

## IMPACTS OF CLIMATE CHANGE ON THE DISTRIBUTION OF *LARIX* SPP. AND *PINUS SYLVESTRIS* AND THEIR CLIMATYPES IN SIBERIA

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**Abstract.** Inter- and intraspecific effects of climate change were assessed for the dominant conifers of Siberia (60–140°E and 48–75°N): *Larix* spp. (*L. sibirica*, *L. dahurica*, and *L. sukaczewii*) and *Pinus sylvestris*. The approach employed a tri-variate (degree-days above 5 °C, degree-days below 0 °C, and a moisture index) estimate of the climatic envelope within which exists the actual ecological distribution of a species and their constituent climatotypes (genotypes physiologically attuned to similar environments). Limits of the actual ecological distribution were approximated by reducing the climatic envelope according to effects of permafrost and interspecific competition. Climatotypes were mapped within the climatic envelope according to the climatic interval that must separate populations for reasonable assurance of genetic differentiation. This interval was calculated from response functions that related 13-year growth and survival of a species to the difference in climate between the provenance of a climatotype and the climate of numerous test sites distributed across Russia. Mapping species' distributions and their climatotypes was done for the contemporary climate and for future climates predicted by the HadCM3GGa1 scenario of Hadley Centre.

The results showed that if the forests of the future are to reflect the adaptedness of today, the distribution of species will shift and genotypes within species will be redistributed. Some contemporary climatotypes are projected to disappear from Siberia while others common elsewhere would evolve. To mitigate these effects, climatotypes should be transferred today to the expected future location of their climatic optima, a distance that is likely to approach 700–1200 km for these species.

**Keywords:** climate change, climatic envelope, climate transfer function, climatotypes, interspecies competition, *Larix sibirica*, *L. dahurica*, *L. sukaczewii*, permafrost, Siberia, tree species *Pinus sylvestris*

### 1. Introduction

Evidence for global warming over the past 200 years is overwhelmingly supported by both direct weather observations, indirect physical and biological indicators such as retreating glaciers and snow/ice cover, rising sea levels, and longer growing seasons (IPCC 2001; Hulme et al. 1999). Recent GCM projections of the Hadley Centre (Gordon et al. 2000) for Siberia show an increase in temperature of 4 °C to 6 °C and an increase in precipitation of as much as 25% by 2100. These changes, moreover, could occur at a rate of 0.1 °C to 0.4 °C per decade (Watson et al. 1996).The

rapid rate of change coupled with the large absolute amount of change is expected to have profound effects on terrestrial ecosystems at all hierarchical levels: from vegetation zones (Tchebakova et al. 2003), to ecosystems (Guisan et al. 1995), to species (Iverson and Prasad 1998; Box et al. 1999), and to populations within species (Rehfeldt et al. 1999b, 2002).

Our goals pertain to the effects of a warming climate on the primary forest tree species of Siberia and their constituent populations: to estimate forest composition of the future and to predict the future distribution of climatypes that would be consistent with the adaptedness of today. The first objective considers the effects of global warming on shifts in the distribution of tree species, and the second considers intraspecific effects. For the second objective, we invoke Turesson's (1925) concept of climatypes, the climatic ecotypes that comprise species.

To meet these objectives, we use a correlative approach with an emphasis on ecological interactions (Guisan and Zimmermann 2000) to model the distribution of the major tree species distributions in Siberia. We first define for each species a tri-variate climatic envelope (Box 1999) which demarks the climatic limits of a species' distribution and within which, therefore, occurs the actual ecological distribution. Actual distributions are approximated by considering the effects of variables other than climate, namely interspecific competition and permafrost.

## 2. Methods

### 2.1. STUDY AREA

Our studies deal with the forests of Siberia (60–140°E longitude and 48–75°N latitude), an area bounded by the Ural Mountains in the west, the Far East in the east, the Arctic ocean in the north, and the southern border of Russia in the south. The base map for this region was a 1 km (0.0083 degree) grid (GLOBE 2000).

### 2.2. MAPPING CURRENT CLIMATES

In our earlier study of global vegetation (Tchebakova et al. 1993), we applied the Budyko approach to predict the distribution of vegetation along two principal climatic variables, radiation balance and dryness index (a ratio of evapotranspiration to annual precipitation). By determining the energy and water balances, these two variables control vegetation zones (Budyko 1974). Potential evapotranspiration, a variable used in many vegetation classifications, was a primary descriptor of the distribution of global vegetation (see Tchebakova et al. 1993). Stephenson (1998) using examples for North America argues that two climatic variables like actual evapotranspiration and deficit may be sufficient and best correlated with the distribution of vegetation types. However, for the Siberian continental climate, low winter temperatures and permafrost, for instance, are crucial limiting

factors controlling tree species distribution (Tchebakova et al. 1994; Nazimova et al. 1990). Moreover, because evapotranspiration customarily is calculated from inter-correlations among commonly measured climate variables (e.g. highly correlated with temperature), precision of the evapotranspiration estimate tends to be low for regions dominated by monsoon, maritime or mountain climates (Budyko 1974). Therefore, for modeling subcontinental Siberian vegetation in detail, climatic indices derived from measured climatic variables like temperature and precipitation and their interactions have proved superior predictors (Tchebakova et al. 1994, 2003).

In this paper, we use growing degree-days, base 5 °C (GDD<sub>5</sub>); negative degree-days, base 0 °C (NDD<sub>0</sub>); and an annual moisture index (AMI), the ratio of GDD<sub>5</sub> to mean annual precipitation. These three variables have proven to be instrumental for our previous analyses addressing plant responses to climate (Rehfeldt et al. 1999a, 2002; Tchebakova et al. 2003). From the physiologic viewpoint, GDD<sub>5</sub> represents temperature requirements for growth and development; NDD<sub>0</sub> defines cold tolerance, and AMI characterizes drought resistence.

For mapping climates, we assembled temperature and precipitation records normalized for the period 1900–1964 from 1000 weather stations across Siberia (Reference books 1967–1970). Hutchinson's (2000) thin plate splines were used to produce climate surfaces of these variables on our base map at a resolution of 1 km. Climatic and topographic images were visualized using IDRISI32 (Eastman 2000). The AMI surface was calculated by dividing the GDD<sub>5</sub> image by the annual precipitation image.

