

Intraspecific responses to climate in *Pinus sylvestris*

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Abstract

Five population-specific response functions were developed from quadratic models for 110 populations of *Pinus sylvestris* growing at 47 planting sites in Eurasia and North America. The functions predict 13 year height from climate: degree-days $> 5^{\circ}\text{C}$; mean annual temperature; degree-days $< 0^{\circ}\text{C}$; summer-winter temperature differential; and a moisture index, the ratio of degree-days $> 5^{\circ}\text{C}$ to mean annual precipitation. Validation of the response functions with two sets of independent data produced for all functions statistically significant simple correlations with coefficients as high as 0.81 between actual and predicted heights. The response functions described the widely different growth potentials typical of natural populations and demonstrated that these growth potentials have different climatic optima. Populations nonetheless tend to inhabit climates colder than their optima, with the disparity between the optimal and inhabited climates becoming greater as the climate becomes more severe. When driven by a global warming scenario of the Hadley Center, the functions described short-term physiologic and long-term evolutionary effects that were geographically complex. The short-term effects should be negative in the warmest climates but strongly positive in the coldest. Long-term effects eventually should ameliorate the negative short-term impacts, enhance the positive, and in time, substantially increase productivity throughout most of the contemporary pine forests of Eurasia. Realizing the long-term gains will require redistribution of genotypes across the landscape, a process that should take up to 13 generations and therefore many years.

Keywords: climate-change impacts, climate response functions, microevolution, population adaptation, genetic responses to climate, predicting responses to change

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Introduction

Forest trees, like most widely distributed plant species, commonly exhibit sub-specific genetic structures that convey adaptiveness to a broad range of climates. *Pinus sylvestris*, for instance, is composed of seven sub-species (Pravdin, 1964; Iroshnikov, 1977) geographically distributed in: (1) eastern Europe, (2) the high elevations in the Crimea and Caucasus Mountains, (3) western and central Siberia, (4) Lapland, (5) the Asiatic steppes of Russia and Kazakhstan, (6) Yakutia of north-east Siberia, (7) Transbaikalia of south-eastern Siberia and Russia's Far East. The subspecies themselves are composed of climatypes (Turesson, 1925) that differ genetically in morphologic and physiologic attributes (Molotkov *et al.*, 1982). Results of numerous designed experiments (e.g. Patlay,

1974; Timofeyev, 1974; Iroshnikov, 1977; Shutyaev, 1983; Kuzmina, 1999) have demonstrated repeatedly that differences in growth potential and cold hardiness among climatypes and their constituent populations are not only genetically controlled but are continuously distributed across the forested landscape (Langlet, 1936; Giertych, 1991).

For species like *P. sylvestris*, the existence of populations physiologically attuned to different climates complicates the adjustment to change. Because sessile trees are not capable of migrating, changes in climate alter population fitness such that growth, productivity, and survival are affected immediately. With continual directional shifts in climate, genotypes other than those of the contemporary population eventually will become better suited to the novel climate. Adjusting to change therefore occurs in

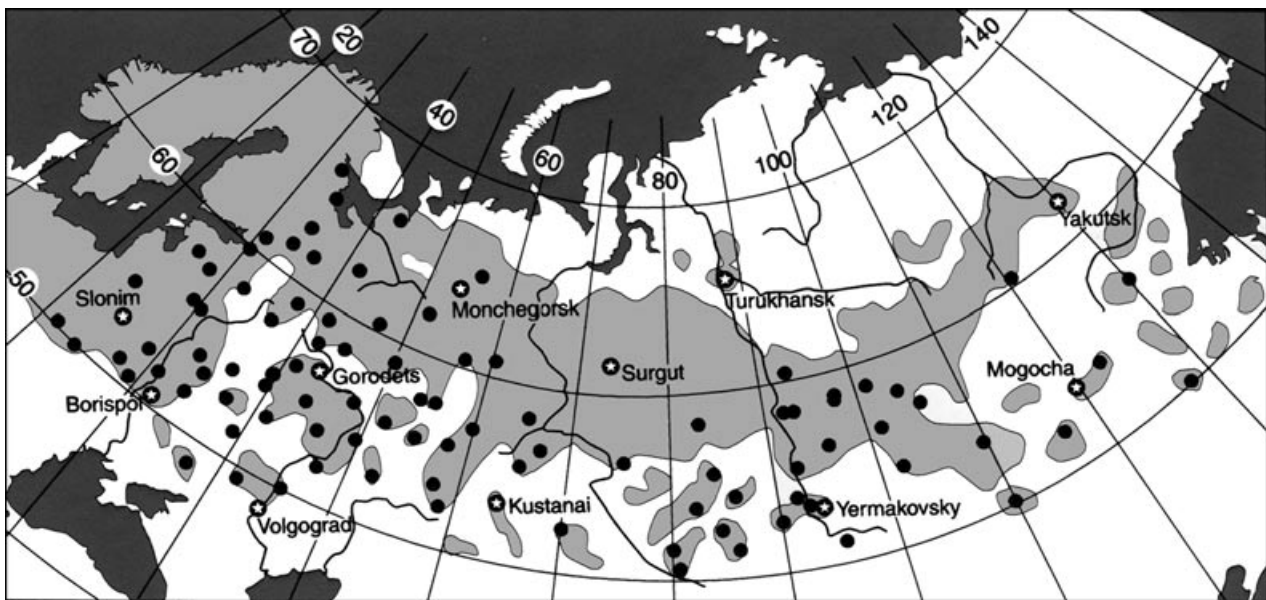


Fig. 1 Distribution (shading) of *P. sylvestris* (after Critchfield & Little, 1966) and location of populations (dots) sampled. Locations that are named are used throughout the paper to illustrate geographical effects.

the short term through physiological plasticity of individuals and in the long term through the evolutionary processes of selection, migration, mutation and drift (see Futuyma, 1979). However, both the short- and long-term adjustments can be pronounced and abstruse (Rehfeldt *et al.*, 1999b). As a result, a changing climate has intraspecific impacts that transcend extirpation and immigration at the margins (Davis & Shaw, 2001).

In this paper, genetic responses to climate are assessed for *P. sylvestris*. Data are collated from a heterogeneous series of designed experiments to develop population-specific response functions driven by climate variables. Throughout this paper, the term 'provenance' is used to designate a geographical location; 'population' refers to the individuals at that location and their wind-pollinated descendants; and a 'provenance test' is a study in which populations from different provenances are grown at the same site. For our purposes, niche-space refers to the Hutchinsonian multivariate hypervolume (Hutchinson, 1958), each dimension of which is represented by a climatic variable. Niche concepts are applied intraspecifically to populations as well as to species themselves.

P. sylvestris has an immense distribution that extends the breadth of Eurasia. Across this vast region, the climate varies tremendously and doubtlessly has been the primary force molding the species' genetic structure into the sub-species, climatypes, and populations that are apparent today. Our studies concern the species' distribution in the former Soviet Union (Fig. 1), a region subdivided from west to east into a European portion

(west of the Ural Mountains, 60°E), western Siberia (60° – 90°E), eastern Siberia ($>90^{\circ}\text{E}$), and the Far East. Alisov (1956) describes distinctive climates for these regions, our summary of which uses for reference the localities either identified in Fig. 1 (and marked with an asterisk in the text) or listed in Tables 1 and 2.

The climate in the north of the European portion (Monchegorsk*) is characterized by cool summers (700 degree-days $> 5^{\circ}\text{C}$) and moderately cold winters. While precipitation is only moderate (650 mm), in combination with the cool summers, moisture indices < 2 are produced, indicating excessive moisture. To the west (Jarva, Slonim*, Borispol*), the climate is mild and warm with sub-maritime features near the Baltic Sea (Jarva). Throughout this region, relatively high precipitation provides sufficient moisture for maintaining conifer and mixed conifer-deciduous forests. However, the south (Volgograd*, Kamyshin, Tsyurupinsk) is hot (2400–2700 degree-days $> 5^{\circ}\text{C}$) and dry (moisture indices > 5) in the summer but yet with cold winters. Here the vegetation is largely steppe. Toward the east, the climate is warm in the summer (Gorodets* and Kovrov) with moderately cold winters (January mean temperatures of about -12°C) that become increasingly colder (-16°C) toward the Urals (Kungur). Moisture in this region is sufficient to support deciduous, mixed conifer-deciduous, and conifer forests.

