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

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Abstract Our objective was to analyze which factors are critical for the dynamics of terrestrial *Asplenium scolopendrium* populations at the northern edge of its distribution. Therefore, a long-term study (1978–1999) on the performance and demography of this fern species has been carried out in three different forest stands (*Picea sitchensis* with *Fagus sylvatica*, *P. sitchensis* with thinning, and *Fraxinus excelsior*) in the Netherlands. We used the recorded demographic data to parameterize 37 transition matrices. The number of frost days in severe winters correlated closely with frond damage and resulted in increased mortality and retrogression. Landslip on the trench banks and intraspecific competition were also found to increase mortality. In the *F. excelsior* plot, plants grew faster and bigger, produced more fronds and formed a more closed fern cover than in the *P. sitchensis* stands, likely due to higher light levels. Life-table response experiments revealed that reproduction contributed greatly to the differences in projected population growth rates: reproduction was importantly higher in the *F. excelsior* and in the thinned *P. sitchensis* plots than in the *P. sitchensis*–*F. sylvatica* plot. These differences can be attributed to an initial difference in light climate and to the accumulation of *F. sylvatica* litter which reduced recruitment. Recruitment occurred on bare soil but also in open moss carpets. We

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expect that the fern *Asplenium scolopendrium* will profit at its northern distribution edge when severe winters will occur less frequently, which is one of the expectations for global climate change.

Keywords Climate change ·
Life table response experiment (LTRE) ·
Long-term demography · Recruitment · Vital rates

Introduction

Demographic studies are useful when investigating a species response to the changes in its habitat, such as those occurring as a result of succession or nature management (Oostermeijer et al. 1996; Jongejans and de Kroon 2005; Lehtilä et al. 2006). Especially, long-term demographic studies can reveal how populations respond to these abiotic and biotic changes in their environment as well as to climatological fluctuations (Økland 1997). However, long-term demographic observations in plants are scarce, which limits the analysis of the effects of rare 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 and Leopold 1992; Pfeifer et al. 2006). However, more long-term datasets and detailed analysis of the pathways through which climate variation impacts population growth are needed to increase a detailed understanding of how weather drives plant population dynamics. Such knowledge is critical if we want to be able to predict how species and ecosystems respond to future climate change (Parmesan and Yohe 2003).

With the rise in temperature, Atlantic species can be expected to 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 few studies have been done on species growing at the edge of their range (e.g., Willems and Bik 1991; Bridle and Vines 2007). A critical climatological factor in this respect 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 plant growth (Sakai and Larcher 1987). However, very few studies (see e.g., Pfeifer et al. 2006) have used long-term demography datasets and population models to examine how different effects of frost and other variables like precipitation affect population growth through various life cycle components (i.e., vital rates: survival, growth and reproduction). Such population-level analyses are important because environmental impacts on a particular vital rate only matter when the population growth rate is sensitive to changes in that vital rate (Horvitz et al. 1997; Jongejans et al. 2008a, b).

In this paper, we therefore investigate the impact of various abiotic (e.g., frost, precipitation) and biotic (e.g., cover by the litter layer and the herb layer) environmental factors on the vital rates and resulting population dynamics of the fern *Asplenium scolopendrium* at the northern edge of its distribution. To that end, we analyse 37 parameterised matrix population models spanning two decades from 1978 until 1999. In order to augment knowledge of conservation management of *A. scolopendrium* populations, we also wanted to get more insight into the response of this species to the light climate in different forest stands and after thinning management. The variation in light intensity is known to be the dominant factor for the distribution and variation in performance in species which grow in the herb layer on the woodland floor (Ellenberg 1982; Barkham 1992; Stoutjesdijk and Barkman 1992; Valverde and Silvertown 1998). We therefore compared fern populations growing in two different stand types and one thinned stand.

Materials 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. *Asplenium 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 et al. 1984). It can be especially abundant in mixed deciduous woodlands in the western part of the UK. In the Netherlands, *A. scolopendrium* is

particularly known as a wall-dwelling species, and sites where plants grow terrestrially are restricted to dunes with calcareous sand (Weevers et al. 1948). However, in the first half of the 1960s, the first terrestrial specimen established in a forest 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 (Bremer 2007). In subsequent years, the species also colonized six other planted woodlands in the same area.

Demography

The demography of *A. scolopendrium* was studied in three permanent plots on trench banks in three contrasting parts in the forest of Kuinderbos, the Netherlands (52°46′N, 5°49′E). The first plot (southwest facing and 3 m × 0.75 m = 2.25 m^2 in size) in a *Picea sitchensis–Fagus sylvatica* stand (PF) was laid out in a site with a high density (30 m^{-2}) of plants. 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 ca. 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 (southwest facing and 2.5 m × 0.9 m = 2.25 m^2) 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 (northeast facing and 1.1 m × 1.1 m = 1.21 m^2) 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 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, with only a shallow water layer (maximum 20 cm) in the trenches in winter. At the latter two sites, the proportional light intensities at the soil were higher in winter than in summer (see Table 1 for details and data of light measurements performed in the plots in 1990 and 1998). Incoming light increased between 1990 and 1998, due to natural gap formation in the 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 the sporangia of adult plants ripened and the sporelings had emerged from the fertilized prothallia that resulted from spores produced in the previous year. In September, hardly any new sporelings emerge. We measured the number of fronds per plant, the number of fertile fronds per plant, and the maximum length of a frond per plant (plant height).