### 2.3. MAPPING FUTURE CLIMATES

For predictions of global warming, we used the greenhouse gas scenario (1% increase per year) from the Hadley Centre, HadCM3GGal (Gordon et al. 2000), for the decade beginning in 2090. We chose this scenario as an extreme example of the vegetation changes that could take place in response to global warming: winter temperature increase of 3 to 9 °C, summer temperature increase of 4 to 6 °C, and annual precipitation changes between –4 and +25% over the study area. First, GCM predicted changes for January and July temperatures and annual precipitation were scaled down from a 2.5 ° by 3.75 ° grid cell to about the 1-km grid cell using the SURFER software. Then, future temperatures and precipitation for each pixel were calculated by adding these changes to the normalized monthly means. Future values of climatic indices GDD<sub>5</sub> and NDD<sub>0</sub> were calculated using the following linear regressions calculated from contemporary data: GDD<sub>5</sub> was calculated from mean July temperature ( $R^2 = 0.90$ ), NDD<sub>0</sub> from January temperature ( $R^2 = 0.96$ ). Future values of AMI were calculated directly by dividing the future GDD<sub>5</sub> image by the future annual precipitation image.

#### 2.4. MAJOR FOREST-FORMING TREE SPECIES OF SIBERIA

The forests across the vast territory of Siberia are composed largely of 8 conifers (Pozdnyakov 1986; Milyutin 1983): 49% *Larix* spp. of which only 1% is the cover dominated by *L. sukaczewi*, 13% by *L. sibirica*, and 83% by *L. gmelini* and *L. cajanderii* and 3% of some far-eastern endemic larches; 13% *P. sylvestris*; 7% *Picea obovata*; 6% *Pinus sibirica* (Siberian cedar); 2% *Abies sibirica*; and 19% hardwoods and other species. The larches and the pine, therefore, are dominant tree species in the Siberian forests. These light-demanding species are commonly referenced in Russian literature as the light-neededled conifers which are seral to the other three shade-tolerant conifers, spruce, cedar and fir, which are referred to as the dark-neededled species (Shumilova 1962). Siberian spruce dominates only in West Siberia, both Siberian cedar and fir dominate on elevated tablelands (Yenisei Ridge) and southern mountains (the Altai-Sayan mountains). Only two tree species, *Larix gmelini* and *L. cajanderii*, dominate the forests in interior Siberia, eastward of the Yenisei River, in the permafrost zone. Note that taxonomically, *L. dahurica* was split into *L. gmelini* and *L. cajanderii* by Bobrov in 1972 (Bobrov 1972). Where parapatric, the latter two species interbreed freely (Abaimov et al. 1998), and because of their genetic, morphologic, and taxonomic similarities, we consider results obtained from *L. gmelini* and *L. cajanderii* to be jointly applicable to their parental species, *L. daurica*. The former nomenclature is used in this report.

#### 2.5. PERMAFROST

Permafrost covers 80% of Siberia and is the primary factor controlling the distribution of vegetation in central Siberia and Yakutia. Forests are capable of developing in this region only because of the melting of permafrost provides additional summer moisture to lands where otherwise the vegetation would be semi-desert (Shumilova 1962; Dylis 1981). Permafrost also limits the northward and eastward spread of the dark-neededled species and also the light-neededled *L. sibirica* and *P. sylvestris*. Within the permafrost zone, these latter two conifers can reach high latitudes only in sandy soils along river valleys and benches where permafrost may thaw to a depth of 1.5–2 m (Shumilova 1962; Pozdnyakov 1986). Only *L. dahurica* (*L. gmelini* + *L. cajanderii*), by contrast, is capable of growing on soils which thaw as little as 10–30 cm during the growing season (Abaimov et al. 1999).

The permafrost border follows the contour marking an active layer of 2 m on the map of Malevich-Malevsky et al. (2001). To map the current position of the permafrost border, we used a regression that predicted the active layer 2 m position from our three climate variables ( $R^2 = 0.70$ ). This regression is valid within the limits of contemporary climate. To map the permafrost border in much warmer 2090, we applied Stefan's theoretical formula (Dostavalov and Kudriavtsev 1967) to the current permafrost border. Note that Stefan's formula predicts this active layer as a function of the ratio between  $GDD_5$  in current and future climates.

2.6. MAPPING DISTRIBUTIONS OF *Pinus sylvestris* AND *Larix* spp.

The contemporary climate envelope of *P. sylvestris*, *L. sibirica*, *L. dahurica* and *L. sukaczewii* and their climatotypes was mapped using three variables: GDD<sub>5</sub>, NDD<sub>0</sub>, and AMI (Table I). Limits of distribution for these variables (Table I) were approximated by considering evidence from four sources: (1) the climatic extremes for provenances included in geneecological studies established throughout the Soviet Union (see Iroshnikov 1977), (2) limits of distribution implied by the transfer distance of populations to test sites in reference to the breadth of transfer functions (see Rehfeldt et al. 2002), (3) the relative climatic tolerances of species (Table II), and (4) the climate estimated for extreme locations on range maps (Figures 1 and 2).

TABLE I

Climatic limits, climatotype breadth, and number of potential climatotypes for the dominant conifers of Siberia for three climate variables: GDD<sub>5</sub>, NDD<sub>0</sub>, and AMI

Statistics		<i>Pinus sylvestris</i>	<i>Larix sibirica</i>	<i>Larix dahurica</i>	<i>Larix sukaczewii</i>
GDD <sub>5</sub> , °C	Lower limit	600	650	400	800
	Upper limit	3000	2350	1850	2400
	Climatotype breadth	480	650	1100	550
	Number of classes	5	3	2	3
NDD <sub>0</sub> , °C	Lower limit	-6000	-4500	-6000	-2200
	Upper limit	0	-1200	-2000	-300
	Climatotype breadth	-1150	-2300	-2000	-1450
	Number of classes	6	2	2	2
AMI	Lower limit	0.6	0.8	0.9	1.0
	Upper limit	7.0	8.5	7.0	5.0
	Climatotype breadth	1.2	1.0	2.4	2.0
	Number of classes	6	8	3	2
Total number of climatotypes		180	48	12	12

TABLE II

Comparative requirements (from low to high) of larches for heat (GDD<sub>5</sub>), cold tolerance (NDD<sub>0</sub>) and drought resistance (AMI) compiled from Polikarpov et al. (1986), with additions from Dylis (1981), Pozdnyakov (1993) and Abaimov et al. (1998)

Climate variable	Tree species		
GDD <sub>5</sub>	<i>L. dahurica</i>	<i>L. sibirica</i>	<i>L. sukaczewii</i>
NDD <sub>0</sub>	<i>L. sukaczewii</i>	<i>L. sibirica</i>	<i>L. dahurica</i>
AMI	<i>L. sukaczewii</i>	<i>L. sibirica</i>	<i>L. dahurica</i>

