Chapter 22
From Vegetation Zones to Climatypes: Effects of Climate Warming on Siberian Ecosystems

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22.1 Introduction

Evidence for global warming over the past 200 years is overwhelming, based on both direct weather observation and indirect physical and biological indicators such as retreating glaciers and snow/ice cover, increasing sea level, and longer growing seasons (IPCC 2001, 2007). On the background of global warming at a rate of 0.6°C during the twentieth century (IPCC 2001), the temperature increase in central Siberia is registered as large as 1–2°C on average for both in summer and winter in the high latitudes, and up to 2–5°C in winter alone in the south (Tchebakova and Parfenova 2006). Recent GCM projections of the Hadley Center (Gordon et al. 2000) for Central Siberia show an increase in temperature of 4–6°C in summer and 2–9°C in winter; an increase in precipitation is shown as much as 30% by 2090. In the south of Central Siberia, January temperature increases by 2000 have already exceeded those predicted by the Hadley Center scenario for 2090. July temperature increase rates for 2000 are of the same order of magnitude as predicted from scenarios 4–6°C for 100 years. Predicted change in rainfall is positive while registered change has been negative (Tchebakova et al. 2008). Predicted changes, moreover, could occur at a rate of 0.1–0.4°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 plants of the boreal forests at all hierarchial levels: from forest zones (Tchebakova et al. 2003), to ecosystems (Guisan et al. 1995), to species (Iverson and Prasad 1998; Box et al. 1999), to populations within species (Rehfeldt et al. 1999b, 2002).

Our goals are to estimate effects of a warming climate on Siberian vegetation, at the highest level of organization, biomes, then at the intermediate level, species, and the lowest level, climatypes. The first considers the effects of global warming on zonal vegetation shifts, the second considers them on major Siberian tree species redistributions, and the third considers intraspecific effects across Siberia within both Siberian plains and the mountains in the south. We invoke Turesson's (1925) concept of climatypes, the climatic ecotypes that comprise species, and illustrate intraspecific effects for *Pinus sylvestris* and *Larix sibirica*.

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22.2 Background

22.2.1 Study Area

Our studies deal with vegetation of Siberia and the forests in particular (within 60–140°E longitude and 50–75°N latitude), an area bounded by the Ural Mountains in the west, eastern Yakutia 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°) grid (GLOBE 1999).

22.2.2 Mapping Current and Future Climates

In this chapter, we use growing degree-days, above 5°C (GDD_5); negative degree-days, below 0°C (NDD_0); and an annual moisture index (AMI), the ratio of GDD_5 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_5 represents temperature requirements for growth and development; NDD_0 defines cold tolerance, and AMI characterizes resistance to moisture stress. The present model does not take into account geographic variations of soils except for presence or absence of the continuous permafrost.

For mapping climates, we assembled temperature and precipitation records normalized for the period 1900–1964 from 1,063 weather stations with precipitation data and 812 weather stations with temperature data across Siberia (Reference books 1965–1970). 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_5 image by the annual precipitation image.

For predictions of global warming, we used the greenhouse gas scenario (1% increase per year) from the Hadley Center, HadCM3GGa1 (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 3–9°C, summer temperature increase of 4–6°C, and annual precipitation changes between −4% and +25% over the study area. Future January and July temperatures and annual precipitation for each pixel were calculated by adding anomalies to the normalized monthly means (Reference books 1965–1970). Future values of climatic indices GDD_5 and NDD_0 were calculated using the following linear regressions calculated from contemporary data: GDD_5 was calculated from mean July temperature ($R^2 = 0.90$), and NDD_0 from January temperature ($R^2 = 0.96$). Future values of AMI were calculated directly by dividing the future GDD_5 image by the future annual precipitation image.

22.2.3 Permafrost

Permafrost covers 80% of Siberia and is the primary factor controlling the distribution of forests and their composition in Central Siberia and Yakutia (Pozdnyakov 1993). In the dry climate of Yakutia, forests are capable of developing in this region only because the melting of permafrost provides additional summer moisture to lands where otherwise the vegetation would be semidesert (Shumilova 1962). Permafrost also limits the northward and eastward spread of the dark-needled (*Picea obovata*, *Pinus sibirica*, *and Abies sibirica*) and also two light-needled (*L. sibirica* and *P. sylvestris)* species. Within the permafrost zone, spruce and pine can reach high latitudes on sandy soils along big river valleys and benches where permafrost may thaw deep enough (Shumilova 1962; Pozdnyakov 1993). Forests from both Siberian pine (*P. sibirica*) and fir (*A. sibirica*) are not found on continuous permafrost zone but found south of permafrost along discontinuous and island permafrost (Pozdnyakov 1993). Only *L. dahurica* (*L . gmelini* + *L. cajanderii*), by contrast, is capable of growing on shallow soils, which thaw as little as 10–30 cm during the growing season (Abaimov et al. 1999; see also Chap. 3).

