

Growth and physiology of *Picea abies* populations from elevational transects: common garden evidence for altitudinal ecotypes and cold adaptation

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Summary

1. There are conflicting reports concerning the adaptive features of tree populations originating from cold, high-altitude environments. We hypothesize that such trees will possess adaptive features that will be demonstrated in a common environment, such as elevated rates of net CO₂ exchange, elevated needle nitrogen concentration and high proportional biomass allocation to roots. To test this hypothesis we measured tree and seed properties of 54 populations of Norway spruce [*Picea abies* (L.) Karst.] located along eight altitudinal transects (from c. 600 to 1500 m) in southern Poland. We also measured growth, biomass partitioning, net photosynthetic capacity (A_{\max}), needle dark respiration (RS) and carbohydrate, nitrogen (N) and chlorophyll concentration of seedlings originating from these populations grown for 2 to 7 years in a common garden at 150 m elevation. Measured *in situ* along the elevational transects, there were linear declines in seed mass, average d.b.h. and height growth increment of seed trees with increased altitude or lower mean annual temperature.

2. In the common garden, the Norway spruce populations from colder, high-altitude habitats had higher N concentration in needles than those from low altitudes. Both A_{\max} and needle RS increased with altitude of seed origin and were significantly related to needle N concentration. High-altitude populations also had higher concentrations of chlorophyll and carotene than those from low elevations. Despite higher photosynthetic rates in high-altitude populations, seedling height and dry mass in the common garden declined with altitude of seed origin. Proportional dry mass partitioning to roots nearly doubled with increasing altitude of origin, while the length of the shoot-growth period was reduced. The high respiration rates, high allocation to roots and reduced shoot-growth period are probably responsible for the low growth rate potential of high-altitude populations, more than offsetting their higher photosynthetic rates.

3. The results of this study showed that Norway spruce populations from cold mountain environments are characterized by several potentially adaptive features. Because these were similar to conifer population responses along a latitudinal gradient of origin, they are probably driven by climate. These climate-driven differences were common to all transects: for a given altitude or mean annual temperature, plant traits were independent of mountain range of origin. However, populations originating from cold high-elevation sites often differed per unit change in altitude or mean annual temperature more than did low elevation populations. The scaling of nitrogen, CO₂ exchange and biomass and allocation patterns may be useful in modelling Norway spruce response on montane forest ecosystems under changing environments.

Key-words: Biomass partitioning, nitrogen, photosynthesis, provenance, respiration

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Introduction

The altitudinal limit of a species distribution depends both on geographic location and on local environmental conditions. For example, the Norway spruce [*Picea abies* (L.) Karst.] tree limit in northern Finland and at the Kola peninsula in Russia ($\approx 68^\circ\text{N}$) is at 400 m, in southern Norway ($\approx 60^\circ\text{N}$) is at ≈ 1000 m and in Macedonia ($\approx 42^\circ\text{N}$) reaches 2100 m (Boratyńska 1998). Elevational differences in climate are often compared to those observed along lowland latitudinal gradients and there are expectations that selection may cause high- and low-elevation trees to become different.

Norway spruce is one of the most common and important timber trees in Europe. Its natural range extends from France in the west (5°E longitude) to the Ural Mountains (55°E) in the east and from 70°N latitude in northern Norway to 42°N in Macedonia. In central Europe Norway spruce is distributed predominantly in montane habitats and in Scandinavia it is equally common in montane and lowland conditions. Owing to its broad biogeographic range, selection has resulted in substantial genetic diversity within Norway spruce (Cieslar 1907; Engler 1913; Giertych 1976). However, if range-wide comparisons are made across both environment and genotype, broad-scale environmental heterogeneity across the range of Norway spruce confounds any tendency for genotypic patterns to be displayed clearly. Therefore, one effective way to examine such patterns is with common garden experiments that separate genotypic from environmental effects. Past research using the common garden approach indicates that Norway spruce populations originating from higher altitudes are characterized by lower above-ground growth rates, survival and greater resistance to snow and drought damage (Schmidt-Vogt 1972; Holzer 1993; Modrzyński 1995). However, these studies were limited either in the number of populations studied or in the scope of tree responses that were measured. Therefore, although it is probable that high-altitude populations usually grow more slowly than populations from lower elevations we are uncertain as to the population traits that are responsible for these differences.

Growth rate is a function of tissue chemistry, metabolism and morphology, coupled with whole-plant biomass partitioning, architecture and phenology (Lambers & Poorter 1992; Oleksyn, Tjoelker & Reich 1992a,b). Unfortunately, very little is known of differentiation among Norway spruce populations from altitudinal gradients in terms of tissue chemistry, biomass allocation, photosynthesis or respiration. There is some evidence that conifer populations from cold rather than warm environments are genetically entrained to have higher tissue nitrogen (N) concentrations (Kral 1961; Giertych & Fober 1967; Reich, Oleksyn & Tjoelker 1996), which is associated with higher respiration rates and photosynthetic capacity

(Reich, Walters *et al.* 1994; Reich *et al.* 1995; Ryan 1995; Reich, Oleksyn & Tjoelker 1996). In general, there are conflicting reports concerning whether dark respiration rates (in a common environment) are higher for cold- than warm-adapted genotypes (Lechowicz, Hellens & Simon 1980; Chapin & Oechel 1983; Körner 1989; Reich, Oleksyn & Tjoelker 1996), although it seems to be true more often than not, and the reverse has never been reported to our knowledge. However, higher %N and net CO_2 exchange rates are usually associated with greater, not lower, growth rates in trees (Reich, Walters & Ellsworth 1992; Reich *et al.* 1998) and thus such presumed patterns, if they exist in Norway spruce, cannot easily explain the patterns of growth differences (higher growth potential in low-elevation populations).

In Scots Pine, *Pinus sylvestris* L., populations from colder native habitats along very broad latitudinal gradients allocate proportionally more to roots than to needles and their low leaf mass ratios and leaf area ratios were associated with low growth rates (Oleksyn, Tjoelker & Reich 1992a), frequently found in interspecific comparisons (Lambers & Poorter 1992; Reich *et al.* 1992). Those Scots Pine populations also differed in the timing of phenological activities, owing to photoperiodic adaptations, which partially explains population differences when grown in common gardens (Oleksyn *et al.* 1992a). It is not known whether Norway spruce populations from altitudinal gradients display similar tendencies.

To quantify differences in growth and associated plant traits among Norway spruce populations from altitudinal gradients, and better understand their relationships, we examined plant growth, partitioning, net CO_2 exchange rates (respiration and photosynthesis), tissue chemistry (%N, TNC, needle pigments) and phenology of 54 Norway spruce populations in both native and common garden environments. The 54 populations collectively represent eight altitudinal transects from four mountain ranges in two regions of southern Poland. To our knowledge this is the most wide-ranging (in terms of numbers of populations and mountain transects), comprehensive (in terms of the range of physiological measures examined) study of altitudinal tree populations made to date.

Materials and methods

SEED COLLECTION AND NURSERY

Cones were collected in autumn of 1987 and 1988 from 540 standing trees in 54 stands (10 trees per stand) in the Carpathian and the Sudety Mountains in southern Poland. All stands were located between $49^\circ 20'\text{N}$ and $50^\circ 18'\text{N}$ latitude and $16^\circ 46'\text{E}$ and $20^\circ 06'\text{E}$ longitude. The location of the Sudety and the Carpathian Mountains as well as the vertical profile of mountains in Poland are shown in Fig. 1. The sites were chosen to span a relatively large area, across

the major mountain ranges with Norway spruce in Poland. In summer of 1988 and 1989, 0.33 ha plots were established in each stand, and elevation above sea level and slope angle recorded. The age of seed stands was provided by local forest records. Diameters at 1.3 m (d.b.h.) were measured in two directions for all trees in all plots. The height of every fifth tree in a plot was measured and the volume and number of trees per ha calculated (Table 1). To compare growth rates between seed stands average stand height and d.b.h. were divided by stand age to calculate height (m year^{-1}) and d.b.h. (cm year^{-1}) increments.

In each transect, cones were collected from four to 16 elevations, from foothill to summit or forest altitudinal limit (Tables 1 and 2). On average the timberline in the Tatra Mountains is at ≈ 1500 m, in the Beskid Wysoki at ≈ 1400 m and in the Kotlina Kłodzka and the Karkonosze at ≈ 1300 m (Fig. 1; J. Zientarski, unpublished data).

Temperature and precipitation data were obtained from published long-term meteorological data sets originating from six stations at different altitudes in the Tatra Mountains (stations at 840 and 1407 m), the

Beskid Wysoki (at 650 and 1400 m) and the Kotlina Kłodzka (at 600 and 1331 m) Mountains. These data (Konček & Orlicz 1974; Chomicz & Samej 1974; Obrebska-Starkłowa 1983; B. Głowicki, unpublished data) were used to calculate mean annual temperature and precipitation. Annual temperature was estimated to vary by 0.41, 0.53 and 0.60 $^{\circ}\text{C } 100 \text{ m}^{-1}$ for the Tatra, the Beskid Wysoki and the Kotlina Kłodzka Mountains, respectively. For the same mountains annual precipitation rate was estimated to vary by 85, 56 and 52 $\text{mm } 100 \text{ m}^{-1}$ (Table 1).