Although the procedure was not mathematically rigorous, the resulting approximations are considered adequate for the purposes of these analyses. The only method available for verifying these procedures was to compare visually the mapped distributions and the range maps of these species. In doing so, one should note, however,

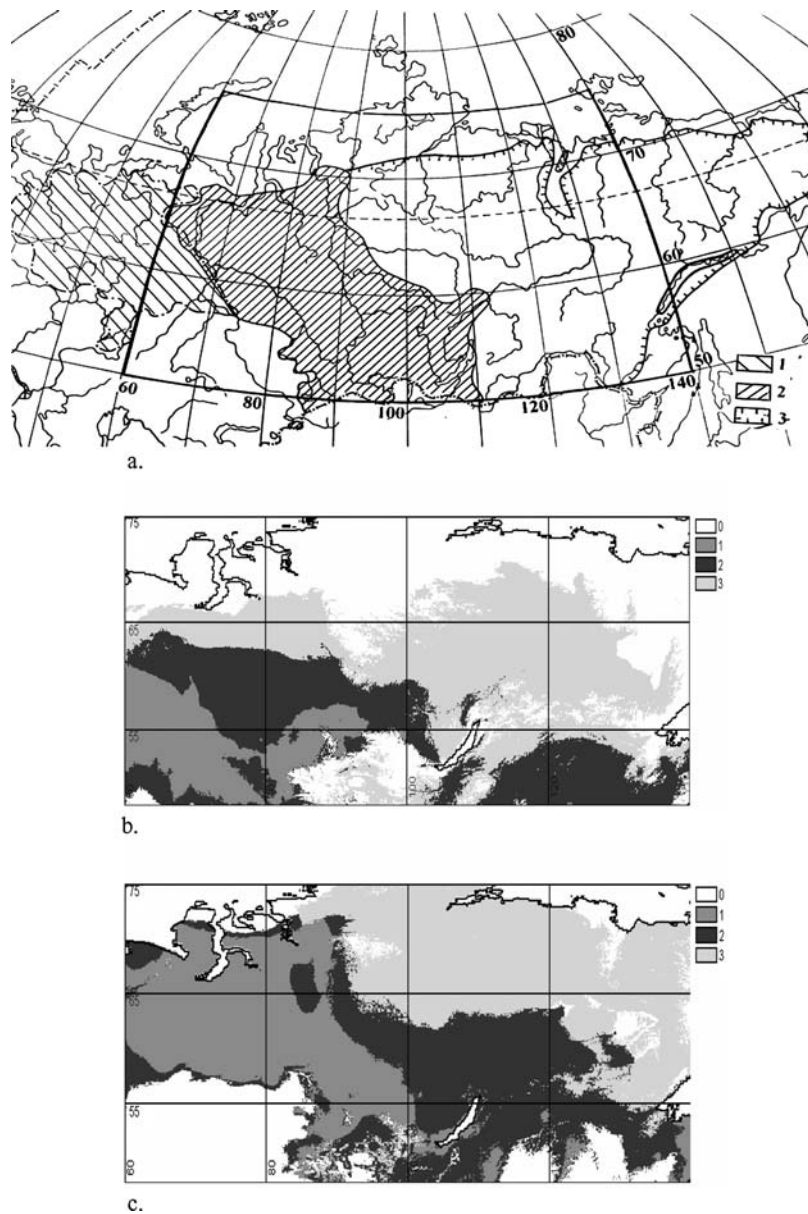


Figure 1. Distribution of *Larix* spp. according to the range map of Sokolov et al. (1977) (a), and modeled actual distribution for the contemporary climate (b), and for the climate projected for the decade beginning in 2090. 0 – not available; 1. *Larix sukaczewii*, 2. *Larix sibirica*, and 3. *Larix dahurica*.

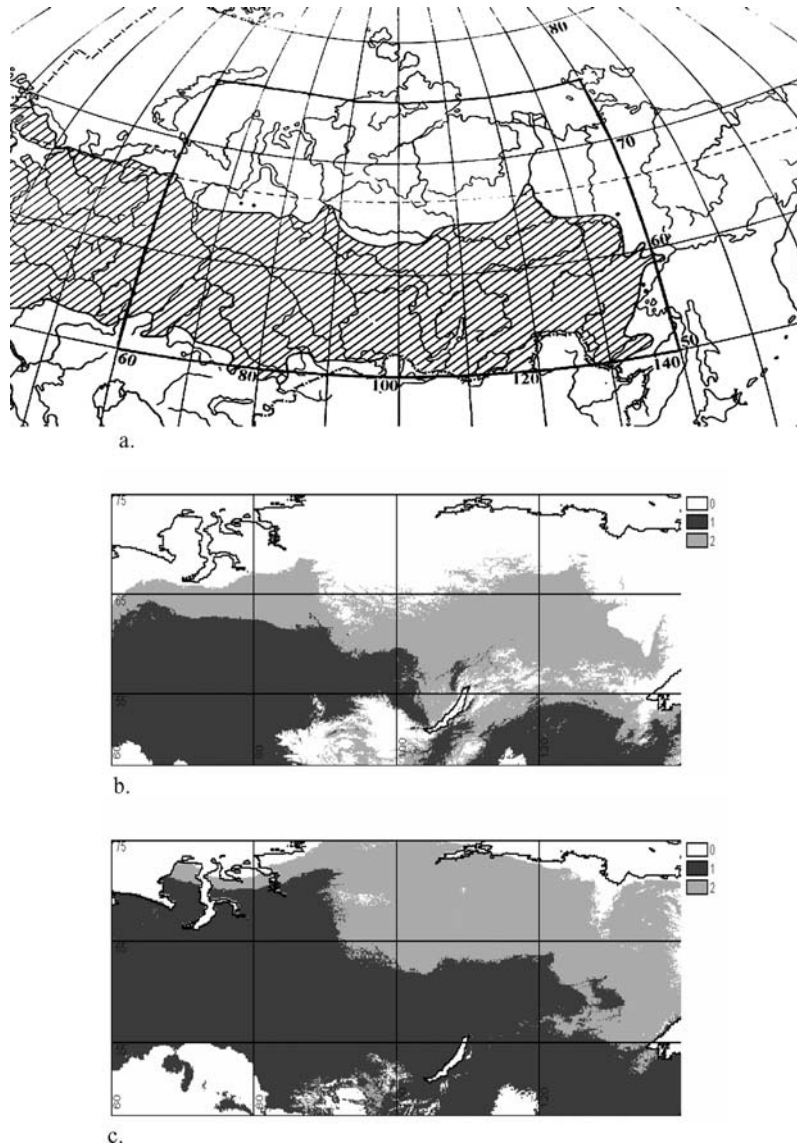


Figure 2. Distribution of *Pinus sylvestris* according to the range map of Sokolov et al. (1977) (a), modeled actual distribution for the contemporary climate (b), and for the climate projected for the decade beginning in 2090. 0 – not available; 1 – beyond permafrost; 2 – on permafrost.

that range maps extend the northern borders of the *L. sukaczewii* and *L. sibirica* distributions in West Siberia beyond the permafrost border to account for the occurrence of these species on sporadic permafrost along the many bays of the big Siberian rivers, the Ob and Yenisei. Our permafrost model predicts only continuous permafrost but ignores its sporadic occurrence.

