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INVITED SYMPOSIA PAPERS

IMPACTS OF CLIMATE CHANGE ON POPULATIONS AND SPECIES DISTRIBUTIONS

Isabelle Chuine, Wilfried Thuiller and Xavier Morin

Centre d'Ecologie Fonctionnelle et Evolutive, CNRS
1919 route de Mende, 34293
Montpellier cedex 05
France
E-mail: isabelle.chuine@cefe.cnrs.fr

Concern about the current climate change is increasing. Ecological (Parmesan and Yohe 2003, Root et al. 2003, Walther et al. 2001) and socio-economic (Keeney and McDaniels 2001, Michaelis 1994, Yohe and Schlesinger 2002) impacts are more and more perceptible. Many studies have already shown that climate change is significantly affecting species development timing (Menzel and Fabian 1999, Parmesan and Yohe 2003, Walther et al. 2001), physiology (Cannell et al. 1998, Hughes 2000, Keeling et al. 1996, Myneni et al. 1997), competition (Hughes 2000), and geographical ranges (Parmesan et al. 1999, Parmesan and Yohe, 2003, Walther et al. 2002). These changes will have major consequences on biodiversity, silviculture, and agriculture (Jingyun et al. 2001, Nicholis 1997). It thus becomes urgent to develop predictive models to draw a picture of species distribution and ecosystem (managed or natural) functioning changes. Forestry should certainly be among the first human activity concerned with such changes, and there are going to be long-term consequences as well as short-term consequences of climate change on trees. The short-term consequences will mainly concern phenology and frost damage. Climate warming mainly advances leaf unfolding and flowering, such that they occur during a period when frost events are more likely (Hänninen 1991, Kramer 1994, Linkosalo et al. 2000). Another short-term consequence of phenology change will be an asynchrony between the phenology of trees and parasites (Bale et al. 2002, Dewar and Watt 1992, Fleming and Candau 1998, Fleming and Volney 1995, Hodar and Zamora 2004).

These short-term consequences will however probably be at low expense compared to the long-term ones, which will concern the distribution of the climatic niche of the species. If the changes observed during the 20th century continue and amplify we could see in a few decades the improvement of the regeneration of the northern range limit of some populations, but at the same time the loss of regeneration of the southern range of populations. How far north species distributions could move within this century is a question of major importance especially in North America where the exploitation of northern latitude timber could be valuable.

To investigate all these questions, we need species distribution models. There are two main kinds of models that are currently used to forecast species' distribution under climate change scenarios: process-based models and so-called niche-based models which are statistical models.

Process-based models simulate biological processes in response to environmental changes using mathematical equations. These equations are derived from experimental results that provide cues to understand how these processes are affected by the environment. Such models have a high predictive power and explanatory power and are particularly robust. The reason for this is that the model parameters are fitted on observations done in natural populations or during experiments of the processes described in the model. They are not fitted on the species present distribution. The main drawbacks of such models are that they require a long phase of development and lots of information on the response of adaptive traits to environment for each species.

Niche-based models either deal with the distribution of species or ecosystems and they statistically relate the presence or absence of the species to environmental variables. This is the principle of the climatic envelope. Such models can be quickly developed as they require the digitized distribution of a species and corresponding environmental information prevailing within and outside the distribution. They can thus be developed for any species providing its distribution is known. One of the main drawbacks of such models is that their robustness is difficult to assess because they use the species' present distribution to fit the parameters and cannot be tested in true external conditions. The use of half of the distribution chosen randomly to fit the model and the other half to validate it does not provide a robust validation as both datasets are highly auto-correlated. However, the use of one continuous part of the distribution to fit and the rest to validate does not provide an accurate model fit either. Validation is therefore an important problem for niche-based models, which is currently driving most attention (Thuiller 2003, 2004). Although niche-based models have good predictive power, they also provide very few insights to understand which key adaptive traits and environmental variables interplay to shape species distribution.

In this paper we use the predictions of temperate tree species' distribution change using a niche-based model, BIOMOD (Thuiller 2003, 2004), and a process-based model, PHENOFIT (Chuine and Beaubien 2001) to draw some conclusions on the impact of climate change.

