THE COLONISATION OF WOODLAND GAPS BY FERNS AND HORSETAILS

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ABSTRACT

In the Voorsterbos, a planted woodland on a former sea-floor (the Netherlands), artificial gaps within stands of *Fagus sylvatica* on boulder clay were monitored for five or six years after cutting. Ten fern species and three species of horsetail established in these gaps, with *Dryopteris cristata, Thelypteris palustris, Matteuccia struthiopteris* and *Equisetum telmateia* not previously known from the Voorsterbos. *Athyrium filix-femina* was most successful and formed dense stands in some gaps. Two species (*Gymnocarpium dryopteris*, *Dryopteris cristata*) established but have since disappeared. *Thelypteris palustris* has built up a sustainable population. It seems plausible that the germination of ferns and horsetails took place during the first season following cutting of the gaps and was derived from a spore bank with an optimal microclimate with constant high moisture and humidity in the shaded part of the gaps. Competition from recruiting trees and shrubs was suppressed in some of the gaps for a period of five year through herbivory by Roe deer.

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 options are available to forest managers. They include a wide range of harvesting systems, regeneration methods and rotation lengths. Various studies have been published on the effects of harvest practices on understory and overstory conditions in managed temperate forest (e.g. Halpern & Spies 1995, Thysell & Carey 2000, Bergstedt & Milberg 2001), but with the exception of one study on *Pteridium aquilinum* (den Ouden 2000), none of them focussed on ferns.

In 1997 the management objective in one of the planted forest in the province of Flevoland (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. We expected gaps would be vegetated by recruiting trees while ferns would play a subordinate role as they had been scarce in the beech stands prior to the gap formation. Natural gaps in beech stands on sandy soil in the Speulderbos (The Veluwe, the Netherlands) showed hardly any role for ferns (two species with little cover) while rejuvenation of trees was suppressed by browsing of deer (personal observations). In the Neuenburger Urwald, an ancient Hornbeam woodland on loamy soil (*Stellario – Carpinetum*), Koop (1989) recorded few fern species colonising the natural gaps.

STUDY SITE

The Noordoostpolder was reclaimed in 1941/1942 and the Voorsterbos (Figure 1) planted in the period 1944 -1955 (Bremer 2001). The area is below mean sea level: the altitude varies from -2.5 to -1m. 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 1 km per ha in the Voorsterbos (boulder clay); their depth ranges from 0.4 m to more than 1.2m. A large area on the boulder clay has a water table at a depth of less than 0.5m in the winter. Currently the trees extract much water, making drainage by trenches less important than in the years after these woodlands were planted. In winter these trenches have a shallow water level, while in summer they are dry, only being filled after heavy rainfall. In the Voorsterbos a management strategy started in 1997, 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 down trees. The diameter of these gaps was 1.5 - 2 times tree height, and their size varied from 0.08 to 0.15ha per gap, with the exception of one gap of 0.25ha (Bremer 2007a). Nearly all the felled trees were transported with heavy equipment, causing soil disturbance over more than 50% of the surface of these gaps. All the gaps were intersected with 0.4 – 1m deep drainage trenches with a density of 1km per ha.

METHODS

This study focuses on 12 gaps in *Fagus sylvatica* stands on boulder clay in which trees were felled at the start of the years 2000, 2001 or 2004; monitoring took place in the

Figure 1. The location of the study area (Voorsterbos) in the Netherlands.

period 2000 – 2008. Each gap was monitored for a period of six years, except for three plots with a five year period. In these gaps the vegetation and recruitment of tree species were mapped, and ferns and horsetails recorded. For those ferns and horsetails that are less common in the Netherlands (listed in Table 1) individuals were mapped on 1:1000 maps, and the length of the longest frond per plant measured and the presence of spore producing fronds noted. Special attention was paid to trenches, as this habitat can be rich in fern species (Bremer 2007b). In the second year following tree felling, a 50m zone surrounding the gaps was surveyed for ferns and horsetails. These `plots` were used as controls. Shade by the trees surrounding the gaps 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) during more or less cloudless weather. 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 has no shade in the period between 21 June and 21 September). The position of each individual fern and horsetail (n = 25) was recorded with reference to these two lines and the number of days with shade for each was determined (Figure 2). For the group of common fern species only *Athyrium filix-femina* was analysed because it is the species most prone to desiccation. This species was analysed using a matrix of 1 x 1m plots in one of the gaps when this gap was five years old and ferns in their subadult or adult phase. Only sporophytes were included in this study, as gametophytes are difficult to monitor. The gametophyte phase was frequent in the first year after tree felling and subsequent sporophytes could be identified when two or three years old. Data were collected in August. Data on cover of the fern layer, herb layer (< 1m) and young shrub layer (> 1m) were estimated per gap in late summer.

