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Nutrient conservation increases with latitude of origin in European *Pinus sylvestris* populations

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Abstract Nutrient availability varies across climatic gradients, yet intraspecific adaptation across such gradients in plant traits related to internal cycling and nutrient resorption remains poorly understood. We examined nutrient resorption among six Scots pine (*Pinus sylvestris* L.) populations of wide-ranging origin grown under common-garden conditions in Poland. These results were compared with mass-based needle N and P for 195 Scots pine stands throughout the species' European range. At the common site, green needle N ($r^2=0.81$, $P=0.01$) and P ($r^2=0.58$, $P=0.08$) concentration increased with increasing latitude of population origin. Resorption efficiency (the proportion of the leaf nutrient pool resorbed during senescence) of N and P of Scots pine populations increased with the latitude of seed origin ($r^2 \geq 0.67$, $P \leq 0.05$). The greater resorption efficiency of more northerly populations led to lower concentrations of N and P in senescent leaves (higher resorption proficiency) than populations originating from low latitudes. The direction of change in these traits indicates potential adaptation of populations from northern, colder habitats to more efficient internal nutrient cycling. For native Scots pine stands, results showed greater nutrient conservation in situ in cold-adapted northern populations, via extended needle longevity (from 2 to 3 years at 50°N to 7 years at 70°N), and greater resorption efficiency and proficiency, with their greater resorption efficiency and

proficiency having genotypic roots demonstrated in the common-garden experiment. However, for native Scots pine stands, green needle N decreased with increasing latitude ($r^2=0.83$, $P=0.0002$), and P was stable other than decreasing above 62°N. Hence, the genotypic tendency towards maintenance of higher nutrient concentrations in green foliage and effective nutrient resorption, demonstrated by northern populations in the common garden, did not entirely compensate for presumed nutrient availability limitations along the in situ latitudinal temperature gradient.

Keywords Scots pine · Nutrient resorption · Climate gradient · Adaptation · Needle longevity

Introduction

Resorption of nutrients from senescing organs has an important role in the plant nutrient economy affecting such key processes as nutrient uptake, competition, productivity and fitness (Chapin 1980; Eckstein et al. 1999; Hörtensteiner and Feller 2002). For example, Lim and Cousens (1986) estimated that in a 46-year-old Scots pine (*Pinus sylvestris* L.) stand in Scotland, nutrient resorption supplies about 55% of nitrogen (N), 64% of phosphorus (P), 56% of potassium (K) and 14% of magnesium (Mg) required for annual aboveground growth. Helmisaari (1992b) estimated that in 15- to 100-year-old Scots pine stands in Finland, retranslocation within the trees supplied between 30% and 50% of N, 23% and 37% of P, 17% and 31% of K and 7% and 20% of Mg required for annual above- and belowground biomass production.

In spite of the expectation that nutrient resorption efficiency (NRE, percentage of the leaf nutrient pool resorbed) will increase with decreasing soil nutrient availability and that plants adapted to low fertility decrease nutrient loss by higher efficiency of resorption, literature reports remain inconclusive. In some studies resorption was found to be more efficient in plants

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growing on infertile soils (Ostman and Weaver 1982; Flanagan and Van Cleve 1983; Boerner 1984; Enoki and Kawaguchi 1999; Hawkins and Polglase 2000; Reich et al. 2001), in others nutrient withdrawal from senescing leaves was higher in more fertile sites (Ryan and Bormann 1982; Chapin and Kedrowski 1983; Nambiar and Fife 1991, Reich et al. 1995), or results were unrelated to soil nutrient availability or inconclusive (Birk and Vitousek 1986; Aerts and De Caluwe 1989; Chapin and Moilanen 1991; Helmisaari 1992b). Inconsistencies in results can originate from variability in sampling protocols, heterogeneity of the controls on resorption, and/or the difficulty in differentiating between phenotypic and genotypic responses of plants to soil fertility (Nambiar and Fife 1991; Pugnaire and Chapin 1993). In the light of the absence of clear evidence for nutrient availability control over NRE, Aerts (1996) suggested that future research should focus on other factors controlling that process.

It is postulated that in habitats with low nutrient availability, selection occurs for plant traits that result in higher nutrient conservation, including longer leaf and root life-span, higher sclerophylly and more efficient nutrient resorption from senescing organs (Chapin 1980; Eckstein et al. 1999). Among habitats where selection for more efficient nutrient resorption can be expected are sites in cold environments of high latitudes or altitudes where low soil temperatures can limit mineralization of organic matter, nutrient release from the mineral soil and biological nitrogen fixation (Körner 1999). Consequently, we hypothesized that genetically based intraspecific differences may exist in the efficiency of nutrient resorption in trees whose geographic range encompasses large-scale climate gradients.

Trees are characterized by wide genetic variation in nutrient concentration, acquisition and productivity (Chapin 1980; Oleksyn et al. 1998, 2002; Raitio and Sarjala 2000). Together with other intrinsic differences in plant traits such as morphology, physiology and biomass allocation, trees can affect nutrient cycling and other ecosystem functions. In previous studies we found that common-garden-grown populations of *Pinus sylvestris* and *Picea abies* originating from latitudinal and altitudinal gradients, respectively, differed in needle macro- and micronutrient concentrations (Reich et al. 1996a; Oleksyn et al. 1998, 2002). These results indicated that plants from cold environments had significantly higher foliage N, P and Mg concentrations when grown in common conditions, and that this may be an adaptive feature that enhances metabolic activity and growth rates under low temperatures of their native habitats (Reich et al. 1996a; Weih and Karlsson 2001).

Given that nutrient limitations and conservation mechanisms can differ along temperature (or latitudinal) climatic gradients (Körner 1999), in this study we assess possible biogeographical differences in NRE in Scots pine (*Pinus sylvestris* L.) trees of wide geographic origin, utilizing a common-garden experiment in western Poland. The natural range of Scots pine is the largest among all

pine species, ranging about 2,700 km in latitudinal, and 14,000 km in longitudinal directions. Within that area of natural distribution, Scots pine occupies a broad range of habitats which encompass a variety of different selection pressures (Giertych and Mátyás 1991; Repo et al. 2001). Gene flow throughout such a vast area is sufficiently restricted to allow genetic differentiation among populations to occur (Wright 1976; Prus-Głowacki 1994).

Owing to the extensive geographic range of Scots pine and broad-scale site and environmental heterogeneity, one effective way to examine intraspecific differences in NRE is in common-garden experiments. In such conditions with uniform soil and climatic factors, and replicate plots it is possible to evaluate and separate genotypic from phenotypic responses. However, a common-garden experiment with diverse populations also introduces photo-periodic, climatic and edaphic factors that can differ from the population's place of origin. Thus we also conducted a literature survey to compare Scots pine foliage and litter concentration of N and P within the European range of Scots pine. Due to importance of foliage longevity in nutrient conservation and litter quality we also analyzed literature reports on needle longevity from the European range of Scots pine. Our study was designed to answer the following questions:

1. Are cold-adapted northern populations of Scots pine more efficient in nutrient resorption than those from southern locations?
2. Are the resorption patterns observed in the common-garden environment similar to those in situ along a temperature gradient in Europe?
3. To what extent do genetic and environmental factors affect foliage nutrient and life span?

Materials and methods

Common-garden experiment

Seeds of Scots pine (*Pinus sylvestris* L.) were collected between 1978 and 1980 in 20 locations in Europe as a part of an international collaborative experiment established under the auspices of the International Union of Forestry Research Organizations. Detailed information about this experiment was presented elsewhere (Oleksyn 1988; Giertych and Oleksyn 1992). In 1984, 2-year-old seedlings of 19 of these populations were planted in the experimental forest, Zwierzyniec, near Kórnik in central Poland (52°15'N and 17°04'E, altitude 70 m). This site consists of seven blocks. Every provenance was planted in three to seven replicated plots (one per block), 7.2 m × 5.2 m. After thinning in 1994, average stocking was 16 trees plot⁻¹ (or 4,328 trees ha⁻¹) (Oleksyn et al. 2000a). Soils at this site are light sands, the chemical properties of which were described in detail earlier (Oleksyn et al. 1999b). The climate of the region is transitional between maritime and continental. Mean annual precipitation is 526 mm and mean temperature 7.7°C, with a mean growing season length of 220 days, calculated as the number of days with mean temperature ≥ 5°C.

