing season, nutrients are withdrawn from the senescing fronds, leaving a large amount of slow-decaying litter after frond death. This way, bracken swards build a physical structure that strongly reduces light levels and smothers plants under collapsed and dead fronds. It builds a thick ectorganic soil profile that is impenetrable for seedlings of most species with light weighted seeds. Mice and voles make preferential use of the protective cover provided by the bracken structure. Consequently, species with larger seeds suffer severe mortality from seed predation and seedling herbivory by these small mammals. The complex chemistry of bracken makes the plant unpalatable to most herbivores, but no allelopathic mechanism is involved in the suppression of neighbouring plant species.

Changes in the vegetation have three general causes: the availability of sites for plants to establish and grow, differential availability of propagules and differential performance of species on the site. Bracken impinges on all of these, and in a dense bracken sward tree recruitment is impossible unless the clones are physically disturbed. In such cases, the established seedlings must attain sufficient height before the bracken canopy closes again. In the studied forests, among the common tree species beech has the highest chances of seedling survival.

Under a forest canopy, the density of the tree canopy determines the density of bracken. However, under most tree species (*Pinus, Larix, Betula, Quercus*) the light levels remain high enough to sustain bracken growth. Only in the thicket and early pole phases of stand development are tree canopies dense enough to suppress bracken completely. Despite the reduced vigour of bracken under a tree canopy it still exerts a strong negative influence on tree seedling establishment and species diversity. On the dry sandy soils, beech is the only tree species that is able to completely inhibit the growth of bracken.

Bracken and forest management

The presence of bracken confronts forest managers with several problems. Where bracken is dominant, species diversity of the community is strongly reduced which may conflict with nature conservation objectives. On the other hand, bracken indicates special natural values due to its almost exclusive presence on ancient forest sites. Because of the severe competition by bracken and its persistence, the use of natural tree regeneration is not an option when bracken is present in the understorey vegetation. Trees have to be planted to ensure sufficient stocking rates.

Eradication of bracken is not feasible, and one has to resign to its presence. Management of forests with bracken in it can focus on preventive measures. Planting a fringe of beech next to the bracken front can impair further spread of clones. The forest canopy should be kept closed prior to stand regeneration by refraining from thinning.

Samenvatting

De adelaarsvaren (*Pteridium aquilinum*) is een van de meest wijdverspreide plantensoorten ter wereld. Zij komt voor op alle continenten (behalve Antarctica) en in verschillende klimaatsgebieden. Onder voor adelaarsvaren gunstige omstandigheden is zij in staat om de vestiging en groei van andere planten te onderdrukken en zo de vegetatie volledig te domineren. In habitats die worden gedomineerd door adelaarsvaren kan de verjonging van boomsoorten eeuwenlang uitblijven. Dit vermogen om de bossuccessie te stagneren heeft adelaarsvaren in vele delen van de wereld de reputatie gegeven van een lastig onkruid.

Net als bij de meeste andere varensoorten is het voorkomen van adelaarsvaren nauw verbonden met de aanwezigheid van een boomvegetatie. In haar natuurlijke leefomgeving, het bos, bereikt de adelaarsvaren zelden hoge dichtheden. Slechts wanneer de kroonlaag van het bos is verdwenen kan de adelaarsvaren zich snel uitbreiden en dichte vegetaties vormen. De aan adelaarsvaren gekoppelde problemen manifesteren zich daarom vooral in open gebieden zoals kapvlaktes of heides waar vroeger bos heeft gestaan. Het is dus logisch dat een grote meerderheid van de studies naar het 'probleem' adelaarsvaren zijn uitgevoerd in dergelijke open vegetaties. Dit proefschrift behandelt de biologie en ecologie van adelaarsvaren in haar natuurlijke bosomgeving met als doel uit te zoeken hoe, en onder welke omstandigheden, de adelaarsvaren ervoor kan zorgen dat de verjonging van boomsoorten langdurig uitblijft en daarmee stagnerende fases in de bossuccessie kan veroorzaken.