Statistical analysis

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

RESULTS

Within three years the gaps were dominated by the herb or initial tree layer (< 1m in height). Fern cover reached a maximum of 21% in the fifth year (Figure 3) and varied from 1– 70% per gap. *Fraxinus excelsior* recruited at a density of more than one sapling per m^2 in 50% of the monitored gaps. In these gaps, after five years, patches of trees were able to build up a young woodland phase despite heavy browsing by Roe deer (*Capreolus capreolus*). In three other gaps shrubs and young trees present before felling were able to cover these gaps within five years. Ten fern species became established in the gaps, of which five were present in adjacent woodland zones, and three species of horsetail (Table 1). The average number of fern species per gap was at its maximum in the early years and decreased slightly after three years (Figure 4). Three fern species (*Thelypteris palustris, Dryopteris cristata, Matteuccia struthiopteris)* and one species of horsetail (*Equisetum telmateia*), had not previously been recorded in the woodland. A single plant of *Asplenium scolopendrium* was found adjacent to one of the gaps; it was not recorded within the gap habitat.

Within the gaps, ferns established on trench banks and on the woodland floor. *Athyrium filix-femina*, the most successful fern coloniser, had its highest density in the trenches ($\chi^2 = 6.5$, $p < 0.05$). The group of less common fern species (Table 1) showed no preference for trench or woodland floor habitat in terms of the population size ($\chi^2 =$

Table 1. Fern species found within 12 gaps of *Fagus sylvatica* stands (5 – 6 years after tree-felling) compared with uncut woodland surrounding these gaps, based on annual monitoring).
n g = number of gaps with species listed, **np g** = total number of estimated or counted plants/colonies in 12 gaps after six seasons, **tr** = number of gaps with species listed growing in drainage 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 %** = average time in shade during the period 21 June - 21 September based on plants/colonies and presented as percentage (e.g. 100% means plants are shaded during the whole season within the 21 June shade line), na = not analysed, **a** = number of 50m zones surrounding gaps with species listed, **np a** = total number of plants in 50m zones surrounding the gaps (data of all these gaps summed) after two seasons, **VB** = species found elsewhere in the Voorsterbos since 2000.

Woodland species	**Woodland gaps**									**50 m zone**			**VB**
	n g	%	np g	tr	%	wfl	%	f	sh %	a	%	np a	
Ferns													
Common species													
Athyrium filix-femina	12	100	> 1000	12	100	12	100	f	na	8	66.7	50 - 100	+
Dryopteris dilatata	11	91.7	200-400	11	91.7	11	91.7	f	na	8	66.7	50 - 100	+
Dryopteris filix-mas	8	66.7	200-400	8	66.7	8	66.7	f	na	8	66.7	50 - 100	+
Dryopteris carthusiana	6	50.0	50-100	6	50.0	5	41.5	f	na	3	25.0	25 - 50	+
Less common species													
Thelypteris palustris	7	58.3	13	3	25.0	5	41.5	n.f	84.6	0	0	0	-
Dryopteris affinis	3	16.6	3	1	8.3	2	16.7	n.f	100	1	8.3	1	+
Matteuccia struthiopteris	2	16.7	2	1	8.3	1	8.3	n.f	70.0	0	0	0	-
Dryopteris cristata	2	16.7	2	2	16.7	0	0	n.f	75.0	0	0	0	-
Gymnocarpium dryopteris	1	8.3	1	1	8.3	0	0	n.f	50.0	0	0	0	+
Polystichum aculeatum	1	8.3	1	0	0	1	8.3	n.f	100	0	0	0	+
Asplenium scolopendrium	0	0	0	0	0	0	0	-	-	1	8.3	1	+
Horsetails													
Common species													
Equisetum arvense	4	33.3	?	0	0	4	100	f	na	0	0	0	+
Equisetum fluviatile	2	16.7	3	0	0	3	100	f	100	0	0	0	+
Less common species													
Equisetum telmateia	1	8.3	2	0	0	2	100	f	100	0	0	0	-