In Siberia, mean temperatures in January average from -17 to -22°C in the west (Kustanai*, Surgut*), -27° to -30°C toward the east (Turukhansk*, Mogocha*), and

Table 1 Location and general climate for 10 of the 47 provenance test sites

Planting site	Latitude °N	Longitude	Mean annual temperature (°C)	Degree-days > 5 °C	Mean temperature in coldest month (°C)	Summer–Winter temperature difference (°C)	Annual moisture index ¹	Mean annual precipitation (mm)
Jarva	59.40	25.90°E	4.2	1240	−6.5	23.1	1.7	712
Pskov	57.83	28.43°E	4.6	1435	−7.5	25.1	2.1	672
Monchegorsk	67.85	32.95°E	−0.7	665	−12.7	26.2	1.1	566
Tsyurupinsk	46.50	32.50°E	10.4	2710	−2.9	26.7	6.0	451
Kovrov	57.20	43.00°E	2.6	1375	−12.1	29.8	2.0	706
Kamyshin	50.17	45.40°E	6.5	2388	−11.0	34.8	5.5	433
Shyekinsky	41.22	47.15°E	11.9	2916	0.0	23.6	3.6	803
Kungur	57.40	56.90°E	1.3	1376	−15.6	33.4	2.1	664
Zvyerinogolovsk	54.50	64.90°E	1.0	1581	−18.2	37.2	2.9	385
Turukhansk	65.80	87.88°E	−7.0	747	−27.1	42.9	1.1	666
Suhobuzimo	56.50	93.25°E	−1.3	1223	−21.4	39.8	3.0	410
Zaudinsk	51.83	107.67°E	−2.9	1258	−26.9	45.1	5.1	246
Svobodny	50.26	128.17°E	−2.2	1533	−27.7	47.9	2.4	647
Crawford	45.10	67.51°W	5.4	1704	−9.4	28.7	1.5	1119
Gunn Park	47.25	93.58°W	3.7	1711	−15.7	35.4	2.4	700
Duck Lake	52.87	106.17°W	1.2	1434	−18.7	36.3	3.5	406
Footner Lake	59.13	117.57°W	−2.4	1013	−23.8	37.8	3.0	386

¹Ratio of degree-days > 5 °C to mean annual precipitation.

approach −45 °C deep inside the Asian continent (Yakutsk*). In Yakutia in fact, a fiercely continental climate with a summer–winter temperature difference of 60 °C is among the world's most severe. Nonetheless, Siberian summers are sufficiently warm (1000–1400 degree-days > 5 °C) to support conifer forests. Precipitation, however, declines toward the east, averaging 600–700 mm near Surgut but only 200–300 mm at Yakutsk. As a result, the distribution of forests in Yakutia is limited more by low precipitation than by the cold.

Russia's Far East (Svobodny) has a monsoonal climate that is cold in the winter (−28 °C), warm in the summer (1500 degree-days > 5 °C), and moist (650 mm annual precipitation). This combination is favorable for the development of conifer and mixed conifer–deciduous forests, and as a result, the Far East has a rich biodiversity.

Methods

During the latter half of the Twentieth Century, numerous *P. sylvestris* provenance tests were established throughout the world. Of these tests, 39 from the Eastern Hemisphere and eight from the Western contained a sample of the same Eurasian populations (Fig. 1) such that genetic responses to climate could be studied. Data from the eastern tests were compiled from Shutyaev & Giertych (1997), Iroshnikov (1977), Cherepnin (1980), and Kuzmina (1985); those from North American tests were

made available by Drs K. C. Carter, University of Maine, Orono, Maine; C. A. Mohn, University of Minnesota, Minneapolis, Minnesota; and N. K. Dhir, Alberta Sustainable Resource Development, Edmonton, Alberta. Together, the tests encompass climates that range from the maritime of Maine in northeastern United States to the continental of eastern Siberia (Table 1).

Of the total number of populations sampled, 110 were in six or more tests, the minimum number accepted for our analyses. The populations represent the species distribution throughout the former Soviet Union (Fig. 1) and thus originate from widely disparate climates (Table 2). On average, each test included 35 populations. The tests, however, were not part of a unified series, and therefore cultural regimes and measurement schedules were not uniform. Although our analyses consider only tree height, the morphometric trait least sensitive to cultural treatments, the ages at which the heights had been measured varied from 7–20. Before analysis therefore, heights needed to be adjusted to a common age such that genetic variation among populations was preserved. Age was defined from the date on which the seeds were sown, regardless of the number of years that planting stock might have been held in nursery or transplant beds.

All analyses used normalized climate data (Environment Canada, 1994; United States Department of Commerce, 1994; Gidrometeoizdat 1966–70). The climate of a planting site or provenance was inferred from that of the

Table 2 General climate of the 11 provenances identified and labeled in Fig. 1

Planting site	Latitude °N	Longitude °E	Mean annual temperature (°C)	Degree days > 5°C	Mean temperature in coldest month (°C)	Summer–winter temperature difference (°C)	Annual moisture index ¹	Mean annual precipitation (mm)
Slonim	52.97	25.37	6.2	1652	−5.4	23.2	2.3	709
Borispol	50.17	32.17	6.8	1940	−6.3	19.6	3.2	564
Gorodets	56.67	43.47	3.3	1490	−11.7	29.8	2.5	586
Volgograd	48.63	44.62	7.5	2536	−9.6	33.8	6.3	403
Monchegorsk	67.85	32.95	−0.7	665	−12.7	26.2	1.1	566
Kustanai	53.33	63.83	1.6	1747	−17.7	37.7	4.7	373
Surgut	61.42	73.33	−3.1	999	−22.0	38.9	1.5	675
Turukhansk	65.80	87.88	−7.0	747	−27.1	42.9	1.1	666
Yermakovskiy	53.00	94.00	0.2	1412	−19.3	37.7	2.4	583
Mogocha	53.74	119.62	−5.5	1048	−30.2	47.4	2.2	470
Yakutsk	62.00	130.00	−10.3	1155	−43.2	61.9	4.7	247

¹Ratio of degree-days > 5 °C to mean annual precipitation.

closest weather station, usually within 30 km. If no stations were within this limit, climate was interpolated from two or more stations.

Adjusting heights to a common age

Population heights were adjusted to a common age in three steps. In the first, a height–age relationship was developed with data from nine sites where repeated measurements were available (Fig. 2a). After performing preliminary analyses of several regression models, we accepted the ecologically sensible model:

$$Y_{i\bullet} = b_0 + b_1(A * D)_i \quad (1)$$

where Y is the height of trees at planting site i averaged across all populations; $A * D$ is the interaction of age and degree-days > 5 °C for site i ; and the b 's are regression coefficients. Thirty observations were available for the regression. Thirteen was the most common age of measurement and therefore was adopted as the standard age.

In the second step, a mean height for each of the 47 planting sites was estimated for the standard age by forcing the regression line in (1) through the observed mean:

$$Y''_{i\bullet 13} = Y_{i\bullet} + Y'_{i\bullet 13} - Y'_{i\bullet} \quad (2)$$

where Y'' is the estimated mean height at age 13 of all populations growing at site i ; Y is the observed mean height of trees at planting site i at the observed age; and Y' is the mean height predicted from [1] at site i for either the observed age ($Y'_{i\bullet}$) or the standard age of 13 ($Y'_{i\bullet 13}$).

Because coefficients of variation in our sample tended to be stable in time (Table 3), genetic variation about the adjusted planting mean was restored in the third step by:

$$Y''_{ij13} = Y''_{i\bullet 13} + \left[Y''_{i\bullet 13} \times \left(\frac{s_i}{Y_{i\bullet}} \right) \times \left(\frac{Y_{ij} - Y_{i\bullet}}{s_i} \right) \right] \quad (3)$$

$$= Y''_{i\bullet 13} \times \left(\frac{Y_{ij}}{Y_{i\bullet}} \right) \quad (4)$$

where Y''_{ij13} is the estimated 13-year height of population i at site j ; $Y''_{i\bullet 13}$ is estimated in [2]; Y_{ij} is the height of provenance j at site i ; s is the standard deviation of population means at site i ; and $Y_{i\bullet}$ is the mean height of all populations at site i .

The effectiveness of the procedure was judged from the error of the estimate between the adjusted and observed height of populations from data (1) on which the model was based and (2) from two independent studies: one (Cunningham, 1973; Cunningham & Van Haverbeke, 1991) which tested 49 populations at a single location in North Dakota, United States (48.28 °N, 100.65 °W, 1920 degree-days > 5 °C), and a second (Beaudoin, 1996) that tested 14 populations at a site in Quebec, Canada (45.68 °N, 73.32 °W, 2046 degree-days > 5 °C). These sources of data provided 20 comparisons for target ages between 11 and 14 (Table 3). The error of estimate was presented as a percentage of the observed mean.