In dit proefschrift heb ik twee hoofdvragen gesteld. Ten eerste: welke mechanismes stellen de adelaarsvaren in staat om de vegetatie volledig te domineren en de verjonging van bomen te verhinderen? Ten tweede: welke factoren bepalen de verspreiding en lokale dominantie van adelaarsvaren in bossen? Na een beknopte inleiding over de biologie en ecologie van adelaarsvaren (hoofdstuk 2) presenteer ik in hoofdstuk 3 en 4 gegevens over de productiviteit en dynamiek van adelaarsvaren in bossen. In de vier daaropvolgende hoofdstukken worden verschillende mechanismen bestudeerd die bijdragen aan de dominantie van adelaarsvaren over andere planten, in het bijzonder zaailingen van bomen. In het laatste hoofdstuk evalueer ik de rol van de adelaarsvaren in de bosdynamiek door gebruik te maken van een hierarchisch successiemodel.

Productiviteit

De productiviteit van adelaarsvaren in bossen werd onderzocht aan de hand van de relatie tussen de beschikbaarheid van licht onder het kronendak en de bovengrondse biomassa productie. De biomassa werd geschat door eerst een relatie te leggen tussen de grootte van een varenblad en zijn drooggewicht, en vervolgens deze relatie toe te passen op meetgegevens van bladeren in plots van 1 m^2.

De totale bladproductie was afhankelijk van de lichtbeschikbaarheid onder het kronendak, en varieerde van >700 $g{\cdot}m^{-2}$ in een grote open plek (100% licht beschikbaar) tot 100 $g{\cdot}m^{-2}$ in een opstand waar slechts 5% van het licht de bodem bereikt. De adelaarsvaren vertoont een hoge plasticiteit in specifiek blad oppervlak in reactie op veranderende lichtniveaus. Gaande van 100% naar 11.5% van het beschikbare licht steeg de verhouding tussen bladoppervlak en bladgewicht van 165 naar 533 $cm^2{\cdot}g^{-1}$. Deze verschillen werden vooral veroorzaakt door verminderde lignine-vorming in de bladeren onder schaduwrijke omstandigheden. Verder werd het verband tussen lichtbeschikbaarheid en de groei vergeleken met de schattingen uit een eerder gepubliceerd groeimodel voor adelaarsvaren. In vol licht schat het model de biomassa in de zelfde orde van grootte als de gemeten biomassa van adelaarsvaren. Echter, onder lagere lichtniveaus onderschat het model de productiviteit van adelaarsvaren.

Dynamiek van aelaarsvaren in bossen

De dynamiek van adelaarsvaren onder een kronendak werd onderzocht door een vergelijking te maken tussen drie kaarten van de verspreiding van adelaarsvaren in het Speulderbos in 1958, 1985 en 1996. De verspreiding van adelaarsvaren en de veranderingen daarin werden gerelateerd aan bodemeigenschappen en de geschiedenis, leeftijd en samenstelling van het bos.

Het algemene verspreidingspatroon van adelaarsvaren hield duidelijk verband met de langdurige aanwezigheid van een boomlaag. Gebieden waar het bos ooit is gekapt en die later weer zijn bebost bevatten nagenoeg geen adelaarsvaren, behalve langs de randen waar vanuit oude bosgroeiplaatsen nieuwe kolonisatie kon optreden. In het bos was de verspreiding en groei van adelaarsvaren gerelateerd aan de samenstelling en structuur van de kroonlaag. In bossen van den (*Pinus*), lariks (*Larix*) en eik (*Quercus*) kan adelaarsvaren zich handhaven onder de transparante kronen. Adelaarsvaren wordt volledig verdrongen uit jonge opstanden van douglas (*Pseudotsuga menziesii*) en kan deze plekken alleen herkoloniseren wanneer het kronendak opener wordt aan het einde van de stakenfase. Bossen van beuk (*Fagus sylvatica*) kunnen de groei van adelaarsvaren permanent belemmeren. Dit is waarschijnlijk een gevolg van de sterke wortelconcurrentie van de beuk, vooral op de droge zandgronden van het studiegebied.

De kolonisatie van adelaarsvaren is volledig afhankelijk van vegetatieve vermeerdering van de rhizomen (wortelstokken). Naast deze laterale groei vanuit de randen kan adelaarsvaren zich ook hervestigen vanuit slapende rhizomen. Omdat deze slapende rhizomen geen bladeren produceren kan de afwezigheid van adelaarsvaren dus niet eenduidig worden afgeleid uit de afwezigheid van bladeren zonder kennis over het eerdere voorkomen van adelaarsvaren op die plaats.