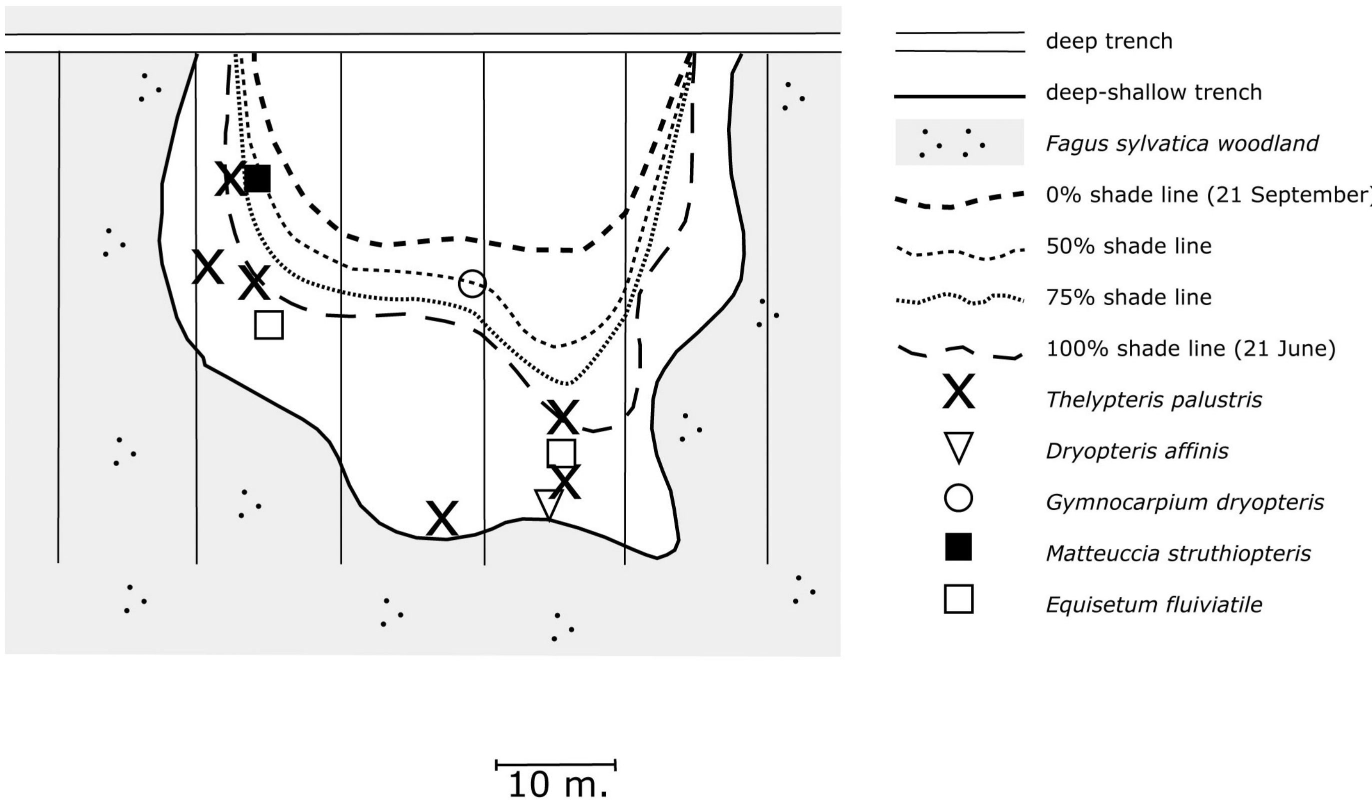

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Figure 2. Woodland gap within *Fagus sylvatica* stand showing the shade lines and the distribution of rare ferns and horsetails.