Needle nutrient resorption pattern was studied in six geographically diverse Scots pine populations from the continuous part of the European range, which originated in Sweden, Russia, Latvia, Poland, Germany and France (Table 1). For this study we selected

Table 1 The origin of seeds of *Pinus sylvestris* used in the study. Provenances are ordered by latitude of origin

Population no. ^a	Stand origin information					
	Country	Latitude (N)	Longitude (E)	Altitude (m)	Precipitation (mm)	Temperature (°C)
15	Sweden	60.18	15.87	185	608	4.5
3	Russia	58.83	29.12	80	616	5.0
4	Latvia	55.75	26.67	165	619	5.4
7	Poland	51.60	20.20	160	575	7.4
12	Germany	49.50	8.50	97	645	9.6
14	France	48.80	7.78	150	850	10.0

^a SP-IUFRO-82 (Giertych and Oleksyn 1992)

populations representing sites across a large range of mean annual temperatures (from 4.5°C in Sweden to 10°C in France), and latitudes ranging from 60.2 to 48.8°N. Samples of needles of a single needle age class cohort (formed in 1996) were collected once or twice per month (total 47 times) between 8 January 1996 and 7 October 1998. On each sampling date, provenance was represented by samples taken from two trees in each of two different blocks. To avoid excessive defoliation and possible confounding effects of crown position (Höhne and Fiedler 1970; Fiedler and Müller 1973; Finer 1994, but see Helmisaari 1992b), and possible differences in NRE between foliage from high and low crown positions (Staaf and Stjernquist 1986), samples were taken from the sun-lit portion of the crown of different trees each date. In order to prevent potential nutrient leaching losses observed after litterfall in litter traps (Nambiar and Fife 1991), senesced foliage was obtained in 7 October 1998 by shaking cut branches. To reduce the possible effect of diurnal variation in needle mass related to carbohydrate accumulation on foliage nutrient concentration, all samples were taken at the same time of day, approximately 4–5 h after sunrise. After collection the samples were placed on ice in a cooler for transportation to the laboratory (distance of 2 km) for further processing.

Measurements of nutrient concentration, resorption and needle morphology

Nutrients were measured on dried (65°C for 48 h) tissue powdered in a Kikro-Feinmühle Culatti mill (IKA Labortechnik Staufen, Germany). For nitrogen analyses the samples were digested by the micro-Kjeldahl method and processed using a BÜCHI Distillation Unit B-322 (BÜCHI Analytical, Switzerland). Analysis of foliar concentrations of P was done simultaneously with an Inductively Coupled Plasma Emission Spectrometer (ICP-AES, model ARL 3560) at the University of Minnesota Research Analytical Laboratory, St. Paul, Minn., USA (<http://ral.coafes.umn.edu/>). The needle projected area was determined using an image analysis system and the WinSEEDLE Software (Regent Instruments, Quebec, Canada).

Given possible impacts of heterogeneity in both green and senesced tissues on estimates of nutrient resorption, we used three different methods to calculate NRE. The three methods involved (1) estimations of NRE on needle area, (2) TNC-free mass, and (3) by utilizing highly significant relationships between needle LMA (needle dry mass divided by the needle projected area) and green foliage N and P concentration throughout the foliage life span, except for the period of foliage senescence. In (3) the nutrient concentration in mature foliage prior to its senescence was calculated as values predicted from the fitted LMA-needle nutrient equation, and nutrient resorption as a departure between expected and observed values for the senesced foliage LMA. Results were similar regardless of method. In this paper we use estimates based on mean area-based green needle concentrations prior to senescence compared with recently senesced and intact needles.

Nutrient resorption efficiency (NRE) was calculated as:

$$\text{NRE} = \frac{N_{\text{MAT}} - N_{\text{SEN}}}{N_{\text{MAT}}} \cdot 100\% \quad (1)$$

where N_{MAT} is the nutrient concentration in mature foliage prior to its senescence and N_{SEN} is the concentration obtained from the last measurement conducted in autumn in senesced leaves. Since nutrient concentration may vary significantly throughout the life-span of needles due to seasonal changes of tissue nonstructural carbohydrates, increasing lignification, changes of secondary metabolites and nutrient retranslocation from green foliage (Oleksyn et al. 1997, 2000b, 2002) usage of a single reference point for N_{MAT} can affect the final value of NRE (see also Nambiar and Fife 1991). In this study to depict average N and P levels over the needle life-span we used data from all sampling dates except the very youngest and oldest needle ages. Therefore, we used as a reference the average concentration for the period prior to senescence when nutrient concentration was relatively stable (Oleksyn et al. 2002). We determined this period by examining the time course of needle nutrient contents and statistically determine the longest period during which needle age was not a statistically significant ($P > 0.1$) factor in repeated-measures ANOVA. For the N_{MAT} for nitrogen resorption, the average value for the period between May 1997 and June 1998 was used and for phosphorus N_{MAT} the period between January and April 1998 was selected.

Nutrient resorption proficiency (NRP), defined as the absolute level to which nutrients are reduced in senescing leaves (Killingbeck 1996) is based on the mean concentration of N or P in senescent leaves. Consequently, plants with a lower concentration of N or P in freshly fallen litter are defined as being more proficient in terms of nutrient resorption than plants with a higher concentration in litter. Although the term proficiency can be debated for this metric, we use it for consistency and comparison with prior studies.

Measurements of nonstructural carbohydrates

Total nonstructural carbohydrate (TNC) concentrations were determined by a modification of the method described by Haissig and Dickson (1979) and Hansen and Møller (1975). Sugars were extracted from oven-dried (65°C, 48 h) tissue powder in methanol-chloroform-water, and tissue residuals were used for starch content determination. Soluble sugars were determined colorimetrically with anthrone reagent at 625 nm within 30 min. Starch in the tissue residual was then gelled and converted to glucose with amyloglucosidase. Glucose concentrations were measured with glucose oxidase by mixing the sample with peroxidase-glucose oxidase-*o*-dianisidine dihydrochloride reagent. Absorbance was measured at 450 nm after 30-min. incubation at 25°C. Soluble carbohydrate concentrations were calculated from standard curve linear regression equations using glucose standard solutions.

Statistical analyses

For all variables, statistical differences among provenances were determined by analysis of variance (GLM procedures). Because different trees and blocks were sampled during the study, and samples were pooled by block, the experimental design was

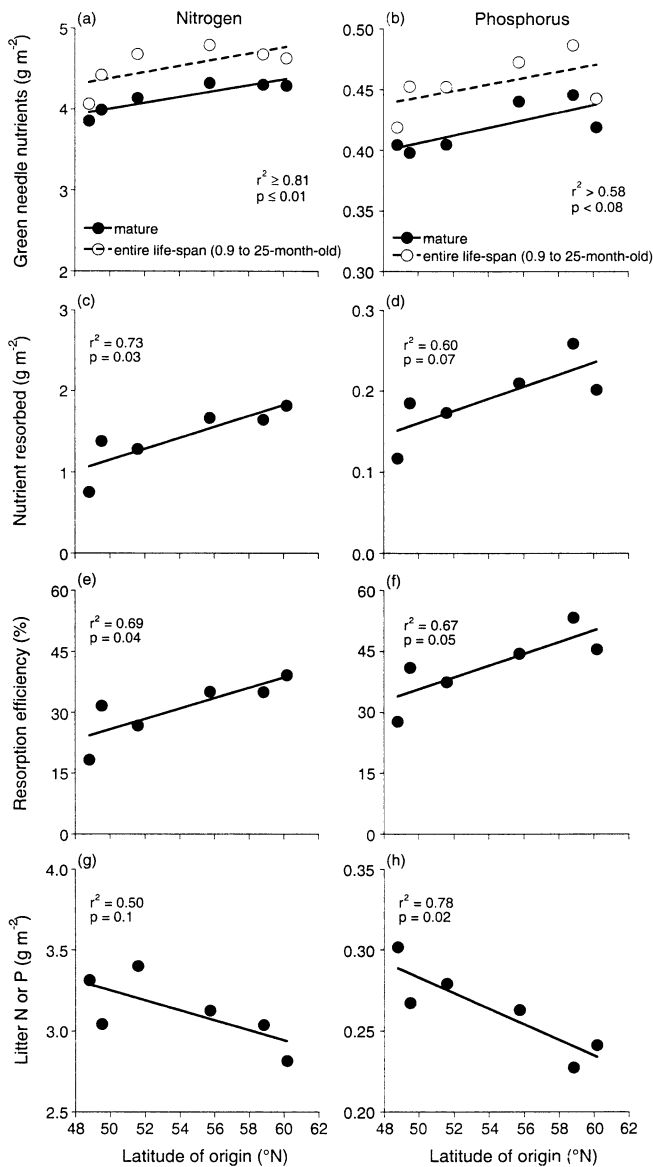


Fig. 1 Latitude of seed origin in relation to green foliage N (a) and P (b) concentration, amount of resorbed N (c) and P (d), nutrient resorption efficiency (e, f) and nutrient content of litter (g, h) in Scots pine populations growing in a common garden in Kórnik, Poland (52°N). *Open circles* (a, b) are average values for the period spanning the entire life of the 1996 needle cohort (between May 1996 and July 1998) except for the 2-month period prior to needle abscission. *Black symbols* represent average N and P concentrations of mature needles prior to senescence used as a reference for nutrient resorption efficiency (see text for explanation). Reductions in litter nutrient contents indicate increased resorption proficiency (g, h). *Dotted lines* (a, b) represent the relationships between each nutrient measure and the latitude of origin, based on the repeated measures ANOVA ($P \leq 0.03$). *Solid lines* (a–h) represent simple linear regressions between the calculated trait and latitude of seed origin

considered completely random. Relationships were assessed using correlation and regression analyses. Repeated measures ANOVA was used to test for latitude of origin relationships with measures of needle N and P over extended time periods (presented in Fig. 1). There was no interaction between needle age and latitude of origin,

and the full model (r^2 ranged from 0.30 to 0.62) and both latitude (P values from 0.03 to 0.0001) and needle age ($P < 0.001$) were significant. For presentation, both correlation and regression are used but we do not assume that direct causal relations are involved. All statistical analyses were conducted with JMP software (version 3.2.2, SAS Institute, Cary, N.C., USA).

