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Biogeographic differences in shoot elongation pattern among European Scots pine populations

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Abstract

Results are presented of shoot elongation of 10-year-old trees of 19 European *Pinus sylvestris* populations growing in a provenance experiment in central Poland. Populations exhibited different shoot elongation patterns with montane southern (40–44°N) and lowland northern (58–60°N) populations having lower growth rates and earlier onset of growth cessation than those from the central lowland part (47–55°N) of European species' range. Average absolute growth rates ranged from 6.6 mm per day for populations of southern origin to 9.2 mm per day for populations from central Europe. Shoot elongation period explained ca. 50–60% and differences in growth rate from 40 to 50% of total differences in annual increment among population groups. There was a linear relationship ($r^2=0.73$, $P<0.0001$) between mean annual temperature (m.a.t.) of seed origin and mean relative growth rate. Populations originating from seeds collected in colder regions (3–6° m.a.t.) had shorter shoot elongation periods than those from warmer (7–10°C m.a.t.) environments. The duration of the shoot elongation period alone explained 86% of total height variation at age 10 years in this experimental site and from 42 to 80% variation in five other sites (in Poland and Croatia) established with same seed lots. Shoot elongation period was negatively related to the proportion of mass allocated to roots, underlying a possible linkage between shoot phenology and below-ground growth. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: *Pinus sylvestris*; Relative growth rate; Provenance; Seed mass; Phenology

1. Introduction

Scots pine (*Pinus sylvestris* L.) is characterized by an extensive area of natural distribution that spans much of Europe and Asia. Scots pine ranges east to west over 14000 km, and north to south nearly 2700 km. Because of large differences in site conditions (including temperature, moisture, photoperiod, growing season length, etc.), and migratory history

during the glaciation and interglacial periods, Scots pine is characterized by having numerous ecotypes with distinct morphological, ecophysiological and growth features (Pravdin, 1969). Due to its economic importance, Scots pine has been planted in central Europe on an ever increasing scale for about 150–200 years leading to its marked presence in numerous countries (Boratynski, 1991). In some localities (Scandinavia, USA) plantations established from unknown seed sources failed to produce good quality trees. Failure of these plantations at the end of the 19th century stimulated recognition of the importance of seed origin in silvicultural practice. Since then several

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large-scale provenance trials to test the influence of origin of Scots pine seed on growth of stands were organized by the International Union of Forestry Research Organizations (in 1907, 1938–1939 and 1982), by Ogievskij (in 1910–1916) in pre-revolutionary Russia and the State Committee of Forestry of the former USSR (in 1970s), and by Wright (NC-51 experiment, late 1950s and beginning 1970s) in the USA (Wright, 1976; Giertych and Oleksyn, 1981, 1992; Shutyaev and Giertych, 1997).

Results of the above-mentioned experiments showed several general trends: (1) movement northward from short day to long day conditions increases height growth compared with local provenances, whereas movement of northern populations southward suppresses height growth; (2) in most cases biometric and physiological characteristics of Scots pine trees vary continuously (clinal) when planted in common gardens, suggesting that these characteristics are, in part, shaped by adaptation to climatic conditions at the seed origin; (3) populations from discontinuous and isolated parts of the species range in the Balkans, Turkey or Spain showed lower growth and limited plasticity.

Most provenance experiments were established to test the influence of origin of seed on growth of plantations, to find regions within which seeds can be safely transferred, and to identify regions with provenances that are productive, resistant to abiotic and biotic factors and produce good wood quality. However, there is relatively little information about the growth traits that distinguish populations from certain regions from others, nor the ecophysiological basis for observed differences. For example, differences in annual height growth increment in a common environment can be explained by variation in growth season length or in growth rate. Such a distinction is important since the former is a phenological attribute, whereas the latter is a physiological characteristic.

Thus, despite a long history of provenance experiments, several questions related to height growth require further studies: To what extent are differences in height growth between diverse populations the result of inherited differences in growth rate or length of the shoot growth period? How do other factors like seed mass or age of plants influence shoot growth rate and growth period? Is the annual pattern of shoot extension unique for populations from different

regions? Is it possible based on such patterns to define biogeographic groups of Scots pine? In order to examine these questions we measured the duration of the shoot elongation period and the growth rate of 19 diverse Scots pine populations grown for 10 years in central Poland. In addition, we also used data from existing provenance experiments established with the same and different seed sources to test the generality of observed patterns.

2. Materials and methods

2.1. Plant material

An experimental site was established in 1984 with seeds of Scots pine (*Pinus sylvestris* L.) collected in 19 locations in Europe (Table 1) as a part of an International Union of Forest Research Organizations Working Party 'Scots pine provenances and breeding' experiment (Oleksyn, 1988). Data on seed germination, mortality, initial seedling growth and mineral contents were presented earlier (Kocięcki, 1985).

In early spring of 1984, 2-year-old seedlings were planted in a permanent plot in the experimental forest, Zwierzyniec, near Kórnik in central Poland (52°15'N, 17°04'E, altitude 70 m). This site consists of seven blocks (each with 7–20 plots). Every provenance was planted in three to seven replicated plots (one per block), 7.2 m × 5.2 m, each with 48 plants (4 rows × 12 plants). Soils at this site are light sands. The climate of the region is transitional between maritime and continental. The average annual precipitation is 526 mm and average temperature 7.7°C, with a mean growing season length of 220 days, calculated as the number of days with an average temperature of 5°C. Soil and needle chemical properties were described in detail earlier (Reich et al., 1994a; Oleksyn et al., 1999).

