

The colonisation of a former sea-floor by ferns

De kolonisatie van een voormalige zeebodem door varens

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The colonisation of a former sea-floor by ferns

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Abstract

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This thesis sets out to answer three main questions on ecology, demography and woodland management related to fern species which established in woodlands on a former sea-floor (province of Flevoland). The study was carried out in the period 1977 - 2007. The thesis first of all addresses the question about distribution and habit preference of fern species in the Netherlands and recent trends that have taken place in population sizes. In the Netherlands 39 species of *Pteropsida* (*Equisetaceae* excluded) were recently reported with most species showing a positive trend. Attention is paid to factors responsible for this trend, including the effect of creation of new habitats and mild winters.

The discovery of a large group of rare ferns in the Kuinderbos in 1977 - 1979 (23 species) offered an opportunity to study the ecology and colonisation process. The area is characterised by deposits of fine calcareous sands on peat (peat erosion area) and intersected by 250 km of drainage trenches. In 1979, 18 of the 23 fern species were found exclusively on trench banks. Attention is paid to preferred soil and canopy composition. As most rare ferns grow in drainage trenches also aspect, relative height up the side of the trench and gradient were involved. The situation in 1979 is compared with that 23 years later, indicating changes, part of them related to clustering around adult plants and canopy composition. Colonisation proved to be related to the size of neighbouring fern populations in the groups of both calcicole and acidophilous fern species. In most rare fern species colonisation started at numerous sites in a short period with spores transported from elsewhere. The role of a sporebank seems plausible

Fifty three woodlands on clay were surveyed on ferns and seed plants. Colonisation of seed plants is depended on woodland age, area (i.e. size), distance to villages and presence of footpaths (rides). More ferns are found in larger woodlands and they are not always the first to establish. Earlier colonists include other anemochoric vascular species and also endozoochoric and epizoochoric woodland vascular species. Ferns are earlier colonist when drainage trenches or *Pinus* stands are present. In case of *Gymnocarpium dryopteris* the Kuinderbos population is compared with other Dutch populations to get more insight in circumstances facilitating a high density in the Kuinderbos (89% of Dutch population). During the period 1979 - 1991 data were collected from 493 colonies. The high density in the Kuinderbos can be attributed to an optimal water supply from a peat subsoil, the composition of the ecto-organic layer consisting of *Picea* needles and an optimal light climate with light intensity between 2 and 5%.

In three plots the demography of *Asplenium scolopendrium* was studied in the peat erosion area (Kuinderbos). Demographic data were parameterized with 37 transition matrices. Light affects the performance of plants and reproduction. It was found that cold winters influence the population growth rate by increasing mortality and retrogression. Mortality was correlated with the number of frost days per winter, but snow cover can protect plants. Recruitment is related to small scale disturbance of trench slopes.

Three experiments by cutting trees were carried out in *Picea sitchensis* and *Fagus sylvatica* stands. Decrease of light intensity had a negative impact on performance and survival of *Gymnocarpium dryopteris*. By thinning the population recovered within seven years to the former population size. In a second experiment repetitive thinning accommodated a mass recruitment of *Asplenium scolopendrium* and *Polystichum aculeatum*. In artificial woodland gaps within stands of *Fagus sylvatica* (Voorsterbos, boulder clay) a spore bank and the microclimate facilitated establishment of 10 fern species.

The fern hot spots in Flevoland can be attributed to the composition of the soil (fine grained sand, boulder clay, light clayey soils), canopy composition (*Picea*, deciduous tree species), variation in relief (drainage trenches) and hydrology. Moreover the colonisation of Flevoland depended on transport of spores by wind from elsewhere, underlining the meaning of populations nearby and time needed to establish and the build up of sporebanks. The thesis advises creating variation in relief prior to planting of new woodlands.

‘Zo langzamerhand kregen we het grondwerk onder de knie en leerden we de kneepjes van het vak kennen, zeker wat het werktempo betreft. Je moest met het verdiende loon de toegestane grens niet overschrijden, waardoor het tarief van de akkoordwerkzaamheden onder druk zou komen te staan. Een duidelijk voorbeeld levert het graven van greppels met een bovenwijdte van 1,15 meter, 60 centimeter diep en 30 centimeter breed. De uitgegraven grond moest aan weerskanten zes meter worden geëgaliseerd tegen een tarief van 9 à 11 cent per meter. Dit variabele tarief was afhankelijk van eventuele wateroverlast. Men moest een boom van een kerel zijn om er zestig meter greppel in één dag uit te gooien’

L. Huizinga, 1987 ‘Pionier Huizinga begint op 1 september 1941’.
De Vriendenkring 27(4): 6 - 13.

Zie ook:

G. van Hezel & A. Pol, 2005. De Flevolandse geschiedenis in meer dan 100 verhalen. Van Gennip, Amsterdam.

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Gymnocarpium dryopteris (Kuinderbos, wood floor)
Gebogen driehoeksvaren



Cyrtomium falcatum (Utrecht, gully cover)
IJzervaren

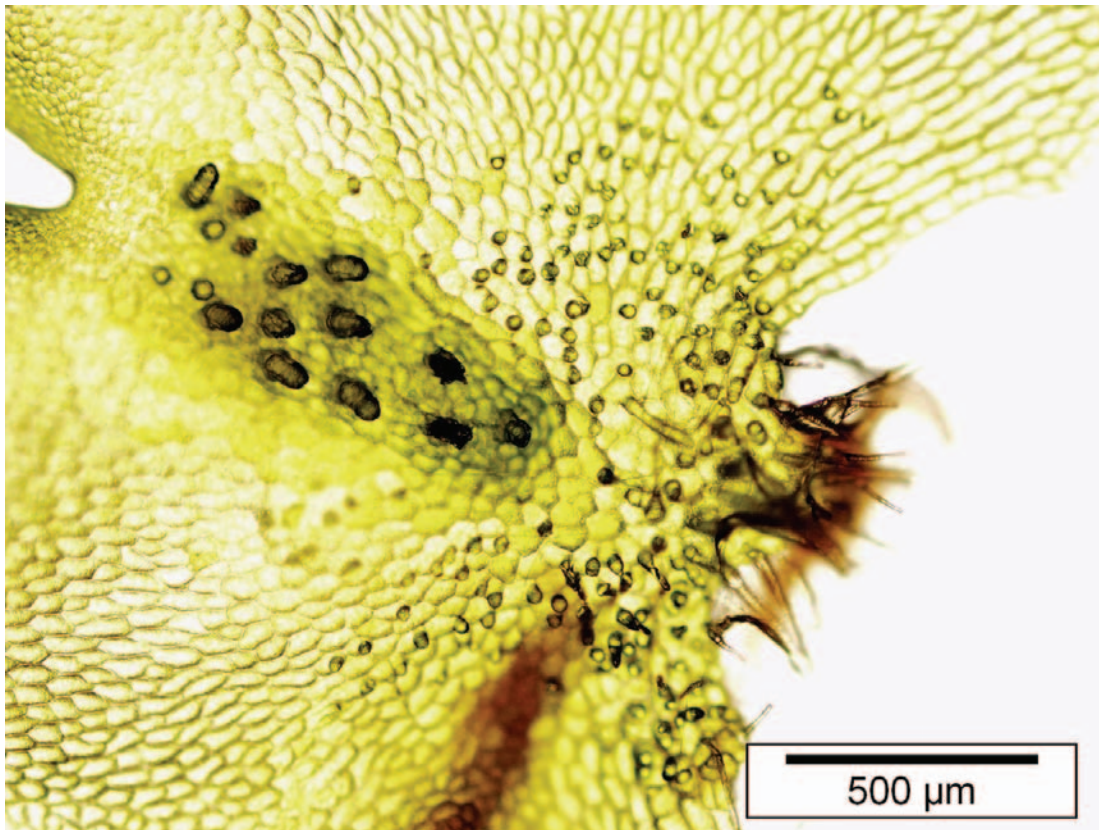


Asplenium adiantum-nigrum (Amsterdam, wall)
Zwartsteel



Asplenium ruta-muraria (Zwolle, wall)
Muurvaren

Introduction



Prothallium of *Asplenium trichomanes* with antheridia and archegonia

Background

Ferns (*Pteropsida*)¹ are an ancient group of plants. Most ferns appeared at the Cretaceous-Tertiary boundary and the ancestors of various groups of ferns that grow on Earth today appeared in the Carboniferous (Collinson 1996, Moran 2000). In the subsequent eons the ferns were able to survive in various habitats. In the Netherlands, ferns are hugely outnumbered by the number of flowering plant species, as they comprise only 2.1 percent of the Dutch flora (Tamis 2005). Nevertheless, they sometimes play a prominent role in the Dutch landscape: *Thelypteris palustris* in reed beds, *Pteridium aquilinum* in *Fagus sylvatica* - *Quercus robur* woods and *Dryopteris dilatata* in *Pinus spp.* plantations and *Quercus robur* woods. *Pteridium aquilinum* is one of the most researched fern species in the world because it is toxic to livestock (Watt 1976, den Ouden 2000). Most of the other *Pteropsida* species have so far received little attention in the Netherlands (Chapter 2; Bremer 2001).

The study of *Pteropsida* has made striking advances during the last fifty years. There was a great leap forward in knowledge of the taxonomy thanks to the work of Manton (1950), who studied the chromosomes extensively by making preparations of spore mother cells undergoing meiosis. Her study triggered a large number of studies on chromosomes (Wagner & Smith 1993), which improved our understanding of speciation within the group of fern species (Haufler 1996). Since 1995, molecular studies based on DNA have intensified, leading to new insights into the phylogenetic relationships. The fern families *Ophioglossaceae*, *Osmundaceae* and Horsetails *Equisetaceae* have proved to be the oldest families, with the latter now being attributed to the *Pteropsida* (Pryer *et al.* 2004). Knowledge of the geographic distribution of taxa in various European countries has also increased, generally as part of mapping projects (Jermy *et al.* 1978, Moreno Saiz *et al.* 1996, Bennert 1999, Groen & Slikke 2000). More recently our knowledge on spore banks and life-cycles has made an important step forward (see section 1.2). But there are still many questions that need to be answered for most fern species. Page (1982) surveyed numerous questions on life-cycles, adaptations to the environment, geographic, edaphic, climatic, biotic and time factors, hampered by the lack of long-term observations.

This thesis originated in the Kuinderbos. This is one of the woodlands in the Noord-oostpolder (Flevoland, the Netherlands), which was reclaimed from the former Zuiderzee in 1941/1942 (Fig. 1.1). Many rare fern species were recorded here for the first time in the period 1977 – 1979. These observations raised questions about the ecology and the colonisation potential of fern species and led to the setting up of a monitoring study aimed to answer questions on the population dynamics of the species involved. The discovery of rare fern species in other woodlands of Flevoland (Fig. 1.1) after 1979 initiated studies on colonisation and its dependence on landscape ecological factors.

About ferns

The *Pteropsida* comprise the ferns and also the Horsetails (*Equisetaceae*). The latter family is not included in this study. Most ferns share a number of life-history features: wind-dispersed spores, hermaphroditic gametophytes, water-induced fertilisation, a perennial life-cycle and the lack of dependence on symbionts (except for some genera) (Werth & Cousens 1990). Ferns do not display secondary growth: the tissues are all primary, derived from a terminal

¹ Nomenclature based on Van der Meijden (2005)

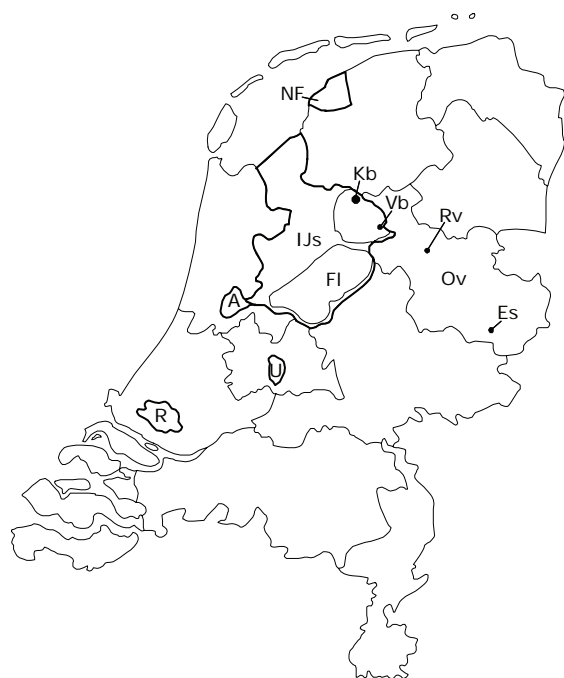


Figure 1.1. Areas and cities mentioned in one or more Chapters of the thesis. IJs = IJsselmeer (in bold, the boundary of the former Zuiderzee), FI = province of Flevoland, Ov = province of Overijssel, Kb = Kuinderbos, Vb = Voorsterbos, Rv = Rouveen (Staphorsterveld), Es = Estate Strootman, NF = North Western part of Friesland, A = Amsterdam, R = Rotterdam, U = Utrecht.

meristem. Pteridopsida have no cambium and they lack cork and secondary vascular tissues (Wagner & Smith 1993). Fern spores are able to be transported over long distances, but most species probably have a leptokurtic distribution of spores dispersed from a parent plant, as demonstrated for *Botrychium virginianum* (Peck *et al.* 1990) and *Asplenium ruta-muraria* (Suter & Schneller 1986). The dispersal of spores not only helps to maintain a population but also assists migration to another population (gene flow) and the establishment of a new population (colonisation).

Most fern species have a so-called homosporous haplodiaplont life-cycle that includes two distinctive and free-living parts (Fig. 1.2). The first of these is the *sporophyte* generation, which is long-lived and contains an internal water-transporting vascular system. This is the fern that can be seen in the field. This phase gives rise to *sori*, mostly underneath the fronds. These *sori* consist of *sporangia*, each containing 64 spores as a rule (apogamous, haploid species contain 32 spores). Sporangia are able to spread the spores actively. The spores are easily dispersed by the wind. They are 24 - 75 μm in diameter (see also Chapter 3, Table 3.6) though *Pilularia globulifera* is exceptional in having large female megaspores. Dispersal by water over small distances is possible too (in the case of wall species; Suter & Schneller 1986). After dispersal a small number of the spores germinate and grow into a separate haploid *gametophyte* generation. Only a fraction will have the chance to germinate. Another part will be added to the spore bank (Dyer & Lindsay 1992, Dyer & Lindsay 1996). They provide opportunities for gametophyte establishment when soil disturbance occurs. Live spores can be found to a depth of 80 cm (or even more) (Esteves & Dyer 2003), which indicates that the spores are able to germinate many years after dispersal. Some species such as *Pteridium aquilinum* do not form these banks (Dyer & Lindsay 1996).

The gametophyte phase comprises the *prothallus*: more or less flat plates of tissue that are usually less than 0.5 cm in diameter, with rhizoids; they resemble liverworts. The prothallus is the sexual generation of the life-cycle and gives rise to female *archegonia* and male *antheridia*. The male gametes are free-swimming, motile organisms that need water in which to swim. Schneller *et al.* (1990) observed in *Athyrium filix-femina* that spermatozooids swim at a speed of 0.1 – 0.2 mm second⁻¹ and that individual sperm are viable for at least 4 - 8 minutes, meaning that they could swim a distance of about 2.4 – 9.6 cm. Farrar (2003)

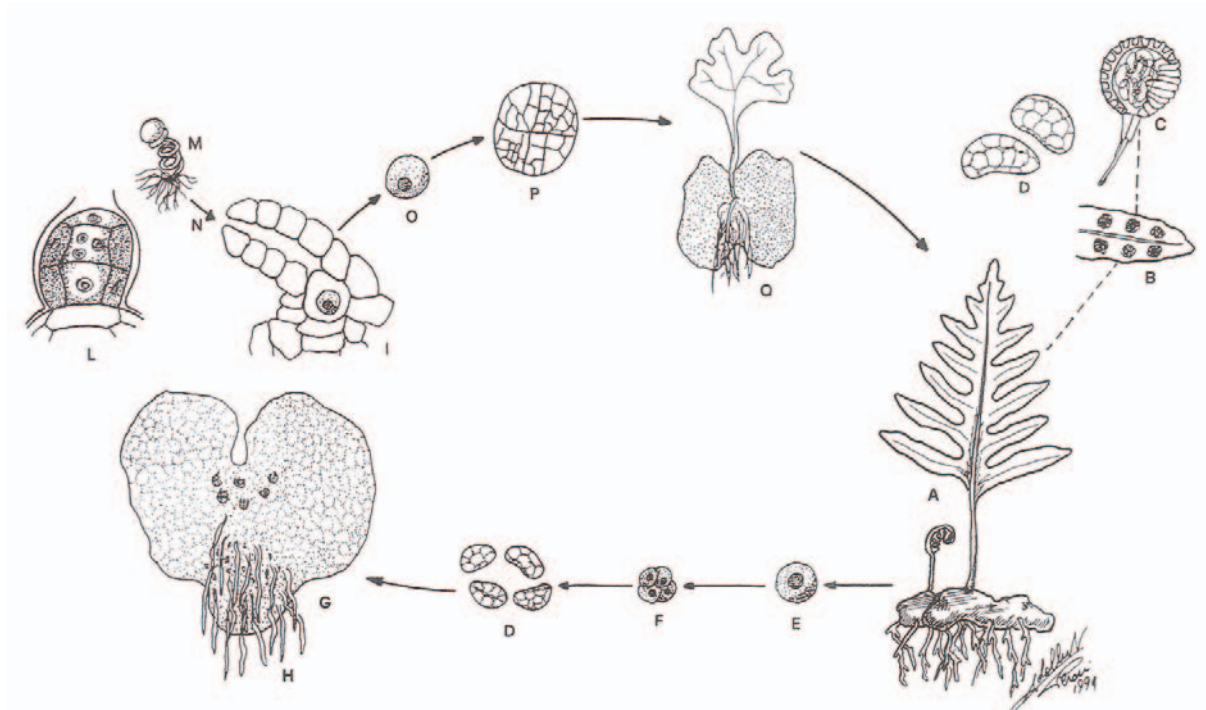


Figure 1.2. The life cycle of ferns (*Pteropsida*) illustrated on *Polypodium vulgare* (after Peroni & Peroni 1997). **A.** sporophyte, **B.** sori, **C.** sporangium, **D.** spores, **E/F.** meiosis, **G.** prothallium, **H.** rhizoids, **L.** antheridium, **I.** archegonium, **M.** spermatozoid, **N.** fertilisation, **O.** fertilised egg cell, **P.** young tissue growing into prothallium, **Q.** prothallium with young sporophyte.

indicates that the gametophyte morphology can be classified into three basic types. The species in this thesis all belong to type I, with cordate or butterfly-shaped gametophytes.

Within ferns three sexual strategies can be found: intragametophytic selfing, intergametophytic selfing (with gametes originating from the same plant) and intergametophytic crossing (Schneller 1987). After germination, a population of bisexual, male and female prothalli can build up, as demonstrated for various species (e.g. *Asplenium scolopendrium*) by Lindsay & Dyer (1996). In the laboratory isolated gametophytes form archegonia only. Without isolation, antheridia are formed in populations of gametophytes, because antheridogen produced by female prothallia induces their development (Schneller *et al.* 1990). In this manner, species are able to outcross. Since antheridogens are secreted by the plant to its environment, they are referred to as a pheromone instead of a hormone (Näf 1979). In *Athyrium filix-femina*, robust plants grow up after outcrossing and smaller plants after selfing (Schneller 1987). Isozyme studies have shown outcrossing to be the principal mode of sexual reproduction (Soltis & Soltis 1989). In laboratory studies of *Asplenium ruta-murari*, Suter & Schneller (1986) found selfing (93% of prothallia). In *Osmunda regalis*, recessive sporophytic lethal alleles were found to be responsible for the death of homozygous individuals after selfing (Klekowski 1973, Zenkteler 1999). Chiou *et al.* (2002) concluded that in the group of fern species they examined, the intragametophytic-selfing species were polyploid, whereas the intergametophytic taxa were diploid. The duplicated loci of polyploid taxa mitigate the expression of recessive alleles after intragametophytic selfing. Some species have the capacity for polyembryony because they have a great variety of archegonia in a long-lived gametophyte, giving rise to a number of sporophytes of different genotypes on a single gametophyte. This has been observed in *Osmunda regalis* (Klekowski 1970). A heterosporous haplodiplont life-cycle is known from some genera, such as *Pilularia*, where male spores and female mega

spores are produced. Genetic diversity is a prerequisite for natural selection and adaptation. In recent decades, the maintenance of genetic diversity has received more attention because of conservation issues (Ellstrand & Elam 1993). Genetic differentiation in ferns has only been studied in some species (Holderegger & Schneller 1994). Genetic diversity has been found to be positively correlated with population age in *Asplenium ruta-muraria*, indicating initial single-spore colonisation and subsequent multiple colonisation events with increasing population age (Schneller & Holderegger 1996).

Ferns are found in many habitats in the Netherlands, especially in woodlands and on walls (Chapter 2). Disturbance plays an important role in the establishment phase. Small-scale disturbances supply micro-habitats for germinating spores. Ferns have been described as “plants which grow in sites where angiosperms most fear to tread” (Page 2002). Demographic studies on ferns are scarce (Montgomery 1990, Gureyeva 2003) and prior to the research described in this thesis, no such study had ever been carried out in the Netherlands.

Research questions and outline of the thesis

This thesis sets out to answer four main questions.

What is the distribution and habit preference of fern species and what trends have taken place in population sizes?

This question is discussed as in Chapter 2. There is a long tradition of collecting floristic data in the Netherlands, including data on *Pteropsida*. Since 1975 the occurrence of species has been recorded per km² grid cell (Groen & Slikke 2000). These data are essential for nature conservation and the protection of species. The resulting database (Florbase²) enables periods to be compared after correcting for differences in survey intensity (Tamis 2005). Also Provincial Boards have build up even more accurate databases. More accurate studies of population trends are scarce, however. Within the *Pteropsida*, such studies have focused on wall species (Maes & Bakker 2002). Extensive surveys on distribution and habitat preference of the *Pteropsida* at a national scale have been assembled by Page (1982) for the UK and by Bennert (1999) for Red List species in Germany. In both publications, little attention has been paid to changes in population size, due to the lack of national long-term monitoring of populations.

What environmental factors allow ferns to succeed in colonising new habitats?

The reclamation of the polders in the former Zuiderzee offered the opportunity to study colonisation by various groups of organisms. In three of the four polders created, the development of flora and vegetation before the reclaimed land was taken into cultivation was documented (Feekes 1936, Feekes & Bakker 1954, Mook *et al.* 1995); this revealed the roles played by water, wind and humans in dispersal. Post-cultivation colonisation by microfungi has been studied on polder farmland (Pugh & van Emden 1969, de Vries *et al.* 1979, van der Aa 2000), while in polder woodlands the colonisation of bryophytes (Bremer & Ott 1990) and macrofungi (van Zanen *et al.* 2000) has been monitored. Lichen colonisation of roadside trees in the polders has also been studied (Bremer 1989). These studies on spore-producing plant groups revealed that long-distance dispersal takes place and that in recently reclaimed polders species

² based on data collected by volunteers and professional organisations (e.g. provinces, nature conservation organisations).

have been able to occupy habitats in which they had not previously been recorded in the Netherlands.

The establishment of many rare ferns in the Kuinderbos was the incentive to study fern colonisation. Various questions arose about the ecology and dispersal of these species: What are the environmental preferences of the rare fern species? Has the environmental preference of these fern species changed within the observation period of 25 years? Is it possible to reconstruct the colonisation and what is the role of the dispersal capacity of the various species? These questions are addressed in Chapter 3.

A second study, described in Chapter 4, examined the colonisation of woodlands on clay soils in the Flevoland polders. The study focused on landscape-scale factors and included other characteristic woodland species. The research questions were: What factors determine the colonisation by woodland species, particularly ferns? What habitats do ferns prefer? How rapidly do ferns colonise newly planted woodlands on clay soils and why is there a difference between the woodland fern flora in the Flevoland polders and on the Dutch mainland? It was hypothesized that fern species would be earlier colonisers than seed plants characterising the woodland. In a third study, described in Chapter 5, the ecological requirements of one particular species – *Gymnocarpium dryopteris* – in the Kuinderbos are compared with the requirements of populations in other parts of the Netherlands.

What abiotic and biotic factors determine the long-term demography of fern populations?

There have been only a few long-term studies on the demography of ferns (Willmot 1984, Cinquemani-Kuehn & Leopold 1992, Gureyeva 2003). Some species with an Atlantic distribution, e.g. *Asplenium scolopendrium* and *Polystichum setiferum*, live in the Kuinderbos at the edge of their range, with the risk of frost damage. To study the effect of frost damage, data must be available for long periods that include years with different numbers of frost days. A dominant operational factor in woodlands is the light climate. Its effect on population parameters can also only be quantified by long-term monitoring. We analysed the effects of frost and light intensity and in addition other factors that play a role. In Chapter 6 of this thesis, a long-term study on *Asplenium scolopendrium* is presented and in Chapter 7 on *Gymnocarpium dryopteris*.

What effect does woodland management have on the dynamics of fern populations?

Chapter 7 focuses on the impact of woodland management on ferns. The traditional way of managing woodland was a thinning regime that ended with clear-cutting (Oldeman 1989, Hunter 1999). There is limited information relating harvest practices to understory and overstory conditions in managed forests (Halpern & Spies 1995, Thysell & Carey 2000, Bergstedt & Milberg 2001). In the Kuinderbos the woodland management focuses on thinning. This method has been used since about 1985 to stimulate the regeneration of commercial trees. Because it was expected that the light climate would have an impact on ferns, two thinning experiments were carried out. In the Voorsterbos (see Fig. 1.1), by contrast, thinning has been more extensive since 1997. As the stands mature, less light reaches the woodland floor. In order to mimic natural processes and to achieve an uneven-aged regeneration mosaic (Koop 1989), 56 gaps were cut in the period 2000 – 2006. Fern colonisation in a selection of gaps was monitored (Bremer 2007).

History of the study

The data discussed in this thesis were collected in the period 1977 - 2007. Some of the thesis chapters are based on previously published work. The inspiration for the research that ultimately resulted in this PhD thesis was the discovery of many rare fern species in Kuinderbos in 1977. In 1979 I was able to investigate the ecology of ferns growing in this forestry as part of my degree in biology at the University of Groningen. In subsequent years I carried out a monitoring study that focused on the ecology and demography of ferns. In 1990 I surveyed the flora and vegetation in the Kuinderbos for Staatsbosbeheer, the national agency that owns the area. This study included also the fern flora (Bremer 1994). A similar study on gap formation in the Voorsterbos was carried out for another national nature conservation organisation (Natuurmonumenten, Bremer 2007). In addition to the study in the Kuinderbos, my study of ferns broadened to include other woodlands in Flevoland and also other woodland species, including bryophytes, lichens, seed plants and macrofungi (Bremer 1989, Bremer & Ott 1990, Bremer *et al.* 2007).

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The distribution, habitat preference and-trends within the fern flora (*Pteropsida*¹) of the Netherlands



Blechnum spicant and *Oreopteris limbosperma* at deep drainage trench bank in the vicinity of Dalfsen (estate Den Berg).

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¹ *Equisetaceae* excluded

Abstract

In the Netherlands 39 species of *Pteropsida* (*Equisetaceae* excluded) were reported during the period 1991 to 2000. Species were most numerous in cities, especially Amsterdam, where ferns grow in the walls alongside canals. Fern species were also numerous in the young woodlands of Flevoland, particularly in the Kuinderbos, where ferns have established on the calcareous sandy banks of drainage trenches. The number of species in the Netherlands has increased over the last 30 years due to afforestation (e.g. the woodlands in Flevoland), a number of mild winters a more intensive survey of canal walls and. The positive trend in 69% of the fern species has also to be attributed to habitat creation from arable fields, ageing of habitats and the strong decrease in SO₂ pollution. Populations of certain species, e.g. *Botrychium lunaria*, have decreased because of N deposition. Wall species, even those protected by law, have suffered as a result of wall restoration. Some species (e.g. *Polystichum lonchitis*, *Marsilea quadrifolia*) have had to bridge a gap of hundreds of kilometres to establish themselves in the Netherlands. Ferns have been found in 75 plant communities. The population size of the various species ranges from some plants (e.g. *Polystichum lonchitis*) to millions of plants (e.g. *Dryopteris dilatata*).

Introduction

This chapter deals with the current distribution and habit preference of fern species in the Netherlands and the trends that have taken place in population sizes. Botanical surveys are a well-established tradition in the Netherlands; they were initiated by the National Herbarium. After FLORON was established in 1988, the studies became more intensive. FLORON coordinates and stimulates volunteers to collect floristic data and has compiled a large database of botanical records, including those on fern species, based on 1 x 1 km grid cells (Florbase¹) (Groen & Slikke 2000). Provincial boards have been systematically mapping species, including ferns, at large scale since 1975 (IAWM 1998). These data can be used to analyse distribution in detail.

Though information about habitat preference has always been included when recording the Dutch flora, it is not based on systematic data collecting (e.g. van der Meijden 2005). Habitats have been studied by provincial boards, which have linked distribution with habitat types, thereby creating a system of habitat types to be used in their mapping projects (the so-called habitat types called IPIs: see IAWM 1985). Habitat preference has been analysed in detail in Drenthe (WFD 1999) and Overijssel (this chapter).

Within Florbase it is possible to compare periods, after correcting for differences in survey intensity (Tamis 2005). More detailed studies of population trends within ferns are scarce, however. Within the *Pteropsida*, such studies have focused on wall species (Maes & Bakker 2002) and the woodlands of Flevoland (Chapters 3, 4). In this chapter, trends are reviewed and related to changes in habitats (e.g. desiccation, atmospheric deposition).

In other countries there have been extensive surveys on the distribution and habitat preference of the *Pteropsida* on a national scale: see Page (1982) for the UK and Bennert (1999) for Red List species in Germany. The lack of (national) long-term monitoring of populations means that both publications pay only limited attention to changes in population size.

From 1950 to 2000, there were 170 publications on fern species in the Netherlands. Most of these studies were done by amateurs; others were done by researchers from Dutch universities (e.g. Segal 1962, Meinders-Groenveld & Segal 1967, Segal 1969, den Ouden 2000). These studies have been taken into account when writing this chapter.

The distribution of ferns

Figure 2.1, based on Florbase, shows the number of fern species in 5 x 5 km grid cells in the Netherlands. The areas poor in ferns are confined to clay and peat soils in the lower-lying part of the country, where suitable habitats (walls, woodlands etc.) are sparse. On the higher sandy part of the Netherlands there are 10 - 14 fern species per grid cell. Grid cells containing over 14 species are found in the eastern part of Overijssel, in the Kuinderbos, in some cities (e.g. Amsterdam, Haarlem) and in the southern part of Limburg. The largest number per grid cell of species (20) was recorded in the Kuinderbos.

In some of the cities, ferns are found growing on canal walls. Figure 2.2 depicts the number of calcicole fern species per 5 x 5 km grid cell. These ferns are concentrated exclusively in certain cities – with the maximum number in Amsterdam – and in the Kuinderbos. Most calcicole species were recorded growing on walls, but some were also found on the woodland floor or at banks of drainage trenches.

¹ Florbase is based on data collected by provincial boards, volunteers, nature conservation organisations and institutes.

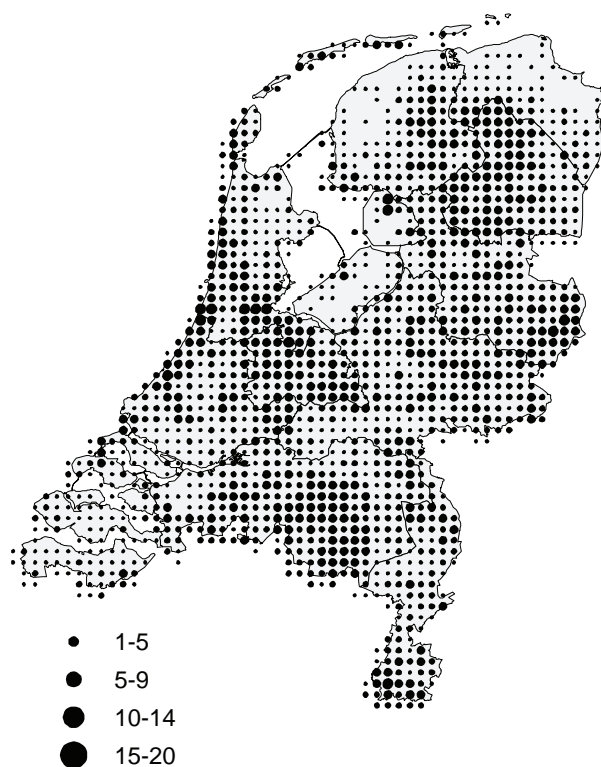


Figure 2.1. The number of fern species (*Pteropsida*, *Equisetaceae* excluded) per 5 x 5 km grid cell in the Netherlands (1975 - 2000) (based on FLORON/ Florbase; database based on data collected by professional organisations and volunteers).

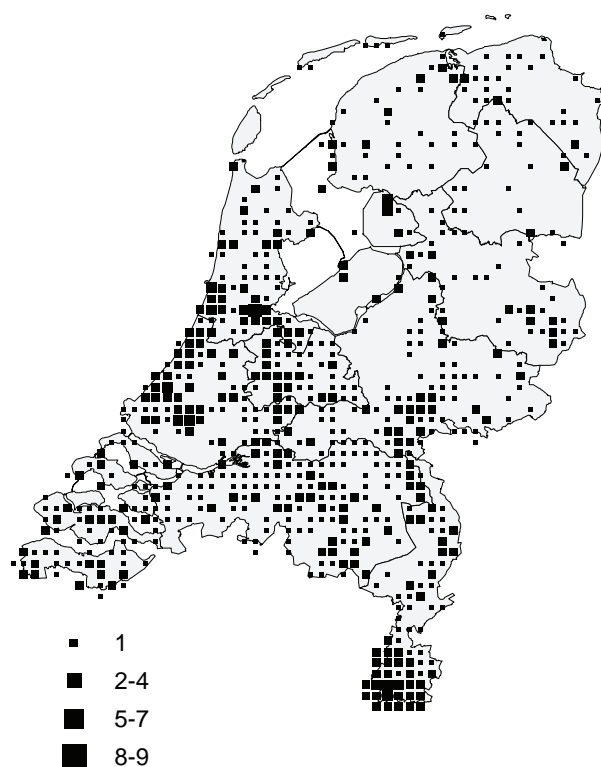


Figure 2.2. The number of calcicole species (*Pteropsida*, *Equisetaceae* excluded) per 5 x 5 km grid cell in the Netherlands (1975 - 2000) (based on FLORON/ Florbase).

Table 2.1. The ferns (*Pteropsida*, excluding *Equisetaceae* and including all fern species except for some recent garden escapes) in the Netherlands (nomenclature based on van der Meijden 2005). **First record:** first year of recording (with reference) is only mentioned for species that established after 1950. In brackets, the year of rediscovery. **RL:** classes based on van der Meijden *et al.* (2000); NT = Near Threatened, V = Vulnerable, E = Endangered, D = Disappeared. **1900 - 1950:** number of 1 x 1 km grid cells occupied in the period 1900 – 1950, based on FLORIVON (*n* = number of grid cells not determined), **1975 – 1998:** number of 1 x 1 km grid cells occupied in 1975 – 1998, based on Floribase. **Tr1:** trend in % between both periods, based on 7374 1 km grid cells surveyed in both periods. **Tr2:** trend based on Tr1 and recent data (e.g. data collected in the province of Overijssel), - negative, ? unknown, + positive. **NH₃:** -- = species negatively influenced by N deposition, + = species positively influenced by N deposition. **Ac:** -- = species negatively influenced by acid precipitation, **Hb:** habitat creation or restoration: + = species positively influenced by creation or restoration of habitats.

Scientific name	First record	RL	1900-1950	1975-1998	Tr1	Tr2	NH ₃	Ac	Hb
<i>Asplenium adiantum-nigrum</i> L.			1	42		+	.	--	.
<i>Asplenium ceterach</i> L.		NT	5	12	-60	-	.	.	.
<i>Asplenium fontanum</i> (L.) Bernh.	1988 (Denters 1990a) ²		0	1	
<i>Asplenium foreziense</i> Le Grand	1988 (Nieuwkoop & Spronk 1989)		0	1		+	.	.	.
<i>Asplenium ruta-muraria</i> L.			426	1023	59	+	.	.	.
<i>Asplenium scolopendrium</i> L.			18	267		+	.	.	.
<i>Asplenium septentrionale</i> (L.) Hoffm.	1990 (Knotters & Bremer 1991)		0	2		-	.	.	.
<i>Asplenium trichomanes</i> L.			51	189		+	.	--	.
<i>Asplenium viride</i> Huds.	1979 (Bremer 1981) ³	NT	0	2		+	.	.	.
<i>Athyrium filix-femina</i> (L.) Roth			<i>n</i>	6109		+	.	.	+
<i>Azolla filiculoides</i> Lam.			<i>n</i>	3116		+	+	.	.
<i>Azolla cristata</i> Kaulf.		D	400	0	-99	-	.	.	.
<i>Blechnum spicant</i> L.		NT	3024	1119	-63	-?	.	--?	+
<i>Botrychium lunaria</i> (L.) Swartz		V	300	200		-	--	.	.
<i>Cyrtomium falcatum</i> (L.f.) C. Presl.			<i>n</i>	6		+	.	.	.
<i>Cystopteris fragilis</i> (L.) Bernh.		E	66	30	-50	-	.	.	.
<i>Dryopteris affinis</i> (Lowe) Fr. Jenkins	Bremer 1998a ⁴		2	31		+	.	.	.
<i>Dryopteris carthusiana</i> (Vill.) H.P. Fuchs			<i>n</i>	10452		+	+	.	+
<i>Dryopteris cristata</i> (L.) A. Gray			194	896	95	+	.	.	.
<i>Dryopteris dilatata</i> (Hoffm.) A. Gray			<i>n</i>	11747		+	+	.	+
<i>Dryopteris expansa</i> (C. Presl) Fraser-Jenk. & Jermy	1988 (Hovenkamp <i>et al.</i> 1990)		0	3		+	.	.	.
<i>Dryopteris filix-mas</i> (L.) Schott			<i>n</i>	6635		+	.	.	+
<i>Gymnocarpium dryopteris</i> (L.) Newm.			33	91	-12	+	.	.	.
<i>Gymnocarpium robertianum</i> (Hoffm.) Newm.		NT	10	14	-67	-	.	.	.
<i>Marsilea quadrifolia</i> L.	1998 (Drok & Weeda 1999) ⁵		0	1		+	.	.	+
<i>Matteuccia struthiopteris</i> (L.) Tod.	1987 (Bremer 2005)		0	1		+	.	.	.
<i>Ophioglossum vulgatum</i> L.			123	337	44	+	.	.	.
<i>Oreopteris limbosperma</i> (All.) Holub			22	46	15	+	.	.	+
<i>Osmunda regalis</i> L.			<i>n</i>	2228		+	.	.	+
<i>Phegopteris connectilis</i> (Michaux) Watt			23	36	5	+	.	.	.
<i>Pilularia globulifera</i> L.			80	162		+	.	.	+
<i>Polypodium interjectum</i> Shivas			<i>n</i>	224		?	.	.	.
<i>Polypodium vulgare</i> L.			<i>n</i>	3656		?	.	--	.
<i>Polystichum aculeatum</i> (L.) Roth		NT	16	14	156	+	.	.	.
<i>Polystichum lonchitis</i> (L.) Roth	1979 (Bremer 1981)	NT	0	3		+	.	.	.
<i>Polystichum setiferum</i> (Forssk.) Woynar	1957 (1980) (Bremer 1980)	NT	1	12		+	.	.	.
<i>Pteridium aquilinum</i> (L.) Kuhn			<i>n</i>	4081		+	.	.	.
<i>Salvinia natans</i> (L.) All.			2	0		-	.	.	.
<i>Thelypteris palustris</i> Schott			<i>n</i>	1013		?	.	.	+

² Plants disappeared in 1992 due to habitat destruction

³ In Amsterdam since 2000 (data T. Denters).

⁴ First recorded in the Netherlands in 1874. For a long time this species was assigned as *Dryopteris x tavelii*. Data on distribution and taxonomy were reviewed in Bremer (1988a).

⁵ In 2006 also found along a brook in the vicinity of Venray (leg. F. Reijerse/T. Verrijdt)

The establishment of previously unrecorded species

Figure 2.3 depicts the number of fern species known from the Netherlands during the period 1931 – 2000 (see also table 2.1). An increase was reported around 1980, following the discovery of many previously unknown species in planted woodlands in Flevoland, especially in the Kuinderbos. *Asplenium viride* and *Polystichum lonchitis* were found growing on trench banks of fine-grained calcareous sand (Bremer 1981), while *Polystichum setiferum* and *Dryopteris affinis* were rediscovered after having been absent from the Netherlands for many years (Bremer 1980, Bremer 1988a, Bremer & Koopman 1994, Bremer 1995). Since 1980, more attention has been paid to ferns growing on walls in cities, especially on canal walls. In 1988 *Asplenium foreziense* was discovered along a canal in the south of the Netherlands (Nieuwkoop & Spronk 1989). *Asplenium fontanum* was found on a quay in the port of Amsterdam, some 600 kilometres outside its previously known range in southern Germany and France (Denters 1990a), but it subsequently disappeared due to habitat destruction. *Dryopteris expansa* may have been overlooked for many years. It was discovered in 1988 by the Belgian pteridologist R. Viane in Drenthe (Hovenkamp *et al.* 1990) in a young woodland on boulder clay. *Asplenium septentrionale* was first reported in 1990 (Knotters & Bremer 1991); it was reported again in 2000, also on a canal wall (Andeweg *et al.* 2001) but subsequently disappeared due to desiccation (data R. Andeweg). *Marsilea quadrifolia* was sighted on the bank in a foreland of the river Waal, 190 km north of its nearest previously known locality. These specimens were found in the *Eleocharito acicularis-Limoselletum*, a moderately eutraphent pioneer vegetation of clayey banks that are drying out. They appeared in a abandoned clay pit (Drok & Weeda 1999). The transformation of hundreds of hectares of farmland along Dutch rivers into wetlands has enlarged the area for the *Eleocharito acicularis-Limoselletum*, increasing the probability of establishment. Since this species is susceptible to frost, the mild winters over the last 10 years may have aided its establishment. In 2006 it was found along a brook in the vicinity of Venray.

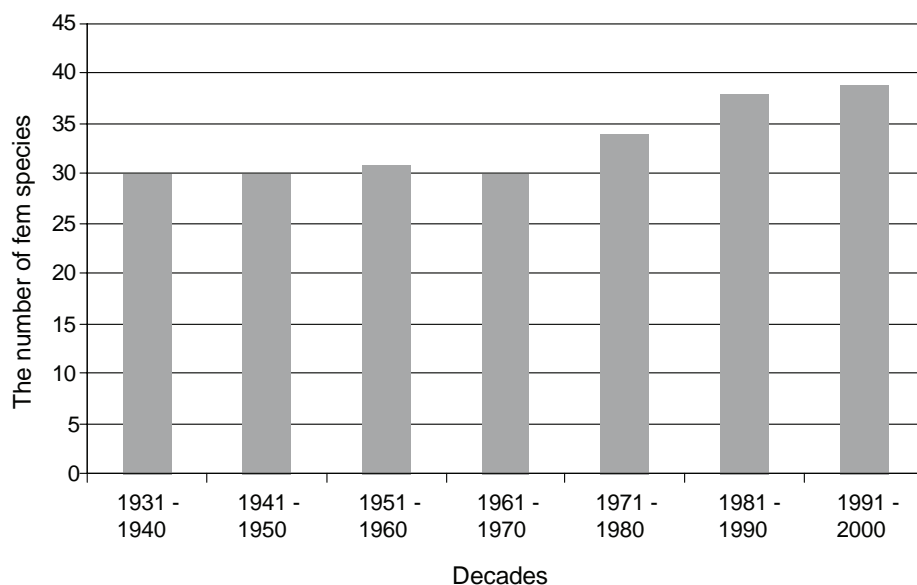


Figure 2.3. The number of fern species (*Pteropsida*, *Equisetaceae* excluded) recorded per decade in the Netherlands.

Table 2.2. Habitats, plant communities and population size in the group of Dutch ferns. **H:** most important habitats in the Netherlands, d = (north-facing) dunes, di = banks of drainage trenches, ditches or other elements with water, gr = grasslands, ma = marshes, p = pollard willows, wa = walls, wb = wooded banks, wo = woodlands/forests. **Diagnostic for communities:** plant community for which species is mentioned as diagnostic (based on Schaminée *et al.* 1995, 1998, Stortelder *et al.* 1999). **Com:** the number of communities in which the species can be found (based on Schaminée *et al.* 1995, 1998, Stortelder *et al.* 1999). **Phr:** phreatophyte, a = aphreatophyte, not associated with the water table, f = phreatophyte; influenced by the water table, h = species living in water, of = obligate phreatophyte = species wholly dependent on the influence of the water table, i = species dependent on inundation, f(a) = phreatophyte, sometimes living under aphreatophytic conditions (according to Londo 1988 and personal observations). **N:** population size. The maximum number of individuals counted in the period 1980–2000. **n:** population size in classes: 1 = 1 – 10, 2 = 11 – 50, 3 = 51 – 100, 4 = 101 – 500, 5 = 501 – 1000, 6 = 1001 – 10⁴, 7 = 10⁴ – 10⁵, 8 = 10⁵ – 10⁶, 9 = > 10⁶ individuals/patches/colonies in the Netherlands, ? = numbers unknown

Scientific name	H	Diagnostic for communities	Com	Phr	N	n
<i>Asplenium adiantum-nigrum</i>	wa	-	2	a		5
<i>Asplenium ceterach</i>	wa	-	1	a		3
<i>Asplenium fontanum</i>	wa	-	-	a	2	1
<i>Asplenium foreziense</i>	wa	-	-	a	2	1
<i>Asplenium ruta-muraria</i>	wa	<i>Asplenietum ruto-murario-trichomanes</i>	4	a		8
<i>Asplenium scolopendrium</i>	wa, wo	<i>Filici-Saginetum</i>	2	f(a)		7
<i>Asplenium septentrionale</i>	wa	-	-	a	1	1
<i>Asplenium trichomanes</i>	wa	<i>Asplenietum ruto-murario-trichomanes</i>	4	a		6
<i>Asplenium viride</i>	wa	-	-	a	16	2
<i>Athyrium filix-femina</i>	wo, di, ma	-	6	f(a)		9
<i>Azolla filiculoides</i>	di	<i>Wollfia-Lemnetum gibbae azolletosum caroliniana</i>	3	h		9
<i>Azolla cristata</i>	di	<i>Lemno-Spirodeletum polyrhizae azolletosum caroliniana</i>	3	h		?
<i>Blechnum spicant</i>	wo, di	-	2	f(a)		7
<i>Botrychium lunaria</i>	gr	<i>Botrychio-Polygaletum</i>	2	a		?
<i>Cyrtomium falcatum</i>	wa	-	-	a		1
<i>Cystopteris fragilis</i>	wa	-	2	f(a)		4
<i>Dryopteris affinis</i>	wo	-	-	f	255	4
<i>Dryopteris carthusiana</i>	wo, di, ma	<i>Stellario-Carpinetum dryopteridetosum</i>	34	f(a)		9
<i>Dryopteris cristata</i>	ma	-	7	of		8
<i>Dryopteris dilatata</i>	wo, ma, di	<i>Betulo-Quercetum roboris dryopteridetosum</i>	35	a		9
<i>Dryopteris expansa</i>	wo	-	-	f	6	1
<i>Dryopteris filix-mas</i>	wo, di	<i>Stellario-Carpinetum</i>	23	f(a)		9
<i>Gymnocarpium dryopteris</i>	wo, di	-	-	f(a)	670	5
<i>Gymnocarpium robertianum</i>	wa	-	1	a		2
<i>Marsilea quadrifolia</i>	ma	-	-	i	3	1
<i>Matteuccia struthiopteris</i>	wo	-	-	f	7	1
<i>Ophioglossum vulgatum</i>	gr, d	-	2	of		6?
<i>Oreopteris limbosperma</i>	wo di	<i>Luzulo-Thelypteridetum</i>	-	f		5
<i>Osmunda regalis</i>	ma di	-	-	f(a)		7
<i>Phegopteris connectilis</i>	wo di	-	-	f(a)		3
<i>Pilularia globulifera</i>	di	<i>Pilularietum globuliferae</i>	7	i		6
<i>Polypodium interjectum</i>	p, d ⁶	-	1	a		6
<i>Polypodium vulgare</i>	wb, wo, d	-	14	a		7
<i>Polystichum aculeatum</i>	wo	<i>Stellario-Carpinetum polystichetosum</i>	1	f(a)		6
<i>Polystichum lonchitis</i>	wo	-	-	f	8	1
<i>Polystichum setiferum</i>	wo	-	1	f(a)	135	4
<i>Pteridium aquilinum</i>	wo	<i>Fago-Quercetum</i>	12	a		?
<i>Salvinia natans</i>	di	-	-	h		?
<i>Thelypteris palustris</i>	wo, ma	<i>Typho-Phragmitetum thelypteridetosum</i> <i>Thelypterido-Alnetum</i>	13	of		?

⁶ Based on collection of the National Herbarium at Leiden, with 33% of plants collected from pollard willows and 26% in dune habitat (n = 72).

The most important habitats

Of the 39 species sighted, 23 were recorded growing on walls. Five species, such as *Asplenium ruta-muraria* and *Asplenium ceterach*, are restricted to walls (Table 2.2). Wall ferns have received much attention in the past 15 years (Denters 1990b, Maes & Bakker 2002). Amateurs and professionals have mapped this group of ferns in all the large cities in the lower-lying part of the Netherlands (e.g. Andeweg 1994, Douwes *et al.* 1999). In most cities, rare species are found, sometimes in large numbers. Amsterdam appears to be the richest in species and number of individuals. Here 18 fern species have been found in the period 1980 - 2000, including rarities like *Asplenium ceterach*, *Asplenium viride* and *Cystopteris fragilis* (Denters 1990b) (Table 2.3.). At the turn of the 19th to the 20th century, the localities with *Asplenium adiantum-nigrum* were mainly terrestrial. During the 20th century the species became nearly totally extinct in this habitat. This loss has been compensated for by an increase in sightings on old walls, especially in the west of the Netherlands (Denters 1997).

Twenty-seven species are found in woodlands. These species occur mainly on the higher-lying sandy soils, which frequently are strongly acidified and species-poor. *Dryopteris dilatata* is the most common species here. In the woods on loamy soil, as well as in the south of the Netherlands, *Polystichum aculeatum* and *Dryopteris affinis* are found. The young woods in Flevoland, planted on land reclaimed from the sea, are rich in species. Fern colonisation in this area has been surveyed and monitored in some woodlands. Monitoring started in 1977 in the Kuinderbos; in the woodlands near Lelystad, it started in 1979 (Bremer 1988b, Smit 1989). Through demographic analysis it has been possible to reconstruct the colonisation in the Kuinderbos (see Chapter 3).

In Overijssel (Fig. 1.1) the distribution of over 600 plant species, including 15 fern species, has been mapped per 50-metre transect (50 x 2 - 4 m) since 1989. This detailed mapping was performed by visiting 1 x 1 km grid cells and surveying at least 100 50-metre transects in all kinds of habitats. Table 2.4 gives an overview of the most important habitats for six most common fern species. All these species show marked preference for one or more habitats. *Blechnum spicant* prefers trench banks (which are often shady). Most of the stands of *Pteridium aquilinum* are found in deciduous woodlands, but patches sometimes occur in coniferous woods. *Polypodium vulgare* achieves its optimum on wooded banks, within woodlands or bordering fields. The distribution of *Athyrium filix-femina* in the eastern part of Overijssel matches the distribution of natural brooks. In the north-western part of this province the species tends to be more concentrated in marshes and ditches than it is in the south-eastern part of the province (Fig. 2.4). The pattern in the latter area corresponds with the distribution of syntaxa characteristic of wet habitats (e.g. *Alno-Padion*).

Vegetation

Since 1985 the vegetation of the Netherlands has been surveyed in detail. 226 plant communities have been distinguished (e.g. Schaminée *et al.* 1995a,b, Schaminée *et al.* 1996, Stortelder *et al.* 1999). Fourteen of the 39 fern species are diagnostic of one or more of these communities (Table 2.2). *Asplenium trichomanes* and *Asplenium ruta-muraria* characterise the wall-bound *Filici-Saginetum*. The *Botrychio-Polygaletum* is a grassland community confined to calcareous dunes, which is characterised by *Botrychium lunaria*. *Thelypteris palustris* is a diagnostic species for alder woodland (*Thelypterido-Alnetum*) and reed beds (*Typho-Phragmitetum thelypteridetosum*). *Azolla filiculoides* characterises the *Wolffio-Lemnetum gibbae*, forming mats several centimetres thick that prevent ditches from freezing over in winter (Schaminée *et al.* 1995b). In a database of 10,000 selected vegetation relevés.

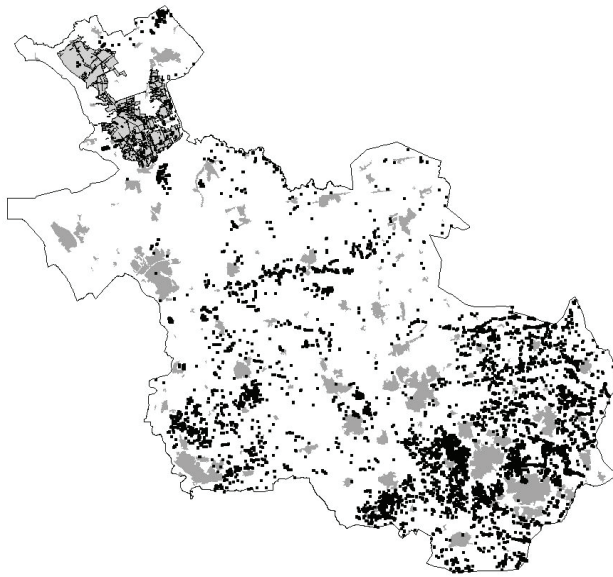


Figure 2.4. The distribution of *Athyrium filix-femina* in the province of Overijssel based on surveying 50-m transects in the period 1984 – 2006 (grey: marshes in the north-west which were incompletely surveyed, the same holds for cities and villages). The distribution pattern in the north-east part of the province matches the distribution of brooks

Table 2.3. The number of fern species recorded in cities and in the woodlands of Flevoland (total number of species 1980 – 2000)

area	area (km ²)	Number of fern species	References
cities (central areas)			
Amsterdam	c. 20	18	Denters (1990b)
Haarlem	c. 5	13	Denters (1991)
Utrecht	c. 5	10	Maes & Bakker (2000)
Rotterdam	c. 25	10	Andeweg (1994)
Groningen	c. 2	8	Douwes <i>et al.</i> (1999)
planted woodlands in Flevoland (former sea-floor)			
Kuinderbos	11	25	Chapter 3
Roggebotzand–Reve–Abbert	15	14	
Voorsterbos–Waterloopbos	7	14	Bremer (2001b)
Lelystad	6	12	Smit (1989)

ferns appeared to be present in 75 plant communities. In nearly all of these communities the probability of finding a fern species is at least 1 %. The communities richest in fern species are the *Filici–Saginetum* and *Asplenietum ruto-murario-trichomanes*: they have 14 species in all examined plots. There are some woodland communities with five or more species, the *Fago–Quercetum* being richest in fern species (e.g. *Pteridium aquilinum*). Some species are confined to one community: *Asplenium ceterach*, for example, is confined to the *Asplenietum ruto-murario-trichomanes*. Most species have an optimum in one community but can be found in others as well. *Dryopteris filix-mas* has its optimum in the *Stellario-Carpinetum*, but it has been found in 23 communities, mainly in woodlands. *Dryopteris carthusiana* and *Dryopteris dilatata* appear to have the widest distribution. Both have been found in more than

30 communities and are sometimes diagnostic at the sub-association level. Recently the *Luzulo luzuloides-Thelypteridetum limbospermae* has been found in various sites, mostly on

Table 2.4. The preference for various habitats of 6 fern species in the province of Overijssel based on 265,864 50-metre transects (flora survey 1984 – 2002). **Bsp** = *Blechnum spicant*, **Ore** = *Osmunda regalis*, **Af** = *Athyrium filix-femina*, **Paq** = *Pteridium aquilinum*, **Dfm** = *Dryopteris filix-mas*, **Pve** = *Polypodium vulgare*. Statistical analysis by χ^2 *** = $p < 0.001$

		Bsp		%	Ore		%	Af		%	Paq		%	Dfm		%	Pve		%
Habitats	<i>No. of</i>	% <i>transects</i>																	
Ditches/ trenches*	113846	42.8	271	81.9	243	57	2541	48	352	9.6	439	31	91	8.5					
Deciduous woods	28626	10.8	21	6.3	36	8.5	915	17	1562	43	329	23	298	28					
Wooded banks	24566	9.2	4	1.2	46	11	390	7.4	770	21	291	21	527	49					
Brooks	4885	1.8	17	5.1	3	0.7	637	12	76	2.1	32	2.3	11	1					
Coniferous woods	18129	6.8	6	1.7	9	2.1	57	1.1	356	8.7	73	5.1	89	8.3					
Open water (edge)	5983	2.2	1	0.1	39	9.2	83	1.6	9	0.1	25	1.8	0	0					
Grassland	9029	3.3	0	0	5	1.2	33	0.6	3	0.1	17	1.2	0	0					
Other habitats	60800	22.9	11	3.3	44	10	614	12	538	15	212	15	54	5					
total no. of transects	265864	99.8	331	100	425	100	5270	100	3666	100	1418	100	1070	100					
χ^2		***		***		***		***		***		***							

* these include also drainage trenches in woodlands, sometimes assigned to the woodland habitat.

trench sides in open coniferous woodlands on heath soils This community is characterised by *Oreopteris limbosperma* and *Blechnum spicant* (Bremer *in prep.*).