Data for the literature survey

To test the generality of the latitude and needle nutrient relationships, we obtained published mass-based N and P data for Scots pine needles grown in situ. The nutritional status of dried samples of green mature needles has often been used as an indicator of nutrient supply in the soil (Johansson 1995). The data for the in situ survey are based upon 58 reports representing 195 different stands or experimental units (Appendix 1).

The survey was limited to undisturbed and untreated stands ranging in age from 5 to 122 years old (median 15), originating from the continuous geographic range of the species in Europe (between 47° and 66°N). Only data for relatively well-developed needles (range, 3–24 months old; median 5) were used. In order to reduce small-scale geographical variation in needle nutrient concentration (in part related to the fact that not all authors indicated precise coordinates of the studied stands) we averaged results within 2° latitudinal increments. We used WorldClimate.com web site as a source of climatic data. At this site historical weather averages are gathered from around 85,000 climate records (<http://www.worldclimate.com>). For missing latitude, longitude or altitude of seed origin we used data obtained from the Global Gazetteer web site (<http://www.calle.com/world/index.html>). This site contains details of geographical locations on >2.8 million of the world's cities and towns sorted by country and linked to a map for each town.

Results

NRE from senescing needles in a common-garden study

The concentrations of N and P in dried samples of green mature foliage or averaged for the period spanning the entire life of the needle cohort increased with the latitude of seed origin (Fig. 1a, b). Relationships with latitude for the entire needle life-span and the stable period prior to senescence were parallel. The amount of P and N resorbed increased linearly with latitude of seed origin by $\approx 35\%$ between 49° and 60°N (Fig. 1c, d). NRE also increased linearly with the seed origin latitude. Among populations originating between the latitudes of 49° and 60°N the nitrogen resorption efficiency increased from 30% in southern European populations to 40% in northern European populations, and P resorption from 35% to 50% (Fig. 1e, f). Moreover, these responses were large enough such that resorption proficiency of N and P increased with increasing latitude of origin (Fig. 1g, h), despite generally higher green tissue nutrient concentrations in the higher latitude populations.

The seasonal pattern of N in green foliage in relation to litterfall phenology in the common garden is shown in Fig. 2. Average needle N concentrations expressed on a TNC-free dry mass basis for 11- to 23-month-old green needles are plotted separately for central (from France, Germany, Poland) and northern European (Latvia, Russia, Sweden) populations, which are grouped for clarity. N

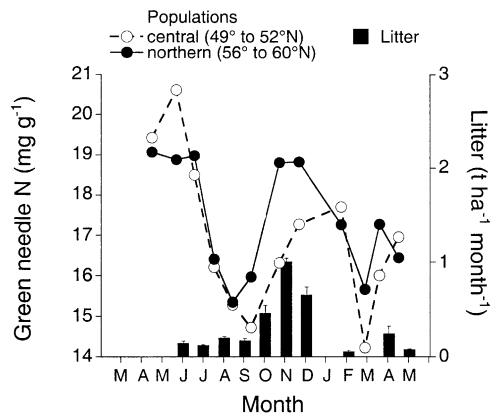


Fig. 2 Seasonal pattern of green needle N (on a TNC-free basis) for central (Poland, Germany and France) and northern (Sweden, Russia and Latvia) groups of Scots pine populations growing in a common garden in Kórnik, Poland (52°N). Changes of N are shown for needles in their second year of life from May 1997 to May 1998, 5 months prior to their senescence and shedding. In the lower portion of the Figure litterfall phenology for a local plantation (51°14'N, 18°10'E, 30 years old) of Scots pine is shown (J. Oleksyn et al., unpublished data)

concentrations of 1-year-old needles declined in both groups of populations during their second growing season (June–September) most likely indicating nutrient retranslocation from mature needles to expanding shoots and to stem growth. An increase of N concentration coincides in both groups with the period of higher litterfall in autumn and winter, most likely due to resorption from senescing foliage. However, the increase in green needle N concentration started earlier and peaked at a higher value in northern than southern populations,

consistent with conclusions from Fig. 1 regarding higher NRE of northern populations (Fig. 2).

In contrast to N and P, we found no evidence of significant population differences in resorption of any other macro- or micronutrients from senescing needles of Scots pine in that experiment.

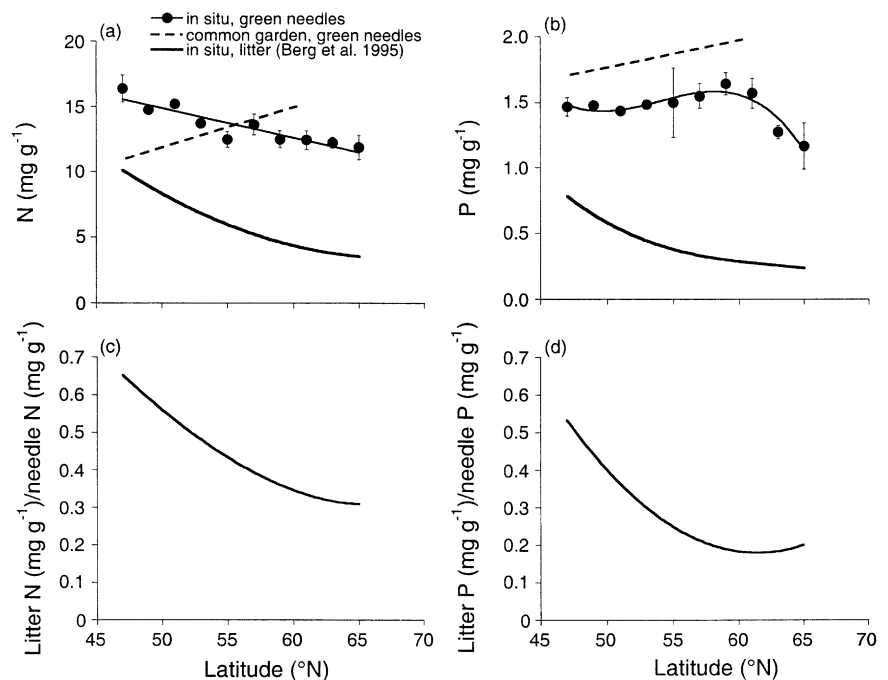
Geographical pattern in needle N and P of in situ and common-garden-grown Scots pine populations

The literature values of in situ foliage N and P concentrations in Scots pine needles are summarized in Fig. 3. Nitrogen concentrations in mature needles (mean of 8 months old) declined linearly with latitude of stand, changing from $\approx 16 \text{ mg g}^{-1}$ at $47 \pm 1^\circ \text{N}$ (Hungary) to 11 mg g^{-1} at $65 \pm 1^\circ \text{N}$ (Fennoscandia, Fig. 3a). A similar declining pattern in in situ N concentration was observed when plotted against mean annual temperature of the stands ($r^2=0.81$, $P=0.0004$; data not shown).

In Fig. 3a, b regression lines are also shown for the latitude of seed origin and mass-based needle N and P concentrations relationships observed in the common-garden-grown (in Kórnik, Poland, 52°N) Scots pine trees. These equations were developed for mature (averaged current- and 1-year-old needles) tissues based on the data reported in this and prior studies (totaling 20 populations) conducted at that site (Reich et al. 1996a; Oleksyn et al. 1999b, 2002, unpublished data). The pattern of latitudinal changes in foliage N in common-garden trees was opposite to that observed in situ (Fig. 3a).