2.2. Measurements and statistical analyses

The total length of the terminal leader was measured weekly on 15 trees per provenance (five trees in each of three blocks) beginning with a measure of dormant bud length on 15 April, 1991. In the course of measurements a few shoots were damaged by *Rhyacionia buoliana* D. et Schiff. or unknown causes, and were excluded from the data set. The number of

Table 1
The origin of seeds of *Pinus sylvestris* used in the study^a

Region	Provenance No. and origin	Country	Latitude (°N)	Longitude (°E)	Altitude (m a.s.l.)	Mean annual temperature (°C)	1000 seed mass (g)	No. of trees measured
North (>58°N)	1 Roshchinskaya Dacha	Russia	60°15'	29°54'	80	3.4 ^b	5.1	14
	15 Sumpberget	Sweden	60°11'	15°52'	185	4.5	4.4	15
	2 Kondezshkoe	Russia	59°58'	33°30'	70	3.7 ^b	5.3	15
	3 Serebryanskoe	Russia	58°50'	29°07'	80	5.0 ^b	5.6	15
Central (55–48°N)	4 Silene	Latvia	55°45'	26°40'	165	5.4	5.8	15
	5 Milomlyn	Poland	53°34'	20°00'	110	7.1	5.3	14
	6 Suprasl	Poland	53°12'	23°22'	160	7.0	6.6	15
	10 Neuhaus	Germany	53°02'	13°54'	40	8.2	7.7	14
	11 Betzhorn	Germany	52°30'	10°30'	65	8.1	6.8	15
	7 Spala	Poland	51°37'	20°12'	160	7.4	6.2	14
	8 Rychtal	Poland	51°08'	17°55'	190	7.1	5.7	15
	13 Ardennes	Belgium	50°46'	4°26'	110	9.2 ^b	9.0	13
	12 Lampertheim	Germany	50°00'	10°00'	95–100	9.6	6.6	15
	14 Haguenuau	France	48°49'	7°47'	130–180	10.0	6.6	13
	16 Zahorie	Slovakia	48°46'	17°03'	160	10.0	8.1	15
	17 Pornoapati	Hungary	47°20'	16°28'	300	9.6	8.2	14
	South (<45°N)	19 Prusacka Rijeka	Montenegro	44°05'	17°21'	800–970	9.6 ^a	7.1
18 Maocnica		Bosnia	43°10'	19°30'	1200	7.4 ^a	6.6	15
20 Catacik		Turkey	40°00'	31°10'	1380–1420	6.5	9.0	14

^a Provenances are ordered by latitude of origin and grouped based on similarities in instantaneous RGR (see text for explanations).

^b From Walter and Leith (1958), other data according to the SP-IUFRO-1982 experiment participants (Oleksyn, 1988).

measured trees was greater than or equal to 13 (Table 1). The final measurement was taken on 29 July, 1991. At the same time the total height of all sampled trees was measured.

Growth data were examined by fitting temporal data from each provenance in each block with the Richards' function (Bates and Watts, 1988) using statistical software (JMP version 3.2.2 for the Macintosh, SAS Institute Inc., Cary, NC, USA). The time trends derived from Richards function fittings are often more biologically meaningful than those of polynomial exponentials, and are recommended for use in plant growth analysis (Venus and Causton, 1979). The form of the function was:

$$Y = a(1 + b e^{-cx})^{1/d}$$

where Y is the total height increment at point of measurement in cm, a the asymptotic value for the function, b , c and d the shape parameters for the function, and x the day of year when last measurement was conducted

Richards' rate constant, c , is of particular importance when viewed in combination with d (Hunt,

1982). When applied to untransformed primary data, the combination $c/(d+1)$ is a weighted mean relative growth rate (average RGR) over the whole period, and $ac/[2(d+2)]$ is the corresponding weighted mean absolute growth rate (average G). When applied to the logarithmically transformed shoot elongation data the latter is a weighted mean instantaneous relative growth rate. Maximal values of RGR (RGR_{max}) and G (G_{max}) were determined from model fits.

For all variables population effects (a fixed effect, 18 d.f.) were analyzed using a randomized complete block design ($n=3$ blocks) in an analysis of variance (general linear model procedures, JMP, SAS Institute Inc., Cary, NC, USA). The average linkage program was used to compute cluster grouping of the Scots pine provenances according to daily changes in instantaneous relative growth rate. Average linkage distance is the average distance between pairs of points in each cluster.

To evaluate relationships between the relative growth rate or seed mass and height growth, we used published data from several sites established with the same (Kocięcki, 1985; Oleksyn, 1988; Gracan, 1989;

Gunia et al., 1991; Rzeznik, 1991) and different seed lots (Wright and Baldwin, 1957, Schreiner et al., 1962). To test whether the shoot phenology is related to the proportional allocation of biomass to roots (as suggested by Ledig et al., 1970), we used published data from the same site at age 12 (Oleksyn et al., 1999).

3. Results

3.1. Growth rate and duration of the shoot elongation period

There were significant differences in 1991 shoot length and tree height among populations (all $P < 0.0001$). Total tree height varied from 206 cm for population 19 (Montenegro) to 438 cm for population

13 (Belgium) and was correlated with final shoot length in 1991 ($r = 0.98$, $P < 0.0001$, Table 2). For both tree height at age 10 and shoot length in 1991, populations ranked in the following order (reasons for such divisions will be presented later): central populations ($54\text{--}48^\circ\text{N}$) > northern ($>55^\circ\text{N}$) > southern ($<45^\circ\text{N}$).

Duration of the shoot elongation period, defined as number of days from 15 April when shoot elongation started to the day when 90% of shoot length was accomplished, was on average 66 days, and varied from ≈ 60 days for both northern and southern populations to ≈ 70 days for populations from central part of European range of Scots pine (Table 2, Fig. 1). Shoot elongation was completed for northern and southern populations on June 14 and for central populations on June 24.