Another factor limiting the tree species distribution in Siberia is forest fire. If even young dark-needled trees can emerge in some favorable habitats, frequent fire events in dry habitats fully eliminate their distribution (Polikarpov et al. 1998). Over the permafrost zone, only *L. dahurica* is adapted to fires, and successfully regenerates in burnt areas. Effects of forest fires on forest distribution were not modeled here.

In this study, we modeled permafrost influence on zones and tree species distribution. The current position of the active layer at the depth of 2 m across Siberia was predicted from the regression relating this layer from the map of Malevsky-Malevich et al. (2001) and our three climate variables ($R^2 = 0.70$). This regression is valid within the limits of contemporary climate. To map the permafrost border in the much warmer climate of 2090, we applied Stefan's theoretical formula (Dostavalov and Kudriavtsev 1967) predicting active layer changes from the ratio between GDD_5 in current and future climates.

22.2.4 Vegetation Zones

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), which control vegetation zones (Budyko 1974). For the Siberian continental climate, low winter temperatures and permafrost are the crucial limiting factors controlling distribution of tree species distribution (Shumilova 1962). To account for these factors, the Siberian bioclimatic model of Tchebakova et al. (1994) was modified to predict vegetation zones (types) from the three bioclimatic parameters and permafrost (Tchebakova et al. 2003; Tchebakova and Parfenova 2006). Forest fire is not included in the model, because we consider only

climax vegetation depending on zonal climate. Fire controls forest successions within a climax vegetation type.

Major zonal (climax) vegetation types recognized by geobotanists on the plains of Central Siberia are as follows: (1) Tundra; (2) Forest-tundra; (3) Dark-needled (*Pinus sibirica, Picea obovata,* and *Abies sibirica*) taiga (subdivided into northern, middle, southern) on elevated tablelands; (4) Light-needled (*Larix sibirica* and *Larix gmelinii, Pinus sylvestris*) taiga (northern, middle, southern); (5) Birch (*Betula pendula* and *Betula pubescens*) and light-needled (*Larix sibirica* and *Pinus sylvestris*) subtaiga; (6) Birch (*Betula pendula* and *Betula pubescens*) and light-needled (*Larix sibirica* and *Pinus sylvestris*) forest-steppe; and (7) Steppe (Shumilova 1962; Nazimova 1995; see also Fig. 1.2 for a similar classification).

In our bioclimatic model (Table 22.1), the AMI separates vegetation into two large types, arboreal and nonarboreal (forests and steppes) and further subdivides the former type into dark-needled and light-needled forests by the AMI index. The cold parameter, NDD_0, equal to 3,500–4,000°C, also tends to separate dark-needled and light-needled tree species. And finally, the permafrost border limits dark-needled species from spreading eastward across Asia, although summers are sufficiently warm to allow survival as far east as Yakutia. The dark- and light-needled forest zones are further separated into latitudinal subzones (e.g. forest-tundra, northern, middle and southern taiga, forest-steppe) by GDD_5. Although temperate steppe, semidesert, broadleaf forest, and forest-steppe types are not found under current Siberian climate, these four classes are included in our model because of their potential importance under a warming climate. In total, therefore, our model considers 14 vegetation types, each of which can be defined climatically from the vegetation ordination in these three climatic variables (Table 22.1).

Table 22.1 Climatic limits for the modified Siberian vegetation model

	GDD_5		AMI		NDD_0	
Vegetation type	Lower limit	Upper limit	Lower limit	Upper limit	Lower limit	Upper limit
Tundra	None	<300	None	None	None	None
Forest-tundra and sparse taiga	300	500	None	None	None	None
Northern dark-needled taiga	500	800	None	<1.5	>−4,500	None
Northern dark-needled taiga	500	800	>1.5	None	None	<−4,500
Middle dark-needled taiga	800	1,050	None	<1.75	>−3,500	None
Middle light-needled taiga	800	1,050	>1.75	None	None	<−3,500
Southern dark-needled taiga and birch subtaiga	1,050	1,250	None	<2.25	None	None
Southern light-needled taiga and subtaiga	1,050	1,250	>2.25	None	None	None
Forest-steppe	1,250	1,650	None	<3.25	None	None
Steppe	1,250	1,650	>3.25	None	None	None
Semidesert/desert	>1,650	None	None	None	None	None
Broadleaf forest	1,250	1,650	None	<1.5	None	None
Temperate forest-steppe	>1,650	None	1.5	3.25	None	None