The simulations of BIOMOD concern European timber trees and they do not take into account effective migration rate and survival rate of the species. They provide a predicted distribution of the climatic envelope of the species. The simulations use the Hadley Center climate model HadCM3 output and two IPCC scenarios, A1Fi which are consumerist individualist scenarios leading to a global mean increase in temperature of 4.5°C by 2100 in Europe and B2 which is a conservationist, communitarian scenario leading to a global mean increase of temperature of 2.5°C in Europe. The simulations of PHENOFIT concern North American timber trees and they do take the migration rate and survival rate of the species into account. The simulations also use the Hadley Center climate model HadCM3 output and two IPCC scenarios, A2 which is consumerist, individualist scenarios leading to a global mean temperature increase of 5.0°C by 2100 in North America and B2 which is a conservationist, communitarian scenario leading to a global mean increase of temperature of 2.2°C in North America.

The response of the species to climate change could be classified into three categories. The first category comprises species whose distribution will be relatively unaffected by climate change. Few of the species studied pertain to this category: common oak (*Quercus robur*) and sessile oak (*Quercus petraea*). Common oak is the least affected species overall. Its sister species, sessile oak, is a little bit more affected, especially in scenario A1Fi in which it disappears from an important part of its present distribution (Fig. 1).

The second category of species comprises species whose distribution will be significantly affected by climate change. This category principally concerns temperate and boreal trees, such as Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) in Europe and lodgepole pine (*Pinus contorta*) and quaking aspen (*Populus tremuloides*) in North America. These species' distributions should contract substantially with climate change, especially in the A1Fi or A2 scenarios (Fig. 2), with migration northward being limited by the sea. The differences between the two scenarios were small.

The third category comprises species whose distribution will be very much affected by climate change and this is mainly Mediterranean and Temperate species such as European larch (*Larix decidua*) and silver fir (*Abies alba*), European black pine (*Pinus nigra*) and maritime pine (*Pinus pinaster*), sugar maple (*Acer saccharum*), and western white pine (*Pinus monticola*). These species should disappear from most of their present distributions (Fig. 3). In Europe, the new colonisable areas may be for some species disconnected from the present ones (*Pinus nigra*, *Pinus pinaster*) (Fig. 4).

These results are in agreement with those of Iverson and Prasad (1998). Using a niche-based model for United States to predict the distribution of 80 species using the Goddard Institute of Space Studies climate model for a doubled level of atmospheric CO_2, they show that species distributions will also shift northward substantially. In their study, *Populus tremuloides* and *Acer saccharum* are among the most affected species by climate change with *Populus grandidentata*, *Abies balsamea*, *Betula papyrifera*, *Pinus resinosa*, and *Thuja occidentalis* also severely impacted. One of the main conclusions of this presentation is that models, either niche-based or process-based, are in agreement. However, only process-based models provide insights to understand species distribution changes.