Seeds were extracted and sown in late April of 1989 in nurseries at the Murowana Gosolina Experimental Forest ($52^{\circ} 33' \text{N}$, $17^{\circ} 06' \text{E}$, 95 m) and the Agricultural University in Poznań ($52^{\circ} 26' \text{N}$, $16^{\circ} 34' \text{E}$, 85 m). At the Murowana Gosolina Experimental Forest seeds were sown in a substrate consisting of a mixture of peat, forest soil and used organic champignon substrate (2:1, $\text{pH}_{(\text{water})} - 5.95$; $\text{P}_2\text{O}_5 - 5.6 \text{ mg g}^{-1}$; $\text{K}_2\text{O} - 0.38 \text{ mg g}^{-1}$; $\text{CaO} - 1.7 \text{ mg g}^{-1}$; $\text{MgO} - 0.28 \text{ mg g}^{-1}$). At the nursery of the Agricultural University in Poznań, seeds were sown in a same type of substrate ($\text{pH}_{(\text{water})} - 5.55$; $\text{P}_2\text{O}_5 - 1.8 \text{ mg g}^{-1}$; $\text{K}_2\text{O} - 0.97 \text{ mg g}^{-1}$; $\text{CaO} - 2.18 \text{ mg g}^{-1}$; $\text{MgO} - 0.74 \text{ mg g}^{-1}$). In both nurseries 2–3 g of seeds of individual trees of each stand were sown in three replicated blocks in 100 cm rows, 10 cm apart. From May to August 1989, seedlings in both nurseries were watered each day. The climate of the region has a transitional character between maritime and continental. The average annual precipitation is 526 mm and average temperature 7.7°C , with a mean growing season length (measured as the number of days with temperature $\geq 5^{\circ}\text{C}$) of 220 days.

GROWTH AND ALLOCATION MEASUREMENTS

Measurements of height after the first and second growing season, hypocotyl length and stem diameter were made for 2-year-old seedlings in the Murowana Gosolina nursery. After the second growing season a harvest was made to determine the dry mass of roots, needles and stem (plus buds) and root length (from root collar to root end). On average 120 plants per population were measured and harvested (range between 20 and 150). The total number of harvested plants was high (6344 plants), because growth of F_1 progeny of individual mother trees was tracked separately. However, in this paper results from all trees are pooled together and family differences are not discussed. Based on these harvest data, we calculated leaf (LWR), stem (StWR), shoot (leaf + stem, ShWR) and root (RWR) dry mass ratios.

COMMON GARDEN IN THE SIEMIANICE EXPERIMENTAL FOREST

In March 1994, 5-year-old trees of 48 out of 54 populations from both nurseries were planted in three

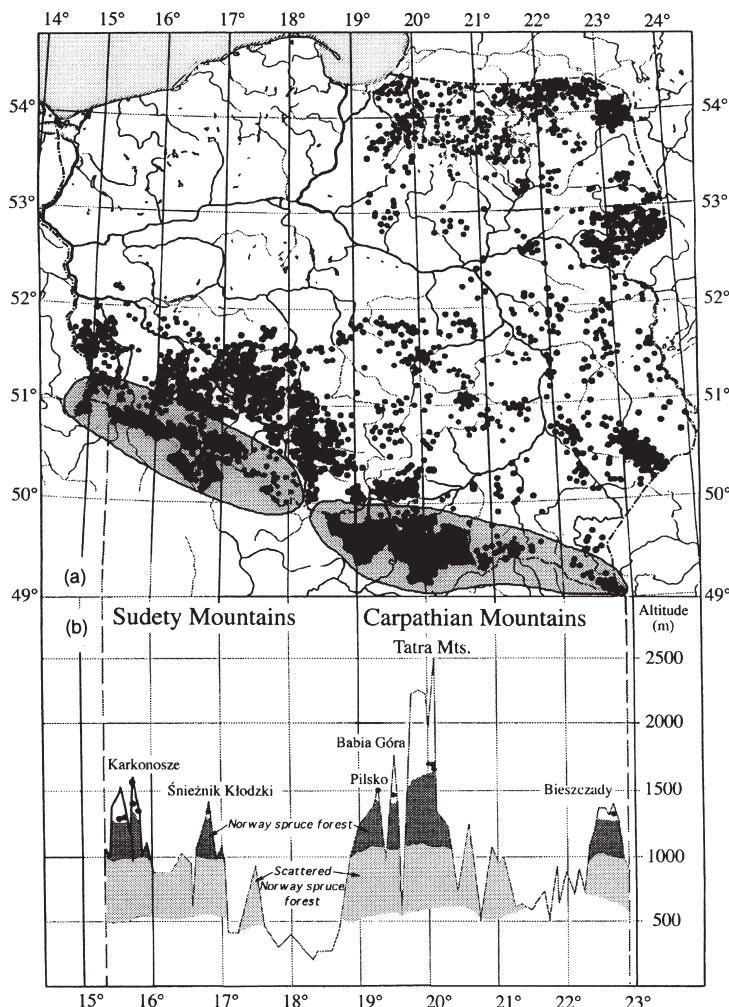


Fig. 1. Distribution of Norway spruce *Picea abies* in Poland: (a) geographic distribution. Dots represent native stands noted in the literature (Boratynski, 1980); (b) altitudinal distribution (Boratynska, 1997). Dots indicate sites above the tree-line.

replicated blocks at the Siemianice Experimental Forest (Dobrygość Forest District, 51° 14' N, 18° 10' E, altitude 150 m). The total area of the experimental site is 0.5 ha. Each block is 19.2 × 67 m and each plot is 4.8 × 5.6 m. On each plot 16 trees (eight

from each nursery) were planted in 1.2 × 1.4 m spacing. The average annual temperature for Siemianice is 7.5 °C, average January and July temperatures are –2.5 °C and 17.6 °C, respectively. The mean length of growing season, measured as the number of days with

Table 1. The origin of seeds of *Picea abies* used in the study and seed stand characteristics

Popu- lation no.	Region	Mountains and geographical location	Transect and location	Altitude (m)	Annual temperature (°C)	Annual precipitation (mm)	Seed stand characteristics									
							Height (m)	DBH (cm)	Volume (m ³)	Number of trees per ha	Age (year)	Seed mass (mg)				
1	Carpathian	Tatra	Dolina Rybiego Potoku	834	4.9	1125	22.4	23.7	579	330	85	8.4				
2				1094	3.9	1342	31.3	42.1	192	407	135	7.1				
3				1245	3.3	1470	27.4	30.9	780	871	125	7.3				
4				1459	2.4	1652	19.7	31.7	441	387	195	6.0				
5				20° 06' E	Dolina Kondratowa	1002	4.2	1263	26.9	41.7	255	476	135	8.5		
6				1175		3.5	1410	25.3	32.2	408	441	80				
7				1427		2.5	1625	14.2	24.0	636	242	155	5.9			
8					Dolina Mietusia	978	4.6	1243	27.3	31.1	624	697	80	8.4		
9				1009		4.2	1383	25.4	33.8	510	616	85	7.4			
10				1203		3.4	1434	26.4	45.1	285	630	140	6.6			
11					Beskid Wysoki	Babia Góra	1478	2.3	1668	19.5	31.8	603	520	195	6.7	
12							925	4.4	1332	29.4	33.7	417	585	85	7.8	
13							1003	4.0	1375	29.2	32.6	315	406	90	9.1	
14							1285	2.5	1533	20.9	38.7	249	356	200	7.5	
15							1308	2.4	1546	19.7	36.4	309	357	200		
16							Pilsko	776	5.2	1248	30.7	42.8	180	492	100	7.8
17								1058	3.7	1406	27.1	32.3	387	450	100	7.9
18								1226	2.8	1500	22.7	34.0	321	382	190	
19							1321	2.3	1554	14.8	27.9	375	271	190		
20	Sudety	Kotlina Kłodzka	Góry Bialskie	705	5.6	1024	24.2	33.4	414	410	95					
22				775	5.1	1060	25.2	37.6	282	372	90	9.1				
21				50° 13' –	844	4.7	1096	29.0	40.5	294	514	140	9.3			
23				50° 18' N	865	4.6	1107	22.0	35.3	408	400	85	8.5			
25				and 16° 58' –	926	4.2	1139	27.4	37.2	255	352	135				
26				17° 01' E	976	3.9	1165	23.7	39.9	249	329	90	9.6			
27					989	3.9	1171	28.4	46.9	150	330	155	8.9			
24					1027	3.6	1191	21.9	42.8	213	294	155				
28					1050	3.5	1203	25.5	51.1	141	319	145	7.9			
29					1060	3.4	1208	19.2	32.2	330	234	135	9.0			
31					1096	3.2	1227	22.3	40.7	186	244	155	8.6			
30					1100	3.2	1229	18.6	36.8	141	137	155				
32					1116	3.1	1237	17.0	28.7	390	211	95	8.0			
38					50° 11' –	Śnieżnik Kłodzki	663	5.8	1002	31.6	44.0	123	268	105	8.5	
33					50° 16' N		666	5.8	1003	30.1	35.3	423	594	100	9.7	
40					and 16° 46' –		798	5.0	1072	28.1	48.9	186	429	95	9.0	
39					16° 52' E		857	4.7	1103	26.0	45.0	255	472	125	8.8	
41					929		4.2	1140	24.6	34.2	384	416	90	8.4		
34					943		4.1	1147	21.7	37.7	303	343	95	8.4		
35					1052		3.5	1204	30.1	48.1	168	408	135	8.7		
47					1094	3.2	1226	19.9	32.2	369	290	105	8.1			
42					1161	2.8	1261	13.4	24.0	510	157	80				
36					1162	2.8	1261	23.7	42.5	249	381	150				
43					1181	2.7	1271	20.0	44.9	177	249	165				
46					1204	2.6	1283	18.6	35.5	267	232	165				
44					1215	2.5	1289	16.9	36.8	273	228	145				
45					1222	2.5	1292	20.7	40.4	180	218	155				
37					1270	2.2	1317	14.3	32.2	342	192	145				
48					1279	2.1	1322	15.5	41.8	165	156	165				
49		Karkonosze	Karkonosze	594	6.2	966				70	9.5					
51		50° 45' –		744	5.3	1041					80					
50		50° 50' N		803	5.0	1075					90	10.4				
52		and 15° 28' –		1103	3.2	1231					110					
53		15° 51' E		1213	2.5	1288					140					
54			1221	2.5	1292					160						

Table 2. Information on sites and data collected

Site	Age of trees (years)	Year of measurements	Description of data collected
54 sites along elevational gradients in the Carpathian and the Sudety Mountains, southern Poland	70–200	1987–1988	On 0.33 ha plots cones were collected from 10 standing trees and measurements of tree height, d.b.h., volume, number of trees ha ⁻¹ were taken. After seed extraction seed mass and per cent of empty seeds were evaluated
Nursery (Murowana Goslina)	1 and 2	1989–1990	Height (at age of 1 and 2 years), hypocotyl height, diameter at root collar, root length, foliage, stem and root dry mass (at age 2 years)
Common garden (Siemianice Experimental Forest)	7	1995–1996	Height, terminal leader length extension, net photosynthesis, needle dark respiration, specific leaf area, glucose, starch, photosynthetic pigments and nitrogen

temperature $\geq 5^{\circ}\text{C}$ is on average 213 days. The soil type at the Siemianice site consists of podzolic soil on loamy sands of medium depth.