Population specific response functions

Response functions were developed for each population to predict 13 year height from each of five climate variables which had demonstrated utility in similar analyses (Rehfeldt *et al.*, 1999a, b): (i) degree-days > 5 °C, (ii) mean annual temperature, (iii) degree-days < 0 °C, (iv) an annual moisture index, the ratio of degree-days > 5 °C to mean annual precipitation, and (v) the summer–winter temperature differential, the difference

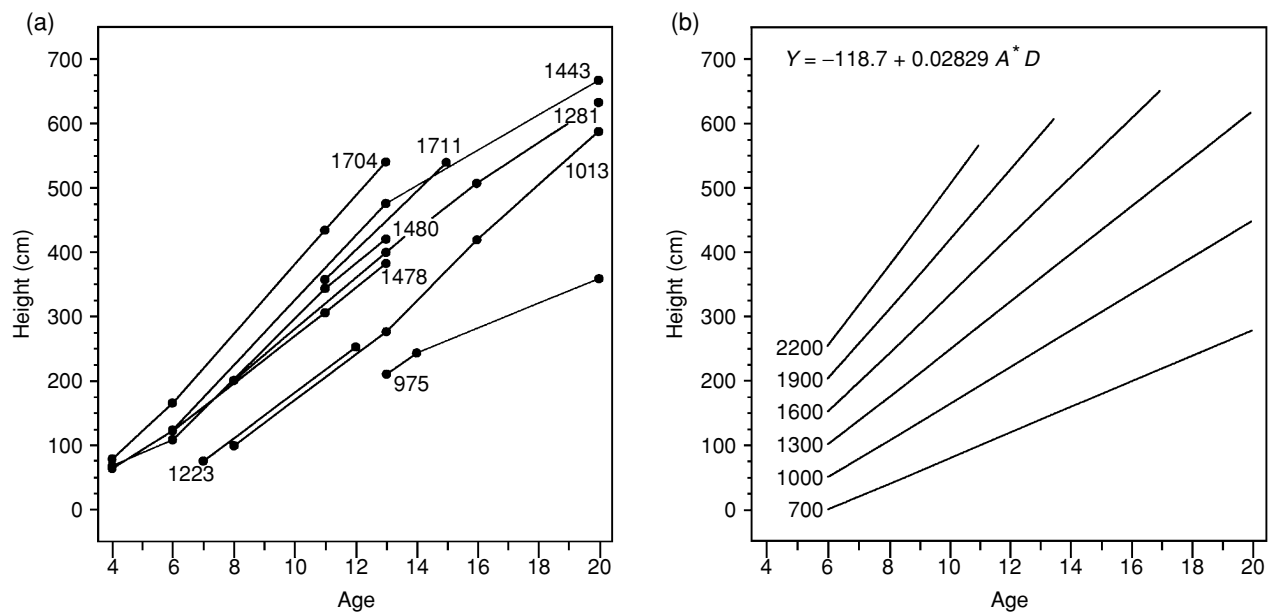


Fig. 2 (a) Relationship of height to age at nine planting sites where measurements were available for multiple ages. Lines connect data points from the same planting site and numbers indicate average degree-days > 5 °C. (b) the regression model developed from data in (a) that was used to adjust heights to a common age. Regression lines illustrate predicted values for sites with different degree-days > 5 °C.

Table 3 Location and general characteristics of provenance tests of Eurasian populations where measurements were available at multiple ages for imbedded data, those on which height–age models were developed, and independent data, those on which the model was tested. Coefficients of variation are of population mean heights and correspond from left to right to the ages in the previous column

Provenance test	Location	Number of provenances tested	Degree-days > 5 °C	Age of measurements	Coefficients of variation (%)
Imbedded data					
Suhobuzimo	Russia	98	1223	7, 12	17, 19
Crawford	United States	49	1704	4, 6, 11, 13	23, 24, 24
Smithtown	United States	47	1478	4, 6, 11, 13	22, 24, 23, 23
Ragmuff	United States	37	1478	4, 6, 11, 13	27, 27, 27, 27
Gunn Park	United States	33	1711	11, 15	16, 14
Duck Lake	Canada	62	1434	6, 13, 20	24, 18, 19
Smoky Lake	Canada	25	1281	8, 13, 16, 20	23, 18, 17, 16
Blue Ridge	Canada	45	975	13, 14, 20	29, 29, 27
Footner Lake	Canada	25	1013	8, 13, 16, 20	12, 14, 13, 12
Independent data					
Quebec	Canada	15	2046	9, 14	30, 27
North Dakota	United States	49	1922	14, 26	30, 9

between the mean temperature in the warmest month and the mean temperature in the coldest month. These five variables are referenced subsequently as the key variables.

A quadratic regression model was used to fit the climate of a planting site to population height for each of the key variables:

$$Y''_{ij13} = \beta_0 + \beta_1 C_i + \beta_2 C_i^2 \quad (5)$$

where Y'' is defined in (3); β_0 , β_1 and β_2 are regression coefficients; and C is one of the key variables at planting site i . This procedure produced 550 univariate regressions (five models for each of 110 populations), which

were based on 6–33 observations. Functions were rejected if the probability of statistical significance (p) was > 0.25 .

Response functions calculated and screened in this manner produced many regressions for which the difference between the roots (values of x for $y = 0$) was ecologically absurd. Because the distance between the roots can be viewed as either the adaptability or the fundamental niche of a population, upper and lower limits to this distance can be set to produce biologically realistic functions (Rehfeldt *et al.*, 2001). To this end, niche breadths were calculated for those functions based on 20 or more observations that were statistically significant ($p \leq 0.05$). Upper and lower limits to niche size then were defined as the maximum or minimum of these values. For any regressions in which niche breadth was outside these limits, the distance between the roots was redefined visually, and regression coefficients were recalculated from the well-known properties (e.g. Brink, 1933) of the quadratic equation:

$$r_1 r_2 = \beta_0 \beta_2^{-1} \quad (6)$$

and

$$r_1 + r_2 = -\beta_1 \beta_2^{-1} \quad (7)$$

where r_1 and r_2 are the roots, and β_0 , β_1 and β_2 , are defined in (5). Note that this procedure does not substantially alter that segment of the curve anchored by data but nevertheless achieves the objective of producing ecologically realistic functions (see Fig. 2, Rehfeldt *et al.*, 2001).

The x - and y -axis coordinates of the vertex of a response function define, respectively, innate growth potential ($Y_{\max}$) and optimal climate (C_{opt}), the climate where the growth potential can be expressed. The optimal climate therefore can be used for testing whether populations ordinarily inhabit their climatic optima. To do so, a t -test of paired observations was used for each of the five key climate variables to determine if the discrepancy between the inhabited and optimal climate (inhabited climate minus optimal climate) differed from zero. Simple correlation was used to relate the disparity between the inhabited and optimal climates to climatic and geographical variables of the provenance.

Generalized response functions

In discarding response functions of (5) when $p > 0.25$, we inadvertently assured that most populations would be represented by fewer than five functions. This meant that predictions would be biased for populations missing one or more of the functions if responses to climate (population adaptations) are controlled by different climate variables across the geographical distribution of the

species. We circumvented this potential problem by using stepwise multiple regression models to predict from provenance climate (i) the height at the vertex ($Y_{\max}$) (ii) the optimal climate (C_{opt}), and (iii) the distance between the roots (RD).

The stepwise models were of the general form

$$Q_{il} = \rho_0 + \rho_1 C_{1i} + \rho_2 C_{2i} \dots \dots \dots + \rho_n C_{ni} \quad (8)$$

where Q is either $Y_{\max}$, C_{opt} or RD for population i and response function l , ρ 's are regression coefficients; and C 's are climate variables for provenance i . Independent variables included the first and second powers of the five key variables, the mean temperature in coldest month, the mean temperature in the warmest month, and the mean annual precipitation. The best fitting regression model was selected according to statistical significance, the value of Mallow's statistic, and the significance of the individual coefficients.

Because the quadratic function is symmetrical about C_{opt} , the roots (r_1 , r_2) for any equation can be derived from $Y_{\max}$, C_{opt} and RD . The parameters of quadratic equation (5) then become:

$$\beta_2 = \frac{4Y_{\max}}{2r_1 r_2 - r_1^2 - r_2^2} = \frac{Y_{\max}}{r_1 r_2 - C_{\text{opt}}^2} \quad (9)$$

$$\beta_1 = (-\beta_2)(r_1 + r_2) = -2\beta_2 C_{\text{opt}} \quad (10)$$

$$\beta_0 = \beta_2 r_1 r_2 \quad (11)$$

Derived functions were validated by comparing predicted heights to observed heights in (i) a provenance test of 44 Eurasian populations planted at a single site in North Dakota, USA (Cunningham, 1973) where degree-days $> 5^\circ\text{C}$ were about 1920, and (ii) a series of provenance tests of 22 Eurasian populations planted at 12 locations in Quebec, Canada (Beaudoin, 1996) where degree-days $> 5^\circ\text{C}$ ranged from 1140 to 2050. Predicted heights for age 13 were correlated with the observed heights at age 26 for the North Dakota test and age 14 for the Quebec tests. Predicted values that were less than zero were equated to zero.

Applications to climate change

The impact of global warming on 13 year height was assessed for the 11 locations identified in Fig. 1. A global warming scenario of the Hadley Center, HadCM3GGA1 (Gordon *et al.*, 2000), was used to calculate for each location the change in mean annual temperature and precipitation expected between 1960 and 1990, the normalized period, and the decades beginning in 2030, 2060, and 2090. Mean annual temperature and precipitation of the future were converted to our key climate variables by using the regressions of Table A1.