Table 1 Characteristics of the three permanent plots for recording *Asplenium scolopendrium* in the Kuinderbos

Stand	Study period	% Light in March	% Light in August
Picea–Fagus (PF)	1978–1999	6.2 ± 1.7 (1990)	1.4 ± 0.3 (1990)
		27.0 (1998)	11.1 ± 1.9 (1998)
Picea thinned (Pthin)	1989–1998	–	3.4 ± 3.1 (1990)
		6.0 ± 0.4 (1998)	11.6 ± 0.6 (1998)
Fraxinus (Fr)	1983–1990	16.2 ± 7.4 (1990)	3.1 ± 0.6 (1990)
		42.2 ± 8.6 (1998)	11.9 ± 6.0 (1998)

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). Light was quantified in March and August in 1990 and 1998 by using a photometer and measuring the incoming light reflected by a white piece of board during with a cloudless sky between 1100 and 1400 hours. Light is expressed as a percentage of the incoming light, with a site without shade as reference ± SD (measuring year in parentheses) ($n = 6$–10 measurements per site per date in most cases). A green spruce aphid (*Elatobium abietinum*) outbreak likely caused the relatively high light level in August 1998 in the Pthin plot, whereas otherwise light levels were always lower in August than in March

After severe winters, the survival of plants was monitored and frost damage per plant was calculated in May, before the sprouting of new fronds, by estimating the area per frond with necrosis. Frond area per plant was calculated for 7 years with the formula $LA = a \, (0.68 \, k^{1.5})$ ($n = 23$, $R^2 = 0.97$, $P < 0.001$) with LA = total area of the frond blades per plant, k = average length of the fronds and a = number of fronds per plant. The average length of the fronds (i.e., stipe plus blade) was based on the maximum frond length per plant (L) using a regression model: $k = 0.65 \, L - 0.86$ ($n = 25$, $R^2 = 0.97$, $P < 0.001$). During the annual monitoring, causes of mortality were deducted. For example, some sporelings and juveniles disappeared after signs of frost damage, herbivory, or desiccation. The microhabitat (i.e., presence of neighboring plants in a 1-cm radius) surrounding recruiting sporelings was also recorded.

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). We present demographic data from three different forest types yielding a total of 37 parameterized transition matrices for *Asplenium scolopendrium*. Within its life cycle we quantify five stages:

1. *sporelings*: small plants that emerge from the prothallium (after fertilization)
2. *juveniles*: plants with a maximum length of the fronds between 2 and 10 cm and which have not sporulated yet in their life
3. *subadults*: plants with a maximum length of the fronds 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 the following spring (Page 1982). They either germinate the next spring or summer, are added to the sporebank, or die (Lindsay and Dyer 1996). We assumed that most sporelings are generated from spores within 1 year. Spores and prothallia were therefore not modeled as separate classes.

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

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

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). Each element of the transition matrix is defined by a combination of vital rates (see Table 2 for a full list of vital rate codes and explanations): σ_j is the

Table 2 Vital rate means for the three plots and various time periods

Vital rates	Years	Pthin	Fr	PF				
		1989–1998	1983–1990	1978–1999	1989–1998[a]	1983–1990[a]	1978–1987[b]	1978–1985[b]
Reproduction: #recruits$_{t+1}$ per adult$_t$	φ	3.242	3.308	1.268	0.745	1.230	2.056	2.542
Survival of sporelings	σ_1	0.701	0.787	0.684	0.658	0.672	0.718	0.808
Survival of juveniles	σ_2	0.777	0.874	0.790	0.716	0.784	0.834	0.871
Survival of subadults	σ_3	0.891	0.866	0.814	0.820	0.812	0.808	0.802
Survival of adults	σ_4	0.758	0.915	0.903	0.880	0.939	0.903	0.917
Survival of postadults	σ_5	0.806	0.643	0.805	0.745	0.819	0.829	0.835
Growth of surviving sporeling$_t$ to juvenile$_{t+1}$	γ_{21}	0.569	0.505	0.433	0.429	0.427	0.441	0.469
Growth of surviving sporeling$_t$ to subadult$_{t+1}$	γ_{31}	0.016	0.016	0.012	0.007	0.003	0.022	0.028
Retrogression of surviving juvenile$_t$ to sporeling$_{t+1}$	ρ_{12}	0.039	0.044	0.052	0.069	0.063	0.047	0.039
Growth of surviving juvenile$_t$ to subadult$_{t+1}$	γ_{32}	0.388	0.394	0.262	0.284	0.294	0.212	0.210
Growth of surviving juvenile$_t$ to adult$_{t+1}$	γ_{42}	0.025	0.022	0.037	0.014	0.018	0.066	0.079
Retrogression of surviving subadult$_t$ to sporeling$_{t+1}$	ρ_{13}	0.060	0.000	0.006	0.001	0.000	0.011	0.014
Retrogression of surviving subadult$_t$ to juvenile$_{t+1}$	ρ_{23}	0.123	0.123	0.220	0.286	0.176	0.186	0.168
Growth of surviving subadult$_t$ to adult$_{t+1}$	γ_{43}	0.301	0.474	0.404	0.437	0.396	0.320	0.370
Growth of new recruit to juvenile$_{t+1}$	γ_{24}	0.038	0.005	0.033	0.059	0.006	0.019	0.024
Retrogression of surviving adult$_t$ to postadult$_{t+1}$	ρ_{54}	0.458	0.124	0.272	0.272	0.214	0.333	0.322
Growth of surviving postadult$_t$ to adult$_{t+1}$	γ_{45}	0.090	0.214	0.410	0.453	0.336	0.376	0.411