FOLIAR GAS EXCHANGE AND SPECIFIC LEAF AREA

Gas exchange rates of 7-year-old trees of 21 populations representing several altitudinal transects were measured with portable photosynthetic systems (LCA-3, Analytical Development Corporation, Hoddesdon, England) used in the differential mode. The system was calibrated against known CO_2 standards. Light-saturated net photosynthesis (A_{max}) was measured on shoots under field conditions at the Siemianice common-garden site, using the Parkinson leaf chamber PLC-C. Measurements of A_{max} were taken on sunny days between 09.00 and 13.00 h (PPFD usually exceeded $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$) between 31 July and 2 August 1995, on current-year needles. During the measurements, air temperature averaged $27.3 \pm 0.1^{\circ}\text{C}$, relative humidity averaged 65% (VPD $\approx 1.25 \text{ kPa}$) and CO_2 concentration averaged $374 \pm 2 \text{ p.p.m.}$

Dark respiration (RS) rate of detached twigs of current-year growth was measured under constant conditions after at least 30 min (usually several hours) in the dark (r.h. 70%, $23 \pm 0.1^{\circ}\text{C}$). For each population six (three trees per two blocks) A_{max} and RS measurements were taken. Current-year Norway spruce needles were fully elongated and thickened at the time of measurements. Therefore, according to the functional model of plant respiration (Ryan 1995), respiration from such foliage represents largely maintenance respiration, because growth (except secondary lignification) and construction respiration decline toward autumn. After gas-exchange measurements, needles were oven dried at 65°C and weighed.

The projected area (one-sided) of fresh 1-year-old needles in the Siemianice common-garden site was determined using the AgVision image analysis system (Decagon Devices, Inc., Pullman, WA, USA).

Needles were oven dried (65°C for 48 h) and weighed. Specific leaf areas (SLA, defined as the projected needle area divided by needle dry mass) were measured on 10 needles per tree for six trees per population (three trees per block, in two blocks). Needles for SLA were collected on 19 April 1996.

MEASUREMENTS OF FOLIAGE PIGMENT CONCENTRATIONS, TNC, NITROGEN AND SHOOT LENGTH GROWTH

Concentrations of needle chlorophyll *a* and *b* and carotene were determined spectrophotometrically, following 4 h extraction of needle fragments at 60°C in dimethyl sulphoxide (Barnes *et al.* 1992). For each population needles from four trees per block in two blocks were sampled. Total non-structural carbohydrate (TNC) concentrations were determined using a modification of the method described by Hassig & Dickson (1979) and Hansen & Møller (1975). Sugars were extracted from oven-dried (65°C , 48 h) needle 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 of sample with peroxidase-glucose oxidase-o-dianisidine dihydrochloride reagent. Absorbance was measured at 450 nm after 30 min incubation at 25°C . Soluble sugars and starch concentration are expressed in mg of glucose g^{-1} dry mass. Glucose concentrations were calculated from standard curve linear regression equations. Data are means of two replications from equally weighed composite samples of five trees for each of two blocks sampled.

Nitrogen was measured on dried (65°C for 48 h) tissue ground in a Mikro-Feinmühle Culatti MFC mill (1.0 mesh, Janke & Kunkel GmbH, Germany), using needles that were used in RS measurements. The

samples were digested by the micro-Kjeldahl method. The sampling procedure and number of replications were the same as for the TNC measurements. Needles for pigment and TNC analyses were sampled on 19 April 1996, after more than 2 weeks with daily temperature between 5 and 14 °C.

Shoot length growth was measured once per week during the seventh growing season on two populations each from high altitudes (nos 11 and 15 from 1478 and 1308 m) and low altitudes (nos 12 and 8 from 925 and 978 m) from the Carpathian Mountains. The measurements started on 14 March and continued for 27 weeks until 12 September 1995. Each week 15 trees per population (five trees per block) were measured. In October 1995 the height of all trees in the experimental site (144 plants per population in three blocks) were measured.

STATISTICAL ANALYSES

For all variables, differences among populations and mountain ranges were calculated using analysis of variance (GLM procedures). Relationships between altitude of origin, annual temperature and other studied traits were made using correlation and regression analyses. For presentation, both correlation and regression are used but we do not assume that direct causal relations are involved, except perhaps for the needle %N-CO₂ exchange and %N-plant pigments patterns. An average linkage, hierarchical method was used to compute cluster groupings of Norway spruce populations based on dry mass partitioning (RWR, LWR, StWR). Other clustering methods (centroid and Ward's) showed comparable results. All statistical analyses were conducted using JMP software (version 3.1.5, SAS Institute, Cary, NC, USA). To test the generality of the altitude and needle %N relationship, we obtained published %N data for Norway spruce needles and total seedlings in common garden experiments (Kral 1961; Giertych & Fober 1967).

Results

SEED AND SEED STAND CHARACTERISTICS ALONG ELEVATIONAL TRANSECTS

The age of seed stands increased linearly with altitude from *c.* 80 years at 600 m to 200 years at high altitudes (Tables 1 and 2). Seed mass decreased linearly with increasing altitude or decreasing mean annual temperature (Fig. 2). On average, seed mass varied from 9–10 mg at 600 m to 6–7 mg above 1400 m (Table 1 and Fig. 2). Seed mass was also linearly related to the seed stand age ($r^2=0.28$, $P=0.001$, data not shown). However, partial correlation analysis including both altitude and mother tree age showed that seed mass was significantly correlated with altitude ($r^2=0.45$, $P<0.001$) and not with the seed stand age ($r^2=0.01$, $P>0.1$). The percentage of empty seeds increased

linearly with altitude (Fig. 2). At high altitudes, above 1400 m, up to 95% of seeds were empty, whereas at lower altitudes that percentage varied between 20 and 50. Both tree diameter and height growth decreased sharply with colder temperatures and higher elevations (Fig. 2).

SEEDLING GROWTH IN COMMON-GARDEN EXPERIMENTS

Populations differed significantly in hypocotyl height as well as in height after the first, second and seventh growing seasons (Table 3). Height declined linearly with altitude of seed origin for 1-year-old ($r^2=0.49$) and 2-year-old ($r^2=0.64$) seedlings ($P<0.0001$, data not shown). Similar, linear relations of tree height with altitude or mean annual temperature were observed after the seventh growing season (Fig. 3). At 7 years old, population height changed with origin at a rate of 25 mm 100 m⁻¹ or 53 mm 1 °C⁻¹. Average population height for overlapping altitudes (776 to 1279 m) was 510 ± 13 mm for the Carpathian Mountains and 467 ± 10 mm for the Sudety Mountains (differences were significant at $P=0.01$). However, no such differences were found when average plant height was compared for overlapping mean annual temperature (2.3 to 4.9 °C): height for the Carpathian Mountains averaged 463 ± 15 mm and for the Sudety Mountains 460 ± 14 mm ($P=0.86$). Seed stand height increment was also correlated with height of 7-year-old trees (Fig. 3). Not surprisingly, height growth differences in 7-year-old trees in a common garden were much more muted than in altitudinal transects, where both genotype and environment work together to result in very large height growth rate differences.

Seed mass and seedling heights were positively correlated. Correlation coefficients between seed mass and seedling height were 0.40, 0.50 and 0.60 for 1, 2 and 7-year-old plants, respectively (all $P\leq 0.02$, data not shown). However, covariance analysis for seed mass using the partial correlation analysis procedure showed that plant height was significantly affected by the mean annual temperature of origin ($r\geq 0.49$, $P<0.01$) and not by seed mass.

Average root system length of 2-year-old seedlings increased with the altitude of seed origin (Table 3, $r^2=0.38$, $P<0.0001$). Root length to shoot length ratio for plants at age two averaged 1.8 and the differences among populations were highly significant (Table 3). Moreover, in contrast to relationships between tree height and the altitude or mean annual temperature this relationship was clearly not linear. Populations originating from altitudes below 950 m (or above 4 °C mean annual temperature) do not show any altitude/temperature related changes. Those from altitudes above 1000 m changed more or less linearly and root length to shoot length ratio increased several-fold between 1000 and ≈1500 m altitude (Table 3).