Boven- en ondergrondse concurrentie

Het belang van bovengrondse en ondergrondse concurrentie werd bestudeerd in een veldexperiment. Jonge beuken en grove dennen (*Pinus sylvestris*) werden geplant in een grove dennenbos en in een grote open plek. In de open plek leidde een reductie van de beschaduwing door adelaarsvaren tot een hogere groei in beide boomsoorten. Het opheffen van ondergrondse concurrentie door adelaarsvaren had geen effect op de groei van beuk in de open plek. De groei van beuk was significant lager wanneer de planten ondergrondse interacties ondervonden in het grove dennenbos. Dit werd toegeschreven aan wortelconcurrentie door de bomen. Dit leidde tot de conclusie dat de verminderde groei van jonge bomen in vegetaties van adelaarsvaren niet het gevolg is van wortelconcurrentie door adelaarsvaren.

Het aantal plantensoorten en de mate waarin zij voorkwamen was, evenals het aantal zaailingen van bomen, aanzienlijk lager in aanwezigheid van adelaarsvaren. Het negatieve effect van de aanwezigheid van adelaarsvaren op de soortenrijkdom van de ondergroei van het bos was gecorreleerd met de totale bladbiomassa. Het late uitlopen van adelaarsvaren stelt een aantal bosplanten is staat samen te leven met adelaarsvaren, in het bijzonder voorjaarsbloeiers. De dichte vegetatiestructuur in plekken met adelaarsvaren lijkt bescherming te bieden aan jonge bomen tegen vraat van grotere herbivoren.

Effecten van strooisel

De adelaarsvaren produceert ieder jaar een grote hoeveelheid strooisel. Dit strooisel verteert langzaam en hoopt zich op tot een dikke ectorganische laag op de bodem. Uit de literatuur blijkt een negatief verband tussen de dikte en bulk dichtheid van de strooisellaag en de vestiging en groei van plantensoorten. Wij onderzochten een andere potentiële fysieke beperking voor de vestiging van planten: de natuurlijke horizontale gelaagdheid van deeltjes in de ectorganische bodemlaag.

De reacties in vroege wortelontwikkeling van zaailingen van grove den op twee niveaus in bulk dichtheid (0.07 and 0.15 $g \cdot cm^{-3}$) in dooreengemengd substraat van adelaarsvaren werden vergeleken met de reacties in turf van gelijke bulk dichtheid en in zand van drie bulk dichtheden (0.37, 0.52, and 0.67 $g \cdot cm^{-3}$). Het effect op de wortelgroei van de natuurlijke horizontale gelaagdheid van organische deeltjes werd bestudeerd door intacte ectorganische bodemprofielen van onder adelaarsvaren te vergelijken met dooreengemengd substraat met dezelfde bulk dichtheid.

De lengtegroei van de wortels was significant lager in organische en minerale substraten met hoge bulk dichtheid. De diameter van de wortel werd niet beinvloed door de bulk dichtheid van het organische substraat, maar werd daarentegen groter met toenemende bulk dichtheid in zand. Vergeleken met dooreengemengde substraten leidde het handhaven van de horizontale gelaagdheid in het intacte ectorganische profiel tot een significante reductie van de wortellengte.

Wortels die groeiden in organisch substraat met hoge bulk dichtheid en in intacte profielen lieten een hoge mate van kronkeling zien hetgeen resulteerde in een geringere diepte die de wortels konden bereiken met hun totale lengte. In zand veranderde de kronkeling van de wortels niet met toenemende bulk dichtheid. Wortels die door een organisch substraat groeien kiezen blijkbaar de weg van de minste weerstand. Dit betekent tevens dat de grootte en oriëntatie van de organische deeltjes belangrijker zijn voor de wortelontwikkeling dan alleen de bulk dichtheid. Verstoring van de ectorganische bodemlaag zal daarom de vestiging van zaailingen bevorderen door vermindering van de mechanische weerstand die de zich ontwikkelende wortel ondervindt.