Population changes

Habitat loss - Changes in the Dutch flora have first of all been attributed to habitat loss (Weeda 1985). The closure of salt water areas (Zuiderzee, SW-part of the Netherlands, Lauwerszee) meant the loss of sites with halophytic seed plant. At the other hand glycophytes colonised embankments and dikes, including numerous fern species. 94.2% of the Dutch bogs have been destroyed, with the loss of very characteristic habitats for various groups of plants and animals, but with no effect on ferns, as these were not found in this habitat. Restoration of walls did have most negative effects on fern species and still has this effect, but more recently protection efforts proved to be more effective (Denters 2005). However, there are still recent examples of habit loss by destruction of old walls (e.g. *Asplenium trichomanes* near Kamperzeedijk in 2006).

Atmospheric deposition - Until well into the 1980s there was heavy SO₂ deposition in the Netherlands, which adversely affected various groups of plants. The SO₂ acidified ponds, negatively affecting the algae (e.g. Roelofs 1986). The establishment and growth of many lichen species were hampered by SO₂ (Barkman 1958, de Wit 1976, van Dobben 1993). In bryophytes, infertility and reduced vitality have also been attributed to SO₂, while the recovery of epiphytic bryophytes correlates with the decrease in SO₂. Van Dam *et al.* (1986) found a strong inverse correlation between the percentage recovery in species distribution and the SO₂ 95 percentile in ten vascular species including *Polypodium vulgare*. Percentage recovery was defined as the percentage of the 5 x 5 km grid cells in which a species was present in 1950 - 1980 as compared with its presence before 1950. *Blechnum spicant* has also decreased markedly over the past 50 years (by 63%, Table 2.1), probably due to high SO₂ levels. Since

1985 there has been a strong decrease in SO₂ levels, with *Asplenium trichomanes* and *A. adiantum-nigrum* profiting (cf. Edgington 2003).

Intensive livestock farming caused concentrations of ammonia in the air to increase from 1960 onwards. The problem was finally acknowledged around 1980 (Berendse & Aerts 1984, van der Knaap 1984). Natural habitats are influenced by high levels of nitrogen deposition. Such deposition has had a profound impact on communities of nitrogen-poor habitats (eutrophication). The nitrification of airborne ammonium also contributes to the acidification of soils (van Breemen *et al.* 1982). Woodlands on sandy soils are strongly influenced by both processes. Sometimes the pH in the topsoil falls to below 3.0. Dirkse (1998) found an increase in *Dryopteris carthusiana*. In stands of Scots pine (*Pinus sylvestris*) there was a positive correlation between the shift in cover between 1984 and 1993 and the NH₃ concentration in the atmosphere in 1993. Boxman *et al.* (1998) experimentally showed *Dryopteris dilatata* to be a nitrophilous species, which decreased significantly after stopping the atmospheric N-input in a Scots pine stand. The Dutch national vegetation monitoring scheme was started in order to evaluate the overall effectiveness of the policy measures related to eutrophication, desiccation and acidification. Since the start of this monitoring in 1999 data are available for two four-year rounds with 10,000 fixed plots (permanent quadrats) (van Duuren *et al.* 2007). A first analysis confirmed a positive significant trend in *Dryopteris dilatata* and *Dryopteris filix-mas*.

Table 2.5. Relation of fern species with changes in land use and processes in the 20th century in the Netherlands. Fern species: n = the (minimum) number of fern species involved, RL = the (minimum) number of Red List fern species involved, based on van der Meijden *et al.* (2000). In this table also data of *Adiantum* species were included.

	Fern species			
	negative		positive	
	n	RL	n	RL
Habitat destruction				
Closure of salty lakes	0	0	6	0
Embankment IJsselmeerpolders (pre-cultivation) ¹	0	0	0	0
Cultivation of bogs (→ arable fields)	0	0	0	0
Cultivation of heaths (→ arable fields)	1	1	0	0
Wall restoration	6	2	0	0
Processes				
Ammonia deposition	1	1	2 - 3	0
Acidification	4	1	0	0
Decrease SO ₂ concentration ²	0	0	4 - 5	1
Lowering of water table (desiccation)	3	0	5	0
Ageing of habitats	0	0	5	0
Climatic change	0	0	8	1
Habitat creation				
Afforestation (from arable fields, former bog/heaths)	0	0	14	1
Afforestation (Zuiderzeepolders) ³	0	0	27	7
Habitat creation from arable fields ⁴	0	0	10	1

¹ = based on Feekes & Bakker (1954), Jans & Drost (1995), ² = decrease from 20 µg m⁻³ in 1985 to 2 µg m⁻³ in 2005, ³ = based on this thesis,

⁴ = based on data collected in Overijssel/Flevoland

Botrychium lunaria disappeared from a canal bank because the vegetation became more luxuriant. Because this vegetation was mown late, nutrients were hardly removed though atmospheric N deposition continued. Recently, restoration experiments have been started, involving the removal of topsoil and earlier mowing (Horsthuis 2002). *Botrychium lunaria* belongs to the group of species characterising heath grasslands, which have severely suffered from acidification and eutrophication (Roelofs *et al.* 1996).

Changes in hydrology - In the last 50 years a major part of the Netherlands has been drained to meet the needs of agriculture. As a result, the groundwater levels in spring may nowadays be 30 - 100 cm lower than before (Runhaar 1999). Although designated nature areas have not been drained, plant communities that required high groundwater levels and were surrounded by farmland have suffered greatly. Seepage of upwelling groundwater diminished and the impact of acid rain increased. A small number of Dutch fern species grow in wet habitats. *Thelypteris palustris* is restricted to such habitats (Table 2.2). Fortunately, most of the large marshes have been designated as nature reserves, which has safeguarded its habitat. The same holds true for *Dryopteris cristata*. This species prefers acidified reed beds (young bog

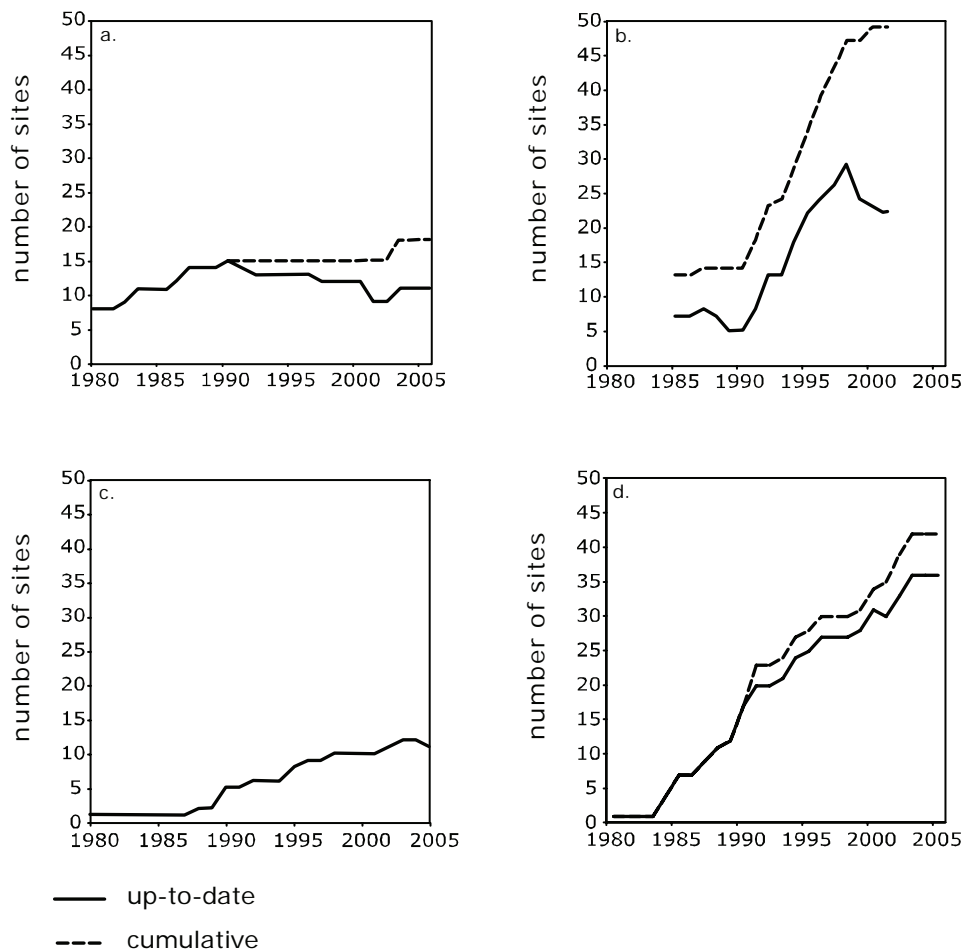


Figure 2.5. The number of current sites of four fern species in Overijssel during more than two decades. The figures also show the cumulative number of sites. The actual number of sites is based on the first year of recording of a particular site, the estimation of the first year of establishment (based on population size and the demographic profile of a population) and (sometimes) the year of disappearance of a particular site. **a.** *Gymnocarpium dryopteris*, **b.** *Pilularia globulifera*, **c.** *Dryopteris affinis*, **d.** *Oreopteris limbosperma*

vegetation, *Pallavicinio-Sphagnetum*). The area of these reed beds has increased as a result of succession and *D. cristata* has multiplied (Table 2.1). In *Gymnocarpium dryopteris* the absolute number of sites increased after 1950, but there was a downward trend in numbers of plants (Table 2.1). Since 1980 the total number of sites increased as exemplified by the situation in the province of Overijssel (Fig. 2.5a). The number of up-to-date sites however did not increase. Some patches probably disappeared because of desiccation. Many coniferous woodlands on sandy soils have been drained and their present hydrological situation may hamper colonisation by this species. In most sites, *Athyrium filix-femina* behaves as a phreatophyte, vulnerable to lowering of the water table. Populations in Overijssel have not shown a significant trend (Fig. 2.6).

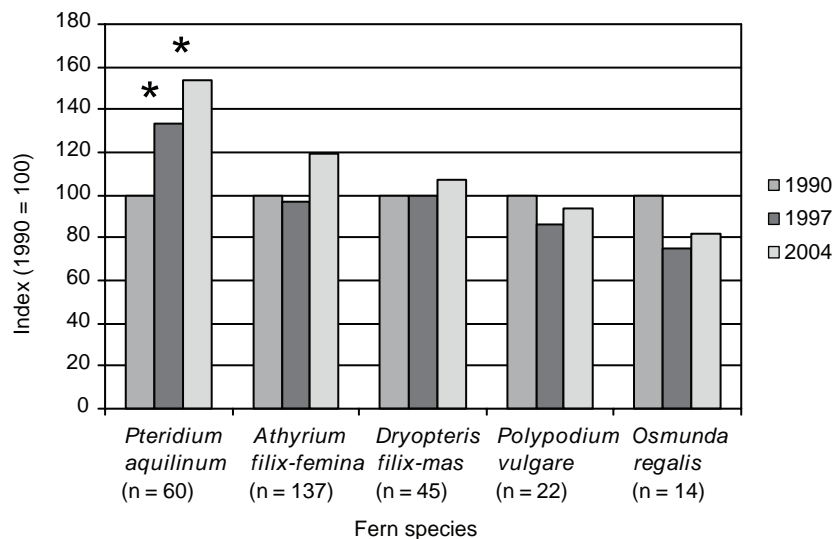


Figure 2.6. The index of five fern species based on the botanical monitoring of more than 3,200 habitat type elements sampled in 92 1 x 1 kilometre grid cells in the province of Overijssel, n = number of elements.

Habitat creation and restoration - In 1990 the Dutch Government published its national Nature Policy Plan, with the aims of reversing this negative trend and enabling nature conservation organisations to buy farmland and to create and restore plant and animal habitats (Ministerie van LNV 1990). On farmland the topsoil was removed, while pools and other small water bodies were dug. Brooks were restored and measures were taken to raise the water table. In Overijssel, habitat creation and restoration on former farmland took place at 88 locations from 1985 to 2000, comprising over 574 ha (Bremer 2001a). In other parts of the Netherlands, too, large areas were restored as natural habitats. In Overijssel ten fern species colonised these habitats, but in most areas they played a subordinate role, with one exception: *Pilularia globulifera* proved to be the most successful fern species in colonising new habitats. In the period 1975 - 2000 the number of *Pilularia globulifera* sites increased from 15 to 50. Half of these new populations developed after habitat creation or restoration measures (Fig. 2.5b). As a result of this success, this fern species lost its status as Red List species (van der Meijden *et al.* 2000). In one area, the Strootman estate in the east of the Netherlands, the establishment and spread of *Pilularia globulifera* was monitored over a five-year period. It seemed plausible that after topsoil removal the spores germinated from a spore bank that was decades old. Although fast-growing, the first cohort was decimated by summer drought. A new cohort arose on the banks of a pond. One patch of the first cohort acted as the source population for dozens of new patches. Within five years the edge of the pond had become overgrown by *Pilularia globulifera* forming a *Pilularietum globuliferae* with e.g. *Juncus bulbosus*, *Hypericum elodes*

and *Eleocharis multicaulis* (Bremer 2002). The effect of afforestation of a former sea-floor (Flevoland) has led to the colonisation of 27 fern species (data presented elsewhere in this thesis). More recently rare ferns were found in the Kralingse bos (Rotterdam, data R. Andeweg). After raising with sand and clay, the area was subsequently trenched and afforested. *Asplenium scolopendrium* and *Polystichum aculeatum* colonised trenches under a canopy of *Picea*.

Ageing of habitats - *Dryopteris dilatata* has become more numerous in woods on sandy soils. This has been attributed to an increased atmospheric input of nitrogen (Boxman *et al.* 1998). Fieldwork has provided circumstantial evidence that dead wood may act as a catalyst for the establishment and development of this species. In a forest reserve, 25 % of the ferns occurred on dead wood above ground and about 60 % on decaying wood in the humus layer. It was concluded that the higher moisture content of dead wood enabled the establishment (de Waal *et al.* 2001). The increase of *Dryopteris affinis* was first assessed in Flevoland in the 1980s, but in subsequent decades the species increased in other parts of the country too, as analysed in detail in Overijssel (Fig. 2.5c). *Oreopteris limbosperma* prefers trench banks surrounded by woodland planted in former heath lands. The increase of both species can be interpreted as a result of this habitat becoming older (Fig. 2.5d). The increase of *Pteridium aquilinum* in Overijssel is related to patches which are expanding (Bremer *et al.* 2004) (Fig. 2.6).

Climatic change - Figure 2.7 depicts trends in two wall species in the city of Amsterdam. In both species the effect of wall restoration (habitat destruction) and management are paramount. But above all, the positive trends in both species can be attributed to the climate. Mild winters have a positive effect on *Asplenium trichomanes* and *Asplenium scolopendrium*, with increase in population size and establishment at less optimal locations (data T. Denters). Some exotic fern species, grown as a houseplant, also profited from mild winters, including *Cyrtomium falcatum*, *C. fortunei*, *Adiantum diaphanum* and *A. raddianum* (van der Ham & Verloove 2002, Denters 2003, Denters & Verloove *in press*). Mild winters might also have influenced the increase of the evergreen *Dryopteris affinis* in woodlands and *Asplenium adiantum-nigrum* at walls (Denters 1997). The effects of severe winters on fern populations in Flevoland will be presented and discussed elsewhere in this thesis.

Overlooked habitats - In the city of Utrecht a total of 11 fern species have been found on 0.8% of the gully covers, the most common being *Dryopteris filix-mas* and *Asplenium scolopendrium* (data W. Vuik). A restricted amount of light penetrates the gully covers, while there is always some water on the bottom of the gully (guaranteeing high humidity). Spores are transported into these pits by water (cf. study on *Asplenium ruta-muraria*, with water as vector, Schneller & Holderegger 1996). This habitat might have been overlooked for years and the ferns have also profited from mild winters.

In Flevoland, *Polypodium vulgare* has colonised the epiphytic habitat. Colonies were found on *Salix alba*, but also on other tree and shrub species such as *Alnus glutinosa*, *Sambucus nigra* and *Ulmus* (data A. Smit). There are also some records from other sites in the Netherlands. The change in habitat preference might be the result of the extent of woodlands planted on clay soils in this area, providing moist habitats with high humidity. Mild winters have played a role as well. The epiphytic colonisation in this species parallels the increase of epiphytic bryophytes, which has been attributed to the decrease in SO₂ deposition, increase of NH₃ deposition and possibly global warming (van Tooren & Sparrius 2007). Epiphytic growth is known from pollarded willows, and growth on boles of trees from the Neuenburger Urwald (Pott & Hüppe 1991) and the UK (Page 1982, Dyer 2005). In the UK, plants become epiphytic

in valleys and ravines along stream courses, in combination with high humidity and greater moss growth.

Population size

Since 1975, eight fern species have been recorded in the Netherlands for the first time. All were growing in small populations, some of which (*Asplenium septentrionale*, *A. fontanum*) included only one or two plants. For most of the species, only the order of magnitude of the population size is known. *Azolla filiculoides*, *Athyrium filix-femina* and *Dryopteris dilatata* constitute the largest populations. *Azolla filiculoides* covers eutrophied ditches with dense mats, while *Dryopteris dilatata* has increased and can form open vegetation, especially in plantations of *Pinus* spp. For some species it was not possible to estimate the population size since the plants grow in dense clones and individuals cannot be recognised in the field without a large-scale genetic analysis (e.g. *Thelypteris palustris*, *Pteridium aquilinum*). The Dutch populations of ferns contribute hardly at all to the world population, except for *Pilularia globulifera* – which has an Atlantic distribution. In the Netherlands, some species have their largest populations in the Kuinderbos (*Asplenium scolopendrium*, *Polystichum setiferum*, *Gymnocarpium dryopteris* and *Dryopteris affinis* (see also Chapter 3), others in cities (e.g. *Cyrtomium falcatum* in Haarlem, *Asplenium ceterach* in Amsterdam).

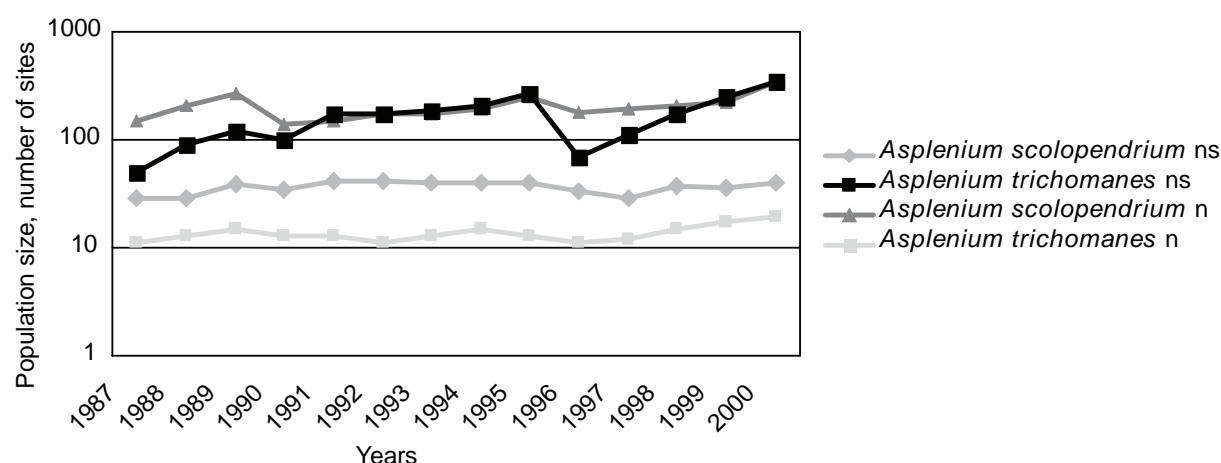


Figure 2.7. Trends in two fern species (*Asplenium scolopendrium*, *A. trichomanes*) in the city of Amsterdam (data from T. Denters, published in Maes & Bakker, 2002), ns = number of sites, n = number of plants.

Protection

In 1991, 12 plant species confined to wall habitats became protected under the Nature Conservation Act, including six fern species, such as *Asplenium trichomanes*, *Cystopteris fragilis* and *Gymnocarpium robertianum*. As a result of this legislation, more attention has been paid to wall ferns. Nowadays, before a wall can be restored, the contractor must obtain a permit from the Ministry of Agriculture, Nature Conservation and Food Quality. In practice, there have been only a few projects for which a permit has been requested. On the other hand, there are examples of wall restoration where the original habitat has been maintained. The first experience was in Utrecht, where parts of walls with rare ferns were dismantled and later reassembled in the same place (Maes & Bakker 2000, 2002). This method has not always been successful, since plants died after replanting because of drought. After wall restoration, many fern habitats disappeared. Portland cement is used nowadays instead of mortar. It takes more

time for ferns to colonise a wall consisting of Portland cement, so the use of mortar is recommended. Woodland ferns are less threatened since woodland destruction is forbidden by law.

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Ecology and colonisation of ferns in an afforested peat erosion area



Trenched *Picea sitchensis* stand in the peat erosion area with luxurious bryophyte and fern vegetation

Abstract

The discovery of a large group (23 species) of rare ferns in the Kuinderbos in 1977 - 1979 offered an opportunity to study the ecology and colonisation in this 1050 ha woodland planted on land reclaimed from the sea. The area is characterised by various soil types. Thick deposits of fine calcareous sands on peat (peat erosion area) are intersected by dozens of km of trenches.

The environmental preference of the ferns in 1979 and 2002 was studied, paying attention to the soil, the composition of the canopy and the trench habitat. Individual plants and patches were mapped and populations monitored during 25 years. Data were also collected on microclimate and hydrology.

In 1979, 18 of the 23 fern species were found exclusively or significantly more on trench banks. Some species showed preference for aspect (e.g. *Asplenium scolopendrium* preferred a SW aspect), relative height up the side of the trench (*Polypodium vulgare* grew higher up the trench sides than other species) and slope (e.g. *Asplenium trichomanes* growing on steep trench sides). Ten species occurred exclusively on the very fine sand deposits in the peat erosion area, while *Dryopteris cristata* grew exclusively on peat soils. *Picea sitchensis* stands proved to be richest in fern species.

In 2002, 15 out of 22 fern species were found exclusively or preferentially on trench sides. There were changes in preference for aspect and gradient, e.g. species preferring shallower gradients (e.g. *Polystichum setiferum*) or change in aspect (e.g. *Asplenium scolopendrium*), the latter related to the clustering of sporelings around adult plants. Various species colonised *Picea abies* stands after thinning, while in former dense mixed stands of *P. abies*, stands of *Acer pseudoplatanus* became available. Only small changes were recorded in preferred soil type.

Various species increased in population size. The two most successful species were *Polystichum aculeatum* and *Asplenium scolopendrium*. In other species the population size stabilised (*Gymnocarpium dryopteris*, *Asplenium trichomanes*), decreased (*Cystopteris filix-fragilis*) or even disappeared from the woodland habitat (e.g. *Dryopteris cristata*). Colonisation was monitored and reconstructed over a period of 50 years, and years of establishment were calculated. Colonisation proved to be related to the size of neighbouring fern populations in the group of calcicole and acidophilous fern species. In all fern species which were able to build up populations a synchronous multi-site colonisation was recorded. A recruitment pattern (clustering) was found in 43% of the rare fern species monitored ($n = 9$), with the highest percentage (99%) in *Polystichum aculeatum*. Clustering was not correlated with ploidy level nor with plants growing in clones or solitary plants. Diploid species were as successful in colonisation as polyploid species.

In future, management and loss of vitality will reduce the role of *Picea* stands. For that reason, *Gymnocarpium dryopteris* will decrease. There is ongoing decalcification, but the soil is buffered by sediments rich in shells. Intense commercial forestry has caused loss of habitat in the short term (increase of *Rubus spp.* in the herb layer), but it is expected that calcicole species will increase further if commercial forestry becomes less intensive and a new generation of trees grows up.

3.1. Introduction

Two processes are crucial for the establishment of plant species: the ability of species to reach a site after some time (dispersal of propagules) and the environmental conditions required for germination and establishment (Mattheus 1992). Colonisation by various groups of wild plant and animal species has been studied in many habitats, but relatively little attention has been paid to the colonisation by ferns (Peck *et al.* 1990, Edgington 2007).

The unexpected discovery of a large group of rare fern species on a former sea-floor in the Noordoostpolder (Bremer 1980a, 1980b) offered the opportunity to study both aspects during a period of more than 25 years. In order to find out what factors were responsible for the unexpected fern species richness, the following research questions were posed:

- What are the environmental preferences of the observed rare fern species?
- Have the environmental preferences of these fern species changed during the monitoring period of 25 years?
- Is it possible to reconstruct the colonisation after the planting of the woodland?
- What is the role of the *dispersal capacity*? Might it be a limiting factor?

In 1979 the environmental preference of the rare ferns was studied, paying attention to various factors that characterise woodlands (e.g. soil and canopy composition, trench habitat, microclimate). The colonisation of such a large number of fern species in a planted woodland had never previously been observed in the Netherlands or neighbouring countries in this extent (Szerdahelyi & Pinter 1996). Studying the environmental preferences of the many fern species offered an opportunity to learn more about the ecology of ferns.

Since the first floral census, changes have been observed in canopy composition, canopy cover (and subsequent light climate) and soil slumps on the trench sides, yet the population of various species has increased, which implies that species are able to respond to a changing habitat. Plants are able to react to new habitats or changing abiotic conditions within a habitat. *Cochlearia danica* colonised road verges as chloride concentrations increased due to spraying with salt in winter (Zonderwijk & Groen 1996), though this species can still be found in its natural habitat (mudflats). Other species in the Netherlands disappeared from their natural habitat (e.g. arable fields) and colonised new ones (e.g. *Sagina apetala*), or colonised new habitats and recolonised its natural habitat (*Corrigiola litoralis*, Peters *et al.* 2004). Changes within one habitat have rarely been documented. In the pioneer phase of colonisation of the woodlands of Flevoland, epizoochoric species established along the paths intersecting the parcels of land, while in the second phase the woodland floor was colonised (Chapter 4). A change in habitat preference can be detected when new microhabitats become available (gaps in woodlands, see also chapter 7).

The inventory of ferns started in 1977 and the first complete survey was finished in the autumn of 1979. In order to reconstruct the colonisation, I started to monitor the fern populations and to study the demography of certain species (e.g. *Asplenium scolopendrium*, *A. trichomanes*) in order to get more data on growth and the period of time between germination and the adult phase. Colonisation was also studied and reconstructed for other vascular species in the woodlands of Flevoland (Bremer 2003, see also chapter 4).

Pteridophyte succession starts with colonisation, which depends on dispersal capacity (primary colonisation), the presence of a spore bank (secondary colonisation) (Mattheus 1992, Miles & Walton 1993) and the mating system (Chiou *et al.* 2002, Flinn 2006). For the Kuinderbos it was hypothesised that spores must have come from source areas outside the polder after the reclamation. Numerous studies have shown that species may be absent because insufficient time has elapsed to enable them to reach the area and plant populations are seed-limited (Nip-van der Voort *et al.* 1979, Turnbull *et al.* 2000, Bremer 2001). After the reclamation of the Noordoostpolder, the vectors important for flowering plants were initially

wind and water. The first plants germinating on the former sea-floor had a seed bank based on seeds transported by these vectors. When the land was taken into cultivation, the anthropogenic impact increased significantly, with humans becoming the dominant vector for many species (Feekees & Bakker 1954). Bakker & van der Zweep (1957) recorded that in the vicinity of Urk anemochoric species dominated and species with a short dispersal distance were scarce. As ferns are wind dispersed and able to cross large distances, I expected dispersal capacity not to be a limiting factor. In order to resolve this, account was taken of spore size, source populations and time of arrival. We expected also a relation to the mating system with polyploid species to be more successful in colonisation than diploid species (Chiou *et al.* 2002, Flinn 2006).

The area

Geology and pedology

The Kuinderbos is on the edge of the Noordoostpolder, one of the reclaimed polders in the former brackish to salty Zuiderzee, which since 1932 has been a freshwater lake: IJsselmeer. Several thousands of years ago, the southern part of the Kuinderbos was a Pleistocene sand area (Wiggers *et al.* 1962). Here a podsol profile developed, which was later overgrown by peat bog. Remnants of this peat area have been saved and are found between the podsol zone and the edge of the polder. Here, in the so-called peat erosion area, some of the peat eroded during the Zuiderzee period (1600 - 1932) and the resulting depressions filled with a very fine-grained sand sediment, the so-called 'Blokzijlzand'. Nowadays this peat erosion area comprises a peat area with a variable layer of Blokzijlzand (20 to 100 cm thick). The soil is called a 'Meer' peat soil when the peat layer is less than 40 cm thick (Lorcher & de Bakker 1994). At the transition from the forest to the Kuinderbuitenpolder is a 'Drecht' vague soil, where acid clay was deposited on top of the peat in the period 250 - 600 AD (during the Dunkirk 2 marine transgression). Sandy soils without a profile ('Vlak' vague soils) originate from the Zuiderzee period and can be found in the north-eastern part of the area (Wiggers *et al.* 1962) (Figure 3.1.).

Climate and severe weather

In the Kuinderbos the average annual rainfall is 825 mm. The average annual transpiration is c. 550 mm. On average the annual total of sunshine is c. 1575 hours and the global radiation is c. 355 kJ/cm². The average wind velocity is c. 5.2 m/sec and the average annual temperature is 9.3°C. There were severe winters in 1978/1979, 1984/1985, 1985/1986, 1995/1996 and 1996/1997, in which there were more than 20 days on which the air temperature was below 0 °C (Heijboer & Nellestijn 2002, period 1971 - 2000). Various storms damaged the woodlands, especially the coniferous plantations at the Westside of the forestry, in 1972, 1973, 1990 and to a lesser extent in 2002. The storm of January 2007 severely damaged the central part of the forestry.

Hydrology

Most of the Kuinderbos is an infiltration area. The only exfiltration area is in the centre. In order to take the reclaimed land into cultivation, 240 km of drainage trenches were dug by hand (up to 0.72 km ha⁻¹ in the peat erosion area) to drain the peat soils. The drainage trenches are shallow (c. 0.5 m) in the centre of the parcels¹ and deeper (up to 1 m) at the

¹ In the Noordoostpolder the basis of cultivation was the layout of the parcels of 800 x 300 meter. These parcels are bordered by deep drainage trenches

edges of the parcels. They parallel with each other and are located from Northwest to Southeast. The trenches in the centre of the parcels contain water for about half of the year (the water level being less than halfway up the trench bank). The trenches at the edges of the parcels contain water for c. 35 % of the year (water level less than 20 % up the trench side). The trenches fill with water in winter and early spring, but may also be filled after heavy rain in summer.

Characteristics of the soil

The main characteristics of the soil have been summarised in Table 3.1. The fine-grained sand has a high CaCO_3 content. In sites with shell banks, the calcium content is much higher. The pH is always higher than 7.2. There is a significant correlation between pH KCl and CaCO_3 concentration ($\text{pH KCl} = 7.39 [\text{CaCO}_3]^{-0.24}$, $R^2 = 0.48$, $p < 0.01$, $n = 50$ soil samples collected in 1979). In the Blokzijl and the humus content is generally low, but it is much higher when a humus layer is present. The water content varies, depending on many factors. The fine-grained sand is highly water-retentive (conductive to 70 cm, Lorcher & de Bakker 1994). The peat has a high water content, high content of organic material, low concentrations of CaCO_3 and concomitantly low pH. The podsol has a low water retention capacity. The concentration of CaCO_3 is low (or even zero), the pH is also low, though may be higher if there are shells in the topsoil.

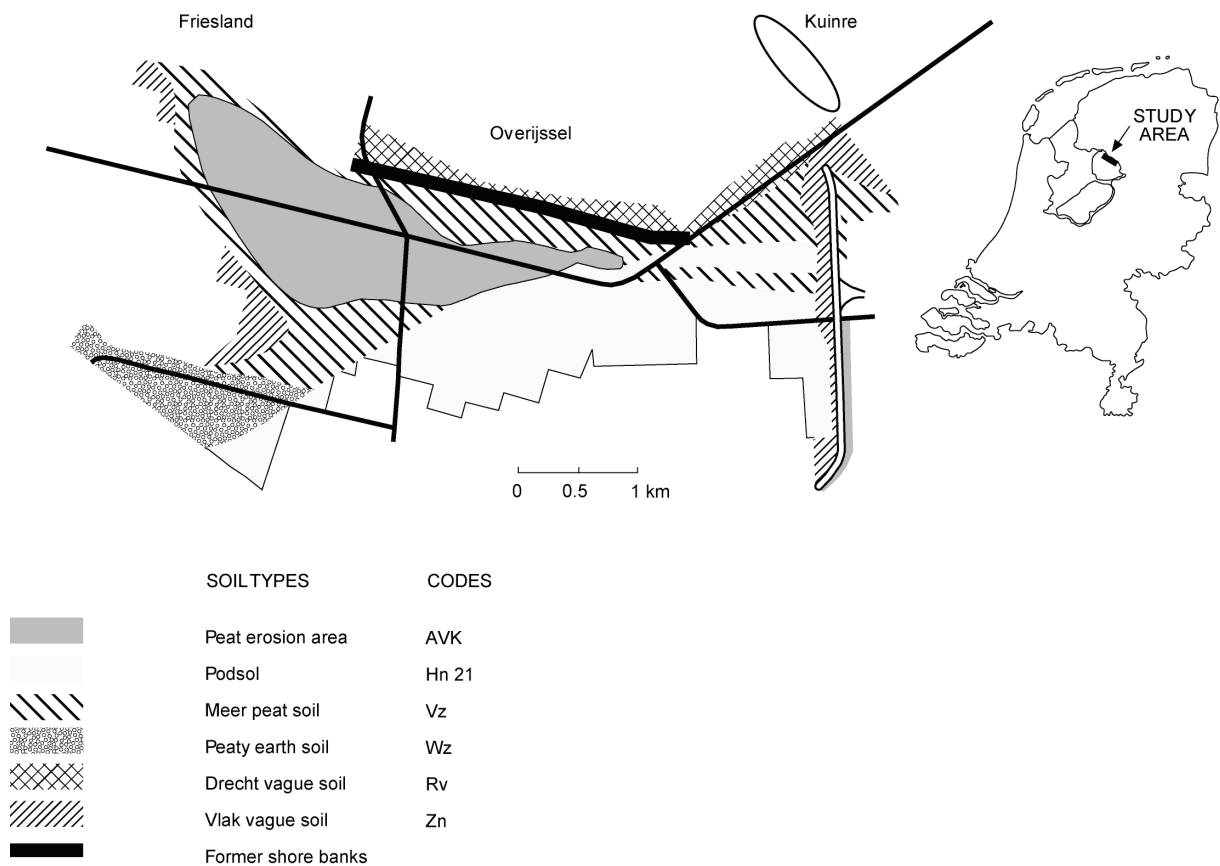


Figure 3.1. Soil map of the Kuinderbos forest area (based on data of the former STIBOKA organisation). Inset: the study area in the Netherlands.

Table 3.1. Some characteristics of the topsoil in the Kuinderbos (Bremer 1980a), n = number of samples. Samples taken from the upper 10 cm (ecto-organic layer not included) in September 1979. % water = water content of soil, % humus = percentage of humus.

	n	% water	% humus	pH-H ₂ O	pH KCl	% CaCO ₃
Blokszjilzand (fine-grained sand)	30	2.6 – 49	1.3 – 12.1	7.2 – 8.4	7.2 – 8.2	0.3 – 5.3
Peat (bog)	10	40.0 - 72.0	17.0 - 56.0	4.7 - 7.0	4.6 - 6.6	< 0.5
Podsol (mineral sand)	5	0.8 – 2.6	2.6 – 5.9	5.8 – 7.7	5.1 – 7.6	0 – 0.8

The humus form

After reclamation, a mull humus form developed in the peat erosion area. The *Ah* horizon in the soil profile of *Fraxinus excelsior* stands is c. 15 cm thick; it is thinner under *Fagus sylvatica* and *Picea sitchensis*. In the Blokszjilzand, earthworms play an important role in converting litter to humus. There are earthworms in the soil under *Picea* stands, despite the acid litter layer (Sevink *et al.* 1986, Sevink *et al.* 1989). These soil types can be designated as mullmoorders (Klinka *et al.* 1981, Kemmers *et al.* 2001). The litter of all the aforementioned tree species lowers the pH, with *Picea* spp. producing the most acids (Ellenberg 1982, de Vries 1994). In stands of *Fraxinus excelsior* there is hardly any impact on the pH. In dense stands of *Picea abies* the ecto-organic layers on trench sides and woodland floor are nearly the same. In the *Picea sitchensis* stands, thinning started earlier, enhancing the impact of rainwater and erosion. Here, trench sides have often slumped. In 1979, heavy rainfall led to erosion on 75 % of the trench slopes in *Picea sitchensis* stands (Bremer 1980a). Erosion can also take place in thick layers of Blokszjilzand during long periods without rainfall. On trench slopes a thin mull soil is present, unless there has been erosion.

Afforestation

Trees were planted from 1949 to 1954. As there was little experience with planting on sandy and peaty soils, various tree species were planted or sown. In the early years, *Picea sitchensis*, *Fraxinus excelsior*, *Acer pseudoplatanus* and *Alnus glutinosa* were planted in large numbers, at densities of more than 10,000 trees or shrubs ha⁻¹. Part of the peat erosion area has been planted with monocultures of *Picea abies* (Wildschut 1992). Selection took place by thinning and self-thinning. In the peat erosion area, sites with thick layers of fine sand are now dominated by *Fraxinus excelsior* and/or *Quercus robur*, though *Picea sitchensis* dominates in the sites with more peat. Current silviculture aims to reduce the proportion of *Picea sitchensis*, as this tree species is susceptible to attack from *Elatobium abietinum* and its vitality and growth have not been optimal. In the *Picea abies* stands, thinning started some 35 years after planting. Within 15 years, most of these stands had deteriorated due to thinning and tree fall due to heavy winds (and infestation by *Ips typographus* and *Heterobasidion annosum*). In most parts of the forest, thinning was in a cycle of 7 - 10 years, but after 1985 this cycle intensified (one thinning per four or five years), to harvest timber and stimulate regeneration of trees. During thinning the boles are removed and the branches are left behind in the parcels, sometimes lying in or across the trenches. For the analysis of the fern flora, ten types of stand/soil were distinguished.

Vegetation

Over the 25 years studied, the composition of the herb, moss and shrub layers changed. In 1980, most stands of *Picea* spp. were in their dense phase, with hardly any vegetation in the understory. Even in *Picea sitchensis* there was no dense cover of ferns. In *Fraxinus excelsior* stands, grasses and *Urtica dioica* dominated. The regeneration of shrubs and tree species became more important after 1980. Bremer (1994) listed 21 regenerating species, the most successful being *Fraxinus excelsior* and *Acer pseudoplatanus*. But at the same time, *Rubus* spp.

Table 3.2. Fern species in relation to the trench habitat. **Aspect:** NE = Northeast aspect, SW = Southwest aspect, n = number of plants, % = percentage of plants, s = statistical testing, s₁ = preferring trench habitat or woodland floor (ignoring area of trenches and woodland floor), s₂ = preferring NE or SW aspect, s₃ = preference for trench habitat and woodland floor, trend analysis 1979 – 2002, s₄ = trend analysis 1979 – 2002 NE/SW aspect. # = population sampled. * p < 0.05 ** p < 0.01 *** p < 0.001 ns = not significant, nt = not tested. *Dryopteris expansa* has been excluded as this species is difficult to identify in the field.

is difficult to identify in the here.

Species			Aspect				s ₁	s ₂	s ₃	s ₄
			NE	SW	other	flat				
<i>Asplenium scolopendrium</i>	1979	n	233	420	-	2	***	***		
		%	35.6	64.1	-	0.3				
	2002#	n	167	130	-	4	***	*	ns	***
		%	55.5	43.2	-	1.3				
<i>Asplenium trichomanes</i>	1979	n	6	5	-	-	***	ns		
		%	54.5	45.4	-	-				
	2002	n	35	3	-	-	***	***	ns	**
		%	92.1	7.9	-	-				
<i>Cystopteris filix-fragilis</i>	1979	n	94	140	-	-	***	**		
		%	40.2	59.8	-	-				
	2002	n	-	2	-	-	nt	nt	nt	nt
		%	-	100	-	-				
<i>Dryopteris cristata</i>	1979	n	92	78	3	5	***	ns		
		%	51.7	43.8	1.7	2.8				
	2002	n	-	-	-	1	nt	nt	nt	nt
		%	-	-	-	100				
<i>Gymnocarpium dryopteris</i>	1979	n	172	189	1	57	***	ns		
		%	41.5	45.1	0.2	13.2				
	2002#	n	59	85	1	130	ns	*	***	ns
		%	21.5	30.9	0.4	47.2				
<i>Gymnocarpium robertianum</i>	1979	n	2	1	-	-	-	-		
		%	66.7	33.3	-	-				
	2002	n	8	1	-	-	**	*	nt	nt
		%	88.9	11.1	-	-				
<i>Phegopteris connectilis</i>	1979	n	-	3	-	-	nt	nt		
		%	-	100	-	-				
	2002	n	64	3	-	1	***	***	nt	nt
		%	94.1	4.4	-	1.5				
<i>Polystichum aculeatum</i>	1979	n	17	29	1	-	***	ns		
		%	36.2	61.7	2.1	-				
	2002#	n	105	121	-	6	***	ns	ns	ns
		%	45.2	52.1	-	2.7				
<i>Polystichum setiferum</i>	1979	n	50	10	-	-	***	***		
		%	83.4	16.6	-	-				
	2002	n	24	18	-	-	***	ns	ns	***
		%	57.1	42.9						
<i>Pteridium aquilinum</i>	1979	n	-	-	1	-	nt	nt		
		%	-	-	100	-				
	2002	n	-	-	1	6	ns	nt	nt	nt
		%	-	-	14.2	85.8				
<i>Thelypteris palustris</i>	1979	n	1	6	12a	3	***	ns		
		%	4.5	27.3	54.5	13.7				
	2002	n	1	-	6a	1	*	nt	ns	nt
		%	12.5		75.0	12.5				

a = the centre of the patches at the bottom of the trenches

and *Urtica dioica* increased in various stand types, at the cost of a more open vegetation with a notable moss layer. In most places the development is towards the *Alno-Padion* woodland community, which is indicated by the successful colonisation by e.g. *Geum urbanum*, *Circaea lutetiana* and *Geranium robertianum* (Bremer 1994). Fern-rich trench sides have much in common with the *Acero-Fraxinetum* (van der Werf 1991).

Stand structure and microclimate

Woodlands have a specific microclimate, for several reasons: rainfall is captured in the canopy, the canopy reflects and absorbs the light, and the woodland itself affects wind speed. Because of extensive thinning, during the study period the average incoming light (expressed as percentage of the light intensity in the open field) increased in all stands. Large changes took place in *Picea abies* stands: they had less than 1% incoming light in 1979 and more than 5% 25 years later. In some stands the canopy composition changed, resulting in a change in light climate. Selective thinning of *Picea abies* in mixed stands of *P. abies* and *Acer pseudoplatanus* led to more incoming light in winter time.

Trench slopes facing SW receive more light compared with those facing NE. This is especially important in spring, before the foliage of broad-leaved tree species such as *Fraxinus excelsior* and *Quercus robur* has emerged. In the evergreen *Picea sitchensis* stands a similar effect was noted. Thinning and the concomitant increase in light intensity also affected the microclimate of the trench habitat.

Methods

Site sampling

The study of ferns in the Kuinderbos area started in 1977. Comprehensive surveys were carried out in 1979, 1990 and 2002. In 1979, 130 km of drainage trenches were checked for rare ferns. During the 1990 census, c. 20 km of trenches were checked. The 2002 census was restricted to the hot spots of rare ferns, comprising c. 9 km of trenches.

During the first census, descriptions were made of the sites inhabited by rare fern species. These descriptions comprised the soil and canopy composition and characteristics of the trench habitat: aspect, slope and relative height up the trench bank (Fig. 3.2a). Groundwater levels were measured with piezometers (Fig. 3.2c). At 75 locations, samples were taken from the top 10 cm of the soil (> 50 g, September 1979). In the laboratory pH H₂O, pH KCl, and CaCO₃ content were measured. Per individual plant number of fronds plant⁻¹, number of fertile fronds plant⁻¹ and the length of the longest frond (plant height) were noted. All rare fern species were mapped in detail. The network of trenches was used to recover individual plants. In 1979, habitat and site descriptions were made of all rare species (i.e. species with less than 50 plants or patches species⁻¹ in the whole area). Samples were taken from *Dryopteris cristata*, *Asplenium scolopendrium*, *Gymnocarpium dryopteris* and *Polypodium vulgare*. In 2002, data were collected on canopy composition, soil composition, habitat, slope, aspect and relative height up the trench side. Eleven species were analysed in detail. In these species 80% of the plants recorded in 2002 appeared after the first census. It was assumed that these species were able to respond to changes in the woodland habitat.

The following parameters considered to be important for the colonisation process were calculated: the number of 5 x 5 km grid cells occupied at the time of establishment within a radius of c. 50 km of the Kuinderbos (Mennema *et al.* 1980, 1985), the number of 1 x 1 km grid cells occupied (Florbase) within the same radius, and a crude estimate of the number of fertile plants in these grid cells. As the distribution data are based on surveys made over long time periods (Florbase started in 1975) it was not possible to estimate the spore production

within a hypothetical area in the year of establishment. The minimum spore size was usually based on measurements of spores collected in the Kuinderbos and for some species based on literature or on collections of spores from elsewhere. The first year of establishment of rare species was calculated or estimated on the basis of the first record, the increase in number of fronds year⁻¹ or increase in plant height. In commoner species, data on population growth were used to extrapolate to the moment of establishment (e.g. *Asplenium scolopendrium*; see also Chapter 6). The distance between Kuinderbos and the nearest locality on the mainland was based on distribution maps (Florbase databank, botanical database of the provincial board of Overijssel).

Statistical analysis

A chi-square test including 2 x 2 contingency tables was used to analyse habitat preference (aspect, trench habitat, canopy and soil composition). Zero data were clustered in this analysis. Differences in relative height up the trench side and slope of the trench side were tested using the t-test or by the Mann-Whitney test. For the landscape ecology analysis, regressions were calculated with SPSS (12.0.1).

Results

Environmental factors in 1979

In 1979, 18 out of 23 fern species were recorded in trenches or on trench sides. *Asplenium trichomanes* and *Gymnocarpium robertianum* preferred the steepest trench slopes, whereas the other species grew on shallower gradients as well. Patch-forming species, such as *Gymnocarpium dryopteris*, carpeted the trench sides (from the floor of the trench up) and also the adjacent woodland floor, reaching maximum numbers at a height just over halfway (59%) up the trench side. *Dryopteris cristata* was the exception: it grew on or near the trench bottom. *Asplenium viride* and *Asplenium adiantum-nigrum* were found only once, both on trench sides with a north-eastern aspect. *Polystichum setiferum* also preferred such sites, but *Asplenium scolopendrium* and *Cystopteris filix-fragilis* preferred the opposite aspect, while *Polystichum aculeatum* showed no preference (Table 3.2, Table 3.3).

Most species were most numerous between 40 and 60 % of the height of the trench side. In these sites the species profited from capillary rise of water from the peat. They behaved like phreatic species (Londo 1988), except for *Polypodium vulgare*, which grew on coarse sand near the top of the trench sides. There was no correlation with the seepage within the peat erosion area. Ten species, including three species of *Polystichum*, were recorded exclusively on the very fine sand deposits rich in shells, particularly on sand layers thicker than 40 cm and with pH KCl ranging from 7.2 to 8.2. They preferred the peat erosion area (Table 3.4). *Dryopteris cristata* preferred the 'Meer' peat soil; this species was found growing on peat in the trench bottoms. *Polypodium vulgare* preferred the podsol area, but in some cases it was also found on calcareous fine sand. Slumping had removed much of the ecto-organic layer and mull micro profile that had accumulated in the dense, juvenile phase of the stands that favoured the establishment of ferns (except for *Gymnocarpium dryopteris*, which requires a well-developed ecto-organic layer on the woodland floor: see Chapter 5). *Gymnocarpium dryopteris* is also able to colonise bare trench sides as well, although most first-year sporophytes are surrounded by bryophytes. The tree canopy plays an important role in filtering the incoming light, influencing the microclimate and the accumulation of litter in the ecto-organic layer. Nearly all the species statistically tested preferred *Picea sitchensis* stands (Table 3.5), with *Gymnocarpium dryopteris* thriving here at a high density.

Table 3.3. Preference of fern species for slope and relative height within the trench habitat in 1979 and 2002. **n79** = number of plants/patches sampled in 1979, **n02** = number of plants/patches sampled in 2002. **s** = testing by comparing situation in 1979 and 2002 with t-test. Mean and standard deviation are given. In species with colonies the highest angle of slope was used, while for the relative height the average value was used (= minimum value + maximum value/2 x 100%). * $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$, ns = not significant, nt = not tested.

Species	Angle of slope (gradient)					Relative Height as % of total height of trench bank		
	n79	n02	1979	2002	s	1979	2002	s
<i>Asplenium scolopendrium</i>	270	203	62±19	47±19	**	54±22	58±26	ns
				*	*			
<i>Asplenium trichomanes</i>	11	36	73±9	58±13	**	59±19	57±23	ns
					*			
<i>Cystopteris filix-fragilis</i>	25	2	60±25	55	nt	41±19	59	nt
<i>Gymnocarpium dryopteris</i>	67	57	40±23	36±9	ns	59±20	57±18	ns
<i>Gymnocarpium robertianum</i>	3	8	67±3	55±12	*	61±9	42±22	ns
<i>Phegopteris connectilis</i>	3	32	50±15	30±9	nt	57±39	56±34	nt
<i>Polystichum aculeatum</i>	47	232	58±14	60±13	ns	48±24	55±24	ns
<i>Polystichum setiferum</i>	60	20	56±13	43±11	**	49±26	39±21	ns
					*			

Polystichum setiferum was found growing under *Fagus sylvatica*. *Dryopteris cristata* was confined to the *Fraxinus excelsior* (- *Quercus robur*) stands, preferring higher light intensities in spring. Only 3.3 % of the plants proved to be fertile.

Change in environmental preference during 25 years

In 1979 most rare species were growing in the trench habitat (Tables 3.2 and 3.3). 25 years later this was still the case, except for *Gymnocarpium dryopteris*, which was found more frequently on the woodland floor. For some species the situation changed profoundly. *Dryopteris cristata* disappeared from its woodland habitat. In 1979 *Pteridium aquilinum* was only known from one site. In the subsequent years, bracken plants established on the woodland floor, especially under *Picea* spp. on peat soils after heavy thinning or natural gap formation. In 2002 four species (*Asplenium trichomanes*, *Gymnocarpium robertianum*, *Asplenium scolopendrium* and *Polystichum setiferum*) were growing on significantly less steep trench sides. In 1979 *Asplenium scolopendrium* preferred a SW aspect, in 2002 it preferred the opposite aspect. Other species lost their preference after 1979 (*Cystopteris filix-fragilis*, *Polystichum setiferum*). In 2002, three species without preference in 1979 preferred a NE aspect (*Asplenium trichomanes*, *Gymnocarpium robertianum*, *Phegopteris connectilis*) and one preferred a SW aspect (*Gymnocarpium dryopteris*). In all species tested there was no difference between 1979 and 2002 in relative height within the trench habitat. *Polystichum setiferum* and *Polystichum aculeatum* did not differ in this respect in 1979, but in 2002 the former preferred the lower part of the trench sides; this was not the case in *P. aculeatum* ($t = 3.2$, $p < 0.01$).

During the 25 years, the only changes recorded in preferred soil type were subtle (Table 3.4). All calcicole species, which in 1979 in the peat erosion area were growing on the fine-grained sand, were still growing on this substrate in 2002. There was no significant change for species common in both years. Nearly all the plants of *Polypodium vulgare* disappeared from the fine-grained substrate. In 1979 *Pteridium aquilinum* was restricted to one site on an acidified clay-on-peat soil. In 2002 four of the seven sites were on the woodland floor, on an acid ecto-organic layer over fine-grained sand.

