Adaptation to Changing Environment in Scots Pine Populations across a Latitudinal Gradient

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Oleksyn, J., Tjoelker, M.G. & Reich, P.B. 1998. Adaptation to changing environment in Scots pine populations across a latitudinal gradient. Silva Fennica 32(2): 129–140.

In several growth chamber and field experiments we examined the growth response of Scots pine (*Pinus sylvestris* L.) populations from a wide latitudinal range to temperature and photoperiod. The duration of the shoot elongation period of one-year-old seedlings was affected by temperature and photoperiod. In contrasting temperatures, 23/20 °C, 20/17 °C, and 17/14 °C (day/night), shoot elongation period for all populations was shortest in the high and longest in the low temperature treatments. The northern populations from 61–57° N ceased height growth earlier than the other populations in the southern 50° N photoperiod. The order of growth cessation among populations at 50° N in the chamber experiment and at 52° N in the field experiment was similar and related to observed population differences in terminal leader growth and total tree height. Since the length of growing season is under strong environmentally-mediated genetic control in Scots pine, potential climatic changes such as increasing temperature will probably alter the length and timing of growth in aboveground tree parts, but likely in the opposite direction (a shorter growing season) than has been often hypothesized (a longer growing season). Tree-ring analyses of a provenance experiment established in 1912 indicate that the main climatic factors that limited ring-width growth in Scots pine were air temperatures in the winter months of December through March. Low winter temperatures were followed by the formation of narrow rings over the next summer. Based on responses to temperature, Scots pine populations from the continuous European range can be divided in several geographic groups along a latitudinal gradient. Our results suggest that in developing new models to predict the response of Scots pine to changing environmental conditions, it is necessary to include intraspecific differentiation in acclimation and adaptation to environmental factors.

Keywords *Pinus sylvestris*, temperature, photoperiod, climate change, growth, provenance
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Accepted 8 May 1998

1 Introduction

Understanding how increased concentrations of greenhouse gases, associated changes in climatic conditions and pollution stress will affect trees and forests is one of the major challenges now facing forest science. Trees with their long life spans are more vulnerable than annual plants to rapid climate changes since they are not able to respond by migration or genetic selection in a short period. Many current models predict that rapid temperature increases as well as other climate changes will occur within the lifetime of one generation of trees (Schwartz 1991, Gates 1993). An especially large increase in temperature is predicted to occur in boreal forests on the order of a 1.5 to 3.5 °C increase in mean annual temperature within the next century (Beuker 1994a). The effects of climatic factors on forest trees have been studied largely by means of predictive models. However, most of these models assume that the trees are genetically adapted to the current climate (Schmidtling 1994). Despite the fact that researchers have long known about intraspecific variation in response to climatic and stress factors and interactions of genotypes with environment, these factors are often ignored in ecophysiological studies of woody plants (Abrams 1994).

In order to examine intraspecific responses of trees to changing environmental conditions, experiments should be established with trees of known genetic background and provenance experiments used in which plants from throughout a species natural range are grown together at the same site. There are many established provenance experiments with the purpose to select populations and regions with the greatest potential in terms of production and as tree-breeding seed sources. During the past decade, these experiments have been used to model climate change effects and to study genotype × pollution interactions (Oleksyn and Bialobok 1986, Oleksyn 1988a, Matyas and Yeatman 1992, Beuker 1994a,b, Matyas 1994, Reich et al. 1994a, Schmidtling 1994). In the present study the results of two field provenance tests and two seedling experiments are used to evaluate the adaptation to changing temperature and environments among diverse European Scots pine populations.

2 Materials and Methods

2.1 Seedling Studies

In 1990 and 1991 two linked growth chamber experiments were conducted to assess the effect of temperature and photoperiod on the growth and physiology of seedlings representing diverse populations of European Scots pine. In the first experiment (for details see Oleksyn et al. 1992a) seedlings of 24 populations were grown from seed for four months in controlled environments under the photoperiods of 50° and 60°N, but with similar temperatures (20/17 °C, day/night) and total daily quantum flux in both photoperiods. The origin of seed used in this study is presented in Table 1 (experiment 1). In the second experiment 15 populations from same seed sources as those in the first experiment were grown from seeds for four months in photoperiod conditions of 60°N and two contrasting temperatures (23/20 °C, and 17/14 °C, day/night). During both experiments the day length was continually changed to simulate the photoperiod from 1 May to 1 September at each latitude. When each population showed signs of height growth cessation (i.e., the development of terminal buds) the number of plants with buds was counted every four days until all individuals within populations set bud. Height growth cessation was defined as the point in time when 50 % of seedlings possessed a terminal bud. Duration of the shoot elongation period of seedlings was defined as the number of days from sowing to 50 % of bud set.