Pthin Population in a thinned *Picea* woodland, *Fr* population in a *Fraxinus* woodland, *PF* population in a *Picea–Fagus* forest

[a] Subset of years to match the observation periods in the other two populations

[b] Same number of years from the start of the monitoring to compare the initial observation period with those of the other two populations (see Fig. 4)

survival rate of individuals in stage j, ϕ the reproduction rate of adults, γ_{ij} the growth rate of surviving individuals progressing from stage j to stage i, and ρ_{ij} the retrogression rate of surviving individuals from j to i (i.e., shrinkage of plants to smaller-size classes or adults becoming post-adults). 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 modeled as 1 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 analyzed how variation in the vital rates caused variation in λ, and how environmental factors related to the λ variation contributions. 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:

$$\lambda^{(q)} \cong \lambda^{(\cdot)} + \beta^{(q)} \qquad (2)$$

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):

$$\tilde{\beta}^{(q)} = \sum_k \left(\tau_k^q - \tau_k^\cdot \right) s_{\tau_k} \Bigg|_{\frac{1}{2}(A^q + A^{(\cdot)})} \qquad (3)$$

in which τ is the kth vital rate of the transition matrix (Eq. 1), $\tau_k^{(\cdot)}$ the overall mean of the vital rates, and $s_{\tau k}$ 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 by 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 mean vital rate values (data from the same period only: 1989–1998) from the reference PF stand. The site effect α was defined as follows:

$$\tilde{\alpha}^{Pthin} = \sum_k \left(\tau_k^{Pthin} - \tau_k^{PF} \right) s_{\tau_k} \Bigg|_{\frac{1}{2}(A^{Pthin}+A^{PF})} \qquad (4)$$

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 (mean vital rates calculated over the period 1983–1990):

$$\tilde{\sigma}^{Fr} = \sum_k \left(\tau_k^{Fr} - \tau_k^{PF} \right) s_{\tau_k} \Bigg|_{\frac{1}{2}(A^{Fr}+A^{PF})} \qquad (5)$$

By comparing the plots with vital rates means calculated over exactly the same years, we controlled for inter-annual climatological differences. However, all three populations showed an increase in size after the monitoring started (Fig. 1). To control for this initial population growth phase, we also compared the vital rate means of the Pthin and Fr plots with the PF means calculated over equal numbers of years from the beginning of the monitoring in the PF plot.

Habitat traits

Cover of the herb and *F. sylvatica* litter layer were estimated annually. The severity of the winters was summarized in the number of frost days. These are defined as days on which the temperature does not exceed 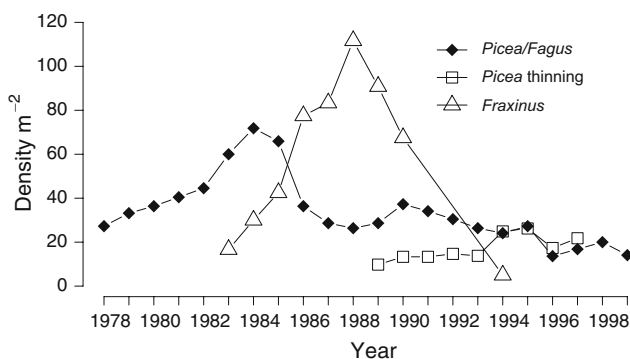0°C. Data on temperature and rainfall were obtained from www.knmi.nl and were interpolated using data from weather stations Eelde and De Bilt in the Netherlands. As precipitation parameters, we used total annual rainfall (mm) during the preceding year and total rainfall during the main growing season when water is most likely to be limiting, separated in spring (April) and summer (May–July). Snow layer depth was measured at 10 random locations among the fern plants in each of the plots after heavy snow fall in 1985.