Table 4 Statistics appropriate for judging the effectiveness of procedures for standardizing heights for a common age for data imbedded in the analyses themselves and for two sets of independent data

Provenance test	Age from which heights were adjusted	Target age	Mean at target age (cm)	Error of estimate ^a (cm)	Percent error
Imbedded data					
Suhobuzimo	7	12	247	4.4	1.7
Crawford	6	13	540	37.6	7.0
Crawford	11	13	540	9.7	1.8
Smithtown	6	13	417	15.7	3.8
Smithtown	11	13	417	-10.7	2.6
Ragmuff	6	13	383	-32.5	8.5
Ragmuff	11	13	383	-6.6	1.7
Gunn Park	15	11	332	11.2	3.4
Duck Lake	6	13	476	68.4	14.3
Duck Lake	20	13	476	94.4	19.8
Smoky Lake	8	13	410	26.1	6.4
Smoky Lake	16	13	410	9.1	2.2
Smoky Lake	20	13	410	28.6	7.0
Blue Ridge	14	13	213	-5.5	2.6
Blue Ridge	20	13	213	44.8	21.1
Footner Lake	8	13	276	34.0	12.3
Footner Lake	16	13	276	-57.0	20.6
Footner Lake	20	13	276	-110.6	39.9
Independent data					
Quebec	9	14	373	-40.4	10.8
North Dakota	26	14	328	-56.9	17.3

^aobserved minus estimated.

Population performance in the future was estimated by using the novel climates as independent variables in the response functions. Short-term responses across the 21st Century were assessed from the changes in 13 year height expected in time for the contemporary population at each of the locations. Long-term effects were assessed from the difference between the future height of the contemporary population and that of the population best suited for each locality for the decade beginning in 2090. The best-suited genotypes were defined as the tallest which therefore would be those favored by the density-dependent selection that accompanies forest development. In calculating population responses, the derived functions of (9), (10), and (11) used were in replacement of those original functions of (5) that failed significance at $P < 0.25$. Predicted responses that were less than zero were equated to zero.

The procedure thus produced for each of 110 populations five estimates of 13 year height at 11 locations for the contemporary climate and for three future decades. In accord with the concept of limiting factors within niche space viewed as a Hutchinsonian hypervolume, the smallest of the five was considered to be the best estimate. To account for competitive interactions among

species, we also assumed that climatic limits of distribution for *P. sylvestris* in the future would be the same as today. Climatic limits were inferred from the 110 provenances of Fig. 1. Predicted heights were equated to zero for future climates lying outside these limits.

Results

Adjusting heights to a common age

The regression for adjusting height for age accounted for 93% of the variance among the data points in Fig. 2(a). The regression, however, was based on only 30 observations and therefore needed validation before confidence could be placed in its use. Two approaches were taken toward validation, one involving independent data and the other using data imbedded in the regression model itself. Because the effects of planting sites were represented in the model quantitatively by degree-days $> 5^{\circ}\text{C}$, even the latter approach was suitable for objectively assessing errors of prediction.

For the 20 comparisons between observed and adjusted heights, the error of the estimate averaged about 10% of the mean (Table 4). Of the eight comparisons for which

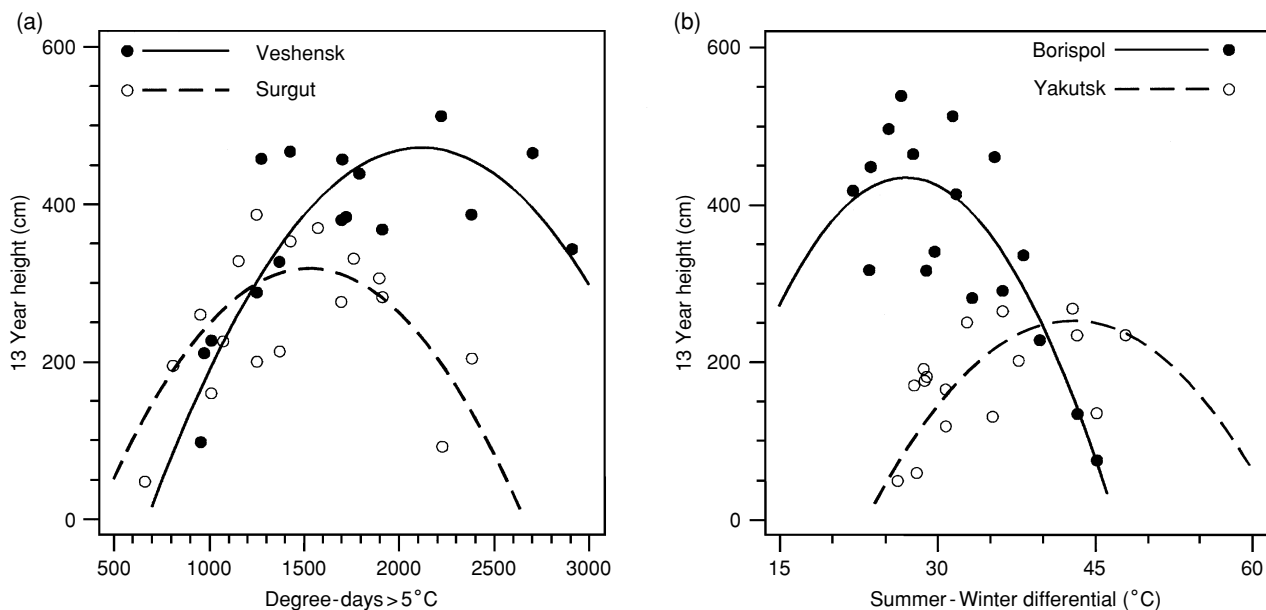


Fig. 3 Relationship between 13 year height and planting site climate for two populations with disparate responses, in (a) according to degree-days > 5 °C, and in (b), according to the summer–winter temperature differential. In both (a) and (b), curves are truncated near the climatic limits of the species.

errors were greater than 10%, seven involved either (i) an age of measurement of 20 or more, or (ii) a discrepancy of seven years or more between the target age and the age from which adjustments were made. Therefore, even though large errors like those for Footner Lake are disquieting, the statistics in Table 4 nonetheless suggest that procedural biases could be minimized by discarding data if their age of measurement was less than seven or greater than 20.

Intraspecific responses to climate

Of the 550 quadratic regressions of (5), 104 (19%) were discarded because $p > 0.25$, leaving 101 driven by degree-days > 5 °C, 97 by the summer–winter temperature differential, 90 by the annual moisture index, 76 by mean annual temperature, and 82 by degree-days < 0 °C. For 20% of the remaining regressions, niche breadth either exceeded our upper limit or was smaller than the lower. For them therefore, distances between the roots were adjusted and regression coefficients were recalculated. Discarding 19% of the original functions meant that all four functions were available for only 51 populations while 28 only had three or fewer.

Figure 3 illustrates both the fit of the response functions and their ecological basis. In Fig. 3(a), the R^2 for the Veshensk regression is 0.56 while that for the Surgut function is 0.60. Veshensk is located 220 km northwest

of Volgograd in European Russia while Surgut is in western Siberia (Fig. 1). Consistent with prevailing views of ecological adaptation, therefore, the Veshensk population (Fig. 3a), originating from a relatively mild climate (Table 2), displays a much higher growth potential ($Y_{\max}$) and warmer ecological optima (C_{opt}) than the population from Surgut. Quite similarly, in comparison to the trees from the severe continental climates of Yakutsk in eastern Siberia (Table 2), trees from Borispol in eastern Europe display a higher innate growth potential that is achieved in continental climates of much less severity (Fig. 3b).

Genetic differences among populations for growth potential and climatic optima are apparent in Fig. 4 as are strong simple correlations (r) between them: 0.72 for the function driven by degree-days > 5 °C (Fig. 4a), -0.49 for the function driven by the summer–winter temperature differential (Fig. 4b), 0.68 for the function driven degree-days < 0 °C, 0.58 for the function driven by mean annual temperature, and 0.34 for the function driven by the annual moisture index. Figures 3 and 4 thus provide further demonstrations that in species of forest trees, populations from mild climates tend to have high growth potentials and low tolerances to the cold, while those from severe climates have high cold tolerances but low growth potentials.

These results are consistent with the view that evolutionary processes have molded the genetic structure of

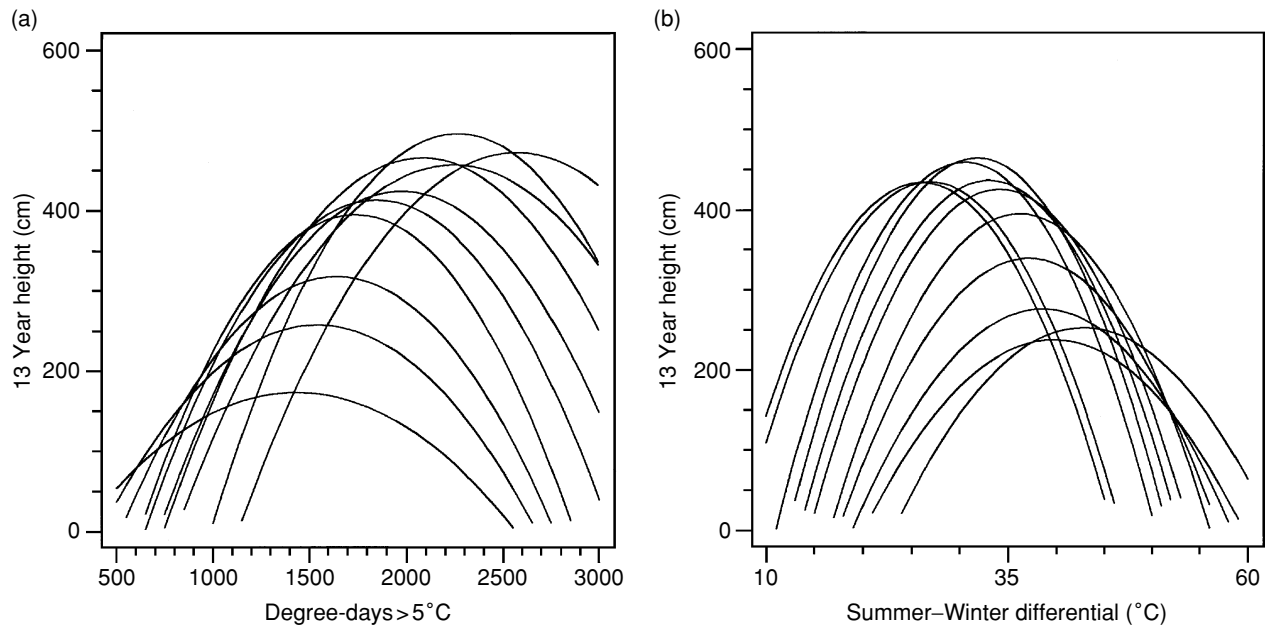


Fig. 4 Response functions for 10 populations in relation to climate: (a), degree-days > 5°C, and (b), the summer–winter temperature differential. In both (a) and (b), curves are truncated near the climatic limits of the species.