22.2.5 Major Forest-Forming Tree Species of Siberia

The forests across the vast territory of Siberia are composed largely of eight conifers (Pozdnyakov 1993): 49% *Larix spp.* of which 1% is *L. sukaczewi*, 13% is *L. sibirica*, and 83% is *L. gmelini* and *L. cajanderii*; and 3% of some far-eastern endemic larches; 13% *P. sylvestris*; 7% *Picea obovata*; 6% *Pinus sibirica*; 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-needled conifers, which are opposed to the other three shade-tolerant conifers, spruce, cedar, and fir, which are referred to as the dark-needled species (Shumilova 1962). Siberian spruce dominates only in Western Siberia, both Siberian cedar and fir dominate on elevated tablelands (Yenisei Ridge) and in the southern mountains (the Altai-Sayan mountains). Only two tree species, *Larix gmelini* and *L. cajanderii*, dominate the forests in vast interior Siberia, the permafrost zone east of the Yenisei River. We consider results obtained from *L. gmelini* and *L. cajanderii* to be jointly applicable to their parental species, *L. daurica* (see Chap. 3).

22.2.6 Distributions of Pinus sylvestris and Larix Species

The contemporary potential and actual climate envelope of *P. sylvestris, L. sibirica, L. dahurica, and L. sukaczewii* and their climatypes was mapped using three variables: GDD_5, NDD_0, and AMI. Limits of distribution for these variables were approximated from the climatic extremes for provenances included in geneco-logical studies established throughout the Soviet Union, limits of the breadth of transfer functions (see Rehfeldt et al. 2002), the relative climatic tolerances of species, and the climate estimated for extreme locations on range maps (Tchebakova et al. 2006).

Actual (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*. The latter factors are recognized as the ecological factors most strongly influencing the distribution of the larches (Dylis 1981; Pozdnyakov 1993; Abaimov et al. 1998). Only *L. dahurica*, for instance, can survive on permafrost with depth of the soil active layer less than 1–2 m. As a result, *L. sibirica* and *L. dahurica* can dominate much of the Siberian forests, 50% of the forest areas in Central Siberia and 80% in Northeastern Siberia, respectively. In the warmer climates of Western Siberia, *L. sukaczewii* can be spread in the south and *L. sibirica* in the north with total 7% of the forest (Polikarpov et al. 1998).

Among larches, *L. sibirica* seems to be competitively superior to *L. daurica* (Polikarpov et al. 1986), outcompeting *L. daurica* on good sites. Yet, *L. sibirica* itself can be excluded from the warm and 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 displace *P. sylvestris* to poor sandy soils on

old alluvial terraces in Western Siberia or along the valleys of large Siberian rivers in the east (Pozdnyakov 1993).

To account for these ecological interactions, we reduced the size of the climatic envelope of the larches using geography of their distribution (Pozdnyakov 1993; Abaimov et al. 1998) according to the following algorithm: (1) the actual distribution of *L. dahurica* is limited by the climatic envelope on the cold fringe and by the permafrost border to the south and west; (2) the actual distribution of *L. sibirica* is determined by the permafrost border on the cold fringe and the climatic limits of *L. sukaczewii* on the warm fringe; (3) the actual distribution of *L. sukaczewii* is determined by its climatic envelope; and (4) the actual distribution of *Pinus sylvestris* is limited primarily by permafrost, although beyond the permafrost zone competition from *L. sibirica* and *L. sukaczewii* tends to relegate *P. sylvestris* only on sandy or boggy soils along wide river valleys.

22.2.7 Mapping Climatypes of Pinus sylvestris and Larix Species

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 Union. 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. 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 the same or similar climate.

The analyses of Rehfeldt et al. (2003) used published data across former Soviet Union within 46–86°N and 24–150°E 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 this study, three transfer functions driven by GDD_5, NDD_0, and AMI were developed. The transfer functions showed that height and survival decrease as the transferred distance 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 (Rehfeldt et al. 1999a). For *P. sylvestris,* these transfer distances were ±240 GDD_5, ±575 NDD_0, and ±0.6 units of AMI; for *L. sibirica* as ±325 GDD_5, ±1,150 NDD_0, and ±0.5 units of AMI; for *L. dahurica*, ±550 GDD_5, ±1,000 NDD_0, and ±1.2 units of AMI; and for *L. sukaczewii*, ±275 GDD_5, ±725 NDD_0, and ±1.0 units of AMI.