Data analysis

For the PF plot, 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, assuming that no autocorrelation occurred among the vital rate contributions of subsequent years. The following explanatory variables were used in these regression models: the number of frost days per winter, the percentage soil coverage by the *F. sylvatica* litter layer and the herb layer, total annual rainfall, total spring rainfall, and total summer rainfall. Linear regression was also used to quantify frost damage in relation to the severity of winters. The total area of the frond blades (in cm^2) was ^{10}log transformed to improve normality for the analysis of correlation with frost damage. Differences between plots in snow cover and fertility were tested by the *t* test, differences in plant height and number of fronds per plant with the Mann–Whitney test because these latter variables were not normally distributed. Chi-square analysis was used to test for differences among the three plots in the microhabitats where sporelings were found and in the causes of plant mortality. 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 3,000 times (Efron 1982). Half-life was based on the survival of cohorts with data of all cohorts summed.

Results

Population dynamics

The number of plants in plot PF increased from 1978 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 from 1989 until 1994. Plot Fr showed a rapid population increase from 1983 until 1988, with a maximum density of 112 plant m^{-2} and a subsequent decline (Fig. 1). Sporelings and juveniles made up the largest proportion of the population in the above-mentioned years of population growth (on average 74%, 68%, and 81% in plots PF, Pthin, and Fr, respectively).

Fig. 1 The total density of plants of *Asplenium scolopendrium* in the three monitored plots

After the growing phase, the population in plot PF comprised all phases (on average: 32% sporelings, 25% juveniles, 9% subadults, 22% adults, and 11% postadults), In the last years of monitoring in plot Pthin, sporulating adults were absent. In the declining population phase, the number of individuals in all stages decreased, while a few large adult plants started to become responsible for much of the fern cover in the plots.

The age was calculated for plants whose moment of establishment as sporophyte was known. The average half-life was 1.8 years in plot PF, 1.7 years in plot Pthin, and 2.8 years in plot Fr (Table 3). The age of the ferns shows a skewed distribution: many plants were short-lived, few plants became old. Adult plants became fertile at an age of 3–10 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.

Table 3 Longevity, fertility and plant performance of the three populations monitored

	PF$_1$	Pthin	PF$_2$	Fr
Longevity				
Number of plants	177	114	299	161
Half-life (in years)	1.64	1.67	1.80	2.81
Confidence interval half-life (min)	1.38	1.43	1.64	2.55
Confidence interval half-life (max)	1.93	1.94	2.01	3.21
Fertility				
Total number of adult plants per plot	6	11	13	21
Range of years before plants become adults	4–8	3–10	4–8	3–6
Average age at which plants become adult	6.0	4.5*	6.3	4.0***
SD	1.9	1.4	1.5	0.9
Plant performance				
Plant height (cohort, in the fifth year)	12.9	17.6 ns	9.0	31.3***
SD	9.0	8.2	6.6	22.4
Number of fronds (cohort, in the fifth year)	4.4	3.9 ns	4.1	7.1*
SD	1.6	1.4	2.2	6.4

In order to compare plots over the same time periods we made subsamples (PF$_1$ and PF$_2$) of the PF data to match respectively the 9 years of data from the Pthin plot and the 8 years of data from the Fr plot

Differences in the average year of becoming adult, plant height and number of fronds per plant were tested

SD Standard deviation. bootstrapped 95% confidence intervals are given for the half-life estimates

* $P < 0.05$, *** $P < 0.001$, ns not significant

Abiotic and biotic environmental impacts 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. 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, that of the σ contribution 0.080, that of the γ contribution 0.046 and that of the ρ contribution 0.023. This shows that the strongest influence on the variation in λ was variation in survival, followed by the variation in reproduction.

Good and poor years alternated irregularly (Fig. 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 4). The F. sylvatica litter layer also had a significantly negative but smaller effect, whereas rain from May to 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 influenced the population growth rate by reducing fern survival and increasing the retrogression of surviving ferns. Among winters with, on average, more than 15% of the frond area showed signs of necrosis, the percentage of frond area damaged per plant in the PF plot was increasingly correlated with plant growth as measured by the annual change in frond area: log (LA_t/LA_{t-1}) as winter become harsher (Table 5). The number of frost days per winter and frond damage were closely correlated ($R^2 = 0.96$, $n = 7$ years).
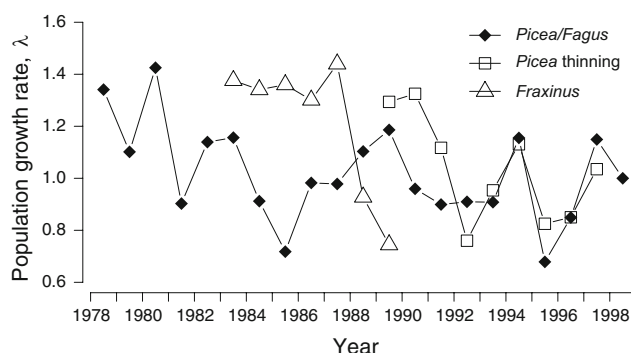

Fig. 2 Projected growth rates (λ) of three Asplenium scolopendrium populations calculated from year-to-year transition matrices