Significant changes related to changes in the canopy composition were found in four species (Table 3.5). In *Polystichum setiferum* there was a shift from a preference for *Fagus*

Table 3.4. The fern species (*Pteropsida*) in the Kuinderbos in relation to soil type. The table presents the number of plants or patches per soil type in 1979 and 2002. n = number of plants per soil type, e = expected number of plants per soil type. Soil types: **AVK** = peat erosion area, **Vz** = ‘meer’ peat soil (fine sand deposits < 0.5 m on bog peat), **Hn** = podsol, **Zn** = ‘vlak’ vague soil (mineral soil without horizons), **Wz** = peaty earth soil, **Rv** = ‘drecht’ vague soil (clay-on-peat). Area = percentage of area matching the soil type. **n_t** = total number of plants, **s₁** = composition of canopy tested, **s₂** = situation in 1979 compared with that in 2002 tested, nt = not tested, significance *** p < 0.001

			Soil types						n _t	s ₁	s ₂
			AVK	Vz	Hn	Zn	Wz	Rv			
Area			31	20	27	6	8	8			
<i>Asplenium scolopendrium</i>	1979	n	649	3	0	3	0	0	655	***	
		e	203	131	177	39	52	52	655		
	2002	n	13128	422	0	0	0	0	13550	***	***
		e	4200	2710	3658	813	1084	1084	13550		
<i>Asplenium trichomanes</i>	1979	n	11	0	0	0	0	0	11	***	
		e	3.4	2.2	3.0	0.7	0.9	0.9	11		
	2002	n	38	0	0	0	0	0	38	***	ns
		e	11.8	7.6	10.3	2.3	3.0	3.0	38		
<i>Cystopteris filix-fragilis</i>	1979	n	234	0	0	0	0	0	234	***	
		e	72	47	63	14	19	19	234		
	2002	n	1	0	0	0	0	0	1	nt	nt
		e	0.3	0.2	0.3	0.1	0.1	0.1	1		
<i>Dryopteris cristata</i>	1979	n	47	231	6	25	3	0	312	***	
		e	97	62	84	19	25	25	312		
	2002	n	-	-	1	-	-	-	1	nt	nt
		e	0.3	0.2	0.3	0.1	0.1	0.1	1		
<i>Gymnocarpium dryopteris</i>	1979	n	343	50	1	1	7	17	419	***	
		e	130	84	113	25	34	34	419		
	2002	n	383	230	1	1	3	2	620	***	***
		e	192	124	167	37	50	50	620		
<i>Gymnocarpium robertianum</i>	1979	n	3	0	0	0	0	0	3	nt	
		e	0.9	0.6	0.8	0.2	0.2	0.2	3		
	2002	n	9	0	0	0	0	0	9	***	ns
		e	2.8	1.8	2.4	0.5	0.7	0.7	9		
<i>Phegopteris connectilis</i>	1979	n	1	2	0	0	0	0	3	nt	
		e	0.9	0.6	0.8	0.2	0.2	0.2	3		
	2002	n	1	67	0	0	0	0	68	***	nt
		e	21.1	13.6	18.4	4.1	5.4	5.4	68		
<i>Polystichum aculeatum</i>	1979	n	44	3	0	0	0	0	47	***	
		e	14.6	9.4	12.7	2.8	3.8	3.8	47		
	2002	n	1076	0	0	0	0	0	1076	***	***
		e	334	215	291	65	86	86	1076		
<i>Polystichum setiferum</i>	1979	n	59	0	0	0	0	1	60	***	
		e	18.6	12.0	16.2	3.6	4.8	4.8	60		
	2002	n	40	2	0	0	0	0	42	***	ns
		e	13.0	8.4	11.3	2.5	3.4	3.4	42		
<i>Pteridium aquilinum</i>	1979	n	0	0	0	0	0	1	1	nt	
		e	0.3	0.2	0.3	0.1	0.1	0.1	1		
	2002	n	2	2	2	0	0	1	7	ns	nt
		e	2.2	1.4	1.9	0.4	0.6	0.6	7		
<i>Thelypteris palustris</i>	1979	n	9	9	0	1	3	0	22	***	
		e	6.8	4.4	5.9	1.3	1.8	1.8	22		
	2002	n	5	2	1	0	0	0	8	ns	ns
		e	2.5	1.6	2.2	0.5	0.6	0.6	8		

Table 3.5. The fern species (*Pteropsida*) in the Kuinderbos in relation to the composition of the canopy (stand). n = number of plants stand type⁻¹, e = expected number of plants stand⁻¹. **Stand types:** Ps = *Picea sitchensis*, Fe = *Fraxinus excelsior*, Qr = *Quercus robur*, Pa = *Picea abies*, La = *Larix*, other = other deciduous or coniferous tree species. Area = percentage of area corresponding with the stand types, **n_t** = number of plants in the chi-square analysis, **s₁** = composition of canopy tested, **s₂** = situation in 1979 and 2002 tested, nt = not tested, significance * p < 0.05, *** p < 0.001.

			Stand types						n _t	s ₁	s ₂
			Ps	Fe Fe/Qr	Qr (Ps)	La	Pa	other			
Area 1979 (%)			7	19	20	11	17	26			
Area 2002 (%)			7	19	20	11	16	27			
<i>Asplenium scolopendrium</i>	1979	n	275	16	105	-	-	260	655	***	
		e	46	125	131	72	111	170	655		
	2002	n	9900	550	320	-	80	330	13520	***	***
		e	946	2569	2704	1487	2298	3515	13520		
<i>Asplenium trichomanes</i>	1979	n	11	-	-	-	-	-	11	***	
		e	0.8	2.1	2.2	1.2	1.9	2.9	11		
	2002	n	37	1	-	-	-	-	38	***	ns
		e	2.7	7.2	7.6	4.2	6.5	9.9	38		
<i>Cystopteris filix-fragilis</i>	1979	n	234	-	-	-	-	-	234	***	
		e	16	44	47	26	40	61	234		
	2002	n	1	-	-	-	-	-	1	nt	nt
		e	0.1	0.2	0.2	0.1	0.2	0.3	1		
<i>Dryopteris cristata</i>	1979	n	10	214	73	5	9	1	312	***	
		e	22	60	62	34	53	81	312		
	2002	n	-	-	-	-	-	1	1	nt	nt
		e	0.1	0.2	0.2	0.1	0.2	0.3	1		
<i>Gymnocarpium dryopteris</i>	1979	n	325	-	53	2	5	24	419	***	
		e	29	80	84	46	71	109	419		
	2002	n	544	1	10	-	30	35	620	***	***
		e	43	118	124	68	105	161	620		
<i>Gymnocarpium robertianum</i>	1979	n	3	-	-	-	-	-	3	nt	
		e	0.2	0.6	0.6	0.3	0.5	0.8	3		
	2002	n	8	-	1	-	-	-	9	***	nt
		e	0.6	1.7	1.8	1.0	1.5	2.3	9		
<i>Phegopteris connectilis</i>	1979	n	3	-	-	-	-	-	3	nt	
		e	0.2	0.6	0.6	0.3	0.5	0.8	3		
	2002	n	68	-	-	-	-	-	68	***	nt
		e	4.8	12.9	13.6	7.5	11.6	17.7	68		
<i>Polystichum aculeatum</i>	1979	n	27	6	11	1	1	1	47	***	
		e	3.3	8.9	9.4	5.2	8.0	12.2	47		
	2002	n	614	299	156	0	7	-	1076	***	*
		e	75	204	215	118	183	280	1076		
<i>Polystichum setiferum</i>	1979	n	7	7	-	-	-	46 *	60	***	
		e	4.2	11.4	12	6.6	10.2	15.6	60		
	2002	n	7	33	-	-	-	2	42	***	***
		e	2.9	8.0	8.4	4.6	7.1	10.9	42		
<i>Pteridium aquilinum</i>	1979	n	-	-	-	-	-	1	1	nt	
		e	0.1	0.2	0.2	0.1	0.2	0.3	1		
	2002	n	2	-	-	1	2	2	7	***	nt
		e	0.5	1.3	1.4	0.8	1.2	1.8	7		
<i>Thelypteris palustris</i>	1979	n	10	9	1	-	-	2	22	***	
		e	1.5	4.2	4.4	2.4	3.7	5.7	22		
	2002	n	5	-	-	-	-	3	8	***	ns
		e	0.6	1.5	1.6	0.9	1.4	2.1	8		

* = 84% of plants growing under *Fagus sylvatica*

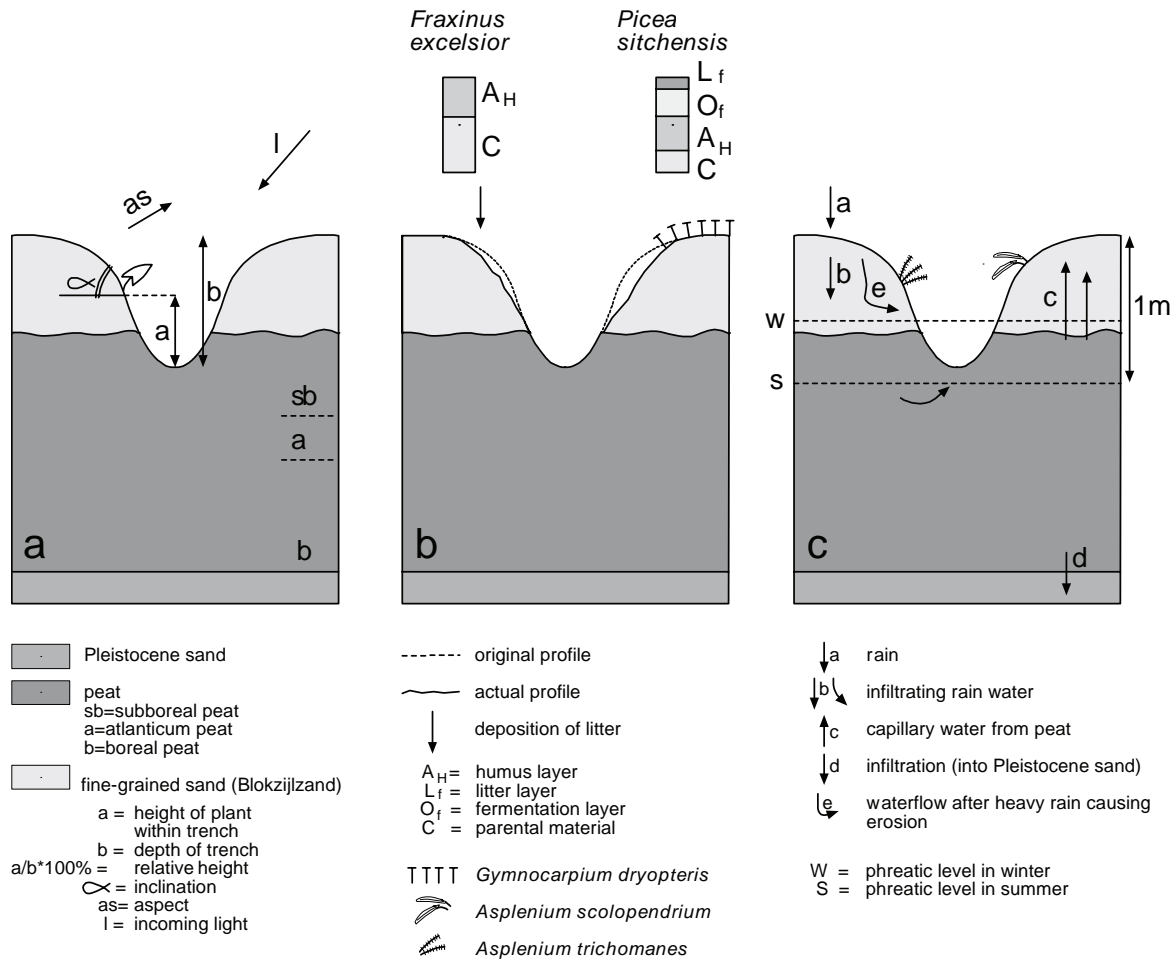


Figure 3.2. Cross-section of trench habitat in peat erosion area

a. trench habitat with some parameters. Relative height up trench side = $a/b * 100\%$

b. trench habitat with soil composition and micro profiles.

c. trench habitat with indication of water level in winter (w) and summer (s) and flow of water.

sylvatica stands towards a preference for stands dominated by *Fraxinus excelsior*. In *Polystichum aculeatum*, too, there was a shift towards stands of *Fraxinus excelsior*. Since 1985, dense stands of *Picea abies* in the peat erosion area have been thinned in a short rotation. Within five years, *Gymnocarpium dryopteris* and *Asplenium scolopendrium* were successful in colonising the thinned stands. Other species were less successful but *Dryopteris affinis* and *Pteridium aquilinum* colonised this new habitat as well, although at a low density. In one part of the peat erosion area, dense mixed stands of *Picea abies* and *Acer pseudoplatanus* were too dark as habitat. In the last 25 years these stands have been thinned selectively, leading to the dominance of *Acer pseudoplatanus*. During the 2002 survey it appeared that numerous rare fern species had colonised the deeper trenches in these stands.

Colonisation and dispersal capacity

A question arising is how much the ability of species to disperse spores to safe sites (dispersal capacity) constrains the colonisation. It was expected dispersal capacity not to be a limiting factor (spore-limitation), with distances to nearby populations to be insignificant. There was an almost significant correlation between the year of colonisation and the distance to a nearby population ($R^2 = 0.13$, $p = 0.07$, $n = 25$). When it was investigated whether there was a correlation between population size of the surrounding population (within a radius of 50 km) and the year of colonisation (with correction for some calcicole species growing in

gardens) (Table 3.6), a significant negative linear correlation was found between the year of colonisation and the number of occupied 1 x 1 km grid cells ($R^2 = 0.22$, $p < 0.01$, $n = 25$). Taking the estimated population size (log transformed) per grid cell into account I found a negative significant linear correlation as well ($R^2 = 0.35$, $p < 0.01$, $n = 25$) (Fig. 3.3). This correlation was also found in the group of acidophilous fern species and in the group of

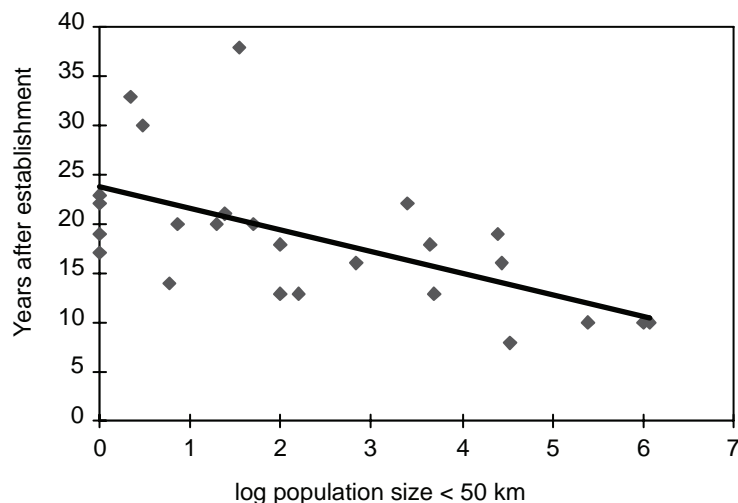


Figure 3.3. The correlation between the $^{10}\log$ number of plants (< 50 km, Kuinderbos at the centre) and the age of the woodland when species established (time scale starting in 1952). With correction for some species growing in gardens.

calcicole species, after correction for species growing in gardens. The population sizes in the Kuinderbos area and in the surrounding area (1979 situation) were correlated in the total group of ferns, but not in the subgroup of calcicole or acidophilous species (Table 3.7). It was also tested whether spore size did have an effect on the time of colonisation. Minimum spore size was used as parameter, but there appeared to be no correlation between spore size and the time of establishment ($R^2 = 0.003$, $p > 0.05$, $n = 25$). Another aspect of colonisation is the dispersal within a particular area. Did rare species establish independently at several sites (a synchronous multi-site colonisation) or did the first colonised site provide the source population for further establishment in the area? And does the distribution pattern say something about the dispersal of spores of the rare fern species? Figure 3.4 shows a population of *Asplenium scolopendrium* monitored for 15 years. In the first year there was only one plant growing at the site in question. After achieving maturity, it produced spores, millions of which were deposited at a short distance from the adult plant. Within a few years juvenile plants had appeared around the adult plant. Within 5 - 10 years, more adult plants were growing at the same spot, probably all of them genetically congenial, although this was not confirmed by gene analysis. This clustering based on recruitment was found in 9 out of the 14 monitored fern species (62.3%), while in 6 species this pattern comprised more than 80 % of the recruitment observed in 2002 and in *Polystichum aculeatum* the corresponding figure was as much as 99 %. The percentage of plants per fern species that was part of these clusters increased significantly in 23 years ($\chi^2 = 5.4$, $p < 0.05$, $n = 21$). Clustering was not correlated with the ploidy level ($\chi^2 = 0.4$, ns, $n = 14$), nor with life-form ($\chi^2 = 0.8$ ns, $n = 14$). In all rare fern species, except those recorded only once or twice, synchronous multi-site colonisation was recorded (Table 3.8).

Asplenium adiantum-nigrum, *Blechnum spicant* and *Pteridium aquilinum* produced sterile plants or patches only. Although 21 species formed fertile populations, successful recruit-

ment was recorded in 13 species (61.9 %); nine of these were rare. Annual recruitment was confined to *Asplenium scolopendrium*, *Gymnocarpium dryopteris* and the common fern species. Eight of the 25 fern species recorded are diploid; the remainder in this group are polyploid (tetraploid) (Table 3.6). Polyploid fern species were twice as successful as diploid species (60 % versus 30 % of fern species), but these differences were not significant ($\chi^2 = 1.5$ ns).

Table 3.6. Landscape ecology parameters and population biology parameters of fern species found in the Kuinderbos. Excluding *Cyrtomium falcatum*, *Matteuccia struthiopteris* and hybrid *Dryopteris x tavelii*. **D** = species studied demographically (> 8 plants/patches monitored). **Landscape ecology parameters:** **Y** = estimated/ calculated age of Kuinderbos at first establishment; **y** = first year of establishment based on demographic studies (d), based on number of plants (n), estimated/ based on other species/ expert judgement (e). **Sp** = minimum spore size. **dB** = distance to fertile population on the mainland at moment of first establishment. **nG** = the estimated number of occupied grid cells (1 x 1 km) within radius of 50 km in 1979 (based on Mennema *et al.* 1980, Mennema *et al.* 1984 and van der Meijden *et al.* 1989 and more recent data of FLORON/ provincial data base). **pS** = 10 log population size (estimated size; $n + 1$) for population within 50 km in 1979. For four species with correction (/.) for plants growing in gardens. **Population biology parameters (1980 – 2004).** **F** = fertility, x = spore-producing plants (adult), - = not fertile, ? = unknown, **Sb** = persistent spore bank (after Dyer & Lindsay 1996), x = with persistent spore bank, - = without persistent spore bank, ? = spore bank not known. **Spl** = cluster of sporelings related to founding adults, **Fs** = frequency of sporeling establishment: a = annual, na = not annual, r = rarely, - = not observed. **Pl** = diploid (d) and/or polyploid (p) (based on: Page 1982, Hegi 1984), **S.e.** = sex expression based on literature; is = intergametophytic selfing, ic = intergametophytic crossing, s = selfing (intragametophytic mating), ap = apomictical.

Species	D	Landscape ecology parameters						Population biology parameters					
	Y	y	Sp	dB	nG	pS	F	Sb	Spl	F s	Pl	S.e.	
‘rare fern species’													
<i>Asplenium adiantum nigrum</i>	-	22	n	35	35	0	0	-	x	-	-	p	s (Edgington 2007)
<i>Asplenium scolopendrium</i>	+	13	n	26	30	1	0.7/2.2	x	x	x	a	d	ic, is (de Groot 2007)
<i>Asplenium trichomanes</i>	+	20	d	24	30	2	1.7	x	x	x	na	p	s (Suter <i>et al.</i> 2000)
<i>Asplenium viride</i>	-	19	n	27	150	0	0	x	x	-	-	d	
<i>Blechnum spicant</i>	-	22	n	30	10	98	3.4	-	x	-	r	d	ic,s (Cousens 1981)
<i>Cystopteris filix-fragilis</i>	-	21	n	30	50	1	1.4	x	x	x	r	p	
<i>Dryopteris affinis</i>	-	20	n	36	200	0	0/1.3	x	x	x	na	p	ap (Fraser-Jenkins 1984)
<i>Dryopteris cristata</i>	-	16	n	50	1.5	140	4.4	x	x	?	?	p	s (Rumsey <i>et al.</i> 2002)
<i>Dryopteris expansa</i>	-	33	n	33	200	0	0.4	x	?	?	?	d	
<i>Gymnocarpium dryopteris</i>	+	14	n	35	35	6	0.8	x	x	x	a	p	s (de Groot 2007)
<i>Gymnocarpium robertianum</i>	+	23	d	41	80	0	0	x	x	x	r	p	
<i>Oreopteris limbosperma</i>	-	38	n	41	30	7	1.5	x	x	-	-	d	
<i>Osmunda regalis</i>	-	16	n	40	4	190	2.8	x	x	-	-	d	ic (Zenktele 1999)
<i>Phegopteris connectilis</i>	+	20	d	34	55	4	0.9	x	x	x	na	p	ap (Dostāl 1984)
<i>Polypodium interjectum</i>	-	30	n	60	150	3	0.5	x	x	-	-	p	
<i>Polypodium vulgare</i>	-	13	n	54	10	250	3.7	x	x	-	r	p	
<i>Polystichum aculeatum</i>	-	13	n	39	100	0	0/2.0	x	x	x	na	p	s (ic) (Pangua <i>et al.</i> 2003)
<i>Polystichum lonchitis</i>	-	17	d	37	200	0	0	x	?	-	-	d	s (is) (Pangua <i>et al.</i> 2003)
<i>Polystichum setiferum</i>	+	18	d	32	250	0	0/2.0	x	x	x	na	d	ic, is (Pangua <i>et al.</i> 2003)
<i>Pteridium aquilinum</i>	+	18	n	30	10	186	3.7	?	-	-	r	p	
<i>Thelypteris palustris</i>	-	19	n	35	5	117	4.4	x	x	-	r	d	
‘common fern species’													
<i>Athyrium filix-femina</i>	-	10	e	27	1.5	490	5.4	x	x	?	a	d	ic (Schneller 1987)
<i>Dryopteris carthusiana</i>	-	10	e	37	1.5	1000	6	x	x	?	a	p	s (Flinn 2006)
<i>Dryopteris dilatata</i>	-	10	e	33	1.5	1180	6.1	x	x	?	a	p	
<i>Dryopteris filix-mas</i>	-	8	e	41	10	340	4.5	x	x	?	a	p	s (de Groot 2007)

Table 3.7. A. Correlation between age of establishment and $^{10}\log$ population size (within radius of 50 km centred on Kuinderbos). **B.** Correlation between $^{10}\log$ population size in the Kuinderbos in 1979 and the $^{10}\log$ population size within radius of 50 km, n = number of fern species. The $^{10}\log$ population size (within radius of 50 km centred on Kuinderbos) has been corrected for the effect of species growing in gardens (four calcicole fern species).

	n	A	sign.	B	
All ferns found (with correction for calcicole species used in gardens)	25	0.59	**	0.73	***
Acidophilous fern species	11	0.54	*	0.34	ns
Calcicole fern species	10	0.70	*	0.07	ns

Changes in density and population diversity

In Figure 3.5 the number of fern species year⁻¹ has been reconstructed for a period of 50 years. The number of species increased between 10 and 20 years after planting, stabilising thereafter. Table 3.8 gives an overview of the trends during 25 years of monitoring. In 1979, 24 taxa were found, and 20 species were classified as rare in the region or in the Netherlands. This group of rare species comprised 1855 individuals. *Asplenium scolopendrium* was the most common (35% of all individuals of rare fern species). One of the taxa, *Dryopteris x tavelii*, was growing between its parents (Bremer 1988). During the 1990 survey the number of taxa was found to have fallen to 22, but the number of individuals increased to 4123, with

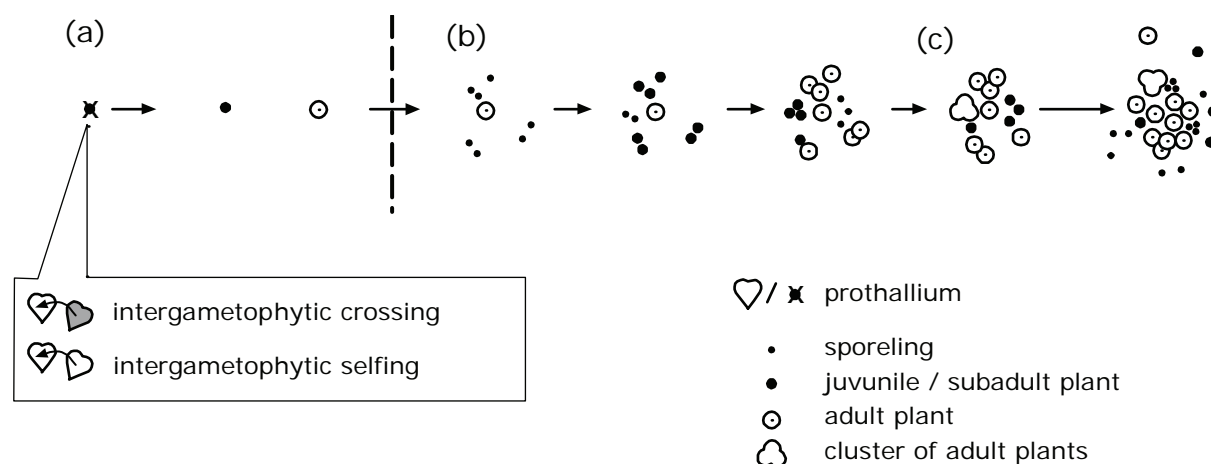


Figure 3.4. Clustering of fern plants based on recruitment with one founding plant of *Asplenium scolopendrium* and leading to an open or dense *Asplenium scolopendrium* vegetation.

a. establishment, **b.** clustering of juvenile and subadult plants, **c.** clustering including all demographic stadia.

Asplenium scolopendrium as commonest species (80%) (see also Figure 3.6). A group of species established at only one site and produced only very small populations, which existed for a short period: *Asplenium viride*, *A. adiantum-nigrum* and *Cyrtomium falcatum* died after the severe winter of 1978/1979. *Dryopteris x tavelii* also disappeared. In 2002, 24 species were found, with 'new' species such as *Polypodium interjectum* and *Oreopteris limbosperma*. 15,598 individuals of rare species were counted or estimated, 88 % of them belong to *Asplenium scolopendrium*. Figure 3.5 also depicts the cumulative number of species. Over the 25 years, 28 taxa were found (one hybrid and two garden escapes not depicted). 91.8% of the plants in the 1979 cohort had disappeared by 2002. Clonal species as group were better able to survive than non-clonal plants (142 clones versus 10 plants) (Table 3.8).

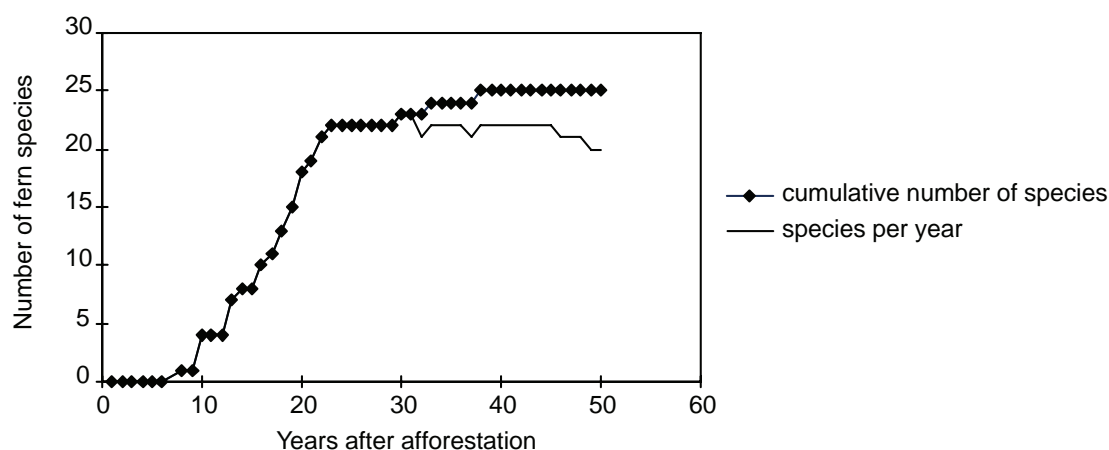


Figure 3.5. The increase in the number of fern species in the Kuinderbos (species listed in Table 3.6). The figure depicts the number of fern species year⁻¹ and the cumulative number of species.

Table 3.8. Clustering (recruitment pattern) in rare fern species. The table compares these clusters between 1979 and 1982. **Sa:** c = whole population monitored, s = monitoring based on samples. **Nex 1979** = number of plants in 1979, **1979 cluster** = number of plants within the spore shadow of an adult plant, **% 1979** = percentage of plants within this clustering, ¹ = estimated number. **Nex 2002** = number of plants in 2002, **2002 cluster** = number of plants within the spore shadow of an adult plant (within distance of 0 – 2-3 m), **% 2002** = percentage of plants within this cluster, **S** = number of plants still alive in 2002 from 1979 cohort. **S%** = percentage of plants in 2002 still alive from the 1979 cohort (percentage based on number of plants in 1979). *Dryopteris expansa* has been excluded as it is difficult to identify in the field. **Multi** = synchronous multi-site colonisation, - = not relevant.

	Sa	Nex 1979	1979 cluster	% 1979	Nex 2002	2002 cluster	% 2002	S	S%	Multi
<i>Asplenium adiantum-nigrum</i>	c	1	0	0	.	.	-	0	0	-
<i>Asplenium scolopendrium</i>	s	655	442	67.5	13530	12800	94.6	0	0	+
<i>Asplenium trichomanes</i>	c	11	0	0	38	36	94.7	1	9.1	+
<i>Asplenium viride</i>	c	1	0	0	.	.	-	0	0	-
<i>Blechnum spicant</i>	c	3	0	0	1	0	-	0	0	+
<i>Cystopteris filix-fragilis</i>	c	234	233	99	1	0	-	1?	0	+
<i>Dryopteris affinis</i>	c	?	?	?	119	c. 100	84.0	?	?	+
<i>Dryopteris cristata</i>	c	312	?	?	1	0	-	0	0	+
<i>Gymnocarpium dryopteris</i>	s	419	3	0.8	655	65 ¹	10.0	109	26.0	+
<i>Gymnocarpium robertianum</i>	c	3	0	0	2	1	50.0	1	33.3	+
<i>Oreopteris limbosperma</i>	c	.	.	.	1	0	-	-	-	-
<i>Osmunda regalis</i>	c	2	0	0	2	0	0	1	50.0	-
<i>Phegopteris connectilis</i>	c	3	0	0	68	66	97.1	2	66.6	+
<i>Polystichum aculeatum</i>	c	47	21	44.7	1076	1073	99.7	3	6.4	+
<i>Polypodium interjectum</i>	c	.	.	.	1	0	-	-	-	-
<i>Polystichum lonchitis</i>	c	2	0	0	1	0	-	1	50.0	+
<i>Polystichum setiferum</i>	c	59	44	74.6	42	34	80.9	4	6.8	+
<i>Polypodium vulgare</i>	c	79	0	0	45	0	0	28	35.3	+
<i>Pteridium aquilinum</i>	c	1	0	0	7	0	0	1	100	+
<i>Thelypteris palustris</i>	c	22	0	0	8	0	0	1	4.5	+

In Figure 3.7 the trends have been summarised for the various combinations of stand and soil types. The density of rare ferns in stands of *Fraxinus excelsior* and *Picea sitchensis* on clayey soils has decreased, but in most stand/soil types the number of species stabilised, while densities increased. In the *Acer pseudoplatanus*/peat erosion area, the colonisation by ferns started after 1990. In the *Picea abies*/peat erosion area, thinning started in c. 1985. Various rare ferns

established, but *Rubus* spp. and *Urtica dioica* also invaded the stands, hampering further colonisation of ferns. Colonisation appeared to be most successful in the *Picea sitchensis*/peat erosion area type. Here the density had increased to more than 300 individuals ha⁻¹ in 2002.

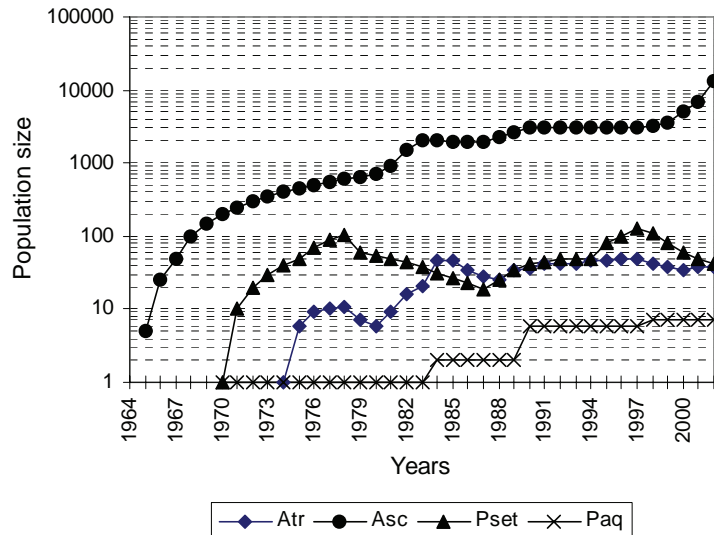


Figure 3.6. Change in population size in a number of rare fern species in the Kuinderbos. Atr = *Asplenium trichomanes*, Asc = *Asplenium scolopendrium* (partly interpolated), Pset = *Polystichum setiferum*, Paq = *Pteridium aquilinum*. Population size prior to 1977 is extrapolated.

Discussion

Ecological requirements

The comparison of the ecological preferences of the fern species in 1979 and 2002 revealed that in both years, rare fern species significantly preferred drainage trenches, especially the sloping sides, whose gradients mimic the natural heterogeneity in woodlands. In a natural woodland, an important part of this heterogeneity is related to fallen trees and their uprooted bases. In the Kuinderbos uprooted bases also occur, especially of *Picea* spp. But their summed perimeter is insignificant compared with the 240 km of drainage trenches. All trees in a stand of *Picea sitchensis* would have to be wind thrown for the summed area of their uprooted bases (c. 3200 m²/ha) to be of the same order as the summed area of the trench slopes (c. 2500 m²/ha)! Trench slopes can be likened to miniature ravines in woodlands. In such habitats in Central Europe large numbers of *Asplenium scolopendrium* can be found (Ellenberg 1982). The shady trench habitat has a higher humidity and on cloudless summer days it remains cooler than the adjacent wood floor (Bremer 1980a).

During the 25-year period studied, the preference for trenches did not change, except in *Gymnocarpium dryopteris*. In 2002, more patches of this species were found on the woodland floor. The species had established on the tracks left by harvesting equipment. Comparing both inventories revealed hardly any change in the preference for gradient. Only *Asplenium trichomanes* and *Gymnocarpium robertianum* preferred the steeper gradients in 1979; this is not surprising, as elsewhere in the Netherlands they are found on vertical walls. These two species and *Asplenium scolopendrium* and *Polystichum setiferum* preferred less steep slopes in 2002 than in 1979. This change in preference is attributable to a change in the trench habitat: slumping had made the trench slopes less steep on average. In one or both inventories, seven species showed a clear preference for a particular aspect. In *Asplenium trichomanes* (Bremer

2004), *Cystopteris filix-fragilis*, *Gymnocarpium robertianum*, *Phegopteris connectilis* and *Polystichum setiferum*, this aspect is related to the recruitment pattern. As there is a concentration of spores below and near fertile plants, recruitment had a much greater probability of succeeding near these founding plants than on the opposite side of the trench. *Gymnocarpium dryopteris* preferred a SW aspect in 2002. On cloudless days, more light falls on trench sides with this aspect, which implies that the temperature is higher there (Bremer 1980a). In 1979 *Asplenium scolopendrium* preferred the SW aspect; in 2002 it preferred the opposite aspect. In 1979, clustering of sporelings was rare and most plants were solitary. In the subsequent years, more sporelings clustered around solitary adult plants. *Asplenium scolopendrium* preferred a NE aspect, especially in *Fraxinus excelsior* stands. In these stands there is a difference in microclimate between NE and SW exposed trench slopes in spring, when much light penetrates to the woodland floor and trenches. At that time of the year, bryophytes may dry out. Bremer (2000a) showed that some pleurocarpous bryophytes in *Fraxinus excelsior* stands preferred a northerly aspect; differences in microclimate seemed the most plausible explanation for this phenomenon. Stoutjesdijk & Barkman (1992) listed various situations in which the slope aspect had an important impact. Van Strien (1991) and also Geertsema (2002) showed that aspect affected the species composition on trench banks. Spores of *Asplenium scolopendrium* can germinate in autumn and spring (Lindsay & Dyer 1996). In spring, these prothallia might be vulnerable to desiccation in sites with a southerly aspect. Elsewhere in Europe, *Asplenium septentrionale* is found on south-facing rocks, probably due to the high temperature requirement for germination and prothallia less vulnerable to desiccation (Dyer & Lindsay 1996).

On average, in both inventories, most of the rare species were found growing at a relative height between 40 and 60 % up the side of the trench. There was no difference in relative height between *Polystichum setiferum* and *Polystichum aculeatum* in 1979, but in 2002 *Polystichum setiferum* was found lower down the trench sides than *Polystichum aculeatum*. This is probably because *Polystichum setiferum* requires a damper habitat, and its sporelings are more prone to desiccation than *Polystichum aculeatum* sporelings. Over the 25 years, *Polystichum setiferum* was able to increase in numbers only in a short period, in contrast with *Polystichum aculeatum*. In the Kuinderbos, *Polystichum setiferum* is at the northern edge of its range. Since 1979 it has been recorded at other locations in the Netherlands as well, but always with only one or two plants per site. Large populations of *Polystichum aculeatum* are found in the southern part of the province of Limburg. Recruitment in these populations proved to be scarce (unpublished data of the author).

The growth of ferns on trench sides is also related to the local hydrology. As trenches may fill with water in winter, most fern species cannot grow on the lowest 20 % or so of the trench side. Patch-forming species can survive a period of inundation if most of the patch is growing above the highest water level. They will even survive when growing on the lowest 20 % of the trench side, as found in *Polystichum setiferum*, if they tolerate short periods of immersion. There is also an upper limit. Water rises to the fine-grained sand from the underlying peat by capillary action over a distance of c. 70 cm (Lorcher & de Bakker 1994). This means that the water supply to trench sides is guaranteed, unless the sand layers are thicker than 70 cm, in which case rainfall is crucial. Desiccation has been recorded in *Asplenium scolopendrium* growing on a thick layer of fine sand. The fine-grained sand deposits rich in shells proved to be an optimal habitat for calcicole fern species. During the observation period, nine calcicole species established on these deposits. The Kuinderbos was the first woodland in Flevoland where these species were recorded. Near Lelystad, after 1979, four calcicole species established on sandy clay, indicating a similarity in composition between

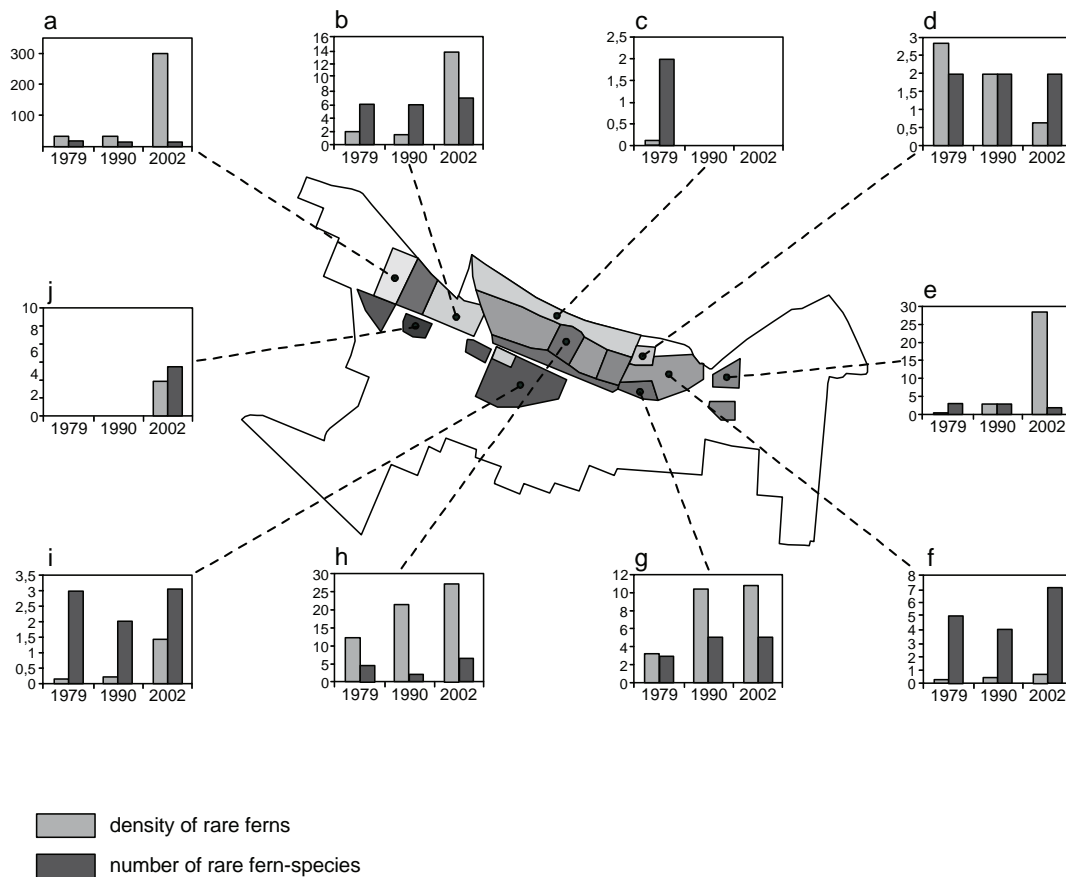


Figure 3.7. Trends in the various soil/stand types in the Kuinderbos. **a.** *Picea sitchensis*/peat erosion area, **b.** *Fraxinus excelsior*/peat erosion area, **c.** *Fraxinus excelsior*/ drecht vague soil (acidified clay), **d.** *Picea sitchensis*/ drecht vague soil, **e.** *Fraxinus excelsior*/meer peat soil, **f.** *Picea sitchensis*–*Quercus robur*/meer peat soil, **g.** *Picea sitchensis*–*Quercus robur*/ peat erosion area. **h.** *Picea sitchensis*/ meer peat soil, **i.** *Picea abies*/ peat erosion area, **j.** *Acer pseudoplatanus*–*Picea abies*/ peat erosion area. Note the different scales on the y-axes.

fine-grained sand and this substrate (Smit 1989). These calcicole species were also found on clayey soils containing more than 5 % silt. On these substrates their density was lower than in the Kuinderbos, due to the low density of trenches and the probability of drowning in winter (mean highest water table < 0.5 m). Some calcicole species have more recently been found at low densities on boulder clay too (Bremer 2001). Boulder clay may dry out in summer and is subject to acidification. *Dryopteris cristata* and *Thelypteris palustris* preferred a peat soil. Both species are very common on peat in marshland, but sometimes occur on acidified mineral soils. *Polypodium vulgare* displayed a preference for the acid podsol. This is in accordance with its preference for Pleistocene soils elsewhere in the Netherlands (see also Chapter 2).

The tree and shrub layers have an important impact on light intensity, atmospheric humidity and on soil formation. *Gymnocarpium dryopteris* showed a strong preference for one tree species: *Picea sitchensis*. In North America, this fern species occurs in stands with *Picea sitchensis* or other conifers. *Gymnocarpium dryopteris* and *Athyrium filix-femina* are the only fern species that the natural *Picea sitchensis* forests and the planted stands in the Kuinderbos have in common (Fonda 1974). *Picea sitchensis* stands were most rich in fern-species in all periods. The *Picea sitchensis* stands in the Netherlands are mostly found on drained, acid sandy soils on which common, mostly acidophilous fern species grow. *Picea sitchensis* has

been planted on thousands of hectares in Scotland and Ireland, but rare ferns are absent there, as all these stands were planted on acid soils (Ford *et al.* 1979) (see also Chapter 5).

Fraxinus excelsior stands only harboured rare (calcicole) species on fine-grained sand in combination with deep trenches and a low water level. *Polystichum lonchitis* grows within this habitat, but elsewhere it has been found in a mixed deciduous stand near Lelystad and in a marl pit in the south of the Netherlands. In mountainous areas it is especially common outside forests in sites more than 900 m above sea level (Dostál & Reichstein 1984). In the peat erosion area, *Picea abies* stands proved to be a 'new' habitat being invaded by *Gymnocarpium dryopteris* and *Asplenium scolopendrium*. The repetitive heavy thinning appeared to have an adverse affect: it encouraged forbs and bramble that outcompeted the fern plants. The trench habitat also played a role, as under the dense *Picea abies* canopy an ecto-organic layer had formed, with hardly any slumping or bare soil that calcicole fern species require for germination. In the sandy part of the Netherlands, *Picea abies* stands are poor in ferns. After thinning, various acidophilous species are found, but the combination of calcareous, fine grained sandy soils on peat and deep trenches is not found elsewhere. *Acer pseudoplatanus* has been described as a ruderal tree species (van der Werf 1991). It is able to recruit in the woodland habitat at a high density. No fern species were exclusively or statistically correlated with this species, but during the 2002 census *Acer pseudoplatanus* stands proved to be inhabited by rare ferns (e.g. *Asplenium scolopendrium*, *Polystichum setiferum*).

It can be concluded that in the Kuinderbos rare fern species do 'behave' differently than in habitats elsewhere in the Netherlands, or even in Europe. It seems that the new habitats here provide new opportunities within the ecological framework characterising each species. The same phenomenon has been observed in bryophytes and fungi. Some calcicole species were found here for the first time in the Netherlands on trench sides: e.g. *Distichium inclinatum* and *Helvella confusa* (Tjallingii 1983, Bremer & Ott 1990). It has been shown that some macrofungi species prefer the trench habitat because they form mycorrhiza with trees that only grow along trenches or because their mycelia are associated with bryophytes that are concentrated on trench sides as here litter does not accumulate. Erosion (resulting in small bare areas) and the microclimate also play a role (Bremer 2000b). Seven out of 128 species of bryophytes recorded in the Kuinderbos were significantly restricted to the trench habitat (5.5 %; Bremer 1994). In ferns, 16 out of 25 species (64.0 %) prefer this habitat.

Figure 3.8 summarises the habitat features facilitating the establishment of a large group of rare ferns in the Kuinderbos. Ferns have a strong link with trenches because of the microclimate and the small-scale erosion required for their germination and establishment. In their haploid phase, ferns have prothallia c. 0.5 cm in diameter, which makes them sensitive to litter; in contrast, bryophytes are able to overgrow litter, while macrofungi (saprophytes) depend on it. The key abiotic factors for the rare ferns in trenches within the Kuinderbos are no litter accumulation, erosion, capillary feeding (constant soil moisture), humidity and 2 - 5 % incoming light.

The 25-year monitoring of populations of rare ferns in the Kuinderbos revealed that the most successful species were *Asplenium scolopendrium*, *Gymnocarpium dryopteris* and *Polystichum aculeatum*. Thirteen species were unable to build up a large population. After apparently establishing they disappeared or their populations remained small and did not increase. *Polystichum aculeatum* has been much more successful than *Polystichum setiferum*, while *P. lonchitis* is teetering on the verge of extinction. The success of these species in the Kuinderbos parallels their behaviour elsewhere in the Netherlands. During the last 25 years these three species have increased in numbers in the Netherlands, with *Polystichum aculeatum* being more successful than *P. setiferum* and *P. lonchitis* still being very rare. In the Kuinderbos the number of *P. setiferum* increased after 1979 to a maximum of 130 plants, and subsequently decreased. Only at one site was a cluster of *Polystichum setiferum* observed,

while *Polystichum aculeatum* formed 12 of these clusters. In both species the presence of high densities of spores around founder plants determined this pattern. Both species react differently to severe winters. *Polystichum setiferum* is an Atlantic species and sensitive to frost. Numbers decreased after severe winters (Bremer 1995). *Polystichum aculeatum*, however, has more leathery fronds which protect it from frost.

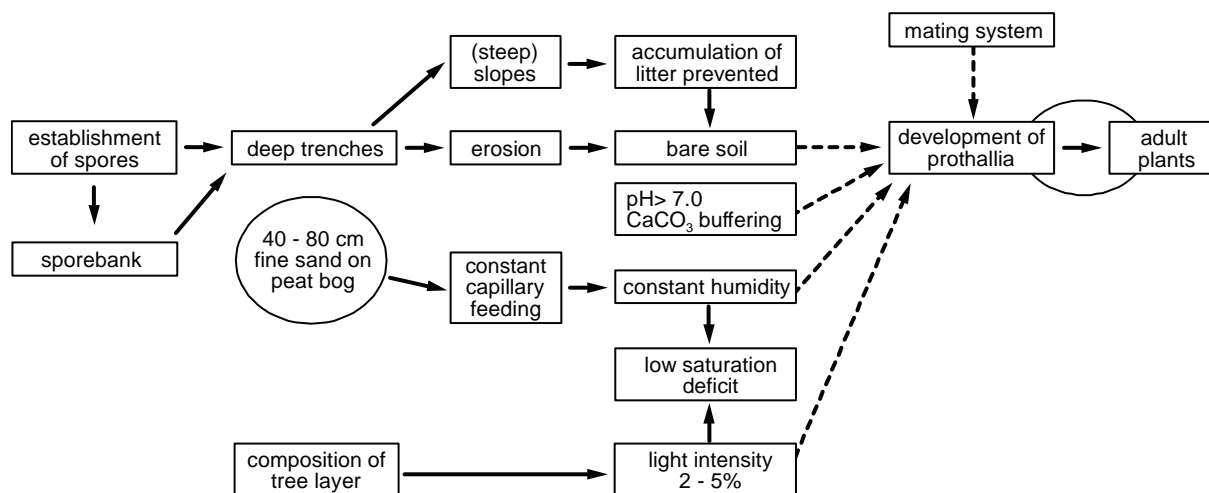


Figure 3.8. Habitat features that facilitated the establishment of a large group of rare (calcicole) fern species in the peat erosion area in the Kuinderbos.

Dispersal capacity

Before 1932 the current woodland floor was under the sea ($2.6 - 4.9 \text{ g NaCl l}^{-1}$, de Beaufort 1954). After the Zuiderzee was closed off from the open sea by a dyke (1932) this NaCl concentration dropped to c. $0.17 \text{ g NaCl l}^{-1}$ within three years. A recent investigation indicates that spore survival is possible in saline conditions (de Groot 2007). This means that spores settled at the bottom of the Zuiderzee and after 1932 at the bottom of the IJsselmeer. They were not transported to deeper parts of the soil (as is the case on land, Esteves & Dyer 2003). After the reclamation of the Noordoostpolder, and prior to planting, a natural vegetation developed, without ferns (Feeke & Bakker 1954). The spore bank had probably been lost from the surface of the ground during 1941 - 1952, when the empoldered land was taken into cultivation. The latter entailed digging trenches to drain the soil and then ploughing (Wildschut 1992). Fern colonisation did not start until later.

Fern spores are able to cross long distances. Due to their high dispersal capacity one may assume that ferns are the first to colonise new (primary) habitats. It was possible to reconstruct the first establishment of the ferns in the Kuinderbos by calculating or estimating the first year of their establishment. I have shown that the moment of colonisation was determined by the size of the nearby source populations. One may argue that the effect of the nearby population is also related to ecology and density. One would expect the more common species to arrive first, followed later by rare species. This was confirmed for the group of ferns as a whole (Table 3.7). But within the groups of acidophilous fern species and calcicole fern species, this correlation does not exist, which indicates the important role of nearby source populations.

Pioneer mass colonisation by rare ferns has not been assessed before in Dutch woodlands, but has been recorded in mural populations (e.g. *Asplenium adiantum-nigrum* and *A. trichomanes*, Denters 1997). On 'old' land, primary colonisation seldom takes place, and spore banks will be present in nearly all terrestrial habitats (Dyer & Lindsay 1992). Grashof-

Bokdam (1997) studied the effects of fragmentation of forest habitat in the past on present occurrence of plant species. In four species (*Dryopteris carthusiana*, *Dryopteris dilatata*, *Polypodium vulgare* and *Pteridium aquilinum*) the effect of area was significant. She found that the probability of encountering these fern species increased concomitantly with the size of the patch of woodland. *Dryopteris filix-mas* was the only fern species that showed a positive correlation with connectivity: the summed area of woodland within a zone of 500 m. As population size was not quantified in this zone it is difficult to state that population size played a role, but in the Kuinderbos study the number of occupied km² grid cells and population sizes in these cells within a radius of 50 km were both correlated with the time of colonisation.

One might argue that the first year of growing from spore to sporophyte is not the same as the first year of arrival of the spores. From the first year after the land had been taken into cultivation spores arrived and were able to build up a 'young' spore bank. It seems likely that species with a large population nearby created more extensive spore banks than species growing further away, or species with small populations. The year of first establishment might be correlated with the size of the spore bank, as all species (except *Pteridium aquilinum*: Dyer & Lindsay 1996) are able to build up such banks. Differences in ecology will have played a role as well. As calcicole species prefer trench sides, their overall potential habitat is less than a tenth in area of that of the wood floor. Various species (e.g. *Dryopteris dilatata*, *D. carthusiana*) depend on dead wood, which also restricts the summed area available in young stands.

On the basis of the collected data and assumptions, the colonisation has been reconstructed in detail, which shows that nearly all species had colonised the area within 20 years when most stands were dense and before the 1972/1973 storms (Fig. 3.5). After these storms and thinning light intensities increased at the woodland floor. A larger area of potential fern habitat became available, which meant a rapid increase in population size in several species. Recruitment took place in the spore shadow of founder plants, which resulted in the clustering of plants. This clustering is related to the fact that wind probably plays a secondary role within the trench habitat, implicating a spore shadow surrounding adult plants (Fig. 3.4). At the same time spores are coming in from elsewhere and build up a sporebank. Even years after the first arrival and establishment, the actual distribution of some species reflects the impact of biotic factors (e.g. competition with forbs) and limitations of dispersal. These data parallel those of Edgington (2007) on the colonisation of *Asplenium trichomanes* and *A. adiantum-nigrum* in the mural habitat in London. In still air (within trenches) spores will be deposited at a very short from a dehiscing sporangium. At mural habitats wind can play an important role which explains the SW - NE distribution in London, which has not been observed in the Kuinderbos.

There are large differences in success among fern species, which are probably not related to habitat or the influx of spores. These differences might be related to the reproductive system and genetic load. Diploid species may have a large genetic load (e.g. *Osmunda regalis*, Zenkteler 1999) and depend on outcrossing, while polyploid species can use selfing. The duplicated loci of polyploid taxa may mitigate the expression of recessive lethal alleles by intragametophytic selfing, whereas genetic load probably maintains the mating systems of the intergametophytic diploid taxa (Chiou *et al.* 2002). Diploid species can only establish successfully if there are at least two prothallia growing a short distance apart. Schneller & Holderegger (1996) observed in *Athyrium filix-femina* that sperms could swim about 2.4 – 9.6 cm. In polyploid species selfing takes place, so isolated spores can result in an adult plant. Eight of the 25 fern species in the Kuinderbos are diploid. Diploid and polyploid species appeared to be equally successful in establishment and population growth. The diploid *Asplenium scolopendrium* was one of the most successful species, while the polyploid *Gymnocarpium robertianum* was not successful, for unknown reasons. De Groot (2007) showed that

although *Asplenium scolopendrium* is an outcrossing species, intra- and intergametophytic selfing can also take place. The species has a strong antheridogen system and high reproductive effort.

Lichens, ferns, bryophytes and fungi all produce spores. Many species within these groups are able to colonise virgin habitats. Miles & Longton (1992) concluded for two bryophyte species that spores are deposited at considerable densities within and immediately outside the parent colony, but that the majority of the spores are dispersed to greater distances. Peck *et al.* (1990) recorded a short distance gradient of spore deposition. They however did not measure all released spores. The ferns were not alone in succeeding to colonise: bryophytes and fungi were also successful. In latter groups, the first year of establishment could only be calculated in some species. The importance of distance to nearby populations and population size in a zone surrounding the area could not be assessed. In fungi this is impossible, as mycelia can be present without fruiting for years.

