Evidence that longer needle retention of spruce and pine populations at high elevations and high latitudes is largely a phenotypic response

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Summary   There is abundant evidence that evergreen conifers living at high elevations or at high latitudes have longer-lived needles than trees of the same species living elsewhere. This pattern is likely caused by the influence of low temperature in combination with related factors such as a short growing season and low nutrient availability. Because it is not known to what degree such patterns result from phenotypic versus genotypic variation, we evaluated needle longevity for common-garden-grown lowland populations of European Scots pine (*Pinus sylvestris* L.) of wide latitudinal origin and Norway spruce (*Picea abies* L.) of wide elevational origin. Nine-year-old trees of 16 Scots pine populations ranging in origin from 47° to 60° N were studied in Kórnik, Poland (52° N) and 18-year-old trees of 18 Norway spruce populations ranging in origin from 670 to 1235 m elevation in southwestern Poland were studied near Morawina, Poland (51° N, 180 m elevation). There was no tendency in either species for populations from northern or high elevation origins to retain needles longer than other populations. All of the Scots pine populations had between 2.5 to 3.0 needle age cohorts and all of the Norway spruce populations had between 6.4 and 7.2 needle age cohorts. Thus, extended needle retention in Scots pine and Norway spruce populations in low-temperature habitats at high elevations and high latitudes appears to be largely an environmentally regulated phenotypic acclimation.

Keywords: genotypic variation, needle longevity, phenotypic variation, Picea abies, Pinus sylvestris, temperature.

Introduction

It has been frequently noted that needle longevity of evergreen conifers such as pine, spruce and fir increases with increasing elevation and latitude (Weidman 1939, Pravdin 1969, Ewers and Schmid 1981, Schoettle 1990, Schoettle and Fahey 1994, Reich et al. 1994). This pattern of increasing needle longevity is paralleled by generally decreasing growth rates and photosynthetic capacities of evergreen conifers in low resource or high stress environments, or both (Reich et al. 1992, 1994). For instance, maximum needle longevity of *Pinus sylvestris* L. (Scots pine) doubles from 3 years at latitude 52° N to 7 or more years at latitude 65° N (Pravdin 1969), and within the genus *Pinus*, needle longevity triples from 4 to 12 years along a 3000 m elevational transect (Ewers and Schmid 1981). Such variation can occur across even relatively small gradients; for example, needle longevity in *Pinus contorta* was 3.6 years greater at 3200 m elevation than at 2800 m elevation (Schoettle 1990).

It is not known whether a long leaf life span is a genotypic feature of evergreen species or populations adapted to cold, low-resource environments, or a phenotypic acclimation driven by low temperatures and associated factors, or both. Analyses among genera and species (but not necessarily populations) suggest that both phenotypic plasticity and genotypic variation contribute to the effects of elevation and latitude on conifer needle longevity (Ewers and Schmid 1981, Chabot and Hicks 1982, Reich et al. 1992, Gower et al. 1993, Reich et al. 1994, Schoettle and Fahey 1994). However, Oohata (1992) grew *Pinus* species from around the world in a common garden in Japan and found no significant interspecific relationship between latitude or climate of origin and needle life span.

With respect to intraspecific differentiation, published reports consistently show longer needle retention in native populations in colder habitats at higher latitudes and elevations than at other sites (Table 1), although other genetic and environmental factors also contribute to local variation. Such intraspecific variation in needle longevity along climate gradients must be the result of either genotypic or phenotypic differences, or both. Ewers and Schmid (1981) identified a significant phenotypic component for individual populations of each of four *Pinus* species. Thus, individuals of given populations showed greater needle retention when grown at higher elevations than at lower elevations in California, USA (Table 2); however, interpopulation differences in needle longevity within three populations of one of these *Pinus* species were less clear when the populations were grown in common gardens (Ewers and Schmid 1981). We have conducted a similar experiment with a relatively large number of populations from two evergreen

Table 1. Observed differences in needle longevity for pine (*Pinus*) and spruce (*Picea*) populations at their native latitudes or elevations. Nebel and Matile (1992) and Ewers and Schmid (1981) reported maximum needle longevities, whereas the other references report average needle longevities.