Table 22.2 Climatic limits, climatype breadth, and number of potential climatypes for the dominant conifers of Siberia for three climate indices (see Sect. 22.2.7)

Statistics		*Pinus sylvestris*	*Larix sibirica*	*Larix dahurica*	*Larix sukaczewii*
GDD_5 (°C)	Lower limit	600	650	400	800
	Upper limit	3,000	2,350	1,850	2,400
	Climatype breadth	480	650	1,100	550
	Number of classes	5	3	2	3
NDD_0 (°C)	Lower limit	−6,000	−4,500	−6,000	−2,200
	Upper limit	0	−1,200	−2,000	−300
	Climatype breadth	−1,150	−2,300	−2,000	−1,450
	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
	Climatype breadth	1.2	1.0	2.4	2.0
	Number of classes	6	8	3	2
Total number of climatypes		180	48	12	12

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 22.2). Climatypes are defined by subdividing the climatic envelope into classes bounded by these limits. For example, the 313 pine provenances used in these tests ranged from 626 to 2,916 GDD_5. Because the transfer functions suggested that the breadth of a climatype should be about 480 degree-days (240×2), 5 classes (2,290/480=4.77) are found. Six classes were needed for both NDD_0 and AMI. All possible combinations of these classes for three climatic indices produced an upper limit to the number of pine climatypes at 180. For the *L. sibirica*, there were 8 classes for the moisture index, 3 for GDD_5 and 2 for NDD_0, which produced a maximum of 48 climatypes; for *L. dahurica*, 3 for AMI, 2 for GDD_5, and 2 for NDD_0 for a total of 12; and for *L. sukaczewii*, 2 for AMI, 3 for GDD_5, and 2 for NDD_0 for a total of 12 (see Table 22.1). Tchebakova et al. (2003) summarized all possible climatypes for each species as combinations of growing degree-days above 5°C, negative degree-days below 0°C, and AMI.

Climatypes of the four species were mapped for all of Siberia using the climate maps of GDD_5, NDD_0, and AMI. Mapping was done for the contemporary climate and for the climate expected by the Hadley GCM for the decade beginning in 2090.

22.3 Effects of Global Warming on Vegetation Shifts

Changes in Siberian zonal vegetation were estimated by applying the Siberian vegetation model to the current climate and the climate change scenario for 2090, taking into consideration predicted changes in the distribution of permafrost (Table 22.3, Fig. 22.1).

In the contemporary climate of Siberia, taiga prevails on 65% of the area, 75% of which consists of light-needled taiga with *Larix sibirica* and *L. dahurica* being

Table 22.3 Vegetation change (%) in Siberia in a warmed climate

Vegetation zone[a]	Area (10^4 km^2) current	Proportion (%)	Area (10^4 km^2) 2090	Change (%)
Tundra	110.8	9.3	7.5	−93
Forest-tundra	91.3	7.7	12.2	−87
Northern dark taiga	1.9	0.2	10.9	+5-fold
Light northern taiga	191.1	16.1	48.6	−75
Dark middle taiga	52.7	4.4	10.2	−81
Light middle taiga	237.0	19.9	66.2	−72
Dark southern taiga	108.3	9.1	127.3	+18
Light southern taiga and subtaiga	98.6	8.3	87.0	−12
Forest-steppe	62.6	5.3	328.1	+5-fold
Steppe	139.2	11.7	176.5	+27
Drysteppe, semidesert	11.7	1.0	78.9	+7-fold
Temperate				
Broadleaved forest	0.03	0.0	2.4	–
Temperate forest-steppe	–	–	28.5	–
Temperate steppe	–	–	216.2	–