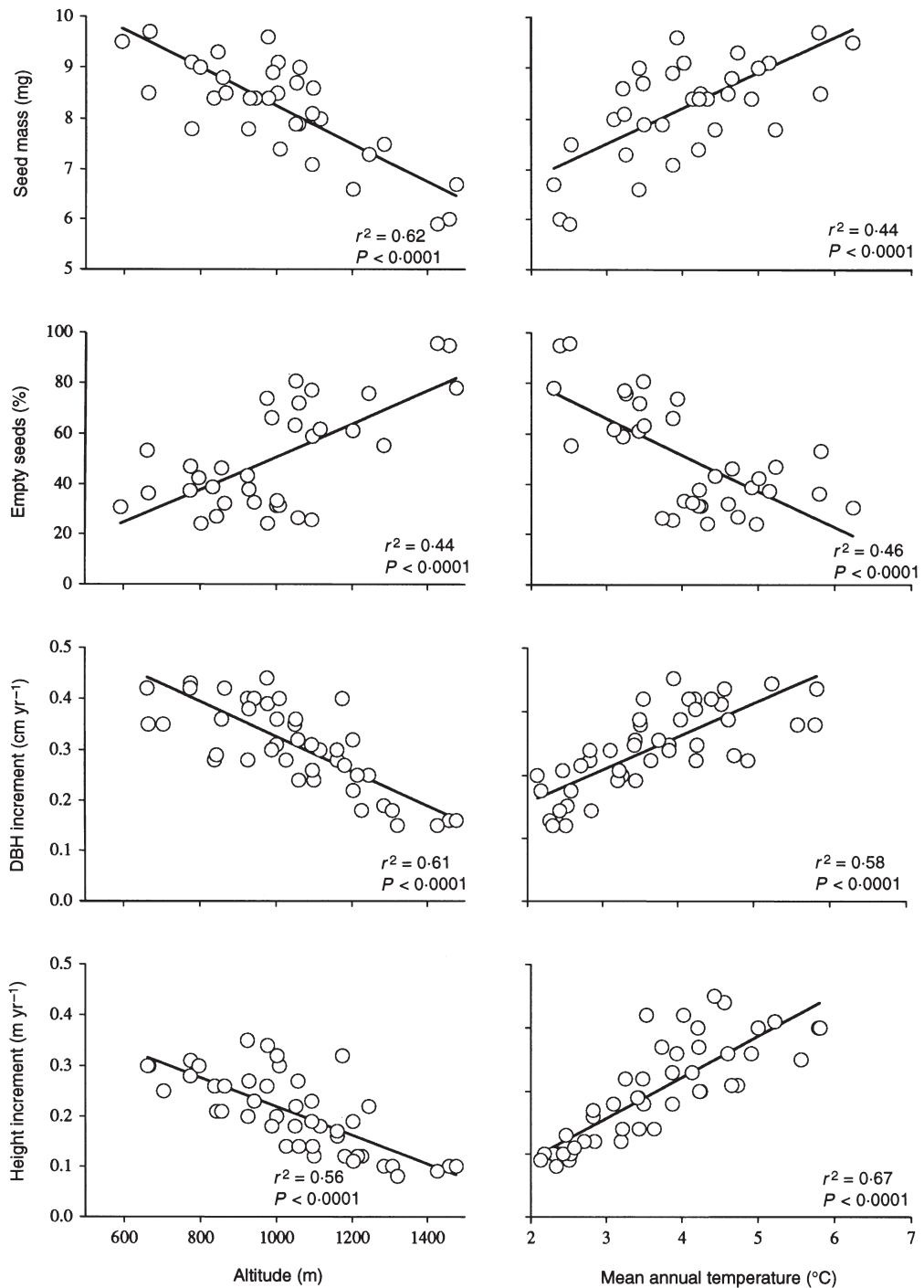


Fig. 2. Seed mass, % empty seeds, d.b.h. and height increment of Norway spruce seed stands in relation to the altitude and mean annual temperature of origin for each stand.

Stem diameter of 2-year-old seedlings varied between 1.8 to 2.8 mm and was significantly different among populations (Table 3). In general, populations originating from locations with average annual temperatures <3 °C had lower than average values of stem diameter, and between 3 and 6 °C there was a plateau in stem diameter. No relationship was found between the stem diameter of 2-year-old seedlings and d.b.h. increment of mother trees ($r^2=0.05$, $P=0.13$, data not shown).

Across all mountain ranges, component and total dry mass of 2-year-old plants and its partitioning differed significantly among populations (Table 3). The lowest mass values were always noted for high-altitude plants (Table 3 and Fig. 4). The relationships were not linear across the entire temperature/altitude range. Needle, stem, root and total plant biomass increased approximately linearly only for populations originating from above 1000 m or below 4 °C. Seedlings originating from sites with mean annual temperatures between 4

Table 3. Mean hypocotyl, 1-, 2- and 7-year-old tree height, stem diameter, root length to shoot length ratio and biomass components of 2-year-old plants for Norway spruce populations. Populations are ordered by altitude of origin. For all population effects $P < 0.0001$

Population no. ^a	Altitude (m)	Hypocotyl height (mm)	(mm) Height at age (year)			Diameter (mm)	Root length (mm)	Root to shoot length ratio	Stem (g)	Needle (g)	Shoot (g)	Root (g)	Total plant (g)
			1	2	7								
49	594	15	31	143	567	2.0	110	0.8	0.48	0.74	1.22	0.23	1.45
38	663	15	30	126	560	2.1	123	1.0	0.44	0.78	1.22	0.28	1.50
33	666	14	25	127	602	1.9	123	1.0	0.42	0.71	1.13	0.24	1.37
20	705	13	30	143	523	2.3	123	0.9	0.59	0.91	1.50	0.32	1.82
51	744	14	26	123	552	1.9	115	0.9	0.39	0.70	1.08	0.22	1.31
22	775				557								
16	776	14	28	127	489	2.1	113	0.9	0.42	0.75	1.17	0.25	1.42
40	798	15	28	135	505	2.1	125	0.9	0.47	0.73	1.20	0.28	1.48
50	803	16	31	130	573	2.2	128	1.0	0.53	0.82	1.35	0.30	1.65
1	834	15	31	147	537	2.2	134	0.9	0.60	0.90	1.51	0.32	1.83
21	844	12	31	152	485	2.2	114	0.7	0.58	0.87	1.45	0.26	1.71
39	857	13	28	136	540	2.1	121	0.9	0.54	0.84	1.38	0.31	1.69
23	865	13	29	144	477	2.2	129	0.9	0.56	0.88	1.44	0.29	1.73
12	925	12	29	138	499	2.1	111	0.8	0.51	0.76	1.27	0.26	1.52
25	926	12	24	109	527	2.2	126	1.2	0.49	0.83	1.32	0.29	1.61
41	929	12	26	127	536	2.0	115	0.9	0.42	0.71	1.13	0.23	1.36
34	943	15	28	111	514	2.0	113	1.0	0.37	0.53	0.90	0.22	1.13
26	976	14	26	93	465	2.4	155	1.7	0.45	0.69	1.14	0.37	1.51
8	978	14	30	126	523	2.1	122	1.0	0.42	0.64	1.05	0.23	1.29
27	989	13	24	72	489	2.1	146	2.0	0.27	0.44	0.71	0.28	0.98
5	1002	14	33	147	493	2.2	136	0.9	0.59	0.82	1.41	0.32	1.73
13	1003	13	31	139	591	2.3	122	0.9	0.59	0.88	1.47	0.31	1.77
9	1009	13	24	116	536	1.9	119	1.0	0.36	0.58	0.94	0.22	1.16
24	1027	13	28	130	464	2.8	142	1.1	0.79	1.20	1.98	0.48	2.46
28	1050	13	23	62	400	2.0	136	2.2	0.25	0.40	0.65	0.29	0.94
35	1052	12	22	82	485	2.5	163	2.0	0.40	0.56	0.96	0.38	1.34
17	1058	14	29	118	534	2.1	123	1.0	0.40	0.66	1.06	0.26	1.31
29	1060	12	23	89	464	2.1	129	1.5	0.36	0.59	0.95	0.27	1.22
2	1094	14	28	118	487	2.0	133	1.1	0.42	0.64	1.06	0.25	1.32
47	1094	11	22	80	411	2.2	177	2.2	0.36	0.58	0.93	0.32	1.25
31	1096	12	22	76	405	2.2	151	2.0	0.30	0.46	0.76	0.29	1.05
30	1100	12	21	66	426	2.1	158	2.4	0.26	0.44	0.70	0.27	0.96
52	1103	13	23	91		2.3	174	1.9	0.48	0.76	1.24	0.38	1.62
32	1116	13	22	67	444	2.1	155	2.3	0.27	0.44	0.71	0.26	0.98
42	1161	13	23	76	441	2.2	178	2.3	0.38	0.63	1.02	0.36	1.38
36	1162	13	21	44	389	1.9	167	3.8	0.15	0.27	0.42	0.22	0.64
6	1175	14	27	120	509	2.3	142	1.2	0.53	0.79	1.32	0.32	1.64
43	1181	13	21	52	409	2.1	196	3.7	0.20	0.32	0.51	0.31	0.82
10	1203	13	28	92	463	2.2	129	1.4	0.34	0.51	0.85	0.26	1.11
46	1204	11	21	75	425	2.1	197	2.6	0.29	0.44	0.73	0.38	1.11
53	1213	14	21	48		2.0	141	2.9	0.19	0.26	0.44	0.23	0.68
44	1215				456								
54	1221	13	22	63		1.9	149	2.4	0.27	0.41	0.67	0.29	0.96
45	1222	13	23	47		2.1	135	2.9	0.15	0.23	0.38	0.17	0.55
18	1226	12	22	64	446	2.2	150	2.3	0.27	0.43	0.71	0.28	0.99
3	1245	14	30	120	518	2.6	159	1.3	0.62	0.81	1.43	0.41	1.84
37	1270	13	20	39		2.1	157	4.1	0.15	0.23	0.38	0.25	0.63
48	1279	12	19	39		1.5	155	3.9	0.11	0.15	0.26	0.18	0.43
14	1285	11	18	45	396	1.8	128	2.8	0.15	0.27	0.42	0.17	0.59
15	1308	11	19	42	353	1.9	144	3.5	0.15	0.26	0.41	0.18	0.59
19	1321	11	18	38	326	1.9	148	3.9	0.13	0.24	0.37	0.19	0.56
7	1427	12	21	53	372	1.9	140	2.6	0.18	0.27	0.45	0.19	0.64
4	1459	13	24	68	418	2.2	171	2.5	0.30	0.41	0.72	0.34	1.06
11	1478	11	17	38	335	1.8	153	4.0	0.13	0.23	0.36	0.17	0.53
Mean		13	25	95	477	2.1	141	1.8	0.37	0.58	0.96	0.28	1.24