Species	Gradient	Site	Needle longevity (year)	Reference
Pinus cembra	Elevation	Switzerland, 560 m	5.2	Nebel and Matile 1992
		Switzerland, 1820–2140 m	6.4 to 7.7	
Pinus contorta	Elevation	California, 15 m	3.9	Ewers and Schmid 1981
		California, 182 m	4.2	
		California, 2697 m	7.9	
Pinus contorta	Elevation	Wyoming, 2800 m	9.5	Schoettle 1990
		Wyoming, 3200 m	13.1	
Pinus monophylla	Elevation	California, 1951 m	8.0	Ewers and Schmid 1981
		California, 2274 m	10.0	
Pinus muricata	Elevation	California, 46 m	2.7	Ewers and Schmid 1981
		California, 182 m	3.5	
Pinus ponderosa	Elevation, climate zone	Coastal and < 1200 m	≈3	Weidman 1939
		Interior, 800–1700 m	≈4 to 6	
		Interior, > 2100 m	≈5 to 8	
Pinus sylvestris	Latitude	Central Europe	3 to 4	Pravdin 1969
		Northern Europe	7 to 9	
Pinus sylvestris	Latitude	Southern Finland (10 sites)	3.7	Jalkanen et al. 1995
		Northern Finland (10 sites)	5.3	
Picea mariana	Latitude	Minnesota	≈5 to 8	Reich, unpublished
		Interior Alaska	≈8 to 15	Hom and Oechel 1983

Table 2. Intraspecific phenotypic differences in maximum needle longevity for pine (*Pinus*) populations of four species grown at two or three different elevations in California, USA. Data adapted from Ewers and Schmid (1981).

Species	Population elevation of origin (m)	Test site elevation (m)	Needle longevity (year)
P. longaeva	3109	287	7.6
		3109	16.8
P. monophylla	1951 and 2274	287	7.6
		1951 and 2274	8.0 to 10.0
P. flexilis	3109	287	3.8
		843	4.8
		3109	9.0
P. muricata	46–182	46 to 182	2.7 to 3.5
		287	3.8
		843	4.7

populations along elevational gradients in the Karkonosze Mountains in southwestern Poland. A detailed understanding of the relative contributions of phenotypic versus genotypic controls on conifer needle traits is critical to our ability to explain conifer adaptative features and to predict responses to potential future climate scenarios. Needle retention is an important trait that is related to a host of other leaf, stand and ecosystem properties (Reich et al. 1992, Gower et al. 1993, Reich et al. 1994).

Materials and methods

Detailed information about the seed sources, populations and experimental conditions are available from Oleksyn (1988) for the Scots pine study and from Modrzynski (1995) for the Norway spruce experiment. The Scots pine experiment was located in the Experimental Forest Zwierzyniec of the Institute of Dendrology, near Kórnik in central Poland (52°15′ N and 17°04′ E). The experiment was established in 1984, under the auspices of the International Union of Forest Research Organization, with the planting of two-year-old nursery seedlings grown from seed collected from 19 locations in Europe. In this study, we largely restrict consideration to 16 populations of lowland origin (< 300 m) within the contiguous range of *Pinus sylvestris*. These populations were planted in blocks of 48 (4 rows × 12 trees) in at least four replicate blocks. Three other populations that inhabit high elevations (900–1400 m) in iso-

conifer species to determine whether climate-driven genotypic variation in needle longevity occurs within species.

We evaluated needle longevity in 16 Scots pine and 18 Norway spruce (*Picea abies* L.) populations growing in common garden experiments at separate locations in western Poland. The Scots pine populations were grown from native seeds collected across a large latitudinal gradient from Scandinavia to Hungary. The Norway spruce populations were from native

lated relict stands in southeastern Europe and Turkey were included in the provenance study. It has been shown that these isolated southern populations differ from those of the continuous central and northern European range and are considered to be separate ecotypes (Oleksyn et al. 1992). Because of this, and the potential confounding of elevation and latitude, these three populations were not included in the analyses.

The Norway spruce experiment was located in the Experimental Forest Siemianice of the Poznan Agricultural University in Morawina, Poland (elevation 180 m, 51°15′ N and 18°05′ E). The seedlings were planted in 1977 from seed collected in 18 locations in the Karkonosze National Park in southwestern Poland. Seed was collected from mother trees that established between 1800 and 1893. All populations were planted in blocks of 16 (4 rows × 4 trees) in at least three replicate blocks. In other common garden studies, these Scots pine and Norway spruce populations have shown large variation in phenology and growth that corresponds to latitude or elevation, and thus are considered natural clinal genotypes (Oleksyn 1988, Oleksyn et al. 1992, Modrzynski 1995, Oleksyn et al. unpublished data).