[a]No bare lands included

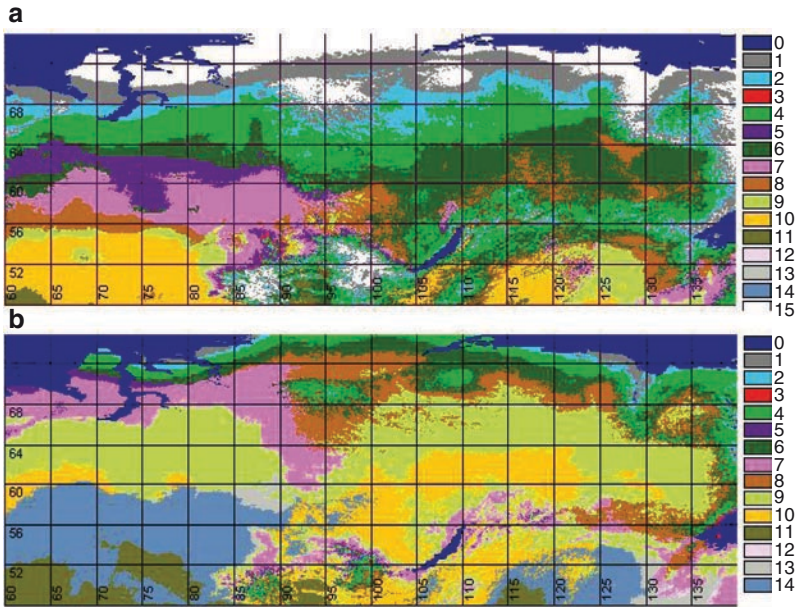

Fig. 22.1 Vegetation distribution in Siberia for the contemporary climate (**a**) and for the climate projected for the decade beginning in 2090 (**b**) (Soja et al. 2007). Numerals indicate the following: Water (0), tundra (1), forest-tundra (2), northern dark (3) and light (4) taiga, middle dark (5) and light (6) taiga, southern dark (7) and light (8) taiga, forest-steppe (9), steppe (10), dry steppe (11), broadleaved (12), temperate forest-steppe (13), and temperate steppe (14) *See* Color Plates

the domimant species. *Pinus sylvestris* can also dominate these forests in the warmer climates of the south or on sandy soils in middle and even northern taiga. Dark-needled taiga (25%) appears in moist and warm climates, such as in the West Siberian Plain, which is west of the Yenisei River, yet along the Yenisei Ridge at the mid-latitudes and in the Mountainous Southern Siberia. At the high latitudes of Putorana Mountains (north of the Artic Circle), only larch taiga can withstand the cold climate and permafrost. *Picea obovata* and *Pinus sibirica* may be mixed with *Larix* in the large river valleys, which tend to be warmer than the surrounding landscape. No grasslands occur north of 56°N (Fig. 22.1a). Nonarboreal types, tundra, and forest-tundra in the north and steppes and forest-steppes in the south, each cover about 17% of the area.

Fire and the melting of permafrost are considered to be the principal mechanisms that will shape new vegetation physiognomies (Polikarpov et al. 1998). In a warmed climate of 2090, taiga is predicted to shrink to half of the present area (Table 22.3, Fig. 22.1b). The southern treeline is being shaped by the forest fire, which rapidly promotes equilibrium between the vegetation and the climate. Tree decline in the southern taiga border in a dryer climate would facilitate the accumulation of woody debris. This accumulation, paired with increased weather suitable for fire, would result in a decreased fire return interval and an increased potential for severe and large fires. Predicted global warming will not be sufficient to melt permafrost deep enough to support dark-needled species in most of Siberia. Still, larch forests would dominate about 60% of Siberian taiga east of the Yenisei River, in Evenkia and in Yakutia. Forest-tundra and tundra should occupy only up to 1.5%. Although forest-steppe, steppe, and semidesert cover about 20% of the area in current climate of Siberia, these vegetation types would occupy more than 60% in the climate of 2090. In fact, large areas of steppe should cover the central Yakutian Plain and the Tungus Plateau, located more than 1,000 km north of the current steppe distribution.

Our Siberian vegetation model also shows that temperate vegetation types such as broadleaved forest, forest-steppe, and steppe climatic limits, which were derived from the global vegetation model (Tchebakova et al. 1993), currently do not exist in Siberia, although they should occur there in a warmed climate. The climate-change scenario we are using predicts the concomitant invasion of temperate broadleaved species such as linden into Western Siberia, which seems reasonable for a warmer climate. This is supported by Khotinsky (1977) who reconstructed mid-Holocene vegetation from pollen depositions and concluded that birch and other broad-leaved forests once were distributed east of the Ural Mountains as far as 70°E and 57°N into the West Siberian Plain.

22.4 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 should

become only slightly more favorable than that of today. Figure 22.2 and Table 22.4 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 Center.

The contemporary climatic envelope of *P. sylvestris* extends across approximately 68% of the area in Siberia, but a more realistic estimate of the actual distribution is only 38% (Table 22.4) because nearly half of the species distribution in Siberia includes sites within the permafrost zone where the species is rare (Fig. 22.2). By 2090, however, both the climatic envelope and the climate associated with the actual distribution should increase 1.5–2 times (Table 22.4), largely because of the melting of permafrost. An increase in area primarily would involve migration out of the valleys in Northeastern Siberia onto the plains and tablelands where it cannot 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 (Fig. 22.2). 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 central part of Mountainous Southern Siberia, the climate suitable for *P. sylvestris* should move upwards in altitude by about 1,000 m by the last decade of the twenty-first century (Rehfeldt et al. 2004).