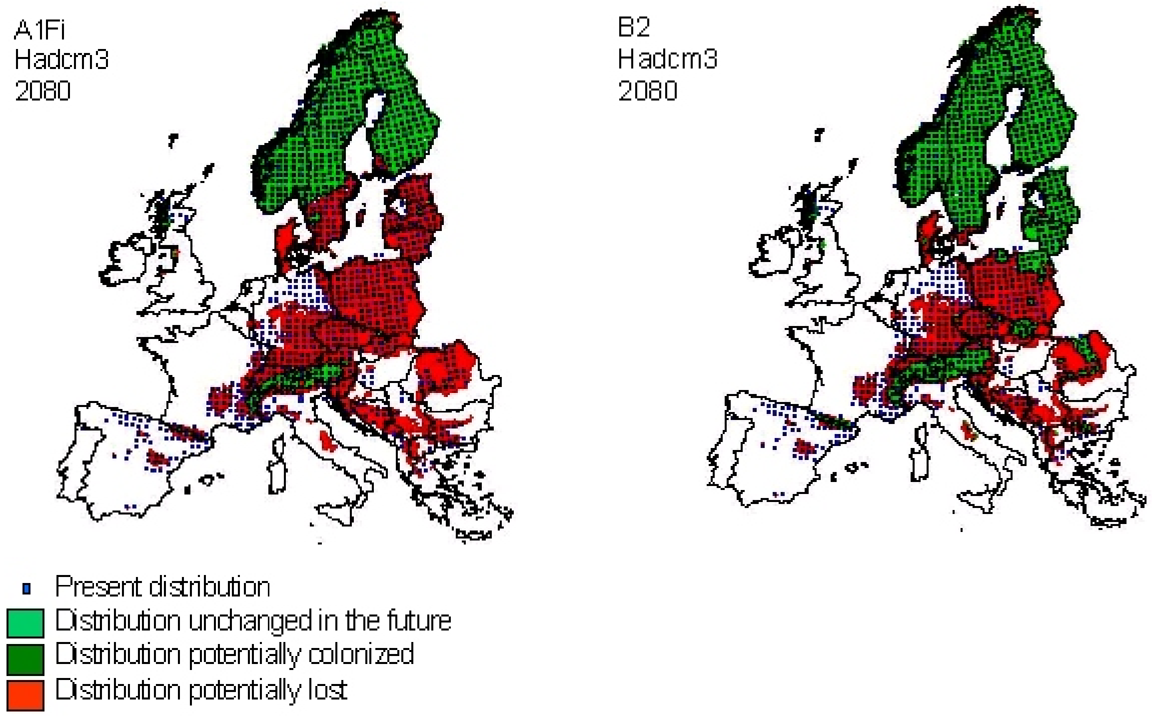

Figure 1. Predicted potential distribution of *Quercus robur*.

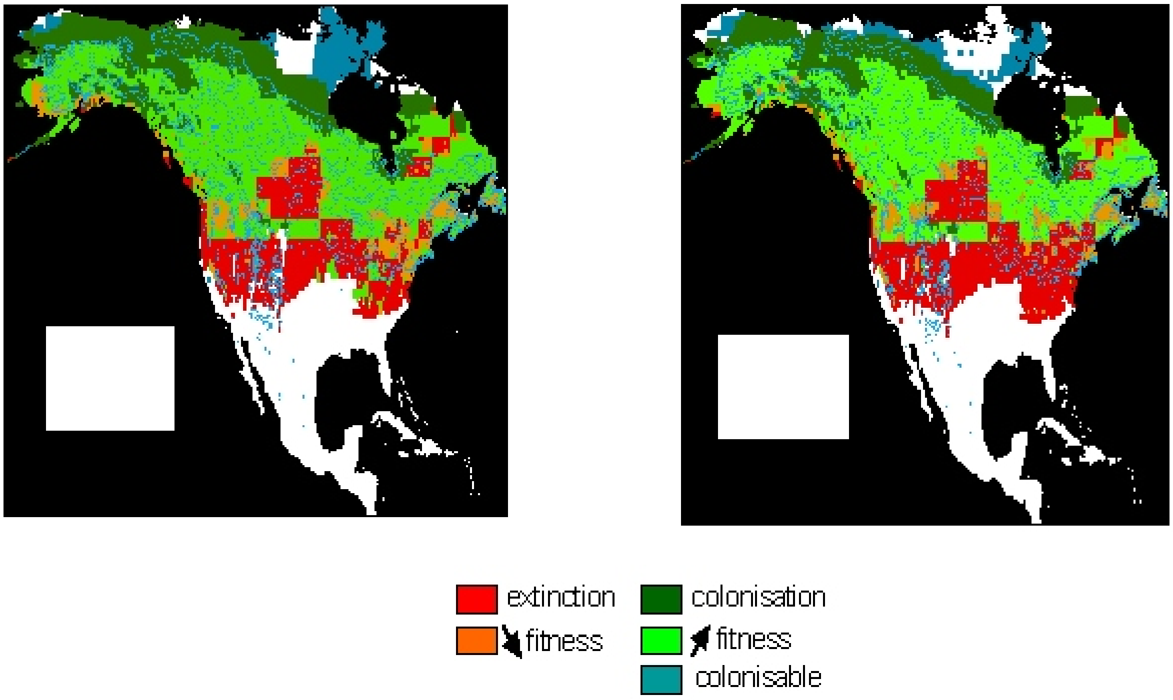

Figure 2. Predicted potential distribution of *Populus tremuloides*.