Needle longevity was assessed by counting annual needle cohorts. Measurements were made in early June 1991 and 1995 for Scots pine and Norway spruce, respectively. Neither Scots pine nor Norway spruce show multiple flushes in these environments. Average needle longevity per branch was assessed by counting the number of annual cohorts that retained a majority (> 50%) of their needles. Thus, our data are relatively representative of average needle life span, not maximum retention as in Ewers and Schmid (1981), although the differences are probably minor. Because shading induces greater needle longevity lower in the crown (Reich et al. 1994, Schoettle and Fahey 1994), we evaluated needle longevity for several upper and lower branches, and used the average values for these analyses. For all populations in the Scots pine experiment we assessed 10 trees in each of four blocks. Because results did not differ by block, we sampled less extensively in the Norway spruce plantation, assessing four trees in each of two blocks.

Results and discussion

There was no correlation (*P* > 0.20) between mean needle longevity and either latitude of origin for Scots pine or elevation of origin for Norway spruce (Figures 1 and 2), or any of several climate indices (datat not shown). All Scots pine populations retained needles for between 1.5 to 2 years (and thus carried 2.5 to 3 needle age classes, including the current-year foliage). All Norway spruce populations retained needles for between 5.4 to 6.2 years (and thus carried 6.4 to 7.2 needle age classes, including the current-year foliage). If genotypic variation driven by climate gradients existed we would expect a positive correlation between number of needle age cohorts and latitude or elevation of origin. Thus, it is clear that in both species there was no genotypic predisposition toward longer-lived foliage for populations from high latitudes or elevations. Both common garden studies were located in the intermediate
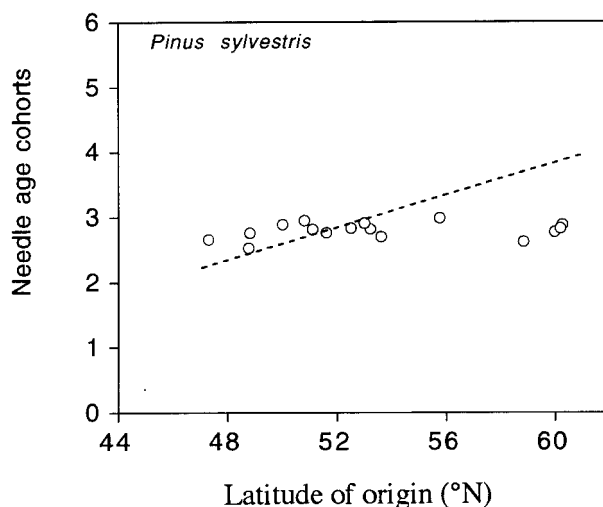

Figure 1. Mean number of needle age cohorts (annual age classes) in a common garden plantation (52° N) in Kórnik, Poland for 16 *Pinus sylvestris* (Scots pine) populations originating in low elevation sites across a latitudinal gradient. Standard deviation of number of needle age cohorts across blocks averaged about 10% of the mean values. There was no significant relationship (*P* > 0.20) between needle longevity and latitude. The dashed line represents a hypothetical relationship between needle longevity and latitude of origin for these populations in this common garden environment if variation in needle longevity had a significant genotypic component (the exact position of the line has no meaning, given that this is an idealized conceptual hypothesis). This hypothesis is not supported.
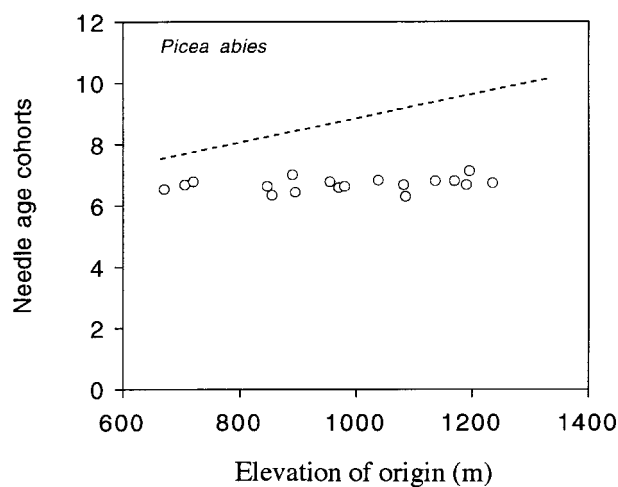