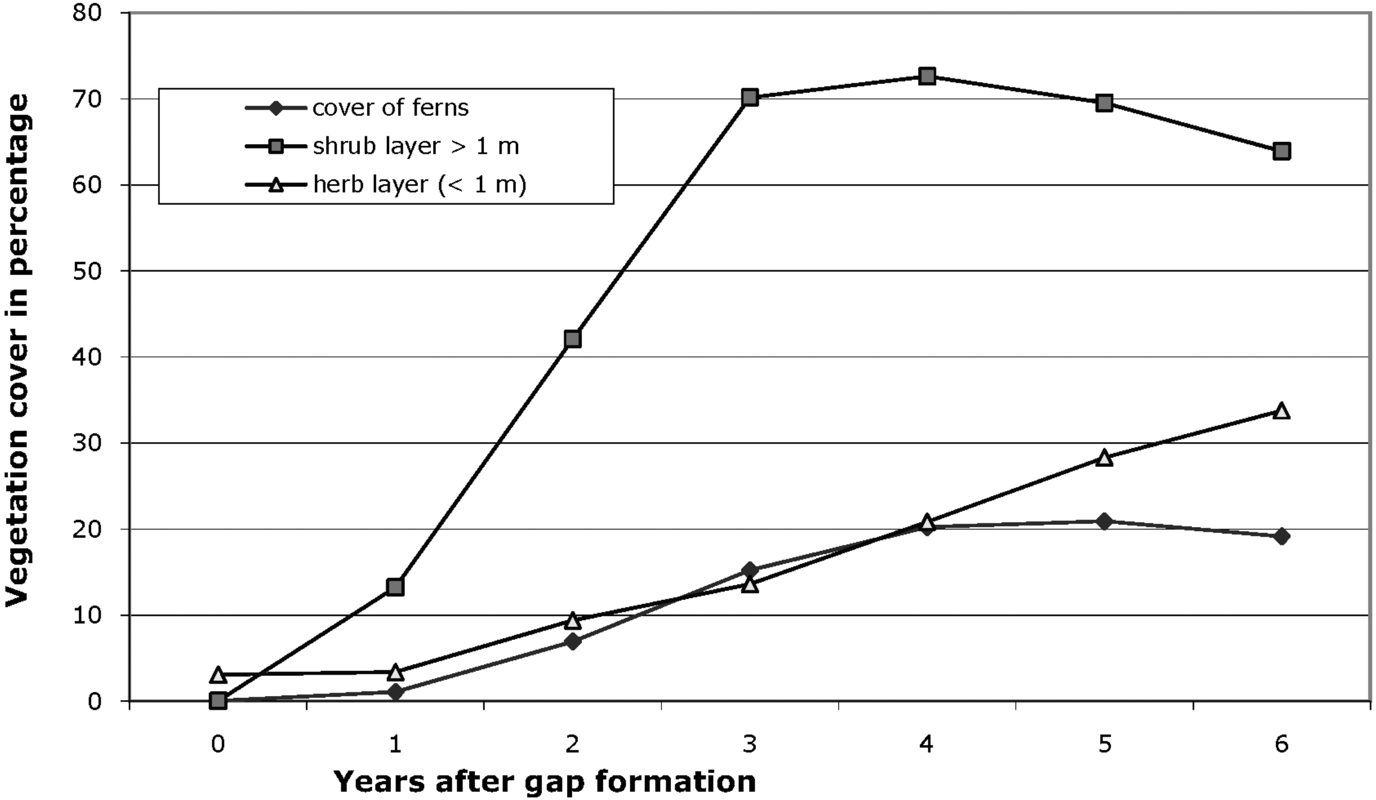

Figure 3. Change in cover layers (average values) during 7 years in woodland gaps in beech stands on boulder clay. The layer of < 1 m comprises the herb layer including recruiting trees, the layer > 1 m comprises the initial tree layer and shrub layer. Data for the sixth year are based on nine gaps (years 1-5 based on 12 gaps). The x-axis gives the number of growing seasons after gap formation.