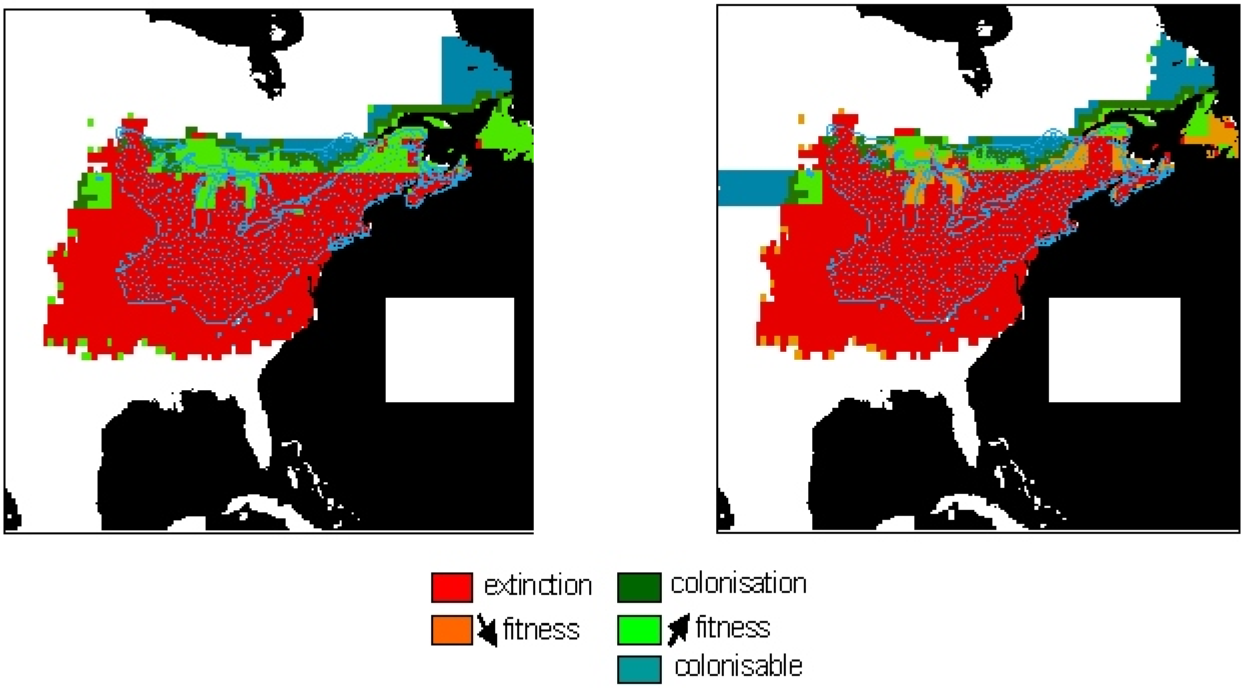

Figure 3. Predicted potential distribution of *Acer saccharum*.