Prospects

The *Picea sitchensis* stands will disappear because of the thinning regime and declining vitality. As these stands harbour the largest number of rare fern species, this process will have implications for the fern populations. At one of the hot spots, avenues of *Fagus sylvatica* will compensate for the loss of *Picea sitchensis*, enabling rare ferns such as *Asplenium scolopendrium* and *Polystichum aculeatum* to maintain or even increase their numbers, as has been observed in recent years. Without human interference *Picea sitchensis* will be replaced by *Acer pseudoplatanus* and *Fraxinus excelsior*, which implies that *Gymnocarpium dryopteris* will decline. The microclimate in these stands will change, as in spring more light penetrates the trench sides under the deciduous trees. But some rare species have sustainable populations in *Fraxinus excelsior* stands, and recruitment of *Acer pseudoplatanus* will suppress forbs and bramble and favour *Asplenium scolopendrium* and *Polystichum aculeatum*. The repetitive heavy thinning and gap formation in *Picea abies* have disqualified this type of stand from being a promising habitat for ferns in the future². These stands will change in composition. Deciduous tree species will enlarge the variation in the forest and within 10 – 20 years a new habitat will be created for ferns in the peat erosion area.

To answer the question about the future of the populations of the rare ferns it must also taken into account that two processes are taking place in the peat erosion area: decalcification and oxidation/mineralisation of the underlying peat. Nine rare calcicole fern species depend on the fine sand deposits. Shells (*Mya arenaria*, but also *Malcoma baltica* and *Cerastoderma edule*) are important for preserving a neutral to slightly alkaline habitat. The content of shells in the deposits varies between 0.3 and 4.5 % (analysed after removing the larger shells in 1979). Acid components and acid rain contribute to the decalcification of the upper soil, the former being more important than acid rain (de Vries 1994). The pH will decrease if the CaCO₃ content is below 0.5 % (Rozema *et al.* 1985). The process of decalcification will be faster in a medium-grained sand soil compared with a fine-grained soil because in the latter soil, water percolates more slowly. Sandy soils (dune area) can decalcify by 0.25% per 100 years (Rozema *et al.* 1985). Ranwell (1972) noted that in British dune areas, most free carbonate is lost from the first 10 cm of surface dune soil within 300 - 400 years. In afforested areas decalcification will proceed more rapidly, as litter contributes to the process. Ott (1990) measured a decrease of the pH in the topsoil (10 - 20 cm, mixed sample) of the fine-grained sand deposits in a period of 17 years (1970 - 1987). An increase of *Acer pseudoplatanus* and *Fraxinus excelsior* will probably slow down the process of decalcification (Ellenberg 1982). As long as there are shells in the soil profile, calcicole ferns are able to grow in the area. It is

² In the heavy storm of 2007 most of the *Picea abies* stands were completely destroyed by windfall

expected that decalcification will continue for several centuries before the CaCO_3 is lost. In the short term, calcicole fern species (and other species as well) will be able to sustain their populations and it seems likely that some calcicole fern species such as *Asplenium scolopendrium* and *Polystichum aculeatum* will even increase in number.

The oxidation and mineralisation of the peat is taking place because of drainage. In the last 50 years the soil level has subsided by an average of over 0.8 m (c. 1.6 cm year^{-1}). The peat layer (0.5 - 2.5 m thick) functions as a sponge, supplying the fine-grained sand deposits with water. The conservation of that sponge is necessary if we wish to protect rare calcicole fern species. Rewetting of the area is essential. At this moment, peat is being lost and the micro topography will become more prominent. On average, loss of peat leads to higher water tables, which will threaten the fern populations in the shallow trenches (already poor in calcicole species). As long as the fine-grained sand deposits on peat continue to co-exist with dozens of kilometres of drainage trenches, there will be opportunities for rare ferns to establish.

Dominance of forbs will not last forever. In the future, *Acer pseudoplatanus* will suppress these competitive species in favour of the rare ferns. Light will only be a limiting factor in dense recruiting stands of *Acer pseudoplatanus*. There will be no return to the past situation of large areas of *Picea* spp. stands. New opportunities will arise and we expect the Kuinderbos to be rich in fern species and numbers for the coming decades.

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Colonisation of polder woodlands on clay by ferns and other vascular plant species

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Abstract

The vascular plant species of 53 woodlands on clay soils in two polders reclaimed from the Zuiderzee, Netherlands – Noordoostpolder and East Flevoland – were surveyed. Total species number per woodland was found to be correlated with woodland age, area (i.e. size) and distance to human settlements, whereas the number of typical woodland species per woodland was correlated with woodland age and area. The number of recruiting tree and shrub species per woodland increased concomitantly with woodland size and proximity to villages. The number of fern species per woodland was only correlated with area. The latter was also true for the abundance of two of the fern species: *Dryopteris filix-mas*, *Dryopteris dilatata*. The occurrence of other woodland species was significantly correlated with one parameter (e.g. *Alliaria petiolata*, *Epipactis helleborine*) or combination of parameters (e.g. *Geranium robertianum*, *Ribes rubrum*). In four species the presence of footpaths or rides contributed to the colonisation (e.g. *Ranunculus ficaria*, *Geum urbanum*). Long-term monitoring in some woodlands demonstrated the effect of woodland age.

Despite their large capacity to disperse, ferns are not always the first to establish in woodlands. Earlier colonists include other anemochoric vascular species of woodlands, and also endozoochoric and epizoochoric woodland vascular species. Ferns are able to colonise trenched woodland within 10 - 20 years after it has been planted. The process takes longer if there are no drainage trenches, as colonisation depends on the availability of safe sites for establishment. The rapid colonisation of pine stands also indicates the importance of the substrate and microclimate for successful establishment.

The presence of trenches within woodlands promotes fern species diversity, especially the diversity of calcicole fern species, which are particularly associated with trenches, though they are mostly present at low densities. In Flevoland, trenched woodlands on clay are much richer in ferns species than woodlands on the mainland (no trenches), mainly because the trenches provide a shady habitat with a calcareous substrate.

Introduction

In 1932 the Zuiderzee was closed off from the sea and subsequently four polders were reclaimed. This study is restricted to two of them: the Noordoostpolder (reclaimed in 1941/1942) and East-Flevoland (reclaimed in 1958) (Fig. 4.1). For over a millennium these areas had been part of the sea floor, overlain by 1 - 4 m of water: freshwater during the Flevo period, brackish in the Almere and brackish to salty from c. 1600 - 1932 during the Zuiderzee period. After the closure of the Zuiderzee in 1932, a freshwater lake, the IJsselmeer, developed. In the reclaimed polders a natural vegetation developed (marshes, reed beds, sometimes grasslands, e.g. Feekes & Bakker 1954, Bakker 1957, Jans & Drost 1995), almost all of which was brought into cultivation within 15 years. After cultivation and drainage, over 5,000 ha of woodlands were planted on clayey soils. Initially, no woodland species were present in the herbaceous layer, so primary colonisation had to take place.

We set out to answer the following questions.

- what factors characterising a planted woodland (e.g. its age, area) have an effect on its colonisation by vascular plants, especially ferns?
- which habitats within woodlands do ferns prefer?
- how rapidly do fern species colonise newly planted woodlands on clayey soils?
- for what ecological reasons is there a difference in fern species composition between woodlands in the polders and those on the mainland ?

Some authors have pointed out that woodlands which are isolated in an agricultural landscape are habitat islands. The number of species in such woodland islands depends on their area, degree of isolation and the duration of the isolation (e.g. Scanlan 1981, Peterken & Game 1984, Grashof-Bokdam 1997). Moreover, the species richness of habitat islands may not always be explicable in terms of the theory of island biogeography alone (McArthur & Wilson 1967). The reason is that the number of species is a function not only of immigration and extinction rates, but also of habitat diversity, successional phase and the history of the area, which are - amongst others - reflected by the seedbank (Hermý 1986). The woodlands we studied are habitat islands surrounded by intensively cultivated farmland. Isolation variables were selected with respect to the mainland and the villages in the polders, since we assumed that the gardens in the villages and also other habitats would be important sources of characteristic woodland species. Connectivity was not taken into account. Although 35 percent of the woodlands examined are linked by shelter-belts, they are rarely connected with other woodlands. Woodland age and area, and silt content were also taken into account (as habitat parameters).

Various trees and shrubs had been planted, and we expected that the most abundant colonisation of woodland species, including the ferns, would be in the more natural stands (*Fraxinus excelsior*, *Salix alba*) corresponding to the *Fraxino-Ulmetum* community (van der Werf 1991), rather than in stands of *Pinus* spp., *Acer pseudoplatanus* and *Fagus sylvatica*, which do not characterise this community in an early phase. Given that the number of fern species in the Kuinderbos was strongly correlated with drainage trenches (Bremer 1980a, b), we expected that woodlands drained by trenches would have more fern species than those without this habitat. There was no reason to assume that other woodland species would prefer this habitat as well.

The a priori assumption was that anemochoric woodland species, especially ferns, would not be influenced by isolation, as the species were presumed to be efficiently dispersed by wind. This had been demonstrated in the Kuinderbos, in the reclaimed Noordoostpolder, where 28

fern taxa were found, some of which were recorded for the first time in the Netherlands. Here, most species established after afforestation on calcareous sands overlying peat (Chapter 3). We expected that isolation would be important, for the other woodland species, especially in relation to the mainland as source of diaspores. For example, it has been demonstrated that the colonisation of road verges started from the mainland and old roadsides were found to be richer in species sooner than young ones (Nip-van der Voort *et al.* 1979). We expected ferns to be the first species to colonise young woodlands and that the number of fern species would achieve saturation within a short period. In the Kuinderbos the number of fern species peaked within 20 years (Chapter 3). We had no reason to assume that colonisation in the clayey woodlands would differ from colonisation on other substrates.



Figure 4.1. The woodlands examined in the province of Flevoland (black). Excluded woodlands (too young or not on a clayey soil) are dotted. The following woodlands are mentioned in the text: Tb = Tollebekerbos, Eb = Emmelerbos, Enb = Enserbos, Jv = Jagersveld.

The deciduous woodlands on drained, clayey soil in the Netherlands have been planted. The best examples are those created on estates from the 17th century onwards (some 12,000 ha, including plantations on undrained soils, Dirkse 1993). The planting of over 5,000 ha of trees in the young polders increased the area of clayey woodlands markedly (Bremer 1997). No rare ferns have been recorded on the mainland; here, the commonest fern species is *Dryopteris dilatata*. There was no reason to assume that in the polders the composition of the fern flora would be different.

The study area

Over 8,300 ha of woodlands have been planted in the polders reclaimed from the Zuiderzee. In the Noordoostpolder 28% of the afforestation was on clayey soils, compared with 73% in East-Flevoland. The composition of the clayey soils varies from slightly clayey (5 - 12% silt) to clay (> 25% silt); they are always calcareous, due to the high density of shells. Most of the woodlands are well drained, with the water table usually at a depth of over one metre in summer. Only a few of the woodlands examined are wet in winter or spring (mean depth of water

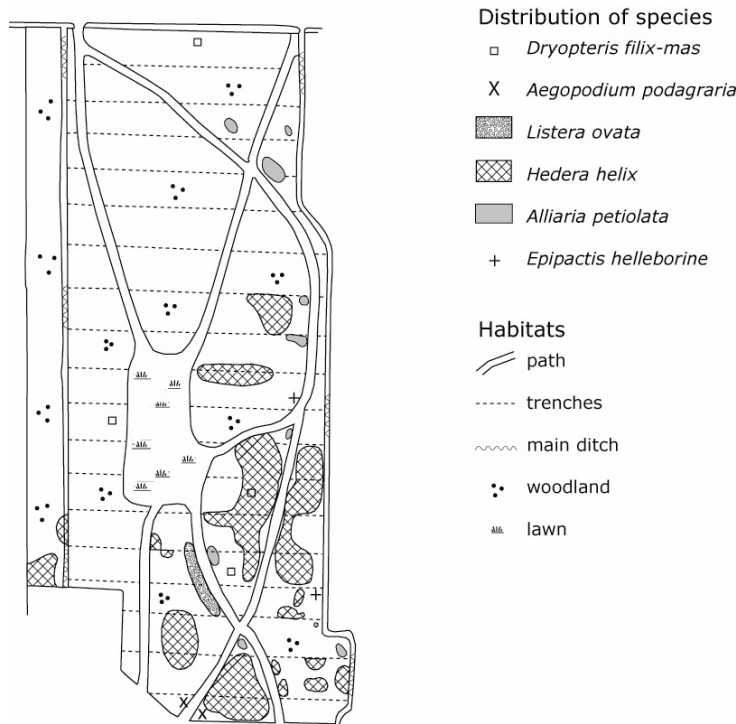


Figure 4.2. An example of a planted woodland on clay (Enserbos, near the village of Ens, see also Figure 4.1) and the distribution of woodland vascular plant species in 1992 (40 years after planting).

table < 0.5 m), due to seepage or water accumulation (on slightly clayey soils or by rewetting, e.g. Hulkesteinse bos). Here trenches have been dug for drainage, at a density of up to 1.1 km ha⁻¹, and on average c. 0.5 m deep. Various tree species have been planted, particularly *Populus x canadensis*, *Quercus robur*, *Fraxinus excelsior*, *Fagus sylvatica*, *Salix alba* and *Acer pseudoplatanus*. At some localities within woodlands, species such as *Pinus* spp., *Picea* spp. and other exotic tree species have been planted. Each woodland is divided into many woodland parcels, separated by deep drainage trenches or ditches. The parcels are bisected (lengthwise) by rides or paths and are drained by trenches running to the main ditch (Fig. 4.2).

Methods

From 1990 to 1994, 53 woodlands were surveyed and the distribution of woodland species in the Noordoostpolder and East Flevoland was mapped (Fig. 4.1, Fig. 4.2). The colonisation in three medium-sized woodlands had been monitored since c. 1970. Estate woodlands on the mainland, planted in the 17th or 18th centuries were used as the reference. In addition, a woodland near Zwolle (Overijssel), planted in 1971, was monitored for more than 20 years (Westerveldse bos). The fieldwork was carried out in late spring or early summer, when there is most chance of finding all species. Small woodlands were visited once, sometimes twice; larger woodlands were visited more frequently. The chosen survey route incorporated all rides, paths and stand types. If trenches were present, they were scrutinised, by walking along them for more than 50 % of their total length. In one of the woodlands (Jagersveld) all trenches were surveyed. The listing and mapping of less common species on the route woodland⁻¹ was deemed finished when no species could be added to the list. On average, 0.1 km ha⁻¹ was sampled. For rare fern species and for other characteristic species of the woodland habitat, the substrate, composition of the canopy and their relationship to habitats were recorded. The abundance of species woodland⁻¹ was assessed with the Tansley scale. In 14 randomly selected woodlands the maximum number of characteristic woodland species ha⁻¹ stand⁻¹ (N_{max}) was based on species mapped with a sampling density of at least 0.3 km ha⁻¹. On the clayey soils a *Fraxino-Ulmetum* community is evolving. Species characterising this community were considered to be true

woodland species (van der Werf 1991, Stortelder *et al.* 1999). Other species with an optimum in woodland communities and woodland edges in the Netherlands, but not known to be characteristic of the *Fraxino-Ulmetum* were also taken into account – including all ferns found (a total of 12 species). The variable ‘number of species woodland⁻¹’ incorporates all species found below the woodland canopy. Species growing on rides without a closed canopy were excluded. The number of endozoochoric species is based on species growing in the herb layer or lower shrub layer. The number of recruiting tree and shrub species encompasses recruitment from species planted and species transported from elsewhere.

Independent variables such as woodland age and area size were calculated using information gathered from plantation maps, isolation variables from topographic maps (at a scale of 1:25,000) and silt content from soil maps (with composition of the soil profile). Data about paths, rides and trenches were collected during the fieldwork. The Jagersveld woodland has been monitored since 1979. In most years, all the rare ferns on trench banks were mapped, and frond characteristics measured. The moment of colonisation was estimated by extrapolating population size and the performance of the plants found. The dispersal types are mainly based on Feeke & Bakker (1954).

Table 4.1. Dependent and independent variables used in the study on woodlands on clayey soils in Flevoland.

Independent variables

patch size

A = woodland area

habitat quality

s = silt content of the upper soil

isolation

d1 = distance to the mainland

d2 = distance to large wooded area (> 100 ha) on the mainland

d3 = distance to nearby woodland, larger than 1 ha

d4 = distance to nearest village

other variables

l = woodland age

p = woodland with footpaths or rides

Dependent variables

s1 = the number of vascular species within the shaded habitat woodland⁻¹

s2 = the number of characteristic woodland vascular species (corrected for some seeded species) woodland⁻¹

s3 = the number of berry-producing species in the herb layer and lower shrub layer woodland⁻¹

s4 = the number of recruiting tree and shrub species woodland⁻¹

s5 = the number of fern species woodland⁻¹

Statistical analysis

The dependent variables were analysed by linear multiple regression. Independent variables (Table 4.1) were added by using stepwise forward selection (Norusis 1986). Because frequency distributions of some of the independent variables were skewed, they were transformed logarithmically (A, d3, d4). For some regressions, the characters within the ordinal Tansley code were transformed into numbers (r = 1, o = 3 etc.). Correlations between independent and dependent variables were calculated as Pearson correlation coefficients. The preference for habitats within the woodland was tested by chi-quadrat analysis.

Results

Species and habitat islands

The total number of plant species recorded in the 53 woodlands was 135. Of these, 43 were characteristic of woodlands: they included 12 fern species (Table 4.2). The most frequent seed plant species (occurring in 77% of the woodlands) was *Ribes rubrum*; the most frequent fern (45% of the woodlands) was *Dryopteris filix-mas*. The most common species in the herbaceous layer were *Galium aparine*, *Poa trivialis*, *Taraxacum* section *Vulgaria* and *Urtica dioica*. All the fern species known from other Dutch woodlands on clay were found. 75 % of the expected woodland species (Table 4.2) were found, although many only appeared in low densities, related with the early phase of colonisation. Various species of ancient woodlands, such as *Corydalis* spp. and *Ranunculus auricomus*, which are known to be poor colonists, were not found in the surveyed woodlands. Some of the fern species found (such as *Polystichum* spp., *Dryopteris affinis* and *Asplenium scolopendrium*) are absent from the woodlands on clay soils on the mainland. The same holds in the examined woodlands for a group of flowering plants, including *Epipactis helleborine*, *Ribes nigrum* and *Lonicera periclymenum*.

A correlation matrix for all variables (Table 4.1) is given in Table 4.3. The area (the size) is only correlated with the silt content and the presence of paths or rides. The soils in younger woodlands have a higher silt content. Woodlands age is correlated with most of the isolation variables. The older woodlands are situated nearer to the mainland, are more isolated from other woodlands in the polders and are closer to villages. The dependent variables all correlated with each other. The total number of species woodland⁻¹ was correlated with area, age and distance to the villages. 56% of the variation could be explained using a multiple regression model with these three variables (Table 4.4).. The best model for the total number of characteristic woodland species woodland⁻¹ incorporates area and age. Age is the variable with a significant effect within the best model for the number of endozoochoric species woodland⁻¹. Recruiting tree and shrub species were more common in larger woodlands and near villages. The number of fern species per woodland was correlated with area and silt content. No correlations were found with isolation and age (Table 4.4). The best model for *Dryopteris filix-mas* and *Dryopteris dilatata* included the area only (Table 4.5). The same holds for *Epipactis helleborine*. Age and distance to villages were significant for *Ribes rubrum* and *R. uva-crispa*, while for *Epilobium montanum* and *Alliaria petiolata* the presence of paths and rides had a significant effect. *Geum urbanum* and *Ranunculus ficaria* were correlated with the presence of paths and rides within the woodlands but also with age. A correlation with silt content was found for *Rubus* section *Corylifolia*. This species prefers woodlands and sandy clay soils. *Ribes nigrum* did not show any correlation with the variables. In six of the 13 species examined, woodland age plays a significant role in the models, but distance to the mainland (d1) or the distance to a large woodland on the mainland (d2) is not important. The explained variation varied from 8% (*Alliaria petiolata*) to 47% (*Ribes rubrum*).

Table 4.2. List of characteristic woodland species in the surveyed woodlands on clay soils in Flevoland, based on van der Werf (1991) and Stortelder *et al.* (1999). **Dt** = dispersal types based on Feekes & Bakker (1954): An1 = anemochoric species: seeds/spores disseminated by wind, transported for kilometres during storms (ferns, orchids), An2 = anemochoric species: seeds disseminated by wind, transported over hundreds of kilometres during storms, An3 = seeds disseminated by wind, transported over no more than 20 – 30 metres during storms, B = barochoric species, En = endozoochoric species, Ep = epizoochoric species, M = myrmecochoric species, H = hydratochoric species. **Np** = frequency in polder woodlands (n = 53), **Np%** = $Np/53 \times 100\%$, **Ne** = frequency in estate woodlands (> 200 years old, n = 3), **Ne %** = $Ne/3 \times 100\%$. * = not observed during the survey, but observed in the preceding period.

<i>Name</i>	<i>Dt</i>	<i>Np</i>	<i>Np%</i>	<i>Ne</i>	<i>Ne%</i>
Ferns					
<i>Dryopteris filix-mas</i>	An1	24	45	2	67
<i>Dryopteris dilatata</i>	An1	13	25	3	100
<i>Athyrium filix-femina</i>	An1	7	13	1	33
<i>Dryopteris carthusiana</i>	An1	5	9	0	0
<i>Dryopteris affinis</i>	An1	5	9	0	0
<i>Polystichum setiferum</i>	An1	3	6	0	0
<i>Asplenium scolopendrium</i>	An1	3	6	0	0
<i>Ophioglossum vulgatum</i>	An1	2	4	0	0
<i>Polystichum aculeatum</i>	An1	1	2	0	0
<i>Polystichum lonchitis</i>	An1	1	2	0	0
<i>Polypodium vulgare</i> ¹	An1	1	2	0	0
<i>Dryopteris cristata</i> ¹	An1	1	2	0	0
Other woodland species					
<i>Urtica dioica</i>	Ep	53	100	3	100
<i>Ribes rubrum</i>	En	41	77	3	100
<i>Ribes uva-crispa</i>	En	30	57	3	100
<i>Epilobium montanum</i>	An2	29	55	3	100
<i>Alliaria petiolata</i>	B	21	40	3	100
<i>Geranium robertianum</i>	Ep	21	40	3	100
<i>Ribes nigrum</i>	En	18	34	1	33
<i>Rubus caesius</i>	En	16	31	3	100
<i>Rubus section Rubus</i>	En	16	31	2	67
<i>Geum urbanum</i>	Ep	16	30	3	100
<i>Epipactis helleborine</i>	An1	16	30	0	0
<i>Rubus section Corylifolia</i>	En	15	28	1	33
<i>Ranunculus ficaria</i>	B	14	26	3	100
<i>Cardamine flexuosa</i>	An2	13	25	3	100
<i>Listera ovata</i>	An1	6	11	2	67
<i>Veronica hederifolia</i>	M	6	11	2	67
<i>Silene dioica</i>	An3	5	9	1	33
<i>Chelidonium majus</i>	M	4	8	1	33
<i>Rubus idaeus</i>	En	4	8	1	33
<i>Circaea lutetiana</i>	Ep	3	6	3	100
<i>Stachys sylvatica</i>	Ep	3	6	2	67
<i>Lonicera periclymenum</i>	En	3	6	1	33
<i>Scrophularia nodosa</i>	An3	2	4	3	100
<i>Poa nemoralis</i>	An3	2	4	3	100
<i>Hedera helix</i>	En	2	4	3	100
<i>Carex remota</i>	H	2	4	3	100
<i>Fragaria vesca</i>	En	1	2	2	67
<i>Impatiens parviflora</i>	Au	1	2	1	33
<i>Chaerophyllum temulum</i>	Ep	1	2	1	33
<i>Deschampsia caespitosa</i>	Ep	1	2	1	33
<i>Ilex aquifolium</i>	En	1	2	1	33

Characteristic Fraxino-Ulmetum species not found in the surveyed woodlands, but found in woodlands on other soil types in Flevoland

Characteristic *Fraxino-Ulmetum* species not found in the woodlands of Flevoland

¹ without durable terrestrial population

² found on roadsides; rare and a late colonising species

³ found in the Voorsterbos on boulder clay in 2005/2006

⁴ planted in the Emmelerbos

Table 4.3. Pearson correlation coefficients between various independent and dependent variables
s = silt percentage, l = age, A = area, d1 = distance to mainland, d2 = distance to large wooded area (> 100 ha) on mainland, d3 = distance to nearby woodland larger than 1 ha, d4 = distance to nearest village, p = paths or rides present (for some abbreviations, see Table 4.1). Significance: * = $p < 0.05$ ** = $p < 0.01$ *** = $p < 0.001$ - = negative correlation.

[illegible]

Table 4.4. Regression equations describing the relationship between various dependent and independent variables of woodland area (A), woodland age (l), distance to villages(d4). Only models with significant regression coefficients ($p < 0.05$) are given. $R^2 \cdot 100\%$ = % variance accounted for by the model, F = groups mean squared deviation/error squared deviation, p = significance. Dependent variables: s_1 = number of species woodland⁻¹, s_2 = number of characteristic woodland species woodland⁻¹, s_3 = number of endozoochoric woodland species woodland⁻¹, s_4 = number of recruiting trees and shrub species woodland⁻¹, s_5 = the number of fern species woodland⁻¹.

	$R^2 \cdot 100\%$	F	p
$s_1 = 3.9 + 9.5 \log A + 0.35 l - 3.7 \log d4$ <0.001 0.04 0.02	56	20.3	<0.001
$s_2 = -1.3 + 3.6 \log A + 0.2 l$ <0.001 0.002	40	16.0	<0.001
$s_3 = 0.2 + 0.1 l$ <0.001	23	14.7	<0.001
$s_4 = 2.3 + 2.3 \log A - 0.8 \log d4$ <0.001 0.03	42	17.2	<0.001
$s_5 = 0.9 + 1.4 \log A$ <0.001	25	16.5	0.002

Table 4.5. Regression equations describing the relationship between the abundance of various characteristic woodland species growing in more than 25 % of the surveyed woodlands (except for *Ribes nigrum*, *Rubus caesius*, *Rubus section Rubus* and *Urtica dioica* which are species without significant correlations with independent variables) and the independent variables: woodland area (A), woodland age (l), silt content (s), distance to villages (d4) and woodland with paths or rides (p). Only models with significant regression coefficients ($p < 0.05$) are given. $R^2 \cdot 100\%$ = % variance accounted for by the model, F = groups mean squared deviation/error squared deviation, p = significance. * $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$. a_s = abundance woodland⁻¹ according to Tansley code numerically transformed.

Species	Model	$R^2 \cdot 100\%$	F	p
Ferns				
<i>Dryopteris dilatata</i>	$a_s = -0.3 + 0.5 \log A$ 0.002	17	11.1	0.02
<i>Dryopteris filix-mas</i>	$a_s = 0.3 + 0.8 \log A$ 0.01	20	12.5	0.001
Other characteristic vascular woodland species				
<i>Alliaria petiolata</i>	$a_s = 0.5 + 1.1 p$ 0.05	8	4.4	0.04
<i>Epilobium montanum</i>	$a_s = 0.4 + 1.3 p$ <0.001	24	15.9	<0.001
<i>Epipactis helleborine</i>	$a_s = 0.005 + 0.5 \log A$ 0.001	19	11.3	0.001
<i>Geranium robertianum</i>	$a_s = -1.9 + 0.08 l + 0.8 \log A$ 0.003 0.006	25	8.0	0.001
<i>Geum urbanum</i>	$a_s = -2.5 + 1.4 p + 0.1 l$ 0.003 <0.001	42	17.3	<0.001
<i>Ranunculus ficaria</i>	$a_s = -0.7 + 0.03 l + 0.5 p$ 0.054 0.032	20	6.0	0.005
<i>Ribes rubrum</i>	$a_s = -0.7 + 0.1 l - 0.9 \log d4$ 0.003 0.005	47	20.8	0.003
<i>Ribes uva-crispa</i>	$a_s = -0.8 + 0.07 l - 0.52 \log d4$ 0.019 0.06	30	10.4	<0.001
<i>Rubus section Corylifolia</i>	$a_s = 0.7 + 0.06 l - 0.3 s$ 0.007 0.017	28	9.5	<0.001

Table 4.6. The maximum number of woodland species ha⁻¹ stand type⁻¹ in a number of selected woodlands. L = age of stands, t = woodland with trenches, n = maximum number of woodland species ha⁻¹ stand⁻¹, nF = the maximum number of fern species ha⁻¹ stand⁻¹, % = nF/n * 100 %, - = woodlands without this type of stand and stand not surveyed.

Name of woodland	L	t	<i>Fraxinus excelsior</i>			<i>Fagus sylvatica</i>			<i>Populus x canadensis</i>			<i>Pinus spp.</i>			<i>Tilia cordata</i>		
			n	nF	%	n	nF	%	n	nF	%	n	nF	%	n	nF	%
Edelkarper	23		2	1	50.0	0	0	0	2	0	0	-	-	-	1	0	0
Biddinghuizen	24	t	6	2	33.3	-	-	-	-	-	-	-	-	-	-	-	-
Larserbos	25		3	1	33.3	0	0	0	2	1	50.0	-	-	-	5	2	40.0
Wisentbos	25		2	0	0	3	1	33.3	1	0	0	6	5	83.4	-	-	-
Harderbos	25		3	1	33.3	1	0	0	4	0	0	5	3	60.0	-	-	-
Bremerbergbos	31	t	3	0	0	1	0	0	8	2	25.0	-	-	-	-	-	-
Tollebekerbos	36		5	1	20.0	3	1	33.3	-	-	-	-	-	-	-	-	-
Enserbos	40	t	7	1	14.2	6	1	16.6	-	-	-	-	-	-	-	-	-
Emmelerbos	43		7	1	14.2	1	0	0	-	-	-	-	-	-	-	-	-

Table 4.7. Ferns and other woodland species in trenched woodlands on clay soils in Flevoland. OSw = Swifterbos-East, OBb = Bremerbergbos, NEn = Enserbos, OHr = Houtribbos, Z7 = Biddinghuizen, OJv = Jagersveld. Total = total number of plants examined. The number of plants found in the trench habitat (t) and woodland floor (wf) are indicated, s = significance: * p < 0.05 ** p < 0.01 *** p < 0.001 (area of trenches/ wood floor involved in analysis). The number of plants woodland⁻¹ is based on samples (more common species) or the total population size (rare species) in the period 1992 – 1994 (except for *Polystichum aculeatum* and *P. setiferum* in the Jagersveld, period 1980 – 1985), ni = not investigated, - = species not present

	OSw		OBb		NEn		OHr		Z7		OJv		total	
Density of trenches (km ha ⁻¹)	0.8		0.8		0.4		1.1		0.3		0.8			
	t/wf s		t/wf s		t/wf s		t/wf s		t/wf s		t/wf s		t/wf s	
Ferns														
<i>Dryopteris filix-mas</i>	123/26	***	190/207	***	0/14	56/15	***	1/0	30/7	***	400/269	***		
<i>Dryopteris dilatata</i>	45/10	***	0/27	*	-	0/4	-	-	ni	-	45/41	***		
<i>Dryopteris carthusiana</i>	9/5	***	0/1	-	-	ni	-	-	ni	-	9/6	***		
<i>Athyrium filix-femina</i>	12/23	***	6/20	-	-	ni	-	-	ni	-	18/43	***		
<i>Polystichum setiferum</i>	1/0	-	2/0	-	-	-	-	-	2/0	-	5/0	-		
<i>Dryopteris affinis</i>	2/0	-	0/1	-	-	-	-	-	1/0	-	3/1	-		
<i>Asplenium scolopendrium</i>	-	-	7/0*	-	-	-	-	-	50/0	***	57/0	***		
<i>Polystichum lonchitis</i>	-	-	-	-	-	-	-	-	1/0	-	1/0	-		
<i>Polystichum aculeatum</i>	-	-	-	-	-	-	-	-	3/0	-	3/0	-		
Other woodland species														
<i>Epilobium montanum</i>	55/109	***	ni	-	ni	0/1	-	ni	-	-	55/110	***		
<i>Ribes uva-crispa</i>	1/4	-	ni	-	2/20	-	-	7/36	**	ni	10/60	*		
<i>Ribes rubrum</i>	10/32	***	ni	-	ni	-	-	11/32	***	2/23	23/87	***		
<i>Ribes nigrum</i>	4/4	***	ni	-	1/1	-	-	2/1	-	-	7/6	*		

The various habitats

The stands

The maximum number of characteristic woodland species ha⁻¹ stand type⁻¹ (N_{max}) varied between 0 and 8 species, while the number of fern species varied between 0 and 5 (Table 4.6). In dense and young stands, the N_{max} is very low; it increases when stands grow older. Stands with *Fraxinus excelsior* are relatively rich in species. In these stands, age and N_{max} are positively correlated (R² = 0.58 p < 0.01 n = 9), but this is not the case for *Fagus sylvatica* stands (R² = 0.26 p > 0.05 n = 8). *Dryopteris filix-mas* is the commonest fern species. In some large

woodlands, *Pinus* has been planted on clay. These stands were the first to be colonised by *Dryopteris* spp. and *Athyrium filix-femina*. In the other stands, *Dryopteris filix-mas* is found at a low density.

Drainage trenches

Eight of the 53 woodlands surveyed are intersected by drainage trenches. The abundances of the majority of fern species are significantly correlated with trenches (Table 4.7). As trenches contain water in the winter period, the ferns are restricted to the trench banks. All fern species prefer trenches in one or more woodlands. Various rare species with only a limited number of specimens, such as *Polystichum lonchitis* and *Polystichum setiferum*, occur only in the trench habitat; others grow inside and outside trenches, but on the trench banks their densities are significantly higher. In one woodland near Ens (Noordoostpolder) *Dryopteris filix-mas* was only found on the woodland floor (Fig. 4.2). *Dryopteris dilatata* showed the least preference for trenches. Though all the phanerogams listed in Table 4.7 (e.g. *Epilobium montanum*, *Ribes nigrum*) prefer the trenches in one or more woodlands, they are not exclusively linked with this habitat.

Other habitats

In young woodlands, sown grass species dominate the rides and the herb layer is poor in species. On lightly clayey soils (silt content 5 – 12%) *Ophioglossum vulgatum* has established at the edge of the rides (Bremer 1988). When the rides are overshadowed (often within 30 years) *Dryopteris filix-mas* can establish. Various epizoochoric species such as *Circaea lutetiana* and *Geum urbanum* are concentrated along paths and rides or start their colonisation there prior to colonisation of the woodland floor.

Colonisation

In four young medium-sized planted woodlands the colonisation was monitored for at least 15 years (Fig. 4.3). The Emmelerbos (no trenches) was planted on slightly clayey to heavy clay soils in the period 1949 – 1954. *Fraxinus excelsior* is currently the dominant tree species. Monitoring started in 1970. The first specimens of *Dryopteris filix-mas* established 18 years planting, followed by acidophilous species on decaying wood of *Pinus* and *Picea* (e.g. *Dryopteris dilatata*). Within 35 years of afforestation, the number of fern species had stabilised (Fig. 4.3), as had the number of characteristic woodland species (Fig. 4.4). Various woodland species established before ferns were recorded. These species are anemochoric (e.g. *Epipactis helleborine*), endozoochoric (e.g. *Ribes* spp.), epizoochoric (e.g. *Geum urbanum*) and some (e.g. *Impatiens parviflora*) are only able to disperse over short distances. Thirty percent of the potential characteristic woodland species are still absent, including late arrivals such as *Festuca gigantea* and *Ornithogalum umbellatum*. A high percentage of species from the group with short-distance dispersal (e.g. myrmecochoric and barochoric species) are absent (Fig. 4.5). The Tollebekerbos (no trenches) was planted in 1957. The first specimen of *Dryopteris filix-mas* established on a bank at the edge of the wood about 25 years after planting. Some years later, *Dryopteris dilatata* was found on decaying wood.

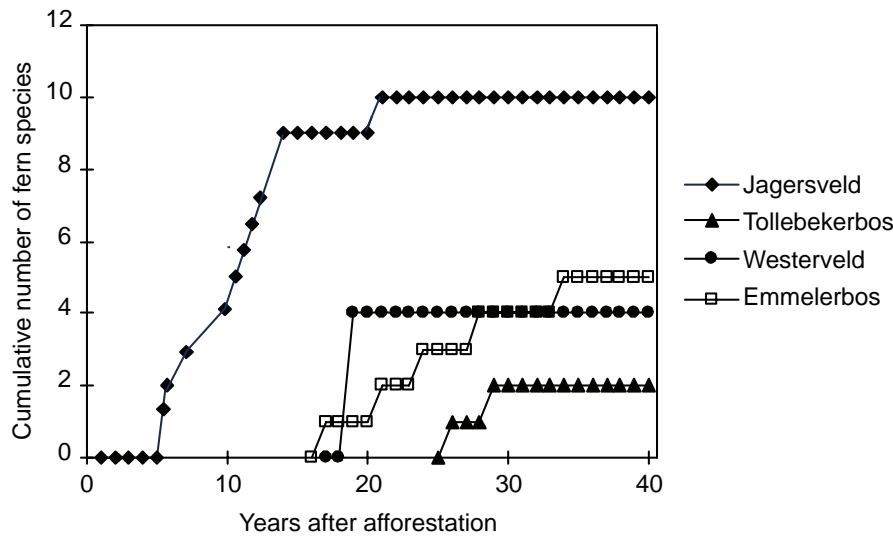


Figure 4.3. The cumulative number of fern species in relation to the age after afforestation, monitored in three woodlands in Flevoland and one near Zwolle (Westerveld). The Jagersveld data have been extrapolated for the period from the year of afforestation (1966) to the 13th year after afforestation. Westerveld was planted in 1971, Tollebekerbos in 1956 and the Emmelerbos in 1949 - 1954.

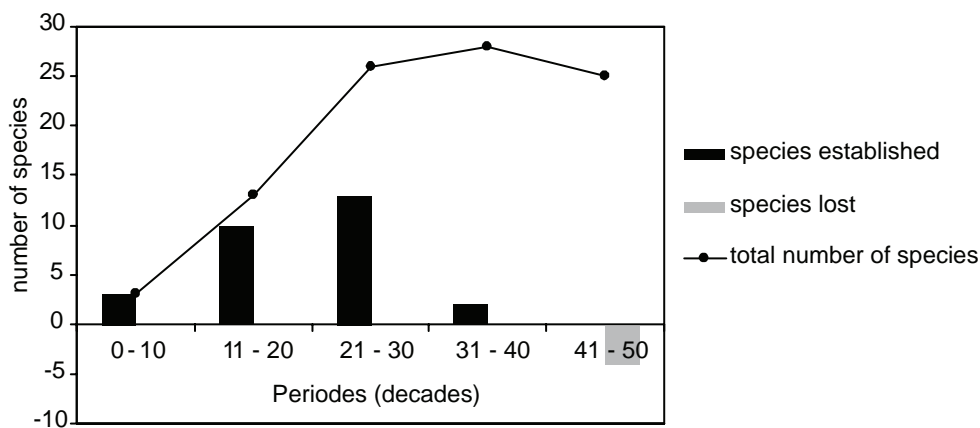


Figure 4.4. The total number of characteristic woodland species, the number of species that established decade⁻¹ and number of species that were lost decade⁻¹ in the Emmelerbos (western part).

The Jagersveld (East-Flevoland) was planted in 1966 on a slightly clayey soil. The trenches (c. 1 km in extent and on average 0.5 m deep) contain water in the winter, but in summer the water table may drop to a depth of more than 2 m (Brinkhorst 1984). Monitoring started in 1979. Eleven fern species established in this woodland, including *Polystichum aculeatum*, *Polystichum setiferum* and *Polystichum lonchitis*. The first sighting of *Dryopteris cristata* in Flevoland was in this habitat, but it disappeared within c. 10 years after establishment. Six species preferred trenches (Table 4.7). As the water table rose in winter, some plants were inundated and died, while others were damaged by frost during severe winters. As a reference, a young woodland (*Fraxinus excelsior*-*Carpinus betulus*) on the mainland, planted on acid clay near Zwolle was monitored from 1983. This small woodland (without trenches) was planted in 1971. There were no ferns at the start of monitoring. After moderate thinning in 1988, four species germinated, including *Dryopteris carthusiana*. Other woodland species were present at that

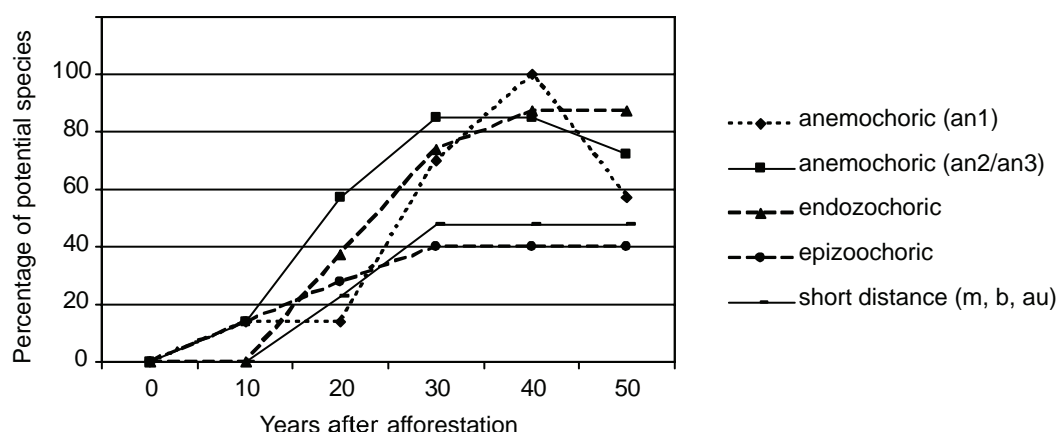


Figure 4.5. The percentage of potential characteristic woodland species per dispersal type (or group of dispersal types) during 50 years in the Emmelerbos. For abbreviations used for the dispersal types, see Table 4.2. The category an1 comprises all fern species and the orchids. Data prior to the 15th year of afforestation are based on extrapolation.

time, some of which (e.g. *Ranunculus ficaria*, *Deschampsia caespitosa*) originated from the grassland present before afforestation. Since 1988 the number of fern species has stabilised, while the number of woodland species has continued to increase.

Rare fern species

Various species found have never been recorded in woodlands on clay soils on the Dutch mainland. *Asplenium scolopendrium* has been found in Flevoland in seven woodlands, the largest population being in the Kuinderbos (see Chapter 3). Populations on clay (in four woodlands) have always been small. Monitoring since 1979 showed that severe winters (1984/1986) had a prolonged impact on the population size, but after 1989 there was a steady increase to more than 100 plants in 2002 (Fig. 4.6). No plants from the early years survived. The oldest recorded plant was 16 years old when it died. 92 % of the plants lived for less than 10 years; about 50 % died in winters with severe frosts. The maximum length of fronds plant⁻¹ also decreased due to severe winters (Fig. 4.7).

Polystichum aculeatum has been found in Flevoland in six woodlands. As in the case of *Asplenium scolopendrium*, the largest population was recorded in the Kuinderbos on calcareous sand (see Chapter 3). On clay there have been three records of plants growing on trench banks. *Polystichum setiferum* has also been recorded in Flevoland in six woodlands, with the largest population in the Kuinderbos (in 1993 128 specimens, Bremer 1995). The plants have always been found growing on trench banks on calcareous sand, boulder clay or clay. There are three clayey woodlands where this species has been found, though with no more than two specimens per woodland. *Polystichum lonchitis* was first recorded in the Netherlands in the Kuinderbos on calcareous sand (Bremer 1981). In addition the species was found in a site near Lelystad, on light clayey soil, in 1986 (Smit 1989). In both areas, the original specimens recorded are still growing. *Ophioglossum vulgatum* can be found in Flevoland in grassland and woodland. In woodland, elliptical patches are found on boulder clay, calcareous sand and clayey soils.

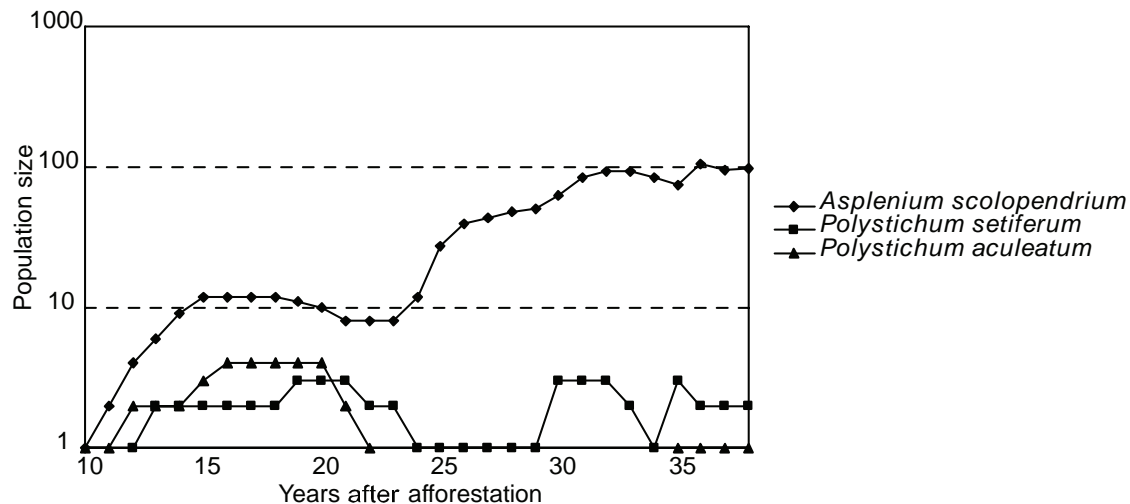


Figure 4.6. The number of specimens of rare ferns at the Jagersveld near Lelystad (East-Flevoland) (planted in 1966). The data for the first period of 13 years after afforestation have been extrapolated.

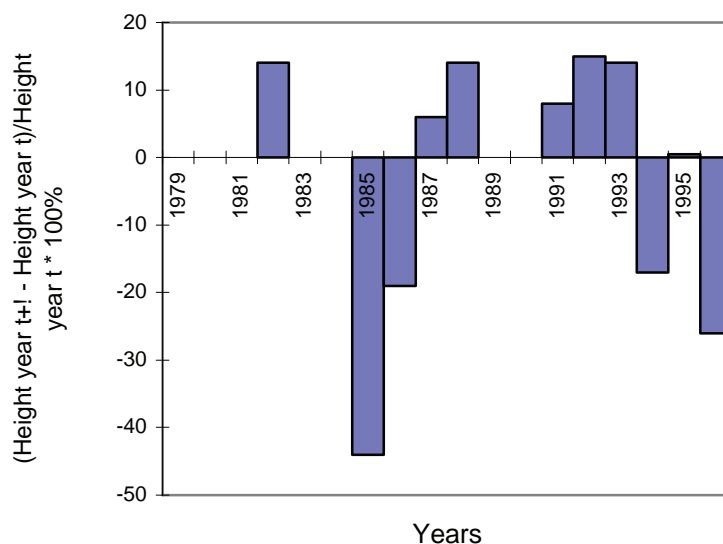


Figure 4.7. The change (percentage) in height (average, based on maximum frond length plant⁻¹) of *Asplenium scolopendrium* as observed in the population in the Jagersveld (1979 – 1996). There were severe winters in 1984 – 1986 and 1995/1996. No data were collected in 1983 and 1989. The figure is based on a paired comparison of subadult and adult plants (plant height > 10 cm, 4 – 10 plants involved in the year on year analysis).

Bremer (1988) surveyed all the localities in woodlands within Flevoland ($n = 16$); 37 % were on clayey soils. In some sites, colonies occur on clay overlying Pleistocene sands with seepage. In other sites, the clay layers are thicker and there is no seepage, but at all localities the water table in springtime is usually less than 0.5 m deep. In all cases the canopy consisted of *Fraxinus excelsior* mixed with other broadleaved trees. In some populations, patches have decreased in vitality or even disappeared during the last 15 years, due to the denser shade and/or the fall of slowly decomposing litter of *Quercus robur* and *Fagus sylvatica*. In the Voorsterbos, *Ophioglossum vulgatum*, which was growing on boulder clay, has even completely disappeared.

Discussion

Habitat islands and colonisation

The number of species on a site depends primarily on area, an almost universal finding, which holds true for true woodland species too (Peterken & Game 1984, Dzwonko & Loster 1989). Grashof-Bokdam (1997) found an area effect for some fern species in the Netherlands, a finding supported by this study. Woodland age is important because the number of species increases concomitantly with it (Fig. 4.3). We may assume that this process is still going on, as older woodlands are richer in species than young ones (e.g. Peterken & Game 1984, Dzwonko & Loster 1989). In the regressions the contribution of age is as important as that of area. We have to take into account that the range in area (0.15 - 790 ha) is much larger than the range in age (16 - 43 years). Considering the effects of isolation, the distance to villages had significant effects, e.g. for some endozoochoric species. Some species (e.g. *Ribes* spp.), have been spread from gardens by birds. Humans (or dogs) will also act as vectors for seeds (e.g. epizoochoric species) along paths and rides in particular. Bijlsma *et al.* (2001) also showed the meaning of this infrastructure as habitat and for the transport of seeds of characteristic woodland inhabiting species.

In a more recent survey Bremer (2007) investigated the woodlands in NW Friesland, where the woodlands are smaller on average (NW-Friesland: 1.7 ha, Flevoland: 54.4 ha) and younger (at average, NW-Friesland: 16 years, Flevoland: 29 years). Here too, age and area contribute to the best model explaining the number of characteristic woodland species woodland⁻¹, while the models explaining the number of recruiting tree and shrub species indicate the importance of the distance to villages. In NW-Friesland the models for particular species do not always agree with our findings in Flevoland. In NW-Friesland the herb layer is dominated by *Anthriscus sylvestris*, while in Flevoland *Urtica dioica* plays a prominent role. In NW-Friesland the colonisation is in an earlier stage. In both areas *Alliaria petiolata* is correlated with the presence of paths or rides and *Geum urbanum* is correlated with woodland age.

The clayey woodlands are habitat islands, isolated by surrounding farmland but connected by a network of ditches and road verges. The island theory predicts equilibrium in number of species, achieved by immigration and extinction. In the woodlands of Flevoland, immigration (colonisation) is in progress, while extinction is more the exception. In the intensively monitored Emmelerbos, 70% of the expected characteristic woodland species have colonised the area and after 40 years the colonisation is counterbalanced by loss of species, indicating an equilibrium in species number. Remarkably, anemochoric species such as *Listera ovata* and *Dryopteris affinis* have lost out, which shows that high dispersal capacity does not always reduce the risk of extinction (Fig. 4.4). As species form seed banks and spore banks, extinction is difficult to prove. The theory also predicts a correlation with distance from the mainland, but we did not find one. The number of plants on road verges did correlate with the distance from the mainland (Nip-van der Voort *et al.* 1979), but it should be remembered that road verges are interconnected, not isolated. Long periods of observations are needed to assess the ratio of colonisation to extinction and its relation to the habitat islands and the role of the seed bank or spore bank. In the Jagersveld, the number of fern species stabilised at a high level. But this species-rich woodland was one of the most isolated. Ferns have a high dispersal potential, not restricted by distances of tens of kilometres. Grashof-Bokdam (1997), however, also found an isolation effect (defined as connectivity) for *Dryopteris filix-mas* in forest patches belonging to the *Quercion roburi-petraea* and for *Dryopteris dilatata* in woodlots and wooded banks 15 - 20 years old, most of them belonging to the *Quercion roburi-petraea*.

Contrary to expectation, ferns were often not the first to colonise the monitored wood-

lands. They were the first to colonise the Jagersveld, but were not the first in the Emmelerbos, Westerveld or Tollebeckerbos. The Jagersveld has trenches, but the other woodland do not. Litter does not accumulate on trench banks and this habitat has its own microclimate, which also means that spores may be present at an early stage and the availability of safe sites (habitat) is restrictive. Various species may be earlier colonists: *Epipactis helleborine*, for example, also dispersed by wind, or species transported by humans (e.g. *Geum urbanum*, *Geranium robertianum*). Prior to afforestation, no species were present in Flevoland, as was observed in the planted woodlands of NW-Friesland where some species were already present in planted grasslands (e.g. *Ranunculus ficaria*) (Bremer 2007). The species colonising these recent woodlands belong to various dispersal types, including those with poor dispersal mechanisms. As indicated by multiple regression, the distance to villages is of importance, suggesting that humans do have a prominent impact on the colonisation of various species.

Some of the fern species recorded here have previously not been observed in clay woodlands elsewhere in the Netherlands. Long-distance dispersal must have taken place for species such as *Polystichum lonchitis*, only a few specimens of which were found in the woodlands of Flevoland. Colonisation might have taken place from the nearest natural populations in the UK or central Europe. Similarly, *Polystichum setiferum* might have reached the area by spores from the rich populations of the south-west of England. Fern spores are capable of being carried long distances and are probably dispersed widely. Lellinger (1985) notes that sometimes spore do germinate and produce sporophytes far outside the usual range of a species. An outstanding example of an out-of-range distribution is that of *Grammitis nimbata*, a Cuban species growing in North Carolina, some thousands of kilometres out of the species' main range. The rarest species (*Polystichum lonchitis*) that had established in the clayey woodlands had probably travelled a mere few hundred kilometres.

The colonisation of woodland species on clay takes decades. When abundance and distribution within woodlands are also monitored, it can be seen that dispersal is restrictive in all species (seed and spore-limitation). The observations suggest that spores probably reach the isolated woodlands, but are not able to germinate (habitat-limitation). Near Zwolle, spores of four species germinated at many sites within a short period after thinning, indicating the presence of a spore bank. In recent years, the presence of viable fern spores in soil has been recognised (Milberg 1991, Dyer & Lindsay 1992). Seeding experiments with ferns however have not been carried out.

The significance of restrictive dispersal in flowering species has also been demonstrated by seeding. Seeding experiments on clay soils were carried out in Flevoland in 1966 and proved to be successful, accelerating the colonisation (e.g. of *Geum urbanum*, *Alliaria petiolata*) (Koridon & Smit 1972). For that reason these species were not incorporated in the regression analysis. More recently a seeding experiment near Zwolle also succeeded: all the species sown established (e.g. *Stachys sylvatica*, *Festuca gigantea*, *Circaea lutetiana*) and the colonisation was most successful in plots with moderate light intensity.

Habitat preference

Most ferns were found in stands with *Fraxinus excelsior* in the canopy. These stands can be assigned to the *Fraxino-Ulmetum* community. Stands rich in ferns near Lelystad are composed of various broadleaved tree species, with *Fraxinus excelsior* being the most important. This woodland resembles the Ash–Maple–Hazel woodlands on heavy, moderately calcareous, poorly drained soils in eastern England, which have more species of flowering plants and ferns than any other woodland of eastern England (Rackham 1980). Young stands of *Pinus* on top of a calcareous clay substrate provide a particularly good habitat for ferns, as the young stands have an acid ecto-organic layer and decaying wood after a first thinning, providing habitat for *Dryopteris* spp. The microclimate might also profit the establishment of ferns. *Asplenium*

scolopendrium established in one of these stands (with no trenches).

Our study shows that trenched woodlands are richer in ferns than woodlands without this kind of drainage. Various species were only found along drainage trenches. Trench banks seem to be an appropriate habitat as there is no accumulation of litter, temperatures are less extreme and on average the relative humidity is higher, especially after heavy rainfall and in the winter when the bottom fills with water. The trenches on clayey soil have much in common with the situation in the Kuinderbos, where rare species occur in large numbers on fine calcareous sand on trench banks and the establishment of species also depends on small-scale land slip and microclimate (see Chapter 3). Drainage trenches elsewhere in the Netherlands mostly have an acidified substrate without calcicole fern species.

Asplenium scolopendrium has not previously been observed on clayey trench banks in the Netherlands, probably because this habitat (with calcareous substrate) is extremely rare on the mainland. It mostly occurs on walls and sometimes terrestrially in the dunes (Weeda *et al.* 1985). The mass growth in trenches was unknown until the first records in the Kuinderbos (Bremer 1980a, b) and the clayey woodlands described here. Probably the trenches mimic more natural habitats, such as the ravine woodlands in Central Europe. *Asplenium scolopendrium* is prone to frost damage. After heavy frost populations can be decimated, as observed on wall populations. In the polder woodlands frost can also be damaging, as demonstrated in the Jagersveld with population decline for some years. The same was observed in the Kuinderbos (see Chapter 6).