Actual or realized distributions are approximated by further reducing the climate envelopes according to the effects of habitat factors, permafrost and interspecific competition among the species of *Larix* (Table II). While the influence of permafrost on the distribution of *P. sylvestris* is well known, these two factors are recognized as the ecological factors most strongly influencing the distribution of the larches (Dylis 1981; Polikarpov et al. 1986; Pozdnyakov 1993; Abaimov et al. 1998). Only *L. daurica*, for instance, can survive on permafrost thawing less than 2 m. As a result, *L. sibirica*, and *L. daurica* can dominate much of the Siberian landscape except (1) in the north or at high altitudes where the cold climate is suitable for only tundra, and (2) in the southern steppe where the climate is too dry. In only the warmer climates of West Siberia, can *L. sukaczewii* be widespread.

Among larches, *L. sibirica* seems to be competitively superior to *L. daurica* (Polikarpov et al. 1986), relegating *L. daurica* to the permafrost zone. Yet, *L. sibirica* itself can be excluded from the moist habitats in Trans-Urals by competition with *L. sukaczewii*, particularly on rich calcareous soils (Dylis 1981). And finally, both of these latter two larches relegate *P. sylvestris* to poor sandy soils on old alluvial terraces in West Siberia or along the valleys of large Siberian rivers in the east (Pozdnyakov 1993).

To account for these ecological interactions, we pared down the climatic envelope according to following algorithm: 1. the actual distribution of *L. daurica* is limited by the climatic envelope on the cold fringe and by the permafrost border to the south and west; 2. actual distribution of *L. sibirica* is determined by the permafrost border on the cold fringe and and the climatic limits of *L. sukaczewii* on the warm fringe; 3. the actual distribution of *L. sukaczewii* is determined by its climatic envelope; 4. the actual distribution of *P. sylvestris* is similar to that of *L. sibirica* and is limited primarily by permafrost.

By considering climate, permafrost, and competition, modeled distributions reflect the relevant ecological interactions controlling distributions of Siberian forest trees. We note that distributions of the light-needled species are further constrained by interspecific competition with the dark-needled conifers, that competition from *L. sibirica* and *L. sukaczewii* tends to relegate *P. sylvestris* onto sandy and boggy soils primarily in West Siberia, and that insects and diseases act to fine tune the ecological distributions of plants. These effects can not yet be modeled.

## 2.7. MAPPING CLIMATYPES OF *Pinus sylvestris* AND *Larix* sp.

Climatic envelopes were subdivided into climatypes by using the results of Rehfeldt et al. (2003). These results were based on common garden studies that had been established across the former Soviet States. In such studies, seeds from numerous native populations are moved to and grown on an array of climatically disparate test sites. Because seeds are transferred along climatic gradients, such studies can also be viewed as climate-change experiments (Mátyás 1994). Differential performance



of populations then reflects adaptive differences that have accrued from natural selection in the climate of the provenance where the seeds originated. The results of such studies can be used to define a climatype as the climatic space occupied by a group of populations whose individuals are adapted to same or similar climate.

The analyses of Rehfeldt et al. (2003) used published data on the height and survival of 313 populations of *P. sylvestris* that had been planted on 36 sites and of 130 populations of larch (63 of *L. sibirica*, 42 of *L. gmelinii*, and 25 of *L. sukaczewii*) planted on 8 sites. These data were used to develop transfer functions that predicted 12-year height from the difference in climate between the provenance of a population and the planting site. The functions were based on a Weibull model which is Gaussian but can be asymmetric. For both height and survival, five transfer functions were developed, but only those driven by GDD<sub>5</sub>, NDD<sub>0</sub>, and AMI were prominent and, consequently, are used herein.

The transfer functions showed that height and survival decrease as transfer distances either increased or decreased from an optimum value which tended to be close to zero, the climate of the provenance. Confidence intervals about the vertex of the function were used to estimate the distance along climatic gradients that genotypes could be transferred without loss of growth potential or survival (see Figure 3, Rehfeldt et al. 1999a). For *P. sylvestris*, these transfer distances were  $\pm 240$  GDD<sub>5</sub>,  $\pm 575$  NDD<sub>0</sub>, and  $\pm 0.6$  units of AMI; for *L. sibirica* as  $\pm 325$  GDD<sub>5</sub>,  $\pm 1150$  NDD<sub>0</sub>, and  $\pm 0.5$  units of AMI; for *L. dahurica*,  $\pm 550$  GDD<sub>5</sub>,  $\pm 1000$  NDD<sub>0</sub>, and  $\pm 1.2$  units of AMI; and for *L. sukaczewii*,  $\pm 275$  GDD<sub>5</sub>,  $\pm 725$  NDD<sub>0</sub>, and  $\pm 1.0$  units of AMI.

It follows, therefore, that populations separated by the breadth of these transfer intervals tend to be genetically different for traits controlling growth and survival (Table I). Climatotypes could then be defined by subdividing the climatic envelope into classes bounded by these limits. For example, because the 313 pine provenances used in these tests ranged from 626 to 2916 GDD<sub>5</sub>, 5 classes, 480 degree-days in breadth, were required to encompass the species climatic distribution. Six classes were needed for both NDD<sub>0</sub> and AMI. Climatype #1, for instance, would include those sites with 600 to 840 GDD<sub>5</sub>, 0 to  $-575$  NDD<sub>0</sub>, and 0.6 to 1.2 AMI; climatype #2 would include those sites with 840 to 1080 GDD<sub>5</sub>, 0 to  $-575$  NDD<sub>0</sub>, and 0.6 to 1.2 AMI. All possible combinations of these classes produced an upper limit to the number of pine climatotypes at 180. For the *L. sibirica*, there were 8 classes for the moisture index, 3 for GDD<sub>5</sub>, and 2 for NDD<sub>0</sub> which produced a maximum of 48 climatotypes; for *L. dahurica*, 3 for AMI, 2 for GDD<sub>5</sub>, and 2 for NDD<sub>0</sub> for a total of 12; and for *L. sukaczewii*, 2 for AMI, 3 for GDD<sub>5</sub>, and 2 for NDD<sub>0</sub> for a total of 12 (see Table I).