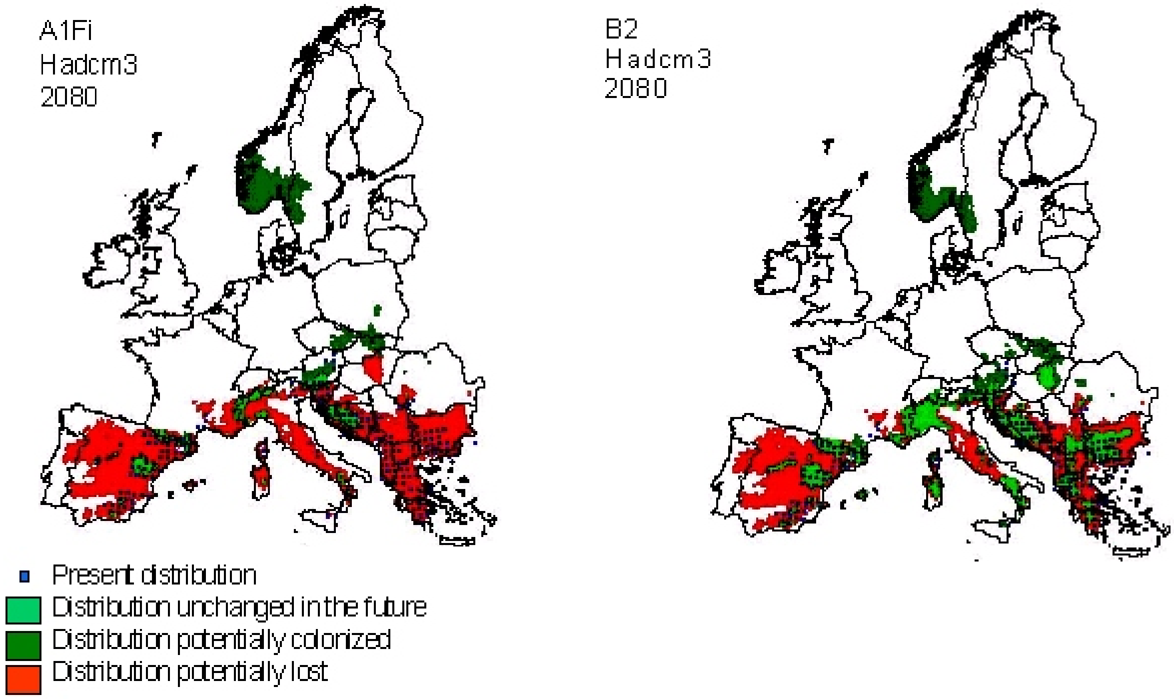

Figure 4. Predicted potential distribution of *Pinus nigra* sp.

During the last major climate change (i.e., from the glacial maximum around 18 000 BP to the climate optimum around 6 000 – 5 000 BP), vegetation showed a major global shift northward. From 10 000 BP to 3 000 BP species distributions shifted northward, at an average rate of 0.3° latitude per century to 1.35° latitude per century for the special case of Scots pine following the migration of their climatic niche. For the 21st century, the model predictions forecast that species' distributions will mostly contract in addition to a northward shift at a rate of 5° latitude per century for species from category one to 15 – 20° latitude per century for species from categories 2 and 3, i.e., 10 times faster than during the last climate change. The model predictions, either niche-based or process-based, are globally in agreement with each other. They show that the distribution of many temperate tree species will be affected, especially the Mediterranean/temperate species that will disappear from most of their current range. They also predict a northward migration and a regression of the southern part of the distribution, but more or less depending on the species. Process-based models show that some species may not be able to follow in real time the migration of their climatic niche.

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IMPACTS OF PAST CLIMATE CHANGE ON SPECIES' DISTRIBUTIONS OF WOODY PLANTS IN NORTH AMERICA

Stephen T. Jackson

Department of Botany
Aven Nelson Building
University of Wyoming
Laramie, WY
82071
E-mail: jackson@uwyo.edu

The modern distributions and genetic structure of North American tree species represent, in part, legacies of climate changes of the past 25 000 years and more. Development of extensive networks of pollen and plant-macrofossil records from lakes, wetlands, and woodrat-middens across North America are revealing the magnitude and complexity of climate-change effects. Paleoecological and paleoenvironmental studies have advanced to the point where some generalizations can be made, which are summarized briefly in this paper.

Ecologically significant climatic change and variability occurs at all timescales, from interannual to tens of thousands of years (Swetnam and Betancourt 1998, Swetnam et al. 1999, Jackson and Overpeck 2000, Jackson 2004). Although trends and cycles can be identified, much of the variability is non-stationary across a range of timescales. The global climate system is continually evolving, and its regional and local manifestations are in continuous flux.

To date, substantial changes in distribution and abundance during the past 25 000 years have been documented for every species and genus of temperate and higher latitudes for which we have good paleoecological records (Huntley and Webb 1988, Betancourt et al. 1990, Jackson et al. 1997, Betancourt 2004, Webb et al. 2004). The extent and nature of the changes varies among species and regions, ranging from major habitat shifts (elevational, edaphic, aspect) to wholesale geographic displacement at scales of thousands of kilometres (Jackson and Overpeck 2000). Some species (e.g., *Pinus remota*) have undergone counterintuitive range shifts, contracting southward since the last glacial maximum (Jackson 2004). Some subalpine species (e.g., *Abies lasiocarpa* and *Picea engelmannii*) appear to have occurred at lower elevations in the southern parts of their ranges than to the north (Jackson et al. 2005). These unexpected patterns probably stem from spatial gradients of seasonal precipitation that differed radically from those prevailing today.