2.2 Field Studies

To compare timing and rates of height growth of 10-year-old trees of the same provenances as those used in the controlled chamber studies, terminal leader length was measured in a field provenance experiment established in 1984 in Kórnik, Poland. Detailed information on the concept, history of establishment, and plan of this experiment is presented elsewhere (Oleksyn 1988b). Terminal leader length was measured once per week starting on April 15 in 12 randomly chosen trees (6 trees × 2 blocks) in 19 populations. At the end

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

Population no.	Origin	Country	Lat. (N) (2	Long. (E) (2	Alt. (m)	Experi-ment no.(1
SP-IUFRO-1982 and seedling experiments						
1	Roshchinskaya Dacha	Russia	60.25	29.90	80	1, 2, 3
15	Sumpberget	Sweden	60.18	15.87	185	1, 2, 3
2	Kondezhkoe	Russia	59.97	33.50	70	1, 2, 3
3	Serebryanskoe	Russia	58.83	29.12	80	3
26	Ostrovskij Forest District	Russia	57.83	28.15	50	1, 2
27	Sebyezhskij Forest District	Russia	57.67	28.17	50	1, 2
4	Silene	Latvia	55.75	26.67	165	1, 2, 3
5	Milomlyn	Poland	53.60	20.00	110	1, 3
6	Suprasl	Poland	53.20	23.37	160	1, 2, 3
10	Neuhaus	Germany	53.00	13.90	40	1, 3
11	Betzhorn	Germany	52.50	10.50	65	1, 3
9	Bolewice	Poland	52.40	16.05	90	1,
7	Spala	Poland	51.60	20.20	160	1, 2, 3
23	Khrenovsk	Russia	51.17	42.00	150	1
8	Rychtal	Poland	51.10	17.92	190	1, 2, 3
13	Ardennes	Belgium	50.80	4.43	110	1, 3
22	Zhitomir	Ukraine	50.50	28.20	300	1, 2
12	Lampertheim	Germany	49.50	8.50	97	1, 3
25	Tsherkasy II	Ukraine	49.52	32.50	50	1
21	Tsherkasy I	Ukraine	49.50	32.17	50	1, 2
14	Haguenau	France	48.80	7.78	150	1, 2, 3
16	Zahorie	Slovakia	48.77	17.05	160	1, 3
17	Pornoapati	Hungary	47.30	16.47	300	3
19	Prusacka Rijeka	Bosnia	44.10	17.35	885	1, 2, 3
18	Maocnica, Montenegro	Yugoslavia	43.20	19.50	1200	1, 2, 3
20	Catacik	Turkey	40.00	31.17	1400	1, 2, 3
1912 Pulawy (Poland) experiment						
4	Arkhangelsk	Russia	63.83	45.17	– (3	4
6	Olonec	Russia	61.50	39.00	–	4
8	Vologda	Russia	59.72	36.87	–	4
10	Novgorod	Russia	59.62	33.55	–	4
15	Tver	Russia	58.63	37.22	–	4
11	Tobolsk	Russia	58.00	63.70	–	4
9	Jenisejsk	Russia	58.00	62.00	–	4
16	Kurland	Latvia	56.12	21.13	–	4
13	Ufa	Russia	55.00	52.00	–	4
1,2	Lublin	Poland	51.40	22.05	–	4
7	Voronez	Russia	51.10	40.28	–	4
14	Kiev	Ukraine	50.83	30.28	–	4
12	Volyniya	Ukraine	50.75	25.30	–	4
5	Kharkov	Ukraine	50.00	36.33	–	4
3	Kars	Turkey	40.50	42.00	–	4

1) *Growth chamber experiments:* 1 – seedlings grown under the photoperiod of 50° and 60°N, temperature 20/17 °C (day/night); 2 – photoperiod of 60°N, temperature 23/20 °C; and photoperiod of 60°N, temperature 17/24 °C; *Field provenance experiments:*3 – ten-year-old trees planted at 52°15’ N (Kórnik, Poland); 4 – 76-year-old trees planted at 51°37’ N (Pulawy, Poland).

2) Geographic coordinates shown in decimal form.

3) Data not available.

of the growing season total height of sampled trees was measured. The duration of the shoot elongation period was calculated (differently than in seedling experiments) as the number of days between beginning of terminal leader extension to the day when 90 % of growth was complete.