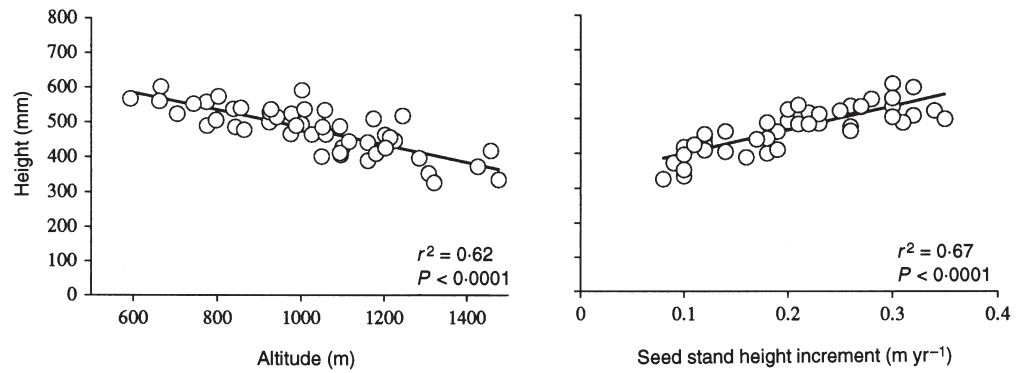


Fig. 3. Height of 7-year-old Norway spruce populations in common garden in relation to the mean annual temperature of population origin and seed stand height increment.

and $\approx 6^\circ\text{C}$ showed a plateau for all biomass parameters. The coefficient of variation for root biomass was 23%, whereas for needles, stem and total plant was 41, 43 and 36%, respectively. On average, total plant biomass for populations originating above 4°C mean annual temperature was $1.5 \pm 0.04\text{ g}$ and dropped to 0.6 g for high-altitude populations originating from sites with a mean annual temperature of $\approx 2^\circ\text{C}$ (Fig. 4).

Populations significantly differed in proportional biomass partitioning, with high-altitude plants having low biomass allocation to stem and needles and high to roots (Table 3 and Fig. 4). We found a strong curvilinear response between mean annual temperature of seed origin and biomass allocation parameters and root to shoot ratio. The biomass allocation of populations originating from sites with a mean annual temperature below $\approx 4^\circ\text{C}$ (or elevation $>1000\text{ m}$) showed nearly linear changes with temperature of seed origin, and above $\approx 4^\circ\text{C}$ (or elevation $<1000\text{ m}$) there were plateaus in these relationships (Fig. 4). On average, in the plateau region between 4 and 6°C mean annual temperature, plants dry mass partitioning averaged 18% to roots, 51% to needles and 31% to stems. Among high-altitude genotypes these values increased up to 2.2-fold for RWR and decreased by 0.7-fold for LWR and StWR.

In order to examine whether RWR of populations is confounded by the ontogenetic drift related to differences in plant mass (observed along the altitudinal transect), we conducted covariance analysis using the natural logarithm of plant mass as the covariate. Accounting for plant mass differences, populations differed in RWR.

Cluster analysis classification techniques were used to group populations with similar biomass partitioning to stem, needles and roots. The results of the cluster analyses are summarized in a dendrogram (Fig. 5). Two distinct cluster groups can be identified. In one group only populations from cold habitats in high elevations are present, ranging in origin from sites with average annual temperatures from 2.1 to 3.9°C . In another are grouped those from sites with average

annual temperature above 4°C , except for population nos 3, 6 and 2 from the Tatra Mountains from sites with average annual temperatures 3.3 , 3.5 and 3.9°C , respectively. These three populations behaved more like low-altitudinal ones in biomass partitioning as well as in total plant biomass and all other growth parameters including plant height at 7 years old (Table 3). Average values of all studied traits for the two identified cluster groups are summarized in Table 4. Biometric traits are all statistically different between those groups except the stem diameter and root mass of 2-year-old seedlings (Table 4).

There were no differences in the time of budburst among two high-altitude (nos 11 and 15) and two low-altitude (nos 8 and 12) populations. The growing season for these four populations started between 10 and 17 May (130 and 137 day of year, Fig. 6). However, the time of terminal leader growth cessation (the date when shoot length reached 95% of final height) of these populations was different and linearly related to the altitude of seed origin (Fig. 6). Despite this phenological difference, the differences in final shoot length were largely related to growth rate and less to growing season length. For example, 61 to 71% of the difference in final shoot length between the high-altitude population no. 11 (from 1478 m) and the other three populations was related to growth rate and only 29 to 39% to the growth period of the terminal leader. The role of growth rate was more pronounced in low-altitude populations (from 925 and 978 m) where only 9% of the difference in final shoot length was related to differences in growth period.

NEEDLE GAS EXCHANGE, PIGMENTS, CARBOHYDRATES AND NITROGEN

The highest measured A_{max} values ($\approx 61\text{ nmol g}^{-1}\text{ s}^{-1}$) were noted for plants originating from the two highest elevations ($\approx 1450\text{ m}$) and the lowest ($\approx 36\text{ nmol g}^{-1}\text{ s}^{-1}$) for the population from the lowest elevation (663 m). Overall, A_{max} of populations growing at 150 m in the

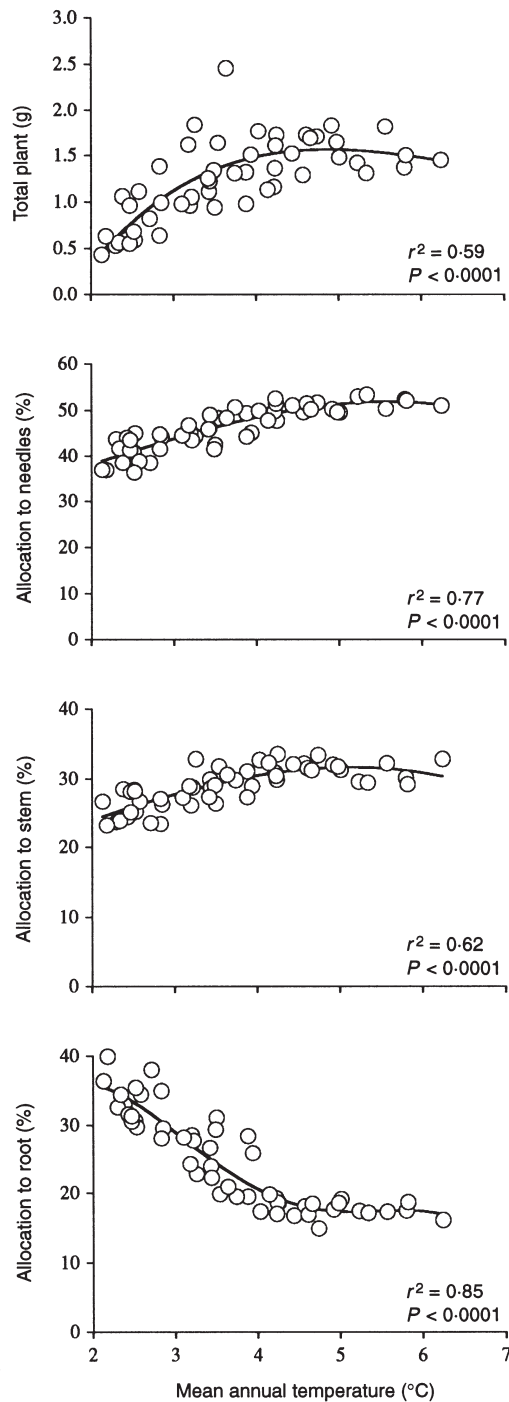


Fig. 4. Total plant mass, proportional biomass allocation to needles, stem and root of 2-year-old Norway spruce seedlings in relation to the annual temperature at place of seed origin.

common garden was highly correlated with the population's altitude of origin (Fig. 7). For common altitudinal (776–1279 m) or temperature (2.3–2.9 °C) gradients there were no statistically significant differences in A_{\max} between the Carpathian and the Sudety Mountains ($P \geq 0.22$, data not shown).

Needle RS values varied among populations between ≈ 8 and $\approx 11 \text{ nmol g}^{-1} \text{ s}^{-1}$. Needle respiration rates were related, but weakly to altitude or mean annual temperature of origin (Fig. 7). Similar to A_{\max} ,

no significant differences between mountain ranges in RS rates were observed.