Climatotypes defined in this manner must be considered as the maximum of the total number possible because (1) they represent the entire climatic envelope and (2) many combinations of the climate variables do not exist (e.g., high GDD<sub>5</sub> coupled with low NDD<sub>0</sub>, or high GDD<sub>5</sub> coupled with low AMI). Other combinations may exist, but on the landscape may be occupied by other species. In the Sayan

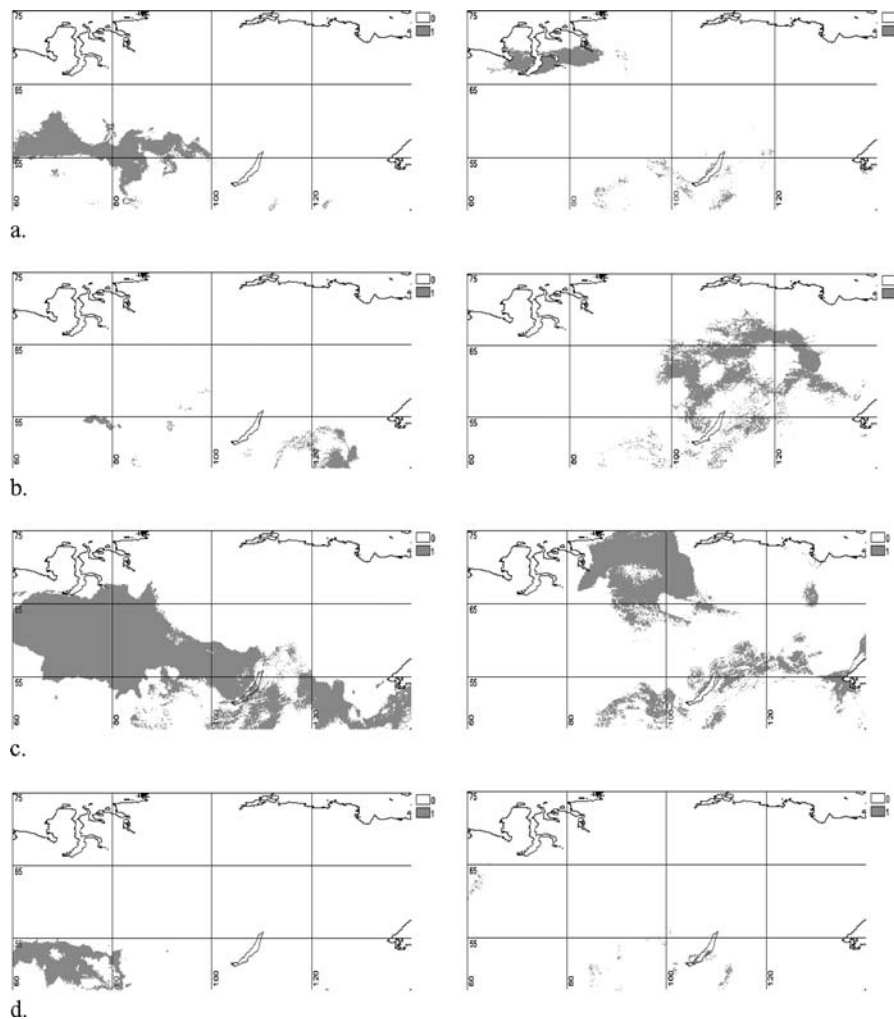


Figure 3. Modeled distributions of single climatypes of four conifers in the contemporary climate (left) and predicted distributions of their climatic optima in decade beginning in 2090 (right): a. *Pinus sylvestris* climatype #46; b. *Larix sibirica* climatype #21; c. *Larix dahurica* climatype #2; and d. *Larix sukaczewii* climatype #7.

Mountains of south-central Siberia, for instance, *P. sylvestris* and *L. sibirica* rarely occur in climates inhabited by the dark-needled conifers even though they are capable of growing there (Ermolenko 2001). The climatypes therefore represent the climatic envelope of a species as if all dimensions of that space were occupied by the species. In presenting the results, no attempt is made to consider actual distributions of the climatypes even though our approach would be amenable. In mitigating the effects of global warming, land managers may chose to plant the seral light-needled species in environments where they may ordinarily have been

competitively excluded by dark-needled species. Or, managers may chose to plant *P. sylvestris* or *L. sibirica* on favorable microsites within the permafrost zone. Climatotypes, therefore, are delimited within the climatic envelope in anticipation of such eventualities.

Climatotypes of the four species were mapped for all of Siberia using the climate maps of GDD<sub>5</sub>, NDD<sub>0</sub>, and AMI described above. Mapping was done for the contemporary climate and for the climate expected by the Hadley GCM for the decade beginning in 2090.

### 3. Results

#### 3.1. MAPPING SPECIES' DISTRIBUTIONS

A visual comparison of the range map of *P. sylvestris* and the modeled map of its climatic envelope (actual distribution + permafrost distribution) shows good agreement (Figure 1), although the mapped climatic envelope, as expected, suggests a distribution that is somewhat broader than that of the range map. By contrast, our estimate of the actual ecological distribution of this species is considerably smaller than the range map. Figure 1 shows that much of northwest Siberia is omitted from our estimate of the actual distribution but is included within the species range. This is a region mentioned earlier where *P. sylvestris* exists on sandy benches along major drainages where permafrost thaws to at least 2 m each summer. The range map, by its definition, outlines the geographic extent of a species distribution and includes, therefore, disjunct populations in the permafrost zone. The range map, therefore, implies a much broader distribution than actually occurs. Yet, by adjusting our climatic envelope for the limits of permafrost, we can not possibly include these outlying populations. While the range map accurately portrays the limits of the biological distribution, our estimate of the actual ecological distribution is more functional. While both approaches are useful, neither is capable of assimilating the full range of environmental factors interacting to determine the ecological distribution of this species.

The visual comparison of the range map with our modeled maps of the actual ecological distribution of the species of *Larix* shows good correspondence for the general as a whole (Figure 2); both suggest that nearly three-fourths of Siberia is climatically suited for species of this genus. However, when the individual species are considered, discrepancies between the range map and our estimates of actual ecological distributions become apparent.