The latitudinal pattern of in situ P concentration was less clear compared to that of N (Fig. 3b). Between 47° and 55°N needle P concentration averaged 1.5 mg g^{-1} and

Fig. 3 Latitude of seed or stand origin in relation to: (a, b) current year fully developed green foliage N and P concentration in Scots pine populations growing in a common garden in Kórnik, Poland (52°N), dashed line (for N $r^2=0.61$, $P=0.003$; for P $r^2=0.64$, $P=0.003$), and in well-developed needles (range, 3–24 months old; median 5) of 195 stands sampled in different sites in Europe (continuous line based on regression, for N $r^2=0.86$, $P<0.0001$). In situ litter N [$N=511 \exp(-0.087 \text{ Lat}) + 1.67$; $r^2=0.77$] and P [$P=514 \exp(-0.144 \text{ Lat}) + 0.194$; $r^2=0.65$] concentration (based on equations from Berg et al. 1995). In situ litter (c, d) N and P divided by green needle concentrations shown in Fig. 3a, b



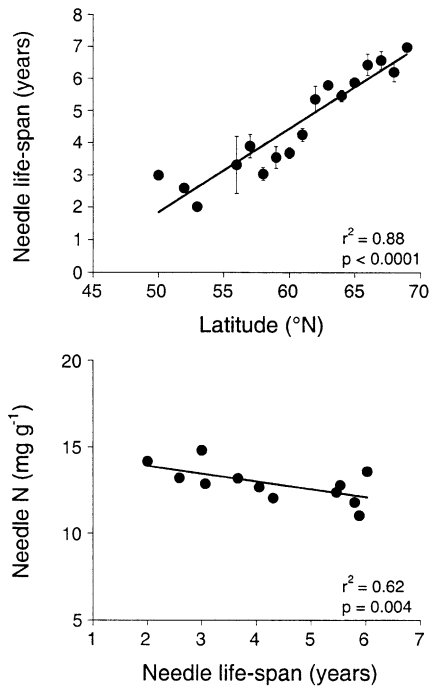


Fig. 4 *Top* Latitude of stand origin in relation to needle life-span (\pm SE) in 112 stands sampled in Europe (see Appendix 2 for data). Results were averaged within 1° latitudinal increments Needle life-span (years) = $-11.15 + 0.26$ Latitude. *Bottom* Relationships between needle life-span calculated based on data presented in Fig. 4a and in young, mature needles (3–24 months, mean 8 months) N (Fig. 3a)

did not differ with latitude ($P=0.52$). Only further north, between 63° and 65°N, was P concentration lower (≈ 1.2 mg g⁻¹). In contrast, mass-based foliar P concentration in the common-garden trees increased with latitude of seed origin. Overall, P values were higher in the common-garden site than in situ. In Fig. 3a, b regression lines are also shown describing relationships between the concentrations of N and P in Scots pine litter and the latitude of the sampled stand. These regressions were developed by Berg et al. (1995) based on the studies of the elemental composition of newly shed litter in Scots pine stands at 31 sites ranging from the Carpathian Mountains to the Barents Sea. Along that transect, N litter concentration decreased from 10 mg g⁻¹ at 47°N to <4 mg g⁻¹ at 65°N. A similar decline was observed for litter P concentration, which declined from 0.75 to 0.25 mg g⁻¹ between 47° and 65°N.

As an index of nutrient conservation we calculated litter nutrient concentration as a proportion of green needle nutrient concentration across the latitudinal gradient (Fig. 3c, d). Lower values of this index should indicate a greater tendency of plants to conserve nutrients (since an index value of 1.0 would indicate identical concentrations in litter and green needles, whereas an index of 0.1 would indicate 10-fold lower concentrations in litter). Scots pine litter in southern Europe is richer in N and P, both in absolute values and as a percent of green needles, than litter in northern Fennoscandia. These data indirectly

suggest that NRE may be higher in northern than in southern Europe in situ.

Nutrient conservation can be accomplished by withdrawing nutrients from senescing tissues or by retaining live tissues for longer. In Fig. 4a the regression line is shown describing the relationship between latitude and Scots pine needle life-span in situ. This regression was developed based on literature data from the European range of Scots pine (Appendix 2). On average, between 50° and 70°N needle life-span increased from 2 to 7 years. We also found that the functional duration of foliage (see Körner 1999 for explanation) changed with stand origin. Needle longevity significantly declined when plotted against average growing season length (calculated as number of days above 5°C) for a given latitude ($r^2=0.71$, $P < 0.0001$, $n=96$; see Appendix 2 for original data). With increasing needle life-span a significant decline of green needle nitrogen in young, mature needles (3–24 months, mean 8 months) was also observed (Fig. 4b). Thus, in situ, northern populations demonstrate all three means of conserving nutrients: extended tissue longevity, low nutrient concentrations in green needles, and apparently greater NRE, based on the indirect index described above.

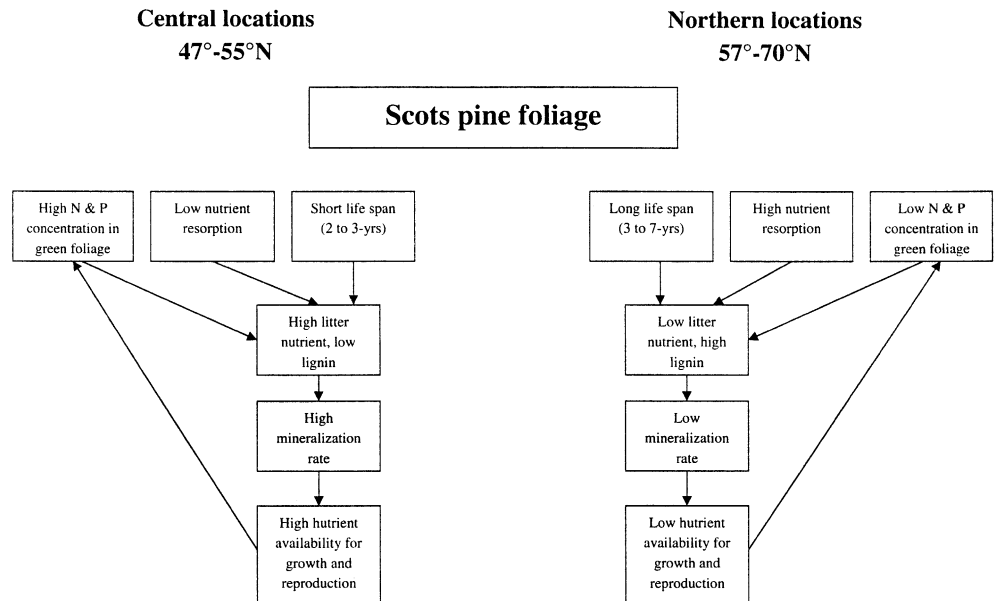
Discussion

Our data indicate that N and P resorption efficiency from senescing foliage increases with latitude in extant Scots pine populations and as well with latitude of seed origin when grown in a common garden (Figs. 1e, f, 3c, d). This latter pattern may indicate that nutrient resorption is under partial genetic control and that this potentially adaptive strategy may contribute to higher nutrient conservation in plants from cold habitats. Enhanced resorption of N and P from senescing needles of northern populations has perhaps evolved as a genetic adaptation to low rates of organic matter decomposition and availability of nutrients observed to occur at colder soil temperatures (Chapin 1987; Heal and Block 1987). The in situ latitudinal gradient in N and P concentration in green foliage of Scots pine (Fig. 3a, b) may also reflect the existence of a nutrient availability gradient, since the higher concentrations in the more southerly populations runs counter to their lower concentrations (compared to northern populations) when grown in a common garden.

Since resorbed nutrients are directly available for plant growth, greater resorption efficiency in Scots pine populations from colder than warmer environments likely represents a nutrient conservation mechanism and a potentially adaptive trait. Nutrient conservation is presumed to increase fitness in nutrient-limited environments, although that is difficult to demonstrate. In more fertile sites, the cost of nutrient resorption may exceed the cost of nutrient uptake from the soil, and NRE may be lower there (Enoki and Kawaguchi 1999).

Evidence of phenotypic and genotypic variation in NRE related to soil nutrient availability is not limited to systems with temperature control over organic matter

Fig. 5 Schematic view of the Scots pine needle and litter attributes and their effects on nutrient dynamics in central (47–55°N) and northern (57–70°N) locations in Europe. Based on data presented in this paper and the literature. See text for additional explanations



decomposition. Reich et al. (2001) reported increased NRE in *Quercus* species along a local fertility gradient in Minnesota, with the response apparently phenotypic in nature. Treseder and Vitousek (2001) reported the existence of genetic variation in nutrient resorption among populations of evergreen tree *Metrosideros polymorpha* from a soil fertility gradient in Hawaii. They found in a common-garden study that the fertile-site population had significantly lower N resorption and higher litter-N than plants from the N-limited site. However, evidence for similar interspecific patterns—wherein species from more infertile sites have greater NRE—is weak (Aerts 1996).

We found different geographic patterns in foliage N and P for populations in the common garden versus those sampled in situ along the latitudinal transect (Fig. 3a, b). In the common-garden green foliage N and P concentrations increased with increasing latitude of seed origin (Fig. 3a, b). In previous studies we found that needles with similar specific leaf area (or LMA) differed by as much as 20% in nutrient concentration among northern and southern European Scots pine populations (Oleksyn et al. 2002). Therefore, the N and P patterns reported here cannot be explained simply as a passive consequence of weaker N dilution in slow-growing northern populations (Oleksyn et al. 2001), but is likely a result of adaptation to lower temperature. An increased ability of cold-adapted, high latitude populations to more effectively accumulate nutrients is consistent with Körner et al. (1989) and Weih and Karlsson (2001) who report that N concentrations in tissues of plants originating from cold sites is higher than those from warmer sites. A similar phenomenon was observed across climatic zones, plant life forms, and species and was not restricted to foliage but also included other plant parts (Körner 1999).

In contrast to the common-garden results, green foliage of plants sampled along the latitudinal/temperature gradient show opposite patterns of decreasing N and to a lesser

extent decreasing P with increasing site latitude (Fig. 3a, b). Our data suggest that the ability of cold-adapted plants to exhibit more efficient nutrient resorption and to maintain higher nutrient concentrations in green foliage (common garden) is not able to entirely compensate for the presumed nutrient availability limitations observed along the temperature gradient, although the observed increases in needle longevity with increasing latitude indicates that nutrient conservation is enhanced through increased mean residence time (Eckstein et al. 1999).