The effect of temperature and precipitation on diameter growth was studied in the oldest Scots pine provenance experiment in Poland, established in 1912 in Pulawy (51°24’N, 22°02’E). A detailed description of this experiment was presented earlier (Oleksyn and Giertych 1984). This experiment includes 15 populations of Scots pine originating from the regions extending from the White Sea in the north to Turkey in the south, and from Poland in the west to Siberia in the east (Table 1 and Fig. 9). Since this site has been subjected to acute pollution impacts since 1966 from a large nearby nitrogen fertilizer plant, only data from the prepollution period, 1925–1965, were analyzed and presented.

In 1988 from 9 to 29 trees from each provenance were sampled for tree-ring analyses. The sample cores were dated and tree ring widths were measured to the nearest 0.01 mm using a computerized measuring machine described by Robins and Evans (1980). An accuracy check of the dating used the computer-assisted method, program COFECHA (Holmes et al. 1986).

The average ring-width series for each provenance was converted to standardized indices using the computer program INDEX (Graybill 1979). The process of standardization effectively removes the trends in growth associated with increasing tree age, a major source of nonstationarity in the time series. A negative exponential curve

$$Y_t = a\, e^{-bt} + k \qquad (1)$$

was fit to each averaged for provenance ring-width series beginning with earliest ring and ending in 1965, the last year of the prepollution period. The values of *a, b* and *k* vary from series to series depending upon the shape of the curve required to fit the data, *e* is the base of natural logarithms and Y_t is the expected growth at given year *t*. The values of *t* vary from 1 to n.

Ring-width indices for each provenance were obtained by

$$I_t = R_t / Y_t \qquad (2)$$

where R_t is the average ring width measurement for year *t* and Y_t is the same as in Eq. 1.

Further information on sampling techniques and methods were described in detail elsewhere (Oleksyn and Fritts 1991, Oleksyn et al. 1993). All meteorological data were from a station located ca. 3 km from the experimental area. The Ward’s Method was used to compute cluster groupings of the Scots pine provenances in response to mean monthly air temperatures from June to December of the year prior to growth and from January to September of the growth year. In this clustering method the distance between two clusters is the ANOVA sum of squares between the two clusters summed over all the variables (JMP, SAS Institute Inc., Cary, NC, USA). The correlation coefficients between the tree-ring indices and temperatures in differing months were used as variables.

3 Results

3.1 Seedling and Young Tree Studies

The duration of the shoot elongation period of European Scots pine populations grown from seeds for four months at simulated 60°N day lengths was significantly affected by temperature. In “cool” conditions of 17/14 °C (day/night) height growth cessation occurred on average after 109±10 days, whereas in “intermediate” (20°/17 °C) and “warm” (23/20 °C) temperatures height growth stopped after 99±5 and 88±2 days, respectively. Differences among populations in timing of growth cessation with respect to night length were larger in the cool conditions of 17/14 °C than in warm conditions of 23/20 °C (Fig. 1). The earlier cessation of growth in all populations was under warm than intermediate or cool conditions and the minimal range among populations in the warm temperature regime suggests that temperature “overrides” any potential photoperiodic response under the warm conditions, probably due to accumulated heat sums (degree days) rather than to photoperiod (duration of night) (Figs. 1 and 2). With decreasing growing

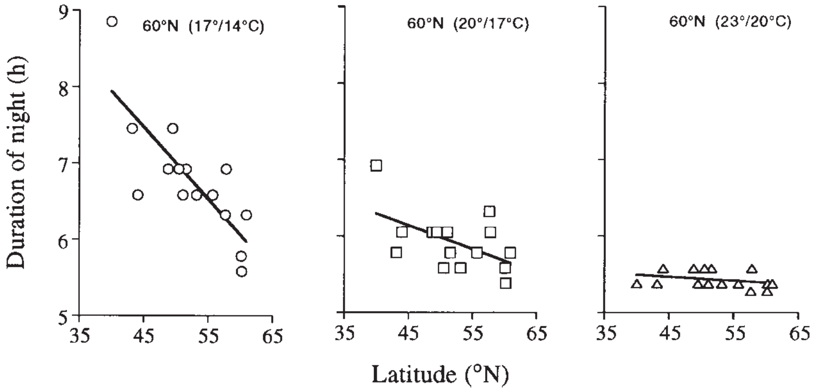

Fig. 1. Length of night at the point of one-year-old seedling height-growth cessation plotted as a function of latitude of seed origin for provenances of Scots pine grown under a 60°N latitude photoperiod under various controlled temperature treatments. In 17 /14 °C conditions, $r = 0.80$, $p = 0.0003$; in 20/17 °C, $r = 0.54$, $p = 0.04$; and in 23/20 °C, $r = 0.30$, $p = 0.28$.