Our map of the ecological distribution of *L. sukaczewii* suggests that the distribution of this species should be much farther toward the east than the range maps show. Putenikhin et al. (2004) recently indicate that near the eastern limits of this species distribution in the southern Urals and Trans-Urals, *L. sukaczewii* occurs in large isolated populations which need to be studied from view point of genetic

structure. While this discrepancy could be in part to errors of estimate from either the small sample of 41 populations represented in trans-Soviet provenance tests or from climate estimates at point locations, Dylis (1981) notes that during warmer epochs, this species ranged farther toward the east than it does today. It is possible, therefore, that warming of the climate during the 20th century has been responsible for a lag between the distribution of *L. sukaczewii* genotypes and the distribution of their climatic optima.

A lack of equilibrium between the climate and the distribution of *L. sukaczewii* in turn would be responsible for the discrepancy between our modeled distribution of *L. sibirica* and the distribution shown on the range map for south-central Siberia (Figure 2). Since our models assume that *L. sukaczewii* would competitively exclude *L. sibirica* from this region, the fact that *L. sukaczewii* does not occur there produces an apparent error in our predictions. In addition, the range map suggests that the distribution of *L. sibirica* extends far north of a latitude of 60° which is north of the permafrost boundary. Like *P. sylvestris* discussed above, *L. sibirica* exists in this region only on those sporadically occurring sites where permafrost thaws to a depth of 2 m. As with the pine, therefore, the range map implies a distribution that is much broader than actually occurs.

Similar arguments account for the discrepancy between the range map and our modeled distribution of *L. dahurica*, the only conifer that can exist on permafrost. Although the distribution of *L. sibirica* is shown by the range map to extend far into the permafrost zone in West Siberia, its occurrence is sporadic. Because *L. dahurica* is the only larch capable of growing there, our algorithm places *L. dahurica* west of its limits shown on the range map in the permafrost zone of West Siberia. The only reasonable explanation for the absence of *L. dahurica* in this region is a lag in the approach of an equilibrium between climate and vegetation distributions.

In assessing modeled distributions of these species, one should be aware that the species of *Larix* are closely related genetically. Hybridization and introgression are common where distributions abut. It is impossible, therefore, to draw a precise range map (see Abaimov et al. 1998). This in part makes the concept of competitively exclusiveness difficult to define. As genecological studies have shown, all three species are capable of growth and survival in the mildest climates of southwest Siberia. Yet, only *L. sukaczewii* actually occurs there. While the range maps indicate discrete distributions, therefore, our maps of the climatic envelopes and actual distributions suggest that the range maps are an over simplification. If the distribution of these larch species should ever approach equilibrium with the climate, one may find that actual distributions are interspersed rather than discrete.

### 3.2. EFFECTS OF GLOBAL WARMING ON SPECIES DISTRIBUTIONS

During the course of the century, the warming climate should become increasingly more suitable for *P. sylvestris*, *L. sibirica*, and *L. sukaczewii* but less favorable for *L. dahurica*. For the *Larix* genera as a whole, however, the climate of the future

TABLE III

Proportions of Siberia (% of the land within the window studied) expected within the tri-variate climatic envelope (predicted actual distribution in parentheses) of conifer species in the current climate and the climate projected by a GCM of the Hadley Centre (HadCM3GGa1) for the decade beginning in 2090

Tree species	Area (% of total)	
	Contemporary climate	Future climate
<i>Pinus sylvestris</i>	68 (38)	87 (62)
<i>Larix sibirica</i>	58 (26)	71 (28)
<i>Larix dahurica</i>	60 (33)	38 (24)
<i>Larix sukaczewii</i>	12 (12)	26 (23)

should become only slightly more favorable than that of today. Figures 1 and 2 and Table III contain estimates of the climatic envelope and the actual distribution of these four conifers for contemporary climate and that expected for the decade beginning in 2090, according to the HadCM3GGa1 scenario of the Hadley Centre.

The contemporary climatic envelope of *P. sylvestris* extends across approximately 68% of Siberia, but a more realistic estimate of the actual distribution is only 38% (Table III). This is because nearly half of the species distribution in Siberia includes sites within the permafrost zone where the species is rare (Figure 1b). By 2090, however, both the climatic envelope and the climate associated with the actual distribution should increase 1.5–2 times (Table III), largely because of the melting of permafrost. An increase in acreage primarily would involve migration out of the valleys in northeast Siberia onto the plains and tablelands where it can not exist today. Since these sites are included within the boundaries of the range map, the geographic extent of actual distribution we predict for the future is seen to be quite similar to the range map of today (Figure 1). Because the future climate of this region is projected to be dry, competition with the dark-needled species should not be a factor because the dark-needled species do not occur under xeric conditions (Polikarpov et al. 1986). Yet, competition with *L. sibirica* should intensify, and this competition may limit the pine to the impoverished sandy soils. Our models also show that in the mountains of south-central Siberia, the climate suitable for *P. sylvestris* should move upwards in altitude by about 1000 m by the end of the decade (Rehfeldt et al. 2004).

For *Larix*, all but the northernmost regions lie within the combined climatic envelopes of *L. sukaczewii*, *L. sibirica*, and *L. dahurica* in the contemporary climate (Table III and Figure 2). Estimates of the actual distributions suggest, in fact, that in total, 71% of Siberia is inhabitable by these species. As the climate warms, this estimate is expected to increase by only 4% by 2090. As suggested by Figure 2c, the climate of the future in the southwest where *L. sukaczewii* now occurs should

slip beyond the contemporary climatic envelope of any these species. This loss of habitat should be more than balanced by an increase in lands to the north and northeast as the climate ameliorates. Nonetheless, the effects of global warming on the individual species of *Larix* are expected to differ greatly. Estimates of the contemporary and future actual distributions suggest that lands climatically suitable for *L. sukaczewii* should increase by about 11%, those suited for *L. sibirica* should increase by a mere 2%, and those for which *L. dahurica* is suited should decrease by about 9% (Table III, Figure 2).

Unlike the projected future distribution of *P. sylvestris*, the future limits to the range of these three species of larch should be displaced considerable distances toward the east and northeast when future distributions approach an equilibrium with the novel climate (Figures 1 and 2). Rough estimates from Figure 1 suggest that the climate associated with the contemporary limits of distribution of *L. sukaczewii* and *L. sibirica* may be found as distant as 10° of latitude (about 700 km) toward the north by 2090. Estimates *L. dahurica* are smaller because northward migration undoubtedly will be impeded by the Arctic Ocean.

### 3.3. EFFECTS OF GLOBAL WARMING ON NUMBER, SIZE, AND DISTRIBUTION OF CLIMATYPES

Because climatypes are composed of genotypes physiologically attuned to climate, a change in climate will disrupt the relationship between the geographic distribution of plants and the distribution of their climatic optima. In assessing the effects of these changes, we assume that the vegetation of the future will move toward and eventually achieve the levels of adaptedness that typify the vegetation of today.