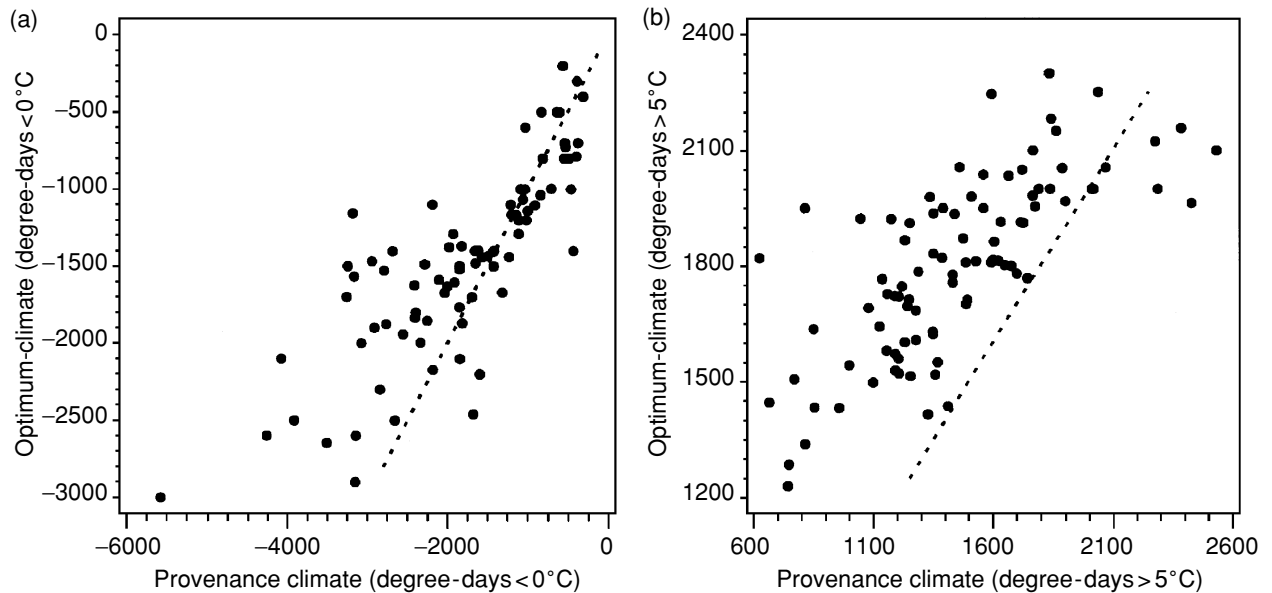


Fig. 5 Relationship between the optimum climate and the provenance climate: (a), degree-days < 0°C, and (b), degree-days > 5°C. In both (a) and (b) the hashed line (–) indicates equality of the inhabited and optimal climates. Populations to the left of this line occupy climates colder than their optima while those to the right occupy climates warmer than their optima.

P. sylvestris. Consequently, strong simple correlations (r) exist between the inhabited and optimal climate: 0.65 for mean annual temperature, 0.77 for degree-days < 0°C (Fig. 5a), 0.71 for degree-days > 5°C (Fig. 5b), and 0.64

for the summer–winter temperature differential. Nevertheless, paired t -tests of the difference between the optimal and inhabited climates were statistically significant ($p \leq 0.01$) for all of the key variables except the

Table 5 Number of observations (n), number of independent variables (v) and goodness of fit (R^2) from stepwise multiple regressions for predicting $Y_{\max}$, the predicted value at the vertex; C_{opt} , the x -axis coordinate of the vertex, and RD , the distance between the roots for the five response functions. Regression coefficients are in Table A2

Dependent variable	Function 1 ($n = 101$)		Function 2 ($n = 82$)		Function 3 ($n = 76$)		Function 4 ($n = 97$)		Function 5 ($n = 90$)	
	v	R^2	v	R^2	v	R^2	v	R^2	v	R^2
$Y_{\max}$	6	0.71**	3	0.61**	4	0.59**	4	0.41**	4	0.56**
C_{opt}	4	0.57**	1	0.64**	3	0.56**	4	0.72**	2	0.13**
RD	3	0.43**	2	0.11**	2	0.03	3	0.14**	3	0.44**

Note: Function 1 is driven by degree-days $> 5^\circ\text{C}$, function 2 by degree-days $< 0^\circ\text{C}$, function 3 by mean annual temperature, function 4 by the summer–winter temperature differential, and function 5 by the annual moisture index. **statistically significant with $p < 0.01$.

summer–winter temperature difference. For our sample of populations, the inhabited climate is colder than the optimum by 351 degree-days $> 5^\circ\text{C}$, 312 degree-days $< 0^\circ\text{C}$, and 2.6°C mean annual temperature; and, it is also 0.7 units of the moisture index (growing season heat per unit of moisture) below the optimum. Even though evolutionary processes undoubtedly are responsible for genetic differentiation of populations, most populations nonetheless occupy climates that are sub-optimal.

Figure 6 shows that in addition, the discrepancy between the inhabited and optimal climate is strongly and negatively correlated (r) with provenance climate: -0.79 for mean annual temperature (Fig. 6a), -0.90 for the summer–winter temperature differential (Fig. 6b), -0.84 for degree-days $< 0^\circ\text{C}$ (Fig. 6c), -0.87 for the annual moisture index (Fig. 6d), and -0.79 for degree-days $> 5^\circ\text{C}$. These correlations, however, are derived from much different effects. First, populations from the warmest regions tend to inhabit climates either near to or slightly warmer than their ecological optima. As the climate becomes colder, however, the discrepancy between the optimum and inhabited climate increases (Fig. 5, 6a and c). Populations inhabiting the coldest regions therefore endure climates far colder than their optima. Second, a moisture index of about three units seems optimal for most populations (Fig. 6d); as the deviation in the absolute value of the moisture index increases from this value, so does the amount by which the inhabited climate is sub-optimal. Third, populations occupying the continental climates of Siberia would achieve their optimal growth in climates less continental than that of their provenance, while those occupying the maritime climate at high latitudes in eastern Europe would achieve theirs in climates that were slightly more continental than that of their provenance (Fig. 6b). For the summer–winter temperature differential, therefore, populations on average occupy their climatic optima, even though few actually do.

Because the severity of the climate across Eurasia is closely related to geography, the discrepancy between the optimal and inhabited climate is correlated with longitude (Fig. 7a) and latitude (Fig. 7b). Populations from the southern portion of the species' range in Eastern Europe tend to occupy climates that are near their optima, while northern and particularly eastern populations inhabit climates that are far colder than theirs. Because of the vastness of Eurasia, climatic gradients across the distribution of *P. sylvestris* are much larger from west to east than from north to south. The difference between the inhabited and optimal climates therefore is correlated much more strongly with longitude than with latitude.

Derived response functions

Stepwise multiple regressions for predicting from provenance climate the height at the vertex ($Y_{\max}$), the optimal climate (C_{opt}), and the distance between the roots (RD) of each response function produced statistically significant regressions for all but one of the dependent variables (Table 5). With values of R^2 as high as 0.72, the regressions were particularly effective in predicting C_{opt} and $Y_{\max}$.

Statistically significant simple correlations between observed and predicted heights using data from independent tests in North America (Table 6) provide strong validation for the response functions, but particularly for that driven by degree-days $> 5^\circ\text{C}$. Regression coefficients for deriving the functions are presented in Table A2; note that for the model lacking statistical significance, predicted values are set equal to the mean.