In the Jagersveld, three *Polystichum* spp. were found. The same was observed in the Kuinderbos, where in one instance the three species were growing on the same trench bank, indicating an overlap in ecology. Though all three species are very rare in the Netherlands, they were able to colonise the same locality independently. *Polystichum lonchitis* is restricted to two locations in Flevoland and it has been present in its first location for more than 35 years. In Scotland, plants occur mainly at c. 600 – 900 m elevation, descending very locally to about c. 150 m (Page 1982), and even c. 50 m (Gent *et al.* 1995). In Central Europe it may descend to an elevation of 300 m, but it prefers the montane and alpine area (Dostál & Reichstein 1984). Other plant species with a montane distribution found on trench banks in the polders included the bryophyte *Distichium inclinatum* (Bremer & Ott 1990). *Ophioglossum vulgatum* is a rare woodland species in the Netherlands, although not mentioned as such in the Dutch flora (Weeda *et al.* 1985). It has been recorded in various types of woodlands such as the *Betulo-Quercetum roboris*, *Pruno-Fraxinetum* and *Stellario-Carpinetum* communities (Bremer 1988) in the Netherlands and Britain. Yet although the species has been found in British woodlands (Tallowin & Swinscow 1986), Page (1982) does not mention woodland as a habitat either. Numerous species previously not recorded in the Dutch broadleaved clayey woodlands have established in Flevoland. The woodland most rich in fern species proved to be Jagersveld. The factors responsible for its richness include the length of trenches, its light clayey soil with long term capacity for water supply, high pH (due to shells) and dominance of *Fraxinus excelsior* in the first tree layer and a second tree layer with trees and shrubs giving a deep shade (e.g. *Corylus avellana*, *Crataegus monogyna*) and suppressing competing species in the herb layer. Other woodlands in the polders on clay are poorer in species, as there is not such a combination of habitat characteristics, with lack of trenches as most crucial factor.

As a reference, three estate woodlands with old stands were investigated. They differ from the woodlands in Flevoland because of the contribution of *stinzenplanten* such as *Corydalis cava* and *C. solida*; naturalised plant species introduced centuries ago that have been able to recruit and spread in woodlands (Bakker & Boeve 1985). However, no ancient or very old natural woodlands of the *Fraxino-Ulmetum* community are found in the Netherlands, as the clay soil has been cultivated within living memory. Hence, a good reference is lacking, hampering a complete analysis of the woodlands in Flevoland. On the other hand, the polder woodlands

proved to be much richer in fern species. The difference can be explained by the fact that there are no drainage trenches in the estate woodlands and the upper soil has decalcified. Deep trenches are also absent in other woodlands on clay, as observed in the ash coppice woodlots in the centre of the Netherlands, or they are shallow, with a high water table in winter. In the woodlands on clay in Flevoland, various characteristic woodland flowering plants from the *Fraxino-Ulmetum* community also established that were not found in the estate woodlands and were not mentioned by Stortelder *et al.* (1999), e.g. *Epipactis helleborine*, *Ribes nigrum* and *Chaerophyllum temulum*. This difference might be attributable to the small sample of relevés used in the syntaxonomical studies on the one hand and on the other hand to the large area of woodlands on clay in Flevoland, which provided species with opportunities they did not have on the mainland (where the woodlots are always small). This is similar to other unexpected vascular species which have colonised the polders, such as the mass colonisation of *Tephrosia palustris* on bare clay soils (Bakker 1960) or *Hieracium caespitosum* in woodlands on boulder clay or calcareous sand (Bremer 1991).

Some of the established fern species have been classified as indicators of ancient woodland. Rackham (1980) mentioned *Ophioglossum vulgatum* and *Dryopteris affinis* as associated with ancient woodland. *Polystichum aculeatum* was associated with ancient woodlands in central Lincolnshire, yet it colonised young planted woodlands in Flevoland. *Polypodium vulgare* has been indicated as a slightly calcifuge species (Page 1982), but in the Kuinderbos it is able to grow on calcareous sand (Bremer 1980b) and near Lelystad it even grows on calcareous sandy clay. This may be an effect of the scarcity of the habitat of trenched woodlands on clayey soils in the Netherlands.

Our study shows that area and age have an effect on the colonisation of woodland vascular species, with settlements having an effect as the source for various seed plant species and the number of fern species woodland⁻¹ being correlated solely with area. Trenched woodlands, although scarce, show a positive effect on the fern flora. The habitat is preferred by all fern species found in these woodlands, with *Dryopteris dilatata* as an exception in some woodlands. Ferns are able to colonise trenched woodland within 10 - 20 years after the woodland has been planted. In the absence of trenches this process takes more time, and establishment depends on safe sites on the woodland floor or decaying wood. The rapid colonisation of pine stands indicates the significance of the substrate and microclimate for successful establishment. Trenched woodlands on clay in Flevoland are much richer in fern species than estate woodlands on the mainland, mainly because the woodlands in Flevoland provide shady trenches and a calcareous substrate.

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The estate woodland on clay of Windesheim (Zwolle) was used as reference

Ecology and syntaxonomy of
Gymnocarpium dryopteris L. in the
Netherlands



Gymnocarpium dryopteris with fronds different in age.

Submitted

Abstract

Distribution, ecology and population size have been studied of *Gymnocarpium dryopteris*, especially during the period 1979 - 1991 by collecting data on 419 colonies in the Kuinderbos (or samples of this population, at least 50 colonies per parameter) and 74 colonies elsewhere in the Netherlands. In this paper the Kuinderbos population is compared with other Dutch populations to get more insight in the ecology of the species and circumstances facilitating a high density. For this reason also populations were studied in Germany as reference.

In the period 1979 - 1991 the species was recorded in the Netherlands with at least 670 colonies, of which 89% in the Kuinderbos, a planted woodland at a former sea-floor. *Gymnocarpium dryopteris* prefers shadowed ditches and drainage trenches, but can grow at various other habitats as well. Especially at the western and southern part of the Netherlands the species grows at walls.

Sites with *Gymnocarpium dryopteris* belong to different communities. In the Kuinderbos stands of *Picea sitchensis* are preferred, while elsewhere in the Netherlands the species prefers the *Quercion roboris-petreae* (*Fago-Quercetum*) or *Pseudotsuga*-stands. *Gymnocarpium dryopteris* is accompanied by 14 fern species, at the Kuinderbos by 12 fern species, with *Athyrium filix-femina* as characteristic species, often indicating potential sites. Rhizomes are shallow creeping, at average 2.6 cm below the surface (0.5 - 8 cm). It grows in the ecto-organic layer or just below this layer. At trench sides it often grows in the mineral layer. Most colonies are within the influence of the watertable. The Dutch colonies are small and colonies with more than 1000 fronds rare. This probably indicates that most colonies are young. Colonies with more than 100 fronds are often fertile, with less than 20 % of the fronds bearing sori. At the wall habitat small-sized individuals may be fertile as well. The high density in the Kuinderbos can be attributed to an optimal water supply from a peat subsoil, the composition of the ecto-organic layer consisting of *Picea* needles and an optimal light climate. The high density in *Picea sitchensis* within the Kuinderbos is unprecedented in Europe and makes these stands resemble the natural habitat of *Picea sitchensis* at the west coast of N.-America.

Introduction

Though *Gymnocarpium dryopteris* is one of the rarest fern species in the Netherlands (Menema *et al.* 1985), it is not endangered (van der Meijden *et al.* 2000). Since 1979, many new sites of this species have been discovered, the most important being in the Kuinderbos. The large number of sites where the density of the species is locally high provided an opportunity to describe the ecology of the species in this woodland (Bremer 1980). In the Kuinderbos, *Gymnocarpium dryopteris* is closely associated with *Picea sitchensis* (Chapter 3), whereas elsewhere in the Netherlands the species has been recorded in woodland, on stream banks and sometimes from very unlikely habitats, such as canal walls (Weevers *et al.* 1948, van Ooststroom 1973). This raises the question: what are the optimal conditions for *Gymnocarpium dryopteris* to develop and form larger patches? To find the answer it was important to do a thorough ecological study of the large population in the Kuinderbos. A more detailed study of colonies elsewhere in the Netherlands was started, to ascertain the conditions under which the species is able to establish but is seldom able to form a population of appreciable size and also to look at the types of vegetation in which *Gymnocarpium dryopteris* occurs. It is the composition of the vegetation and the abundance of its constituent species that provide information about the abiotic conditions and management (e.g. Grootjans 1985, Schaminée *et al.* 1995), in so far that constraints to dispersion do not strongly influence the composition of the vegetation, and provided the communities are saturated. When comparing populations, aspects of performance were also considered, measured from the size and fertility of the colonies. It is the small and young colonies that provide information about the potential for establishment: the microhabitat in which they have established is often still discernable in the field. The colonies that have been able to survive in certain places for a long time yield different information. The environment in which prothallia can establish successfully may differ greatly from the environment of the mature colonies, as is the case for *Pteridium aquilinum* (Page 1982).

Methods

A questionnaire on the characteristics of the locality and site was compiled and sent out to botanists and vegetation scientists who had sent in observations to the National Herbarium. In total, 26 respondents completed the questionnaire or supplied other information. In addition, documentation at the National Herbarium (Leiden University) was consulted, including the descriptions in the herbarium collection. I visited 60% of the sites in the Netherlands where the species has been found and described them. Most of the data on the Kuinderbos were collected in 1979 (Bremer 1980). Data on the other sites elsewhere in the Netherlands were collected from 1979 to 1990. I used my own system to classify the habitats of the locations visited. The composition of the tree layer was noted per species. The soil composition was determined by taking multiple samples of the top 30 cm with a soil auger and describing the soil composition (e.g. Wiggers *et al.* 1962). The pH was determined at 28 locations, from soil collected from the root zone (ecto-organic layer plus soil from the underlying 5 cm layer). This entailed collecting 15 g of soil and mixing it with 20 ml of distilled water (pH H₂O) in the laboratory. The next day the mixture was shaken and then analysed. The pH KCl was measured after adding 2.5 ml 1 N KCl. The thickness and composition of the ecto-organic layer were determined by carefully scraping off this layer several times in each colony (Klinka *et al.* 1981). In the Kuinderbos, the water table was determined from the water levels in piezometers (filter at 80 - 100 cm). Elsewhere, the mean highest water table (MHWT) was estimated from the water table in nearby watercourses or using soil features (rust phenomena). The accompanying fern species were those within a radius of 3 m from the edge of a patch. If there were height differences in the site (as was particularly the case in drainage trenches slope was measured with a clinometer. Aspect

was determined from the topographical map. In all colonies the number of fronds colony⁻¹ and the number of fertile fronds were counted. The data supplied by respondents were not always complete. This accounts for the differences between the numbers of colonies for which data on the aforementioned parameters are available.

Vegetation relevés were made at 37 locations in the Netherlands (in woodlands 10 x 15 m in size). Data were analysed with TWINSpan (Hill 1979). Data on vegetation and other aspects were also collected from colonies in four mountain areas in Germany (Harz, Weserbergland, Teutenerwoud, Allgäu). A chi-square test was used to analyse the data.

Results

Distribution

Prior to 1950 the species had been recorded in 56 5 x 5 km grid cells¹. In the period 1950 - 1984 it was recorded in 78 5 x 5 km grid cells (Mennema *et al.* 1985). In the period 1979 - 1991 the species was recorded in 51 5 x 5 km grid cells (Fig. 5.1; a separate symbol has been used to indicate recent data). These finds were almost always in 1 or 2 km² grid cells per 5 x 5 km grid cells, except for the Kuinderbos. Outside the Kuinderbos, 81% of instances were of one colony found 1 km⁻² grid cell; occasionally there were several clones – up to a maximum of 6 colonies 1 km⁻² grid cell (in the park of Het Loo palace). In total, for the period in question there were 74 colonies in the Netherlands (excluding Kuinderbos). In the Kuinderbos there was a maximum of about 300 colonies per 1 km² grid cell. In 1979, a total of 419 clones were recorded here, but in the period 1979 - 1991 the number exceeded 600: 89% of the entire Dutch population.

Most of the localities where the species has been recorded are in the eastern half of the Netherlands. Elsewhere in the Netherlands the populations are limited in extent. Though *Gymnocarpium dryopteris* has been found in 7 localities in Amsterdam, the clones are small, with no more than 6 fronds colony⁻¹ (Denters 1990).

Ecology

Gymnocarpium dryopteris can be found in a large number of different habitats (Table 5.1). There are significant differences in the distribution of the sites over the various habitats in the Netherlands prior to and since 1979 ($\chi^2 = 52.8$, $p < 0.001$, d.f. = 5). Prior to 1979, the species was found in a larger number of different habitats. In the period since 1979, the habitat preference in the Kuinderbos has been very different to that elsewhere in the Netherlands ($\chi^2 = 305.0$, $p < 0.001$, d.f. = 8); it is strongly related to the great preference in the Kuinderbos for treed coniferous woodland. *Gymnocarpium dryopteris* occurs mostly in locations with some differences in height: this applies to 89% of the clones in the Kuinderbos and 75% of the clones elsewhere in the Netherlands. The differences in height are often associated with sides of trenches, but this category also includes walls. In the past, the species has also been recorded on pollarded willows, in wells and on wooded banks, but there have been no recent sightings in these habitats. Only since 1984 have individual specimens been recorded growing between the

¹ Until c. 1980, the Dutch flora was mapped on the basis of presence of plant species in 5 x 5 km grid cells; since then, 1 x 1 km grid cells have been used.

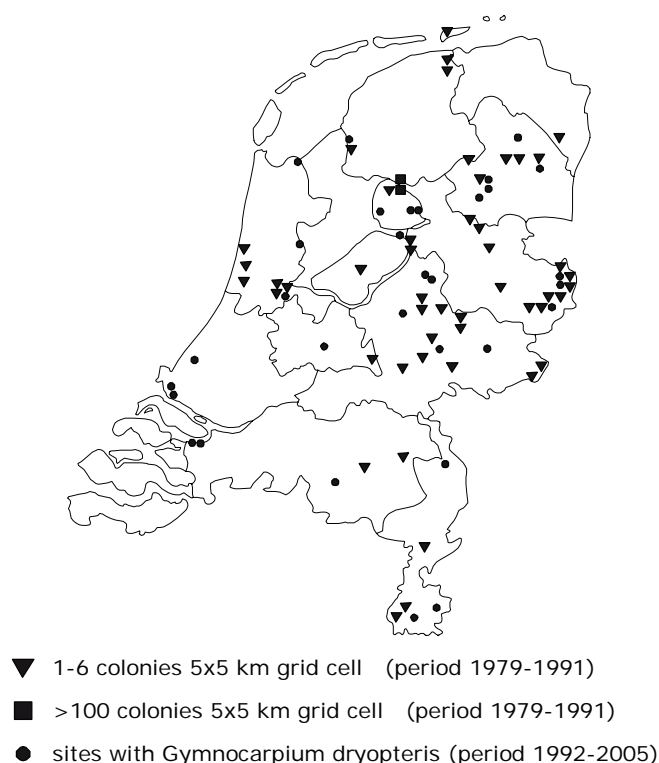


Figure 5.1. Distribution of *Gymnocarpium dryopteris* in the Netherlands in the period 1979 – 1991 and the period 1992 – 2005 (data not used in the analysis, data FLORON).

basalt blocks on former sea dikes (Lauwersmeer and IJsselmeer dikes: van der Ploeg 1984). In the Netherlands, *Gymnocarpium dryopteris* occurs most in stands of *Pseudotsuga menziesii* and *Quercus robur*. Eighty seven percent of sites in the west and south of the Netherlands have something to do with walls ($n = 15$). In the Kuinderbos, 79% of the clones were found under *Picea sitchensis* (Table 5.2). The distribution over Kuinderbos sites with different tree species is significantly different from that elsewhere in the Netherlands (period 1979 - 1981) ($\chi^2 = 289.1$, $p < 0.001$, d.f. = 5). For the entire country and the period 1979 - 1991, two clones (3.1%) occurred under *Fagus sylvatica*. In the Kuinderbos there was also a different preference in relation to the distribution of the top 10 cm of soil compared with the rest of the Netherlands ($\chi^2 = 105.2$, $p < 0.001$, d.f. = 9) (Table 5.3). In the Netherlands, *Gymnocarpium dryopteris* occurs most often on moderately fine, coarse and loamy sandy soils, whereas in the Kuinderbos the soil composition is humic to peaty fine sand. Outside the Kuinderbos the soil is lime-poor with a measured pH-KCl of $3.9 (\pm 1.0, n = 12)$. In the Kuinderbos the fine sand is always calcareous, whereas peat and clay are lime-poor. In 52 of the 141 sites studied where clones were found, limy material occurred in the top 10 cm (Bremer 1980) and the mean pH-KCl was $6.6 (\pm 0.9, n = 16)$. The average maximum thickness of the ecto-organic layer within patches is 4.7 cm outside the Kuinderbos but 1.5 cm in the Kuinderbos (Table 5.4). The difference is not statistically significant ($\chi^2 = 9.2$, $p = 0.06$, d.f. = 4). The thin average ecto-organic layer in the Kuinderbos is associated with the marked preference for trench banks. On these banks the ecto-organic layer is either less developed or is absent due to erosion, while litter decomposition is faster because the pH is high. Here, the rhizomes are at a shallow depth in a basic soil, whereas at the top of the trench, fronds of the same clone are usually growing in the ecto-organic layer, where the pH is much lower (Table 5.5). Elsewhere in the Netherlands, the pH at the top of trenches and on the trench sides is low.

Table 5.1. Habitat preference of *Gymnocarpium dryopteris* in the Netherlands. The table shows the number of colonies per habitat. A distinction is made between populations that disappeared prior to 1979 and have not been recorded since, populations present in the period 1979 - 1991 (excluding Kuinderbos) and populations in the Kuinderbos (benchmark population: the entire population in 1979). Values ≤ 3 were clustered in the chi-square analysis.

	Netherlands				Kuinderbos	
	number of colonies before 1979	%	number of colonies 1979 – 1991	%	number of colonies in 1979	%
Soil under conifer stands			6	9.2	57	13.6
Soil under broadleaved stands			9	13.8	1	0.2
Trench in coniferous woodland			9	13.8	347	82.8
Trench in deciduous woodland			1	1.5	14	3.3
Not shaded ditch/drainage trench			10	15.4	-	
<i>subtotal woodlands/trench</i>	24	35.8	35	53.7		
Stream	8	11.9	8	12.3	-	
Canal wall/quay wall	16	23.9	8	12.3	-	
Brick wall (dry)	8	11.9	2	3.1	-	
Basalt dike	-		9	13.8	-	
Roadside verge	-		3	4.6	-	
Wooded bank	3	4.5	-		-	
Drainage canal	2	3.0	-		-	
Pollarded willow	2	3.0	-		-	
Well	2	3.0	-		-	
Hollow way	1	1.5	-		-	
Edge of steep drop	1	1.5	-		-	
<i>Total</i>	67	100	65	100	419	100

Table 5.2. Habitat preference in relation to dominant tree species in the tree layer. A distinction is made between populations that disappeared prior to 1979 and have not been recorded since, populations present in the period 1979 – 1991(excluding Kuinderbos) and populations in the Kuinderbos (benchmark population: 1979). * indicates no information on tree species. Values ≤ 3 were clustered in the chi-square analysis.

	Netherlands				Kuinderbos	
	number of colonies before 1979	%	number of colonies in 1979 – 1991	%	number of colonies	%
<i>Pseudotsuga menziesii</i>	2	3.0	16	25.1	-	
<i>Pinus spp.</i>	5	7.5	2	3.1	-	
<i>Picea abies</i>	1	1.5	2	3.1	5	1.2
<i>Quercus robur</i>	1	1.5	10	15.6	53	12.6
<i>Picea sitchensis</i>	-		2	3.1	325	77.5
<i>Fagus sylvatica</i>	-		2	3.1	5	1.2
<i>Larix sp.</i>	-		2	3.1	2	0.5
<i>Betula spp.</i>	-		5	7.8	-	
Other tree species	22*	32.8	5	7.8	29	6.9
Other habitats	36	53.7	18	28.2	-	
<i>Total</i>	67	100	64	100	419	100

Table 5.3. Composition of the top 10 cm of soil under clones of *Gymnocarpium dryopteris* in the Netherlands (excluding Kuinderbos, period 1979 - 1991) and in the Kuinderbos (1979).

Soil composition	Netherlands		Kuinderbos	
	number of colonies	%	number of colonies	%
Humic, moderately fine sand	16	27.2	-	
Moderately coarse sand	14	23.7	16	11.3
Sand on loam or loamy sand	10	16.9	-	
Stony substrate	10	16.9	-	
Between basalt blocks	8	13.6	-	
Loam	1	1.7	-	
Humic, very fine sand	-		59	41.9
Peaty, very fine sand	-		27	19.1
Peat	-		30	21.3
Clay	-		9	6.4
<i>Total</i>	<i>59</i>	<i>100</i>	<i>141</i>	<i>100</i>

Table 5.4. Thickness of the ecto-organic layer in sites of *Gymnocarpium dryopteris* in the Netherlands (excluding Kuinderbos) and in the Kuinderbos. The highest value is given for each clone.

Thickness (cm)	Netherlands		Kuinderbos	
	number of colonies	%	number of colonies	%
0.0 - 2.0	6	31.6	67	68.0
2.1 - 4.0	3	15.8	18	18.0
4.1 - 6.0	4	21.0	11	11.0
6.1 - 8.0	1	5.3	3	3.0
8.1 - 10.0	5	26.3	0	0.0
<i>Total</i>	<i>19</i>	<i>100</i>	<i>99</i>	<i>100</i>
<i>mean</i>	<i>4.7</i>		<i>1.5</i>	

Shallow rooting also occurs in places where clones are growing in roadside verges and where there is no accumulation of litter. Here, the rhizomes grow in the mineral soil. Where colonies are growing on level ground under *Picea* spp. or *Pseudotsuga mensiezii*, the rhizomes may be growing in the mineral layer or the fermentation layer (litter layer), depending on the thickness of both these layers. Near Warnsveld, clones are growing in a trench with 2 - 10 cm litter overlying a fermentation layer that is up to 8 cm thick. Here, the rhizomes are mostly growing in the litter layer. The rooting depth varied from 0.5 to 8 cm.

The mean rooting depth based on measurements in three areas in the Netherlands is 3.3 cm ($n = 82$, Table 5.5a-c), in the Kuinderbos 1.8 cm (four populations together, 2.6 cm). Rooting depth also varies greatly in natural sites outside the Netherlands (Table 5.5e-f). On walls, the rhizomes of *Gymnocarpium dryopteris* grow shallowly, between the bricks. In the Kuinderbos, most clones are growing within the influence of the groundwater. This is particularly true for the clones growing lowest down the sides of trenches. Sometimes these clones endure brief soaking or even submergence. Elsewhere in the Netherlands, clones (or their parts) also generally occur within the influence of groundwater, but they can live outside this influence too (Table 5.6; $\chi^2 = 23.3$, $p < 0.001$, d.f. = 4).

Table 5.5. The depth of rhizomes at various sites in the Netherlands and elsewhere. The measurements are based on 1 – 4 different colonies per area. The depth for each clone has been determined for places where the stipes are attached to the rhizomes. n = number of observations. **a.** Delden, shady roadside drainage trench. **b.** Lonnekerberg, shady roadside drainage trench, **c.** 't Velde estate, shady trench, **d.** Kuinderbos, clones on forest soil and trench sides under *Picea sitchensis*, **e.** Harz, Bremketal, in *Luzulo-Fagetum*, on mountainside, 51°40'N 10°20'E, **f.** Allgäu (southern Germany), Wiederhofen, in *Abieti-Fagetum* on mountainside 47°26' N 10°25' E. Total = total number of determinations.

Depth (cm)	Netherlands				Kuinderbos				Germany			
	a		b		c		d		e		f	
	n	%	n	%	n	%	n	%	n	%	n	%
1	10	71.4	17	100	-	-	32	42.7	-	-	24	48.0
2	-	-	-	-	6	11.8	16	21.3	4	6.2	18	36.0
3	4	28.6	-	-	1	2.0	9	12.0	8	12.3	5	10.0
4	-	-	-	-	7	13.7	12	16.0	21	32.3	3	6.0
5	-	-	-	-	8	15.7	2	2.7	20	30.8	-	-
6	-	-	-	-	19	37.2	4	5.3	3	4.6	-	-
7	-	-	-	-	9	17.6	-	-	5	7.7	-	-
8	-	-	-	-	1	2.0	-	-	3	4.6	-	-
9	-	-	-	-	-	-	-	-	1	1.5	-	-
<i>Total</i>	14	100	17	100	51	100	75	100	65	100	50	100
<i>mean</i>	1.3		0.5		4.8		1.8		4.3		1.5	

Table 5.6. Mean highest water table (MHWT) in metres for clones of *Gymnocarpium dryopteris* in the Netherlands (excluding Kuinderbos) and in the Kuinderbos.

MHWT	Netherlands		Kuinderbos	
	number of colonies	%	number of colonies	%
≤ 0.4	15	38.4	23	46.0
0.41 - 0.8	4	10.3	27	54.0
0.81 - 1.2	1	2.6	-	-
> 1.2	9	23.1	-	-
on walls	10	25.6	-	-
<i>Total</i>	39	100	50	100

Many clones (55.3% outside the Kuinderbos, 88.5% in the Kuinderbos, both for the period 1979 – 1991) grow on unstable, steep, trench sides. The huge difference between the Kuinderbos and the rest of the Netherlands in the slope of the sites ($\chi^2 = 39.5$, $p < 0.001$, d.f. = 8) is because outside the Kuinderbos the sites include walls and quays (with a slope of 80° – 90°), whereas in the Kuinderbos many clones are growing on the level woodland floor (Table 5.7). Within the Dutch population, the species is found significantly more often on northerly aspects than on southerly aspects ($\chi^2 = 8.2$, $p < 0.01$, d.f. = 1) (Table 5.8). Most of the trenches in the Kuinderbos run NW – SE, but there is no preference for either aspect ($\chi^2 = 0.8$, $p > 0.1$). Hence there is a difference between the distribution of the colonies in the Kuinderbos compared with elsewhere in the Netherlands ($\chi^2 = 99.1$, $p < 0.001$, d.f. = 3).

Composition of the vegetation

Gymnocarpium dryopteris co-occurs with 97 higher plants and 38 mosses and liverworts (n = 40 relevés). Several clusters are discernable in the synoptic table (Table 5.9). In general, the clusters do not fit into one syntaxon exactly. Group I comprises wall vegetations. Among the species accompanying *Gymnocarpium dryopteris* here are *Dryopteris filix-mas* and *Thelypteris*

Table 5.7. Inclination of colonies on walls and in trenches in the Netherlands (excluding the Kuinderbos). Inclination per colony is based on the highest value.

Inclination	Netherlands		Kuinderbos	
	number of colonies	%	number of colonies	%
< 10°	2	4.6	17	25.5
11 - 20°	5	11.7	2	3.0
21 - 30°	5	11.7	1	1.4
31 - 40°	2	4.6	5	7.4
41 - 50°	13	30.2	12	17.9
51 - 60°	3	7.0	20	29.9
61 - 70°	1	2.3	6	8.9
71 - 80°	0	0.0	4	6.0
81 - 90°	12	27.9	0	0.0
<i>Total</i>	<i>43</i>	<i>100</i>	<i>67</i>	<i>100</i>

Table 5.8. Aspect of sites in the Netherlands with slope > 10° (excluding Kuinderbos) and in the Kuinderbos.

Aspect	Netherlands		Kuinderbos	
	number of colonies	%	number of colonies	%
NW-NE	26	42.6	172	41.0
E or W	12	19.7	0	0.0
SW-SE	9	14.7	190	45.4
none	14	23.0	57	13.6
<i>Total</i>	<i>61</i>	<i>100</i>	<i>419</i>	<i>100</i>

palustris. These vegetations are related to the *Asplenietum trichomano-ruta-murariae*. Group II comprises vegetations with relatively many acidophile species. Some of the relevés were in stands of exotics. The relevés display a clear relationship with the *Quercion roboris-petreae* (and within this, with the *Fago-Quercetum* and also the *Betulo-Quercetum*). The relevés made under *Picea sitchensis* (Kuinderbos) also fall into this group. Group III comprises relevés in which species such as *Sorbus aucuparia*, *Fagus sylvatica* (seedling or juvenile) and *Lonicera periclymeum* are differentiating. These relevés are clearly assignable to the *Fago-Quercetum*, actually being a damp form of this association with *Athyrium filix-femina* and *Lysimachia vulgaris*. Group IV comprises a single relevé which includes, among others, *Geranium robertianum*, *Aegopodium podagraria*, *Oxalis europaea* and *Conocephalum conicum*, which are assignable to the *Pruno-Fraxinetum*. Group V comprises relevés with relatively many grasses. The characteristic species for this group include, among others, *Festuca rubra*, *Holcus lanatus*, *Cerastium fontanum* and *Taraxacum*, *Vulgaria* section. These sites are of *Gymnocarpium dryopteris* on basalt dikes and in roadside trenches; the relevés contain many species that occur in the adjacent roadside verges. The site in the *Calamagrostis epigejos* brushwood in Knarbos also falls into this category. There are no vegetation relevés related to the *Stellario-Carpinetum* in Table 5.9. A single clone in south Limburg, for which there is no known relevé, lies on the transition from *Stellario-Carpinetum* to *Fago-Quercetum*. The most reliable accompanying species of *Gymnocarpium dryopteris* are *Athyrium filix-femina*, *Dryopteris dilatata*, *Rubus fruticosus* s.l., with *Athyrium filix-femina* in particular being an indicator of potential sites of *Gymnocarpium dryopteris*. Accompanying fern species were recorded for 128 colonies in total. The commonest within the Dutch population are *Athyrium filix-femina*, *Dryopteris filix-mas*, *D. dilatata* and *D. carthusiana*. Outside the Kuinderbos there are 14 fern species that occur as accompanying species: on average, 2.2 species colony⁻¹. The various uncommon species recorded as accompanying fern species on canal walls include *Gymnocarpium robertianum*, *Polystichum aculeatum*

and *Asplenium trichomanes*. In the Kuinderbos, *Gymnocarpium dryopteris* is accompanied by 12 fern species (Table 5.10). Four of the five patches of *Phegopteris connectilis* in the Kuinderbos are accompanied by *Gymnocarpium dryopteris*. In some localities outside Kuinderbos, both species occur directly next to each other or in the same area. The frequencies of *Gymnocarpium dryopteris* in the Kuinderbos and in the rest of the Netherlands being accompanied by other fern species are significantly different ($\chi^2 = 13.1$, $p < 0.001$, d.f. = 4); this is primarily because of the high frequency of *Dryopteris carthusiana* in the Kuinderbos.

Size of colonies

Sixty-nine percent of the colonies in the Netherlands have fewer than 100 fronds. Large specimens with over 1000 fronds are a rarity: in the period 1979 - 1981, this occurred in only a single patch (in the park of Het Loo palace). In this respect the distribution for the Kuinderbos (1990 situation) is very similar to that for the rest of the Netherlands (Table 5.11), though the Kuinderbos has relatively more colonies with more than 1000 fronds (maximum is 3000). Various populations in this woodland were monitored over 15 years (see also Chapter 7). In heavy shade, individuals may remain the same size for a long time. If the light increases suddenly (e.g. as a result of storm damage), the number of fronds may increase over a number of years, at a maximum rate of 400 fronds year⁻¹. Seventy-five percent of the colonies in the Netherlands are smaller in extent than this annual increase. Young clones lack a clear shape. As they grow larger, patches become clearly discernable. They are often oval or round in shape. If the centre dies, a fairy ring may arise. Along trenches or streams, the oval shape may become elongated. Old patches may break up, making it appear that several clones occur next to each other. This has seldom been recorded in the Netherlands, because the clones are relatively young and limited in extent. In the Netherlands (outside Kuinderbos), 74 clones were recorded in the research period (1979 - 1991). By 1992, 7 (= 10%) had disappeared. Sites on walls are always small and vulnerable, but large patches, too, can decay in a couple of years. Eighty-eight percent of the 41 Dutch colonies whose age was known or could be estimated were no older than 20 years. After long-term monitoring of four research plots in the Kuinderbos it was found that after 15 years, 43.7% of the population ($n = 190$) had disappeared (Chapter 7). The half-life varied from 3.5 to 4.6 years, with some colonies older than 30 years.

Other observations on colonies

Gymnocarpium dryopteris is a non-evergreen species. Its fronds usually unfurl in early May, though they may appear at the end of April if the winter has been mild. The species is vulnerable to damage from late night frosts, as evidenced after the April frosts of 1991. Frost can also accelerate die-back in October, but even without frost, most fronds have died before November. Severe thunderstorms may also cause damage, as if bent, the fragile fronds will die. New fronds can be formed until September, though they are usually smaller. *Gymnocarpium dryopteris* rarely suffers pest damage. Sawfly caterpillars (*Symphyla*, indet.) are regularly found on the fronds of specimens in the Kuinderbos, but rarely do they destroy entire fronds. Similar pest damage has been found on populations elsewhere in the Netherlands. Slug damage is rare. *Gymnocarpium dryopteris* growing on dikes in small crevices between basalt rocks may be damaged by browsing livestock. Fertile fronds generally occur in specimens with more than 50

Table 5.9. Synoptic table based on relevés with *Gymnocarpium dryopteris*. The data have been classified on the basis of a TWINSpan computation of 37 relevés, two of which were made in Germany (Teutoburgerwoud) and the rest in the Netherlands. The table does not show the mosses, liverworts and vascular plant species recorded only once. Tree and shrub layer were not included in computation. The table gives the number of relevés per relevé group in which the species in question was found. Exclusive characteristic species have been printed in grey. These are species that have only been recorded in a single species group, with a presence of 25% or more. I = wall vegetations, II = exotic stands, III = *Fago-Quercetum*, IV = *Pruno - Fraxinetum*, V = vegetation of dikes and ditch banks.

Relevé group	I	II	III	IV	V
Number of relevés	4	16	8	1	8
<i>Gymnocarpium dryopteris</i>	4	16	8	1	8
<i>Asplenium ruta-muraria</i>	2	-	-	-	-
<i>Asplenium trichomanes</i>	2	-	-	-	-
<i>Thelypteris palustris</i>	3	-	-	-	-
<i>Sagina procumbens</i>	2	-	-	-	-
<i>Capsella bursa-pastoris</i>	2	-	-	-	-
<i>Rubus idaeus</i>	-	7	-	-	-
<i>Betula pendula</i>	-	5	-	-	-
<i>Ceratocarpus claviculata</i>	-	5	-	-	-
<i>Quercus robur</i>	-	4	-	-	-
<i>Cardamine pratensis</i>	-	3	-	-	-
<i>Viola palustris</i>	-	2	-	-	-
<i>Festuca ovina</i>	-	2	-	-	-
<i>Humulus lupulus</i>	-	2	-	-	-
<i>Eupatorium cannabinum</i>	-	2	-	-	1
<i>Chamaenerion angustifolium</i>	-	6	-	-	1
<i>Oxalis europaea</i>	-	1	-	1	-
<i>Lonicera periclymenum</i>	-	-	6	-	-
<i>Equisetum arvense</i>	-	-	2	-	-
<i>Luzula multiflora</i>	-	-	2	-	-
<i>Oxalis stricta</i>	-	-	2	-	-
<i>Cerastium fontanum</i>	-	-	-	-	4
<i>Taraxacum vulgare</i>	-	-	-	-	6
<i>Tussilago farfara</i>	-	-	-	-	3
<i>Lolium perenne</i>	-	-	-	-	2
<i>Athyrium filix-femina</i>	2	7	8	1	1
<i>Dryopteris filix-mas</i>	4	4	3	1	2
<i>Dryopteris dilatata</i>	1	14	4	-	-
<i>Rubus sp.</i>	4	9	6	-	-
<i>Epilobium sp.</i>	1	1	-	-	1
<i>Stellaria media</i>	-	2	1	1	1
<i>Urtica dioica</i>	-	3	4	1	2
<i>Agrostis capillaris</i>	-	3	6	-	1
<i>Galium aparine</i>	-	1	3	-	2
<i>Lysimachia vulgaris</i>	-	2	6	-	1
<i>Hieracium laevigatum</i>	-	2	2	-	1
<i>Juncus effusus</i>	-	4	1	-	1
<i>Poa trivialis</i>	-	2	1	-	2
<i>Dryopteris carthusiana</i>	-	2	2	-	1
<i>Polypodium vulgare</i>	1	1	-	-	-
<i>Senecio vulgaris</i>	1	-	-	-	1
<i>Holcus mollis</i>	-	5	3	-	-
<i>Deschampsia flexuosa</i>	-	4	3	-	-
<i>Sorbus aucuparia</i>	-	1	6	-	-
<i>Fagus sylvatica (j)</i>	-	1	5	-	-
<i>Galium saxatile</i>	-	2	2	-	-

<i>Molina coerulea</i>	-	1	2	-	-
<i>Rumex obtusifolius</i>	-	1	1	-	-
<i>Ajuga reptans</i>	-	1	1	-	-
<i>Phegopteris connectilis</i>	-	1	-	-	1
<i>Galium palustre</i>	-	1	-	-	1
<i>Heracleum sphondylium</i>	-	1	-	-	1
<i>Calamagrostis epigejos</i>	-	2	-	-	2
<i>Phragmites australis</i>	-	3	-	-	2
<i>Holcus lanatus</i>	-	4	-	-	5
<i>Ranunculus repens</i>	-	-	2	1	-
<i>Geranium robertianum</i>	-	-	1	1	-
<i>Anthriscus sylvestris</i>	-	-	1	1	-
<i>Angelica sylvestris</i>	-	-	1	1	-
<i>Festuca rubra</i>	-	-	1	-	7
<i>Potentilla erecta</i>	-	-	1	-	1
<i>Prunella vulgaris</i>	-	-	2	-	1

Table 5.10. Accompanying fern species (within a distance of approx. 3 m from the clone) in the Netherlands (excluding Kuinderbos) and in the Kuinderbos (n = number of clones) For chi-square analysis, species with a frequency < 5 were clustered in a single category.

Species	Netherlands (n = 63)		Kuinderbos (n = 65)	
	number of colonies	%	number of colonies	%
<i>Dryopteris dilatata</i>	40	63.5	50	76.9
<i>Athyrium filix-femina</i>	36	57.1	35	53.8
<i>Dryopteris filix-mas</i>	22	34.9	25	38.5
<i>Dryopteris carthusiana</i>	14	22.2	40	61.5
<i>Asplenium trichomanes</i>	4	6.3	1	1.5
<i>Phegopteris connectilis</i>	4	6.3	3	4.6
<i>Blechnum spicant</i>	4	6.3	-	-
<i>Polypodium vulgare</i>	3	4.8	1	1.5
<i>Thelypteris palustris</i>	3	4.8	-	-
<i>Pteridium aquilinum</i>	2	3.1	-	-
<i>Asplenium ruta-muraria</i>	1	1.6	-	-
<i>Polystichum aculeatum</i>	1	1.6	2	3.1
<i>Gymnocarpium robertianum</i>	1	1.6	1	1.5
<i>Asplenium scolopendrium</i>	1	1.6	4	6.1
<i>Polystichum setiferum</i>	-	-	2	3.1
<i>Dryopteris affinis</i>	-	-	1	1.5
<i>Mean no. of species per colony</i>	2.2	-	2.5	-

fronds, except in the case of wall specimens, where though fronds are few, they may be fertile. Usually, less than 20% of the fronds of large colonies are fertile. In some large colonies, more than 50% of the fronds were found to be fertile. In general, fertile fronds are longer than sterile fronds and extend beyond the other fronds.

Discussion

Gymnocarpium dryopteris is a very rare species in the Netherlands (van der Meijden 2005). In the period 1979 – 1991 670 clones were recorded in 51 5 x 5 km grid cells. In most grid cells, only one clone was recorded. The only high density recorded was in the Kuinderbos. Here, the fern was closely associated with *Picea sitchensis* in 1979, regardless whether the ecto-organic layer was overlying fine sand, peat or clay. The rhizome is frequently very shallow, and thus the species reacts strongly to the composition of the ecto-organic layer, which is determined by

the dominant tree species. It is striking that all the sites have peat in the subsoil. This peat deposit can be likened to a thick sponge that continually supplies the uppermost deposits with water by capillary action, assuring a very stable moisture supply. In long droughts, like the one that occurred from May to August 1992, many specimens may display reduced vitality, but

Table 5.11. The size of colonies of *Gymnocarpium dryopteris*, based on the number of fronds colony⁻¹ n = number of colonies, % percentage of colonies. **a.** Dutch population 1979 – 1991 (excluding Kuinderbos), **b.** population in Kuinderbos in 1979, **c.** population in Kuinderbos in 1990, **d.** Harz, Bremketal (1989), in *Luzulo-Fagetum dryopteridetosum* 51°40'N 10°20'E, **e.** Weserbergland (1989), in Steinköpfe ancient woodland in *Fago – Quercetum*, 51° 28'N, 9° 20'E, **f.** Allgäu (1991) in *Abieti-Fagetum* 47°26' N 10°25' E.

Size	Netherlands		Kuinderbos		Germany							
	a		b		c		d		e		f	
	n	%	n	%	n	%	n	%	n	%	n	%
1-10	11	17.2	35	17.2	19	10.9	1	1.8	-	-	2	14.2
11-100	29	45.3	124	60.8	75	43.1	13	24.1	5	12.8	6	42.9
101-1000	23	35.9	45	22.0	72	41.4	18	33.3	18	46.2	6	42.9
1001-10000	1	1.6	-	-	8	4.6	15	27.8	14	35.9	-	-
10001 - 10 ⁵	-	-	-	-	-	-	4	7.4	2	5.1	-	-
10 ⁵ - 10 ⁶	-	-	-	-	-	-	3	5.6	-	-	-	-
Total	64	100	204	100	174	100	54	100	39	100	14	100

there is no massive die-back of fronds. The reason that rhizomes on trench banks are shallower than in the woodland may be that the moisture supply is better than in the adjacent woodland. Here, clones often occur almost as far as the bottom of the trench. In the Kuinderbos, most colonies are growing within the influence of the groundwater; elsewhere they also occur outside this sphere of influence. The species can thus be designated a local phreatophyte (Londo 1988). Although it does not tolerate waterlogging in the root zone (Britten undated), parts of clones will tolerate brief submergence. In the Netherlands the rooting depth varies from 0.5 - 8 cm, which is more than the 2 - 3 cm mentioned by Page (1982). The mean value does agree with Page (1982). In the Netherlands (excluding Kuinderbos) *Gymnocarpium dryopteris* grows on acid sites. Exceptions are the sites on canal walls, where the mortar has a high pH. In the Kuinderbos the pH is generally high, but this could be an artefact of the soil sampling, as the ecto-organic layer is thin and when the root environment is being sampled, some of the underlying soil was also sampled. Clones growing on the transition from trench side to woodland floor may be growing in calcareous fine sand in the trench side, but in an acidic fermentation layer on the woodland floor. Hence within a single clone, the pH of the root zone may vary by several units. Page (1982) notes that in the United Kingdom, *Gymnocarpium dryopteris* can grow in various pH values. Dostál (1984) reported the species on limestone overlain by a layer of raw humus, on soils with a mull or a moder profile. In North America the species prefers weakly acid substrates (Lellinger 1985). Ellenberger (1982) called the species a moder indicator, because it grows on litter, under *Picea abies*, for example. For Westhoff & Den Held (1969), the species is the character species for the *Stellario-Carpinetum*. The present study did not find this: the species was in no way associated with any single community. It occurs in various woodland types, such as the *Fago-Quercetum* and *Pruno-Fraxinetum*, always in relatively damp places and often accompanied by *Athyrium filix-femina*. The data presented by Stortelder *et al.* (1999) are in agreement with this. Outside the Kuinderbos, stands of *Pseudotsuga mensiezii* are an important habitat. These have often been planted in places where the potential woodland type is the *Fago-Quercetum*. Sissingh (1970) goes so far as to call it a *Dryopterido-Pseudotsugetum* with, among others, acidophile mosses and various ferns, including *Gymnocarpium dryopteris* as characteristic species. *Gymnocarpium dryopteris* is

found in natural Douglas fir forests in N.-America (Snyder 1993). The only localities in the Netherlands where the species has been observed in stands of *Picea sitchensis* are Abbertbos (East Flevoland) and the Kuinderbos, especially the latter. On the west coast of the United States and Canada the species frequently occurs in the natural Sitka forests (Fonda 1974) and is common in the *Polystichum munitum* - *Picea sitchensis* association which has been described as a closed coniferous forest thriving on the most foggy and rainy coasts of British Columbia. It is also common in other associations of the montane and subalpine forests e.g. the *Gymnocarpium dryopteris* - *Abies amabilis* community (Peinado *et al.* 1997). The species has not been reported from the extensive plantations of *Picea sitchensis* in Scotland (Ford *et al.* 1979, Peterken 1985), but can be expected on places where moisture is guaranteed.

After 1985 it was found that *Gymnocarpium dryopteris* could rapidly establish in many places in the Kuinderbos where very dense stands of *Picea abies* had been severely thinned. This suggests it is not strictly associated with *Picea sitchensis*. If the Kuinderbos had been planted with *Pseudotsuga mensiezii* rather than *Picea sitchensis*, similar densities could have been expected, given the similarities between both conifers in terms of the light climate and build-up of the ecto-organic layer. The colonisation of thinned stands of *Picea abies* is in line with the behaviour of the species in Central Europe. In southern Germany, *Gymnocarpium dryopteris* has been reported in 31 forest types (out of a total of 68); in 8 forest types its frequency was more than 20%. The woodlands in question were in ravines (*Ulmo glabrae-Aceretum pseudoplatani*), or were beech forests (such as *Dentario-Fagetum* and *Aceri-Fagetum*) and *Picea abies* (such as *Asplenio-Piceetum*) (Oberdorfer 1992). In the Harz mountains, it occurs in all types of beech forest, in subassociations in shady, places with a high relative humidity (Böttcher *et al.* 1981). The centre of gravity of the species' distribution in the United Kingdom is in the birch and oak woodlands in Scotland (Page 1982), but it also occurs along brooks with woodland vegetation related to the *Pruno-Fraxinetum* (Tansley 1965). Rodwell (1991) calls it from *Juniperus communis* - *Oxalis acetosella* woodland with *Betula spp.* in the tree layer. In Scandinavia, the species is common in spruce, pine and birch forests (Aune 1982, Havas & Kubin 1985), and also in *Carpinus betulus* forests (Mäkirinta 1982). In the farthest north it also occurs outside woodland, in grasslands (Westhoff & Schoof-van Pelt 1982). Its occurrence in grazed vegetations on basalt dikes is thus not unexpected, as this vegetation too is unshaded. The fact that *Gymnocarpium dryopteris* is often accompanied by *Phegopteris connectilis* is striking. In the Netherlands it co-occurs with *Gymnocarpium dryopteris* in 7 places. In the Kuinderbos, *Phegopteris connectilis* almost always co-occurs with *Gymnocarpium dryopteris*. It has been reported (Rasbach & Willmans 1976) that in Central Europe *Gymnocarpium dryopteris* establishes on weathering chalk soils earlier than *Phegopteris connectilis* (Rasbach & Willmans 1976) especially if an acid layer has formed on top of these soils. Page (1982) mentions that the ecological difference is that *Phegopteris connectilis* grows on slightly drier slopes. The ecological differences appear to be minor. It remains noteworthy that in the Netherlands and elsewhere, *Phegopteris connectilis* is much rarer than *Gymnocarpium dryopteris*. In the 1980s, the Dutch population of *Gymnocarpium dryopteris* was at least 670 clones, with approximately 80000 fronds, compared with an estimated maximum of 50 clones of *Phegopteris connectilis* (according to FLORON data, in the period 1975 – 1998, *Phegopteris connectilis* was recorded in 36 1 x 1 km grid cells). In its favoured sites (montane areas), more than 100 000 fronds may occur within 1 ha, as has been recorded in the Harz mountains. Colonies with more than 1000 fronds form 2% of the population in the Netherlands, 5% of the population in the Kuinderbos and 41% in the studied populations in the Harz mountains and Weserbergland. Although clones can increase their size rapidly if conditions are favourable, in the Netherlands they remain small.

There are no really old sites. Many of the sites of establishment are woodlands planted

since 1850. The species used to occur in Beekbergerwoud, before this last surviving ancient Dutch woodland was felled in 1871. The oldest existing sites are in the park of Het Loo palace, where the species was first recorded in 1853. It is possible that the same clones are still present, which must therefore be at least 150 years old. Most of the clones are younger than 20 years, which suggests many recent establishings, but also high mortality. In the Kuinderbos the mortality is related to the lack of light that causes clones to gradually diminish in size and to disappear after some years (Chapter 7). Elsewhere in the Netherlands, colonies have disappeared for reasons such as the destruction of biotopes, heavy trampling and structural depletion of groundwater. Colonies mostly remain discernable as clearly delimited patches. Oinonen (1971) established that in Finland, colonies were still discernable after 450 years. Only in ancient, undisturbed forests do such clones break up and become indistinguishable. Peterken (1985) mentioned this phenomenon in rhizome geophytes in old deciduous woodland. In one of the most undisturbed ancient woodlands in Europe, the Bialowieza, *Gymnocarpium dryopteris* has been observed to have a very dispersed manner of growth that is interrupted only where the rootballs of windthrown trees have created a new habitat and there has been a concentration in the fronds per colony. The final conclusion is that the population in the Kuinderbos differs from that in the rest of the Netherlands in many aspects. The high density of clones in this area makes it possible to identify which factors are important. These are: a good, constant supply of moisture from underground peat, the presence of an acid ecto-organic layer with both a litter layer and a fermentation layer, and a favourable light climate. These conditions can be met in moderately dense *Picea* stands. Although in the Kuinderbos the species is closely associated with *Picea sitchensis*, its occurrence elsewhere in the Netherlands under *Pseudotsuga menziesii* and the colonisation of *Picea abies* within the Kuinderbos indicate that moisture supply and the presence of the acid ecto-organic layer of Spruce needles are more important than the presence of *Picea sitchensis* in particular.

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Frost and forest stand effects on the population dynamics of *Asplenium scolopendrium* L.

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Adult plant of *Asplenium scolopendrium* on the bank of a drainage trench

submitted

Abstract

Our objective was to analyse the factors critical for the demography of *Asplenium scolopendrium* within populations of plants growing terrestrially. A long-term study (1977 - 1999) on this fern's performance and demography has been carried out in the Kuinderbos, one of the woodlands planted on land reclaimed from the Zuiderzee (province of Flevoland). Three plots (*Picea sitchensis* - *Fagus sylvatica*, *Picea sitchensis* with thinning and *Fraxinus excelsior*) were studied in more detail. We used the recorded demographic data to parameterise 37 transition matrices.

It was found that cold winters influence the population growth rate by reducing survival and increasing retrogression. Average frond damage and mortality correlated closely with the number of frost days winter⁻¹. In the *Fraxinus excelsior* plot, snow cover protected fronds and reduced the impact of frost. Land slip of trench banks and intraspecific competition were also found to increase mortality.

A key factor affecting the performance of *Asplenium scolopendrium* was found to be light. In the *Fraxinus excelsior* plot, plants grew faster, produced more fronds and became larger than in the *Picea sitchensis* stand. In the *Fraxinus excelsior* plot, the ferns were able to form a closed fern cover, but in the shadier plots in the *Picea sitchensis* - *Fagus sylvatica* plot they were not. Life-table response analysis revealed that reproduction contributed greatly to the differences in projected population growth rates. Reproduction was importantly higher in the *Fraxinus excelsior* and the thinned *Picea sitchensis* plots than in the *Picea sitchensis* - *Fagus sylvatica* plot. These differences can be attributed to an initial difference in light climate. Moreover, in the *Picea sitchensis* - *Fagus sylvatica* plot the accumulation of litter reduced reproduction.

Frost, competition and land slip showed to be the most important mortality factors. Recruitment took place on bare soil but also in open mats of pleurocarpous moss species and on bare soil with vegetations developing into the *Fissidentietum taxifolii*. It is expected that in the Netherlands *Asplenium scolopendrium* will profit from global warming, since severe winters will become rarer and summers wetter.

Introduction

Demographic studies are especially useful when comparing different habitat types and when demographic parameters are related to the changes in the habitat, such as those occurring as a result of succession, nature management or climatological fluctuations (Oostermeijer 1996, Jongejans & de Kroon 2005, Lehtilä *et al.* 2006). Long-term demographic studies can reveal how populations respond to these abiotic and biotic changes in their environment. However, long-term demographic observations in plants are scarce, which limits the analysis of the effects of extreme environmental conditions, such as prolonged droughts and harsh winters. The few long-term studies that do exist show that weather does influence demography (Tamm 1972, Cinquemani-Kuehn & Leopold 1992, Pfeifer *et al.* 2006). An example of a critical climatological factor is frost, as it can determine the northern border of the range of Atlantic plant species that are prone to frost damage (Page 1982, Cinquemani *et al.* 1988). Frost may have an impact by increasing the mortality rate and reducing growth (Sakai & Larcher 1987).

With changing climate, i.e. the rise in air temperature and more humid summers, Atlantic species might expand their range. In this context a long-term demographic study at the northern border will contribute to our understanding of the factors that limit a species range. To date, only a very few studies have been done on species growing at the edge of their range (e.g. Willems & Bik 1991, Bridle & Vines 2007).

In this paper we investigate the importance of frost for the population dynamics of the frost-sensitive fern *Asplenium scolopendrium*. To that end we analyse 37 parameterised matrix projection population models, spanning two decades from 1978 until 1999. We also study the role of the light climate by comparing fern populations growing in different stand types. The variation in light intensity is known to be the dominant factor in woodlands; it explains the distribution and variation in performance in species which grow in the herb layer on the woodland floor (Ellenberg 1982, Stoutjesdijk & Barkman 1992). In managed woodlands light climate is strongly influenced by management practices, such as thinning. In order to augment the conservation management of *Asplenium scolopendrium* populations we wanted to get more insight on the response of this species on the light climate.

Material and methods

Species studied

Asplenium scolopendrium L. is a long-lived perennial fern with gametophyte and sporophyte phases (this study focuses on the sporophyte phase). *A. scolopendrium* is a markedly calciphile, evergreen species, requiring habitats which are more or less permanently moist. It thrives on soils with a high pH, and in mineral soils with very little humus (Page 1982, Dostál & Reichstein 1984). It can be especially abundant in mixed deciduous woodlands in the western part of the UK. In the Netherlands, *Asplenium scolopendrium* is particularly known as a wall-dwelling species, and sites where plants grow terrestrially are restricted to the dunes with calcareous sand (Weevers *et al.* 1948). However, in the first half of the 1960s the first terrestrial specimen established in a woodland planted on a former sea floor (the Noordoostpolder, reclaimed from the sea in 1941/1942). The distribution and ecology of this species were studied in 1979 (Bremer 1980) and in 2002 (Chapter 3). In subsequent years the species also colonised six other planted woodlands in the same area.