Nitrogen concentrations in current-year needles of 7-year-old trees of 21 populations ranged from 1.3 to 2.2% and the differences among populations were statistically significant (Table 5). Needle %N concentrations were correlated with the altitude of population origin ($r^2 = 0.48$, $P = 0.0005$) or mean annual temperature ($r^2 = 0.38$, $P = 0.002$). In two other common-garden studies reported in the literature (Kral 1961; Giertych & Fober 1967), there were statistically significant relationships between the altitude of seed origin and needle or total plant %N ($r^2 \geq 0.52$, $P \leq 0.01$). Pooling data from all three studies, there was a significant relationship between altitude and needle or plant %N (Fig. 8). Both A_{\max} and RS rates were positively correlated with needle %N concentrations (Fig. 7). We do not report here area-based gas exchange because SLA measurements were taken on the same trees but at a different time as measurements of A_{\max} and RS. However, because there was no relation between SLA and climate of seed origin, relationships between area-based measurements of A_{\max} , RS and N and mean annual temperature of origin likely should be similar to those on a mass basis. Calculation of these parameters on an area basis

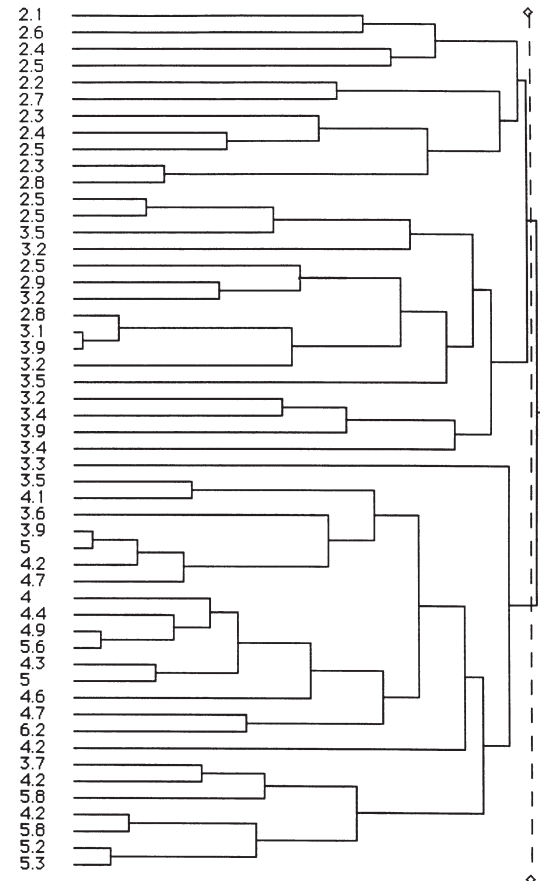


Fig. 5. Dendrogram of cluster groupings of populations of Norway spruce based on similarity of second-year biomass partitioning to stems, needles and roots. For each population the annual temperature at place of seed origin is shown.

(using our SLA values) is consistent with this idea (data not shown).

The contents of all studied pigments were significantly different among 21 populations at the Siemianice common garden (Table 5). Chlorophyll *a*, carotene (Fig. 9) and chlorophyll *a+b* ($r^2=0.20$, $P=0.04$) were significantly correlated with altitude or mean annual temperature of origin. High-altitude populations tend to have higher concentrations of these pigments than those from low elevations. Changes of chlorophyll *b* and *a:b* ratio were unrelated to temperature or elevation of seed origin. Chlorophyll *a*, *a+b* and carotene contents were significantly correlated with A_{max} (Fig. 9). All chlorophyll and carotene values were also significantly correlated with needle %N (all $r^2 \geq 0.35$, and all $P \leq 0.004$).

On average, the concentration of glucose was 162, starch 67 and TNC 228 mg g⁻¹ (Table 5). However, differences among populations were not significant and unrelated to altitude or mean annual temperature of seed origin.

For all populations, average specific leaf area for plants in the Siemianice experiment was ≈ 46 cm² g⁻¹,

Table 4. Mean values of biometric and physiological parameters for two Norway spruce altitudinal ecotype groupings (with mean annual temperature below and above 4 °C)

Parameter	n	Mean annual temperature at place of origin		ANOVA effects $P > F$
		<4 °C	>4 °C	
Seed mass (g)	34	7.7	8.7	0.004
Empty seeds (%)	34	67	36	<0.0001
Hypocotyl height (mm)	52	13	14	0.0007
Height, 1 year old (mm)	52	23	29	<0.0001
Height, 2 year old (mm)	52	72	132	<0.0001
Height, 7 year old (mm)	52	434	533	<0.0001
Root length, 2 year old (mm)	52	153	121	<0.0001
Root:shoot length, 2 year old	52	2.4	0.9	<0.0001
Stem diameter, 2 year old (mm)	52	2.1	2.1	0.90
Stem mass, 2 year old (g)	52	0.30	0.49	<0.0001
Needle mass, 2 year old (g)	52	0.47	0.77	<0.0001
Shoot mass, 2 year old (g)	52	0.77	1.26	<0.0001
Root mass, 2 year old (g)	52	0.28	0.27	0.49
Root:shoot, 2 year old	52	0.41	0.21	<0.0001
RWR, 2 year old (%)	52	29	18	<0.0001
StWR, 2 year old (%)	52	27	31	<0.0001
LWR, 2 year old (%)	52	44	51	<0.0001
ShWR, 2 year old (%)	52	71	82	<0.0001
Needle N, 6 year old (%)	21	1.83	1.55	0.0009
Chlorophyll <i>a</i> , 6 year old (µg g ⁻¹)	21	4.5	3.9	0.01
Chlorophyll <i>b</i> , 6 year old (µg g ⁻¹)	21	1.1	1.0	0.25
Chlorophyll <i>a+b</i> , 6 year old (µg g ⁻¹)	21	5.6	4.9	0.03
Chlorophyll <i>a/b</i> , 6 year old	21	4.1	3.9	0.17
Carotene, 6 year old (µg g ⁻¹)	21	1.4	1.2	0.004
Glucose, 6 year old (µg g ⁻¹)	21	159	165	0.26
Starch, 6 year old (µg g ⁻¹)	21	65	70	0.26
TNC, 6 year old (µg g ⁻¹)	21	224	235	0.14
SLA, 6 year old (cm ² g ⁻¹)	21	46	46	0.77
A_{sat} , 6 year old (nmol g ⁻¹ s ⁻¹)	21	54.6	45.1	0.0002
RS, 6 year old (nmol g ⁻¹ s ⁻¹)	21	10.1	9.3	0.08
A_{sat} : RS	21	5.5	5.0	0.02

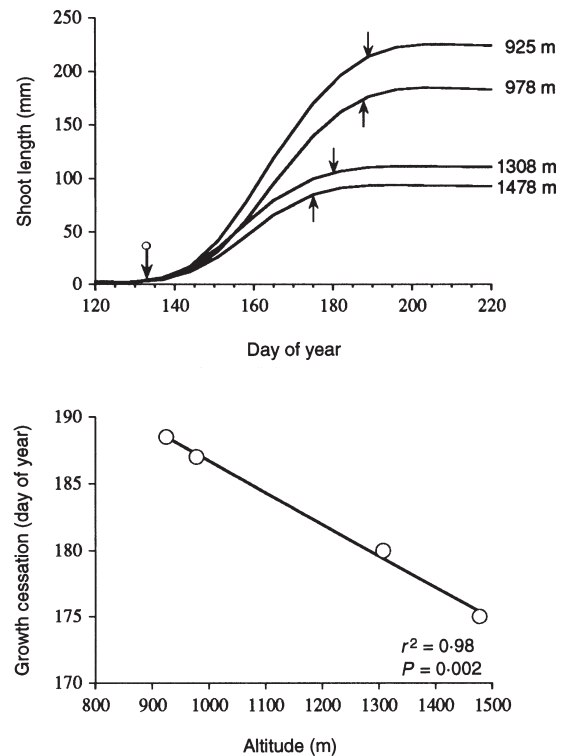


Fig. 6. Seasonal time course of shoot length growth of two low- and two high-altitudinal populations of Norway spruce. Mean values of terminal leader shoot length were recorded during the seventh growing season in a common garden (upper graph). Growth cessation was calculated as the day of year when 95% of final shoot height was attained (indicated by arrows) and is shown in relation to the population's altitude of origin (bottom graph).

and the differences among populations were statistically significant (Table 5). However, variation in SLA, needle length, mass or projected area among populations was unrelated to the altitude or temperature at place of origin.

Discussion

PHYSIOLOGICAL TRAITS

The Norway spruce populations from the colder, higher altitudes showed higher needle %N than those from low altitudes (Table 5 and Fig. 8). Similar results were also obtained in two other reports of Norway spruce altitudinal populations from Poland and the Alps grown in common-garden conditions (Kral 1961; Giertych & Fober 1967; Fig. 8). Similar to results presented here, we found a linear relationship between needle %N and mean annual temperature in place of origin in *P. sylvestris* populations from a broad latitudinal range (Reich, Oleksyn & Tjoelker 1996).

A linear relationship between the altitude of seed origin and needle %N could be a result of genetic adaptations to an altitudinal nitrogen availability gradient, related to the slow mineralization of litter,

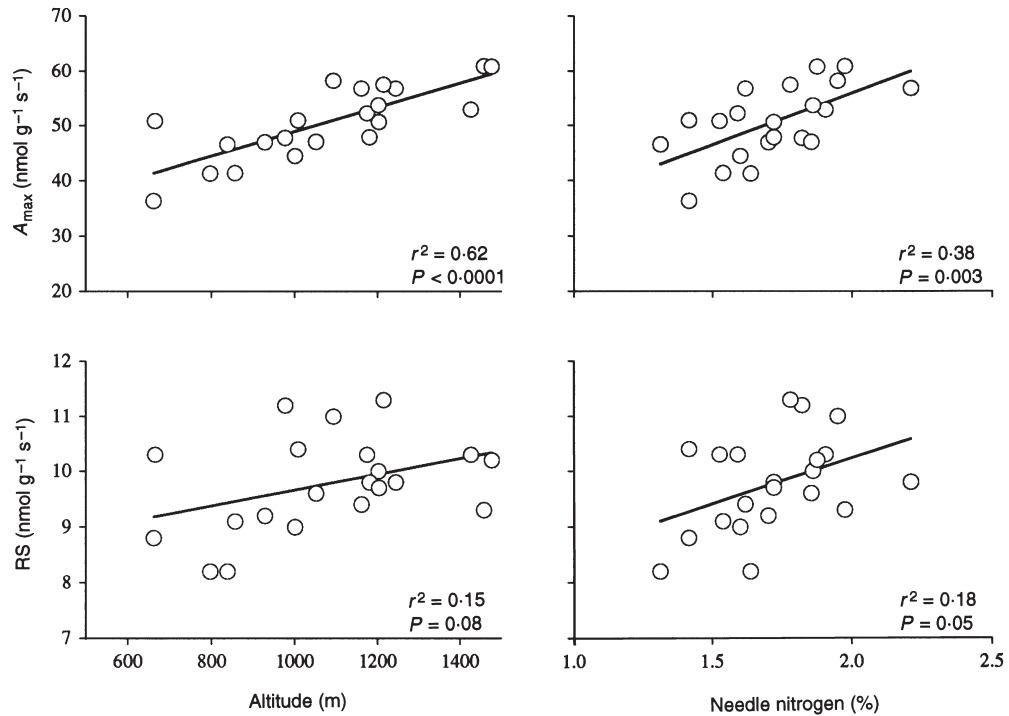


Fig. 7. Mean needle light-saturated net photosynthesis (A_{\max}) and respiration (RS) rates in Norway spruce populations growing in common-garden conditions in relation to the altitude of origin or needle nitrogen concentration of each population.