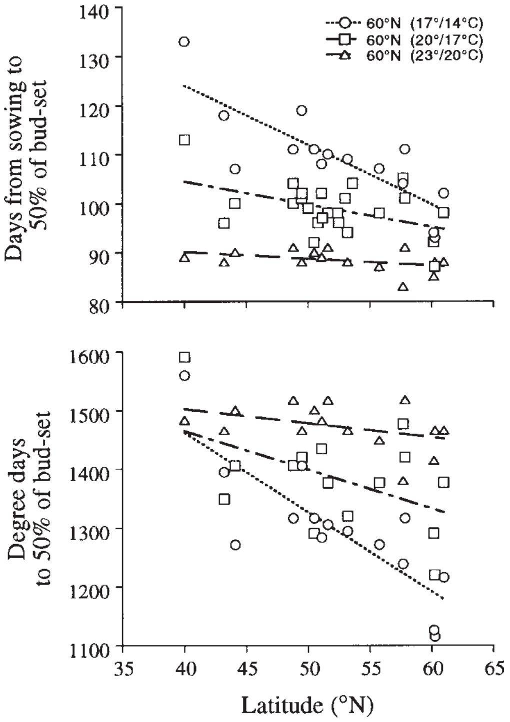

Fig. 2. Duration of the shoot elongation period and total degree days at the point of height growth cessation (50 % bud set) for provenances of Scots pine grown under a 60°N latitude photoperiod in relation to latitude of seed origin. For the 17/14 °C and 20/17 °C treatments, $r^2 \geq 0.22$ and all $p \leq 0.06$.

season temperatures, the populations response became increasingly differentiated along the latitudinal gradient of origin with northern populations having an earlier onset of height growth cessation, at lower degree days and shorter nights than those from central and southern parts of the European range of Scots pine (Figs. 1 and 2).

Height growth of different provenances of Scots pine seedlings grown at various temperatures under the 60° N photoperiod showed a similar pattern with latitude of origin (Fig. 3A). In all 60° N treatments height growth of central and northern populations was comparable and significantly higher than those found in pines from Turkey and former Yugoslavia.

The pattern of variation in height of one-year-old seedlings grown in simulated 50° N photoperiod and 20/17 °C temperature (Fig. 3A) was similar to that found in 1-year-old and 10-year-old trees grown in a field experiment in central Poland at 52°15’N (Fig. 3B). Central populations were taller than northern or southern ones. Over time in the field, populations of southern origin showed a greater growth decline (in ranking of performance among populations) than was found in seedlings grown in controlled chambers or in the field. This can be explained by the heavier seeds of the southern populations which can mask genetic differences in tree growth capacity between populations of Scots pine in the first five years of age (Reich et al. 1994b). After

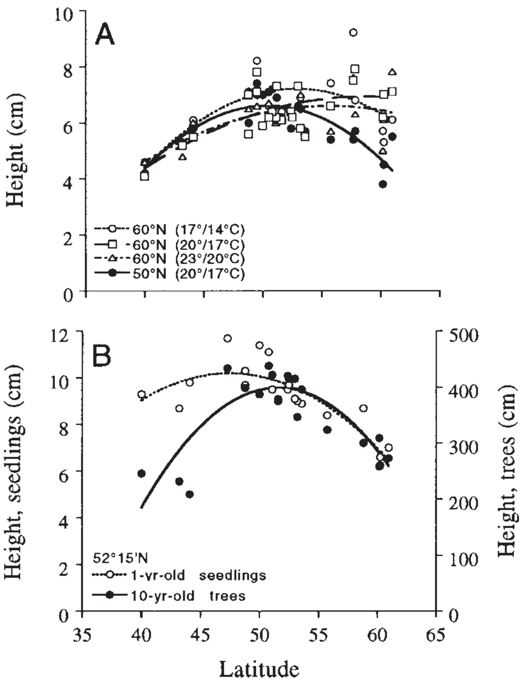

Fig. 3. (A) Mean seedling height after growth cessation in provenances of Scots pine grown under 50° and 60°N photoperiods and different temperatures. Data for the 20 /17 °C treatment are from Oleksyn et al. (1992a). (B) Mean one-year-old seedling height and 10-year-old trees of the same provenances grown at a field site in central Poland (52°15'N). For all curves $r \geq 0.62$ and all $p < 0.05$.

excluding the three southernmost populations, there were statistically significant correlations between the height of one- and 10-year-old trees ($r = 0.70$ and $p = 0.003$).