Demography

The demography of *A. scolopendrium* was studied in three permanent plots in three contrasting parts in the forest of Kuinderbos, the Netherlands (52° 46' N, 5° 49' E). The first plot in a *Picea sitchensis* - *Fagus sylvatica* stand (PF) was laid out in a site with a high density (30 m⁻²) of plants (Table 6.1). This plot was monitored for 22 years (1978 - 1999). After 1978 the population of *A. scolopendrium* in the Kuinderbos increased, as did the number of trench banks with high concentrations of ferns (more than c. 10 plants m⁻²). In 1987 a thinning took place in a *Picea sitchensis* stand where no thinning had taken place in recent years. Here the second plot was laid out (Pthin) in order to compare the demography and performance with the PF plot without thinning. This second plot was studied from 1989 until 1998. The third plot was laid out in a stand of *Fraxinus excelsior* (Fr plot) in 1983 in order to compare the performance and demography of the species with that in the PF plot, since light intensity is higher in *Fraxinus* stands, especially in spring (Table 6.1). The annual monitoring was carried out from 1983 to 1990 and repeated once in 1994. The three plots (PF, Pthin and Fr) were laid out in the peat erosion area (Table 6.1), with only a shallow depth of water (maximum 20 cm) in the trenches in winter. At two sites, the proportional light intensities at the soil were higher in winter than in summer. Incoming light increased between 1990 and 2000, due to natural gap formation in the

Table 6.1. Characteristics of the three permanent plots in the Kuinderbos. The demography of *Asplenium scolopendrium* was studied in stands dominated by the tree species *Picea sitchensis* and *Fagus sylvatica* (PF), a thinned *Picea sitchensis* stand (Pthin), and a stand dominated by *Fraxinus excelsior* (Fr). Nt = number of transitions, As = aspect (Southwest or Northeast) of the plot. Light was measured in March and August in 1990 and 1998 and is expressed as percentage of the incoming light, with a site without shade as reference (in brackets: measuring year) (n = 6 - 10 measurements site⁻¹ date⁻¹). No measurements were taken in the Pthin plot in March 1990.

Stand	Period	Nt	Plot length x width (m)	Plot Size (m ²)	As.	Light in March (%)	Light in August (%)
<i>Picea/Fagus</i> (PF)	1978 - 1999	21	3.0 x 0.75	2.2	SW	6.2 ± 1.7 (1990) 27.0	1.4 ± 0.3 (1990) 11.1 ± 1.9 (1998)
<i>Picea</i> thinned (Pthin)	1989 - 1998	9	2.5 x 0.9	2.2	SW	- 6.0 ± 0.4 (1998)	3.4 ± 3.1 (1990) 11.6 ± 0.6 (1998)
<i>Fraxinus</i> (Fr)	1983 - 1990	7	1.1 x 1.1	1.2	NE	16.2 ± 7.4 (1990) 42.2 ± 8.6 (1998)	3.1 ± 0.6 (1990) 11.9 ± 6.0 (1998)

PF plot and to thinning in the other two plots. The corners of the permanent plots were fixed by means of a piece of metal. All plants were mapped and marked by a metal peg. Monitoring took place between early August and mid September, which is when adult plants have their sporangia ripened and the sporelings have emerged from the fertilised prothallia that resulted from spores produced in the previous year. In September hardly any new sporelings emerge. We measured the number of fronds plant⁻¹, the number of fertile fronds plant⁻¹ and the maximum length of a frond plant⁻¹ (plant height). After severe winters the survival of plants was monitored and frost damage plant⁻¹ was calculated in May, before the sprouting of new fronds, by estimating the area frond⁻¹ with necrosis. Frond area plant⁻¹ was calculated for seven years with the formula $LA = a(0.68l^{1.5})$ (n = 23, R² = 0.97, p < 0.001) with LA = frond area plant⁻¹, l = average length of the frond area and a = number of fronds plant⁻¹. The average length of the frond area was based on the maximum frond length plant⁻¹ (L) according to the regression: $l = 0.65L - 0.86$ (n = 25, R² = 0.97, p < 0.001). During the annual monitoring, causes of mortality were noted. For example, some sporelings and juveniles had become detached from the soil, while others disappeared after frost damage (combination of data collected in May and August/September). The microhabitat of recruitment for sporelings was also noted in relation

to the surrounding bryophyte vegetation. Numerous populations were sampled in the UK as reference for this recruitment microhabitat as terrestrial growth is rare in the Netherlands.

Life stages and matrix population models

We used stage-based matrix projection models of the form $n_{(t+1)} = An_{(t)}$, in which n is a stage-structured population size vector, and A a matrix in which the elements represent annual transitions among stages (Caswell 2001). Such models have successfully been applied in comparative demographic studies of plant species (Silvertown *et al.* 1993, Silvertown & Franco 1993) and have led to new insights into the demography of species in relation to their habitat (Silvertown & Franco 1993, Oostermeijer 1996, Jongejans & de Kroon 2005). We present demographic data from three different forest types yielding a total of 37 parameterised transition matrices for *Asplenium scolopendrium*. Within its life-history cycle we quantify five stages:

1. *sporelings*: small plants that emerge from the prothallium (after fertilisation)
2. *juveniles*: plants with a maximum frond length between 2 and 10 cm and which have not sporulated yet in their life
3. *subadults*: plants with a maximum frond length exceeding 10 cm and which have not sporulated yet in their life
4. *adults*: plants with at least one mature frond bearing ripe sori.
5. *postadults*: sterile plants which had previously been adults.

Spores are dispersed from late summer to next spring (Page 1982). They either germinate the next spring or summer, are added to the sporebank, or die (Lindsay & Dyer 1996). We assumed that most sporelings are generated from spores within one year. Spores and prothallia were therefore not modelled as separate classes. in which the columns give the transitions from the five stages (from left to right: sporelings, juveniles, subadults, adults and postadults) to each of those five stages in the next year (rows).

We constructed a 5 x 5 stage-structured transition matrix for the *A. scolopendrium* populations:

$$\begin{pmatrix} \sigma_1(1 - \gamma_{21} - \gamma_{31}) & \sigma_2\rho_{12} & \sigma_3\rho_{13} & \phi(1 - \gamma_{24}) & 0 \\ \sigma_1\gamma_{21} & \sigma_2(1 - \rho_{12} - \gamma_{32} - \gamma_{42}) & \sigma_3\rho_{23} & \phi\gamma_{24} & 0 \\ \sigma_1\gamma_{31} & \sigma_2\gamma_{32} & \sigma_3(1 - \rho_{13} - \rho_{23} - \gamma_{43}) & 0 & 0 \\ 0 & \sigma_2\gamma_{42} & \sigma_3\gamma_{43} & \sigma_4(1 - \rho_{54}) & \sigma_5\gamma_{45} \\ 0 & 0 & 0 & \sigma_4\rho_{54} & \sigma_5(1 - \gamma_{45}) \end{pmatrix}$$

equation 1

Each element of the transition matrix is defined by a combination of vital rates: σ_j is the survival rate of individuals in stage j , ϕ the reproduction rate of adults, γ_{ij} the growth rate of surviving individuals (old or new) progressing from stage j to stage i , and ρ_{ij} the retrogression rate of surviving individuals from j to i . Adult reproduction ϕ was calculated by dividing the number of new sporelings in a plot by the number of sporulating adults in the previous year. Stasis, i.e. surviving plants remaining within the same class, was modelled as one minus the growth and retrogression rates of the surviving plants in that stage class. These notations for the different types of vital rates are similar to those used by Franco and Silvertown (2004) and

Jongejans *et al.* (2006). We calculated the dominant eigenvalue of each transition matrix, which can be interpreted as the deterministic projected population growth rate, λ .

Life table response experiments

To investigate how environmental factors influenced the vital rates and consequently the projected population growth rate of *A. scolopendrium*, we analysed how variation in the vital rates caused variation in λ , and how environmental factors related to the variation in vital rates. We used the fixed factor life-table response experiments (LTRE) technique to decompose the variation in λ into contributions from the deviations in the vital rates (Horvitz *et al.* 1997; Caswell 2001). First we decomposed the temporal variation in λ of the *PF* plot into year effects with the following LTRE model:

$$\lambda^{(q)} \cong \lambda^{(\cdot)} + \beta^{(q)} \quad \text{equation 2}$$

in which a given λ of year q is written as the sum of the dominant eigenvalue of the mean of all matrices, $\lambda^{(\cdot)}$, and the effect of year q , $\beta^{(q)}$. This year effect can be estimated by the sum of the products of the vital rate deviations from their overall means and vital rate sensitivity values (Horvitz *et al.* 1997):

$$\tilde{\beta}^q = \sum_k (\tau_k^q - \tau_k^{(\cdot)}) s_{\tau_k} \left| \frac{1}{2} (A^q + A^{(\cdot)}) \right. \quad \text{equation 3}$$

in which τ is the k^{th} vital rate of the transition matrix (eqn. 1), $\tau_k^{(\cdot)}$ the overall mean of the vital rates and s_{τ_k} the λ -sensitivity value of τ_k . This sensitivity of λ to small perturbations in τ_k is determined in a transition matrix halfway between the matrix of interest, A^q , and the overall mean matrix, $A^{(\cdot)}$. In this way the year effects are decomposed into positive or negative contributions to the deviations in the vital rates. Note that if a given matrix has a λ smaller than the λ of the overall mean matrix, the sum of all LTRE contributions will be negative.

Next we investigated how differences in vital rates between plots contributed to differences in population growth rate between those plots. We calculated the means of the vital rates observed over the years in the Pthin stand and compared them to vital rate means (data from the same period only: 1989-1998) from the reference PF stand. The site effect α was defined as follows:

$$\tilde{\alpha}^{Pthin} = \sum_k (\tau_k^{Pthin} - \tau_k^{PF}) s_{\tau_k} \left| \frac{1}{2} (A^{Pthin} + A^{PF}) \right. \quad \text{equation 4}$$

in which the sensitivity values were determined for a transition matrix in which all vital rates were set halfway between the Pthin and PF means. Similarly, we decomposed the difference in λ between the *Fraxinus* (Fr) and PF plot (vital rate means calculated over the period 1983-1990):

$$\tilde{\alpha}^{Fr} = \sum_k (\tau_k^{Fr} - \tau_k^{PF}) s_{\tau_k} \left| \frac{1}{2} (A^{Fr} + A^{PF}) \right. \quad \text{equation 5}$$

Habitat traits

Cover of the herb and litter layer were estimated annually. The severity of the winters was summarised in the number of frost days. These are defined as days on which the temperature does not exceed 0 °C. Data on temperature and rainfall were obtained from www.knmi.nl and

were interpolated using data from weather stations elsewhere in the Netherlands. Rainfall during the preceding year and rainfall in summer and in April were used as parameters.

Microclimate

Light measurements were carried out in 1990 and 1998, using a photometer and measuring the incoming light reflected on a white piece of board during with a cloudless sky between 11:00h and 14:00h. As reference, the incoming light outside the woodland was measured. In some winters, temperature was measured with a minimum-maximum thermometer suspended between the fronds of *Asplenium scolopendrium* for several weeks in January.

Data analysis

Linear regression analysis was used to study which habitat parameters could explain the variation in the λ year effect and in the contributions to the variation in the different types of vital rates, as calculated for the PF plot. Linear regression was also used to quantify frost damage in relation to the severity of winters. The frond area (in cm^2) was $^{10}\log$ transformed to analyse the correlation with frost damage. Differences in snow cover and fertility were tested by the t-test, differences in plant height and number of fronds plant^{-1} with the Mann–Whitney test. Chi-square analysis was used to test the preference of sporelings for microhabitats and to analyse the mortality factors in the three plots. We calculated 95% confidence intervals for our estimations of the half life of the plants in the different plots by bootstrapping the ages of the individuals 3000 times (Efron 1982).

Results

Trends in population size

The number of plants in plot PF increased until 1984, but decreased in the subsequent years to about 20 plants m^{-2} , despite a small recovery in 1989/1990. In plot Pthin, plant density increased until 1994. Plot Fr, however, showed a rapid population increase, with a maximum density of 112 plant m^{-2} and a subsequent decline (Fig. 6.1).

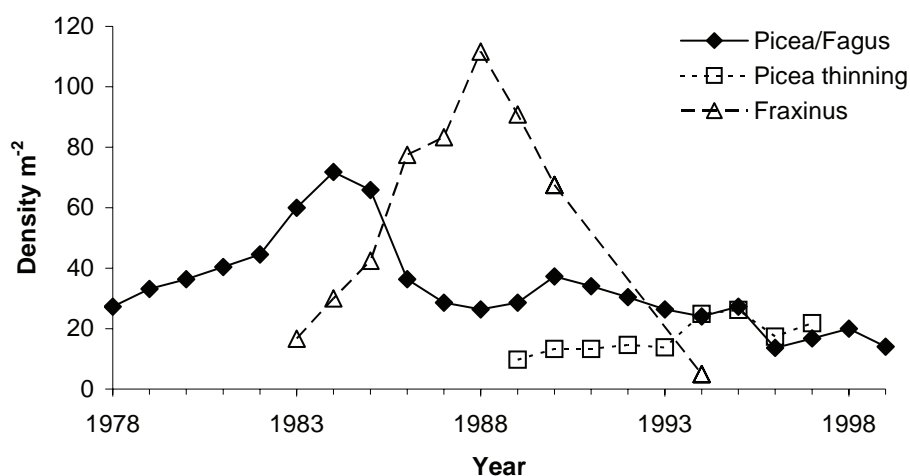


Figure 6.1. The density of plants of *Asplenium scolopendrium* in the three plots

Population structure

In all plots, sporelings and juveniles dominated in the first years. In each growing population they made up the largest proportion of the population. After the growing phase, the population in plot PF comprised all phases. In plot Pthin, subadults played a more important role and in the last years of monitoring, sporulating adults were absent. In plot Fr there was more recruitment than in the other plots. But after reaching the maximum density, all phases decreased eventually leading to the dominance and complete cover by some adult plants.

The longevity was calculated for plants whose moment of establishment as sporophyte was known. The average half life was 2.0 years in plot PF, 1.9 years in plot Pthin and 3.0 years in plot Fr. Comparing plots PF and Pthin for the same period, the half life is nearly the same, but in plots PF and plot Fr for the same period, the half lives are different (Table 6.2). The longevity shows a skewed distribution: many plants were short-lived, few plants became old. Adult plants became fertile at an age of three to ten years (5.3 years on average). Plants took longest to become adult in plot PF. Sporulating and surviving adults had a 29% probability of becoming non-reproductive (postadult) the next year. A comparison of a cohort of plant 7 years in plots PF and Pthin revealed that only 20% of them had become adult in plots PF and Pthin in this period, compared with 40% in plot Fr.

Climatological effects on the population dynamics of *Asplenium scolopendrium*

The projected growth rates of the fern populations ranged from 0.68 (declining) to 1.44 (increasing) (Fig. 6.2). The LTRE analysis quantified the effect of each year in the longest monitored PF plot. The magnitude of the year effect, β , was on average 0.153. We decomposed β into contributions to the variation in λ by the variation in reproduction, survival, growth and retrogression. The latter three are summations of the individual contributions of that type: for instance, σ is the sum of the contributions of, σ_1 , σ_2 , σ_3 , σ_4 and σ_5 . The magnitude (absolute value) of the ϕ contribution was on average 0.061, σ 0.080, γ 0.046 and the absolute ρ contribution was on average 0.023. This shows that the strongest

Table 6.2. Longevity, fertility and plant performance of the three populations monitored in plot PF, Fr and Pthin.. In order to compare the same periods with the plots Fr and Pthin, plot PF was divided into two periods (PF₁ and PF₂). Differences in the average year of becoming adult, plant height and number of fronds plant⁻¹ were tested. SD = standard deviation, * $p < 0.05$ *** $P < 0.001$, ns = not significant, - = no testing. Bootstrapped 95% confidence intervals are given for the half-life estimates.

	Pthin	PF ₁		Fr	PF ₂	
number of years	9	9		8	8	
Longevity						
number of plants	114	177		161	299	
half life (in years)	1.67	1.64		2.81	1.80	
Confidence interval half life (min)	1.43	1.38		2.55	1.64	
Confidence interval half life (max)	1.94	1.93		3.21	2.01	
Fertility						
total number of adult plants per plot	11	6	-	21	13	-
range of years before plants become adults	3 - 10	4 - 8	-	3 - 6	4 - 8	-
average age that plants become adult	4.5	6.0	*	4.0	6.3	***
SD	1.4	1.9		0.9	1.5	
Performance						
Plant height (cohort, in the fifth year)	17.6	12.9	ns	31.3	9.0	***
SD	8.2	9.0		22.4	6.6	
Number of fronds (cohort, in the fifth year)	3.9	4.4	ns	7.1	4.1	*
SD	1.4	1.6		6.4	2.2	

influence on the variation in λ was variation in survival, followed by the variation in reproduction.

Good and poor years alternated irregularly (Fig. 6.2). Multiple regression analysis showed a strong and very significant negative effect of cold winters (high number of frost days) on the year effect β (Table 6.3). The litter layer also had a significantly negative but smaller effect, whereas rain from May until July had a small, positive effect. Linear regressions of the ϕ , σ , γ and ρ contributions showed that the number of frost days was very important for the year-to-year variation in survival and retrogression, but not for reproduction. This shows that cold winters influence the population growth rate by reducing fern survival and increasing the retrogression of surviving ferns. Not one of the variables examined could explain the variation in the contributions of the growth of surviving plants. The contribution of reproduction was only explained by the litter layer, which showed an inverse correlation. The herb layer did affect the survival, but was not significantly related to the overall year effect.

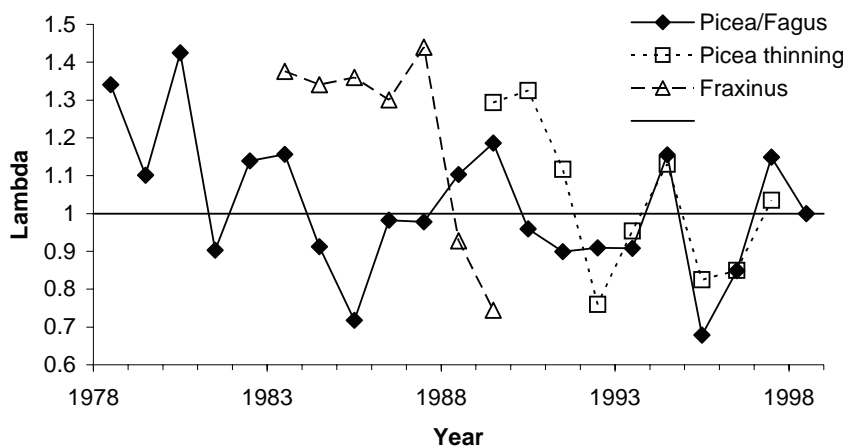


Figure 6.2. Projected growth rates (lambda) of three *Asplenium scolopendrium* populations calculated from year-to-year transition matrices. The populations were in different forest stand types.

When we examined the separate effects on λ of winter coldness, the litter layer, May-July rain and the herb layer, only the number of frost days showed a significant, inverse relationship (Fig. 6.3). The first year, from 1978 to 1979 was exceptional: the winter was the coldest (32 frost days) of the study period, but λ was high: 1.34. This was partly because survival was still above average, but also because the effects of the cold winter were compensated for by high reproduction ($\phi = 4.0$) later that year.

Effects of stand type on the population dynamics of Asplenium scolopendrium

Stand type may have influenced population growth in different ways: for instance through an increasing cover of the litter layer or through increasing light levels. In PF the litter layer did indeed increase from 1978 (10% cover) to the late 1990s (70% cover), which could partly indeed explain the negative contributions to λ from reduced reproduction and survival and from increased retrogression. There was no litter cover in both other plots. The light

Table 6.3. Results of linear regressions modelling the LTRE year effect (β) and contributions of the combined sexual reproduction (ϕ), survival (σ), growth (γ) and retrogression (ρ) rates to the year effects in plot PF based on 20 years of monitoring. The factors investigated were the number of frost days, the percentage coverage of the litter and herb layer, and rain [mm] from May until July, April and the whole year. Level of significance: (*) $0.05 < p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Non-significant factors were removed from the regression models.

	Year effect, β			ϕ contribution		σ contribution			γ contribution		ρ contribution			
	effect	t		effect	T		effect	t		Effect	t	effect	t	
Frost days	-0.115	-3.59	**			ns	-0.070	-5.49	***		ns	-0.020	-4.80	***
Litter layer	-0.004	-2.83	*	-0.002	-3.15	*	-0.002	-3.09	**		ns			ns
						*								
Rain May-July	0.001	2.25	*			ns	0.001	3.18	**		ns			ns
Herb layer			ns			ns	-0.002	-1.86	(*)		ns			ns
Rain April			ns			ns					ns			ns
Rain whole year			ns			ns					ns			ns

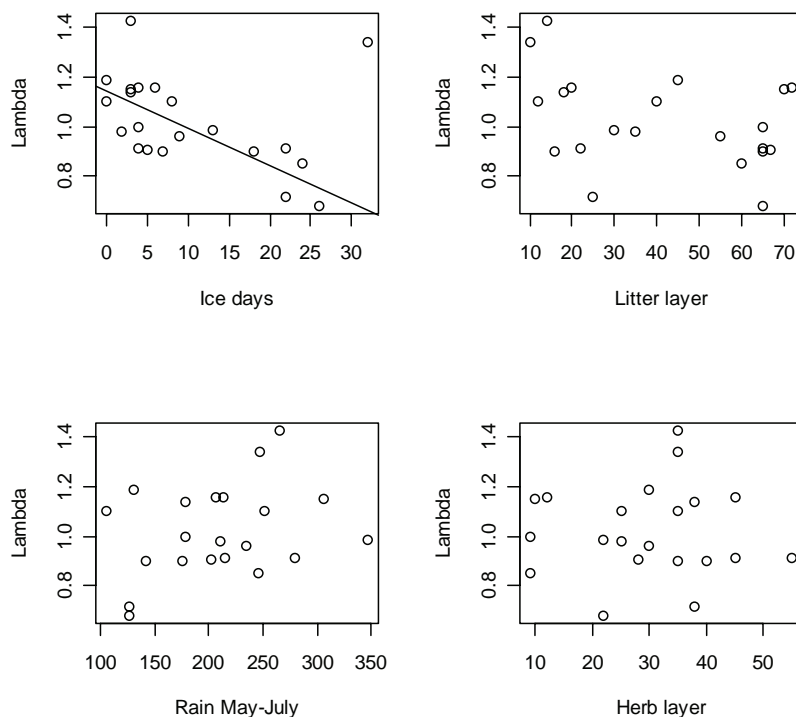


Figure 6.3. Relationship between abiotic (number of frost days, rain [mm] from May until July) and biotic (percentage coverage of the litter and herb layer) factors and the projected growth rate of the *Asplenium scolopendrium* population in the *Picea/Fagus* stand (the PF plot). A significant linear regression line is depicted for the λ -number of frost days relationship (the outlier year 1978-1979 was omitted from this regression analysis).

measurements in 1990 and 1998 showed an increase in light availability (Table 6.1). The comparison of the *Picea-Fagus* plot with the population in the thinned *Picea* stand, however, provides additional clues on the role of stand composition on populations of terrestrial *A. scolopendrium*. Over the period in which both plots were studied (1989 - 1998) the projected population growth rate was higher in the Pthin plot ($\lambda = 1.04$) than in the untouched *Picea-Fagus* plot ($\lambda = 0.92$). Decomposition of this λ difference into contributions from differences in vital rates between the two populations (Fig. 6.4) revealed an overwhelming contribution from the difference in reproduction, which was higher in the thinned forest ($\phi = 3.24$) than in the undisturbed forest (mean $\phi = 0.75$ for plot PF). Interestingly, λ was very similar between

the two populations in the last five years (Fig. 6.2), perhaps because the initial effects of thinning, with increase of light intensity, were less prevalent after five years. Light levels did indeed appear to be the same in both plots in August 1998 ($t = 0.83$ ns) (Table 6.1). Surprisingly, the comparison with the fern population in the Fr plot in the period (1983 -1990) showed very similar trends: λ was lower in the *Picea-Fagus* plot (1.01 vs. 1.24). Once again, the main reason for the difference in projected population growth rate was the higher reproduction rates (mean $\phi = 3.31$ vs. 1.23: see Fig. 6.4b). In early spring, light levels were higher in the *Fraxinus* plot than in the *Picea-Fagus* plot (Table 6.1). The full list of vital rate codes and explanations can be found in Table 6.4.

Table 6.4. Vital rate means for the three plots and various time periods

Vital rates		PF			Pthin	Fr
		'78-'99	'89-'98	83-'90	'89-'98	83-'90
Reproduction: #recruits _{t+1} per adult _t	ϕ	1.268	0.745	1.230	3.242	3.308
Survival of sporelings	σ_1	0.684	0.658	0.672	0.701	0.787
Survival of juveniles	σ_2	0.790	0.716	0.784	0.777	0.874
Survival of subadults	σ_3	0.814	0.820	0.812	0.891	0.866
Survival of adults	σ_4	0.903	0.880	0.939	0.758	0.915
Survival of postadults	σ_5	0.805	0.745	0.819	0.806	0.643
Growth of surviving sporeling _t to juvenile _{t+1}	γ_{21}	0.433	0.429	0.427	0.569	0.505
Growth of surviving sporeling _t to subadult _{t+1}	γ_{31}	0.012	0.007	0.003	0.016	0.016
Retrogression of surviving juvenile _t to sporeling _{t+1}	ρ_{12}	0.052	0.069	0.063	0.039	0.044
Growth of surviving juvenile _t to subadult _{t+1}	γ_{32}	0.262	0.284	0.294	0.388	0.394
Growth of surviving juvenile _t to adult _{t+1}	γ_{42}	0.037	0.014	0.018	0.025	0.022
Retrogression of surviving su-adult _t to sporeling _{t+1}	ρ_{13}	0.006	0.001	0.000	0.060	0.000
Retrogression of surviving subadult _t to juvenile _{t+1}	ρ_{23}	0.220	0.286	0.176	0.123	0.123
Growth of surviving subadult _t to adult _{t+1}	γ_{43}	0.404	0.437	0.396	0.301	0.474
Growth of new recruit to juvenile _{t+1}	γ_{24}	0.033	0.059	0.006	0.038	0.005
Retrogression of surviving adult _t to postadult _{t+1}	ρ_{54}	0.272	0.272	0.214	0.458	0.124
Growth of surviving postadult _t to adult _{t+1}	γ_{45}	0.410	0.453	0.336	0.090	0.214


Causes of mortality and frost damage


In the three plots 616 plants died for various reasons (Table 6.5). The most important factor was frost damage, especially in the PF plot, where land slip of the trench bank and litter accumulation also played a role. Density-dependent mortality due to crowding of plants in all stages led to self thinning and caused the highest death rate in the Fr plot. In the two *Picea sitchensis* plots (PF and Pthin), crowding of adult plants played a less important role. Self thinning probably also took place at the sporeling phase, but was not quantified.

In winters with on average more than c. 15% of the frond area damaged by necrosis there were significant correlations between the ratio in frond area plant⁻¹ ($\log(LA_t/LA_{t-1})$) and the percentage of frond area damaged plant⁻¹ in the PF plot. In more severe winters these correlation coefficients account for more of the variation found ($R^2 = 0.66$, $n = 5$). The number of frost days winter⁻¹ and frond damage are closely correlated ($R^2 = 0.96$, $n = 7$ years) (Table 6.6). In plot Fr the effect of severe winters was less.

Table 6.5. Factors responsible for mortality in the plots monitored in the Kuinderbos. **A.** total number of plants that died (all years of monitoring are incorporated in this table). **B.** factors responsible for mortality (as percentage of A). Frost damage data are based on field observations and regression analysis (see also table 6.6). * numbers estimated on micro distribution of sporelings.

	Plot PF	plot Pthin	Plot Fr	total
A				
total mortality (number of plants)	365	88	163	616
B				
Frost	39.7	38.6	8.0	31.2
Competition (self thinning)	6.8*	5.6*	47.8	17.5
Land slip of trench bank	8.2	3.4	3.7	6.3
Litter accumulation	3.8	0	0	2.3
Herbivory	0.3	0	0	0.2
Desiccation	0.3	0	0	0.2
Factors unknown	40.8	52.3	40.5	42.3

Table 6.6. Frost damage in two monitored plots with *Asplenium scolopendrium*.. **n fr** = number of frost days, **FD** = frost damage to plot, based on average percentage necrosis plant⁻¹, **R²** = explained variation between the ratio in frond area plant⁻¹ and percentage of frond area damaged plant⁻¹, **mortality**: percentage of plants that died in winter, - = plot monitored, parameters not measured.  = plot not monitored * p < 0.05 ** p < 0.01

Winter	n fr	Plot PF			Plot Fr		
		FD	R ²	mortality	FD	R ²	mortality
1978/79	32	65	0.36**	12			
1979/80	8	16	0.08*	11			
1980/81	3	13	<0.01	8			
1981/82	18	35	0.07*	14			
1982/83	3	-	-	8			
1983/84	4	-	-	14	-	-	-
1984/85	22	-	-	20	-	-	-
1985/86	22	39	0.07*	38	12	-	9
1986/87	13	20	-	25	9	-	7
1987/88	2	0	-	17	-	-	-

Conditions for establishment

The composition of the micro-vegetation in which sporelings were found differed significantly between the three plots (Table 6.7, $p < 0.001$). In all the plots, recruitment took place in the *Fissidentietum taxifolii* bryophyte community or in the community of *Fissidens bryoides* (Bremer 1999). In plot PF, there was land slip of the trench banks, which accounts for the high percentage of plants found on bare soil. In this plot recruitment also took place at the base of adult plants, even if these had died. In plot Pthin 40% of the area was covered by *Mnium hornum* and *Eurhynchium striatum*. No sporelings were found in these bryophyte mats. In plot Fr the *Fissidentietum taxifolii* interspersed in an open vegetation of *Brachythecium rutabulum* and *Eurhynchium praelongum*, which was also important as microhabitat for recruitment. The summed data from the Kuinderbos plots are similar to data collected at various sites in the UK in 1988 ($\chi^2 = 8.92$, ns).

Table 6.7. The vegetation within a radius of 1 cm around sporelings in the first year in the three plots in the Kuinderbos and in sites in Devonshire/Wye valley (UK, 3 plots) as reference (data collected in 1988). PF = plot in *Picea sitchensis*/*Fagus sylvatica* stand, Pthin = plot in *Picea sitchensis* stand, Fr = plot in *Fraxinus excelsior* stand.

	Plot PF %		plot Pthin %		plot Fr %		total %		UK %	
<i>Fissidentietum taxifolii</i> / <i>Fissidens bryoides</i> com.	19	27.9	16	44.4	25	33.3	60	33.5	20	40
bare soil	23	33.8	0	0	7	9.3	30	16.8	11	22
open <i>Brachythecium rutabulum</i> mat	1	1.5	0	0	34	45.3	35	19.6	3	6
open <i>Eurhynchium praelongum</i> mat	1	1.5	10	27.8	9	12.0	20	11.2	4	8
litter	4	5.9	1	2.8	0	0	5	2.8	0	0
at the base of adult <i>Asplenium scolopendrium</i>	20	29.0	5	13.9	0	0	25	14.0	10	20
other surrounding vegetation	0	0	4	11.1	0	0	4	2.2	2	4
Total number of plants	68	100	36	100	75	100	179	100	50	100

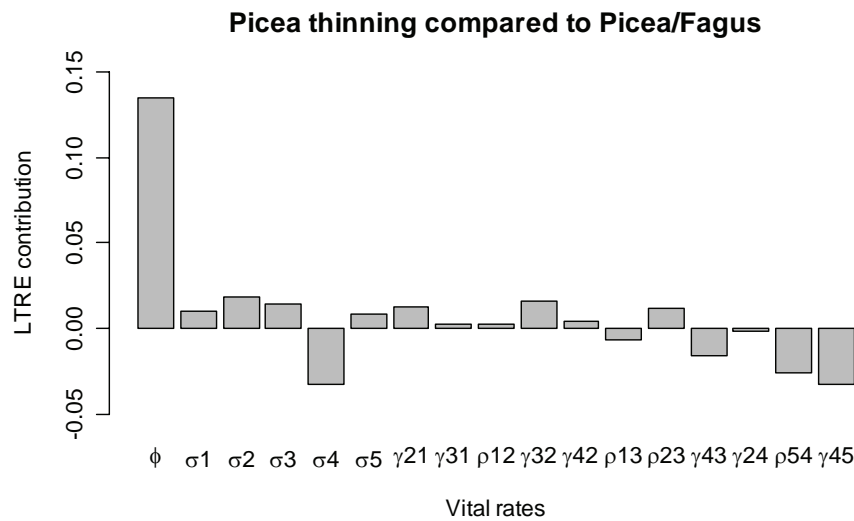
Discussion

Effects of frost on plant performance and population dynamics

Our analyses show that frost strongly reduces the population growth rate by reducing survival and increasing retrogression. Frost has three effects on plant performance: in severe winters many ferns are killed, while other plants become stunted or sterile (postadults). The highest mortality was observed in the winter of 1985/1986, when 38 % of the plants died. In this winter a mortality of as high as 88% was recorded within a wall-dwelling population in Langbroek (in central Netherlands) exposed to freezing wind. The trench-dwelling populations in the Kuinderbos were more protected since wind speeds in these trenches are low.

In New York, Cinquemani *et al.* (1988) attributed the variation in population size of *Asplenium scolopendrium* populations to drought (sites exposed to wind), the light climate (shade cast by *Tsuga canadensis*) and the amount of snow. The soil below *Tsuga canadensis* tends to freeze during the winter months, while adjacent soils, under hardwood canopies, are protected by deep snow cover, and do not freeze. In frozen soils without snow cover the supply of water may also be limiting (Cinquemani *et al.* 1988, Peck *et al.* 1990). Our results are consistent with those findings. On 30 November 1985 the snow cover in the PF plot was 0.9 ± 0.8 cm on average ($n = 10$), compared with 6.6 ± 1.2 cm ($n = 10$) in the Fr plot ($p < 0.001$), where snow protected the fronds. That winter, frost accounted for 38% of the mortality in the PF plot, while mortality due to frost in plot Fr was much lower (9%). There were no differences in minimum temperatures within the *Asplenium scolopendrium* vegetation. Peck *et al.* (1990) also confirm the importance of snow cover in protecting fern plants from desiccation. Temperature remains at zero after snow accumulation (McHaffie 2006). Frost resistance of ferns has been studied in Japan (Sakai & Larcher 1987). Evergreen species in the northern part of Japan were tolerant to freezing to -40°C . During the severe winter of 1978 - 1979, temperatures in the Kuinderbos fell to -23°C . In winter, the perennating organs, such as the fronds of the evergreen *Asplenium scolopendrium*, are dormant, which is associated with enhanced frost hardiness. If cell membranes are damaged and intracellular freezing takes place, the cells die (Sakai & Larcher 1987). Hardiness leads to an increase in the volume of membranes (Willemot 1975, Singh *et al.* 1975) and changes in the composition of phospholipids. The latter are an important compound of membranes. Phosphatidylcholine (PC) seems to be most related with frost hardiness (Smolenska & Kuiper 1977, Kedrowski & Chapin 1978). Bremer *et al.* (1984) have reported higher concentrations of PC in fronds of *Asplenium scolopendrium* in winter than in summer.

a)



b)

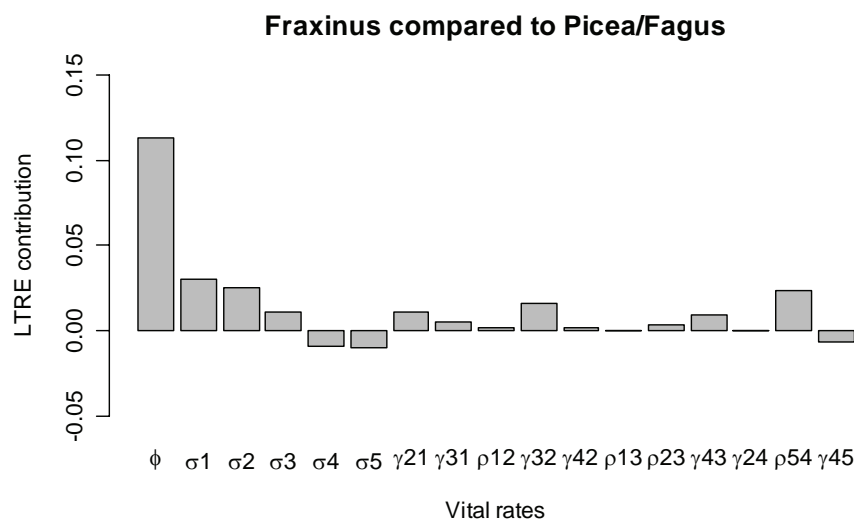


Figure 6.4. Vital rate LTR contributions showing how differences in vital rates contributed to deviations of the projected growth rate (λ) of the *Asplenium scolopendrium* populations in the thinned *Picea* woodland (a) and *Fraxinus* woodland (b) from λ of the *Picea-Fagus* woodland population. Separate sub samples of the reference *Picea-Fagus* data set were used in the comparisons to match the years in the two shorter data sets. Equation 1 shows how sexual reproduction (ϕ), survival (σ), growth (γ) and retrogression (ρ) define the annual transitions between the life stages.

In the Kuinderbos, frost damage was observed in nine fern species and frost-induced mortality in at least four species. But in none of these species was frond damage (necrosis) as pronounced as in *Asplenium scolopendrium*. In *Asplenium trichomanes* growing in the same Kuinderbos sites as *Asplenium scolopendrium*, frost did not cause necrosis. However, in this species too, decreases in population size correlated with the number of frost days winter⁻¹, although only above a threshold of 15 frost days (Bremer 2004). In *Asplenium scolopendrium*, significant effects of frost damage on frond production (when the average necrosis exceeded c. 15% of the frond area) oc-

curred from about eight frost days per winter. This indicates that *A. scolopendrium* is more sensitive to frost than *Asplenium trichomanes*.

Frost damage was also observed in other hardy species. After the severe winter of 1985/1986, necrosis was seen on more than 50% of the foliage area of *Hedera helix* and *Vinca minor*, for example (P. Bremer, unpublished results). There are few studies on the impact of frost damage at population level, as long-term demographic studies of evergreen plant species are scarce. However, a long-term study by Willems & Bik (1991) attributed high mortality and a low flowering percentage in a Dutch *Orchis simia* population to low winter temperatures.

Effects of stand type on plant performance and population dynamics

In the *Picea sitchensis* - *Fagus sylvatica* plot the projected population growth rate was lower than in the thinned *Picea sitchensis* plot or the *Fraxinus excelsior* plot. In both cases, higher reproduction rates (ϕ) were responsible for the differences. It seems plausible that the dominant factor resulting in differences in demography of the plots is the light climate. Light also has a major effect on plant performance. In the Pthin and Fr plots, plants became adult at a younger age than in plot PF. In the Fr plot there is much incoming light in spring prior to frond emergence of *Fraxinus excelsior* trees, while in the Pthin plot, thinning caused light intensity to increase. Despite the increased light intensities in this plot in subsequent years, subadults did not become fertile. The reason for this is unknown.

Measurements of incoming light in 1990 and 1998 indicated an increase of light intensity on the woodland floor in all plots. Under such circumstances, it could be hypothesised that the cover of *Asplenium scolopendrium* on the trench banks would exceed 90%, as in plot Fr, for instance. However, this was not the case, since litter accumulation hampered recruitment in plot PF, whereas in plot Pthin, 40 % of the plot area was covered by *Eurhynchium striatum* and *Mnium hornum*, which also hampered recruitment.

Accumulation of *Fagus* litter only played a role in plot PF. The gradual increase in the amount of litter on the plot had a negative impact, which might explain the difference in reproduction rates compared with the other two plots. The increase of the litter layer reduced the microhabitat for recruiting sporelings, as prothallia die under litter and spores do not germinate in litter. Bodziarczyk (1992) also reported that beech litter hinders the regeneration of *Asplenium scolopendrium*. This phenomenon has been reported in other plant groups. Bryophytes avoid the litter deposition in woodlands by growing on trench banks, trunks and trees. Adult plants produce their own litter as the fronds fade and droop down, over the soil or trench banks. In the *Fraxinus excelsior* plot, *Asplenium scolopendrium* accounted for over 90% of the herb cover. Below adult plants the light climate was restricted (light intensity < 1%) and a litter of wilted fronds accumulated. The same phenomenon has been observed in other hardy fern species, e.g. *Polystichum aculeatum* and *Polystichum setiferum* (Bremer 1995).

In all three plots *Asplenium scolopendrium* dominated the herb layer over the years. Intraspecific competition therefore played a considerable role in all plots, probably during all life stages. In the Fr plot nearly 50% of the population died as a result of intraspecific competition, because in some years only few plants became adults, overgrowing their neighbours, causing self-thinning. Only a few individuals were able to survive under a canopy of *Asplenium scolopendrium* fronds. These juveniles are comparable to the tree saplings growing below a closed forest canopy, waiting for growth after gap formation (Hunter 1999).

Other habitat traits and recruitment

Land slip of the trench banks caused up to 8% of the mortalities. The trench banks erode because water percolates through the fine sand overlying the peat, but when it reaches the peat it triggers small-scale slumping. This type of erosion also plays a role in other rare fern popula-

tions in the Kuinderbos. In 1979 many adult plants of *Asplenium trichomanes* died from major erosion of trench banks after heavy rain and subsequent drowning in the trench bottom (Bremer 2004). Peck *et al.* (1990) reported that freeze-thaw erosion in winter eliminated many gametophytes. Cinquemani *et al.* (1988) linked the number of plants of *Asplenium scolopendrium* per site with the influence of drought (or in fact indirectly to the impact of the wind). In our study there were dry summer periods with drought damage. Although some plant in the plots had desiccated fronds, no mortality due to drought was observed. However, in adjacent populations, summer drought did seem to contribute to sporeling mortality. The thick layers of fine-grained sand are fed by capillary rise of groundwater, which suggests that conditions for fern growth are optimal, but after weeks of drought in late summer, the upper layer (several cm) of the fine-grained sand dries out. We investigated three parameters related to rainfall in our regressions, but only early summer (May - July) rainfall were (positively) correlated with population growth. This corresponds with *Asplenium scolopendrium* growing optimally under moist conditions with high relative humidity (Page 1982).

Although herbivory by snails and slugs can damage fronds, herbivory had no impact on demographic parameters in our study. During all the years of monitoring inside and outside the plots, mass feeding on adult plants by snails (*Arianta arbustorum*) was observed only once. No evidence for herbivory by roe deer (*Capreolus capreolus*) was found in the plots, although one adult plant was defoliated by deer in another woodlands in Flevoland in 2002. Roe deer browse other fern species too.

The presence of sporelings correlated with an open bryophyte vegetation (aspect of pleurocarpous species) or bare soil that had been concomitantly colonised by *Fissidens* spp. or *Pellia endiviifolia*. For spores to be able to germinate and become prothallia, there must be open microsites. Here the prothallia have to compete with bryophyte species. In our study we did not monitor the fate of these prothallia. However, contrary to our findings, Ostlie (1990) argues that bryophyte beds enhance sporeling regeneration by providing a favourable site for fertilisation, spore germination and gametophyte growth. Peck *et al.* (1990) also mention that competition with bryophytes is detrimental for ferns. Bodziarczyk (1992) describes recruitment in two distinct microhabitats on stony slopes in Poland: rock with a sparse layer of bryophytes and interstone space filled with humic soil. Prothallia were found on the stabilised disaggregated rock in the bryophyte layer, but no prothallia were found on unstabilised soil. In the Kuinderbos trench banks eroded but subsequently stabilised and a cover of bryophytes re-established. The substrate has to be sufficiently stable to permit the development of the frail gametophytes. On walls, plants recruit in the inter brick space.

We conclude that the dynamics of *Asplenium scolopendrium* populations are affected by various factors, the dominant one being light. In a more favourable light climate (under *Fraxinus excelsior* stands, for instance) plants grow faster, produce more fronds, become larger and reach maturity sooner. It took a few years for these fern plants to form a closed cover. A closed cover was not formed in the more shady plots in the *Picea sitchensis* stand, where the composition of the bryophyte layer also played a role. *Fagus sylvatica* litter accumulation hampered recruitment.

Long-term population dynamics

Long-term studies are needed to quantify the effect of extreme weather conditions, yet most demographic studies do not exceed three or four seasons. Our study shows that over two decades the vital rates can vary profoundly. The effect of cold winters would not have been properly assessed in a short study lasting only three or four years. Variance decomposition analysis of the population growth rate proved to be a very elegant tool for identifying those life history

components that not only were affected by weather conditions but also contributed considerably to the variation in λ . We were therefore able to ascertain that the effects of frost on plant performance are really important for the population dynamics of the fern species we studied at the northern edge of its range.

The Kuinderbos has being colonised by *Asplenium scolopendrium* in the first half of the sixties (Chapter 3). The population growth received a setback in the 1980s, when severe winters damaged and killed plants. Since then, the strong increase is concentrated in an optimally managed habitat (a part of the *Picea sitchensis* - *Fagus sylvatica* stand, without plot) where the population size increased to more than 10,000 plants after a woodland thinning in 1998. Numbers increased after the thinning, which suggests that light was the trigger factor, as also found after analysing our data from the plots.

Long-term monitoring of *A. scolopendrium* in the cities of Amsterdam (data T. Denters in Maes & Bakker 2002) and Utrecht (Maes & Bakker 2002) showed that these populations increased tenfold in the period 1987 - 2000. The size of these wall-dwelling populations was much smaller than in the Kuinderbos, as walls provide only a small number of safe sites for establishment. Moreover, populations on walls are threatened by wall cleaning and restoration (Denters 2005), while during severe winters mortality can be as high as 88 % as stated before. Long-term monitoring has been carried out for over seventy years on six central New York populations of *Asplenium scolopendrium* var. *americana*. None of these six American populations increased as dramatically as the Kuinderbos population has done in recent years (Cinquemani *et al.* 1988).

Mean global temperature is rising as a result of increased concentrations of carbon dioxide, especially from the burning of fossil fuel. Climate change is likely to vary from country to country. It seems probable that the Netherlands will become warmer and wetter in the near future, as already experienced in the extreme summer of 2006. There will be also direct effects of increasing CO₂ concentrations on plant growth (Cannell 1990), and new species from warmer climates have been reported in the Netherlands (e.g. various species of lichens and seed plants, van Herk *et al.* 2002, Tamis 2005). Taking into account the data on population dynamics, mortality risks and distribution data, we expect *Asplenium scolopendrium* to increase in the Kuinderbos and elsewhere in the Netherlands. Severe winters will still occur sporadically, but our long-term monitoring shows that *Asplenium scolopendrium* is able to survive these events and to build up and maintain large populations at the current northern edge of its range.

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Mass recruitment in *Asplenium scolopendrium*.

The effect of woodland management on ferns



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Abstract

The effect of woodland management on ferns was tested in the field by three experiments. A thinning experiment was carried out in which populations of *Gymnocarpium dryopteris* were monitored in a plot before and after thinning and in a control plot. Two other plots were monitored in the same period over a period of 15 years in the Kuinderbos forest. Colonies were mapped and number of fronds colony⁻¹ counted annually. In the thinning experiment, mortality was 51%, compared with 63% in the control plot. Colonies lost fertility, became smaller and eventually died. After forest thinning the fern population recovered within seven years to the former population size. The experiment showed the impact of the light climate. In a reference plot with a clay topsoil, the number of fronds colony⁻¹ increased, but no recruitment was observed, probably due to the dense moss layer on the woodland floor and trench banks. In a second reference plot in the peat erosion area, *Gymnocarpium dryopteris* reacted positively (by recruitment) to forest thinning while windfalls in preceding years had a positive effect on the size of the fern patches.

In a second experiment, two stands of *Picea sitchensis* - *Fagus sylvatica* were monitored after repeated thinning at an interval of six years. With thinning the light climate improved (to between 2% and 5% light intensity), allowing mass recruitment of *Asplenium scolopendrium* and *Polystichum aculeatum* to take place. *Gymnocarpium dryopteris* reacted by forming larger patches.

In the Voorsterbos, artificial gaps within stands of *Fagus sylvatica* on boulder clay were monitored for three years after cutting. Ten fern species established in these gaps, including two species not known from the area. *Athyrium filix-femina* formed dense stands. Various species (e.g. *Gymnocarpium dryopteris*, *Dryopteris cristata*) behaved as pioneers but were unable to build up a population. *Thelypteris palustris*, however, did build up a population. It seems plausible that the mass colonisation was related to a spore bank and an optimal microclimate with constant high moisture and humidity in the shaded part of the gaps. In the gaps, mass recruitment of *Fraxinus excelsior* was suppressed by herbivory of Roe deer for a period of five years, but variation in browsing was subsequently responsible for a heterogeneous dense recruitment pattern.

Introduction

Woodlands are the climax vegetation over much of the Earth and do not need any human intervention to be sustained. As humans need timber and fibre, they manage woodlands and harvest boles. Numerous silvicultural tools are available to forest managers; they include a wide range of harvest systems, regeneration methods and rotation lengths. Various studies have been published on the effects of harvest practices on understory and over story conditions in managed forests (e.g. Halpern & Spies 1995, Thysell & Carey 2000, Bergstedt & Milberg 2001), but none of them focused on ferns. In the Netherlands, the long-term monitoring of unmanaged woodlands pays attention to the herb layer (Koop 1989, Broekmeyer *et al.* 1993), while the effect of management has been documented for *Pteridium aquilinum* (den Ouden 2000). Silviculture is focused on the tree layer and the recruitment of trees.

In the Noordoostpolder (province of Flevoland, Fig. 1.1), woodlands such as Kuinderbos and Voorsterbos were planted after reclamation, for timber production but also for recreation and as habitat for plants and animals. After planting, the stands were managed intensively by thinning in order to select for certain tree species. Thinning varies in terms of the return interval, the severity (the number of trees cut) and the spatial pattern (Hunter 1999). In Chapter 3 some attention was paid to silviculture and its relation to the fern flora, but at the start of the survey (1977) little knowledge on this topic was available. For that reason two thinning experiments were set up in the Kuinderbos in a *Picea sitchensis* - *Fagus sylvatica* stand already rich in fern species and with high density of various species. One of these experiments focused on *Gymnocarpium dryopteris*, the other on the complete group of rare fern species.

In 1997 the management objective in the Voorsterbos changed from timber production to ecological forestry. Homogeneous thinning with a short return interval was banned and replaced by heterogeneous thinning, artificial gap formation and longer periods of no management, in order to increase the variation within the stands and to convert single cohort stands into stands with a mosaic of phases (Koop 1989, Koop & Siebel 1993, van den Burgh *et al.* 1995, Hunter 1999). The first series of gaps in the Voorsterbos offered an opportunity for studying the effect of these gaps on the herb layer, especially on the fern population. We hypothesised that gaps would be vegetated by recruiting trees while ferns would not expand as they had been scarce prior to the gap formation.

The study area

The Noordoostpolder was reclaimed in 1941/1942 and the Kuinderbos was planted in the period 1949–1954 and the Voorsterbos in the period 1944–1955 (Bremer 2001). Both sites are below mean sea level: the altitude varies from -3.1 to -1.2 m in Kuinderbos, and from -2.5 to -1 m in the Voorsterbos. About 40% of the Kuinderbos has been classified as peat erosion area (Bremer 1980, Chapter 3, see also Fig. 3.1), with a rich fern flora. On the peat soils, many trees were planted in mixed stands at a density of up to more than 10,000 trees ha⁻¹. *Picea sitchensis*, *Picea abies*, *Quercus robur* and *Fraxinus excelsior* are now growing in pure and mixed stands. Broad-leaved species have become dominant on the soils with the deepest cover of fine sand, while *Picea sitchensis* dominates the peat soils without much sand cover. The Voorsterbos has been planted on sand and boulder clay. Here, *Quercus robur* dominates (48 % of the area), while other tree species are less important: *Pinus* spp. (12%), *Fagus sylvatica* (8%) and *Fraxinus excelsior* (7%) (Bremer 2001). Drainage trenches were dug at a density of up to 0.7 km ha⁻¹ (peat erosion area) in the Kuinderbos and up to 1 km ha⁻¹ in the Voorsterbos (boulder clay); their depth ranges from 0.4 m to more than 1.2 m. The depth to the water table is always more than 0.5 m in the peat erosion area, but a large area on the boulder clay has a water table at a depth of less than 0.5 m in the winter. Currently the trees extract much water, making drainage

by trenches less important than in the years after these woodlands were planted.

Methods

First experiment

Gymnocarpium dryopteris populations were monitored in four plots in the Kuinderbos during the period 1979 – 1992. The canopy of these stands consists of *Picea sitchensis*. Plots I and II were located in the peat erosion area (Bremer 1980). Plot III was in an area of acidified clay on peat. There was some variation in the density of trenches and in windfalls that occurred during the storms in 1985 and 1990. There was no systematic variation in the depth of trenches (Table 7.1).

In 1987, 26% of the trees were cleared on part of plot I, which was designated plot Ia. The uncleared part of plot I was designated plot Ib (control plot). In 1989, plots II and III were lightly thinned (c. 20 % of the trees cleared). The plots were monitored annually, at the end of August. In patches of ferns with less than 100 fronds the fronds were counted; in larger patches, frond numbers were estimated. Colonies were mapped at a scale of 1:2500 so they could be monitored. In 1992 the number of fertile fronds colony⁻¹ was recorded. The average moss and herb cover were surveyed in 1979, 1993 and in some plots also in 1986.

The windfalls in plots II and III were also mapped. Light intensities several cm above the woodland floor were measured in plots Ia and Ib with a Lunasix 3 light meter on 30 August 1990 during unclouded weather in the middle of the day.

Second experiment

A second experiment was started in 1993. A *Picea sitchensis* - *Fagus sylvatica* stand unmanaged since 1977 was thinned in 1993 and 1998. The control plot was plot Ib mentioned above (no thinning since 1977). For the thinning, c. 20% of the trees was harvested and some *Fagus sylvatica* trees were girdled. Rare ferns were mapped and their numbers monitored during three inventories.

Third experiment

In the Voorsterbos a management strategy started in 1990, aiming to produce a shifting mosaic by making artificial gaps in various stands (Koop & Siebel 1993). In the period 2000 - 2006, 54 gaps were created by cutting trees. This study focuses on 12 gaps in *Fagus sylvatica* stands on boulder clay, cut in 2000, 2001 or 2004, monitored for at least three years. Here the mass establishment of fern sporelings and juveniles occurred in the first year after cutting. In these gaps the vegetation and recruitment of tree species were mapped and data were collected on the distribution of rare ferns and their growth. Individual plants of rare fern species were counted. In the second year after cutting, an area adjacent to the gaps was surveyed for fern species. These 'plots' were used as control. Shade was mapped on or near 21 June (with largest area of gap floor receiving direct light) and 21 September (the end of the astronomical summer, approximately the end of the growing season). The shade line of 21 June is defined as the 100% shade line (the part of the gap south of this line is always in shade), while the shade line of 21 September is defined as the 0% shade (the part of the gap north of this line in the period between 21 June and 21 September has no shade). The position of rare fern individuals was recorded with reference to these two lines. The density of *Athyrium filix-femina* was measured within a matrix of 1 x 1 m plots in one of the gaps.

Statistical analysis

A chi-square test was used to analyse habitat preference. A Kruskal–Wallis test was used to analyse a gradient in density of *Athyrium filix-femina* in one of the gaps. A Mann-Whitney test was used to analyse mortality.