Table 2

Final 1991 shoot and 10-year-old tree height, shoots relative and absolute growth rate^a, and shoot elongation period (\pm S.D.) of Scots pine populations grown in central Poland

Region	Provenance	Final height (cm)		Relative growth rate, RGR (mm/cm/day)		Absolute growth rate, G (mm/day)		Shoot elongation period (days)
		Shoots	Trees	Average	Maximal	Average	Maximal	
North ($>58^\circ\text{N}$)	1	52 (10)	260 (82)	0.32 (0.03)	0.43 (0.06)	6.2 (1.8)	9.8 (0.3)	60 (3)
	15	60 (1)	309 (24)	0.31 (0.01)	0.40 (0.01)	7.6 (0.3)	10.9 (0.7)	61 (4)
	2	58 (4)	273 (57)	0.29 (0.03)	0.39 (0.04)	7.1 (0.9)	10.0 (1.7)	62 (4)
	3	56 (2)	300 (9)	0.33 (0.02)	0.44 (0.02)	7.4 (0.5)	10.7 (1.2)	59 (3)
	Mean	56 (3)	285 (23)	0.31 (0.02)	0.41 (0.02)	7.1 (0.6)	10.4 (0.5)	60 (1)
Central ($55\text{--}48^\circ\text{N}$)	4	67 (0)	324 (11)	0.35 (0.01)	0.48 (0.01)	8.4 (0.3)	12.8 (0.7)	66 (2)
	5	80 (1)	396 (54)	0.33 (0.03)	0.46 (0.06)	9.4 (0.2)	14.4 (0.2)	71 (4)
	6	70 (3)	347 (45)	0.34 (0.05)	0.46 (0.08)	8.4 (0.5)	12.9 (0.6)	67 (1)
	10	84 (5)	420 (22)	0.36 (0.02)	0.51 (0.04)	9.7 (1.1)	15.1 (1.5)	72 (1)
	11	81 (7)	415 (29)	0.35 (0.01)	0.48 (0.02)	9.4 (1.0)	14.7 (1.5)	71 (4)
	7	76 (6)	379 (45)	0.35 (0.01)	0.48 (0.02)	9.9 (0.7)	14.5 (2.6)	69 (1)
	8	82 (5)	422 (51)	0.35 (0.00)	0.46 (0.02)	9.5 (0.7)	14.8 (1.2)	71 (3)
	13	85 (4)	438 (43)	0.36 (0.01)	0.49 (0.00)	10.0 (0.6)	16.2 (0.8)	71 (2)
	12	82 (1)	387 (40)	0.37 (0.03)	0.51 (0.04)	9.7 (0.2)	15.5 (1.1)	71 (3)
	14	77 (4)	399 (35)	0.36 (0.01)	0.50 (0.01)	9.1 (1.0)	14.4 (1.6)	71 (3)
	16	66 (3)	339 (12)	0.39 (0.02)	0.53 (0.03)	8.0 (0.8)	13.3 (1.5)	70 (1)
	17	78 (2)	432 (20)	0.35 (0.01)	0.47 (0.02)	9.2 (0.6)	14.8 (0.9)	71 (2)
	Mean	77 (6)	392 (38)	0.36 (0.01)	0.49 (0.02)	9.2 (0.6)	14.4 (1.0)	70 (2)
South ($<45^\circ\text{N}$)	19	43 (3)	206 (27)	0.35 (0.01)	0.47 (0.03)	6.0 (0.6)	9.1 (0.6)	60 (3)
	18	50 (6)	232 (36)	0.34 (0.02)	0.43 (0.02)	6.6 (0.9)	10.2 (1.3)	60 (6)
	20	55 (2)	246 (24)	0.35 (0.01)	0.46 (0.03)	7.2 (0.6)	10.9 (0.7)	61 (3)
	Mean	49 (6)	229 (19)	0.35 (0.01)	0.45 (0.02)	6.6 (0.6)	10.0 (0.9)	60 (1)
Mean		68 (14)	344 (80)	0.35 (0.03)	0.46 (0.05)	8.4 (0.4)	12.9 (2.5)	66 (6)
	$P > F$	<0.0001	<0.0001	0.002	0.002	<0.0001	<0.0001	<0.0001

^a Calculated over the shoot elongation period.

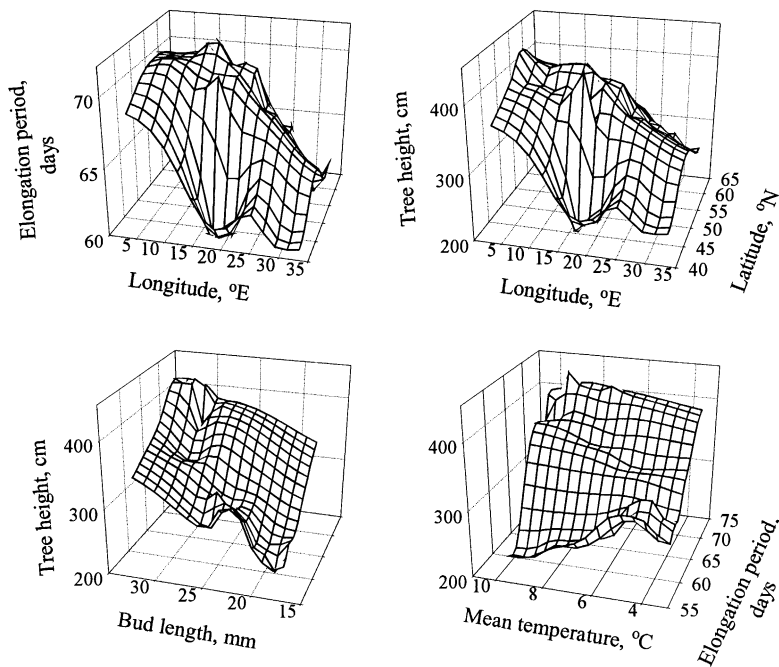


Fig. 1. Three-dimensional models of shoot elongation period and tree heights in relation to longitude and latitude of seed origin, bud length and elongation period. All regression models were significant statistically ($P < 0.01$). See Table 1.

Populations differed in instantaneous relative growth rate (RGR), maximal RGR (RGR_{max}), and average (G) and maximal (G_{max}) absolute growth rates (all $P = 0.004$, Table 2). RGR averaged for the period from the onset of growth to 90% of terminal leader growth cessation explained only 17 and 19% of total height and shoot length among populations, respectively ($P = 0.08$ and 0.06). Slightly better correlations were found between RGR_{max} and total height and shoot length ($r = 0.52$, $P = 0.02$, and $r = 0.54$, $P = 0.02$, respectively).