Table 4 Results of multiple linear regressions which analyzed the LTRE year effect (β) and contributions of the combined sexual reproduction (ϕ), survival (σ), growth (γ) and retrogressin (ρ) rates to the year effects in plot PF based on 20 years of monitoring

	Year effect, β			φ Contribution			σ Contribution			γ Contribution			ρ Contribution		
	Effect	t		Effect	t		Effect	t		Effect	t		Effect	t	
Frost days (no.)	−0.115	−3.59	**			ns	−0.070	−5.49	***			ns	−0.020	−4.80	***
Litter layer (% cover)	−0.004	−2.83	*	−0.002	−3.15	**	−0.002	−3.09	**			ns			ns
Rain May–July (mm)	0.001	2.25	*			ns	0.001	3.18	**			ns			ns
Herb layer (% cover)			ns			ns	−0.002	−1.86	+			ns			ns
Rain April (mm)			ns			ns						ns			ns
Rain whole year (mm)			ns			ns						ns			ns

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

Table 5 Frost damage in plot PF in five winters with necrosis measurements

Winter	Number of frost days	Frost damage	R^2	Mortality
1978–1979	32	65	0.36**	12
1979–1980	8	16	0.08*	11
1980–1981	3	13	<0.01	8
1981–1982	18	35	0.07*	14
1985–1986	22	39	0.07*	38

Frost damage was quantified by the average percentage necrosis per *Asplenium scolopendrium* plant. R^2 is the proportion of the variability in the annual change in frond area (log (LA_t/LA_{t-1})) per plant that is accounted for by the damaged frond area damaged per plant. Mortality is the percentage of plants that died in winter

* $P < 0.05$, ** $P < 0.01$

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 *F. sylvatica* litter layer, which showed an inverse correlation. The herb layer did affect the survival, but was not significantly related to the overall year effect.

When we examined the separate effects on λ of frost days, *F. sylvatica* litter, May–July rain, and herbs, only the number of frost days showed a significant, inverse relationship (Fig. 3). The first year, from 1978 to 1979, was exceptional: that 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 *F. sylvatica* litter layer or through increasing light levels. In the PF plot, the *F. sylvatica* litter layer did indeed increase from 1978 (10% cover) to the late 1990s (70% cover), and litter cover significantly reduced the reproduction and survival contributions to λ (Table 4). There was no cover of leaf litter of deciduous trees in both other plots. Light availability increased in all plots during the study period, both due to thinning and due to natural increases in canopy gaps (Table 1).

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. 4a) revealed an overwhelming contribution from the difference in reproduction, which was higher in the thinned forest ($\phi = 3.24$) than in the undisturbed forest ($\phi = 0.75$; Table 2). When the same number of years were compared from the start of monitoring in each of the two plots (controlling for the initial population growth phase), the difference in ϕ still made the largest positive contribution (Fig. 4b) even though reproduction was also important in the initial growth phase of the population in plot PF. Interestingly, λ was very similar between the two populations in the last 5 years (Fig. 2), perhaps because the initial effects of thinning were less prevalent after 4 years.

The comparison with the fern population in the Fr plot in the period (1983–1990) showed similar trends: λ was lower in the *Picea–Fagus* plot (1.01 vs. 1.24). The main reason for the difference in projected population growth rate was again a higher reproduction rates (mean $\phi = 3.31$ vs. 1.23: see Fig. 4c and Table 2): plants were taller and consisted of significantly more fronds in the Fr plot compared to the plants in the PF plot (Table 3). Larger reproduction rates were also important when we controlled for the initial population