With increasing latitude or lower mean annual temperature a decrease in litter N and P concentrations has been observed for Scots pine stands (Fig. 3a, b; Berg et al. 1995; Johansson 1995). It was suggested (Killingbeck 1996) that in order to avoid complications related to the relative measurements of NRE caused by variations in green leaf concentrations, a nutrient resorption proficiency (NRP, the absolute level to which nutrients are reduced in senescing leaves) should be used. Litter N and P variation presented in Fig. 3a, b correspond with Killingbeck's nutrient resorption proficiency and indicate ca. 3-fold increase in NRP between 47° and 65°N, and may be indicative of differences in nutrient conservation among Scots pine populations. Along the same latitudinal gradient in situ (but not in common garden, see Reich et al. 1996b), needle retention changes by almost the same magnitude as NRP. Thus, overall, these data indicate that populations from colder habitats have higher nutrient resorption efficiencies and proficiencies (Fig. 1).

The observed and expected feedbacks between foliage attributes, litter quality, and nutrient cycling among central and northern populations of Scots pine are shown schematically in Fig. 5. Foliage of pines from northern locations is distinguished by a long life span (3–7 years at 57° to 70°N vs 2–3 years at 47° to 55°N; Fig. 4), higher NRE (Fig. 1), and lower concentration of N and P in green and senescent foliage (Fig. 3). Combinations of

these traits result in marked differences in litter production and quality among high and low latitude populations (Fig. 5). Green foliage N and P concentrations decline with increasing age, mainly due to nutrient dilution in increasing mass of foliage structural elements, resulting from secondary lignification that takes place throughout the life span of the foliage (Oleksyn et al. 1997, unpublished data). Therefore, differences in foliage persistence alone, can create a gradient of litter quality along the European latitudinal transect. Among species long-lived foliage is typically characterized by low nutrient concentrations, which is the case here as well, since high latitude populations have long needle life-span and low N concentration, as observed more generally (Reich et al. 1997). More than 4-fold variation in foliage longevity within the European latitudinal transect versus <1-fold variation in nutrient resorption underlines the relative importance of leaf-life span as a nutrient conservation mechanism (Reich et al. 1992). The increase of foliage longevity with latitude of stand was also statistically significant when accounting for needle functional duration (*sensu* Körner 1999).

In northern locations the combination of litter that is low in nutrients and high in lignin, and low temperatures result in slow litter decomposition rates. Litter with a high lignin: N or C: N ratio decomposes more slowly than litter with low ratios of these constituents (Stump and Binkley 1993), especially during initial phases of decomposition (Melillo et al. 1989). Data from the European transect study show that decomposition rates of Scots pine litter, measured as a percent of dry matter loss during the first year, decreased markedly with increasing latitude of site, from 47% in southern Poland (50°N; 7.4°C m.a.t.) to 7% in Finland (70°N; -1.7°C m.a.t.; Vucetich et al. 2000). Since the rate of decomposition is directly related to nutrient cycling in ecosystems (Hobbie 1992) variation in NRE and other traits affecting litter quality may feed back to affect soil characteristics.

In northern environments, interactions of low temperature, low mineralization rates, and poor litter quality can limit nutrient availability for growth and reproduction. In cold habitats, due to substantially longer foliage life span and higher N and P resorption efficiency (Fig. 5) a much longer residence time of both macronutrients in foliage is expected which may further reduce soil nutrient availability. This may also imply that Scots pine stands growing in nutrient-limited soils in high altitudes, by means of longer nutrient residence time and slow litter decomposition, will reinforce the species competitive ability due to a positive feedback with low soil fertility.

In addition to the above-mentioned nutrient conservation mechanisms employed by Scots pine populations from cold habitats, there are also several other strategies instrumental in sustaining the necessary metabolic activity required for maintaining their competitive ability in nutrient-limited conditions. Among them are: (1) an increase in needle scleromorphicity (Langlet 1936; Gunia et al. 1991); (2) a decrease in plant growth rate (Oleksyn et al. 2000, 2001; Vucetich et al. 2000); (3) higher

biomass allocation to roots (Oleksyn et al. 1992a, 1992b; Oleksyn et al. 1999a); and (4) lower frequency of masting years (Sarvas 1962; Henttonen et al. 1986). Most of the nutrient conservation strategies listed above, together with higher cold hardiness of high latitude populations of Scots pine (Repo et al. 2001) can increase their survival success in nutrient-poor soils and in cold environments. The evidence of that can be seen in recently published survival data from the most comprehensive Scots pine provenance experiment series established in the mid-1970s in Russia (Shutyaev and Giertych 2000).

Along with the resorption of nutrients from senescing foliage we also observed significant N resorption from green foliage during the growing season and into green foliage in autumn (Fig. 2). From July to August, 1-year-old foliage of Scots pine lost ca. 30% of N. These data underline the importance of internal nutrient withdrawals from green foliage for the support of new growth. In the autumn, during the period of high litter fall, green foliage N concentrations returned to pre-growing season levels for northern populations but remained at lower levels in those from central Europe (Fig. 2). This pattern is consistent with the data on nutrient resorption from senescing foliage.

In summary, we observed significant differences in N and P resorption efficiency and proficiency among European Scots pine populations when grown in a common garden. The intrinsic qualities of Scots pine foliage along large temperature or nutrient availability gradients may provide significant feedbacks on nutrient cycling. At high latitude sites, nutrient availability may be reduced in part owing to lower litter quality, and rise to some degree at the warmer more fertile sites of central Europe. Therefore, intrinsic differences in nutrient resorption capacity, together with other nutrient conservation strategies employed by Scots pine populations may affect nutrient cycling, competition, productivity and fitness along large climatic gradients.

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Appendix 1

Average N and P concentration (mg g⁻¹) in mature green foliage (3–24 months old) of different Scots pine (*Pinus sylvestris* L.) stands within species' continuous range in Europe

See text for additional information. (*FI*, Finland; *SE*, Sweden; *RU*, Russian Federation; *EE*, Estonia; *LT*, Lithuania; *DE*, Germany; *PL*, Poland; *BY*, Belarus; *UA*, Ukraine; *CZ*, Czech Republic; *HU*, Hungary. 1, Average of different crown height; 2, Average for different crown or branch position; 3, seed orchard; 4, average of multiple stands; 5, average of stands sampled in different years; 6, Stand on silicate substrate; 7, Stand on carbonate substrate)