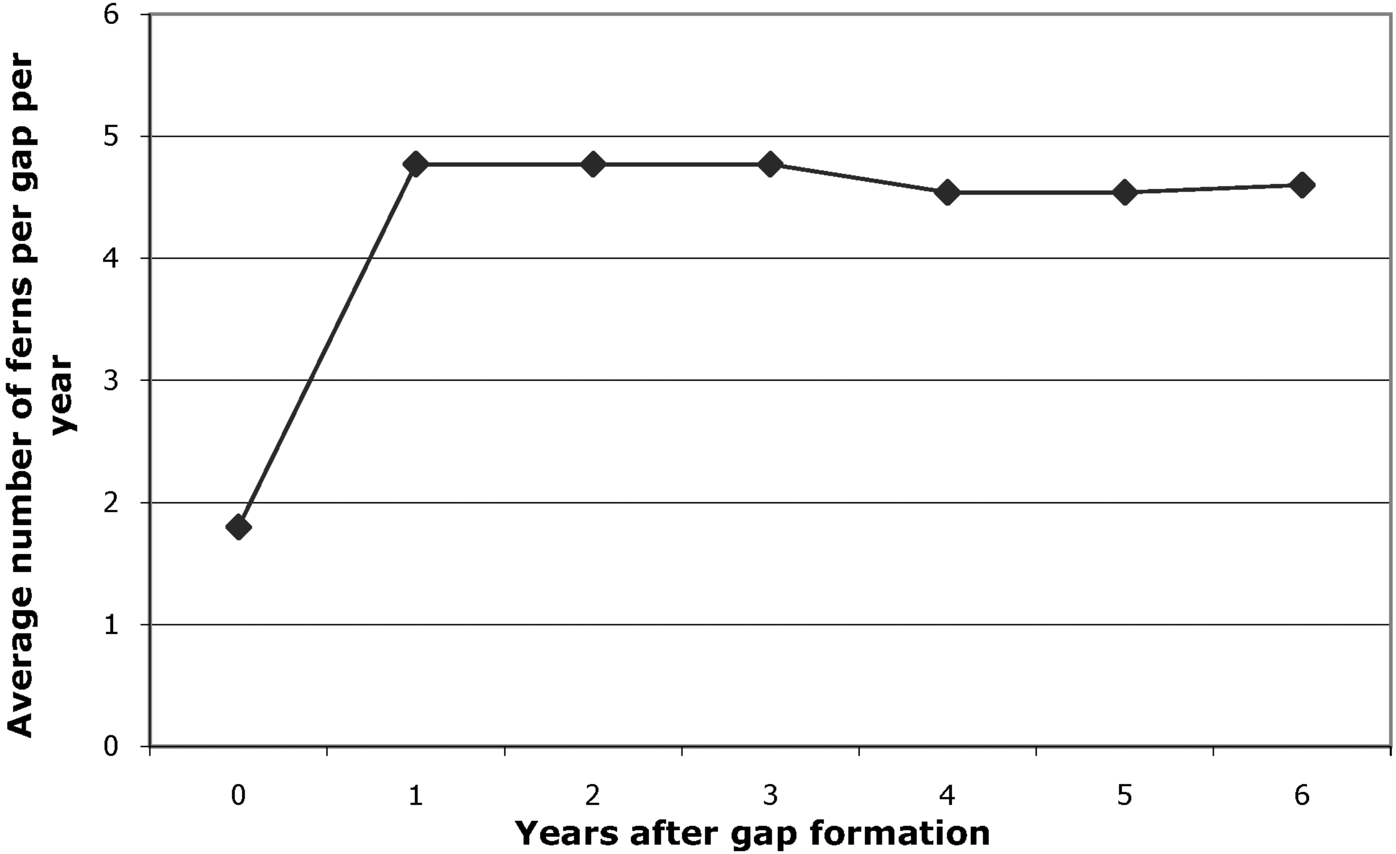

Figure 4. The average number of fern species found in the woodland gaps each year from the year before gap formation (year = 0) to six years after gap formation. Data for the sixth year are based on nine gaps (instead of 12).

0.5 n.s), but when densities were corrected for the area of both habitats there was a preference for the drainage trench habitat ($\chi^2 = 12.7$ $p < 0.001$). Plants of *Thelypteris palustris* showed no preference, while *Equisetum telmateia* was found only on the woodland floor. Fertility within four years after establishment was observed only in the group of the most common species (present in more than 49% of the gaps). Some plants of *Athyrium filix-femina* reached the adult phase in the third season after cutting and became co-dominant in five out of the 12 gaps, growing alongside horsetails, grasses and bryophytes.

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 almost exclusively within this line. *Gymnocarpium dryopteris* and *Matteuccia struthiopteris* were found within the 75% shade line (Figure 2) 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 shade in the summer period ($\chi^2 = 10.8$ $p < 0.01$). Three species of *Equisetum* became established: *Equisetum arvense* was co-dominant with *Athyrium filix-femina* in three gaps, *Equisetum telmateia* colonised neutral boulder clay in one gap, while *Equisetum fluviatile* established within the 100% shade line in two gaps. Forty-two gaps were created in other stand and soil types. Sandy soils with low pH were poor in fern species. *Dryopteris dilatata* was present prior to tree felling and increased afterwards. In a stand of *Carpinus betulus* on boulder clay, gaps were created by bark ringing trees. Although this led to a gradual increase of light intensity, no ferns or horsetails established in these gaps, but young trees, already present in high density prior to the girdling, formed a dense stand.