Allelopathie

Verschillende studies naar de potentiële giftigheid van adelaarsvaren voor andere plantensoorten concludeerden dat allelopathie een belangrijk mechanisme is in de verdringing van plantensoorten van plekken die worden gedomineerd door adelaarsvaren. De remming van de kieming, strekking van de kiemwortel of groei van de zaailing na blootstelling aan substraat van adelaarsvaren werd meestal geweten aan het voorkomen van fenolische verbindingen.

Wij onderzochten de mogelijke fytotoxiciteit van adelaarsvaren door zaden van groveden, fijnspar (*Picea abies*) en ruwe berk (*Betula pendula*) bloot te stellen aan extracten uit bladeren van adelaarsvaren, en dit te vergelijken met blootstelling aan extracten van bladeren van beuk en eik. De bladeren werden geëxtraheerd gedurende 1, 2 en 4 dagen, en extracten werden gemaakt van vers gevallen bladeren en bladeren die een winter lang buiten konden uitlogen. De extracten lieten een grote variatie zien aan concentraties van fenolen, maar bij alle testsoorten had dit geen effect op de strekking van de kiemwortel. Het enige significant negatieve effect werd gevonden bij berk in extracten van het vers gevallen blad van adelaarsvaren welke waren geëxtraheerd gedurende een periode van 4 dagen.
Wij vergeleken tevens de potentiële fytotoxiciteit van extracten met de in het veld aanwezige bodemoplossing onder adelaarsvaren. Er werd geen enkel effect gevonden voor wat betreft kieming of wortelstrekking in zaden van grove den, fijnspar en rankende helmbloem (*Ceratocapnos claviculata*).

In een ander experiment werd vers en uitgeloogd blad van adelaarsvaren en beuk door minerale grond gemengd en werd de groei van hierin geplante grove den en fijnspar zaailingen gevolgd gedurende 11 weken. Het blad van adelaarsvaren had geen enkele invloed op de groei van zaailingen. Het blad van beuk veroorzaakte verminderde droge stofproductie in beide soorten. De hypothese dat reductie in groei van zaailingen in door de grond gewerkt blad van adelaarsvaren het gevolg is van stikstof-immobilisatie kon niet worden bevestigd.

Op basis van de uitkomsten van deze, en vele andere, studies is er geen reden aan te nemen dat allelopathie een belangrijk mechanisme is waarmee adelaarsvaren de regeneratie en vestiging van andere plantensoorten belemmerd.

Muizen habitat en zaadbeschikbaarheid

Vegetaties van adelaarsvaren bieden bescherming aan muizen en woelmuizen. De aanwezigheid van deze knaagdieren kan via verspreiding en predatie een sterke invloed hebben op de beschikbaarheid van zaden. We onderzochten het effect van de habitatstructuur, hier bepaald door adelaarsvaren, op de snelheid waarmee zaden verdwijnen en het patroon van zaadverspreiding van *Quercus robur* eikels door bosmuis en woelmuis.

De activiteit van knaagdieren was significant hoger in vegetaties van adelaarsvaren dan in de omringende vegetatie. De rosse woelmuis werd bijna altijd aangetroffen onder adelaarsvaren, maar de bosmuis werd ook regelmatig buiten de beschermende dekking van adelaarsvaren aangetroffen. Zaden verdwenen sneller van onder adelaarsvaren, en deze verdwijnsnelheid was gecorreleerd met de hoeveelheid knaagdieren ter plekke. De zaden die verdwenen werden opgegeten of verstopt voor later.

Zaden die buiten de adelaarsvaren vegetatie waren neergelegd werden gemiddeld verspreid in de richting van de hoogste activiteit van muizen onder de varens. De afstand waarover zaden werden verspreid was gerelateerd aan de zaadproductie van bomen. In een jaar waarin er geen eikels werden geproduceerd was de gemiddelde afstand waarover de eikels verspreid werden twee maal zo groot als in een mastjaar met veel zaadproductie. Deze studie toont aan dat de vegetatiestructuur een indirect effect kan hebben op de beschikbaarheid van zaad via verspreiding van zaden in de richting van plekken met een grote structuur variatie. Muizen en woelmuizen kunnen verder de aantallen zaden en zaailingen via predatie drastisch reduceren.