Table 5. Mean CO_2 exchange, specific leaf area (SLA) glucose, starch, total non-structural carbohydrates (TNC) and pigment concentrations of current-year foliage for Norway spruce populations. Populations are ranked by altitude of origin

Population no. ^a	Altitude (m)	A_{\max} (nmol $\text{g}^{-1} \text{s}^{-1}$)	RS (nmol $\text{g}^{-1} \text{s}^{-1}$)	SLA ($\text{cm}^2 \text{g}^{-1}$)	Glucose (mg g^{-1})	Starch TNC (mg of glucose g^{-1})		Chlorophyll (mg g^{-1})				Carotene (mg g^{-1})	Needle nitrogen (%)
								<i>a</i>	<i>b</i>	<i>a+b</i>	<i>a/b</i> ratio		
38	663	36.3	8.8	44.2	160	65	226	3.41	0.87	4.27	4.0	1.07	1.42
33	666	50.8	10.3	43.4	156	76	232	4.46	1.06	5.52	4.2	1.26	1.53
40	798	41.2	8.2	49.1	159	63	222	3.43	1.12	4.55	3.5	1.15	1.64
1	834	46.5	8.2	48.8	190	62	252	3.77	0.95	4.72	4.0	1.19	1.31
39	857	41.3	9.1	42.6	167	66	233	2.93	0.69	3.62	4.2	0.98	1.54
41	929	46.9	9.2	43.1	157	66	223	4.60	1.16	5.77	4.0	1.29	1.70
8	978	47.7	11.2	52.5	163	79	242	4.51	1.19	5.71	3.8	1.36	1.82
5	1002	44.4	9.0	44.9	170	80	250	4.25	1.22	5.47	3.5	1.36	1.60
9	1009	50.9	10.4	45.9	160	65	224	3.57	0.89	4.45	4.0	1.12	1.42
35	1052	47.0	9.6	40.5	153	52	205	4.09	0.93	5.01	4.4	1.22	1.85
2	1094	58.2	11.0	39.5	143	60	203	5.49	1.59	7.09	3.6	1.63	1.95
36	1162	56.8	9.4	40.7	156	59	216	4.64	1.06	5.71	4.4	1.40	1.62
6	1175	52.2	10.3	46.7	159	83	242	3.88	0.99	4.86	3.9	1.24	1.59
43	1181	47.8	9.8	51.7	167	65	232	4.72	1.08	5.80	4.4	1.38	1.72
10	1203	53.7	10.0	49.7	156	69	224	3.77	0.96	4.72	4.0	1.24	1.86
46	1204	50.6	9.7	45.7	160	47	207	4.40	1.02	5.41	4.3	1.36	1.72
44	1215	57.5	11.3	44.3	182	72	254	4.68	1.11	5.79	4.2	1.39	1.78
3	1245	56.8	9.8	42.4	141	61	203	4.65	1.36	6.01	3.5	1.51	2.21
7	1427	52.9	10.3	50.5	165	62	227	4.39	1.12	5.51	3.9	1.39	1.91
4	1459	60.9	9.3	44.6	157	80	238	4.63	1.11	5.75	4.2	1.37	1.98
11	1478	60.8	10.2	50.3	173	67	241	4.58	1.02	5.60	4.5	1.37	1.88
Mean		50.5	9.8	45.8	162	67	228	4.23	1.07	5.30	4.0	1.30	1.72
Population effects, <i>P</i> > <i>F</i>		0.006	0.39	0.04	0.58	0.42	0.70	0.003	<0.0001	0.001	0.002	<0.0001	0.05

^aSee Table 1 for origin.

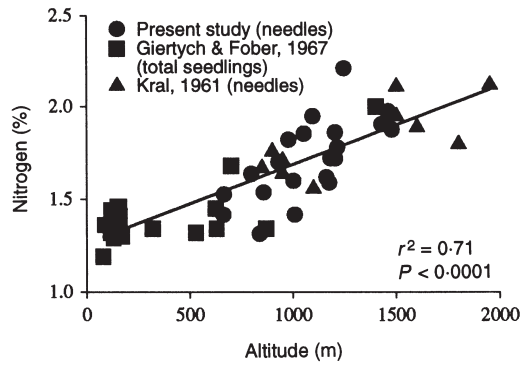


Fig. 8. Needle or total plant nitrogen concentrations in Norway spruce populations in a common garden in the present study and those of Kral (1961) and Giertych & Fober (1967) in relation to the population's altitude of origin. Relationship between altitude of seed stand and needle or plant %N were significant for each study ($r^2 \geq 0.48$, $P \leq 0.01$).

increased N leaching owing to the acidity of the raw humus layers and the frequent waterlogging at high altitudes (Larcher 1995). Plants that are found in nutrient-deprived habitats employ efficient strategies to achieve the necessary metabolic activity required for maintaining their competitive ability despite a shortage of nutrients (Larcher 1995). An increase in biomass partitioning to roots (Fig. 4) can be considered as a factor that may increase the uptake of mineral substances. Similarly, lower above-ground biomass (Fig. 4) and slower growth rate (Fig. 6) make possible better utilization of the available supplies of nitrogen for dry matter production (Körner 1989; Larcher 1995).

The lack of a significant correlation between altitude or mean annual temperature of seed origin and SLA or other needle parameters (such as length, projected area or mass) suggests that higher %N in high elevation populations is unlikely a result of its 'dilution' (for low-altitude populations) or 'concentration' in high-altitude populations as suggested previously (Kral 1961). The lack of clear trends in SLA among such diverse ecotypes may also indicate that the frequently observed decrease with altitude in needle length and other dimensions of width and thickness (for review see: Tranquillini 1979) may be largely a phenotypic response. Similarly, we found that longer needle retention in Norway spruce and Scots pine observed *in situ* in high elevations and high latitudes is most probably not under genetic but under environmental control (Reich, Oleksyn, Modrzyński & Tjoelker 1996). However, the lack of significant altitudinal trends in SLA may be also influenced by lack of lowland populations in our experiment (from altitudes <600 m) and/or changes in needle shape.

Mean needle A_{\max} values ranging from ≈ 36 to $61 \text{ nmol g}^{-1} \text{ s}^{-1}$ observed for current-year needles are in the usual range reported for Norway spruce (Gross

1976; Wedler, Weikert & Lippert 1995). Both A_{\max} and needle RS were significantly related to altitude or mean annual temperature. Results of two earlier studies suggested that such patterns might occur, but these were limited in comparisons of only three or four populations (Pelkonen & Luukkanen 1974; Gross & Hettesheimer 1983).

Both A_{\max} and RS were significantly correlated with needle %N (Fig. 7). Site and species variation in A_{\max} are frequently associated with changes in leaf N (Field & Mooney 1986; DeLucia, Schlesinger & Billings 1989; Reich *et al.* 1992, 1995; Reich, Walters *et al.* 1994). However, in some studies, variation in foliar N among different tree populations or species was unrelated or had little or inconsistent relation to variation in A_{\max} (Sheriff, Namibar & Fife 1986; Reich & Schoettle 1988; Schoettle 1994; Reich, Oleksyn & Tjoelker 1994b).

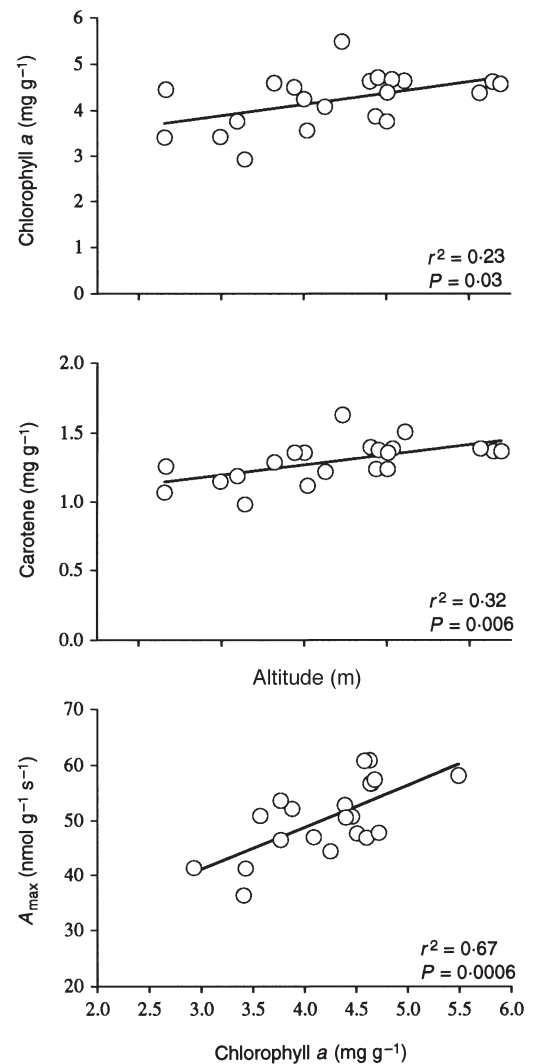


Fig. 9. Chlorophyll *a* and carotene concentration in 1 year-old needles of 7-year-old Norway spruce populations in a common garden in relation to the population's altitude of origin (upper two graphs), and mean needle light-saturated net photosynthesis (A_{\max}) in relation to chlorophyll *a* concentration.