Response to global warming

The changes in climate predicted by the Hadley Model are both pronounced and disparate for the 11 sites of Fig. 1 (Table 7). When the Hadley predictions were

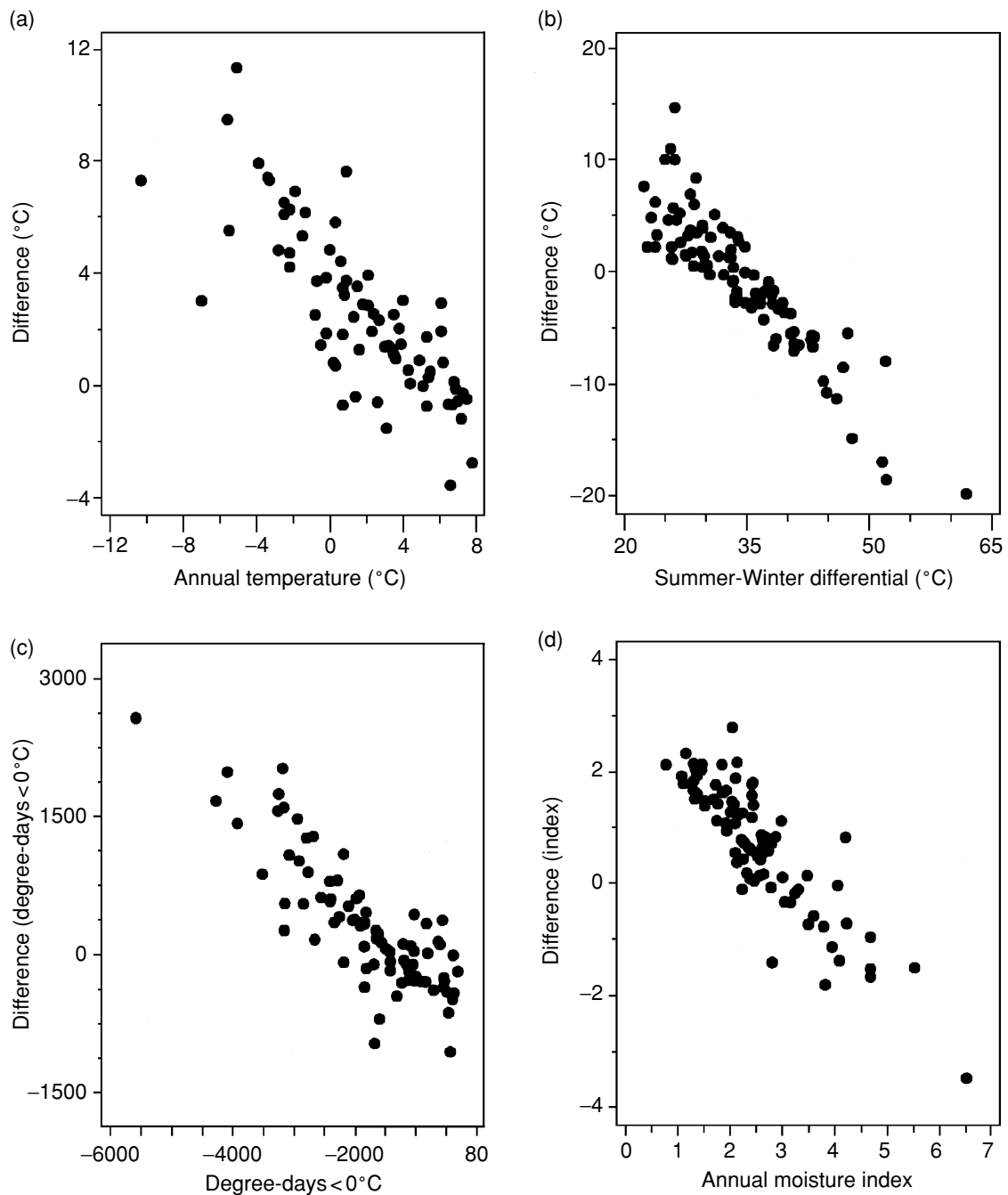


Fig. 6 Relationship of provenance climate with the difference between the optimum climate and the inhabited climate: (a), mean annual temperature; (b), summer–winter temperature differential; (c), degree-days < 0 °C; and (d), annual moisture index.

converted to our key variables (Table A1) and used to drive the response functions, the results depicted for Eurasia short and long-term responses to global warming that are highly variable geographically (Table 8).

Short-term responses fell into three categories (Table 8). At one extreme was the mortality and therefore the

demise of pine forests predicted for Volgograd and Monchegorsk by the end of the 21st Century; at Volgograd, because the predicted climate becomes too hot and dry (functions driven by the moisture index and degree-days > 5 °C predicted a height of zero), and at Monchegorsk because the climate becomes too

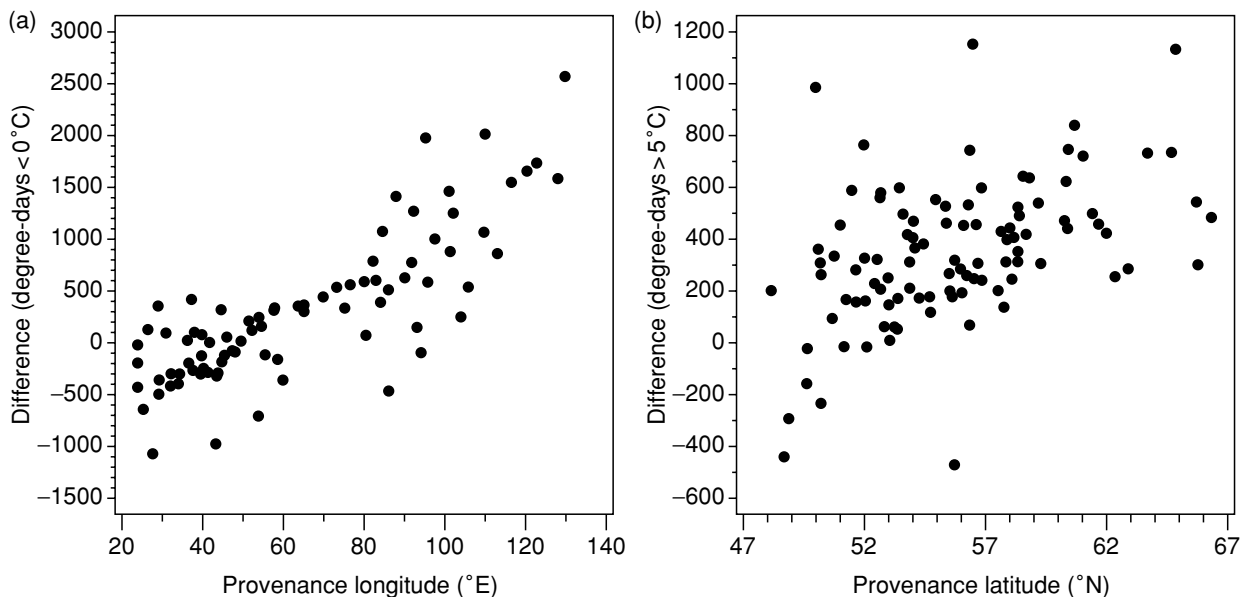


Fig. 7 Relationship of provenance location with the difference between the provenance climate and the optimum climate. (a), for degree-days $< 0^{\circ}\text{C}$ and longitude; and (b), degree-days $> 5^{\circ}\text{C}$ and latitude.

maritime (the function driven by the summer–winter temperature differential predicted a height of zero). A second category consists of those populations that today inhabit climates that are either near or only slightly colder than their ecological optima. Thus, at Slonim, Borispol, Gorodets, Kustanai, and Yermakovskiy, growth of the contemporary population should slowly decline as the climate changes, with losses in height eventually reaching maximums between 13% and 50%. The third category includes those populations that exist today in climates that are far colder than their optima. At Surgut and Turukhansk, for example, a warming climate should increase 13 year height by about 30%; at Mogocha by 200%; and at Yakutsk by 450%.

Our models also predict that the genotypes best suited to future climates will be other than the inhabitants of today (Table 8). Long-term responses therefore will depend on either the immigration or evolution of genotypes suited to the novel climates. For instance, at Volgograd in particular, but also perhaps at Slonim and Borispol, immigration may involve species other than *P. sylvestris*. No populations existed in our samples that today inhabit climatic conditions expected in the future at these three locations. Whether suitable populations exist in western Europe is not known, but it is nonetheless doubtful that *P. sylvestris* genotypes currently exist that are capable of inhabiting a climate with the 3400 degree-days $> 5^{\circ}\text{C}$ and moisture indices of 7.8 (see Tables 1 and 2) that are projected for the future at Volgograd. Yet, at most locations (Table 8) throughout

Table 6 Simple correlations of heights observed in two North American provenance tests with those predicted from each of five derived response functions (Table A2), the mean of the five predictions, and the smallest of the five predictions. All coefficients are significant with $p < 0.01$

Source of predicted value	Quebec ^a	North Dakota ^b
Function 1, degree-days $> 5^{\circ}\text{C}$	0.71	0.81
Function 2, degree-days $< 0^{\circ}\text{C}$	0.47	0.75
Function 3, annual temperature	0.54	0.80
Function 4, summer–winter differential	0.34	0.57
Function 5, annual moisture index	0.55	0.72
Average of the five predicted values	0.67	0.79
Minimum of the five predicted values	0.52	0.79

^atree ages, 14; number of observations, 67.