Results

*First experiment: the effect of thinning on *Gymnocarpium dryopteris**

The density of patches of the four plots was high, ranging from 6 to 57 colonies hectare⁻¹ with plot Ia showing the highest density in the Netherlands. Major changes occurred in a period of 15 years: plot I showed a decrease in density from 1979 until 1986, when high mortality occurred. After thinning in 1987, the density increased again, until after six years the original density had been re-attained (Fig. 7.1). In plot Ib, where there was no thinning, the density remained at a low level after 1986. In plot II, the density of colonies remained constant until 1989, when after thinning the density increased. In plot III, the density hardly fluctuated over the 15 years of monitoring (Fig. 7.1). In the period 1982 – 1986, plots Ia and Ib showed a high level of mortality, but mortality was low in plots II and III. The survival rate (Table 7.3 h) was notably low in plot Ia, indicating a high turnover. The number of newly established stands was high in plots Ia and II. Figure 7.2 shows the fluctuations of the average number of fronds colony⁻¹. In plot Ib the average number of fronds patch⁻¹ present at the annual census decreased from 1983 until 1988, after which an increase occurred. No patches of over 1,000 fronds were found. The same holds for plot Ia except that after 1989, patches of over 1,000 fronds were found. Plots II and III showed a conspicuous increase in the average patch size; colonies of over 1,000 fronds were present in both plots after 1992. Figure 7.3 shows the average patch size with respect to the patch age. All the colonies that had established since 1979 were incorporated. In plot Ia there appears to be a linear correlation. In plot Ib patch size appears to decrease after an age of three years. No graphic representation can be given for plot III, because of insufficient recruitment. Table 7.4 shows that in colonies that established between 1979 and 1993, the mortality in colonies less and more than two years old was not different ($\chi^2 = 0.5$ ns). The percentage of adult colonies increased with patch size (Fig. 7.4). Colonies with less than 50 fronds are usually sterile. In colonies of 51 – 100 fronds, fertility varied from 0% in plot Ib to 100% in plot III. The percentage of fertile fronds colony⁻¹ increased with colony size, except in plot Ib. Fertile fronds are larger than the sterile fronds and often grow in a separate layer above them. In plot Ia the light intensity in 1990 was 3.4%, compared with an average of < 2% in the control plot Ib (Table 7.5). In plot Ia colonies had on average 13 fronds colony⁻¹ in the last year of recording (before dying), in plot Ib this was at average 18 fronds. These differences were not significant ($p = 0.38$).

Second experiment: the effects of a repeat thinning

In the control plot the herb layer cover remained low (< 2 %) while in the thinning plot the herb layer increased after thinning, with light intensity increasing to 2 - 5 % (Table 7.5). Rare ferns decreased in the control plot. Patches of *Gymnocarpium dryopteris* became smaller, the numbers of *Asplenium scolopendrium* stabilised and *Cystopteris filix-fragilis* faded away. In the thinned plot there was mass establishment of *Asplenium scolopendrium* and of *Polystichum aculeatum* (which increased to 391 individuals in 2002). The plot was the most successful site within the Netherlands in view of recruitment and population size (Table 7.6). The congenial *Polystichum setiferum* hardly responded to the increase in light intensity.

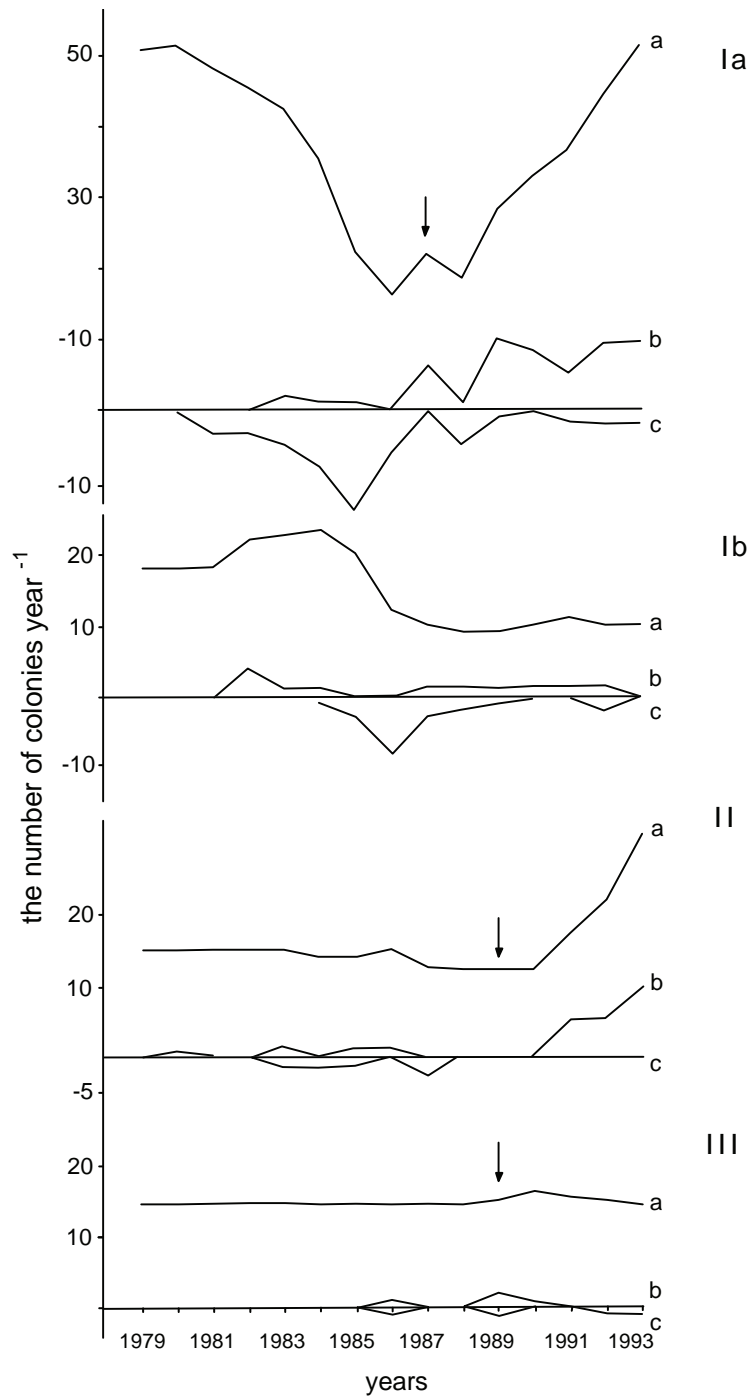


Figure 7.1. The number of *Gymnocarpium dryopteris* colonies year⁻¹ in four plots in stands of *Picea sitchensis* in the Kuinderbos (the Netherlands) **(a)**, the number of colonies arriving year⁻¹ **(b)**, and number of colonies lost year⁻¹ **(c)**. ↓ = year of thinning.

Plot Ia. Plot in peat erosion area, thinned in 1987.

Plot Ib. Plot in peat erosion area, not thinned since 1978.

Plot II. Plot in peat erosion area (other parcel than Ia/Ib), thinned in 1989, windfall since 1985.

Plot III. Plot with peat soil and clay/sand deposits, thinned in 1989.

Table 7.1. Some features of the Kuinderbos plots (Noordoostpolder, The Netherlands). **plot:** designated number, see Fig. 7.1, **area:** area in ha, **soil:** p.e.a₁ = peat erosion area with fine-grained sand deposits > 0.4 m deep overlying peat, p.e.a₂ = same, deposits < 0.4 m, cl = acidified clay on peat, **dt** = density of trenches in km ha⁻¹; **depth:** depth of trenches in m, **thinning** = year of thinning, - = no thinning, **d Pc** = average density of *Picea sitchensis* 100 m² in 1990, **windfalls:** the percentage of the area with windfalls, - = no gaps occurred.

Plot	area	soil	dt	depth	thinning	d Pc	windfalls
Ia	0.9	p.e.a ₁	0.62	0.7 - 1.0	1987	8.6	1979: 0% 1990: 0%
Ib	0.5	p.e.a ₁	0.62	0.5 - 0.9	-	11.6	1979: 0% 1990: 5 %
II	0.8	p.e.a ₂	0.4	0.5 - 0.7	1989	6.4	1979: 0% 1986: 4% 1990: 12%
III	2.5	cl	0.4	0.6 - 0.9	1989	6.7	1979: 0% 1990: 1.5%

Table 7.2. The estimated moss and herb layer cover (in %) in four plots for certain years. For plot number, see Fig. 7.1.

plots	years	trench banks		woodland floor	
		moss layer	herb layer	moss layer	herb layer
Ia	1979	50	30	50	30
	1986	15	5	15	5
	1993	85	20	75	10
Ib	1979	50	30	50	30
	1986	15	5	15	5
	1993	15	5	15	5
II	1979	80	10	80	10
	1993	80	10	95	10
III	1979	90	35	90	25
	1993	90	35	90	25

Table 7.3. Population fluctuations of *Gymnocarpium dryopteris* in four plots in the Kuinderbos (The Netherlands) for the period 1979 – 1993. For plot number, see Fig. 7.1.

	Plot number	Ia	Ib	II	III
A	Number of colonies in August 1979	51	18	15	15
a1	density of colonies (ha ⁻¹)	56.7	36.0	18.7	6.0
B	number of colonies in August 1993	51	10	31	14
b2	density of colonies (ha ⁻¹)	56.6	20.0	38.7	5.6
C	net change (b-a)	0	-8	16	-1
D	rate of increase (b/a)	1.0	0.6	2.1	0.9
E	number of colonies that arrived between August 1979 and August 1993	52	12	23	4
F	total number of colonies lost between August 1979 and August 1993	52	19	7	5
G	colonies present in August 1979 and still alive in August 1993	11	10	9	12
H	percentage survival of colonies present in 1993 (g/a x 100%)	21.6	55.6	60.0	80.0
I	expected time for complete turnover years (14/ 100 - h) x 100)	19.1	33.8	37.5	75
J	total number of colonies recorded during study	103	30	38	19
K	percentage mortality over 15 years of all patches (f/j x100%).	50.5	63.3	18.4	26.3

Table 7.4. The mortality (number of plants) within the cohort which established between 1979 and 1993, in relation to their age. For plot number, see Fig. 7.1.

Age/plot	Ia	Ib	II	III	total
< 2 years	4	1	1	1	7
> 2 years	28	7	8	3	46
total	32	8	9	4	53



Gymnocarpium dryopteris

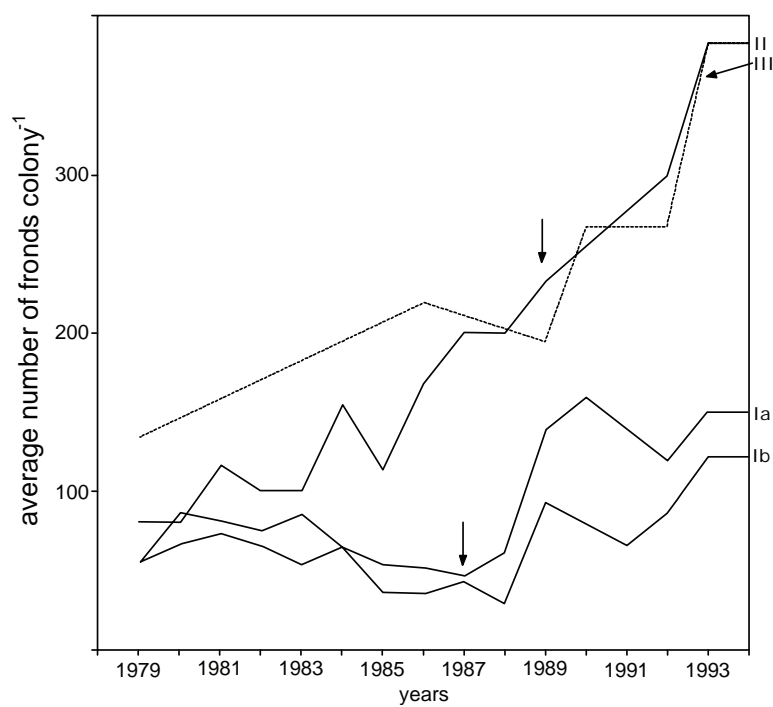


Figure 7.2. The average number of fronds patch⁻¹ year⁻¹ of *Gymnocarpium dryopteris* for four plots. The designated numbers of the plots are the same as in Fig. 7.1. ↓ = year of thinning.



Figure 7.3. Average number of fronds colony⁻¹ in relation to age of colonies, for all colonies which arrived after 1979 (plot III not shown due to low recruitment).

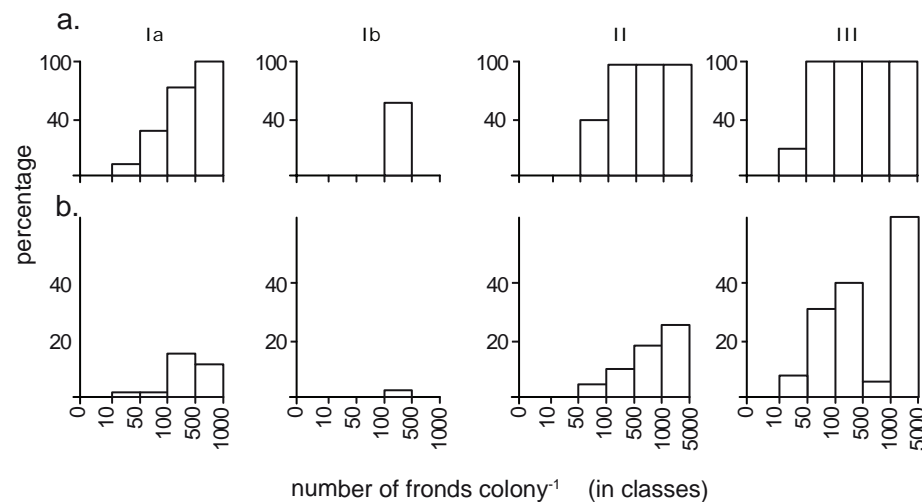


Figure 7.4. Fertility in *Gymnocarpium dryopteris* in 1992 in four plot, n = number of colonies plot⁻¹: Ia n = 45, Ib n = 12, II n = 22 and III n = 15.

a. the percentage of colonies with fertile fronds size class⁻¹.

b. the percentage of fertile fronds based on the total number of fronds⁻¹ size class⁻¹.

The designated number of plots is the same as in Figure 7.1.

Table 7.5. Light intensity at woodland floor (as percentage of light intensity in unshaded situation) in thinned and control *Picea sitchensis* stands on 30 August 1990. Measurements were carried out between 13.10 h and 13.30 h with an unclouded sky, n = number of measurements, SD = standard deviation.

	n	Average	SD
Control plot without thinning	15	1.9	1.5
Plot with thinning			
Track	20	3.7	2.5
trench bank	15	2.5	1.3
between track and trench	20	3.8	2.4

Third experiment: the effect of creating gaps in Fagus sylvatica stands

In the period 2000 - 2006, 54 gaps were created in the Voorsterbos. Twelve of these, in 50-year-old stands of *Fagus sylvatica* on boulder clay, were monitored. These gaps were 1.5 - 2 times tree height, and their size varied from 0.08 to 0.15 ha gap⁻¹, with one gap of 0.25 ha (Bremer 2007). Within three years the gaps were dominated by the herb or shrub layer. *Fraxinus excelsior* recruited at a density of more than one sapling m⁻². After five years, patches of trees were able to build up a young woodland phase despite heavy Roe deer (*Capreolus capreolus*) browsing. In these gaps, ten fern species established (five of which were known from the adjacent zone: Table 7.7). Three fern species which established in one gap or more had previously been recorded in the woodland within a radius of 1 km from the gaps. *Thelypteris palustris* and *Dryopteris cristata* had not been found recently in this woodland, while *Matteuccia struthiopteris* grows in gardens in the vicinity. *Asplenium scolopendrium* was found adjacent to one of the gap; it was the only fern not found within the gap habitat.

Within the gaps, ferns established on trench banks and the woodland floor. *Athyrium filix-femina*, the most successful fern species, had its highest density in the trenches ($\chi^2 = 6.5$, $p < 0.05$). The group of rarer fern species (established in less than four gaps) showed no preference for trench or woodland floor habitat considering the population size ($\chi^2 = 0.5$ n.s), but when densities were corrected for the area of both habitats there was a preference for the trench habitat ($\chi^2 = 12.7$ $p < 0.001$). Plants of *Thelypteris palustris* only established on the woodland floor. Fertility was only observed in the group of the most common species (present in more than 50% of the gaps). Some plants of *Athyrium filix-femina* reached the adult phase in the third season after cutting and became codominant in 5 out of the 12 gaps with a vegetation that can be described as a 'hochstaudenflur' (Ellenberg 1982). The establishment of ferns was most successful in the southern parts of the gaps, within the 100% shade line: *Thelypteris palustris*, *Dryopteris cristata*, *Dryopteris affinis* and *Polystichum aculeatum* were found exclusively within this line. *Gymnocarpium dryopteris* and *Matteuccia struthiopteris* were only found within the 75% shade line (Fig. 7.5) and *Athyrium filix-femina* reached its highest density in this zone ($\chi^2 = 8.3$ $p < 0.01$ $n = 12$). Within the largest gap (0.25 ha) the average herb layer cover in the fifth year was 92%, with *Athyrium filix-femina* contributing 17%. In this gap, a gradient in density of *Athyrium filix-femina* could be correlated with the period of shadow in the summer period ($\chi^2 = 10.8$ $p < 0.01$). Three species of *Equisetum* established. *Equisetum arvense* became codominant, *Equisetum telmateia* colonised neutral boulder clay in one gap, while *Equisetum fluviatile* also established within the 100% shadow line in two gaps. In one of the gaps *Scirpus sylvaticus* established with numerous clones. Forty-two gaps were created in other stand and soil types. Sandy soils low in pH were poor in fern species. *Dryopteris dilatata* was present prior to the cutting and increased afterwards. No rare ferns established. In a stand of *Carpinus betulus* on boulder clay, gaps were created by girdling trees; though this led to a gradual increase of light intensity, no ferns established, while young trees formed a dense stand.

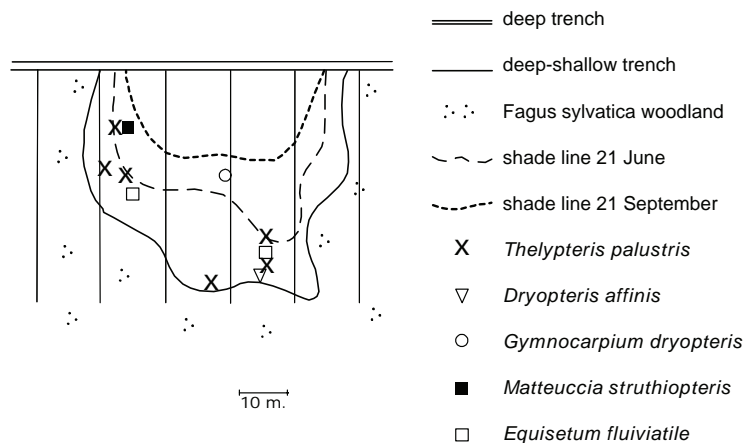


Figure 7.5. Woodland gap within *Fagus sylvatica* stand showing the shade lines and the distribution of rare ferns and horsetails.

Table 7.6. The impact of thinning in a *Picea sitchensis* stand with avenues of *Fagus sylvatica*, c = control plot without management after 1978, p = plot with no management between 1977 and 1993, with thinning in 1993 and 1998. Before / = the summed number of colonies, behind / the number of fronds in *Gymnocarpium dryopteris*. Both plots have the same area (2 ha) and have a trench length of 0.8 km.

		1979	1994	1995	2002
Herb layer cover	c	35%	5%	5%	5%
	p	35%	5%	10%	25%
<i>Asplenium scolopendrium</i>	c	73	541	519	563
	p	18	237	659	2198
<i>Gymnocarpium dryopteris</i>	c	22/?	19/?	19/597	6/1150
	p	17/?	19/3490	21/3523	22/7000
<i>Cystopteris fragilis</i>	c	183	10	3	2
	p	48	0	0	0
<i>Polystichum setiferum</i>	c	3	5	2	3
	p	0	1	1	5
<i>Polystichum aculeatum</i>	c	0	0	0	0
	p	2	42	46	391
<i>Gymnocarpium robertianum</i>	c	0	0	0	0
	p	1	0	0	0

Discussion

There are very few published accounts of the effect of woodland management on ferns. I observed that the establishment of colonies and the growth of *Gymnocarpium dryopteris* were influenced by changes in the canopy structure through cutting, girdling or windfall that increase light intensity at the woodland floor and on trench banks. When fern plants experience low light intensities, fern patches grow slowly (or even decrease) and have low fertility. Under these conditions the light intensities were less than 2%. Increase of light intensity, due to canopy thinning or windfall, resulted in a high growth rate, higher percentage of fertile colonies (adults) and recruitment.

The trend in plot Ia paralleled that in plot Ib, but after thinning, the number of fronds colony⁻¹ in plot Ia was higher, due to an increase in light intensity (Figure 7.2). The increase in plot Ib was unexpected; it is related to the formation of some small gaps without human interference. The establishment of new patches (with a low number of fronds colony⁻¹) also had an impact on the average in plot Ia. In plot II, stress due to light conditions was reduced after 1985, through windfall. The gaps created by windfalls increased in size after 1990. In the centre of these gaps *Gymnocarpium dryopteris* was overgrown by *Eupatorium cannabinum*, however, and later by recruiting trees (e.g. *Betula*, *Acer pseudoplatanus*) and shrubs¹. In plot III, thinning was done in 1989, after which the number of fronds increased steadily over the years. Prior to thinning, the moss and herb layer were more luxuriant than in the other stands, which suggests that a clay soil, through its higher nutrient content, may partially compensate for any stress due to lower light conditions (Ellenberger 1982). Recruitment was very low in this plot, despite the presence of favourable trench banks with appropriate light conditions.

Table 7.7. Fern species found within gaps of *Fagus sylvatica*/ boulder clay stands (3-7 years after cutting, 8-17 are gap⁻¹) compared with uncut woodland adjacent to the gaps, based on annual monitoring, n = 12), **n g** = number of gaps with species listed, **np g** = total number of estimated or counted plants/colonies in 12 gaps after two seasons, **a** = number of 50 m zones surrounding gaps with species listed, **np a** = total number of plants in 50 zones (all gaps summed) after two seasons, **tr** = number of gaps with species listed growing in trenches, **wfl** = number of gaps with species listed growing on the woodland floor, **f** = fertility of plants after establishing in the gaps; **f** = with fertile fronds within four years, **n.f** = not fertile within four years, **sh** = percentage of time with shadow cast in period 21 June -21 September based on number of plants/colonies as mentioned in *n plant gaps*, **na** = not analysed, **VB** = species found elsewhere in the Voorsterbos (including Waterloopbos) or on its border in the period after 1990, between brackets; population in gardens near the woodland.

Woodland species	Woodland gaps						50 m zone						VB
	n g	%	np g	tr	%	wfl	%	f	sh	a	%	np a	
<i>Athyrium filix-femina</i>	12	100	> 1000	12	100	12	100	f	na	8	66.7	50 - 100	+
<i>Dryopteris dilatata</i>	11	91.7	200-400	11	91.7	11	91.7	f	na	8	66.7	50 - 100	+
<i>Dryopteris filix-mas</i>	8	66.7	200-400	8	66.7	8	66.7	f	na	8	66.7	50 - 100	+
<i>Dryopteris carthusiana</i>	6	50.0	50-100	6	50.0	5	41.5	f	na	3	25.0	25 - 50	+
<i>Thelypteris palustris</i>	5	41.7	13	1	8.3	5	41.7	n.f	84.6	0	0	0	-
<i>Matteuccia struthiopteris</i>	2	16.7	2	1	8.3	1	8.3	n.f	70.0	0	0	0	(+)
<i>Dryopteris cristata</i>	2	16.7	2	2	16.7	0	0	n.f	75.0	0	0	0	-
<i>Gymnocarpium dryopteris</i>	1	8.3	1	1	8.3	0	0	n.f	50.0	0	0	0	+
<i>Polystichum aculeatum</i>	1	8.3	1	0	0	1	8.3	n.f	100	0	0	0	+
<i>Dryopteris affinis</i>	2	16.6	2	1	8.3	1	8.3	n.f	100	1	8.3	1	+
<i>Asplenium scolopendrium</i>	0	0	0	1	8.3	0	0	-	-	1	8.3	1	+

¹ In 2004 it was observed that numerous colonies survived this phase.

The dense mats of *Mnium hornum* and *Eurhynchium praelongum* may have had a negative effect on recruitment. In the Kuinderbos, dense 40-year-old stands of *Picea abies* were thinned for the first time after 1985. These stands are similar to those of *Picea sitchensis* which are also located in the peat erosion area (Bremer 1980) and have high densities of trenches. After thinning, the amount of light reaching the soil increased from less than 1% to 3 - 4%, facilitating the establishment of *Gymnocarpium dryopteris*.

The effect of light conditions on plants growing in woods has often been demonstrated (Anderson 1963, Eber 1972, Peterken 1981, Ellenberger 1982). Oinonen (1971) showed that *Gymnocarpium dryopteris* in Finland did not establish from spores. He stated that vegetative propagation was responsible for its abundance. In the Netherlands, *Gymnocarpium dryopteris* mainly occurs in one or a few colonies per location that rarely expand (Chapter 5). The situation in the Kuinderbos is an exception: here establishment from spores was found in stands of *Picea sitchensis* and more recently in *Picea abies*.

Table 7.4 shows that in colonies that established between 1979 and 1993 mortality did not differ between colonies younger and older than two years old ($\chi^2 = 0.5$ ns). This indicates that the colonies were all influenced by the same mortality factors. The causes of this juvenile mortality were hard to assess from our observations. Some colonies died because of small-scale land slips on the trench banks. Low light conditions may have been a factor as well. It must be borne in mind that young sporophytes were only visible when they had some fronds. Some of them may have been overlooked.

The recruitment, expressed as the number of colonies $\text{ha}^{-1} \text{y}^{-1}$, is high when compared to other Dutch localities, where recruitment is almost non-existent. Still, the recruitment level in *Gymnocarpium dryopteris* is low by comparison with other fern species. High recruitment levels have been published for *Dryopteris dilatata* (Willmot 1984) and *Polystichum setiferum* (Page 1982). In the Kuinderbos a high level of recruitment has been observed in various species, especially *Asplenium scolopendrium*, *Polystichum aculeatum*, *Athyrium filix-femina* and *Dryopteris spp.* (see also Chapters 3 and 6). In the second experiment there was a thinning interval of five years. The thinning led to an increase in the herb layer cover. On average, light intensities did not exceed 5%, preventing *Rubus* species or *Urtica dioica* from dominating. *Rubus* species in particular can overgrow rare fern species and outcompete them when light intensities exceed 5% (Bijlsma 2004). The thinning favoured *Gymnocarpium dryopteris* (especially the number of fronds colony⁻¹), but also *Polystichum aculeatum* and *Asplenium scolopendrium*. The mass recruitment of *Asplenium scolopendrium* had not previously been observed in the Kuinderbos. Optimal light conditions and a succession of mild winters may have favoured this species as well (Chapter 6). Both experiments showed that thinning in dense stands favours the fern flora. Without thinning less than 2% of the light penetrates to the woodland floor, which allows only some fern plants to establish. Thinning might be favourable, but its severity is crucial (Fig. 7.6). Long return intervals and moderate thinning seem to be the most effective, as a short return interval (five years) and severe thinning in *Picea spp.* stands led to forbs and *Rubus* species invading and outcompeting the rare ferns, and also to the recruitment of trees. Thysell & Carey (2000) compared a stand that was thinned twice within 80 years with an even-aged *Pseudsuga menziesii* control stand in Washington (Pacific Northwest). Species richness, diversity and understory cover were higher after thinning. *Polystichum munitum*, *Athyrium filix-femina* and *Pteridium aquilinum* had greater cover after thinning. Thinning also implies less interception of rainfall and less root competition from *Picea sitchensis*. Differences in moisture between the thinning plot and control might play a role, but there are no indications that fern patches died from drought. Less root competition and also disturbance due to harvesters might have played a role, but the dominant factor was probably light. Gap formation in *Picea sitchensis* on peat soil initiated a 'hochstaudenflur', which was succeeded by a dense

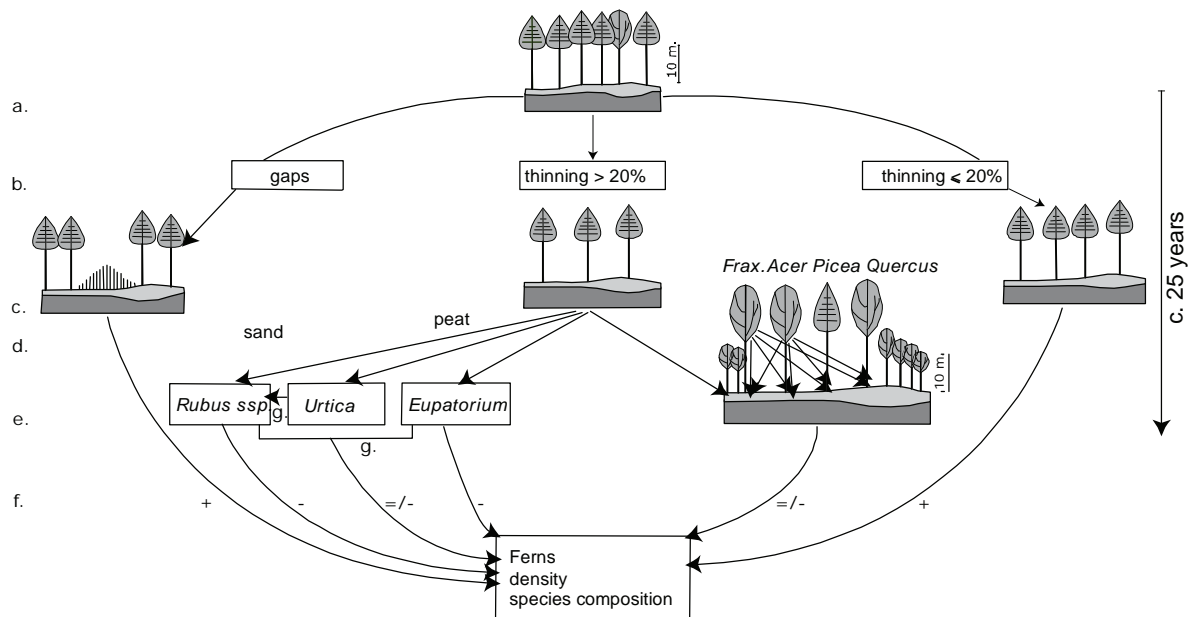


Figure 7.6. Management regime and effect of management on fern species composition within *Picea sitchensis* stands in the Kuinderbos as recorded in a period of 25 years. **a.** *Picea sitchensis* stands c. 1980, **b.** management regime with gap formation (once), thinning > 20% (once every five years) and thinning ≤ 20 %, c. once every 10 years) **c.** profile of stands after 25 years of management, **d.** Soil composition, **e.** composition of herb layer, **f.** effect of management on ferns (density, species composition) + = positive effect, - = negative effect, = : neutral effect, g = effect of repeated thinning.

phase with trees and shrubs. In this dense phase *Rubus* species and *Eupatorium cannabinum* are suppressed, facilitating the survival of *Gymnocarpium dryopteris*. Natural gaps in *Picea sitchensis* in the peat erosion area were dominated by *Urtica dioica* and by recruiting trees.

Artificial gaps on boulder clay were studied in the Voorsterbos. Recruiting trees were expected to form a dense juvenile stand, contributing to the horizontal and vertical structure of the woodland. On boulder clay, *Fraxinus excelsior* recruits successfully, but the knee-height saplings were intensely browsed by Roe deer in the first five years, preventing a dense phase and facilitating a 'hochstaudenflur' with dominance of *Athyrium filix-femina* or even dominance of *Phragmites australis*. Other ferns were present from the outset, with *Athyrium filix-femina* outcompeting *Gymnocarpium dryopteris*. On the boulder clay, ten fern species established, including *Dryopteris cristata* and *Matteuccia struthiopteris*. It seems likely that their spores were present prior to the gap formation. *Gymnocarpium dryopteris*, *Matteuccia struthiopteris*, *Dryopteris cristata* and *Thelypteris palustris* had never previously been observed in this kind of habitat – which underscores the uniqueness of this habitat: small gaps on neutral boulder clay. *Dryopteris cristata* and *Thelypteris palustris* have very large populations in the marshes of NW Overijssel, so spore dispersal combined with a persistent spore bank might have been crucial (Dyer & Lindsay 1996). Spores of *Athyrium filix-femina* were found to be the most frequent in the soil bank in a boreal old-growth spruce forest, yet there were no plants in the herb layer (Rydgren & Hestmark 1996). The same probably holds for the gaps examined on the boulder clay, where there was mass recruitment of this species though there were no plants on the spot before the trees were felled. Gaps do have a characteristic microclimate (Moore & Vankat 1986, Stoutjesdijk & Barkman 1992). Gaps with a diameter of less than 0.7 times the tree height do not get any direct sunshine, while in gaps with a diameter equal to the tree height; c. 80% of the gap area is shaded when the foliage is fully developed. Gaps with a diameter 1 - 2 times the tree height deviate most from the adjacent woodland, having a microclimate that is more Atlantic in summer and more continental in winter (Stoutjesdijk & Barkman 1992). As rainwater is not

intercepted any longer by the canopy (in *Fagus sylvatica*, interception and stem flow account for 30%) and without tree transpiration, the soil in these small gaps becomes constantly wet, with on average a low saturation deficit during the growing season, while in winter there is more radiation. In the Voorsterbos, most gaps are 1 - 2 times the tree height which is an optimal habitat for ferns and also for horsetails. The dominance of *Athyrium filix-femina* is related to soil conditions (boulder clay with reduced percolation, moisture and neutral substrate). Godefroid *et al.* (2006) show an effect of light intensity but also a combined effect of the air temperature and air humidity on the occurrence of this species in clear cuts. My finding that most of the rarer species are confined within the 100% shade line indicates that they prefer a constantly wet soil and high air humidity. Comparing gaps with and without girdling indicates that cutting and the concomitant soil damage (disturbance) is also a precondition for the germination of fern spores. *Equisetum fluviatile*, *E. telmateia*, *Scirpus sylvaticus* and to some extent *Matteuccia struthiopteris* are indicators of seepage (e.g. Grootjans 1985), indicating a flux of pH neutral groundwater. That these species were found growing on impermeable boulder clay shows that seepage is not the dominant factor, but that a continuously moist, pH neutral habitat is needed, which can also be accomplished by rainwater stagnating on pH neutral boulder clay. Gaps on sandy soils do not facilitate the growth of ferns, as the water percolates to the water table and the soils are acid. When constant high humidity can be assured, one might expect species such as *Blechnum spicant* and *Oreopteris limbosperma* to establish. In unmanaged forest, natural gaps are recolonised by trees and shrubs, but ferns can play an important role in gaps as described for the *Stellario-Carpinetum* in the Neuenburger Urwald (Koop 1989).

When they manage woodland, humans have a great impact on the composition of the herb layer and recruitment of trees. In all three experiments, management facilitated the establishment and expansion of fern populations. It seems likely that the crucial factor is light. Creating woodland gaps allows ferns to profit from their anemochoric dispersal capacity and sporebank, and to develop prior to the phase in which seed plants might become dominant.

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General discussion



Terrestrial growth of *Asplenium trichomanes* with cluster of plants accompanied by the pleurocarpous bryophyte *Thuidium tamariscinum*.

In this thesis on fern species the first question addresses the current distribution, the preferred habitats and the trends in the Dutch populations. The hotspots of fern species in the Netherlands are concentrated in cities and the planted trenched woodlands of Flevoland (Table 8.1). In neighbouring countries most fern species are found in mountainous areas (Page 1982, Ben-nart 1999). In fact, the wall habitat mimics the rocky habitats, while drainage trenches share many characteristics with ravine woodlands. The canal wall habitat is not found to such an extent in other countries (e.g. Amsterdam with 100 km of canal walls, 15% with significant fern growth, Denters 1990), while nowhere else in the world is there a trenched peat erosion area. The woodlands on sandy clay in the Netherlands are devoid of drainage trenches, while boulder clay has decalcified and acidified (Table 8.1).

Trenches and canal walls have in common that they vary in aspect and humidity, while litter accumulation does not take place. They also provide a pH-neutral habitat, where some permanent dampness is guaranteed. In the peat erosion area this is because of the underlying peat layer. In the canal wall habitat, water is provided by the earth bodies behind the construction (Maes & Bakker 2002). In neighbouring countries, fern species inhabit unique habitats as well: e.g. limestone grikes (on average 2.5 m long, 0.25 m wide, 1 m deep) in the UK (Porter 1994). The habitat preference of fern species differs from the habitat preferred by other vascular plant species. Ferns are not found in habitats where seed plants thrive, such as arable fields, bogs and saline coastal banks and marshes. Perennial fern species are not adapted to annual ploughing (habitat dominated by annuals) or to high salt concentrations. Though 23% of the Dutch seed plant species are found growing in grasslands (Arnolds & van der Maarel 1979), only two fern species characterise this habitat (5.1% of the fern species).

26% of the Dutch fern flora is listed as threatened (10 species). Reconsidering the species data we must conclude that 6 species (15%) are really endangered. In the seed plant flora, 460 species (34%) are threatened. 69% of the fern species (including those that have established for the first time) have increased at a national scale, which is a much higher percentage than in the seed plants. Negative trends in ferns have been attributed to habitat destruction, acidification, eutrophication and desiccation. Positive trends are related to the reclaiming of land from the sea, afforestation, eutrophication, global warming ageing, lowering of the water table and decrease in SO₂ concentration. Lowering of the water table has had a very negative effect on phreatophytic species (Runhaar 1999), probably including some fern species. On the other hand, lowering has sometimes offered new opportunities, with bare ditch banks as new habitat (unpublished data, province of Overijssel). The total area of woodlands in the Netherlands increased from 334,000 ha in 1983 to nearly 360,000 ha in 2005 (Daamen *et al.* 2007). Various fern species colonised these new habitats, although the extensive Pine forests on mineral soils are still poor in species. Here *Dryopteris dilatata* is often the dominant fern species, profiting from NH₃ deposition (Boxman *et al.* 1998), or having increased from existing colonies (*Pteridium aquilinum*; van Dort *et al.* 1999, den Ouden 2000). Some trends in the Netherlands are similar to trends abroad. In the UK, *Polystichum setiferum* and *Asplenium scolopendrium* have increased their range, benefiting from milder winters (Braithwaite *et al.* 2006).

The second question addresses the environmental factors that allow ferns to succeed in colonising new habitats in the planted woodlands in Flevoland. First of all, more than 95% of the hotspots of fern species in Flevoland are related to drainage trenches, which provide altitudinal variation in aspect and slope (Table 8.1). The effects of different aspects (peat erosion area) are not uniform in most species. In 1979 and 2002 in the whole group of rare ferns a SW aspect was preferred, to some extent related to clustering around adult plants. In *Asplenium scolopendrium* the preferred aspect changed from SW (1979) to NE (2002). In this species, population size increased while the significance of clustering increased. In mountainous areas, slopes with N aspect are often covered with woodland communities characterised by ferns,

profiting from the microclimate (Ellenberg 1982), but north slopes are also preferred in other habitats (dunes, canal walls, canals). Some species prefer a restricted range in relative height along the trench bank. *Dryopteris cristata*, for example, grew on the trench bottoms, but most species prefer a relative height between 40 - 60%. Here water supply is guaranteed while immersion is insignificant. Relative height also plays a role in bryophytes growing on trench banks, but also in seed plants along ditches.

Table 8.1. Hotspots of fern species (part of hotspot with at least 10 fern species 10 ha⁻¹) in trenched woodlands of Flevoland, related to environmental factors.

	<u>peat erosion area</u>	<u>boulder clay</u>	<u>sandy clay</u>
Woodland	Kuinderbos	Voorsterbos	Jagersveld (Lelystad)
<i>Fern hotspots</i>			
Area size (ha)	c. 80	c. 8	c. 10
Total number of fern species (1980 – 2005)	25	15	11
Population size 'rare' fern species (2002)	15600	50	110
<i>Drainage trenches inhabited by rare ferns</i>			
sum of length	80 km	5 km	1 km
depth (m)	0.5 - 1.2	0.5 - 1.2	0.4 - 0.6
Annual erosion rate	> 8%	4%	?
Stable woodland gaps	< 10	20	0
Soil	fine-grained sand (peat)	boulder clay	sandy clay, silt < 12%
Water capacity soil	moderate	high	moderate/high
Guarantee of water supply	nearly always	not always	always
pH H ₂ O	6.0 – 7.5	3.7 – 4.5/ 6.7 – 7.5	> 7.0

In the peat erosion area, disturbance by small-scale land slips plays an important role in creating habitats for recruiting calcicole fern species. This has been analysed in detail in *Asplenium scolopendrium* but has also been recorded in e.g. *Asplenium trichomanes*, *Polystichum aculeatum* and *Polystichum setiferum*. On boulder clay, fern hotspots are much poorer in species and number of plants (Table 8.1). In an earlier study (Bremer 1998) I reported on the *Fissidentium taxifolii* community in the peat erosion area and boulder clay, with annual erosion rates of 4% on boulder clay and at least 8% in the peat erosion area. The differences in erosion rate could be one of the reasons why rare fern species on boulder clay have established at a low density. Long-term monitoring also revealed that this was not the only reason, as artificially created microsites were not colonised by ferns. Microsites created by local disturbances are important as safe sites for recruitment. These safe sites offer opportunities to germinate and establish without significant competition from other plants (Grubb 1977, Huston 1994, Page 2002). Conditions in water supply are important in fern species, although species differ in their requirements (e.g. *Athyrium filix-femina* is very prone to desiccation, while the opposite holds for *Polypodium vulgare*). Water supply is guaranteed by the water capacity of a silty soil or the sponge function of the peat subsoil (peat erosion area). Submerged plants can succumb, as was observed near Lelystad (data A. Smit), so the water table should not rise above 0.4 m below the woodland floor. In the boulder clay, water tables might be high in spring, but can be low in summer (> 1.5 m below the woodland floor). In dry periods the upper trench banks may even become crusted. This can be more distinctive after thinning, with more light coming in and temperatures rising in the trench habitat. It is one of

the reasons why fern density (number of fern species, population size) is much lower on boulder clay than in the peat erosion area.

Canopy composition and the related composition of the ecto-organic layer has important effects on *Gymnocarpium dryopteris*, as the creeping rhizomes depend on this layer. In this species it was shown that the relation with *Picea sitchensis* is not unique and rhizomes can grow in the ecto-organic layers of other coniferous and sometimes deciduous tree species. Rhizomes of *Pteridium aquilinum* do not depend on the ecto-organic layer and may be found deep in the soil (Watt 1940). For the other rare fern species¹, canopy composition plays an important role in intercepting radiation and creating deep shade on the woodland floor. Most fern species were found in woodland with a light intensity between 2 and 5%. When water supply is guaranteed, fern species can grow in sites with more incoming light, in as far as competition with seed plants is suppressed or avoided by early establishment, as shown in the woodland gaps on boulder clay.

In Flevoland, three hotspots of fern species are found (Table 8.1). Fine-grained sand and light clayey soils differ in their silt content (< 5% and 5 - 12%). The differences in species richness between both hotspots can be attributed to the total length of trenches and probably also to the variation in depth of these trenches. Hotspots of rare fern on boulder clay are scarce, due to the effect of desiccation, low incidence of disturbance and an acidified soil (trench banks), while the area of woodland gaps is small. All hotspots have in common that they have developed on neutral soils (pH 6.0 - 7.5).

Bremer & Ott (1990) have attributed the relatively successful establishment of many bryophyte species in the woodland of Flevoland to the reduced levels of competition. After the closing of the canopy 'ruderal' seed plants faded away. At the same time, seed plant species adapted to a low light intensity started their colonisation. So there was a vacuum of species, to be described as a situation of *under saturation* due to limited dispersal capacity (spore limitation) (Hermy *et al.* 1992, Turnbull *et al.* 2000, see also Schaminée *et al.* 1995 for other reasons for under saturation). Bryophytes - and also fern species - profited from this situation and colonised the woodlands. It has also been suggested that the complex network of relations controlling germination and establishment of spores, in which micro-organisms might be essential, has not yet been fully developed in the new polders (During & van Tooren 1987). This hypothesis had not been tested by other studies however, and more studies are needed to clarify the role of the soil as biological network. In this respect it is also worth noting that the trench banks (e.g. in the peat erosion area) provide a large 'catchment area' for spores. This has perhaps also contributed to the success of fern species in the peat erosion area. The size of catchment area probably also plays a role in the colonisation of the Biesbosch and Horsterwold by various rare epiphytic bryophytes (van der Pluijm 2000, 2004). Van Tooren *et al.* (1990) attributed the inability of pleurocarpous perennial bryophytes to colonise the plots in their experiments to the lack of sexual and asexual propagules but also to the size of the 'catchment area'.

The second question also concerns the dispersal of fern species. In Chapter 3 it is demonstrated that the size of the surrounding fern populations has an impact on the colonisation rate of fern species in the Kuinderbos. The larger the source population, the earlier a species established in this area. Besides the large dispersal capacity in ferns, spore banks also play a role (During & Ter Horst 1983, Dyer & Lindsay 1992). In our study the mass colonisation of a planted woodland near Zwolle and colonisation of woodland gaps on boulder clay were best explained by spore banks. In both areas the maximum number of fern species was reached in a very short time, even within one year. Above all, in the woodland gaps within the Voorsterbos, *Athyrium filix-femina* demonstrated a mass colonisation, even though the species was not

¹ See Table 3.6

on the spot prior to cutting and the populations in the adjacent woodland were restricted in size.

When comparing the (reconstructed) colonisation in both Kuinderbos (Chapter 3) and Jagersveld (Chapter 4), the establishment in both show the same trend (colonisation within 10 - 20 years after afforestation). The reconstruction of the moment of establishment was based on extrapolating data on population size, frond length or number of fronds. However, due to phenotypic plasticity, plants can become old with minimal growth, as shown in tree species (Hunter 1999). Rich *et al.* (1995) used the annual average growth rate of patches to reconstruct the population age structure in *Hymenophyllum tunbrigense*, while elsewhere I used the annual growth rate of patches in the bryophyte *Hylocomium brevirostre*, indicating colonisation 10 - 22 years after afforestation (Bremer 2003a).

Dispersal capacity also impacts the micro distribution of plant individuals. Strong clustering was found in nine fern species in the peat erosion area, but also in other woodlands, e.g. *Asplenium scolopendrium* on sandy clay and more recently in the Kralingse bos (data R. Andeweg). In bryophytes spore deposition patterns fit well to the inverse power law, but when these curves are extended to infinity they fail to explain all spores being dispersed in species examined. Probably by thermal updrafts spores contribute to long distance dispersal (Miles & Longton 1992, Sundberg 2005). In ferns, only short distance dispersal has received attention (Raynor *et al.* 1976, Conant 1978, Peck *et al.* 1990), but both 'mechanisms' have not been studied simultaneously in ferns at all (information A.F. Dyer), although fern spores are found at greater height (data Elkerliek Ziekenhuis, team Pollenonderzoek). Yet the colonisation within a period of 10 - 20 years and the clustering of individuals in various species suggests that both 'mechanisms' are also operational within the group of the ferns. Wind speed within the trench habitat might play a crucial role in clustering, with most spores deposited within metres of the parent plants. It seems probable that founder plants originated from spores transported from elsewhere (by long distance dispersal), while spores of founder plants on trench banks are not able to spread over long distances within the woodland, due to sheltered windless conditions. This might not be the case in *Gymnocarpium dryopteris*, patches of which are growing up to the top of the trench banks, and in the more common species growing on the wood floor. Edgington (2007) estimated an expansion of populations of two species of *Asplenium* at up to 1 km per year in London. The fact that wind speeds generally increase with height will favour dispersal in mural species over trench-dwelling ferns. Edgington (2007) found a predominance of sites to the north-east of the presumed initial locations, which seems to be consistent with the prevalence of south-westerly winds.

It can take years before an adult fern is surrounded by a new generation. This crowding can be explained by the high numbers of spores deposited near adult plants (and the subsequent role of the spore bank) combined with a low chance of germination. In this respect the mating system might play a role. One would expect successful establishment in the sequence autogamic, selfing and intergametophytic species. In the autogamic *Phegopteris connectilis* and *Dryopteris affinis*, prothallia grow into sporophytes without fertilisation. But even in the former species it took 20 years before clustering was found near a founder colony. In *Phegopteris connectilis*, clustering started concomitantly with the sudden increase of light intensity. In the tetraploid *A. trichomanes* it took 10 years before sporelings established near founder plants, while in the diploid *Asplenium scolopendrium* the recruitment started within 10 years. *Asplenium scolopendrium* depends on intergametophytic crossing or selfing, while in *Asplenium trichomanes*, intragametophytic selfing is the rule. One would expect the latter species to be more successful, which was not the case in the Kuinderbos. In Amsterdam the population size of both species is, however, of the same magnitude (Maes & Bakker 2002, data T. Denters). In the tetraploid *Polystichum aculeatum* and diploid *P. setiferum* the percentage of clustered plants was of the same order but the number of clustered plants was much lower in

the latter species. *Polystichum setiferum* probably depends on intergametophytic crossing, with successful establishment of sporelings depending on the spore shadow of an adult plant and deposition of at least one spore from a genetically different plant. Peck *et al.* (1990) studied fern populations in the Woodman Hollow State Preserve (USA) for 20 years, and found 39% ($n = 13$ fern species) able to recruit. Differences in life history attributes (spore production and mating system) correlated with population size and recruitment for the species studied in detail, with bisexuals without genetic load being most successful. In the Kuinderbos 75% of the fern species ($n = 24$ species) were able to recruit, but there were no significant differences between diploids and polyploids. The hypothesis that polyploid species would be more successful in colonising new habitats than diploid species (Flinn 2006) could not be confirmed. The relation between colonisation, clustering and mating system poses questions still to be answered by more experimental studies.

In the group of seed plants the role of source populations and clustering can be seen in all kinds of habitats after construction or reconstruction (e.g. reconstructed ditch sides, Melman 1991). Clustering results from founder plants using rhizomes or stolons to expand, or depends on recruitment from seed. Clustering due to seed recruitment has much in common with clustering found in ferns. The spread of seed plants might be much faster. After topsoil removal in a peat area, founder plant related clusters were found in numerous species. The initial clusters of *Drosera intermedia* disappeared within c. 6 years, as the species colonised all potential sites in an area of 4.5 ha. *Carex hostiana* individuals were still clustered within less than 3 metres around founder plants 10 years after these established on bare peat soil (Bremer *et al.* in prep). The success of long-distance dispersal in fern species has also been observed in other groups of spore-producing taxonomic groups within the woodlands of Flevoland. Macrofungi have a high capacity for dispersal. Spore size varies between 4 and 40 μm (on average 7.9 μm , based on sample of 313 spp.). We assumed that nearly all species were transported by wind from nearby populations in the Netherlands or even from other European countries (Bremer *et al.* 2007). A number of species could have arrived in the root balls of trees. No attention was paid to the role of a spore bank, although there are indications of a spore bank in hypogeous macrofungi (Miller *et al.* 1994, Kj  ller & Bruns 2003).

Epiphytic lichens have also been studied in Flevoland (Bremer 1990). Lichens are able to spread not only by spores, but also by numerous vegetative propagules (soredia, isidia, pycnidio-spores). The consequence is a strong clustering of thalli. All epiphytic species found were known from the adjacent areas. As some species do not produce spores in the Netherlands, the spores must have come from abroad, or colonisation must have taken place by means of vegetative propagules. Bremer & Ott (1990) present data on the colonisation of woodlands by bryophytes. In a study of 12 plots, 35% of the potential species were present within c. 10 years after planting. In a chronosequence study, 60% of the potential species were present within 20 years. There is only one terrestrial species which started its colonisation c. 25 years after afforestation: *Thamnobryum alopecurum*. In the Voorsterbos, 87% of all the expected terrestrial bryophytes were present within 25 years. At that time, only 33% of the potential true woodland seed plants were present (Bremer 2003b). In seed plants, anemochoric species such as orchids can arrive early, as observed in the woodlands on clay (*Epipactis helleborine*), but the colonisation of most species is influenced by humans, directly or indirectly as shown in Chapter 4. Seeds are transported by people (or their dogs) or by birds dispersing berries from gardens into woodlands. The results in Flevoland agree with those from a study on woodlands on clay in NW-Friesland (Bremer 2007). Here, anemochoric species are favoured in all plant groups, which implies that the vegetations built up are seed limited, as already noted by Bakker & van der Zweep (1952) in their study in the vicinity of Urk. More recently, the role of seed limitation has been shown in various habitats (Tillman 1997, Turnbull *et al.* 1999). In chapter 1 it was hypothesised that in all cases, of all the true wood-

land species, ferns would be the first to colonise the woodland habitat. Within planted woodlands on clay on the mainland, soils have a diaspore bank and colonisation by characteristic seed species can start even before the woodland is planted (e.g. *Ranunculus ficaria*, *Deschampsia caespitosa*; Bremer 2007). The same was observed along a brook in the eastern part of Overijssel, where the effect of tree planting along a former not shaded brook was monitored during 15 years. Seed plants were probably transported by water and all expected fern species ($n = 4$) established 9 - 15 year after the tree planting, with the tree layer partly suppressing the competing seed plants (data botanical monitoring, province of Overijssel) (Fig. 8.1a).

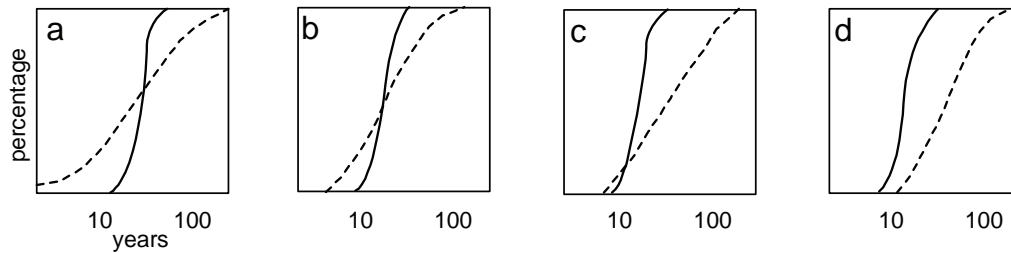


Figure 8.1. Colonisation process of ferns (—) and characteristic seed plants (- -) as observed in the monitored woodlands, presented as percentage of maximum number of species to be expected (100 %).

- a.** colonisation of habitats on the mainland with existing seed and spore banks.
- b.** colonisation in Flevoland, with establishment of characteristic seed plants starting earlier than the colonisation by ferns.
- c.** starting point for colonisation by ferns and characteristic seed plants nearly the same.
- d.** colonisation, with ferns the first to arrive.

When drainage trenches are absent, ferns start the colonisation of woodlands on clay at a later moment than characteristic seed plants. In small woodlands the difference between both groups is even larger than in large woodlands (Fig. 8.1b). Colonisation of trenched woodlands can have the same starting point for both groups, as observed in fern-rich sites in Kuinderbos and near Lelystad (Fig. 8.1c). The long period colonisation took on boulder clay is exceptional: the first calcicole fern species arrived c. 35 years after afforestation. In a fourth pattern, ferns were the first to arrive, as observed in *Pinus* spp. stands on clay, but also in trenched woodlands on clay (Jagersveld) (Fig 8.1d). The different sequential patterns are primarily correlated with the presence of drainage trenches. In trenched woodlands the colonisation by ferns can be observed at an earlier stage, which means that late colonisation by ferns is not determined by dispersal capacity but exclusively by lack of habitat (e.g. no trenches and/or decaying wood). But how to explain the late colonisation in the Voorsterbos? I think this exception is related to the low density of microhabitats suitable for establishment, as noted above. In one intensely monitored parcel with Ash and Hornbeam, *Asplenium scolopendrium* established c. 45 years after planting, while the number of occupied sites and plants of the more common species (*Dryopteris* spp.) increased at a low rate. Clusters of 'rare' ferns were not observed through the 55-year period. As the *Fissidentietum taxifolii* faded away in this parcel and pleurocarpous bryophytes became dominant, the number of suitable micro sites decreased sharply. I assume that despite the decrease in number of safe sites, more spores of calcicole species accumulated in the soil. The third question in this thesis addresses the factors that determine the long-term demography of fern populations. Long-term studies offer the opportunity to analyse temporal factors such as weather, climate change, inundation time etc. In this thesis, two demographic studies were presented, i.e. on *Gymnocarpium dryopteris* and *Asplenium scolopendrium*. The first showed the dominant effect of the light climate on de-

cline and recovery. In the second species the impact of severe winters and effect of light were documented. Demographic studies were also carried out in the Kuinderbos on *Gymnocarpium robertianum*, *Phegopteris connectilis* and *Asplenium trichomanes* with effect of light in *Phegopteris connectilis*. Severe winters have a negative impact on the population dynamics of *Asplenium scolopendrium* but also on *A. trichomanes*. Frost damage implied a decline in population size, sometimes for years. In *A. scolopendrium*, frost damage had a positive effect on retrogression and mortality. Severe winters also had a negative impact on evergreen fern species such as *Polystichum setiferum* and *Asplenium trichomanes* (Bremer 2004), while necrosis was not observed. It is difficult to understand why a severe winter would have an effect on recruitment some years later, which seems to be the case in the diploid *Polystichum setiferum*. One might hypothesise that severe winters harm the spore bank. In *Asplenium scolopendrium*, frond production is related to necrosis in the preceding winter. This means that the evergreen fronds are probably important for the production in two ways: stored assimilates will be transported from the old fronds to the new ones, and old fronds in spring have a net production of assimilates that can be transported to the new generation of fronds.