Country and remarks	Lat. (N)	Long. (E)	Mean annual temperature (°C)	N (mg g ⁻¹)	P (mg g ⁻¹)	Stand or tree age (years)	Source
FI	65.87	26.12	1.1	13.6	0.9	50	Pietiläinen (1984)
FI	64.97	26.40	1.1	10.3	1.3	70	Vuorinen et al. (2000)
FI	64.79	26.79	1.0	11.8	1.5	20	Silfverberg et al. (1999)
SE	63.67	17.97	3.8	10.8	1.4	23	Örlander et al. (1990)
FI	63.51	26.59	3.1	14.0	1.6	22	Reinikainen et al. (1983)
FI	63.35	19.32	2.3	11.5	1.6	45	Silfverberg et al. (1999)
FI, 1	62.85	30.88	2.2	14.9	1.6	50	Finer (1994)
FI, 1	62.85	30.88	2.2	14.2	1.1	50	Finer (1994)
FI	62.78	30.97	2.0	11.5	1.3	100	Helmisaari (1990)
FI	62.78	30.97	2.0	10.9	1.1	15	Helmisaari (1990)
FI	62.78	30.97	2.0	11.1	1.1	35	Helmisaari (1990)
FI, 2	62.78	30.97	2.0	11.0	1.1	35	Helmisaari (1992a)
FI, 2	62.78	30.97	2.0	10.0	1.0	100	Helmisaari (1992a)
FI	62.78	30.97	2.0	11.2	1.1	15	Helmisaari (1992a)
FI	62.23	20.83	3.7	11.3	1.3	85	Finer (1992)
FI, 1	62.23	30.83	2.4	12.2	1.2	85	Finer (1994)
FI	62.20	25.23	2.7	15.4	1.1	35	Silfverberg et al. (1999)
FI	62.12	22.18	3.7	13.6	1.5	13	Reinikainen et al. (1983)
FI	62.06	25.29	2.7	12.3	1.3	65	Silfverberg et al. (1999)
FI	61.92	23.73	3.8	12.5	1.6	30	Jokela et al. (1997)
FI	61.78	20.73	3.6	13.2	1.5	20	Raitio (1987)
RU	61.70	50.90	0.2	10.5	2.1		Rusanova et al. (1977)
FI, 3	61.57	26.30	2.6	16.0	1.6		Lukina et al. (1994)
FI	61.50	24.00	3.6	11.1	1.7	20	Nuorteva et al. (1993)
FI	61.18	21.97	4.0	14.4	1.4	40	Silfverberg et al. (1999)
SE, 2	60.82	16.50	4.9	9.7		20	Troeng et al. (1982)
FI	60.44	24.29	4.3	12.1	1.1	13	Silfverberg et al. (1999)
SE, 2	59.87	18.92	5.8	14.3	1.5		Tamm (1955)
RU, 4	58.26	84.45	4.3	12.3	1.6	8	Koschelkov et al. (1973)
RU	58.26	84.45	4.3	16.1	2.2		Koschelkov (1967)
RU	58.26	84.45	4.3	13.1	1.8		Koschelkov (1967)
RU, 4	58.26	84.45	4.3	13.2	1.8		Koschelkov (1967)
RU, 4	58.26	84.45	4.3	11.8	1.6		Koschelkov (1967)
RU, 4	58.26	84.45	4.3	11.5	1.5		Koschelkov (1967)
RU, 4	58.26	84.45	4.3	10.6	1.4		Koschelkov (1967)
RU, 4	58.26	84.45	4.3	9.7	1.4		Koschelkov (1967)
EE, 4	58.00	27.00	5.5	16.4	1.7		Porgasaar (1977)
UK, 2	57.58	-3.87	8.0	13.3	1.5	64	Wright et al. (1958)
UK	57.58	-3.87	8.0	10.6	1.2	18	Wright et al. (1958)
UK	57.58	-3.87	8.0	14.6	1.9	28	Wright et al. (1958)
UK	57.58	-3.87	8.0	14.2	1.5	64	Wright et al. (1958)
SE, 5	57.17	14.83	5.8	12.7	1.5	30	Sikström (1997)
LT	54.88		6.5	13.1	1.8		Stefan et al. (1997)
LT, 4	54.88		6.5	11.9	1.2		Skoudene (1997)
DE, 5	53.68	13.85	8.5	16.2	1.7	5–15	Heinsdorf (1973)
RU	53.33	34.20	5.3	11.0	1.7		Krasnikov (1976)
PL	53.20	23.37	6.7	15.2	1.4	15	Oleksyn et al. (unpublished data)
DE, 5	53.12	13.50	8.7	14.6	1.6	70	Trillmich et al. (1982)
DE	52.92	13.87	8.7	10.9	1.3	7	Heinsdorf (1976c)
DE	52.92	13.87	8.7	11.0	1.3	14	Heinsdorf (1976c)
DE	52.92	13.87	8.7	13.0	1.6	33	Heinsdorf (1976c)
DE	52.92	13.87	8.7	14.4	1.7	47	Heinsdorf (1976c)
DE	52.92	13.87	8.7	14.5	1.6	85	Heinsdorf (1976c)
DE	52.87	13.40	8.5	16.5	1.7	5	Heinsdorf (1966)
DE	52.87	13.40	8.5	16.6	1.6	6	Heinsdorf (1966)
DE, 5	52.87	13.75	8.7	16.2	1.6	42–46	Heinsdorf et al. (1976)
DE	52.83	13.88	8.9	14.9	1.4	35	Ritter et al. (1978)
DE	52.83	13.88	8.3	14.3	1.4	55	Riedel (1986)
DE	52.83	13.88	8.3	13.1	1.4	40	Hippeli (1976)
DE	52.66	13.73	8.5	15.8	1.6	5	Heinsdorf (1966)
DE	52.66	13.73	8.5	14.9	1.6	6	Heinsdorf (1966)
DE, 4	52.41	13.50	8.5	15.1		57	Tölle et al. (1970)
DE	52.36	14.07	8.5	13.1	1.5	5	Heinsdorf (1966)
DE	52.36	14.07	8.5	15.2	1.7	6	Heinsdorf (1966)
DE	52.36	14.07	8.5	13.1	1.4	6	Heinsdorf (1967)
DE	52.36	14.07	8.5	11.2	1.2	6	Heinsdorf (1967)
PL	52.35	20.30	7.5	15.9	1.7		Kurczynska et al. (1997)
PL, 5	52.30	23.85	6.2	13.8	1.4		Unpublished data of the Forest Research Institute in Warsaw

Country and remarks	Lat. (N)	Long. (E)	Mean annual temperature (°C)	N (mg g ⁻¹)	P (mg g ⁻¹)	Stand or tree age (years)	Source
PL	52.25	17.07	7.7	11.5	1.3	11–15	Oleksyn et al. (unpublished data)
PL	52.25	17.07	7.7	12.6	1.8	29	Oleksyn et al. (unpublished data)
BY, 4	52.25	31.00	7.1	15.1	1.5	8–10	Morozov et al. (1981)
DE, 5	52.23	12.17	8.5	12.3	1.3	5–15	Heinsdorf (1973)
DE, 5	52.23	12.17	8.5	12.0		15–19	Heinsdorf (1978)
DE	52.23	12.17	8.5	12.7	1.3	5	Heinsdorf (1976b)
DE, 5	52.22	12.85	8.5	13.4	1.4	5–11	Heinsdorf (1973)
DE	52.20	12.77	8.5	12.6	1.3	5–6	Heinsdorf (1966)
DE	52.20	12.77	8.5	10.6	1.1	6	Heinsdorf (1967)
PL	52.17	20.90	7.5	16.7	1.7		Kurczynska et al. (1997)
DE, 5	52.05	13.60	8.5	11.0	1.2	6–16	Heinsdorf (1973)
DE	52.00	13.00	8.5	13.5	1.5	5–6	Heinsdorf (1973)
DE, 5	51.95	13.23	8.5	11.8	1.3	6–15	Heinsdorf (1973)
DE	51.95	13.23	8.5	12.3	1.5	5–6	Heinsdorf (1966)
DE	51.95	13.23	8.5	10.1	1.2	6	Heinsdorf (1967)
DE	51.90	13.22	8.5	12.3	1.3	5–14	Heinsdorf (1973)
DE	51.90	13.22	8.5	13.4		15–18	Heinsdorf (1978)
DE	51.87	13.43	8.5	17.1	1.8	5–6	Heinsdorf (1966)
DE	51.87	13.43	8.5	13.3	1.5	5–6	Heinsdorf (1967)
PL	51.80	14.97	8.0	12.0	1.4	60	Rzeznik et al. (1968)
DE	51.62	14.02	8.4	13.2	1.3	6–7	Heinsdorf (1976a)
DE	51.55	14.10	8.4	18.0	1.3	5–6	Heinsdorf (1976a)
DE	51.50	13.80	8.4	11.6	1.1	6–7	Heinsdorf (1976a)
DE	51.41	14.25	7.9	13.7	1.4	7	Heinsdorf (1987)
DE	51.40	12.88	8.5	17.1	2.0	37	Czerney et al. (1969)
DE	51.40	12.88	8.5	18.3	1.7	39	Czerney et al. (1969)
DE	51.40	12.88	8.5	17.8	1.8	52	Czerney et al. (1969)
DE	51.40	12.88	8.5	18.1	1.8	56	Czerney et al. (1969)
DE	51.40	12.88	8.5	17.8	1.8	63	Czerney et al. (1969)
DE	51.40	12.88	8.5	17.9	1.8	77	Czerney et al. (1969)
DE	51.40	12.88	8.5	16.1	1.7	88	Czerney et al. (1969)
DE	51.40	12.88	8.5	16.0	1.6	97	Czerney et al. (1969)
DE	51.40	12.88	8.5	17.6	1.4	108	Czerney et al. (1969)
DE	51.40	12.88	8.5	16.7	1.7	118	Czerney et al. (1969)
DE	51.40	13.90	9.1	13.5	1.5	50	Höhne et al. (1970)
DE, 5	51.40	14.00	8.5	10.7	1.1	7–11	Heinsdorf (1982)
DE	51.37	14.52	8.4	14.0	1.4	5–6	Heinsdorf (1976a)
DE	51.32	14.33	9.1	13.8	1.5	9	Fiedler et al. (1967)
DE	51.32	14.33	9.1	14.8	1.3	15	Fiedler et al. (1967)
DE	51.32	14.33	9.1	14.8	1.3	29	Fiedler et al. (1967)
DE	51.32	14.33	9.1	15.5	1.2	41	Fiedler et al. (1967)
DE	51.32	14.33	9.1	16.3	1.2	52	Fiedler et al. (1967)
DE	51.32	14.33	9.1	15.3	1.5	78	Fiedler et al. (1967)
DE	51.32	14.33	9.1	14.8	1.5	89	Fiedler et al. (1967)
DE	51.32	14.33	9.1	12.7	1.3	9	Fiedler et al. (1967)
DE	51.32	14.33	9.1	12.8	1.2	15	Fiedler et al. (1967)
DE	51.32	14.33	9.1	14.8	1.2	29	Fiedler et al. (1967)
DE	51.32	14.33	9.1	15.3	1.0	41	Fiedler et al. (1967)
DE	51.32	14.33	9.1	17.4	1.1	52	Fiedler et al. (1967)
DE	51.32	14.33	9.1	14.4	1.3	78	Fiedler et al. (1967)
DE	51.32	14.33	9.1	14.5	1.4	98	Fiedler et al. (1967)
DE	51.30	14.33	8.6	14.7	1.6	105	Leube et al. (1975)
DE, 5	51.30	14.45	8.5	13.3	1.5	6–16	Fiedler et al. (1970)
DE	51.28	12.98	7.3	16.1	1.6	24	Czerney et al. (1969)
DE	51.28	12.98	7.3	17.5	1.8	33	Czerney et al. (1969)
DE	51.28	12.98	7.3	19.1	1.6	37	Czerney et al. (1969)
DE	51.28	12.98	7.3	17.7	1.7	41	Czerney et al. (1969)
DE	51.28	12.98	7.3	17.6	1.6	47	Czerney et al. (1969)
DE	51.28	12.98	7.3	19.8	1.4	44	Czerney et al. (1969)
DE	51.28	12.98	7.3	21.3	1.4	47	Czerney et al. (1969)
DE	51.28	12.98	7.3	17.6	1.6	50	Czerney et al. (1969)
DE	51.28	12.98	7.3	17.6	1.4	60	Czerney et al. (1969)
DE	51.28	12.98	7.3	19.3	1.7	61	Czerney et al. (1969)
DE	51.28	12.98	7.3	17.0	1.7	65	Czerney et al. (1969)
DE	51.28	12.98	7.3	19.8	1.5	65	Czerney et al. (1969)
DE	51.28	12.98	7.3	19.9	1.5	69	Czerney et al. (1969)
DE	51.28	12.98	7.3	17.6	1.4	77	Czerney et al. (1969)
DE	51.28	12.98	7.3	17.0	1.4	80	Czerney et al. (1969)
DE	51.28	12.98	7.3	19.2	1.3	82	Czerney et al. (1969)