Average G_{max} for all populations was ≈ 13 mm/day, and different groups of populations ranked in similar order to those for total height and shoot length: central populations (≈ 14 mm/day) > northern (≈ 10 mm/day) = southern (≈ 10 mm/day) (Table 2). G_{max} was highly correlated with both total height and shoot length ($r = 0.96$, $P < 0.0001$).

3.2. Shoot growth in relation to latitude and temperature of seed origin

The relationship between latitude of seed origin and dormant bud length of terminal leaders was curvi-

linear with southern montane and high latitude populations having smaller buds (Fig. 2). The duration of the shoot elongation period was linearly related to mean annual temperature of seed source ($r^2 = 0.39$, $P = 0.004$ for all populations and $r^2 = 0.76$, $P < 0.0001$ after excluding mountain populations 18, 19 and 20). The relationship between latitude and mean RGR was curvilinear. However, when plotted against the mean annual temperature of seed origin, RGR showed a linear relationship with a gradual increase from colder to warmer climatic conditions (Fig. 2). The data presented in Fig. 2 suggest the existence of linear changes of growth parameters when plotted against temperature conditions and curvilinear when plotted against latitude of seed origin for populations grown in a common garden at $52^\circ N$.

For these populations, shoot elongation period and tree height gradually decreased with increasing longitude and reached its maximal values between 47 and $54^\circ N$ latitude of seed origin. Both dormant bud length and shoot elongation period were significantly related to tree height (Fig. 2) and together accounted for 90% of variation in tree height (Tree Ht. = $-393.4 + 6.23$

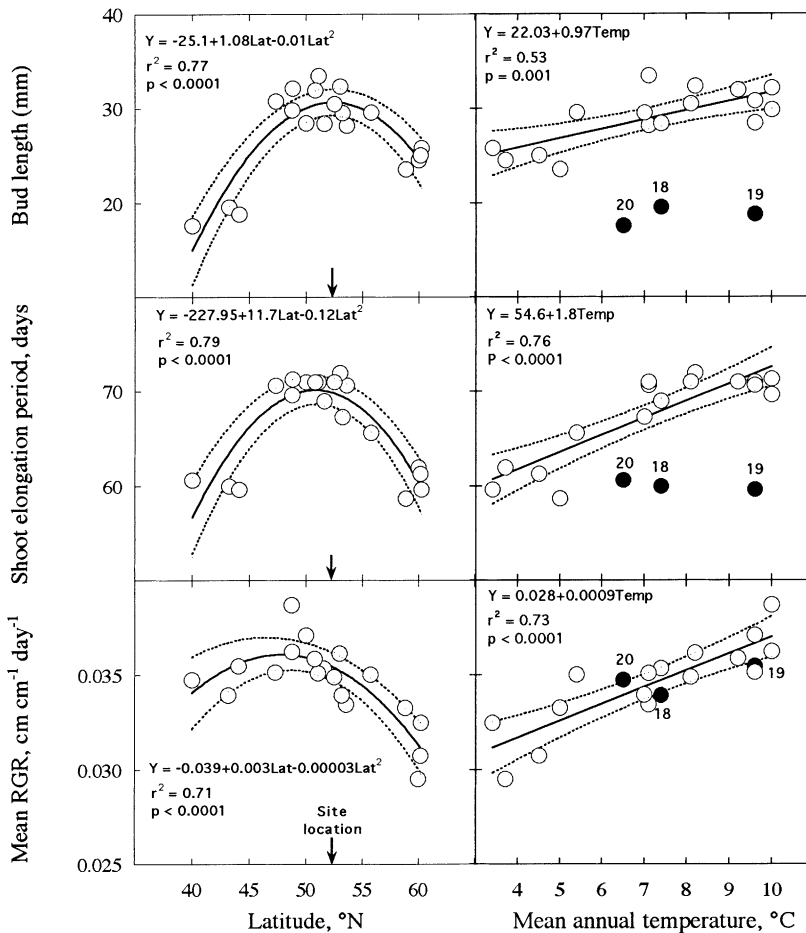


Fig. 2. Mean dormant bud length, shoot elongation period and mean relative growth rate (RGR) in Scots pine populations growing in a provenance experiment in Kórnik, Poland (52°N), in relation to the latitude and mean annual temperature of origin for each population. Southern montane populations from discontinuous range of Scots pine (# 18, 19 & 20) are marked. These populations were excluded from the correlation with mean annual temperature of seed origin. Dotted lines indicate the upper and lower 95% confidence limits for the fitted model.

Bud Lt. (mm)+8.52 Shoot Elongation Period (days)). Similarly, a highly significant multiple regression was noted for tree height as a function of both shoot elongation period and m.a.t. ($r^2=0.89$, $P<0.0001$, not shown).

3.3. Population groups of European Scots pine based on seasonal growth patterns

Seasonal changes of RGR, G, and cumulative growth differed between northern, central and southern populations (Fig. 3). The RGR for central populations was higher for the entire shoot elongation period

than for the other two groups, and RGR for southern populations was higher or equal to those of northern populations.

Absolute growth rate at the beginning of the shoot elongation period until beginning of May was slightly higher for northern populations, followed by those from central and southern populations (Fig. 3). Starting from the middle of May, central populations exhibited much higher G than pines from two other groups. Maximal values of G occurred on 2 June (± 2 days, S.E.M), 28 May (± 1 day) and 27 May (± 3 days) for central, southern and northern populations, respectively (Fig. 3).

Since northern and southern populations reached growth cessation exactly at the same time, differences between them are mostly due to growth rate and not due to shoot elongation period. However, the greater height growth of the central populations compared to the two other groups resulted from both 30 to 40% higher growth rates and a 10-day increase in shoot elongation period (Fig. 3).