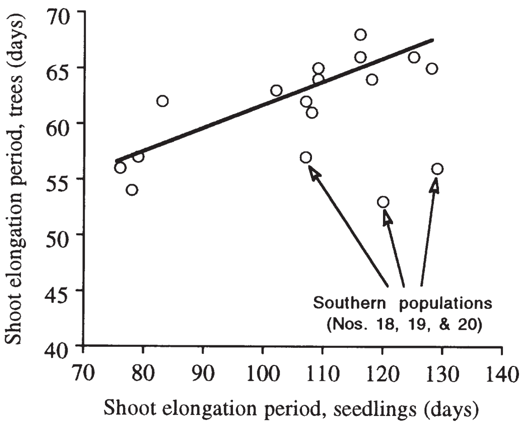

Fig. 4. Duration of the shoot elongation period of one-year-old seedlings grown at simulated 50°N photoperiod conditions and 20/17 °C in relation to shoot elongation period of 10-year-old trees of the same provenances at a field site in central Poland (52°15'N). After excluding data for southern populations (nos. 18, 19 & 20), $r = 0.82$, $p = 0.0003$.

There were significant positive correlations ($r = 0.82$, $p = 0.0003$) between duration of the shoot elongation period of one-year-old seedlings of central and northern populations grown in simulated 50° N photoperiod and 20/17 °C temperature and those found in 10-year-old trees grown in a field experiment in central Poland at 52°15'N (Fig. 4). Seedlings have a markedly longer shoot elongation period than trees, 106±16 versus 61±5 days, respectively. It is unclear why the shoot elongation period for trees and seedlings of southern populations do not follow the same linear relationship. This may be a result of generally poor performance in the field (short duration of the shoot elongation period corresponds to low 10-year height growth). Alternatively, in seedlings the time of bud-set is used as a measure of growth cessation, and this method may not always be an accurate measure of height growth period. It is possible that southern pines ceased growth earlier than the terminal leader bud became visible.

3.2 Long-Term Effects of Temperature on Diameter Growth in a 1912 Provenance Experiment

Dendroclimatological studies conducted in a 76-year-old provenance experiment in Pulawy, Poland (51°24'N), revealed significant effects of temperature on diameter growth of diverse Scots pine populations. In general, temperature during the current growing season had a negative or no effect on tree-ring indices of the studied provenances (Fig. 5). Higher temperatures either in the prior or current summer were correlated with lower growth. However, our findings also demonstrate that the greatest differentiation among provenances in the strength of the correlations between

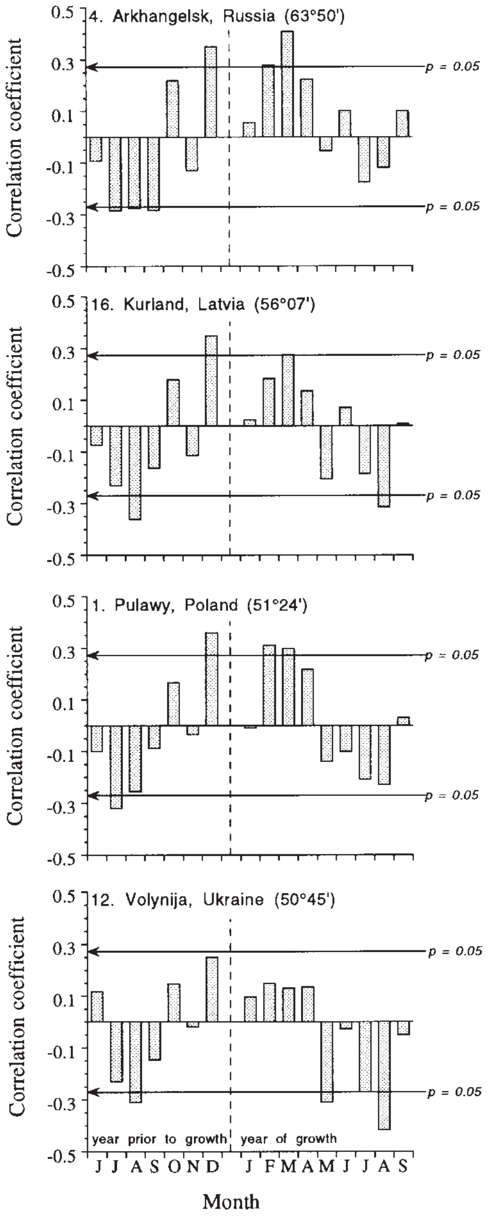

Fig. 5. Correlation coefficients between tree-ring indices of provenances selected from different cluster groups (see Figs. 8 & 9) and mean monthly air temperatures for June–December of year prior to growth and January–September of the growth year. Horizontal lines indicate significance at $p = 0.05$. Data in Figs. 5–9 originated from the provenance trial established in 1912. The data on tree-ring indices and temperature were collected during the period 1925–1966.