^btree ages, 26; number of observations, 44.

the species' contemporary distribution, the enhanced growth potential of those genotypes best suited to the future climate eventually should allow any negative short-term impacts to be overcome while yielding long-term increases in growth and productivity. As measured by 13 year height, long-term gains could range from about 17% at Kustanai to over 530% at Yakutsk when those genotypes best suited to the future climate actually occur there.

Table 8 also shows that in our sample of populations, the genotypes best suited to the climate of 2090 currently

Table 7 Changes (Δ) in mean annual temperature and daily precipitation expected between the contemporary period (1961–90) and three decades beginning in 2030, 2060, and 2090 as projected by the Hadley Model (HadCM3GGa1) for the 11 locations labelled in Fig. 1

Location	Δ Temperature ($^{\circ}\text{C}$)			Δ Precipitation (mm/day)		
	2030	2060	2090	2030	2060	2090
Slonim	2.45	3.19	4.66	−0.17	−0.28	−0.17
Borispol	2.60	3.64	5.19	−0.12	−0.11	−0.07
Gorodets	2.59	3.52	5.43	−0.04	−0.09	0.07
Volgograd	2.19	3.19	4.41	−0.04	−0.08	−0.12
Monchegorsk	2.24	3.58	5.76	0.08	0.11	0.36
Kustanai	2.82	4.03	5.49	−0.02	−0.06	0.02
Surgut	2.36	3.79	5.85	0.13	0.15	0.29
Turukhansk	2.65	3.94	5.72	0.20	0.23	0.36
Yermakovsky	1.95	3.12	4.41	−0.11	0.00	0.00
Mogocha	2.27	3.82	4.98	0.13	0.10	0.29
Yakutsk	2.82	4.59	5.68	0.18	0.32	0.38

Table 8 Thirteen-year heights (cm) predicted at 11 locations (Fig. 1) for (i) the contemporary population in the contemporary climate and in the Hadley GCM's projected climate for the decades beginning in 2030, 2060, and 2090, and (ii) the population best suited for the climate of the decade beginning in 2090. Numbers in parentheses in final column are approximate geographical distances (km) between the location and the contemporary provenance of the best-suited population in 2090

Location	Contemporary population				Best-suited population for 2090
	1961–1990	2030	2060	2090	
Slonim	350	322	314	298	–
Borispol	429	424	408	360	–
Gorodets	383	372	350	296	447 (1200)
Volgograd	284	174	80	0	–
Monchegorsk	84	35	4	0	395 (2200)
Kustanai	355	271	191	177	414 (1625)
Surgut	212	243	269	270	448 (3000)
Turukhansk	136	176	180	177	354 (1800)
Yermakovsky	329	325	308	284	434 (2700)
Mogocha	188	242	262	269	385 (3775)
Yakutsk	21	68	101	118	135 (1075)

exist at large distances (> 1000 km) from the site of their future optima. To be sure, we analyzed only a sample of the *P. sylvestris* climatotypes, but, nevertheless, these distances are astonishingly large. They illustrate therefore the extent of the long-term evolutionary adjustments necessary before global warming can be accommodated.

The statistics in Table 8 imply that the response functions could be used to map the shifts in distribution expected from a warming climate. For example, screening the coldest of 1200 Siberian weather stations to find locations climatically suitable for *P. sylvestris* in the novel climates of 2090 suggested that the Yakutsk population (Table 2) should survive in the future climate at Iansk

(68.7 $^{\circ}\text{N}$, 134.5 $^{\circ}\text{E}$) and Ust-Moma (66.5 $^{\circ}\text{N}$, 143.2 $^{\circ}\text{E}$). In fact, according to our models, for only those locations where degree-days $> 5^{\circ}\text{C}$ currently are < 400 (north of about 72 $^{\circ}\text{N}$) the future climate still would be too cool during the growing season for *P. sylvestris*. One might conclude therefore that global warming would produce a shift in the distribution of the species at least 800 km toward the northeast. Such a conclusion, however, would fail to take into consideration the physiognomy of the region and the ecology of the species. To be suitable for *P. sylvestris*, the permafrost that now covers most of Yakutia must thaw to a depth of 2 m during summer months (Pozdnyakov, 1983). Yet, the thawing of

permafrost itself may create extensive bogs (Velichko *et al.*, 1995) that presumably would be unsuitable for this pine. Mapping shifts in distribution therefore becomes a complex problem that must integrate factors additional to the atmospheric climate.

Discussion

Height adjustments

Our approach for adjusting tree heights to a common age is probably as realistic biologically as is statistically possible with only 30 observations. Consider, first, that the regression was based on a linear relationship between height and age when, in fact, height-age relationships tend to be logistic. Yet, for the ages under consideration, a linear model obviously was suitable (Fig. 2a). Second, to accommodate the well-known fact that tree growth is dependent on temperature, the approach incorporated into the regression coefficient a variable (degree-days $> 5^{\circ}\text{C}$) reflecting the temperature regime of the planting site. Third, because tree growth is determined by many environmental factors (e.g. soils, competition, insects) in addition to climate, the regressions were forced through the observed data points to arrive at an expected height at a target age of 13 and finally, because coefficients of variation remained relatively constant in time (Table 3), provenance variation about an adjusted site mean could be reintroduced at the target-age.

Nevertheless, the approach doubtlessly introduces errors that most likely accrue from two primary factors. First, growth rates of trees are determined as much by the genotypes that are planted on the site as by environmental conditions of the site itself (Monserud & Rehfeldt, 1990). In the data we assembled, a sub-sample of only 35 of the populations was grown at each site, and this factor undoubtedly biased site means. Second, tree growth is influenced by cultural conditions (e.g. density, spacing, vegetation control), biotic effects (e.g. insects, diseases), and abiotic factors (e.g. droughts, unseasonable frosts) for which our approach could not account. Because of these sources of error and because of the general problem foresters historically have faced in developing site-specific relationships between height and age, perhaps it should be satisfying for errors of estimate to be only 10% (Table 4). Still, errors can be quite large (e.g. Footner Lake, Table 4), but by limiting the discrepancy between the target-age and the age from which adjustments were made, they should be acceptable. Our approach therefore seems to be a reasonable means of assembling heterogeneous data from disparate series of provenance tests. For such data, genetic responses to climate could not be assessed without adjusting height for age.

Ecological adaptation

The results demonstrate principles of ecological genetics that are well known for plants in general (see Brown & Gibson, 1983) and for forest trees in particular (e.g. Rehfeldt, 1988, 1989): species consist of populations that differ in innate growth potential and cold hardiness, the two of which are negatively correlated. Adaptation of populations, first and foremost, appears as a balance between selection for growth potential in mild climates and selection for cold tolerance in severe. While evolutionary processes undoubtedly have produced the climatypes that characterize the genetic system of *P. sylvestris* in Eurasia, our results also lead toward the seemingly antithetical conclusion that natural populations exist in climates that are sub-optimal to their growth and survival.

Still, these results are essentially the same as for *P. contorta* (Rehfeldt *et al.*, 1999b), and therefore as with *P. contorta*, the only reasonable explanation for these seemingly antithetical results is for the distribution of genotypes to be determined as much or more by competition than by adaptation to the physical environment. Put simply, density-dependent selection, a universal component of forest development, and selection by the physical environment are seen as the driving forces controlling the distribution of genotypes. For instance, if seeds from Veshensk and Surgut were dispersed across a site with 1500 degree-days $> 5^{\circ}\text{C}$, both undoubtedly could grow superbly (Fig. 3a). Yet, genotypes from Veshensk would be 75 cm taller after 13 years than those from Surgut, and in time, therefore, the density-dependent selection that accompanies self-thinning would favor genotypes from Veshensk. This means that genotypes from Surgut would be competitively excluded from their climatic optima. Competitive exclusion is initiated by the fastest growing genotypes, which by virtue of their high growth potential, are capable of excluding genotypes of other populations from their optima (Fig. 4).

As argued by Arthur (1987), the realized niche becomes that part of the fundamental niche where a group of genotypes is, first, adequately adapted but, second, competitively exclusive. Sexual reproduction in the face of the high levels of gene flow that typify these two wind-pollinated species disassembles in each generation those genotypes best suited for a given site. Consequently, the balance between high growth potential (competitive exclusiveness) and adaptation to the climate must be reestablished each generation. Asymmetric gene flow along a climatic gradient from the center of distribution toward the periphery (Kirkpatrick & Barton, 1997; Garcia-Ramos & Kirkpatrick, 1997) couples with strong density-dependent selection to prevent populations from inhabiting their

ecological optima (Rehfeldt *et al.*, 1999b). For populations toward the periphery, the discrepancy between the optimal and inhabited climates then becomes larger as the climate becomes more inhospitable.

Because two widespread conifers have responded to climate so similarly, it is tempting to consider that this process by which populations are relegated to sub-optimal climates may reflect a general principle controlling the distribution of genotypes in tree species of the temperate and boreal forests. Nearly all of the broadly distributed species of these forests are composed of populations that have different innate growth potentials and climatic optima. Nearly all, moreover, exhibit clinal patterns of genetic variation for growth potential and cold hardiness, the two of which tend to be negatively correlated. For all, density-dependent selection is an integral component of forest development. Perhaps it is typical therefore for the distribution of genotypes within forest tree species as well as the distribution of species themselves to be governed by a tradeoff between adaptation and competition. Populations of many species indeed may inhabit climates that are sub-optimal for their growth and development.