De rol van adelaarsvaren in de bosdynamiek

De adelaarsvaren is goed aangepast aan de milieuomstandigheden in het bos, maar lijkt op de Nederlandse droge zandgronden niet in staat te overleven buiten de bescherming van een kronendak. Omdat regeneratie vanuit sporen vrijwel niet voorkomt is de dynamiek in populaties van adelaarsaren volledig het gevolg van sterfte en vegetatieve vernieuwing van bestaande rhizomen. Het verband tussen adelaarsvaren en oude bosbodems is daarom vooral historisch bepaald, en niet het gevolg van de huidige eigenschappen van dergelijke bodems.

Haar 'guerrilla' groeivorm stelt de adelaarsvaren in staat om nieuwe plekken te koloniseren en geschikte plekken volledig te bezetten en benutten. Onder gunstige omstandigheden kunnen de bladeren tot 2.5 m hoog worden en een dicht bladerdak vormen. Aan het einde van het groeiseizoen worden voedingsstoffen uit de afstervende bladeren onttrokken, waardoor na bladsterfte een grote hoeveelheid slecht verteerbaar strooisel achterblijft. Op deze wijze bouwt adelaarsvaren een fysieke structuur dat het lichtnivau sterk verlaagt en planten verstikt onder geknakte en dode bladeren. Onder adelaarsvaren ontstaat een dikke ectorganische laag die ondoordringbaar is voor zaailingen van de meeste soorten met kleine zaden. Muizen en woelmuizen maken bij voorkeur gebruik van de beschermening die adelaarsvaren hen biedt. Als gevolg hiervan ondervinden plantensoorten met grote zaden hoge sterfte door zaadpredatie en herbivorie van de zaailingen door deze kleine knaagdieren. De complexe chemie van adelaarsvaren maakt deze oneetbaar voor de meeste herbivoren, maar allelopathie speelt geen rol in de belemmering van de groei van andere plantensoorten.

Veranderingen in de vegetatie hebben drie algemene oorzaken: de beschikbaarheid van plaatsen waar planten kunnen vestigen en groeien, verschillen in zaadbeschikbaarheid en verschillen in de groei en ontwikkeling van soorten in relatie tot hun omgeving. Adelaarsvaren grijpt in op al deze drie. De verjonging van boomsoorten is onmogelijk in dichte vegetaties van adelaarsvaren, tenzij de klonen fysiek worden verstoord. In dergelijke gevallen moet de opgekomen verjonging snel voldoende hoogte bereiken voordat het bladerdak van adelaarsvaren zich weer kan sluiten. Van de algemene boomsoorten heeft de beuk de meeste kans te overleven onder adelaarsvaren.

De dichtheid van het kronendak bepaald de dichtheid van adelaarsvaren. Onder de meeste boomsoorten (*Pinus*, *Larix*, *Betula*, *Quercus*) blijft voldoende licht beschikbaar voor de groei van adelaarsvaren. Alleen in de dichte fase en vroege staken fase wordt het kronendak dicht genoeg om adelaarsvaren volledig weg te drukken. Ondanks de lagere dichtheid onder een kronendak blijft adelaarsvaen een sterke negatieve invloed uitoefenen op de verjonging van soorten en de soortsdiversiteit. Op de droge zandgronden is de beuk de enige boomsoort die in staat is om de groei van adelaarsvaren volledig te verhinderen.

Adelaarsvaren en bosbeheer

De aanwezigheid van adelaarsvaren confronteert bosbeheerders met een aantal problemen. Waar adelaarvaren tot dominantie komt verlaagt dit de soortsdiversiteit hetgeen in strijd kan zijn met natuurbehoudsdoelstellingen. Daarentegen duidt, vanwege het exclusieve voorkomen in oude bosgroeiplaatsen, de aanwezigheid van adelaarsvaren op speciale natuurwaarden. Vanwege de grote concurrentiekracht en standvastigheid van adelaarsvaren is natuurlijke verjonging van boomsoorten geen optie wanneer adelaarsvaren aanwezig is in de ondergroei. Bomen moeten worden aangeplant wanneer voldoende bezetting gewenst is.