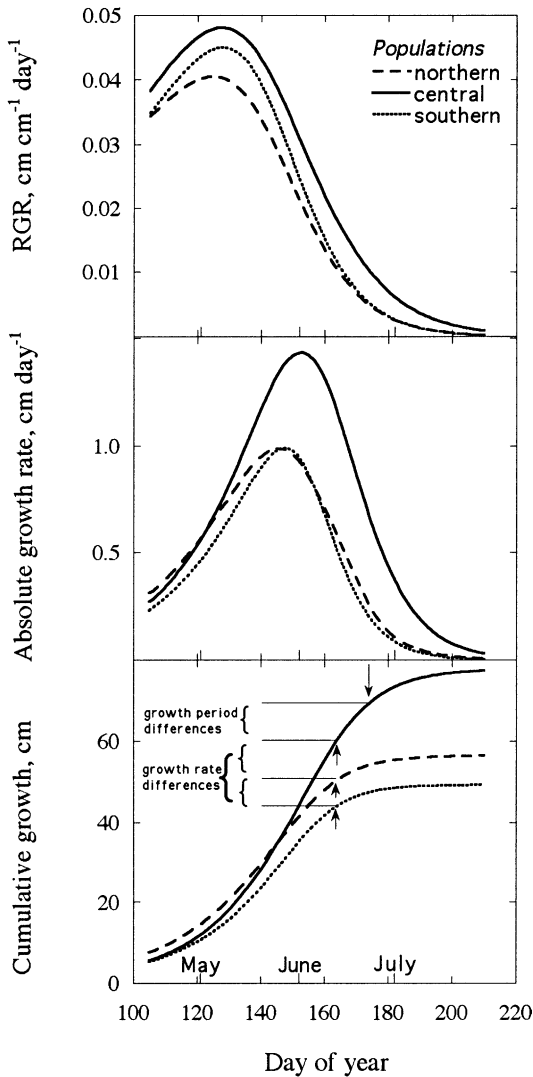


Fig. 3. Mean relative growth rate (RGR), absolute growth rate (G) and cumulative growth for northern (>58°N) central (55–48°N) and southern (<45°N) Scots pine populations growing in a provenance experiment in Kórnik, Poland (52°N). See text for explanations.

A cluster analysis classification technique was used to group provenances according to their instantaneous RGR from 15 April to the time when 90% of shoot growth was complete. The results of the analyses from an average linkage clustering method are summarized in a dendrogram (Fig. 4). Other clustering methods (Ward’s minimum variance method, single linkage, and centroid) showed similar results. Three distinct clusters were identified. In one group only northern populations from Russia and Sweden, ranking in origin from 60°15’ to 58°50’N appear. In another are grouped those from central regions (≈55–48°N) in Latvia, Poland, Germany, Belgium, France, Slovakia and Hungary. Three populations from a discontinuous southern part of the European range of Scots pine in Bosnia, Montenegro and Turkey (latitudes from ≈40 to 44°N) formed a third group. The geographic distribution of these groups is shown in Fig. 4. When populations were grouped based strictly on height growth or terminal leader growth, slow growing southern and northern populations were clustered in one group, separately from those from central latitudes. The presented data indicate that it is possible to define biogeographic groups of Scots pine based on the annual pattern of shoot extension.

3.4. Shoot elongation period, RGR and seed mass as predictors of height growth and biomass allocation

Shoot elongation period in the plantation in Kórnik was a good predictor of populations total height growth, both in the Kórnik experiment and in other sites established with the same seed lots. Examples from one Croatian and three Polish sites are shown in Fig. 5. Shoot elongation period shown on x-axis of this figure was from Kórnik site, since no phenology data from other sites are available. All correlations between the shoot elongation period and tree heights were highly significant. In contrast, height and m.a.t were unrelated at each site ($P=0.16$). Even in the southernmost site at 45°N in Croatia, population shoot elongation period in Poland (52°N) was correlated with height growth of plants at the age of six (Fig. 5). Sperman’s rank–order correlations computed on the ranks of the data values for shoot elongation period and tree height were also highly significant ($R_{ho}=0.58$, $P=0.009$, data not shown).