Many species that are geographically extensive and/or regionally dominant today (e.g., *Betula papyrifera*, *Pinus ponderosa*, *P. strobus*, *P. edulis,* and *Tsuga canadensis*) occurred as localized, dispersed populations during the last glacial maximum (Betancourt et al. 1990, Jackson et al. 2000, Betancourt 2004). Others (*Juniperus osteosperma*, *Pinus banksiana*, and *Picea glauca*) have been widespread and dominant since the last glacial period, but their ranges have shifted by 100s to 1000s of km while many of the extensive and dominant species of the last glacial period (e.g., *Pinus flexilis* and *P. remota*) are now localized and highly fragmented compared to the past. At least one species (*Picea critchfieldii*) that was dominant in the lower Mississippi Valley and extensive in the unglaciated Southeast during the last glacial maximum is now extinct (Jackson and Weng 1999).

Changes in distribution and abundance were widespread and rapid during the glacial-interglacial period, 15 000–10 000 years ago. Many species expanded rapidly into new territory during this period in both eastern and western North America (Webb 1988, Betancourt et al. 1990, Clark et al. 1998). Recent genetic evidence suggests that this rapid expansion may have been facilitated by existence of northern outlier populations during the last glacial maximum (McLachlan 2003, McLachlan and Clark 2004). The late-glacial period is characterized by extensive areas of vegetation with no modern counterpart, particularly in the mid-continent (central and western Great Lakes, Upper Mississippi Valley, Ohio Valley, and adjacent uplands) (Williams et al. 2001, Jackson and Williams 2004). This vegetation consisted of mixed forests of *Picea*, *Quercus*, *Fraxinus nigra*, and *Ostrya/Carpinus* (presumably *Ostrya*). This no-analog vegetation shows spatial patterns and temporal changes, but these are poorly resolved at present. Nevertheless, the records show unique plant communities and landscape patterns during this period, and populations of *Fraxinus nigra* and *Ostrya* were much larger over more extensive areas than today. When these species declined at the opening of the Holocene 10 000 years ago, they were replaced in the central-western Great Lakes region by *Ulmus* populations, again more abundant than anywhere today. Late-glacial vegetation in much of western Canada and adjacent Alaska also lacked modern analogs (Anderson et al. 1989, Williams et al. 2004).

The past 10 000 years – the Holocene – have seen continued movements of species and community reorganizations. However, aside from human activities, the magnitude of both environmental and biotic change has been generally lower than that of the glacial-to-interglacial transition. Tree species migrated over extensive areas of North America during the Holocene, expanding into new territory, abandoning old territory, shifting along edaphic and elevational gradients, and changing in abundance. These changes are recorded at innumerable local paleoecological sites distributed throughout the continent (Betancourt et al. 1990, Grimm et al. 2001, Shuman et al. 2004, Anderson et al. 2004, Grimm and Jacobson 2004), and are visible in mapped time-series of pollen abundances and macrofossil presence/absence (Webb 1988, Jackson et al. 1997, Gajewski et al. 2000, Williams et al. 2000, 2004). All of these ecological and biogeographic changes are related ultimately to climate change. However, the underlying climate change was not always gradual or monotonic. Recent intensive studies of late Holocene migrations, in both eastern and western North America, are revealing that decadal to millennial-scale climate variability have regulated species invasions, resulting in alternating periods of stasis and rapid expansion (Peñalba and Payette 1997, Jackson and Booth 2002, Shuman et al. 2002, Lyford et al. 2003, Booth et al. 2004).

Climate change and variability have emerged as the dominant drivers of changes in the distribution and abundance of tree species of the late Quaternary. Climate is multivariate, and important climate variables (e.g., seasonal temperature and precipitation) can change independently through time, resulting in continual recombinations of climate variables and reconfigurations of climate gradients across the continental landscape (Jackson and Overpeck 2000). Because different species respond in different ways to the array of climate variables, species have shifted their geographic ranges independently, often migrating in different directions and at different rates. Development of independent paleoclimate records are allowing delineation of the climate controls on these movements (e.g., Shuman et al. 2004).