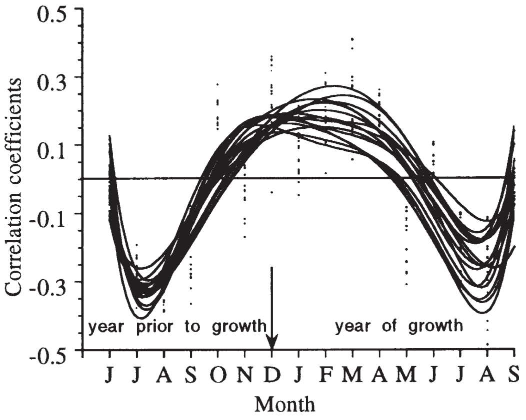

Fig. 6. Correlation coefficients between tree-ring indices of 15 Scots pine populations and mean temperatures for June–December of year prior to growth and January–September of the growth year. Temporal trends are shown using polynomial splines.

temperature and ring-width growth occurs during the current year from February through August (Fig. 6). Data presented in Figures 5 and 6 indicate that another main climatic factor limiting ring-width formation in all Scots pine populations is temperatures in winter months of December through March. Low temperatures during this time of year were followed by the formation of narrow rings during the following summer. On average, winter temperatures explained 32±0.6 % of diameter growth variance. The population least responsive to winter temperature was the population from Kharkov, Ukraine (18 % of diameter growth explained by winter temperatures), and most responsive were those from Arkhangelsk (Russia) and Lublin (local Poland), 43 and 44 %, respectively (Fig. 7).

A cluster analysis technique was used to group provenances by similar responses to temperature. To make the groupings, correlation coefficients between tree-ring indices and mean temperatures for 16 consecutive months starting in June of the year before growth were used. From these analyses we excluded populations no. 3, 9, 11, and 13 from the southeast, discontinuous range of Scots pine, which also had low stocking densities in the experiment. The results of the cluster analyses are summarized in a dendrogram (Fig. 8) and a geographic distribution of

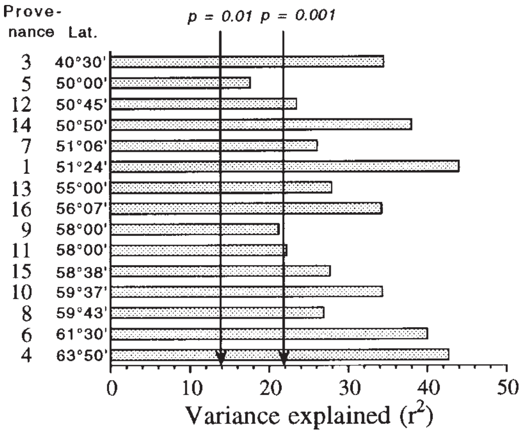

Fig. 7. Diagram of variance explained (r^2)by the regression between the average of the monthly temperatures from December through March and ring-width indices. The vertical lines show significance at $p = 0.01$ and $p = 0.001$.

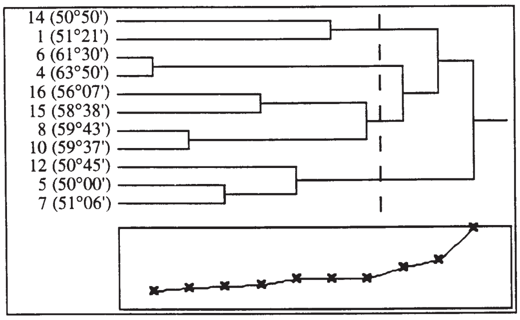

Fig. 8. Dendrogram of cluster groupings of provenances of Scots pine based on similarity of their response to mean monthly temperatures. As variables the correlation coefficients between the tree-ring indices and temperatures of different months were used (see Fig. 6). The plot beneath the dendrogram presents points for each cluster. The distance and curvature between the points represents the distance between the clusters.

groups is shown in Figure 9. Four distinct clusters can be identified. In one group only the northernmost Russian populations (nos. 4 and 6, from 63°50’N and 61°30') appear. These populations were characterized by small and nonsignificant declines in radial growth relative to temperatures of May-August of the growth year and a highly significant positive effect of warm temperatures in December and February-March. Another group consists of populations from the Baltic region (provenance nos. 8, 10, 15, 16), roughly between 50° and 56° N and considerably southwest of the two northern Russian populations. In comparison with the previous group, populations from the Baltic region appeared to be more sensitive to warm temperatures in July-September of prior growth season and August of the current year. Three populations from ca. 50° N (nos. 5, 7, 12) were included in a group, because they differed from all other groups by having a much smaller response to winter temperatures and the highest negative effects of warm summer temperatures during the current growing season. A local Polish population (no. 1,2) and those from Kiev, Ukraine, constitute a fourth group. In comparison with previous groups these populations showed a higher positive response to warm winter temperatures and a less pronounced negative effect of warm temperatures in August of the current year. Precipitation (data not shown) had a generally positive effect in June and July of the current growing season and July-August of the previous year. Winter time precipitation for most populations had no effect and only for four of them (nos. 3, 4, 11, 16) there were negative effects of high precipitation in February or March.