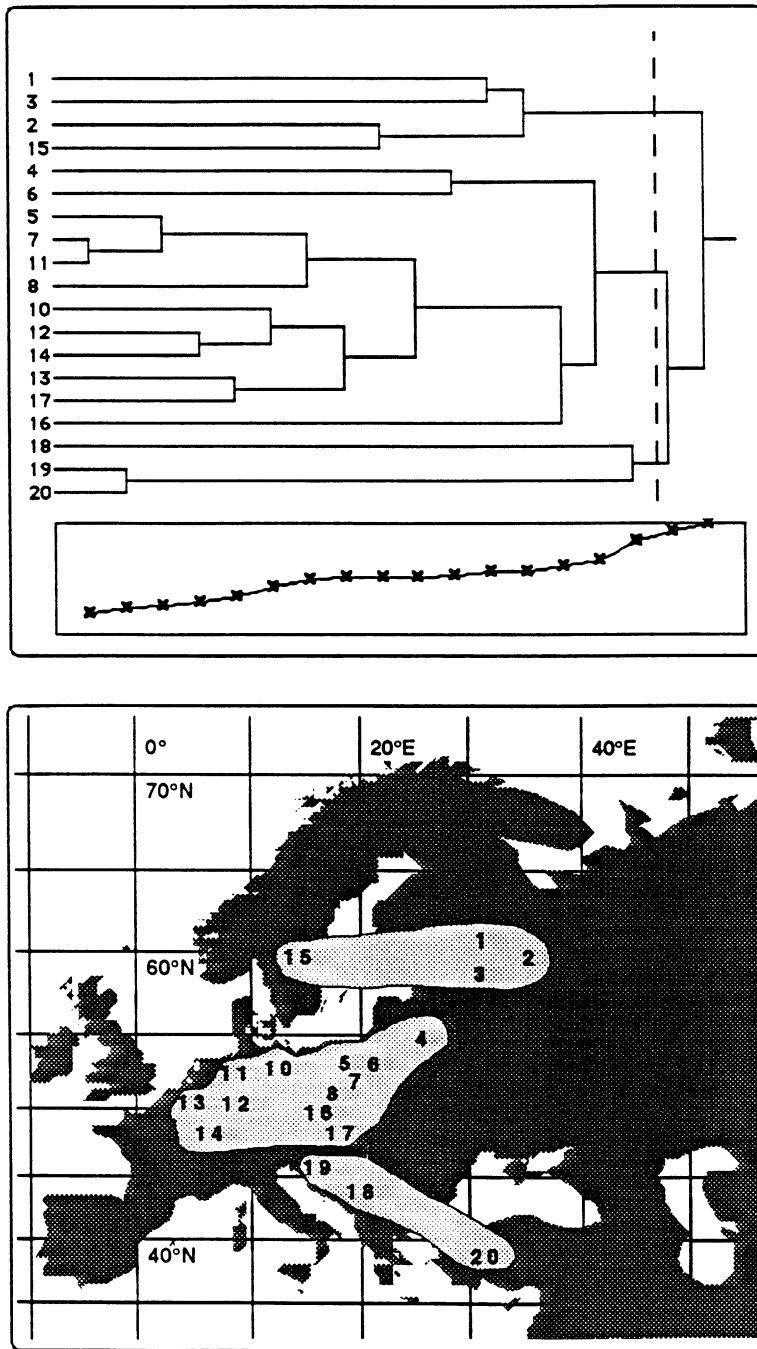


Fig. 4. Upper panel: Dendrogram of cluster groupings of provenances of Scots pine based on similarity of instantaneous relative growth rate (RGR). The daily values of RGR from 15 April to the day when 90% of shoot length was complete were used as variables. The plot beneath the dendrogram represents points for each cluster. The distance and curvature between the points represents the distance between the clusters. Lower panel: The geographic origin of provenances of Scots pine of the marked cluster groups shown.

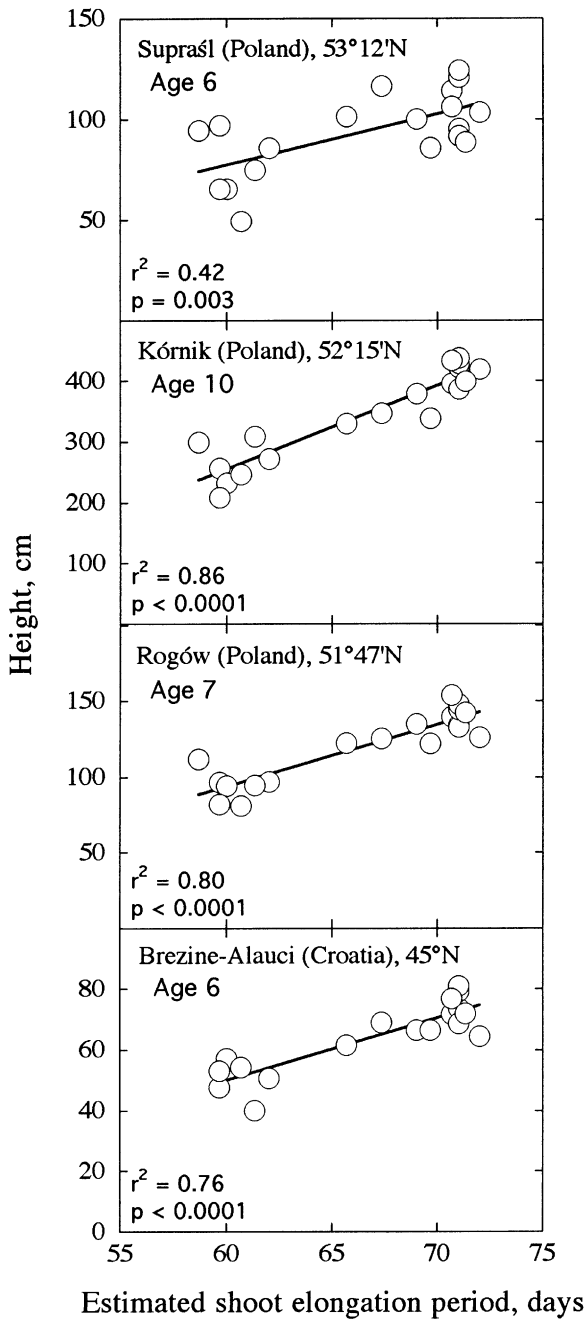


Fig. 5. Mean height of trees in Scots pine populations originating from the same seed lots in four sites in relation to estimated shoot elongation period based on the Kórnik site.

Polynomial regression equations developed for the Kórnik site between the latitude of seed origin and the shoot elongation period or RGR (Fig. 2.) were used to predict the height of diverse populations originating from different seed lots at other sites. For this purpose, we used published data from the IUFRO-1938 Scots pine experiment from Fox State Forest, NM, USA (Wright and Baldwin, 1957) and Herkimer State Forest, NY, USA (Schreiner et al., 1962). In both cases, estimated shoot elongation period or RGR were each highly correlated with height growth at the two sites (Fig. 6).

The strength of the relationship between shoot elongation period and tree height increases with age of trees, from $r^2 \approx 0.4$ for 1- or 2-year-old plants to $r^2 > 0.8$ for 10-year-old pines at the Kórnik plantation (Fig. 7a). The relatively small effect of shoot elongation period on height of young plants could be masked by strong seed mass effects on tree height at that time (Fig. 7). Both seed mass and shoot elongation period values were significant in multiple regression equation in the first 2 years of plant growth and jointly accounted for ≈ 70 and 55% of height growth variance in years 1 and 2, more than either shoot elongation period or seed mass alone (Fig. 7). At older ages (5 and 10 years) the seed mass effect was not statistically significant.

We tested whether these relationships show a similar pattern in different experiments. We used shoot elongation period values calculated in a similar way as presented earlier in Fig. 6; and seed mass and height for 1, 2, and 3-year-old Scots pine plants from NC-51 experiment, as published by Wright and Bull (1963). In this comparison we limited data only to European populations, and excluded Spanish provenances, which were not tested in our study. Similar to data presented in Fig. 7a, we observed an increase of percent of variation explained by estimated shoot elongation periods from $\approx 60\%$ in 1-year-old plants to $\approx 70\%$ in 3-year-old plants. Seed mass effect was highest for 1-year-old plants and diminished with age. The combination of seed mass and estimated shoot elongation period together explained $\approx 80\%$ of height growth variance, more than either factor alone (Fig. 7).