Country and remarks	Lat. (N)	Long. (E)	Mean annual temperature (°C)	N (mg g ⁻¹)	P (mg g ⁻¹)	Stand or tree age (years)	Source
DE	51.28	12.98	7.3	17.6	1.4	100	Czerney et al. (1969)
DE	51.28	12.98	7.3	15.6	1.1	87	Czerney et al. (1969)
DE	51.28	12.98	7.3	18.0	1.4	97	Czerney et al. (1969)
DE	51.28	12.98	7.3	17.8	1.5	118	Czerney et al. (1969)
DE	51.28	12.98	7.3	16.5	1.1	111	Czerney et al. (1969)
DE	51.28	12.98	7.3	16.9	1.6	121	Czerney et al. (1969)
DE	51.28	12.98	7.3	17.6	1.2	122	Czerney et al. (1969)
DE	51.28	12.98	7.3	17.6	1.6	10	Czerney et al. (1969)
DE	51.28	14.42	9.1	13.3	1.5	97	Fiedler et al. (1967)
DE	51.27	14.33	9.1	15.0	1.4	107	Fiedler et al. (1967)
DE	51.27	14.33	9.1	12.5	1.4	10	Fiedler et al. (1967)
DE	51.27	14.33	9.1	14.4	1.4	17	Fiedler et al. (1967)
DE	51.27	14.33	9.1	12.4	1.5	27	Fiedler et al. (1967)
DE	51.27	14.33	9.1	12.9	1.5	41	Fiedler et al. (1967)
DE	51.27	14.33	9.1	12.8	1.5	50	Fiedler et al. (1967)
DE	51.27	14.33	9.1	13.2	1.5	61	Fiedler et al. (1967)
DE	51.27	14.33	9.1	12.7	1.5	81	Fiedler et al. (1967)
DE	51.27	14.33	9.1	13.7	1.4	110	Fiedler et al. (1967)
DE	51.27	14.33	9.1	15.2	1.3	107	Fiedler et al. (1967)
DE	51.27	14.33	9.1	11.1	1.2	10	Fiedler et al. (1967)
DE	51.27	14.33	9.1	12.4	1.4	17	Fiedler et al. (1967)
DE	51.27	14.33	9.1	12.4	1.6	27	Fiedler et al. (1967)
DE	51.27	14.33	9.1	12.1	1.5	41	Fiedler et al. (1967)
DE	51.27	14.33	9.1	11.4	1.4	50	Fiedler et al. (1967)
DE	51.27	14.33	9.1	12.4	1.5	61	Fiedler et al. (1967)
DE	51.27	14.33	9.1	13.8	1.6	81	Fiedler et al. (1967)
DE	51.27	14.33	9.1	14.4	1.5	110	Fiedler et al. (1967)
PL	51.23	18.17	7.5	13.2	0.9	29	Oleksyn et al. (unpublished data)
DE	50.90	11.60	8.7	15.0	1.6	12–13	Fiedler et al. (1987)
DE	50.77	11.63	8.0	13.5	0.8	77	Fiedler et al. (1969)
DE	50.77	11.63	8.0	14.5	1.0	58	Fiedler et al. (1969)
DE	50.77	11.63	8.0	15.8	1.0	72	Fiedler et al. (1969)
UA	50.55	48.35	7.1	16.3	1.4	40	Patlai (1973)
UA	50.55	48.35	7.1	15.6	1.7	5	Patlai (1973)
PL	50.03	20.37	7.7	12.4	1.5	15	Oleksyn et al. (unpublished data)
DE	50.00	8.69	9.8	17.9	1.2	100	Busch et al. (1997)
DE	50.00	12.30	7.1	14.3	1.6	111	Sauter (1991)
DE	50.00	12.30	7.1	14.2	1.6	80	Sauter (1991)
DE	50.00	12.30	7.1	15.0	1.6	81	Sauter (1991)
RU	49.93	36.28	6.9	16.3	1.4	40	Patlai (1973)
DE	49.77	11.93	8.0	13.3	1.4	86	Sauter (1991)
DE	49.75	11.55	8.0	14.0	1.5	70	Sauter (1991)
DE	49.65	14.08	7.9	16.0	1.5	15	Oleksyn et al. (unpublished data)
DE, 4	49.40	11.00	8.6	15.2	1.4		Gulder et al. (1993)
DE	49.26	12.32	8.0	13.5	1.6	62	Sauter (1991)
DE	49.26	12.32	8.0	13.4	1.5	70	Sauter (1991)
DE	49.26	12.32	8.0	13.9	1.5	100	Sauter (1991)
DE	49.20	12.03	8.0	14.3	1.4	105	Sauter (1991)
CZ, 6	49.10	17.57	8.9	14.7	1.4	85	Heinze (1996)
CZ, 7	49.10	17.57	8.9	17.4	1.6	85	Heinze (1996)
DE	49.03	10.98	7.6	13.2	1.5	89	Sauter (1991)
DE, 4, 5	49.00	11.00	7.6	14.1	1.4	40	Wehrmann (1961)
HU, 6	47.68	16.16	10.3	14.0	1.7	85	Heinze (1996)
HU, 7	47.68	16.16	10.3	14.5	1.4	85	Heinze (1996)
HU, 6	47.55	17.75	10.4	20.7	1.2	85	Heinze (1996)
HU, 6	47.45	17.03	9.7	17.8	1.4	85	Heinze (1996)
HU, 7	46.77	17.25	10.0	15.1	1.5	85	Heinze (1996)
HU, 6	46.68	19.68	10.8	16.3	1.6	10	Heinze (1996)

Appendix 2

Needle longevity (years) in different Scots pine (*Pinus sylvestris* L.) stands within species' continuous range in Europe

See text for additional information. [FI, Finland; SE, Sweden; RU, Russian Federation; EE, Estonia; PL, Poland;

UA, Ukraine; GB, Great Britain. *Lat.*, latitude (in decimal values); *Long.*, longitude; *Alt.*, altitude; *M.a.t.*, mean annual temperature. Growing season length was calculated as the number of days with mean temperature $\geq 5^{\circ}\text{C}$]