Figure 2. Mean number of needle age cohorts (annual age classes) in a common garden plantation (at 180 m elevation) in Morawina, Poland for 18 *Picea abies* (Norway spruce) populations originating in southwestern Poland along an elevational gradient. Standard deviation of number of needle age cohorts across blocks averaged about 10% of the mean values. There was no significant relationship (*P* > 0.20) between needle longevity and elevation. The dashed line represents a hypothetical relationship between needle longevity and elevation of origin for these populations in this common garden environment if variation in needle longevity had a significant genotypic component (the exact position of the line has no meaning, given that this is an idealized conceptual hypothesis). This hypothesis is not supported.

or warmer end of the biogeographic population gradient. It is not known whether interpopulation differences might occur in high latitude or high elevation common gardens where conditions conducive to extended needle longevity would be greater.

The three Scots pine populations from isolated southern montane habitats all had shorter mean needle retention (1.2 to 1.3 years, 2.2 to 2.3 needle age cohorts) than the central or northern populations. However, when data for these three populations were included with data for the16 lowland populations, there was no significant correlation ($P > 0.20$) between needle retention and several indices of average climate (e.g., mean annual temperature or growing season length). The three southern populations had shorter needle retention ($P < 0.05$) than populations originating at sites with similar mean temperatures (from further north but at low elevations) (data not shown). These differences may reflect interracial or ecotypic differences that are common between these isolated southern populations and populations from the contiguous zone of Scots pine further north (Oleksyn et al. 1992).

The tendency of evergreen conifers such as pine and spruce to have long-lived foliage compared with other plant species is part of a set of intrinsic leaf and whole-plant genotypic traits (Reich et al. 1992, 1994). In contrast, these intraspecific characteristics of Scots pine and Norway spruce populations suggest that long needle life span at high elevations and high latitudes (see Table 1) is likely not a genotypic adaptation of local populations, but a phenotypic acclimation driven by environmental conditions acting on the internal regulatory mechanisms of leaf life span (Reich et al. 1992, Schoettle and Fahey 1994, Reich 1995). For example, needle retention in *Pinus contorta* was inversely related to shoot growth both within tree crowns (Schoettle and Smith 1991) and across elevational gradients (Schoettle 1990), suggesting that the plasticity of needle longevity in evergreen conifers may enable a consistency in crown architecture among environments (Weidman 1939, Schoettle and Fahey 1994). Variation in needle longevity among populations in their native environment was more closely related (and inversely) to variation in temperature regime than to elevation or latitude *per se* (Weidman 1939, Jalkanen et al. 1995).

Direct proof of phenotypic rather than genotypic control would be data showing patterned variation in needle longevity for the Scots pine and Norway spruce populations in this study grown across their natural climate gradients (elevational and latitudinal). Weidman (1939) found such patterns in native environments (see Table 1), but not in a common garden. Other published data also show intraspecific differences in needle longevity for populations along natural latitudinal and elevational gradients (see Table 1); a comparable increase in needle longevity within a population when planted at increasing elevations (Table 2); and no intraspecific differences in needle longevity for populations when grown in common gardens (Figures 1 and 2, and Burger 1931, Nageli 1931, Weidman 1939).

Collectively, there are now nine studies (those cited in Tables 1 and 2, plus Burger 1931, Nageli 1931, and the present study) that have yielded data that do not support the idea of genotypic differences in needle longevity among conifer populations found along climatic gradients, but that indicate a strong control over needle longevity patterns due to climate or associated factors (such as soil fertility). It is interesting that needle longevity appears not to vary genotypically among spruce and pine populations that occur along marked climatic gradients, because these same populations vary appreciably and predictably in common gardens with respect to needle chemistry, respiration rates, phenology and growth (Oleksyn 1988, Oleksyn et al. 1992 and unpublished data, Modrzynski 1995, Reich et al. 1996). This lack of intraspecific differentiation contrasts with the large observed interspecific differentiation; species differ in leaf life-span genotypically over a 50-fold range among all trees, and at least several-fold within the *Pinus* genus.

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