It has also been questioned what effect woodland management has on the dynamics of fern populations. Woodland management (thinning) results in changes to the light climate (increase of light intensity), which has an impact on the undergrowth. When incoming light exceeds a certain level (c. 5 %) forbs become dominant (*Urtica dioica* or *Rubus spp.*) or trees are able to rejuvenate (see also Siebel 1998). Dominance of *Rubus spp.* has a detrimental effect on ferns; they are overgrown and disappear. In the peat erosion area, thinning has been intense and frequent in the last 20 years, with negative effects on the actual and potential area of the fern populations. In one of the experiments, thinning had a positive effect on fern density, but thinning also weakened the stand stability, implying a larger chance of wind throw. After canopy closure, management without cutting (no interference), cutting gaps or selective thinning are possible, and in my view should depend on the pteridological value of the hot-spots in Flevoland. In these stands, tree harvesting should have a subordinate role.

The observations in Flevoland show that colonisation by ferns is spore-limited for scores of years. As spore banks hardly play a role in these young woodlands, colonisation depends on transport from elsewhere. The first cohort of adult plants functions as source population, with very short distance dispersal for species thriving on trench banks. Differences in success between species might to some extent also be related to the breeding system. Habitat limitation in ferns is related to the light climate, which is largely controlled by woodland management. The potential fern habitat in the peat erosion area was at first suppressed by a lack of incoming light (e.g. dark *Picea abies* stands) and later on by too much incoming light. While the role of spore limitation is still decreasing (effect of increase of population size and build-up of spore bank), this does not hold for the habitat limitation.

The creation of woodlands has received much attention from researchers, including the position of the characteristic woodland species (Ferris-Kaan 1995), and their seeding and planting (Gilbert & Anderson 1998). The data presented in this thesis has increased our knowledge about the conditions required by fern species and other characteristic woodland species. This knowledge can be used to describe the optimal conditions for these plants when developing new woodlands on clay soils. In future, more afforestation can be expected in the Netherlands, e.g. as part of the policy to bind CO₂ in biomass (e.g. the Wendelerbos, planted in the period 2005 - 2007). The colonisation by true woodland species will be speeded up if woodlands are created near villages (Chapter 4) and if trees are planted on former grasslands instead of on former arable fields (Hermy *et al.* 1993). Variation in canopy structure is needed, with gradients from light to dark: the optimum for ferns is 2 - 5% of the incoming light reaching the woodland floor (e.g. with *Fraxinus excelsior* or *Salix alba* stand alternating with *Carpinus betulus* or *Corylus avellana* in the shrub layer) (Fig. 8.2b).

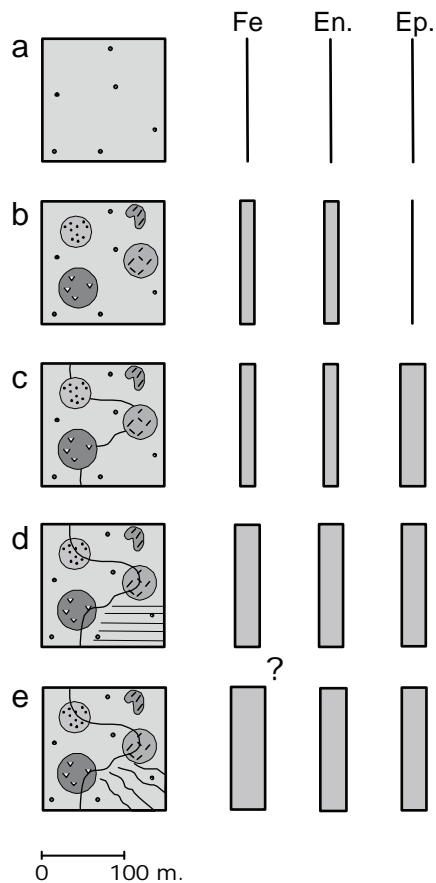


Figure 8.2. The position of ferns (Fe), endozoochoric woodland species (En) and epizoochoric woodland species (Ep.) in relation to the creation of new woodlands on clayey soils. The width of the bars represents the relative effect of the layout on the group of plants, ? = relation hypothesised, not proved. **a.** woodland planted with one dominant deciduous tree species (e.g. *Fraxinus excelsior*, *Salix alba*), **b.** woodland planted with mosaic of tree species (developing light-shade gradients e.g. *Carpinus betulus*, *Tilia cordata*, *Acer pseudoplatanus*, *Ulmus glabra*), **c.** woodland intersected with paths, **d.** woodland (c) with drainage trenches, **e.** Woodlands with more meandering drainage trenches and isolated trenches. Dots represent small clusters of e.g. *Corylus avellana*, *Crataegus monogyna* and *Prunus padus*.

Paths intersecting the parcels stimulate the colonisation by seed plants, but have no impact on fern colonisation (Fig. 8.2c, with *Ophioglossum vulgatum* as the exception). However, as this thesis shows, ferns profit from variation in relief. In Flevoland, drainage trenches provide these conditions (Fig. 8.2d), but other artificial forms of topographic variation may be applied as well, e.g. making trenches more meandering (Fig. 8.2e) and improving site heterogeneity (Buckley & Knight 1989). Meandering trenches mimic the natural habitat of shaded brooks. In Overijssel 10 fern species have been found along brooks (data provincial board of Overijssel).

Fern hotspots in the peat erosion area and the boulder clay area are unique from a geological and pteridological point of view. The more recent colonisation by rare ferns in the trenched Kralingse bos (Rotterdam, with 4 - 5 m thick, artificial deposits of clay and sand) shows that an optimal fern habitat can also be developed by man, accidentally or on purpose. This knowledge can also be used to develop new fern habitats deliberately, or to develop these habitats within existing woodlands. Artificial variations in relief within existing woodlands might provide new habitats for fern species, e.g. small marl pits in shady places in S-Limburg.

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Summary



Matteuccia struthiopteris established on boulder clay (Voorsterbos) after cutting gaps in *Fagus sylvatica* stands.

This thesis attempts to answer questions on distribution, trends and habitat preference of ferns in the Netherlands. It is focused on ecology, demography, dispersal capacity and management of fern species in planted woodlands on a former sea-floor in the province of Flevoland.

Chapter 2 addresses questions about distribution and habitat preference of fern species in the Netherlands and recent trends that have taken place in population sizes. In the Netherlands 39 species of *Pteropsida* (*Equisetaceae* excluded) were reported during the period 1991 to 2000. Species were most numerous in cities, especially Amsterdam, where ferns grow at canal walls. Fern species were also numerous in the young woodlands of Flevoland, particularly in the Kuinderbos, where ferns have established on the calcareous sandy banks of trenches. The number of species in the Netherlands has increased over the last 30 years due to afforestation (e.g. the woodlands in Flevoland), a number of mild winters and a more intensive survey of canal walls in cities. The positive trend in 69 % of the fern species has also to be attributed to habitat creation on former arable fields, ageing of habitats and the strong decrease in SO₂ pollution. Despite the increase in the number of species, populations of certain species, e.g. *Botrychium lunaria*, have decreased because of increased N deposition. Wall species, even those protected by law, have suffered as a result of wall restoration. Some species (e.g. *Polystichum lonchitis*, *Marsilea quadrifolia*) have had to bridge a gap of hundreds of kilometres to establish themselves in the Netherlands. Ferns have been found in 75 plant communities. The population size of the various species ranges from some plants (e.g. *Polystichum lonchitis*) to millions of plants (e.g. *Dryopteris dilatata*).

The establishment of many rare fern species in the Kuinderbos was the incentive to study fern colonisation. It was questioned what environmental factors allowed ferns to succeed in colonizing the Kuinderbos. **Chapter 3** addresses the question about ecology (environmental preferences and change in preferences) and dispersal capacity of the fern species. The discovery of a large group (23 species) of rare ferns in the Kuinderbos in 1977 - 1979 offered an opportunity to study the ecology and colonisation in this 1050 ha woodland planted on land reclaimed from the sea. The area is characterised by various soil types. Thick deposits of fine calcareous sands on peat (peat erosion area) are intersected by dozens of km of drainage trenches.

The environmental preference of the ferns in 1979 and 2002 was studied, paying attention to the soil, the composition of the canopy and the trench habitat. Individual plants and patches were mapped and populations monitored during 25 years. Data were also collected on microclimate and hydrology. In 1979, 18 of the 23 fern species were found exclusively or significantly more on trench banks. Some species showed preference for a certain aspect (e.g. *Asplenium scolopendrium* preferred a SW aspect), relative height up the side of the trench (*Polypodium vulgare* grew higher up the trench sides than other species) and slope (e.g. *Asplenium trichomanes* growing on steep trench sides). Ten species occurred exclusively on the very fine sand deposits in the peat erosion area, while *Dryopteris cristata* grew exclusively on peat soils. *Picea sitchensis* stands proved to be richest in fern species. In 2002, 15 out of 22 fern species were found exclusively or preferentially on trench sides. There were changes in preference for aspect and gradient, e.g. species preferring change in aspect (e.g. *Asplenium scolopendrium*) or shallower gradients (e.g. *Polystichum setiferum*), with preference for aspect also related to the clustering of sporelings around adult plants. Various species colonised *Picea abies* stands after thinning, while in former dense mixed stands of *P. abies*, after 25 years of thinning stands of *Acer pseudoplatanus* became available. Only small changes were recorded in preferred soil type.

Various species increased in population size. The two most successful species were *Polystichum aculeatum* and *Asplenium scolopendrium*. In other species the population size stabilised (*Gymnocarpium dryopteris*, *Asplenium trichomanes*), decreased (*Cystopteris filix-fragilis*) or the species even disappeared from the woodland habitat (e.g. *Dryopteris cristata*).

Colonisation was monitored and reconstructed over a period of 50 years, and years of establishment were calculated. Colonisation proved to be related to the size of neighbouring fern populations both in the group of calcicole and acidophilous fern species. In all rare fern species which were able to build up populations a synchronous multi-site colonisation was recorded. A recruitment pattern (clustering) was found in 43% of the rare fern species monitored ($n = 9$), with the highest percentage (99%) in *Polystichum aculeatum*. Clustering was not correlated with the ploidy level nor with plants growing in clones or as solitary plants. Diploid species were as successful in colonisation as polyploid species. In the soil there is an ongoing decalcification, but the soil is buffered by sediments rich in shells. Intense commercial forestry has caused loss of appropriate habitats (increase of *Rubus spp.* in the herb layer), and it is expected that calcicole species will increase further if commercial forestry becomes less intensive and a new generation of trees grows up.

In **Chapter 4** the question about the environmental factors allowing ferns to succeed in colonising new habitats was worked out for 53 woodlands in the Noordoostpolder and East-Flevoland. These woodlands had been planted on clay soils. In this study also seed plants were incorporated. Total species number per woodland was found to be correlated with woodland age, area (i.e. size) and distance to human settlements, whereas the number of true woodland species per woodland was correlated with woodland age and area. The number of recruiting tree and shrub species per woodland increased concomitantly with woodland size and proximity to villages. The number of fern species per woodland was only correlated with area. The latter was also true for the abundance of two of the most common fern species: *Dryopteris filix-mas* and *D. dilatata*. The occurrence of other woodland species was significantly correlated with one parameter (e.g. *Alliaria petiolata*, *Epipactis helleborine*) or combination of parameters (e.g. *Geranium robertianum*, *Ribes rubrum*). In four species the presence of footpaths or rides contributed to the colonisation (e.g. *Ranunculus ficaria*, *Geum urbanum*). Long-term monitoring in some woodlands also demonstrated the effect of woodland age. Despite their large capacity to disperse, ferns are not always the first to establish in woodlands. Earlier colonists include other anemochoric vascular species of woodlands, and also endozoochoric and epizoochoric woodland vascular species. Ferns are able to colonise trenched woodland within 10 - 20 years after it has been planted. The process takes longer if there are no trenches, as colonisation depends on the availability of safe sites for establishment. The rapid colonisation of pine stands also indicates the importance of the substrate and microclimate for successful establishment. The presence of trenches within woodlands promotes fern species diversity, especially the diversity of calcicole fern species, which are particularly associated with trenches, though they are mostly present at low densities. In Flevoland, trenched woodlands on clay are much richer in ferns species than woodlands on the mainland (no trenches), mainly because the trenches provide a shady habitat with a calcareous substrate.

Chapter 5 focuses on *Gymnocarpium dryopteris*. In this paper the Kuinderbos population is compared with other Dutch populations to get more insight in the environmental preference of the species and circumstances facilitating a high density. For this reason also populations were studied in Germany. During the period 1979 - 1991 data were collected on the ecology on 419 colonies in the Kuinderbos (or samples of this population, at least 50 colonies per parameter) and 74 colonies elsewhere in the Netherlands. In this period the species was recorded in the Netherlands with at least 670 colonies, of which 89% occurred in the Kuinderbos. *Gymnocarpium dryopteris* preferred shadowed ditches and drainage trenches, but can grow at various other habitats as well. Especially at the western and southern part of the Netherlands the species grows at walls. Sites with *Gymnocarpium dryopteris* belong to different communities. In the Kuinderbos especially plantations of *Picea sitchensis* are preferred, while elsewhere in the Netherlands the species prefers the *Quercion roboris-petrae* (*Fago-Quercetum*) or *Pseudotsuga*-plantations. *Gymnocarpium dryopteris* is accompanied by 14 fern species, at the

Kuinderbos by 12 fern species, with *Athyrium filix-femina* as characteristic species, often indicating potential sites. Rhizomes are shallow creeping, at average 2.6 cm below the surface. Here it grows in the ecto-organic layer and just below this layer. At trench sides it is often found in the mineral layer. Most colonies are within the influence of the water table. The Dutch colonies are small and colonies with more than 1000 fronds rare. This probably indicates that most colonies are young. Colonies with more than 100 fronds are often fertile, with less than 20% of the fronds bearing sori. At the wall habitat small-sized individuals may be fertile as well. The high density in the Kuinderbos can be attributed to an optimal water supply from a peat subsoil, the composition of the ecto-organic layer consisting of *Picea* needles and an optimal light climate. The high density in *Picea sitchensis* within the Kuinderbos is unprecedented in Europe and makes these stands resemble the natural habitat within *Picea sitchensis* forests at the west coast of N.-America.

In **Chapter 6** our object was to analyse the factors critical for the demography of *Asplenium scolopendrium* within populations of plants growing terrestrially by long-term observations. A study on this fern's performance and demography has been carried out in the Kuinderbos. Three plots (*Picea sitchensis* - *Fagus sylvatica*, *Picea sitchensis* with thinning and *Fraxinus excelsior*) were studied in more detail (1977 - 1999). We used the recorded demographic data to parameterize 37 transition matrices. A key factor affecting the performance of *Asplenium scolopendrium* was found to be light. In the *Fraxinus excelsior* plot, plants grew faster, produced more fronds and became larger than in the *Picea sitchensis* stand. In the *Fraxinus excelsior* plot, the ferns were able to form a closed fern cover within a few years, but in the shadier plots in the *Picea sitchensis*- *Fagus sylvatica* plot they were not. It was found that cold winters influence the population growth rate by increasing mortality and increasing retrogression. The average frond damage was closely correlated with the number of frost days per winter. Mortality was correlated with the number of frost days per winter. In the *Fraxinus excelsior* plot, snow cover protected fronds and reduced the impact of frost. Erosion of trench banks and intraspecific competition were also found to increase mortality. Life-table response analysis revealed that reproduction contributed greatly to the differences in projected population growth rates. Reproduction was higher in the *Fraxinus excelsior* and the thinned *Picea sitchensis* plots. These differences can be attributed to an initial difference in light climate. Moreover, in the *Picea sitchensis* - *Fagus sylvatica* plot the accumulation of litter reduced reproduction. Recruitment took place on bare soil but also in open mats of pleurocarpous moss species and on bare soil with a vegetation developing into the *Fissidentietum taxifolii*. It is expected that *Asplenium scolopendrium* with its Atlantic distribution will profit from global warming, since severe winters will become rarer and summers wetter.

Chapter 7 studies the effect of woodland management on ferns in the field by three experiments. A thinning experiment was carried out in which populations of *Gymnocarpium dryopteris* were monitored in a plot before and after thinning and in a control plot. Two other plots were monitored in the same period over a period of 15 years in the Kuinderbos forest. Colonies were mapped and number of fronds per colony counted annually. In the period prior to thinning mortality was 51%, compared with 63% in the control plot. Colonies lost fertility, became smaller and eventually died. After forest thinning the fern population recovered within seven years to the former population size. The experiment showed the impact of the light climate. In a reference plot with a clay topsoil, the number of fronds per colony increased, but no recruitment was observed, probably due to the dense moss layer on the woodland floor and trench banks. In a second reference plot in the peat erosion area, *Gymnocarpium dryopteris* reacted positively (by recruitment) to forest thinning while windfalls in preceding years had a positive effect on the size of the fern patches. In a second experiment, two stands of *Picea sitchensis* - *Fagus sylvatica* were monitored after repeated thinning at an interval of six years.

With thinning the light climate improved (from < 2% to 2.5 - 4% light intensity), allowing mass recruitment of *Asplenium scolopendrium* and *Polystichum aculeatum* to take place. *Gymnocarpium dryopteris* reacted by forming larger patches.

In the Voorsterbos, in artificial gaps within stands of *Fagus sylvatica* on boulder clay were monitored during a period of three years. Ten fern species established in these gaps, including two species not known from the area. *Athyrium filix-femina* formed dense stands. Various species (e.g. *Gymnocarpium dryopteris*, *Dryopteris cristata*) behaved as pioneers but were unable to build up populations. *Thelypteris palustris*, however, did build up a population. It seems plausible that the mass colonisation was related to a spore bank and an optimal microclimate with constant high moisture and humidity in the shaded part of the gaps. In the gaps, mass recruitment of *Fraxinus excelsior* was suppressed by herbivory of Roe deer for a period of five years, but browsing was subsequently responsible for a heterogeneous dense recruitment pattern of Ash trees. By cutting gaps the *Fagus sylvatica* stand is transformed into a *Fraxinus excelsior* vegetation, in which various fern species probably will be preserved.

In **Chapter 8** (General discussion) the meaning of spore-limitation is stressed. In the first 20 years after afforestation the sequence of establishment of fern species is determined by the population size of the particular fern species in the adjacent area. But after establishment spore limitation is still important, even after 50 years, as concluded on the widespread distribution of fern plants in the peat erosion area and the small scale clustering around adult plants. Colonisation is still a combination of spores coming in from outside the area and of local dispersal, with differences between species, due to differences in habitat preference and breeding system. The clustering pattern was observed in the peat erosion area but also on clay, but can even be observed on canal walls in the city of Amsterdam (e.g. colonisation by *Asplenium adiantum-nigrum*). Seed-limitation also plays a very important role in most of the characteristic woodland species, but seed plants differ from ferns in having source areas more nearby (role of villages as source area) and with other operating vectors (humans, dogs). Habitat limitation is related to the light climate (which is largely controlled by woodland management). The potential fern habitat was at first suppressed by a lack of incoming light (e.g. dark *Picea abies* stands), while since 1985 there is on average too much incoming light (leading to forb dominance or rejuvenation of trees). While the role of spore limitation has decreased (effect of increase of population size and build up of spore bank), the role of habitat limitation has increased.

In Chapter 8 also attention is paid to the planning and creation of woodlands based on the conclusions of the thesis. For the purpose of the development of the woodland flora woodlands have to be large, to be situated nearby villages (or even better nearby ancient woodlands or wooded banks), with variation in relief (drainage trenches, if functional), with footpaths and stand variation at a small scale. In this mosaic patches tree species which give deep shade (e.g. *Carpinus betulus*, *Acer pseudoplatanus*), alternate with species with transmitting more light to the wood floor (e.g. *Fraxinus excelsior*, *Salix alba*).

In the peat erosion area woodland management has to be focused completely on the pteridological values. This means restrictions in tree harvesting and to focus any human management interference on its effect on the herb layer including the fern flora. Moreover, conservation of the peat erosion area also means hydrological measures in keeping the peat sponge as wet as possible.

Samenvatting



De *Rechte driehoeksvaren* (*Gymnocarpium robertianum*) komt al ca. 35 jaar in het veenafbraakgebied voor. Van de oorspronkelijke drie vestigingen is er nog één over. Hier vond vanuit één kloon slechts gedurende enkele jaren verjonging plaats. Bij het dunningsbeheer is rekening gehouden met deze groeiplaats.

Dit proefschrift gaat over varens. Het gaat in op vragen die betrekking hebben op trends, habitatvoorkeur en verspreiding van varens in Nederland. Het spitst zich toe op de ecologie, demografie en dispersie van soorten en het beheer van het varenleefgebied in de Flevolandse bossen. In dit proefschrift krijgt het varenrijke Kuinderbos (Noordoostpolder) veel aandacht.

Hoofdstuk 2 is gericht op trend, habitatvoorkeur en verspreiding van varens in Nederland. In de periode 1991 - 2000 kwamen 39 soorten varens voor (Paardenstaarten zijn in dit proefschrift niet bij de varens gerekend, ondanks een gewijzigde taxonomische visie op deze groep van sporenplanten). In Nederland kunnen steden rijk aan varens zijn. Vooral Amsterdam heeft een rijke varenflora, waarbij varens groeien op grachtkanten in de voegen tussen (basalt)stenen. Ook jonge polderbossen kunnen rijk zijn aan varensoorten. Het Kuinderbos is momenteel het meest soortenrijke gebied in Nederland, waarbij veel bijzondere varensoorten groeien op greppelkanten en wortelen in het kalkhoudende, zeer fijne zand. Het aantal varensoorten in Nederland is de laatste 30 jaar toegenomen vanwege de aanplant van bossen (bijv. in Flevoland). Voor 69% van de soorten geldt dat het aantal groeiplaatsen is toegenomen. Dit heeft te maken met aanplant van bossen, omvorming van boerenland naar natuur en de klimaatsverandering. Ook speelt het ouder worden van de bossen en de sterke afname van de SO₂ vervuiling. Er zijn ook soorten waar het minder goed mee gaat. De Maanvaren (*Botrychium lunaria*) is achteruitgegaan door het weelderiger worden van de vegetatie vanwege de hoge stikstofdepositie, terwijl nog steeds groeiplaatsen van beschermde varensoorten verloren gaan door restauratie of afbraak van (gracht)muren.

Sommige soorten die in de laatste 30 jaar voor het eerst in ons land verschenen (bijv. Lansvaren *Polystichum lonchitis*, Klaverbladvaren *Marsilea quadrifolia*) bleken in staat om een afstand van enkele honderden kilometers te overbruggen met hun sporen. Varens kunnen in ons land worden aangetroffen in 75 plantengemeenschappen. Veertien soorten zijn diagnostisch voor één of meer van deze gemeenschappen. De populatieomvang van de Nederlandse varens varieert van enkele planten (bijv. Lansvaren, *Polystichum lonchitis*) tot vele miljoenen exemplaren (bijv. Brede stekelvaren, *Dryopteris dilatata*).

De vestiging van vele zeldzame varensoorten in het Kuinderbos vormde de reden om een studie te beginnen naar ecologie en kolonisatie. De vraag werd gesteld welke omgevingsfactoren de kolonisatie in dit gebied tot een succes hebben gemaakt. In **hoofdstuk 3** wordt deze vraag verder uitgewerkt naar ecologie (bepaalde voorkeur voor omstandigheden, verandering in deze voorkeur in periode van bijna een kwart eeuw) en het vermogen van varens zich te verspreiden (dispersie capaciteit). Bijzondere varens werden vrijwel uitsluitend in bosgreppels gevonden. In totaal werd 130 km van de in totaal 240 km aan bosgreppels onderzocht. Het Kuinderbos is 1050 ha groot en werd in de periode 1949 - 1954 geplant op allerlei bodemsoorten, waaronder op meerveengrond en een veenafbraakgebied. Op deze bodemtypen ligt een laag schelphoudend (dus kalkrijk) fijn zand op eeuwenoud, zuur zegge- en hoogveen. De zandlaag varieert in dikte van 20 tot 100 cm. Vrijwel alle bosgreppels lopen in het bos van het noordwesten naar zuidoosten.

De habitatvoorkeur werd zowel in 1979 als in 2002 onderzocht waarbij aandacht werd besteed aan bodemsamenstelling, samenstelling van de boomlaag en eigenschappen van de bosgreppels: hoogte van planten op greppelkanten, richting (expositie), steilte van de kanten (inclinatie). Alle bijzondere soorten werden nauwkeurig gekarteerd en per plant/kloon gegevens over aantal bladeren en maximale bladlengte verzameld. Er werden eveneens gegevens verzameld over microklimaat (lichtmetingen) en waterhuishouding (grondwaterbuizen). In 1979 werden van de 23 varensoorten 18 uitsluitend of significant meer op greppelkanten gevonden. Sommige soorten hadden een voorkeur voor een bepaalde expositie (bijv. de Tongvaren, *Asplenium scolopendrium* voor het Zuidwesten) of voor de relatieve hoogte binnen het greppelmilieu. De Kamvaren (*Dryopteris cristata*) kwam alleen onderin greppels voor op de veenbodem. De Gewone eikvaren (*Polypodium vulgare*) echter prefereerde de bovenzijde van

greppel kanten, op plaatsen waar deze verzuurd Pleistoceen zand aansnijden. Sommige soorten vertoonden ook een voorkeur voor een bepaalde inclinatie. De Steenbreekvaren (*Asplenium trichomanes*) groeide alleen op de steilste kanten. Tien soorten werden enkel op het fijne Blokziltzand gevonden in het veenafbraakgebied. Opstanden van de Sitkaspar (*Picea sitchensis*) bleken het rijkst aan varensorten. In 2002 hadden 15 van de 22 varensorten een voorkeur voor de greppelkanten. In vergelijking met 1979 waren er soorten waarvan de plaatsvoorkeur was veranderd. De Zachte naaldvaren (*Polystichum setiferum*) groeide in 2002 lager in greppels dan in 1979, terwijl de Tongvaren nu een significante voorkeur voor het Noordoosten vertoonde. Veranderingen in het microklimaat kunnen bij deze soorten een rol spelen. Bij andere soorten wordt het effect vooral bepaald door verjonging (vestiging van nieuwe planten) rondom ouderplanten op dezelfde greppelkant. Diverse bijzondere varensorten koloniseerden opstanden van de Fijnspar (*Picea abies*). Deze opstanden waren in 1979 nog zeer dicht (in een stakenfase) en te donker voor varens. Na dunningen, die begonnen in 1985, werden deze opstanden enige tijd gunstig voor varens (om vervolgens door te veel kap en daarmee samenhangende lichttoename en verruiging ongunstig te worden voor varens). Door dunningen veranderden ook zeer dichte gemengde Fijnspar - Gewone esdoorn (*Acer pseudoplatanus*) opstanden in Gewone esdoorn opstanden, die daarna door diverse kalkminnende varens werden gekoloniseerd. In de periode 1979 - 2002 namen diverse soorten sterk toe. Het meeste succesvol waren de Tongvaren en Stijve naaldvaren. Andere soorten namen amper toe (Steenbreekvaren, Gebogen driehoeksvaren *Gymnocarpium dryopteris*), namen af (o.a. Blaasvaren) of verdwenen zelfs (o.a. Kamvaren).

De kolonisatie van het gebied werd gereconstrueerd door het berekenen van het eerste jaar van vestiging per soort. Het jaar van vestiging bleek te zijn gecorreleerd met de omvang van varenpopulatie in de omgeving (zone van 50 km). Analyse van afzonderlijke varengroepen (kalkminners, zuurminners) maakt het aannemelijk dat dit deels te verklaren is als dispersie-effect (beschikbaarheid van sporen). Opvallend tijdens de kolonisatie was het tegelijk verschijnen van soorten op diverse locaties binnen het bos. Na vestiging vond rondom volwassen planten (dus met vorming van sporen) een sterke vestiging van nieuwe planten (verjonging) plaats bij 43% van de bijzondere varensorten. Dispersie lijkt dan ook te spelen op heel korte afstand (clustering) en op grote afstand (tot honderden km). Na vestiging van sporen gaat het voortplantingssysteem een rol spelen. Uit sporen groeien prothallia die zowel mannelijk als vrouwelijk organen dragen. Zelfbestuiving is niet de regel, omdat dit bij diploïde soorten kan leiden tot sterfte door recessieve erfelijke eigenschappen. In het Kuinderbos bleken polyploïde soorten (veelal erfelijke eigenschappen in viervoud, minder kans op sterfte bij zelfbestuiving) succesvoller (ontwikkelde grotere populaties op meer locaties) dan diploïde soorten, maar de verschillen waren niet significant.

Het inklinken van de bodem en ontkalking kunnen op de lange termijn een bedreiging zijn voor de varenpopulaties in het veenafbraakgebied. Op korte termijn bleek vooral bosbeheer (houtoogst) van grote invloed, waarbij groeiplaatsen verloren gaan door verruiging. Verruiging met bramen is fnuikend. Op lange termijn is bij ecologisch bosbeheer enig herstel te verwachten door ontwikkeling van nieuwe generatie bomen.

In **hoofdstuk 4** is de vraag welke omgevingsfactoren die van invloed zijn op de kolonisatie van bosplanten uitgewerkt voor 53 op zavel en klei gelegen bossen in de Noordoostpolder en Oostelijk Flevoland. Deze studie was gericht op zowel zaadplanten als varens. Er komen per bos meer soorten zaadplanten voor als het bos groter is, ouder is en dichter bij dorpen ligt. Het aantal voor het bos *kenmerkende* soorten zaadplanten is hoger naar mate het bosoppervlak groter is en het bos ouder. Het aantal zich verjongende bomen en struiken per bos is hoger in grotere bossen of als het bos dicht bij dorpen ligt, wat wijst op aanvoer van soorten uit dorpen (bijv. Aalbes, *Ribes rubrum* en Kruisbes, *Ribes uva-crispa*).

De kans om varens aan te treffen in een bos is hoger naar mate een bos groter is. Dit geldt ook voor twee afzonderlijk onderzochte soorten (Brede stekelvaren en Mannetjesvaren, *Dryopteris filix-mas*). De mate van voorkomen van andere bosplanten per bos hield direct verband met één parameter (bijv. Brede wespenorchis, *Epipactis helleborine*, hogere kans op voorkomen in grotere bossen) of combinatie van parameters (bijv. Robertskruid, *Geranium robertianum*, met hogere kans op voorkomen in grotere en oudere bossen). Bij vier soorten neemt de kans op voorkomen toe als bospaden aanwezig zijn (bijv. bij Speenkruid *Ranunculus ficaria* en Geel nagelkruid *Geum urbanum*), wat wijst op verspreiding door de mens of meelopende honden. Langdurige monitoring in enkele bossen laat ook overtuigend het effect van leeftijd zien op het voorkomen van soorten. Hoewel varens een groot vermogen hebben om zich met sporen te verspreiden zijn ze niet altijd de eerste bosplanten die zich vestigen. Zaadplanten die met de wind worden verspreid (bijv. Orchideeën), maar ook soorten met bessen (bijv. Aalbes) of soorten waarvan zaden aan de vacht blijft haken (bijv. Geel nagelkruid) kunnen zich eerder in een bosgebied vestigen dan varens. Als greppels aanwezig zijn vindt tussen de 10 en 20 jaar na aanplant kolonisatie door varens plaats. Zonder greppels kan het veel langer duren waarbij milieuomstandigheden en dispersie beide een rol spelen. De tamelijk snelle kolonisatie van denopstanden (op zavel, klei, maar ook op zand) laat net als bij de greppels het belang van een geschikt habitat zien. Begreppeling van kleibossen is gunstig voor de varenrijkdom en dat geldt met name voor kalkminnende soorten. Het mooiste voorbeeld betreft het bij Lelystad op lichte zavel geplante Jagersveld, dat geldt als één van de hotspots voor varens in Flevoland. Kleibossen op het oude land zijn relatief arm aan varens, wat mede samenhangt met het ontbreken van greppels (in feite dus reliëf).

Hoofdstuk 5 gaat over de Gebogen driehoeksvaren waarbij allerlei groeiomstandigheden van de Kuinderbos-populatie vergeleken zijn met die van populaties elders in Nederland. Ook populaties in Duitsland (bedoeld als referentie) zijn bij de vergelijking betrokken. In de periode 1979 - 1991 kwamen in Nederland 670 klonen van deze soort voor, waarvan 89% in het Kuinderbos. Zowel in als buiten het Kuinderbos komt de soort vooral langs greppels voor. De habitatkeuze buiten het Kuinderbos is breder, met in het westen en zuiden van ons land ook groeiplaatsen op grachtmuren. In het Kuinderbos is de Gebogen driehoeksvaren van alle varensoorten het sterkst gebonden aan opstanden van de Sitkaspar, terwijl elders in ons land de soort ook in loofbos en onder Douglasspar (*Pseudotsuga menziesii*) voorkomt. De wortelstokken van de Gebogen driehoeksvaren groeien vooral in de ecto-organische laag (strooisellaag en de gefermenteerde laag daaronder) op een gemiddelde diepte van 2,6 cm, maar soms ook in de minerale laag daaronder. De soort wordt in het Kuinderbos begeleid door 12 andere varensoorten, elders in Nederland door 14 verschillende varensoorten. Kenmerkend is het samen optreden met de Wijfjesvaren (*Athyrium filix-femina*). De meeste klonen liggen binnen de invloedssfeer van het grondwater. Klonen zijn veelal klein en zelden groter dan 1000 bladeren per kloon, wat zowel geldt voor het Kuinderbos als klonen elders in Nederland. Deze grootte wijst op een relatief jonge leeftijd. Klonen zijn meestal fertiel als er meer dan 100 bladeren zijn, waarbij in de regel minder dan 20% van de bladeren sporangia dragen. Juist op muren kunnen klonen met een heel geringe omvang wel fertiel zijn. De hoge dichtheid van deze soort in het Kuinderbos in vergelijking met de rest van Nederland kan worden verklaard uit de combinatie van een optimale waterhuishouding (veenondergrond die de bovenlaag capillair voedt), de aanwezigheid van een ecto-organische laag van de Sitkasparnaalden en een optimaal lichtklimaat. De vergelijking met groeiplaatsen elders in Nederland laat zien dat de relatie met de Sitkaspar geen strikte voorwaarde is. De hoge dichtheid in opstanden van de Sitkaspar is van elders in Europa niet bekend en doet deze opstanden in het Kuinderbos lijken op het natuurlijke habitat in Sitkasparbossen aan de westkust van Noord-Amerika.

Hoofdstuk 6 gaat in op de demografie van de Tongvaren in het Kuinderbos, waarbij in de periode 1977 - 1999 in drie proefvakken planten zijn gevolgd. Jaarlijks werden in deze proefvakken planten opgemeten en ingetekend zodat deze als individu te volgen waren. De drie proefvakken lagen in opstanden van Sitkaspar-Beuk, Es en Sitkaspar. Eerstgenoemd proefvak is 20 jaar gevolgd, de andere twee korter. Voor analyse van de data werd gebruik gemaakt van matrixrekenen, waarbij de overgang van de verschillende levenstadia werd geanalyseerd. Licht bleek een sleutelfactor die van invloed is op de groei van de Tongvaren. In het proefvak onder Essen groeiden planten sneller, produceerden zij meer bladeren per plant en werden groter dan in beide andere proefvakken. Onder Es bleek de Tongvaren in staat binnen enkele jaren een aaneengesloten vegetatie te vormen, wat niet het geval was in beide andere proefvakken. Koude winters beïnvloedden de populatiegroei door een grotere rol van sterfte en toename van retrogressie (bijv. planten die in het ene jaar nog volwassen waren, in het daaropvolgende steriel). Bladschade (necrosis) en ook sterfte waren sterk gecorreleerd met het aantal vorstdagen per winter. In het Es proefvak was de invloed van strenge winters geringer door bescherming van de bladeren met sneeuw. Erosie van greppelkanten en competitie waren eveneens een oorzaak van sterfte. Matrix analyse liet zien dat reproductie (verschijnen van kiemplanten) eveneens in belangrijke mate het verschil bepaalde tussen het Sitkaspar - Beuk proefvak en beide andere proefvakken. Het lichtklimaat verklaart een deel van deze verschillen. Hierbij speelde dat in eerstgenoemde proefvak door strooiselophoping de betekenis van reproductie afnam. De vestiging van kiemplanten vond in de proefvakken plaats op kale zandgrond (waar zich tegelijk met de prothallia ook Veder mossen, *Fissidens* spp. vestigden), maar ook in open vegetaties van slaapmossen. Gezien de onderzoeksresultaten is de kans groot dat de Tongvaren zal profiteren van het warmer wordende klimaat, omdat verwacht wordt dat strenge winters minder vaak zullen voorkomen en zomers vochtiger worden.

Hoofdstuk 7 gaat in op de relatie tussen bosbeheer en varens aan de hand van drie experimenten. Een experiment in een Sitkaspar-opstand werd uitgevoerd waarbij in een bosgedeelte eenmalig werd gedund (dunningsvak) en in het controlevak niet. Ook twee andere bosgedeelten werden gevolgd in een periode van 15 jaar (met dunningen halverwege). In de periode voor dunning werden klonen jaarlijks kleiner en vormden geen fertiele bladeren meer (voorbeeld van retrogressie!). In het dunningsvak was de sterfte 51% en in de controleplot 63%. Na dunning trad herstel op. Het duurde zeven jaar voordat de oorspronkelijke situatie van voor de achteruitgang werd bereikt. Het experiment toonde de grote rol van lichtklimaat voor deze soort. In een referentieproefvak op klei nam het aantal bladeren per kloon wel jaarlijks toe, maar vond geen verjonging plaats, mogelijk vanwege de dichte moslaag op bosbodem en greppelkanten. In een ander referentieplot reageerde de Gebogen driehoeksvaren positief op dunning en op het ontstaan van een stormgat. Het positieve effect bleek hier vooral uit de grootte van de klonen.

In een tweede experiment werden twee bosgedeelten met een Sitkaspar-Beuk samenstelling gevolgd, waarbij het ene deel twee maal werd gedund met tussenpoos van 6 jaar en het andere als controle diende. Deze dunning initieerde een massale verjonging van de Tongvaren en Stijve naaldvaren. De Gebogen driehoeksvaren reageerde ook hier vooral met het vormen van grotere klonen.

Een derde experiment werd uitgevoerd in het Voorsterbos (Noordoostpolder) waarbij bosgaten werden gekapt in opstanden van Beuk op neutrale keileem. Na kap vestigden zich in totaal 10 varensoorten, waaronder twee soorten die niet bekend waren van het gebied. De Wijfjesvaren (*Athyrium filix-femina*) vormde dichte vegetaties. Verschillende soorten (o.a. de Kamvaren!) gedroegen zich als pioniers en waren niet in staat duurzame populaties op te bouwen. De Moerasvaren (*Thelypteris palustris*) was wel in staat dit te doen. Het lijkt waarschijnlijk dat de massale kolonisatie te maken had met een al bestaande sporenbank

(sporenvorrada in bodem met sporen die meerdere jaren hun kiemkracht bewaren) en een optimaal microklimaat met constante hoge bodem- en luchtvochtigheid in het beschaduwde deel van de bosgaten. In de bosgaten vestigden zich diverse als kwelindicator bekend staande soorten (Bosbies *Scirpus sylvaticus*, Holpijp *Equisetum fluviale*, Reuzenpaardestaart *Equisetum telmateia*), wat duidelijk indiceert dat niet de kwelflux maar een basisch, constant vochtig milieu essentieel is voor deze soorten. In de bosgaten wisten Reeën (*Capreolus capreolus*) gedurende vijf jaar de massale verjonging van de Es (*Fraxinus excelsior*) te onderdrukken, waarna deze doorschoten. Beukenbos wordt via deze gaten omgevormd in essenbos, waarbinnen naar verwachting diverse varensorten zich zullen kunnen handhaven.

In **hoofdstuk 8** (discussie) wordt een aantal aspecten van het onderzoek nog eens op een rij gezet. Uit het onderzoek in de Flevolandse bossen blijkt duidelijk dat het dispersievermogen een 'bottle neck' is in de eerste 20 jaar, waarbij de volgorde van vestiging van varensorten mede bepaald wordt door de populatieomvang direct buiten het gebied. Het aanbod van sporen (sporenlimitatie) blijft ook nadien een belangrijke rol spelen. Dit blijkt uit het patroon van een eerste cohort van zich gevestigde planten uit sporen die van elders zijn aangevoerd en een tweede cohort van vestigingen die direct samenhangen met sporenproductie door ouderplanten en vestiging rondom deze ouderplanten (clustering). Dit patroon is vooral waargenomen in Kuinderbos en Jagersveld, maar ook elders (o.a. bij de Zwartsteel *Asplenium adiantum-nigrum* en Tongvaren op de Amsterdamse grachtmuren). Zaadlimitatie speelt ook langdurig een belangrijke rol bij vestiging van zaadplanten in de Flevolandse bossen. In tegenstelling tot de varens blijken bij zaadplanten de dorpen een belangrijk brongebied. Zowel de mens als huisdieren spelen hier een belangrijke rol bij de verspreiding. Habitatlimitatie heeft voor wat betreft de varens vooral te maken met het lichtklimaat (en beheer). Het hele veenafbraakgebied zou vol kunnen staan met varens, ware het niet dat voorheen grote delen te donker waren, en thans grote delen verruigd zijn of zich met bomen verjongen. Terwijl sporenlimitatie over de decennia heen een minder grote rol gaat spelen (grotere varenpopulaties, bijv. bij de Tongvaren, opbouw van grotere sporenbank), geldt dit niet voor habitatlimitatie. Het oppervlak geschikt habitat is recent afgenomen en hangt samen met het dunningsbeheer.

In het laatste hoofdstuk wordt ook aangegeven hoe de ontwikkeling van de bosflora kan worden begunstigd in nog aan te planten bossen. Het is gunstig als deze groot zijn, dicht bij dorpen of steden liggen (of nog beter dicht bij oude boskernen en eeuwenoude houtwallen, wat niet geldt voor Flevoland), bestaan uit een mozaïek van schaduwgevende boomsoorten (bijv. Haagbeuk *Carpinus betulus*, Gewone esdoorn) en minder schaduwgevende boomsoorten (Es, Schietwilg *Salix alba*), er sprake is van reliëf (bijv. in de vorm van bosgreppels) en het bos ontsloten is met bospaden.

Op grond van de resultaten beschreven in dit proefschrift moet worden aanbevolen het bosbeheer in het veenafbraakgebied binnen het Kuinderbos in haar geheel af te stemmen op ecologische waarden. Dat betekent dat de beheerder zeer terughoudend moet zijn met houtoogst en deze geheel dient af te stemmen op de kruidlaag (met name de varens). De duurzame instandhouding van het veenafbraakgebied (behoud van de veenspons) kan alleen als de veen ondergrond zo nat mogelijk wordt gehouden (vernatting).

Geprezen Gij, EEUWIGE, die begenadigt met weten¹
Uit: *Sidoer - Achttiengebed*

Dankwoord

Een `eerste` woord van dank is gericht is aan mijn ouders. Beiden werden geboren in het jaar van de voltooiing van de Afsluitdijk en groeiden op aan de rand van de vroegere Zuiderzee en maakten mee dat de Noordoostpolder droogviel. Zij gaven mij alle vrijheid om mij te kunnen ontwikkelen, niet in het minst in de tienerjaren in Emmeloord, toen de CJN (later ACJN) mij ruimschoots de mogelijkheid bood ecologische kennis en ervaring op te doen en deze ook weer in praktijk te brengen. Het was dr. Ger Londo die mij in 1999 stimuleerde om een proefschrift te gaan schrijven. Het idee was om dat te doen over nieuwe natuur in Flevoland. Vervolgens heb ik de kolonisatie van de Flevolandse bossen ook overwogen, maar uiteindelijk is de keuze gevallen op kolonisatie van deze bossen door met name varens. Het schrijven van een verhaal over Nederlandse varens in het boek *Pteridology in the New Millennium* (ed. S. Chandra & M. Srivastava) was mede de prikkel om deze keuze definitief te maken. Het verschijnen van een proefschrift is niet mogelijk zonder een promotor. Na een eerste briefwisseling stemde prof. dr. Frank Berendse er in toe om verder met mij in zee te gaan. Frank bedankt voor dit besluit en het daarna getoonde geduld. Het kostte de nodige tijd mij te overtuigen om het aantal van 12 hoofdstukken terug te brengen tot het wenselijk aantal en doelmatigheid en scherpte voor ogen te houden. Het is gemakkelijker een promovendus vanaf het begin van onderzoek te begeleiden dan een promovendus die alles al heeft onderzocht en dan een beroep op je doet voor begeleiding in de laatste fase.

Het proefschrift besteedt veel aandacht aan het Kuinderbos. Hier begon mijn interesse voor varens ongewild. Dat was tijdens een paddenstoelenexcursie met het onvergetelijke echtpaar Frans² en Dien³ Tjallingii in september 1977 op kavel L 69. De opstand bevond zich toen nog in de stakenfase en het kostte ons de nodige moeite om ons tussen de sparren te wringen. Kleine sparrerussula (*Russula nauseosa*) and Sparreveertje (*Pterula multifida*) werden gevonden evenals diverse plekken met de Tongvaren. Dat was het begin om in de winter van 1977/1978 de nodige kilometers aan bosgreppels af te lopen (struinen door de waterhoudende greppels en in dichte opstanden). Het leverde bij elk bezoek voor het gebied nieuwe varensoorten dan wel nieuwe vindplaatsen op. Op de fiets van Emmeloord naar het gebied. Een paar kilometer sjouwen door greppels en vermoeid, vaak smerig, maar voldaan terug naar het ouderlijk huis. In 1979 kreeg ik tijdens mijn biologiestudie aan de Groningse Universiteit op het Laboratorium voor Plantenecologie de kans om in een doctoraalonderwerp de uitzonderlijke varenrijkdom in het Kuinderbos nader te onderzoeken. Dr. Wouter Joenje was bereid de studie te begeleiden na het plotselinge overlijden van prof. dr. D. Bakker, die eigenlijk de begeleiding op zich zou nemen. Het onderzoek in het Kuinderbos was mogelijk door een langjarige en goede samenwerking met Staatsbosbeheer. Dat was al zo tijdens de doctoraalstudie toen ik maandenlang bivakkeerde in een caravan bij de familie Bovendeur⁴ achter de werkschuur. En ook daarna. Een eerste dunningsproef kon plaatsvinden dankzij inspanning van Fred Mijnten. In 1990 was ik zelfs voor een jaar één dag per week in dienst bij Staatsbos-

¹ `weten` wordt ook vertaald met `wetenschap`

² Dr. F. Tjallingii overleed in 2007

³ D. Tjallingii-Beukers overleed in 1990

⁴ H. Bovendeur overleed in 1997

beheer om het Kuinderbos goed in kaart te brengen voor wat betreft flora en vegetatie. Dat bood ook de mogelijkheid de data over varens te actualiseren. Ook de namen van Harco Bergman, de veel te vroeg overleden Jan van den Bosch⁵, Jeroen Bredenbeek, Ties Hanssens en Henny Olthof moeten hier worden genoemd. In het begin van de jaren negentig heb ik veel tijd besteed om meer zicht te krijgen op de ontwikkelingen van de bosflora (vaatplanten) in de kleibossen van Flevoland. Bram Smit had al omstreeks 1979 de bijzondere varenflora in het Jagersveld ontdekt en begon hier een monitoring met sterke overeenkomsten met mijn onderzoek in het Kuinderbos. Het is dan ook niet voor niets dat Bram medeauteur is van hoofdstuk 4. Sieuwke van der Werf⁶ gaf commentaar op een eerdere versie van dit hoofdstuk.

Hoofdstuk 5 is in belangrijke mate gebaseerd op een enquête die werd verzonden naar ontdekkers van groeiplaatsen van de *Gebogen driehoeksvaren*. Gegevens werden beschikbaar gesteld door: dr. André Aptroot, prof. dr. J. Barkman⁷, Fred Bos, S. van de Brand, dr. Rienk-Jan Bijlsma, Onno de Bruijn, P. Chardon, J. Cortenraad, Ton Denters, Ate Dijkstra, Bert Dijkstra, Fons Eijssink, J. Hermans, M.T. Jansen⁸, J.R. Marquart, Henk Menke, H. Leys, D.T.E. van der Ploeg⁹, Jan Schreurs, F. Sollman, dr. Bart van Tooren, Eddy Weeda, W. van der Weerd, Sieuwke van der Werf, Jan Werschkull, dr. Cor Zonneveld en Otto Zijlstra.

Hoofdstuk 6 gaat over de demografie van de Tongvaren. Het jarenlang jaarlijks opnemen van individuele planten vereiste de nodige discipline. Bij het uitwerken, en mede dankzij de hulp van dr. Eelke Jongejans, bleek in het materiaal meer te zitten dan ik via de klassieke methode had kunnen blootleggen.

Hoofdstuk 7 betreft zowel proeven in Kuinder- als Voorsterbos. Hoewel het onderdeel van dit proefschrift over het Voorsterbos beperkt is, is het relatief gezien wel een belangrijk onderdeel. Juist in het Voorsterbos, onder leiding van Jan Akkerman en met ondersteuning van Dick Buitenhuis, Lykele Zwanenburg en Klaas Althuis, is de afgelopen 10 jaar een sterk op natuur gericht beheer gevoerd. Dat bood de mogelijkheid op grote schaal bosgaten te realiseren en de effecten op de vegetatie te onderzoeken. Het Voorsterbos was voor mij de afgelopen 10 jaar als een jongensdroom. Voor elk goed ecologisch voorstel vond ik hier een gewillig gehoor.

In meerdere gedeelten van dit proefschrift wordt informatie gebruikt die ontleend is aan de uitgebreide florakartering in de provincie Overijssel. Deze kartering werd uitgevoerd in de jaren 1983 - 2006 door Ruud Beringen, Piet Bremer, Johan Brouwer, dr. Marijke Creveld, Bert Dijkstra, Paul ten Den, Martin Heinen, Coen Knotters, Theo de Kogel, Jan Schreurs, Klaas van der Veen en Bart Vreeken. In meerdere hoofdstukken zorgden tekenaars van de provincie Overijssel voor de nodige ondersteuning. Ik noem hier Gerrit van Vilsteren, Sander Wijsman en Rob Houthuijzen. Pieter Hendriksma, Marcel Horsthuis en Michiel Brouwer worden hier genoemd voor allerlei vormen van ondersteuning. FLORON (Leiden) stelde data uit Florbase meer dan eens beschikbaar. Een speciaal woord van dank geldt voor Wout van der Slikke. Dr. Erik van Dijk heeft jarenlang voor belangrijke PC ondersteuning gezorgd. Dr. Peter Hovenkamp gaf commentaar op hoofdstuk 3, evenals dr. A.F. Dyer. Ook dank aan Ton Denters, Wim Vuik en Remko Andeweg voor hun informatie over de ontwikkelingen in het stedelijk gebied. Het team pollenonderzoek van het Elkerliek ziekenhuis (Helmond) verzamelde gegevens over varensporten in luchtmonsters. De beide paranimfen Geertjan Smits en Pieter Hendriksma namen het proefschrift door in de laatste fase en checkten allerlei zaken die zo makkelijk mis kunnen gaan (echter, fouten van welke aard dan ook zijn geheel voor

⁵ J. van den Bosch overleed in 1998

⁶ S. van der Werf overleed in 1998

⁷ J. Barkman overleed in 1990

⁸ M.T. Jansen overleed in 1994

⁹ D.T.E. van der Ploeg overleed in 2006

rekening van de auteur!). Dr. J. Burrough heeft de concepttekst op Engels taalgebruik gecorrigeerd en één hoofdstuk vertaald. Staatsbosbeheer, de Nederlandse Varenvereniging en Provincie Overijssel droegen bij tot het tot stand komen van het proefschrift. Tenslotte een speciaal woord van dank aan Désirée Rooswinkel en onze dochters Hannah en Leah. Désirée, ook na het afronden van het proefschrift, zal ik `s avonds nog wel eens boven zitten.....



Zachte naaldvaren (*Polystichum setiferum*)
Kuinderbos (greppelkant)



Gewone eikvaren (*Polypodium vulgare*)
Kadoelermeer (op Schietwilg)



Geschubde mannetjesvaren (*Dryopteris affinis*), Deventer (begraafplaats)



Mannetjesvaren (*Dryopteris filix-mas*) en
Brede stekelvaren (*Dryopteris dilatata*)
(met Vermiljoenhoutzwam, *Pycnoporus cinnabarinus*), Voorsterbos (bosgat)

Curriculum Vitae



Wooded bank near Oldemarkt with ancient coppice stools

Piet Bremer was born in Wolvega, the Netherlands, on 6 June 1956. He attended primary school in Oldemarkt, and was ecologically imprinted with the marshes of the Weerribben and wooded banks of Paaslo. His secondary school was the Christelijke Scholengemeenschap in Emmeloord (Noordoostpolder). He read biology at Groningen University from 1975 to 1982. His master's project was on the fern colonisation in the Kuinderbos (supervised by Dr. W. Joenje). Other projects were on the population dynamics and ecology of the shrimp *Neomysis integer*, frost resistance in wild plants and the taxonomy of the bryophyte genus *Dicranum*. In the period 1982 - 1983 he worked at the Rijksinstituut voor Natuurbeheer (Leersum) on epiphytic lichens and SO₂ pollution. Since 1983 he has worked as an ecologist for the provincial board of Overijssel, supervising and participating in the mapping of the meadow birds, vegetation and vascular plant species of the province. He uses these data to advise the provincial authority on environmental, rural and ecological issues.

Besides his provincial work he has executed various ecological projects, e.g. the mapping of epiphytic lichens in Flevoland (province of Flevoland) and the mapping of the flora and vegetation in the Kuinderbos, Bremerbergbos (Staatsbosbeheer), Urkerbos, Schokkerbos (Flevolandschap), Voorsterbos and Waterloopbos (Natuurmonumenten). Since 1997 he has advised Natuurmonumenten on developing nature reserves on farmland, and on woodland management. He is active in nature conservation in the Noordoostpolder.

In his spare time he has functions within the FLORON volunteer organisation and the Dutch Mycological Society (Werkgroep Mycologisch Onderzoek IJsselmeerpolders). He has published reports and papers in local, regional, national and international journals on bryophytes, lichens, vascular plants, macrofungi, breeding birds, mammals and various groups of invertebrates. Most of these reports and papers are focused on ecology.

More reading:

G. van Hezel & A. Pol, 2005. De Flevolandse geschiedenis in meer dan 100 verhalen. Van Gennip, Amsterdam.



Smalle beukvaren (*Phegopteris connectilis*)
Landgoed Den Berg

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