4 Discussion

The earlier onset of growth cessation under 23/20 °C than in two other temperature treatments in seedling studies (Fig. 1) can indicate that in a warm growing season scenario a longer period of active growth cannot necessarily be expected, as often predicted in global climate change models. Several simulation models, laboratory experiments, and one field study predict an increase in growth period based on the earlier onset of height growth in spring (Cannell and Smith 1986, Murray et al. 1989, Hänninen et al. 1993). To date a number of models developed describing tree responses to temperature have concentrated on a simulation of the timing of shoot growth onset in relation to the incidence of frost damage to trees (see Hänninen 1990 and Hänninen et al. 1993 for review). Our results suggest that both the geno-

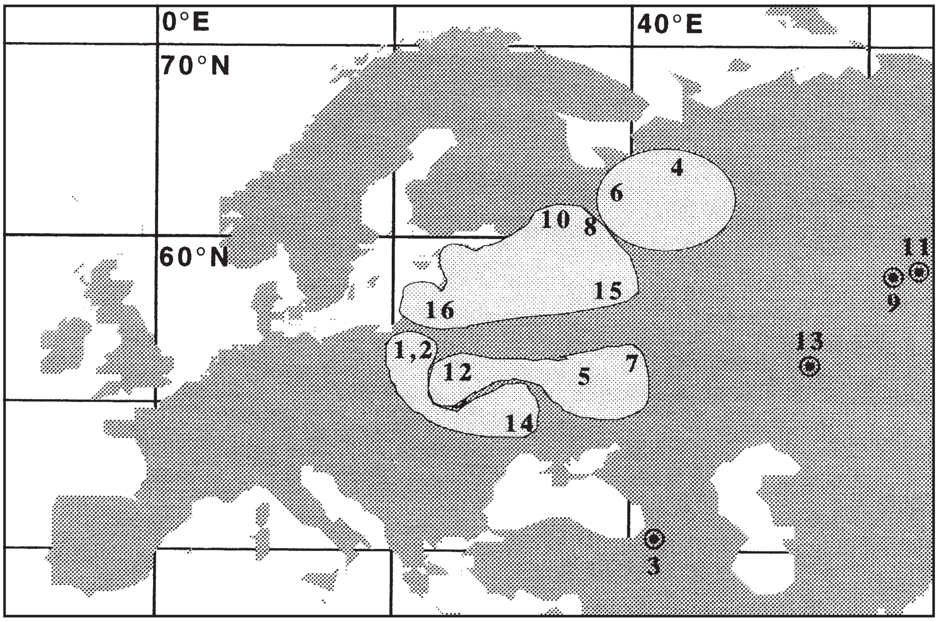

Fig. 9. Geographic origin of provenances of Scots pine of the marked cluster groups shown in Fig. 8.

type x temperature interaction in timing of growth cessation and temperature environment can affect projected growing season length, and both should be considered in models predicting the results of climate warming. However, it is important to consider that shoot elongation in Scots pine occurs during a ca. six week period, whereas stem diameter growth takes place over a period of about three months, needle elongation for more than five months (Jankiewicz 1976, Rook 1985) and photosynthetic activity as long as conditions are above freezing. Therefore, a shorter period of shoot growth extension observed in warm conditions (Figs. 1 and 2) does not mean that overall wood production will be negatively affected.

The mechanisms controlling the onset of shoot growth cessation have been described using various models based on: (1) heat sum accumulation (expressed as degree days), which reflects the joint effect of time and temperature; (2) a critical length of the photoperiod; and (3) the joint effect of degree-day accumulation and photoperiod (see Oleksyn et al. 1992a). Our results suggest that the duration of night (photoperiodic) component of growth cessation occurs only in a certain range of growing season temperatures. In warm conditions of 23/20 °C all populations ceased growth without relation to latitude of origin at the same time after reaching on average 1273±39 degree-days (Fig. 2). This indicates that under such conditions temperature alone can be responsible for shoot growth cessation (as was suggested by Sarvas 1972). A decrease in growing season temperature uncovered the photoperiodic component in growth cessation which (at least for northern Scots pine populations) is a result of the joint effect of degree-day accumulation and photoperiod (Koski and Sievänen 1985, Paus et al. 1986, Oleksyn et al. 1992a). There is no indication that shoot growth cessation of southern pines is controlled in any way by photoperiod in the same way as populations from northern Europe and these populations appear responsive to temperature (Figs. 1 and 2).