For *Larix*, all but the northernmost regions lie within the combined climatic envelopes of *L. sukaczwei*, *L. sibirica*, and *L. dahurica* in the contemporary climate (Table 22.4, Fig. 22.2). 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 was suggested in Fig. 22.2, the climate of the future in the southwest where *L. sukaczewii* now occurs should pass beyond the contemporary climatic envelope of all these species. This loss of habitat should be more than balanced by an increase in suitable 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

Table 22.4 Proportions of Siberia of conifer species (%, predicted actual distribution in parentheses) in the current climate and the climate projected by a GCM of the Hadley Center (HadCM3GGal) for the decade beginning in 2090 (Tchebakova et al. 2006)

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

Note that the first numerals in each cell include areas overlapping with distribution of other species, and do not add up to 100%

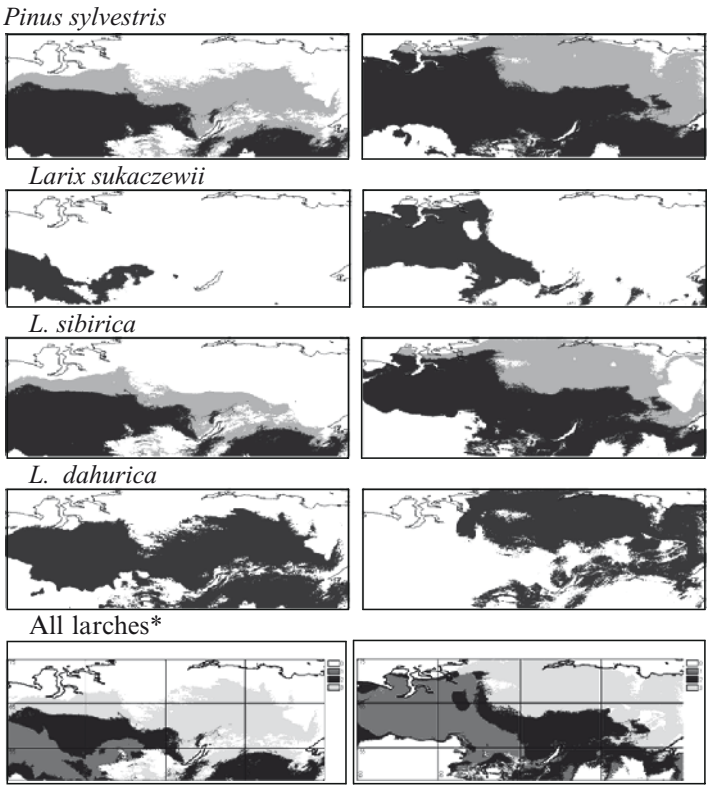

Fig. 22.2 Potential distributions of *P. sylvestris* and *Larix spp* modeled for the contemporary climate (*left*), and for the climate projected for the decade beginning in 2090 (*right*). *Gray* is part of the potential distribution of *L. sibirica* and *Pinus sylvestris* over the permafrost zone. *L. sukaczewii* occurs beyond the permafrost zone and *L. dahurica* occurs only on permafrost. (Asterisk) Actual distributions of *L. spp* depend on the effects of permafrost and interspecific competition among the larches (Tchebakova et al. 2006; shades of *gray*): *dark – L. sibirica*, *medium – L. sukaczewii*, *light – L. dahurica*

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 22.4, Fig. 22.2).

Unlike the projected future distribution of *P. sylvestris*, the future range limits 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 (Fig. 22.2). Rough estimates from this figure suggest that the climate associated with the contemporary limits of distribution of *L. sukaczewii* and *L. sibirica* may be found as distant as 10° in latitude (about 700 km) toward the north by 2090. Estimates for *L. dahurica* are smaller because northward migration will halt at the Arctic Ocean.

22.5 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.

22.5.1 Pinus sylvestris

Of the 180 possible climatypes in the climatic envelope of *P. sylvestris,* most are small; only ten account for 55% of the species' climatic envelope and 63 comprise the species tri-variate envelope in Siberia (Table 22.5). 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 22.5). 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.

Of the 101 climatypes expected for the future, only one-half exist there today (Table 22.5). Nonetheless, like today's distribution of climatypes, those 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.