Fig. 3 Relationship between abiotic [number of frost days (**a**), rain (mm) from May until July (**b**)] and biotic [percentage coverage of the litter (**c**) and herb (**d**) layer] factors and the projected growth rate (λ) of the *Asplenium scolopendrium* population in the *Picea–Fagus* forest (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)
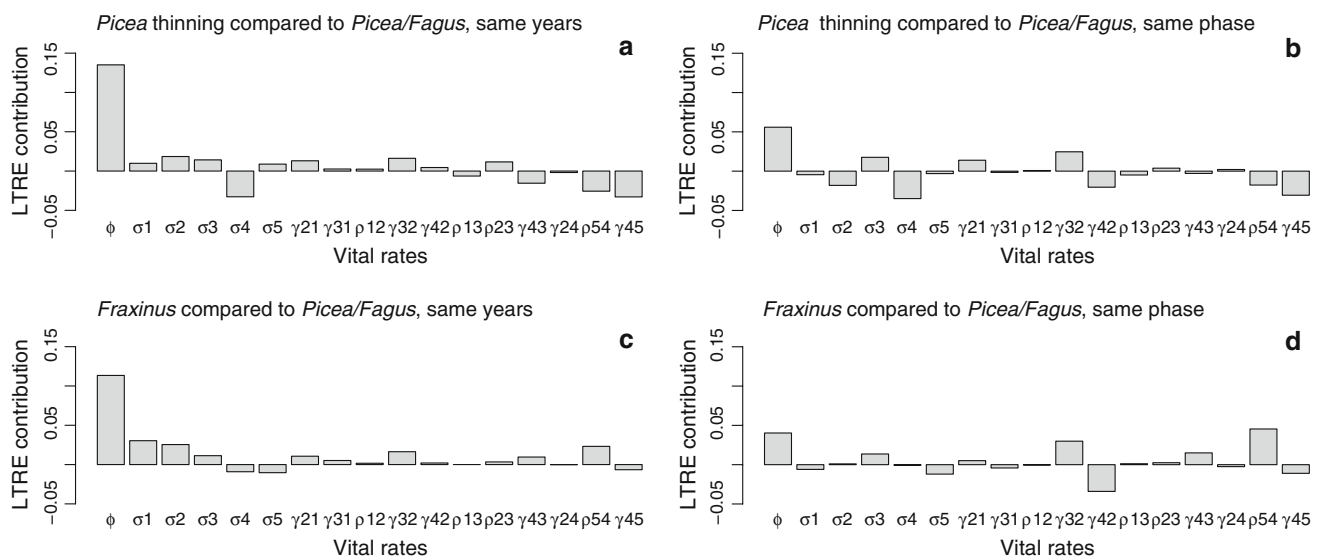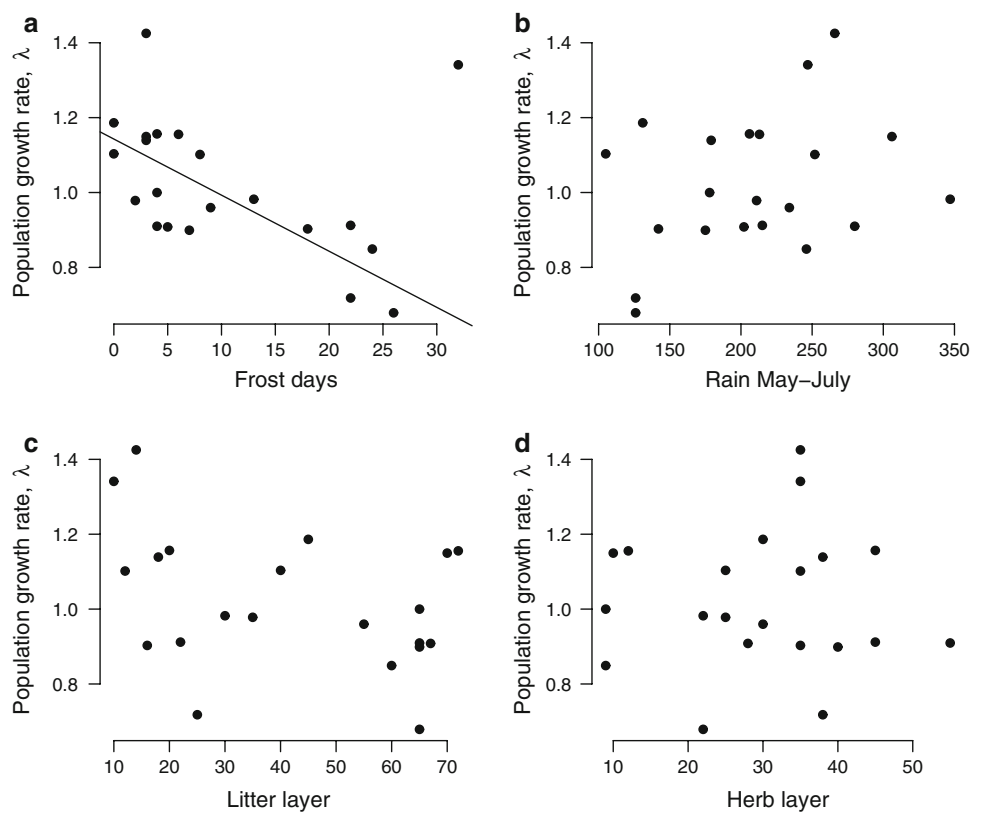
Fig. 4 Vital rate LTRE contributions showing how differences in vital rates contributed to deviations of the projected growth rate (λ) of the *Asplenium scolopendrium* populations in: **a**, **b** the thinned *Picea* woodland, and **c**, **d** the *Fraxinus* woodland from λ of the *Picea–Fagus* woodland population. Separate sub-samples of the reference *Picea–Fagus* data set were used in the comparisons to match the two shorter

data sets with: **a**, **c** the exact same years or **b**, **d** the same number of years from the beginning of the monitoring in each population. Equation 1 shows how sexual reproduction (ϕ), survival (σ), growth (γ), and retrogression (ρ) define the annual transitions between the life stages

growth phase, although the increase in the juvenile-to-subadult-growth rate (γ_{32}) and the decrease in the retrogression-to-postadult rate (ρ_{54}) contributed as much to

the difference in λ, while the lower juvenile-to-adult-growth rate buffered the higher λ for the Fr plot somewhat (Fig. 4d).