Shoot elongation period was negatively correlated with the percent of biomass allocated to roots of studied populations at the age of 12 (Fig. 8, Oleksyn et al., 1999). We found that plants with longer above-ground growing period tend to allocate proportionally less biomass to roots.

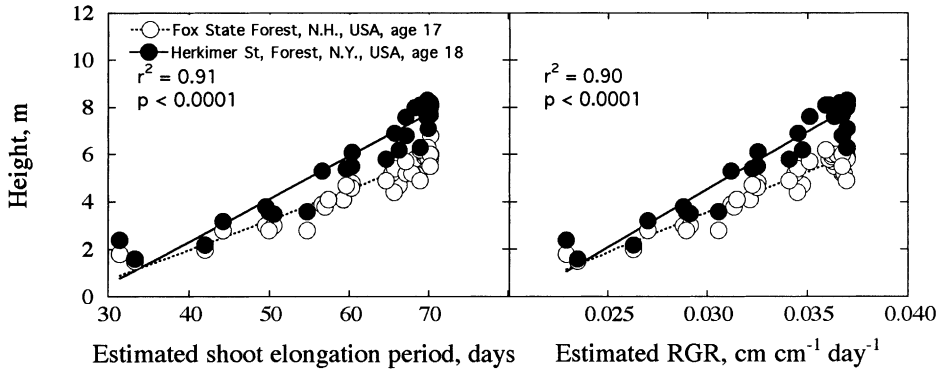


Fig. 6. Mean height of trees in Scots pine populations from the IUFRO-1938 experiment in relation to estimated shoot elongation period and estimated RGR based on the Kórnik site.

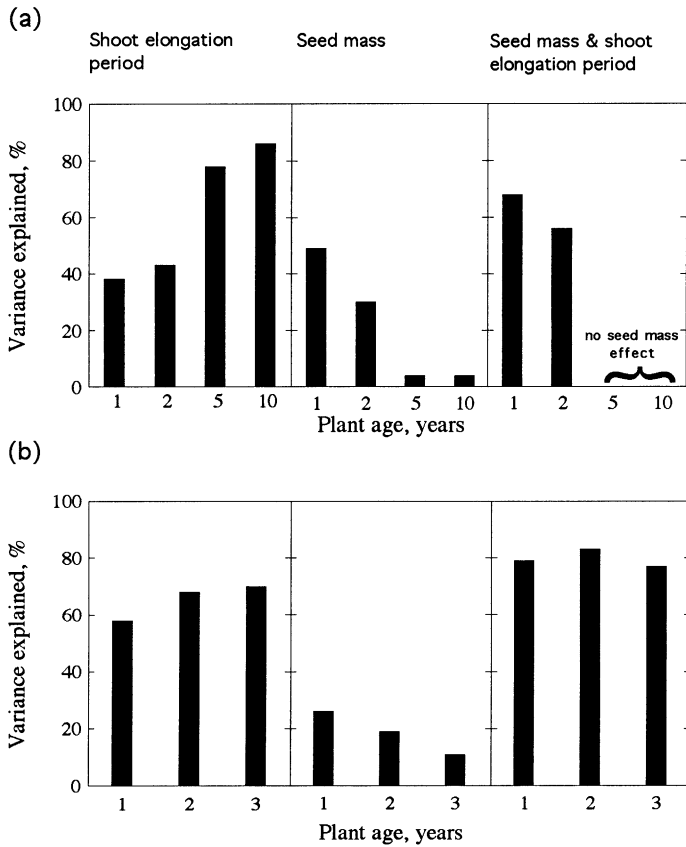


Fig. 7. Percent of variance in height growth accounted for by shoot elongation period, seed mass and its joint effects in relation to plant age in (a) Kórnik site, Poland and (b) in the NC-51 experiment, Michigan, USA (Wright and Bull, 1963). Estimated shoot elongation periods are based on the Kórnik site.

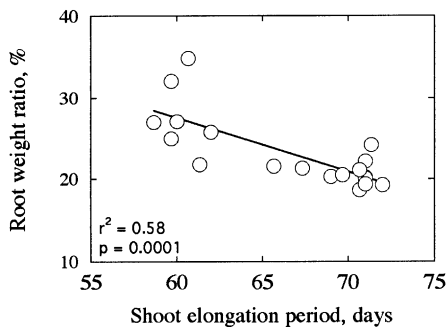


Fig. 8. Root weight ratio measured at the age of 12 (Oleksyn et al., 1999) in Scots pine populations growing in a provenance experiment in Kornik, Poland, in relation to shoot elongation period.

4. Discussion

Populations from the central part of the European range of Scots pine had greater shoot and height growth than those from northern and southern latitudes (Table 2). This type of pattern occurs in all experiments with diverse Scots pine populations (Giertych, 1979; Giertych and Oleksyn, 1981, 1992). Growth depression of northern populations after southward transfer of more than 2–3°N is a well known phenomenon, and appears to be related to growth phenology. Among the environmental factors usually considered responsible for triggering earlier height growth cessation are photoperiod or a combined short-day and thermoperiodic mechanism (Koski and Sievänen, 1985; Oleksyn et al., 1992a, 1998).

Inferior growth of southern populations from a discontinuous and isolated part of the species range in former Yugoslavia and Turkey can be a result of a combination of several factors like: 'inbreeding depression', specialization to arid and warm climate, high susceptibility to biotic stress factors or montane origin (Pravdin, 1969; Prus-Glowacki and Stephan, 1994). Even in their native ranges these populations grew slower than those introduced from central Europe (Saatçioğlu, 1967; Gracan, 1989). However, it is necessary to emphasize that, to our knowledge all provenance trials in southern conditions were established in lower altitudes than seed source stands. Therefore, it is impossible to separate the result

of their montane origin from other previously listed factors.