Table 22.5 Effects of global warming on the number of climatypes in four Siberian species (Tchebakova et al. 2006)

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

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 (Fig. 22.3). 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 Fig. 22.3, however, the future location of climates inhabited by contemporary climatypes is expected to shift geographically. The shift, in fact, may amount to 500–1,000 km.

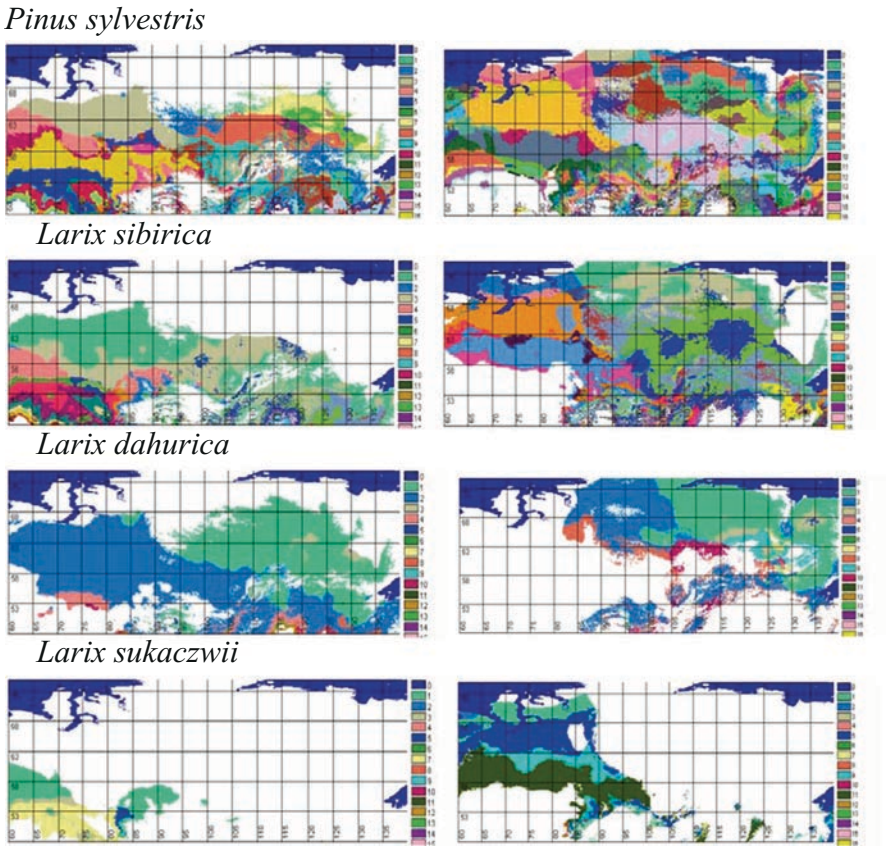

Fig. 22.3 Distributions of climatypes in Siberia for *Pinus sylvestris* and Siberian Larches (*Larix sibirica*, *L. dahurica,* and *L. sukaczewii*) in the contemporary climate (**a**) and in decade beginning in 2090 (**b**). For each species, one color corresponds to a single climatype of 180 possible climatypes for *Pinus sylvestris,* 48 for *Larix sibirica*, 12 for *L. dahurica*, and 12 for *L. sukaczewii* (see Table 22.5, Tchebakova et al. 2003) *See* Color Plates

22.5.2 *Larix sibirica*

Of the 48 possible climatypes, 31 comprise the species' contemporary climatic envelope in Siberia (Table 22.5). 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 22.4) while their distribution 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 22.5). Three minor climatypes (<0.5% of the area) are expected to disappear while 28 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 (Fig. 22.3).

22.5.3 *Larix dahurica*

Of the four species being considered, *L. dahurica* occurs in the coldest climates and is the only species endemic to permafrost; the cold fringe of its distribution thus 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 22.4). As the envelope shrinks, however, the number of climatypes that comprise it should remain constant at 12, with neither new climatypes arising nor contemporary climatypes lost (Table 22.5). The two most important climatypes of today, which currently occupy 91% of the species climatic envelope, also are expected to be dominant at the end of the century but by then should occupy only 68%. As shown in Fig. 22.3 for one of the two, the future areal extent of these two climatypes should be reduced by about 50% while their geographic position shifts to the northeast.

22.5.4 *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 climatypes are also similar. Because of an increase in the climatic envelope from 12% of Siberia to 26% (Table 22.4), the number of climatypes is expected to increase from 5 to 10

(Table 22.5). During the course of the century, the two climatypes 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, which is expected 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 climatypes should arise even though no contemporary climatypes are expected to be lost. The novel climatypes quite likely exist today west of the Ural Mountains.