Table 6 Causes of mortality (in percentages) of *Asplenium scolopendrium* monitored in the Kuinderbos

	PF	Pthin	Fr	Total
Frost	39.7	38.6	8.0	31.2
Intra-specific competition	6.8	5.6	47.8	17.5
Landslip 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
Mortality cause unknown	40.8	52.3	40.5	42.3
Total number of observed deaths	365	88	163	616

All years of monitoring are incorporated in this table. Frost damage data are based on field observations and regression analysis

PF Plot in *Picea sitchensis–Fagus sylvatica* stand, *Pthin* plot in *Picea sitchensis* stand, *Fr* plot in *Fraxinus excelsior* stand

Causes of mortality

Over the course of the study, 616 plants died for significantly different reasons in the three plots (Table 6; $\chi^2 = 161$, $P < 0.001$, with 'litter accumulation', 'herbivory', and 'dessication' added to the unknown mortality causes to deal with too low numbers for the analysis). The most important factor (39%) in the PF and Pthin plots frost damage, although only 8% of fern mortality was due to frost in the Fr plot. *Fagus sylvatica* litter accumulation and land slip of the trench bank also played a role in that plot. Crowding of plants in all stages was the main cause of mortality in the Fr plot. In the two *Picea sitchensis* plots (PF and Pthin), crowding of adult plants played a less important role. Mortality due to crowding probably also occurred in the sporeling phase, but was not quantified.

Conditions for establishment

The composition of the micro-vegetation in which sporelings were found differed significantly between the three plots (Table 7; $\chi^2 = 112$, $P < 0.001$, with 'litter' added to the 'other vegetation' category). In all the plots, recruitment took place in the *Fissidentietum taxifolii* bryophyte community or in the community of *Fissidens bryoides*. 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 living or dead adult plants. 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 *Eurhychium praelongum*, which was also important as microhabitat for recruitment.

Table 7 The vegetation (in percentages) within a radius of 1 cm around *Asplenium scolopendrium* sporelings in three plots in the Kuinderbos

	PF	Pthin	Fr	Total
Fissidentietum taxifolii/ Fissidens bryoides com.	27.9	44.4	33.3	33.5
Bare soil	33.8	0.0	9.3	16.8
Open *Brachythecium rutabulum* mat	1.5	0.0	45.3	19.6
Open *Eurhynchium praelongum* mat	1.5	27.8	12.0	11.2
Tree leaf litter	5.9	2.8	0.0	2.8
At the base of adult *Asplenium scolopendrium*	29.4	13.9	0.0	14.0
Other surrounding vegetation	0.0	11.1	0.0	2.2
Total sporelings studied	68	36	75	179

Litter in the Pthin plot consisted of *P. sitchensis* needles. See Bremer (1999) for a full description of the moss communities

PF Plot in *Picea sitchensis–Fagus sylvatica* stand, *Pthin* plot in *Picea sitchensis* stand, *Fr* plot in *Fraxinus excelsior* stand

Discussion

Effects of frost on plant performance and population dynamics

Our analyses show that frost significantly reduces the projected population growth rate by reducing survival and increasing retrogression (Table 4). Frost has three effects on plant performance: in severe winters, many ferns are killed, while other plants become stunted or even sterile (postadults). The highest mortality was observed in the winter of 1985–1986, when 38% of the plants died (Table 5). In this winter, mortality as high as 88% was recorded within a wall-dwelling population in Langbroek (in central Netherlands) exposed to freezing wind (P. Bremer, unpublished data). The trench-dwelling populations in the Kuinderbos were more protected since wind speeds in these trenches are very low.

In New York, Cinquemani et al. (1988) attributed the variation in population size of *Asplenium scolopendrium* populations to the low amount of snow below *Tsuga canadensis* trees: the soil 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 harsh winter with 22 frost days, frost accounted for 38% of the mortality in the PF plot while mortality due to frost in the more snow-covered plot Fr was much lower

(9%). 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 *A. scolopendrium*, are dormant and have enhanced frost hardiness: Bremer et al. (1984) have reported higher concentrations of the cell membrane phospholipid phosphatidylcholine in fronds of *A. scolopendrium* in winter than in summer.

In the forest where our study was situated, Kuinderbos, frost damage was observed in nine fern species and frost-induced mortality in at least four species (Bremer 2007). But in none of these species was frond damage (necrosis) as pronounced as in *A. scolopendrium*. In *Asplenium trichomanes*, frost did not cause necrosis. However, in this species too, decreases in population size correlated with the number of frost days per winter, although only above a threshold of 15 frost days (Bremer 2004). In *A. scolopendrium*, significant effects of frost damage on frond production (when the average necrosis exceeded ca. 15% of the frond area) occurred in winters with more than ca. 8 frost days.

There are few studies on the impact of frost damage at population level, as long-term demographic studies of plant species are scarce. However, a long-term study by Willems and Bik (1991) attributed high mortality and a low flowering percentage in a Dutch *Orchis simia* population to low winter temperatures. Here, we used matrix models, life-table response experiments, and multiple regression models of LTRE contributions to analyze explicitly through with vital rates frost influenced the projected population growth rate of a frost-sensitive fern at the northern edge of its distribution. This approach is very powerful because it shows directly which impacts of environmental factors on vital rates matter at the population level.