Results of shoot growth patterns revealed that shorter shoot elongation period and lower absolute growth rate are both partially responsible for the slow total annual growth of both northern and southern populations, compared to those from central Europe, (Table 1, Fig. 3). Photoperiod or temperature cues may regulate growth phenology (Koski and Sievänen, 1985; Oleksyn et al., 1992a, 1998). In the Kórnik plantation, the short-day photoperiodic conditions of southern latitudes likely reduces the length of the growth period of northern populations. Likewise, movement of southern or central populations northwards, to longer day photoperiods, should increase the length of the above-ground plant growth period. Therefore, the mechanism controlling height growth phenology for southern and central populations, most probably, is not strictly photoperiodic in nature. Results of seedling studies conducted in controlled environment using the same seed lots also support the notion that it is unlikely that a single mechanism can account for the growth phenology differences among both southern and northern populations (Oleksyn et al., 1998). Given the potential for genotype–environment interactions in various phenological traits, we expect that actual shoot elongation periods will differ between sites that differ in photoperiod or temperature; however, our analysis suggests that the pattern of population rankings may be conserved across sites.

The duration of the shoot elongation period differed between populations, with northern and southern populations ceasing growth earlier than those from central Europe (Table 2, Fig. 3). The latter group also has a higher RGR and G. However, the cumulative growth of central European populations exceeded those for other groups only later in the season (Fig. 3). Superior growth of central populations over the two other groups is a result of both higher growth rate and longer summer growing season. These relative differences can be due to two factors (Cannell et al., 1976): (1) inherent differences in response to the environmental factors, such as temperatures when elongation occurs; or (2) differences in number of stem units (internodes, together with the nodal appendages) originally present in the winter buds. The first factor depends on climatic conditions when the shoot is elongating and second on climate during

the previous growing season. We found that a highly significant correlation exists between the dormant bud length and shoot and tree height (Fig. 1). Since the bud length reflects the number of stem units (Kozłowski et al., 1973), it supports Cannell et al. (1976) conclusion that potential shoot length of monocyclic pines such as Scots pine is governed by the number of stem units present in the bud.

The results of the cluster analysis presented in Fig. 3 indicate the existence of three main groups with similar course of RGR: northern ($>58^{\circ}\text{N}$), central ($55\text{--}48^{\circ}\text{N}$) and southern ($<45^{\circ}\text{N}$). Very similar groups were found when interaction between 50 and 60°N simulated photoperiod and growth was studied for first-year seedlings of the same populations as used in this experiment (Oleksyn et al., 1992a). These groupings agree with existing taxonomic divisions of Scots pine based on other morphological characters (Pravdin, 1969; Molotkov and Patlaj, 1991).

The shoot elongation period length was significantly related to the height of plants (Fig. 1). There is general agreement that the times when shoots elongate differ greatly between years and sites irrespective of genotype, but the relative differences in timing between genotypes are often the same (Cannell et al., 1976). Therefore, if these differences are related to adaptation to climatic conditions at seed origin (Fig. 2) we should see the same pattern of height growth and climate in other experiments. We tested this hypothesis for trials established with the same seed lots (experiment SP-IUFRO-1982) and with unrelated experiments from the IUFRO-1938 series (Figs. 5 and 6). In the latter study, shoot elongation period (and RGR) were calculated from equations relating these parameters with latitude of seed origin (Fig. 2). The aim of comparisons was to reveal how much variance in height growth can be attributed to these factors. In the SP-IUFRO-1982 experiment, shoot elongation period explained from 42 to 86% of height growth variance for sites between 53 and 45°N latitudes (Fig. 5). An even higher portion of height growth variance ($\approx 90\%$) was explained by shoot elongation period in the IUFRO-1938 experiments (Fig. 6), suggesting that this factor is indeed related to height growth and can be used for predicting relative height growth rankings of diverse Scots pine populations. We predict that this type of relation will hold for all sites in central and southern latitudes, but

not necessarily for northern latitudes, where height growth can be substantially modified by the combination of long-day photoperiod, short growing season and nutrient limitations (Oleksyn et al., 1992a). Also in studies with Norway spruce it was found that the duration of the growth period accounted for a large part of the variation in shoot growth (80%) among diverse provenances (Skrøppa and Magnussen, 1993).

Among the factors modifying the relationship between growth and shoot elongation period can be the age of trees. In many studies a positive correlation was observed between seed mass (or size) and seedling size (see Reich et al., 1994b). We found that the magnitude of the seed mass effect is the largest for 1-year-old seedlings, and it gradually declined or disappeared by the age of 10 (Fig. 7; see also Reich et al., 1994b). Opposite to the trend in seed mass effect, the shoot elongation period effect on height growth cumulates with plant age, explaining $\approx 40\%$ of height growth variation in 1-year-old seedling and $>80\%$ for 10-year-old trees (Fig. 7). The joint effect of shoot elongation period and seed mass was the most effective for explaining early growth of different Scots pine populations (Fig. 7). We found that the same type of relationship was true also for other experiments, like the NC-51 Scots pine experiment in Michigan, USA (Wright and Bull, 1963; Fig. 7).

Termination of height growth extension is generally associated with a switch of dry mass accumulation from the shoot to the root (Ledig et al., 1970) and most of the root growth of Scots pine growth occurs after shoot growth cessation (Lyr and Hoffmann, 1967). Despite relatively small (≈ 10 days) differences in time of height growth cessation between different groups of Scots pine populations (Table 2), the overall effect is cumulative over time. We found that the shoot elongation period was significantly negatively related to the proportional distribution of biomass between shoots and roots, with northern populations having both earlier height growth cessation and a higher proportion of biomass in roots (Fig. 8). A higher proportion of biomass in roots is associated also with higher respiratory costs (Linder and Troeng, 1981; Oleksyn et al., 1992b) and can further adversely affect growth rates in northern and southern populations.

In summary, we found that shoot elongation period and growth rate differ among diverse different Scots pine provenances and is strongly associated with

cumulative height growth differences among diverse Scots pine populations. The seasonal patterns of shoot RGR and elongation are unique for different groups of populations and three distinct latitudinal groups of European Scots pine populations were identified. The percent of variation explained by shoot elongation period increases with increasing plant age, and for young plants (1–3 years-old) a combination of seed mass and shoot elongation period can better account for height growth variance than any of these factors alone. These findings underscore the importance of phenology as a determinant of productivity differences among diverse seed sources.

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