Data from this study are consistent with the idea of a general CO₂ exchange–nitrogen relationship. A positive relationship between %N and A_{\max} can be a result of direct participation of roughly half of leaf nitrogen in the photo- and biochemical photosynthetic processes (Mooney 1986). It is possible that a higher assimilation rate potential of plants from cold habitats represents a genetic adaptation to such environmental conditions, possibly by maintaining higher %N.

Higher RS of Norway spruce populations from colder habitats (Fig. 7) is consistent with similar patterns noted in other species (Mooney 1963; Larigauderie & Körner 1995; Reich, Oleksyn & Tjoelker 1996). The ≈20% differences in maintenance respiration we observed in this study were smaller than those we found in Scots pine populations (≈50%) from along a continuous latitudinal range of 48 to 60°N (mean annual temperature range from 4.7 to 9.5 °C) grown at common-garden conditions at 52 °N in Poland (Reich, Oleksyn & Tjoelker 1996).

The beginning of the growing season in Norway spruce is associated with sharp increase in starch content in needles (Linder 1995). In our studies there were no significant differences among Norway spruce populations in needle starch concentration, and no relationship was found between starch (or glucose) and the altitude of seed origin (Table 5). This finding and the lack of differences in timing of shoot extension among Norway spruce populations from contrasting altitudinal habitats (Fig. 6) indicate that there is very little (if any) difference in time of the beginning of growing season among such diverse populations. Therefore, growth differences among populations cannot be explained by earlier onset of growth.

SEEDS, GROWTH AND BIOMASS ALLOCATION

The average (8.2 mg) and range (5.9–10.4 mg) of seed mass of Norway spruce populations in this study is consistent with the range (3–12.5 mg) usually noted for Poland (Gunia 1995). It is interesting that seed mass in north-eastern Poland (Fig. 1), despite its lowland origin, is consistently ≈20% lower (Dutkiewicz 1968) than those found in this study, except for the highest altitudes. We found a similar pattern in *P. sylvestris*, where seeds originating from high altitudes in south European countries of Turkey, Bosnia and Montenegro were heavier than those from lowland regions further to the north (Reich *et al.* 1994a).

The seed mass of Norway spruce from mountains of southern Poland gradually declines with altitude or with decrease of mean annual temperature of stand origin (Table 1 and Fig. 2). In mountain conditions, plants tend to reduce frequencies of seed years, and the mass and number of seeds produced (Tranquillini 1979; Körner & Renhardt 1987). In our study, seed

mass may also have been influenced by stand age. It is known that trees produce heavier seeds when young than when old (Giertych 1974; Bergsten 1985). Calculated separately, the altitude of seed stand accounted for 60% of seed mass variation, whereas the mean annual temperature and the age of seed stands accounted for 44% and 28% of seed mass variation, respectively (all $P \leq 0.001$). However, multiple regression analysis revealed that only altitude (or mean annual temperature), but not the age of seed trees, was significantly correlated with seed mass.

With increasing altitude there was a significant increase in per cent of empty seeds, to as much as 95%. A decreasing cone and seed mass, a decreasing number of seeds per cone, an increasing proportion of empty seeds, and a reduction in seed quality in Norway spruce were observed previously in a limited number of sites in mountain conditions (Lehotsky 1961; Tranquillini 1979), and most probably, similar to the phenomenon observed in northern Scandinavia (Sarvas 1956; Koski & Malmivaara 1974), associated with inadequate pollination.

Seedling height growth in common garden declined linearly with altitude of seed origin by as much as 80% (Fig. 3 and Table 3). Similar results were also found in studies conducted in different mountain regions (e.g. Schmidt-Vogt 1977; Holzer 1979; Modrzyński 1993).

Height growth variation among populations was significantly correlated with seed mass. However, the correlation with altitude or mean annual temperature of seed origin was stronger than those of seed mass and partial correlation analysis showed that plant height was significantly correlated with mean annual temperature and not seed mass. Moreover, it has been shown in several studies that the persistence of seed mass effects and differences in these effects among populations usually disappear within the first 2–6 years (Reich *et al.* 1994a) and should not play a significant role in height differences among 7-year-old trees.

Norway spruce populations are characterized by high variability and heterozygosity (Lundkwist 1979; Kleinschmidt, Lunderstädt & Svolba 1981; Kleinschmidt, Sauer-Stegmann *et al.* 1981) and they may undergo selection during one generation. Consequently the offspring populations are usually substantially different from the parent populations in terms of phenological and growth characteristics (Holzer 1985). However, there is a possible alternative explanation for the close association and adaptation of populations to mountain conditions resulting from direct selection during the sexual reproduction (either at the haploid pollen level or postzygotic diploid level), rapid genomic changes or epigenetic effects (Johnsen 1989a,b; Johnsen *et al.* 1994). If indeed the environmental conditions during sexual reproduction of Norway spruce can significantly affect the growth and phenology of progeny, then the

entire idea of 'identification' of maternal populations based on progeny traits (Holzer 1967, 1985; Schmidt-Vogt 1972, 1976; Modrzyński 1993, 1995 and other) will be marginally useful.

Several traits such as root to shoot length, needle, stem, root and total plant biomass and proportional biomass allocation showed non-linear responses to altitude or mean annual temperature of seed origin (Fig. 4 and Table 3). In all cases except root mass we found no significant seed origin effect in populations originating from locations with mean annual temperatures between ≈ 4 and 6°C (≈ 600 m to 1000 m elevation), and gradual changes in listed traits for populations originating from sites with a mean annual temperature less than 4°C (>1000 m). This pattern refutes the Wright (1976) hypothesis that 'the rate of gene exchange is much higher between different elevations of the same mountain than between populations of few hundred miles apart. Such continuous gene exchange tends to keep the high- and low-elevation populations from diverging genetically'. The relationship between dry mass allocation and population origin was tested using a cluster analysis technique. The results (Fig. 5 and Table 4) indicate the existence of two main groups: those with mean annual temperatures below 4°C vs above. Based on our data we hypothesize that at low elevations there is a high rate of gene exchange between different populations, and that only in locations with mean annual temperatures below $\approx 4^\circ\text{C}$ are there barriers (most probably phenological) preventing continuous gene exchange. Existence of such phenological barriers could genetically diverge different high-elevation populations more than occurs among different low elevation populations.

The lack of gradual changes of traits for the entire range of altitudes (Fig. 4 and Table 3) is interesting because often continuous clinal changes of growth traits with seed source altitude or latitude have been reported (Giertych 1976). It is possible that non-clinal growth changes among populations are visible mainly when biomass or especially biomass partitioning is assessed, whereas in most of the studies only non-destructive measurements like tree height and/or diameter were conducted. In such measurements, as in Fig. 3, there is no indication of any non-clinal growth changes. Because allocational differences are not related to seed mass (Reich *et al.* 1994a) they are probably better than tree height in assessing altitude–population relationships at a young age.

Extensive production of fine roots and high partitioning of biomass to roots is observed in many plant populations from the cold end of large altitudinal and latitudinal gradients (Holzer 1961; Körner & Renhardt 1987; Oleksyn *et al.* 1992a,b) and has been considered as an adaptation to unfavourable climatic conditions where nutrient supplies are limited. However, because allocation often varies with plant

size (small plants have high root allocation), it is impossible to tell from those earlier studies whether cold-adapted populations do allocate more to roots, or merely had smaller plants at the time of measurements. The extensive sampling approach taken in our study enabled us to evaluate those alternative explanations, with the conclusion that cold-adapted plants do in fact allocate more to roots, even after differences in plant size are accounted for. In addition, there are also other possible factors contributing to increased root over shoot growth of altitudinal Norway spruce populations. There is a close relation between the altitude of seed source and the terminal leader growing season length (Fig. 6). Termination of shoot extension is generally associated with a shift of dry mass accumulation from the shoot to the root (Ledig, Bormann, Wegner 1970) and most of the root growth of *P. abies* occurs after shoot growth cessation (Lyr & Hoffmann 1967).

Differences in the length of the active shoot growth period among populations from different altitudes (Fig. 6) can be controlled by photoperiod and/or temperature. According to Holzer (1966) there are two main photoperiodic groups among altitudinal Norway spruce populations: one growing at lower altitudes, with a 12–14 h day requirement (short-day ecotypes) and the other at higher altitudes with an 18–20 h day requirement to maintain normal growth (long-day ecotypes). Differentiation into these two groups may be associated with time of growing season, which starts in southern Poland at high altitudes in June when the longest daylengths occur and at low elevations in early May when the daylength is much shorter. Because high-altitude populations are sensitive to short days, in lowland conditions they show early growth cessation. However, growing period length alone is responsible for 30 to 40% of the differences in height between high- and low-altitude populations, with the majority of the differences between these groups owing to growth rate differences (Fig. 6); thus both are important and should be considered in models of altitude \times growth interaction.

In summary, the results of this study showed that Norway spruce populations from cold mountain environment are characterized (under common-garden conditions) by reduced growth rate and shorter period of shoot extension, higher proportional biomass partitioning in roots, higher needle nitrogen and pigment concentration and higher rates of photosynthesis and respiration. Enhanced metabolic activity and reduced growth rate are most likely genetically controlled adaptational features across plant species originating from cold environments (Reich, Oleksyn & Tjoelker 1996). Although metabolic rates of high-altitude populations *in situ* are probably lower than those of low-altitude populations, their genotypic predisposition to elevated metabolic rates probably reduces the degree to which their *in situ* rates differ. The degree to which realized growth and

physiological traits of trees along altitudinal gradients are influenced by their genetic differences can considerably affect our current projections of the consequences of expected global climatic changes. However, because some of the patterns vary in a predictable manner it opens the possibility for modelling plant response from cold environments under changing environments.

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