#### 3.3.1. *Pinus Sylvestris*

Table IV shows that of the 180 possible climatypes in the climatic envelope of *P. sylvestris*, 63 comprise the species tri-variate envelope in Siberia. Most of these climatypes are small; only ten, in fact, would account for 55% of the species' climatic envelope. As the climate of the future becomes more favorable to *P. sylvestris*, the number of climatypes suited to the future climate should increase to 101 by the end of the current century (Table IV). During this period, 15 of the contemporary climatypes should be lost as the climate for which they are best suited dissipates. These 15, however, tend to be small, accounting for only 2% of the lands within the climatic envelope of today.

Meanwhile, 53 novel climatypes should appear in association with the appearance of climates currently not found in Siberia. While novel to Siberia, these climatypes undoubtedly exist today west of the Ural Mountains in Eastern Europe. These novel climatypes, should make an important contribution to the future flora, accounting for approximately 36% of the species climatic envelope by the end of the century.

TABLE IV  
Effects of global warming on the number of climatypes in four Siberian species

Tree species	Number of climatypes					
	Total possible	Contemporary climate	Future climate	Lost by 2090	Novel by 2090	Unchanged
<i>Pinus sylvestris</i>	180	63	101	15	53	48
<i>Larix sibirica</i>	48	31	42	3	14	28
<i>Larix dahurica</i>	12	12	12	0	0	12
<i>Larix sukaczewii</i>	12	5	10	0	5	5

Of the 101 climatypes expected for the future, only one-half exist there today (Table III). Nonetheless, like today's distribution of climatypes, that of the future should be dominated by a few large climatypes, the largest 10 of which should be suited to about 74% of the species climatic envelope.

While the number of climatypes suited to the future climate is increasing, the size and geographic position of the climatypes would also be changing. The five climatypes that currently dominate the pine forests of Siberia are expected to be reduced to approximately one-third of their contemporary distributions (Figure 3a). Of the five largest climatypes expected for the future, one is absent today and three are minor (<1%). Still, 48 climatypes that should exist in Siberia throughout the century should be suitable for about 63% of the future distribution. As shown in Figure 3a, however, the future location of climates inhabited by contemporary climatypes is expected to shift geographically. The shift, in fact, may amount to 500 to 1000 km.

### 3.3.2. *Larix Sibirica*

Of the 48 possible climatypes, 31 comprise the species' contemporary climatic envelope in Siberia (Table IV). As with *P. sylvestris*, the contemporary envelope of *L. sibirica* is dominated by a small number of large climatypes. Five, in fact, account for 73% of the species' climatic distribution. Projected effects of global warming show that the proportion of Siberia climatically suitable for this species should increase slightly (Table III), the distribution of the optimal climates should advance toward the east and north. As a result, the number of climatypes expected by the end of the century should increase from 31 to 42 (Table IV). Three minor climatypes (<0.5% of the area) are expected to disappear while 14 climatypes not presently in Siberia should appear. Twenty-eight climatypes should exist throughout the century, and these 28 should account for 73% of the future climatic envelope. However, the two huge climatypes of today should be reduced to one-fourth of their contemporary size, while the dominant climatype of the future currently comprises only 4% of the contemporary climatic envelope.

Figure 3b illustrates the present and projected distribution of a single climatype. This climatype occupies 4% of the species contemporary climatic envelope but should occupy nearly 15% of the future envelope. The figure also illustrates the geographic shift in climatotypes that will be required for the vegetation to adjust to the novel positions of their climatic optima.

### 3.3.3. *Larix Dahurica*

Of the four species being considered, *L. dahurica* occurs in the coldest climates and is the only species endemic to permafrost (Table II); the cold fringe of its distribution borders the tundra. This means that the potential for migration to the northeast during global warming is limited ultimately by the presence of the Arctic Ocean. The most prominent effect of global warming, therefore, should be a reduction of the species climatic envelope to approximately 2/3 of its contemporary distribution by the end of the century (Table III). As the envelope shrinks, however, the number of climatotypes that comprise it should remain constant at 12, with no new climatotypes arising or contemporary climatotypes being lost (Table IV). The two most important climatotypes of today, which currently occupy 91% of the species climatic envelope, also are expected to be dominant at the century but by then should occupy only 68%. As shown in Figure 3c for one of the two, the future areal extent of these two climatotypes should be reduced by about 50% while their geographic position shifts to the northeast).

### 3.3.4. *Larix Sukaczewii*

Because projected effects of global warming on *L. sukaczewii* are similar to those on *L. sibirica*, anticipated effects on the number and distribution of climatotypes also are similar. Because of an increase in the climatic envelope from 12% of Siberia to 26% (Table III), the number of climatotypes is expected to increase from 5 to 10 (Table IV). During the course of the century, the two climatotypes that dominate the species envelope today (>89%) are expected to become insignificant by the end of the century (<13.5%). Meanwhile, the climate at the end of the century should become optimal for a single climatype, expected then to account for 41% of the future climatic envelope. This climatype does not occur in Siberia today. Likewise, during the course of the century, four other novel climatotypes should arise even though no contemporary climatotypes are expected to be lost. The novel climatotypes quite likely exist today west of the Ural Mountains.

Figure 3d shows the present distribution of a climatype of *L. sukaczewii* in the contemporary climate along with the projected future location of its optimal climate. This climatype, one of the two that dominate the contemporary distribution of the species in Siberia, accounts for 47% of the species climate envelope. By the end of the century, however, the climate occupied by this climatype should account for only 3% of the climatic envelope and should arise at a geographic location far removed from its present location (Figure 3d).



#### 4. Synthesis

It is well known that the distribution of forest trees is either directly or indirectly related to climate. It is also well known that genetic variability within species of forest trees is arranged along clines that parallel climatic gradients. It follows, therefore, that a change in climate will have prominent inter- and intra-specific effects across the landscape. Our analyses describe these effects for four of the dominant species of Siberia. The results show that if the vegetation of the future is to maintain the adaptedness characteristic of today's vegetation, species distributions will shift toward the north and east, regulated largely by the melting of permafrost. Maintaining adaptedness intraspecifically will require a concomitant redistribution of genotypes across the landscape in order that genotypes become realigned with their climatic optima.