Effects of habitat on plant performance and population dynamics

In the *Picea sitchensis–Fagus sylvatica* plot the projected population growth rate was lower than in the thinned *P. sitchensis* plot or the *Fraxinus excelsior* plot. In both cases, higher reproduction rates (ϕ) were responsible for the differences (Fig. 4). It seems plausible that the dominant factor resulting in differences in demography of the plots is the light climate. Light may also have had a major effect on plant performance. In the Pthin and Fr plots, plants became adult at a younger age than in plot PF (Table 3). In the Fr plot, there is much incoming light in spring prior to frond emergence of *F. excelsior* trees, while in the Pthin plot, thinning caused light intensity to increase initially.

Light intensity increased on the woodland floor in all plots during the 1990s (Table 1). Under such circumstances, it could be hypothesized 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 in plot Pthin where 40% of the plot area was covered by *Eurhynchium striatum* and *Mnium hornum*, which hampered recruitment, suggesting that light limitation as substituted by microsite limitation.

Valverde and Silvertown (1998) showed that light intensity can impact demographic parameters in the understorey herb *Primula vulgaris*. In their study there was a positive correlation between λ and the light intensity caused by higher growth rates in lighter environments. They also reported more recruitment with increasing light, which is consistent with our findings.

Accumulation of *F. sylvatica* litter only played a role in plot PF, where it limited recruitment. 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 *Fagus* litter layer reduced the microhabitat for recruiting sporelings, as prothallia die under litter and spores do not germinate in litter (Bodziarczyk 1992). Adult plants produce their own litter as the fronds fade and droop down over the soil or trench banks. Below adult plants the light climate was restricted: light intensity < 1% (P. Bremer, unpublished data) and wilted fronds accumulated. This has also been observed in other hardy fern species, e.g., *Polystichum aculeatum* and *Polystichum setiferum* (Bremer 1995).

Landslip 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. Peck et al. (1990) reported that freeze–thaw erosion in winter eliminated many gametophytes.

Cinquemani et al. (1988) linked the number of plants of *A. scolopendrium* per site not only to snow cover and light climate but also to drought (or in fact indirectly to the impact of the wind). Although some plants in our plots had desiccated fronds in dry summers, no mortality due to drought was observed. This was probably due to the local conditions: thick layers of fine-grained sand are fed by rising groundwater, which suggests that conditions for fern growth are optimal. Of the three precipitation parameters in our regressions, only early summer (May–July) rainfall was (positively) correlated with population growth (Table 4). This corresponds with *A. scolopendrium* growing optimally under moist conditions (Page 1982).

The Nature Conservancy (1990) argues that bryophyte beds enhance sporeling regeneration by providing a favorable site for fertilization, spore germination, and gametophyte growth. However, in our study, the presence of sporelings was correlated with an open bryophyte vegetation or bare soil that had been concomitantly colonized by *Fissidens* spp. or *Pellia endiviifolia*.

Long-term population dynamics

Most demographic studies do not exceed three or four seasons, yet long-term studies are needed to quantify the effect of extreme weather conditions. With the 21 annual transitions (from 1978 to 1999) in plot PF, we were therefore able to ascertain that the effects of rare cold winters on plant performance are really important for the population dynamics of this fern species at the northern edge of its range. *Asplenium scolopendrium* colonized the Kuinderbos in the first half of the 1960s. The population growth received a setback in the 1980s, when severe winters damaged and killed plants. Since then, the strong increase is concentrated in another part of the *P. sitchensis–F. sylvatica* stand, where the population size increased to more than 10,000 plants after a woodland thinning in 1998. This is consistent with long-term monitoring of *A. scolopendrium* in the cities of Amsterdam (Denters in Maes and Bakker 2002) and Utrecht (Maes and Bakker 2002) which showed that these populations increased tenfold in the period 1987–2000. Long-term monitoring has been carried out for over 70 years on six central New York populations of *A. scolopendrium* var. *americana* (Cinquemani et al. 1988), but no population models have been constructed from those data. None of these six American populations increased at any time as dramatically as the Kuinderbos population has done in recent years.

Global warming and increasing CO_2 concentrations affect plant growth (Cannell 1990), and new lichen and seed plant species from warmer climates have been reported in, e.g., the Netherlands (van Herk et al. 2002; Tamis 2005). Unforeseen additional effects of climate change warrants carefulness with predictions of aspects of climate change on a particular species. However, we expect the frost-sensitive fern *Asplenium scolopendium* to increase at the northern edge of its distribution when we consider (1) the current distribution of *A. scolopendrium*, (2) our data on climate correlations with plant mortality and population dynamics, and (3) expectations of increasing winter temperature in the Netherlands (van den Hurk et al. 2006). Severe winters will still occur sporadically, but our long-term monitoring shows that *A. scolopendrium* populations are able to survive such cold winters and to build up and maintain large populations at the current northern edge of its range.

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