Location (country)	Lat (N)	Long (E)	Alt (m)	M.a.t. (°C)	Growing season (days)	Needle longevity (years)	Reference
Murmansk (RU)	68.97	33.04	46	0.2	126	7.0	Pravdin (1969)
Jukkasjärvi (FI)	68.00	20.61	320	-1.5	111	7.4	Sylven (1916/1917)
Lokka (FI)	67.77	27.75	255	-0.7	126	5.7	Jalkanen et al. (1995)
Ainijärvi (FI)	67.75	29.48	265	-0.9	125	5.8	Jalkanen et al. (1995)
Särkijärvi (FI)	67.72	23.83	280	-1.3	128	6.2	Jalkanen et al. (1995)
Nuttio (FI)	67.67	25.97	220	-0.7	126	6.0	Jalkanen et al. (1995)
Aska (FI)	67.27	26.72	175	-0.7	126	6.0	Jalkanen et al. (1995)
Sätsi (FI)	67.25	29.22	225	-0.8	127	6.4	Jalkanen et al. (1995)
Pajala (SE)	67.22	23.40	168	0.5	137	5.8	Sylven (1916/1917)
Kalix (SE)	66.85	23.13	11	0.2	141	5.6	Sylven (1916/1917)
Ängesa (SE)	66.73	22.30	182	0.8	142	6.5	Sylven (1916/1917)
Raneträsk (SE)	66.70	20.00	263	-0.7	126	7.2	Sylven (1916/1917)
Pärlälven (SE)	66.70	18.40		-1.2	127	7.8	Sylven (1916/1917)
Kulveikonvaara (FI)	66.70	27.82	255	-0.7	133	5.5	Jalkanen et al. (1995)
Jockmock (SE)	66.59	19.89	255	-1.2	127	8.0	Sylven (1916/1917)
Kaarnijärvi (FI)	66.45	26.80	200	0.4	138	6.0	Jalkanen et al. (1995)
Storbacken (SE)	66.38	20.71	43	-1.2	126	7.4	Sylven (1916/1917)
Tennilä (FI)	66.38	26.48	135	0.4	137	5.2	Jalkanen et al. (1995)
Arjeplog (SE)	66.03	17.80	430	0.6	134	6.2	Sylven (1916/1917)
Malmesjaur (SE)	66.03	19.17		-1.2	127	6.4	Sylven (1916/1917)
Ranea (SE)	66.00	22.30	11	1.3	142	5.4	Sylven (1916/1917)
Vargisa (SE)	65.88	20.32	104	-1.2	127	7.2	Sylven (1916/1917)
Tornaea (SE)	65.83	24.13	3	1.0	138	5.2	Sylven (1916/1917)
Sivakkavaara (FI)	65.80	24.67	35	1.3	138	4.5	Jalkanen et al. (1995)
Arvidsjaur (SE)	65.58	19.17	378	-1.2	127	6.8	Sylven (1916/1917)
Övre Byske (SE)	65.40	19.72		-1.2	127	6.6	Sylven (1916/1917)
Älvsby (SE)	65.30	18.55	17	0.3	138	5.6	Sylven (1916/1917)
Stensele (SE)	65.09	17.20	327	0.3	118	6.2	Sylven (1916/1917)
Jörn (SE)	65.03	20.15	296	-1.3	118	6.4	Sylven (1916/1917)
Norsjö (SE)	64.92	19.48	300	3.1	159	5.6	Sylven (1916/1917)
Frostviken (SE)	64.65	13.77	337	2.0	148	5.4	Sylven (1916/1917)
Vilhelmina (SE)	64.62	16.65	341	1.1	144	5.6	Sylven (1916/1917)
S. Lycksele (SE)	64.60	18.67	223	1.2	144	5.6	Sylven (1916/1917)
Burträsk (SE)	64.52	20.65	81	2.4	160	6.0	Sylven (1916/1917)
Tasjö (SE)	64.22	15.90	248	0.9	144	5.7	Sylven (1916/1917)
Degerfors (SE)	64.20	19.72	217	2.5	159	5.0	Sylven (1916/1917)
Asele (SE)	64.17	17.33	312	1.0	144	5.4	Sylven (1916/1917)
Fredrika (SE)	64.08	18.40	293	1.1	144	5.8	Sylven (1916/1917)
Anundsjö (SE)	63.43	18.15	123	3.5	162	6.4	Sylven (1916/1917)
Are (SE)	63.40	13.07	371	1.7	156	6.0	Sylven (1916/1917)
Bräcke (SE)	63.38	14.00	295	2.5	156	5.8	Sylven (1916/1917)
Hallen (SE)	63.37	13.45	386	1.7	139	5.4	Sylven (1916/1917)
Östersund (SE)	63.18	14.50	367	2.5	154	6.0	Sylven (1916/1917)
Junsele (SE)	62.83	16.90	195	3.4	168	5.9	Sylven (1916/1917)
Härnösand (SE)	62.60	18.00	8	3.5	161	5.5	Sylven (1916/1917)
Medelpad (SE)	62.53	17.39	4	3.4	163	5.4	Sylven (1916/1917)
Rätan (SE)	62.47	14.55	351	2.4	159	5.6	Sylven (1916/1917)
Hede (SE)	62.41	13.50	439	0.5	140	8.0	Sylven (1916/1917)
Västra (SE)	62.40	14.00		2.4	159	5.0	Sylven (1916/1917)
Kalttila (FI)	62.00	24.10	110	2.6	160	4.3	Jalkanen et al. (1995)
Norra (SE)	61.83	14.00		2.4	158	5.0	Sylven (1916/1917)
Karelya (RU)	61.82	34.27	110	2.5	159	6.0	Bobkova et al. (1999)
Ranta-Halola (FI)	61.80	29.33	90	2.8	163	4.4	Jalkanen et al. (1995)
Särna (SE)	61.70	13.10	437	1.5	150	6.0	Sylven (1916/1917)
Vesijako (FI)	61.33	28.05	130	3.6	172	4.0	Jalkanen et al. (1995)
Österdalarna (SE)	61.28	14.55		0.9	175	5.2	Sylven (1916/1917)
Piikajärvi (FI)	61.27	22.18	45	3.6	170	4.1	Jalkanen et al. (1995)
Gästrikland (SE)	61.20	16.80		4.5	179	4.1	Sylven (1916/1917)
Transtrand (SE)	61.08	13.32	368	1.5	150	6.8	Sylven (1916/1917)
Ojajoki (FI)	60.67	24.35	130	4.5	173	3.9	Jalkanen et al. (1995)
Grönbo (SE)	60.60	15.47	215	4.9	183	3.0	Sylven (1916/1917)
Halkivaha (FI)	60.60	24.40	120	4.5	173	3.8	Jalkanen et al. (1995)
Kaksoiskivi (FI)	60.60	24.52	120	4.5	173	4.0	Jalkanen et al. (1995)
Torpparinmäki (FI)	60.53	26.45	30	4.5	175	4.2	Jalkanen et al. (1995)
Ruotsinkylä (FI)	60.35	24.95	60	4.3	171	4.1	Jalkanen et al. (1995)
Kopparberg (SE)	60.25	14.98	229	4.9	183	4.0	Sylven (1916/1917)
N Roslag (SE)	60.25	17.40		5.8	189	3.0	Sylven (1916/1917)

Location (country)	Lat (N)	Long (E)	Alt (m)	M.a.t. (°C)	Growing season (days)	Needle longevity (years)	Reference
Örbyhus (SE)	60.23	17.70	21	5.9	189	3.5	Sylvén (1916/1917)
Västerdalarna (SE)	60.17	14.50		5.8	183	4.8	Sylvén (1916/1917)
Solböle (FI)	60.03	23.03	40	3.8	171	4.0	Jalkanen et al. (1995)
Kloten (SE)	59.90	15.28	263	5.4	180	3.2	Sylvén (1916/1917)
Arvika (SE)	59.67	12.63	74	5.4	188	3.8	Sylvén (1916/1917)
Västerås (SE)	59.58	16.60	6	5.9	194	3.0	Sylvén (1916/1917)
Enköping (SE)	59.50	17.07	10	6.0	194	3.2	Sylvén (1916/1917)
Älvdal (SE)	59.40	13.50		5.6	188	4.4	Sylvén (1916/1917)
Karlstad (SE)	59.40	13.50	55	5.6	188	3.8	Sylvén (1916/1917)
Örebro (SE)	59.30	15.20	33	5.4	185	3.0	Sylvén (1916/1917)
Askersund (SE)	59.00	14.80	175	6.1	183	3.0	Sylvén (1916/1917)
Tartu (EE)	58.30	26.70		5.5	191	2.5	Tullus (1991)
Northern (GB)	57.86	-4.79	203	6.7	196	3.4	Steven et al. (1959)
Wester Ross (GB)	57.55	-5.42	210	6.8	196	3.3	Steven et al. (1959)
Strath Glass (GB)	57.31	-4.91	301	6.1	191	3.2	Steven et al. (1959)
Speyside (GB)	57.16	-3.72	369	6.1	190	3.9	Steven et al. (1959)
Deeside (GB)	57.00	-3.10	325	6.4	190	3.8	Steven et al. (1959)
Great Glen (GB)	56.99	-5.11	305	7.0	238	3.5	Steven et al. (1959)
Moskovsk. obl. (RU)	56.80	37.00	100	3.8	178	6.0	Bobkova et al. (1999)
Rannoch (GB)	56.63	-4.33	294	6.7	238	3.9	Steven et al. (1959)
Southern (GB)	56.48	-4.79	252	7.2	235	3.0	Steven et al. (1959)
Moskovsk. obl. (RU)	55.80	37.60	156	4.2	178	5.0	Bobkova et al. (1999)
Bryansk. obl. (RU)	53.33	34.22	162	4.9	185	2.0	Bobkova et al. (1999)
Kornik (PL)	52.25	17.07	70	7.7	220	2.6	Reich et al. (1996a)
Lvov (UA)	49.80	24.00	325	7.3	210	3.0	Pravdin (1969)
Lvov (UA)	49.80	24.00	325	7.3	210	3.0	Pravdin (1969)
Lvov (UA)	49.80	24.00	325	7.3	210	3.0	Pravdin (1969)
Lvov (UA)	49.80	24.00	325	7.3	210	3.0	Pravdin (1969)
Lvov (UA)	49.80	24.00	325	7.3	210	3.0	Pravdin (1969)

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