Our analyses suggest that by the end of this century, the climate of Siberia should be more amenable for *P. sylvestris*, *L. sibirica* and *L. sukaczewii* than it is today, but less suited for *L. dahurica*. As the melting of permafrost allows, *P. sylvestris* should migrate out of the broad valleys of northwest Siberia onto the plains and tablelands. The altitudinal displacement within the mountains of southern Siberia should approach 1000 m. For *Larix*, the distribution of *L. dahurica* should shift toward the north and east, regulated by rates of permafrost thaw on the cold fringe and competitive exclusiveness of *L. sibirica* immigrants on the warm fringe. In the milder climates to the west, *L. sukaczewii* should advance into regions now occupied by *L. sibirica* but should be excluded from the advancing steppe on the southern front.

While the distributions of these species shift, the distribution of climatypes within species is expected to become reorganized. Adjusting to global warming will require genotypes to be redistributed across the landscape to realign genotypes with their climatic optima if optimal forest growth and productivity is to be maintained (Rehfeldt et al. 2001). The prominent climatypes of today should either be absent from or minor in the future forests. Likewise, the most prominent climatypes of the future seem to be either absent or minor in Siberia today. Even those climatypes that should remain on the landscape throughout the century are expected to change in position and importance. To be sure, global warming as predicted by the Hadley GCM (HadCM3GGa1) should have widespread effects on the distribution of genotypes within these species.

Figure 3 illustrates the scope of the intraspecific effects expected from global warming. To be sure, the geographic position of the climates inhabited by contemporary climatypes may shift more than 1000 km. As a further example, consider projections (Tchebakova et al. 2003) for the Sayan Mountains of south-central Siberia. Of the three *P. sylvestris* climatypes expected to dominate future forests, one is a minor component of the contemporary array. This climatype, however, is much more prevalent today toward the southwest in the foothills of the Altai Mountains, nearly 700 km away. The other two which will be new to the Sayan Mountains,

are currently present as isolated populations in Kazakhstan and Bashkiria, about 1500 km and 20 degrees of longitude to the west. For *L. sibirica* the most prominent climatype expected in the future for the Sayan Mountains is also common in the Altai Republic, but the future climate is also expected to be suited to *L. sukaczewii*. It is likely, therefore, that the dominant larch of the Sayan Mountains at the end of the century will be interspecific hybrids (see Abaimov et al. 1998). Nonetheless, it is clear that the genotypes expected to be of importance to the future forest vegetation of Siberia currently reside at long distances from their future optima. These distances further illustrate the magnitude and complexity of the intraspecific adjustments necessary for the forest vegetation of the future to become physiologically attuned to the novel distribution of climates.

These results are essentially the same as those obtained for the same species in the Sayan Mountains of south-central Siberia (Tchebakova et al. 2003; Rehfeldt et al. 2002) and for *P. contorta* (Rehfeldt et al. 1999) and *Picea engelmannii* (Rehfeldt 2004) of western North America. The conclusion seems inescapable that global warming will initiate a complete redistribution of genotypes within most species (Rehfeldt et al. 2004). Response to climate-change, therefore, is much more than a shifting of species distributions (Davis and Shaw 2001). Indeed, effects of a changing climate reverberate throughout a species distribution as genotypes become reshuffled across the landscape (Rehfeldt et al. 1999b, 2002).

The evolutionary processes by which these inter- and intraspecific changes will occur are well known (see Futuyama 1979) but nonetheless will differ from each other. While migration is the only feasible means by which immigration can take place, natural selection and gene flow are the processes most amenable to the restoration of population adaptedness (for discussion, see Rehfeldt et al. 1999b, 2001, 2003). One must be aware that genotypes physiologically attuned to a climatic regime cannot migrate across a climatic gradient without being subjected to selection. Genotypes of sessile forest trees quite simply can not track their climatic optima during times of change. There is no question, therefore, whether the vegetation is capable of adjusting to the predicted changes. However, evolutionary processes by which these adjustments will occur to accommodate the changes needed for Siberian forests require periods of time that far exceed the rates that the climate is expected to change.

At the interspecific level, migration of forest species in Siberia is largely dependent on rates of thawing of permafrost. These rates are much slower than projected rates of climate change (Velichko and Nechaev 1992), and as a result, a migration lag (Davis 1989) can be anticipated. One must also realize that migration through a closed forest canopy can not commence until the physiological plasticity of the existing forest has been exhausted and the resulting forest demise creates the openings required for reproduction (Rehfeldt et al. 2001). Therefore, the fact that forest sites are currently occupied should exasperate the lag between the change in climate

and the appropriate vegetation response. Thus, even the modern synthesis of plant migration, which proposes migration rates of as much as 1 km per year instead of a few meters per year (Clark et al. 1998; Higgins et al. 2003), is insufficient to account for rates that must occur if the vegetation is to closely track the climate as it changes across Siberia.

At the intra-specific level, responses to selection can be rapid, but there are limits to the amount that genetic systems can change in a single generation of selection. Estimates for *P. contorta* (Rehfeldt et al. 2001) and *P. sylvestris* (Rehfeldt et al. 2002) suggest that 5 to 10 generations may be required for the evolutionary process to adjust to global warming. This process, therefore, may take several centuries even where species' distributions are not changing (see Rehfeldt et al. 2002).

A series of analyses on a disparate group of species thus demonstrate the far-reaching effects of a changing climate on the ecologic distribution and genetic composition of future forests. Forest zones and species boundaries are expected to change at the same time that genotypes within species will be redistributed. Because analogs to the future forests of Siberia exist contemporarily, one can confidently assume that the vegetation doubtlessly is capable of adjusting to the predicted changes. Current estimates, however, suggest that redistribution of forest zones, tree species and their climatypes will require long periods to adjust to the amount of change being predicted. From the ecological perspective, therefore, it is the speed of warming rather than the absolute amount of warming that is most foreboding.

We believe that mitigating the effects of global warming will require a proactive stance by forest managers. Mankind must participate in the evolutionary processes to lessen the lag between the timing of the change and the appropriate response of the vegetation. Forest management as viewed by Noss (2000) during a changing climate will suffice only to the point where the amount of change exceeds the ability of plastic physiological systems to adjust. Because there is little doubt that the amount of change predicted for the world's temperate and boreal forests will exceed the plasticity of contemporary forests (see Rehfeldt et al. 1999b, 2002, 2003), managers will need to assist the natural processes to maintain the goods and services demanded of today's forests.

From the practical viewpoint, therefore, it seems obvious that maintaining optimal levels of productivity for Siberian forests will require the participation of mankind in the evolutionary processes to assure that the appropriate species and their proper genotypes track their climatic optima in a timely manner. Assistance would take the form of massive planting programs to transfer seeds from their contemporary location to the future site of their climatic optima. Maps such as Figure 3 can serve as blueprints for guiding the long-distant transport of seeds from their contemporary location to the novel location of their climatic optima for selected periods (e.g., 2025) during the coming decade.

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