Due to the design of seedling experiments which lasted only for four months, we were not able to make any conclusive observations on possible temperature or photoperiod induced budbreak. Ekberg et al. (1979) found that *Pinus sylvestris* and *P. contorta* seedlings frequently produce a second flush under photoperiods longer than the optimum photoperiod for height growth. Since the possibility of second flush can be important for the prediction of the effects of global warming, more observations in this direction will be necessary.

Inferior growth and limited plasticity of southern populations from a discontinuous and isolated part of the species range, in former Yugoslavia and Turkey is most probably a result of their "inbreeding depression", narrowing their genetic variation and to their specialization to a warm and arid climate (Pravdin 1969, Szmidt and Wang 1993). Recent studies on genetic variation of southern Scots pine showed that populations in this region have unique alleles not present in populations from eastern and northern Europe (Prus-Glowacki and Stephan 1994). Therefore, these populations are most likely relicts of Tertiary flora that did not take part in reforestation of Europe after the last glaciation (Mirov 1967, Prus-Glowacki and Stephan 1994). This study also indicates that these pines have distinct ecophysiological differences in comparison with plants from other parts of the European range of Scots pine.

The negative effect of low winter temperatures on diameter growth of different Scots pine populations in 1912 experiment could be related to needle injury caused by frost or winter drought. Positive direct responses of Scots pine populations to winter temperatures can indicate that at least in Polish conditions, the risk of premature shoot growth onset and the possibility of subsequent frost damage as a result of climatic warming has no significant effect on radial growth, even in northern populations. The possibility of such damage in trees of the boreal region was indicated by a simulation study of Hänninen (1991). However, a field test of this model indicated that the predicted climate warming will not increase the risk of frost damage in trees as much as was suggested by the initial simulations (Hänninen 1991). Dendroclimatological studies conducted in more northern conditions (for example in Scandinavian countries) using old provenance experiments could help evaluate the risk of winter damage following mild spells in winter and the possible magnitude of a genotype × temperature interaction in wood production.

Along with a positive effect of high winter temperatures on diameter growth, high temperatures in July, August, and September of the year before growth and July and August of the growth year had a negative effect on ring-widths (Figs. 5 and 6). Therefore, the influence of possible global climate warming on Scots pine diameter growth will be a result of both positive and negative effects, depending on seasonal variation in mean temperatures.

Long-term responses to temperature of Scots pine trees of different populations can be significantly modified by local climatic conditions. Plants of northern latitudes are typically less responsive to environmental variables than those in the south (E. Vaganov, pers. com.). Results obtained in our study suggest that answers to the question "How large is the genetic component in the relationship between temperature regimes and growth of different populations?" can be obtained by applying dendroclimatological methods. In such analyses, existing and well-documented IUFRO 1907 and 1938/1939 Scots pine experiments could be used (for list of sites see Giertych and Oleksyn 1992). Dendroclimatic studies can shed light on mechanisms of population response to climatic changes, and with other models, for example, Beuker's (1994a) wood production model, could help develop improved models useful for the prediction of large-scale responses of Scots pine to climate changes.

In summary, these studies showed that there is a genetic component in population response to environmental factors such as temperature and photoperiod that clearly has evolved along latitudinal (i.e., climate) gradients up to the point where geographic discontinuities among populations may have interfered with the ability to adapt such mechanisms. Since the length of the growing season is under strong genetic control, potential global warming normally assumed to make conditions more favorable for tree growth probably will not increase the seasonal period of growth in aboveground tree parts. However, prolonged periods of warmer temperatures after shoot-growth cessation could substantially increase biomass allocation to roots and cause an increase in overall respiratory costs (Oleksyn et al. 1992a,b). Furthermore, seasonal variation in temperature will both positively and negatively affect radial growth depending on the month of year. Thus, simple predictions about the magnitude or even direction of change in tree growth due to climate change remains a challenge at present.

Acknowledgments

This research was supported by the Institute of Dendrology (Poland), the University of Minnesota, and the U.S. National Science Foundation (IBN – 9630241).

An earlier version of this paper was presented at IUFRO S.2.02-18 symposium "Scots pine Breeding and Genetics", Kaunas-Girionys, Lithuania, 13-17 September 1994.

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