DISCUSSION

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. We had expected that ferns would not expand as they had been scarce prior to the gap formation, yet they proved to be successful both in cover and number of species. On boulder clay, *Fraxinus excelsior* recruits successfully, but the >1m saplings were intensely browsed by Roe Deer in the first five years, preventing a dense growth and facilitating vegetation with local dominance of *Athyrium filix-femina* at the southern parts of gaps. Other ferns were also present from the outset with, e.g., *Athyrium filix-femina* outcompeting *Gymnocarpium dryopteris*. On the boulder clay, ten ferns and three species of horsetail established; this included species not previously recorded in the area. From records of young sporophytes it appears that all these species established from spores in the first year following tree felling and soil disturbance. Spores of these species may have been derived from dry and wet spore rain to colonise the disturbed areas. However, there was a high density (establishment of >50 plants per m^2) of *Athyrium filix-femina* in five out of 12 gaps. As *Athyrium filix-femina* grew only at a low density prior to tree felling there may have been an extensive accumulation of spores preserved in the spore bank. Viable spores of *Athyrium filix-femina* were reported to be the most frequent type of fern spore in the soil spore bank in a boreal old-growth spruce forest, yet there were no plants in the herb layer (Rydgren & Hestmark 1996). In contrast in the Kuinderbos fern colonisation by numerous fern species (with no extensive spore bank) always started with one fern individual at a particular site, followed in subsequent years sometimes by mass colonisation in the spore shadow of adult plants (Bremer 2007).

In the group of less common fern and horsetail species, the almost simultaneous colonisation within two years suggests that the spore bank may play a dominant role rather than spore rain; the spore bank here has had c. 60 years to accumulate. There appears to be no relationship between the burst of colonisation in the new gaps and the fern diversity of surrounding populations. This contrasts with the long term study (50 years) of fern colonisation in the Kuinderbos (also on a former sea floor), where Bremer (2007b) showed that colonisation of 25 fern species was correlated with the population size within 50 km from the forest.

Gymnocarpium dryopteris, *Matteuccia struthiopteris*, *Dryopteris cristata* and *Thelypteris palustris* had not previously been recorded from boulder clay in this kind of habitat within the Netherlands. All three species were able to colonise the bare soils, and thrive until eliminated by competition. A similar observation was made for a group of seed plants in the gaps, with establishment of pioneer species (e.g. *Puccinellia distans*, *Juncus gerardii*). These plants established on the boulder clay between the period of reclamation of the sea floor (1942) and afforestation (c. 1948) and must have survived the period 1948 – c. 2000 through a seed bank.

Gaps 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 sunlight, 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 by the canopy in these gaps and without tree transpiration, the soil in these 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, the diameter of most gaps is 1-2 times the tree height which is an optimal habitat for many terrestrial woodland ferns and 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. The results of this study show that the less common species were confined mostly within the 100% shade line; this indicates that they prefer a constantly wet soil and high air humidity. Comparing gaps formed through tree-felling with those developed through bark-ringing demonstrates that cutting and concomitant soil disturbance is important for the germination of fern spores. *Equisetum fluviatile*, *E. telmateia* 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 achieved 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. When constant high humidity can be assured, one might expect species such as *Blechnum spicant, Osmunda regalis* and *Oreopteris limbosperma* to establish. *Matteuccia struthiopteris* is a common garden plant in the Netherlands, and occurrences of *M. struthiopteris* outwith gardens are nearly always related to garden rubbish deposited at the edge of woodlands by man. The species established for the first time naturally in one of the planted woodlands of E.-Flevoland (province of Flevoland) in 1988 and still grows there. In the Voorsterbos it was recorded for the first time on boulder clay; a habitat not known from neighbouring countries (Bremer 2005).

In the woodland experiment, felling trees in *Fagus sylvatica* stands on boulder clay in order to make gaps facilitated the establishment and expansion of fern and horsetail populations with large differences in microclimate between gaps and the adjacent woodland. It seems likely that the crucial factors are soil composition (weakly acid - pH neutral boulder clay), moisture, and the light regime. Creating woodland gaps allows ferns to gain from their anemochoric dispersal capacity and the cumulative effect of spore dispersal (i.e. spore bank) and from the ability to develop prior to the phase in which seed plants might become dominant. Ferns, horsetails, bryophytes and liverworts are the first to establish before seed plants become dominant. Cutting woodland gaps on soils prone to desiccation would not be beneficial to the fern flora.

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