Volledige bestrijding van adelaarsvaren is niet uitvoerbaar, en men moet zich dus neerleggen bij haar aanwezigheid. Het beheer van bossen met adelaarsvaren in de ondergroei kan zich richten op preventieve maatregelen. Om te voorkomen dat adelaarsvaren zich verder verspreid kan langs de buitenkant van het verspreidingsgebied van adelaarsvaren een strook met beuk worden geplant. Wanneer het bos verjongd moet worden dient het kronendak van het bos van te voren zoveel mogelijk gesloten te blijven door het nalaten van dunningen.

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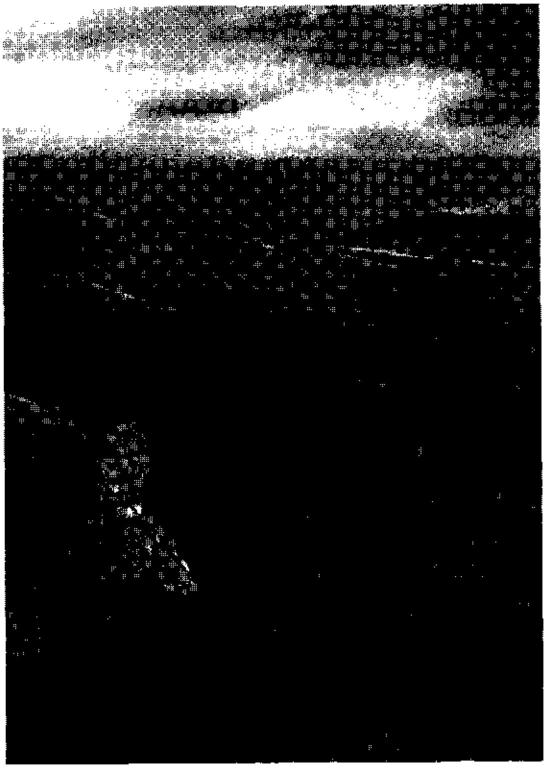

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Curriculum vitae

Jan den Ouden werd geboren op 20 januari 1963 te Streefkerk, in een van de strengste winters van de twintigste eeuw. Het eerste deel van de middelbare school bracht hij door op de Christelijke Scholengemeenschap De Lage Waard te Papendrecht. Snel nadat hij bijna van die school was verwijderd omdat hij het had gewaagd tijdens de eerste les geschiedenis (Adam en Eva) te informeren naar de evolutietheorie, veranderde hij van school en heeft aan het Van der Putt-lyceum te Eindhoven in 1981 zijn VWO-diploma behaald.

Vanaf zijn kleuterschooltijd wilde hij al boswachter worden, maar meer geïnteresseerd in het waarom dan het hoe ging hij Bosbouw studeren aan de Landbouw Hogeschool te Wageningen. Na een afstudeervak in de bosteelt der gematigde streken zocht hij de kou weer op en ging naar Alaska voor zijn stage, waaraan hij vervolgens een afstudeervak vegetatiekunde koppelde. In 1988 studeerde hij met lof af aan de Landbouwuniversiteit Wageningen.

Na zijn afstuderen heeft hij als vrijwilliger voor Natuurmonumenten een inventarisatie gemaakt van de vegetatie op de Imbos, en bij Oranjewoud in Heerenveen een analyse gemaakt van gegevens over de vitaliteit van Europese bossen. In 1990 kreeg hij de kans om aan het Forestry Sciences Lab in Juneau, Alaska verder te werken aan zijn onderzoek aan successie van mossen in bossen. Verder heeft hij daar veel (nog) ongerepte delen van het gematigde regenwoud in kaart gebracht.

Na enige omzwervingen kwam hij in 1992 terug naar Nederland. In die tijd waren AIO-banen dun gezaaid, en dus greep hij zijn kans toen de Landbouwuniversiteit vijf plaatsen beschikbaar stelde voor onderzoeksprojecten die door de aspirant AIO's zelf moesten zijn geformuleerd. Als een van de gelukkigen begon hij in 1993 aan zijn promotieonderzoek aan adelaarsvaren, dat met dit proefschrift is afgerond.
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