22.6 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. In this paper, we estimate the future distribution of the climates in which the vegetation exists today. Potential biological impacts are qualified by use of the word "should."

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 genetic variability across the landscape such 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 Mountainous Southern Siberia should approach 1,000 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 so that optimal forest growth and productivity are 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 climatypes within these species.

Figure 22.3 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 1,000 km. As another indication of this scope, it is also instructive to assess the contemporary location of the climatypes expected to be of future importance in Siberia. Of the three *P. sylvestris* climatypes expected to dominate future forests, one, No. 40, is a minor component of the contemporary array. Nevertheless, this climatype is much more prevalent today toward the southwest in the foothills of the Altai Mountains, nearly 700 km away (Rehfeldt et al. 2004). Climatypes No. 82 and No. 88, which will be new to the Sayan Mountains, are currently present as isolated populations in Kazakhstan and Bashkiria, about 1,500 km and 20° of longitude to the west (Rehfeldt et al. 2004). And, for *L. sibirica,* climatype No. 20, which is to be of future importance, is present today in the Altai Republic. However, the climatic conditions with which this climatype is associated, can also be found west of the Ural Mountains in European Russia (Rehfeldt et al. 2004). Because the dominant larch west of the Ural Mountains is *L. sukaczewii,* it is possible that the future climates of Siberia may be suited to a mixture of larch species and their hybrids (see Abaimov et al. 1998; Chap. 3). Nevertheless, it is clear that the genotypes expected to be of importance to the future vegetation currently reside at long distances from their future habitat (Fig. 22.3). 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 climate.

These results are essentially the same as those obtained for *Pinus contorta* (Rehfeldt et al. 1999b) and *Picea engelmannii* (Rehfeldt et al. 2004) of western North America. The conclusion seems inescapable that global warming will initiate a redistribution of genetic variability within most species (Rehfeldt et al. 2004) such that in time genotypes also become redistributed. Response to climate-change, therefore, is much more than a shifting of species distributions (Davis and Shaw 2001; Davis et al. 2005). Indeed, effects of a changing climate reverberate throughout a species distribution as genetic variability becomes 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 Futyama 1979; Davis et al. 2005). 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; Davis et al. 2005). One must be aware that genotypes physiologically attuned to a climatic regime are subject to selection and recombination during migration. Genotypes of sessile forest trees quite simply cannot 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 the projected rates of climate change (Izrael et al. 2002), and as a result, a migration lag (Davis 1989) can be anticipated. One must also realize that migration through a closed forest canopy cannot 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 the rates that must occur if the vegetation is to closely track the climate as it changes across Siberia.

At the intraspecific 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 5–10 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).

These analyses on disparate species thus demonstrate the far-reaching effects of a changing climate on the ecological 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 (2001) during a changing climate will suffice only to the point where the amount of change exceeds 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 and cause widespread mortality in existing populations (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 assist migration such 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 (see Rehfeldt

et al. 2004; St Clair and Howe 2007). Maps such as Fig. 22.3 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. 2020) during the coming decade.

22.7 Conclusions

Impacts of global warming on the Siberian vegetation will be pronounced if GCM scenarios are allowed to reach their 2090 projections. Effects should shift vegetation zones, alter species distributions, and produce populations within species that no longer are physiologically attuned to their environment.

Shifts in zonal vegetation could result in a taiga that is only one-half of the current area while steppe and semidesert vegetation should proliferate, increasing in area from about 20% of the total to 60%. The future climate may also be suited to temperate broadleaved species, which do not inhabit Siberia today. Fire and the melting of permafrost are viewed as the principal mechanisms promoting establishment of new vegetation and, therefore, the shifting vegetation zones.

The shifts in zonal vegetation will result from migration of species as they attempt to track their climatic optima. The 2090 climate of Siberia should be increasingly more suitable for *P. sylvestris*, *L. sibirica*, and *L. sukaczewii* but less favorable for *L. dahurica.* Suitability of the future habitat, however, will depend as much on permafrost melting, a process that lags behind the change in climate.

Genetic structure of species will be disrupted, as the changing climate becomes less and less suited to extant populations. The area suitable for the climatypes of today should undergo tremendous change as minor climatypes of today become important for the future. The future location of climates optimal for the climatypes of today is projected to recur at distances measured in hundreds of kilometers from their contemporary location.

Extent of the projected impacts is so profound that maintaining a semblance of equilibrium between plant distributions and climate will require humans to assist in plant migration.

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