Climate change

Projected impacts of global warming on *P. sylvestris* (Table 8) parallel closely those for *P. contorta* (Rehfeldt *et al.*, 1999b, 2001). They also are surprisingly compatible with the conclusions of Persson (1998) with *P. sylvestris* of Scandinavia, Schmidting (1994) with *Picea abies* of Western Europe, and Carter (1996) with several species from northeast United States, all of whom used transfer functions rather than response functions. Studies of all of these species dealt with tree heights at relatively young ages. In this regard, a comparison of the results of Rehfeldt *et al.* (1999b) with Rehfeldt *et al.* (2001) unequivocally demonstrates that even small percentage changes in height at young ages are magnified exponentially when extrapolated to volumes of wood per unit area. Height differences at young ages also provide the fuel for density-dependent selection, and, for these reasons, seemingly insignificant changes in tree height at young ages are indicative of much larger effects on future productivities. Consequently, genetic variation in juvenile height is well suited for assessing the impact of a changing climate on forest trees.

Our results suggest that even without considering augmented atmospheric CO₂ or nitrogen deposition, global warming will have both short and long-term impacts on the growth and survival of *P. sylvestris* that will be both pronounced and complex. Immediate short-term responses should be highly negative in populations that currently inhabit mild climates but strongly positive for

populations inhabiting severe climates. Yet, in the long term, when the novel climates of the future are inhabited by the best suited genotypes, productivity should increase throughout much of the species distribution, thereby ameliorating negative short-term impacts while enhancing the positive. While extirpation on some fronts should be balanced against immigration on others, the long-term impacts of global warming on *P. sylvestris* are strongly positive for Eurasia in general and Siberia in particular.

Achieving the expected long-term increases in productivity requires, first, a redistribution of genotypes throughout the contemporary distribution and, second, immigration into lands that are currently unsuitable. Achieving the potential therefore will be dependent on concomitant rates of microevolution and migration (Davis & Shaw, 2001). Although seed dispersal is the only means by which distributions expand, this form of migration is not feasible for redistributing genotypes within existing distributions (Davis, 1989; Solomon & Kirilenko, 1997). To be sure, the genotypes best suited to future climates currently reside at large distances from their future optima (Table 8), and, therefore, migration of pre-adapted genotypes by means of seed dispersal would require many generations (Davis, 1989). However, in light of the rapid rate that climates are changing (IPCC, 2001), a leisurely migration of pre-adapted genotypes cannot take place across a climate gradient (Table 7) without the migrants being subjected to selection. Descendants of genotypes adapted to climatic conditions at one time and place simply cannot arrive in a similar climate in a new time and place without undergoing change. Consequently, the redistribution of genotypes required to optimize adaptedness in the novel climates of 2090 undoubtedly will be dependent on directional selection acting on systems of genetic variability enriched each generation by gene flow rather than from the migration of pre-adapted individuals.

When genetic variances are large and selection is intense, genetic systems can respond rapidly to change (see Falconer, 1981). Even so, in *P. contorta* the amount of genetic change required to convert contemporary genotypes to those best suited for future climates is often greater than can be achieved in a single generation of intense selection (Rehfeldt *et al.*, 2001). In fact, for *P. contorta*, as many as twelve generations may be required to accommodate global warming. For *P. sylvestris*, genetic gains in height of about 10% of the mean are readily attainable under strong selection during the first generation of domestication (Rosvall *et al.*, 1998). Conversion of the heights expected for the contemporary population in 2090 to those of the best suited population (Table 8) would require therefore about one generation at Yakutsk; five at Surgut, Yermakovskiy, and Mogocha; 10

at Turukhansk; and 13 at Kustanai. Because generations in *P. sylvestris* generally are discrete and last more than 100 years, the lag in genetic response to global warming could be more than 1500 years.

Such calculations and their conclusions tacitly assume that future climates will stabilize, when, in fact, stabilization is problematic (IPCC, 2001). Without stabilization, evolutionary processes in forest trees of long generation will perpetually lag far behind the change in climate, causing future productivities to fall far short of their potential. To the evolutionary geneticist therefore, the projected speed of global warming is more daunting than the absolute amount of change. To ecological modelers, the redistribution of genotypes that is necessary for accommodating a changing climate may produce a perpetual lag between adaptiveness and climate that will effectively preclude the formation of the high latitude terrestrial carbon sink anticipated by some researchers (Schulze *et al.*, 2001; White *et al.*, 2001).

As pointed out clearly by Davis & Shaw (2001), the impact of a changing climate encompasses much more than shifts in the distribution of species. Response to change reverberates throughout a species' genetic system and therefore throughout its distribution. The present results join with those for *P. contorta* (Rehfeldt *et al.*, 1999b, 2001) to demonstrate for two of the northern hemisphere's most widespread conifers the importance of considering intra-specific effects when assessing responses to a changing climate. This work was supported in part by a grant from International Programs, US Forest Service and to the Sukachev Institute of Forest.

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Appendix

Table A1 Regression equations and their associated R^2 for predicting degree-days $< 0^\circ\text{C}$, mean temperature in the warmest month, mean temperature in the coldest month, and degree-days $> 5^\circ\text{C}$ from mean annual temperature. Regressions were based on 1023 observations (Gidrometeoizdat, 1966–70) and all were statistically significant at $p < 0.01$

Dependent variable	R^2	Equation
Degree-days $< 0^\circ\text{C}$	0.97	$-2234.9 + 219.4 X_1 - 4.397 X_1^2$
Warm month temperature	0.96	$1.5 + 2.23 X_1 - 0.0197 X_1^2 - 0.0076 X_2$
Cold month temperature	0.97	$4.9 - 1.07 X_1 + 0.0453 X_1^2 + 0.0112 X_2$
Degree-days $> 5^\circ\text{C}$	0.99	$-542.6 + 55.18 X_1 + 2.48 X_1^2 + 104.2 X_3$

X_1 = mean annual temperature, X_2 = degree-days $< 0^\circ\text{C}$, X_3 = mean temperature in the warmest month.

Table A2 Regressions for predicting the vertex ($Y_{\max}$), climatic optima (C_{opt}), and distance between the roots (RD) for five response functions. Functions are labelled according to their independent variable

Regression equations

Function 1, degree-days $> 5^{\circ}\text{C}$

$$Y_{\max} = -241.3 + 0.471X_1 - 9.28 \times 10^{-5}X_1^2 - 2.53 \times 10^{-5}X_2^2 + 0.821X_3^2 + 18.1X_4 - 0.481X_4^2$$

$$C_{\text{opt}} = 1240.9 + 0.250X_1 - 4.03 \times 10^{-5}X_2^2 + 0.951X_3^2 + 41.8X_5$$

$$RD = 2166.2 + 4.56 \times 10^{-5}X_2^2 + 133.0X_5$$

Function 2, degree-day $< 0^{\circ}\text{C}$

$$Y_{\max} = 56.9 + 0.370X_1 - 7.96 \times 10^{-5}X_1^2 - 3.92 \times 10^{-6}X_2^2$$

$$C_{\text{opt}} = -1694.8 + 121.2X_5$$

$$RD = 4846.5 + 0.290X_2 + 7.84 \times 10^{-5}X_2^2$$

Function 3, mean annual temperature

$$Y_{\max} = 406.2 + 0.104X_1 + 0.172X_2 - 11.5X_3 - 16.7X_5$$

$$C_{\text{opt}} = 3.21314 + 6.41 \times 10^{-3}X_2 - 0.682X_3 + 3.03 \times 10^{-3}X_6$$

$$RD = 22.8$$

Function 4, summer–winter temperature differential

$$Y_{\max} = 236.9 + 0.128X_1 - 0.0829X_5 - 1.711X_7$$

$$C_{\text{opt}} = 36.5 - 2.99 \times 10^{-3}X_1 + 2.20 \times 10^{-7}X_2^2 - 0.452X_5 + 0.139X_7^2$$

$$RD = 10.4 + 2.49 \times 10^{-2}X_1 - 7.39 \times 10^{-6}X_1^2 + 6.12 \times 10^{-2}X_5^2$$

Function 5, annual moisture index

$$Y_{\max} = 11.8 + 0.585X_1 - 1.42 \times 10^{-4}X_1^2 - 0.104X_4^2 - 11.8X_5$$

$$C_{\text{opt}} = 2.46 + 1.55 \times 10^{-7}X_1^2 + 7.33 \times 10^{-4}X_6$$

$$RD = 4.64 + 1.58 \times 10^{-3}X_1 + 0.12835X_5 + 1.42 \times 10^{-2}X_5^2$$

X_1 = degree-days $> 5^{\circ}\text{C}$, X_2 = degree-days $< 0^{\circ}\text{C}$, X_3 = mean temperature in the coldest month, X_4 = summer–winter temperature differential, X_5 = mean annual temperature, X_6 = mean annual precipitation, X_7 = annual moisture index.