Evidence for pre-Columbian human impacts on forest composition and geography is sparse. Impacts appear to have been local or occasionally regional in scope. Undoubtedly, the sophisticated agricultural civilizations of the mid-continent (Mississippian cultures) and the desert Southwest (Pueblo cultures) cleared extensive land areas, but evidence is largely lacking, in part owing to a dearth of suitable paleoecological sites that might have recorded such impacts. The Anasazi culture certainly had substantial effects, which are well-recorded at Chaco Canyon. There, local populations of piñon (*Pinus edulis*) were exterminated (Betancourt and Van Devender 1981), and *Abies* and *Picea* logs were transported some 75–100 km from adjacent mountains for use as timbers in pueblo construction (English et al. 2001). The best evidence for human impacts on vegetation in eastern North America come from pollen work at Crawford Lake, Ontario, where an Iroquoian village was established in the 14th Century and a few hectares of forest were cleared for cultivation for a few decades (McAndrews and Boyko-Diakonow 1989). However, such small-scale activities are difficult to detect in pollen records (Jackson 1997). Human impacts have accelerated in the past 300 years, and such events as agricultural land-clearance and the pathogen-induced declines of *Castanea dentata* and *Ulmus americana* are well-documented in pollen records.

Human-induced changes in tree species abundance and distribution will continue indefinitely, owing to continued land-use practices and to introduction of exotic invasive species and pathogens. In the next few decades, however, ecological impacts of human-induced climate change will become increasingly apparent, potentially overshadowing and certainly interacting with the effects of land-use, invasives, and diseases. The paleoecological record of the late Quaternary can provide important perspectives on these changes (National Research Council 2005). Populations, communities, and ecosystems have been exposed to both rapid changes (National Research Council 2002) and large-magnitude changes (Bartlein et al. 1998) in the past, but the combination of rapid and large-magnitude changes has been uncommon, particularly at broad spatial scales (Jackson and Overpeck 2000). One of the most potentially disruptive climate-change impacts, which has been inadequately studied, is rapid reconfiguration of climate gradients (Jackson and Williams 2004). Climate change will consist not only of changes in individual variables (e.g., annual or seasonal temperature and precipitation), but of fundamental recombinations of these variables. Climate realizations of the near-future may be as different from those of the 20th Century as those of the late-glacial period (see Fig. 10 in Jackson and Williams 2004), when forest composition over much of North America had no modern analogs (Williams et al. 2001). This presents a major challenge to our ability to predict biotic responses to climate changes of the coming decades and centuries. Paleoecological studies of ecological responses to past climatic changes may help identify the critical climatic controls of the distribution and abundance of individual species. Integrating paleoecological studies with the ecology and genetics of modern populations will provide benefits not only for science but society as we pass through a period of profound environmental change.

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GENETIC RESPONSES TO CLIMATE AND CLIMATE CHANGE IN CONIFERS OF THE TEMPERATE AND BOREAL FORESTS[1]

Gerald E. Rehfeldt[2], Nadezda M. Tchebakova[3] and Elena I. Parfenova[3]

[2] U.S. Department of Agriculture
Forest Service
Rocky Mountain Research Station
1221 S. Main
Moscow, ID
83843
E-mail: grehfeldt@fs.fed.us

[3] Sukachev Institute of Forest
Siberian Branch
Russian Academy of Sciences
Akademgorodok
Krasnoyarsk
660036
Russia

ABSTRACT

The availability of climate data and sophisticated software for high speed computers has made it possible to assess the climatic factors underlying geographic patterns of genetic variation in forest trees. Analyses have demonstrated anew that the clines in genetic variation that typify most tree species indeed have been molded by and are perpetuated by the climate. Yet, distribution of genotypes across the landscape is controlled by an interaction between adaptation to climate and competition, the same factors governing the distribution of species. Genotypes occur where they can be competitively exclusive, but most, nonetheless, have been competitively excluded from their climatic optima. Most populations, therefore, exist in climates that are colder than the optimal for their growth, productivity, and survival, with the discrepancy between the inhabited and the optimal climate increasing with the severity of the climate.

Responses to climate change can be viewed 1) as short-term plastic responses that accrue in endemic populations as physiological systems adjust to change, and 2) as long-term evolutionary processes that realign genetic variability with environmental diversity. Immediate short-term responses to a warming climate are dependent on the discrepancy between the inhabited and optimal climates. Responses, therefore, should be highly negative in populations occupying the mildest climates but positive in the coldest. As a result, expected short-term responses in *Pinus sylvestris* and *Larix sibirica* of Siberia are strongly positive while those of *Picea engelmannii* of western United States are highly negative. Accommodating global warming in the long term will require a redistribution of genotypes within species to match genotypes with the climate for which they are best suited. The process undoubtedly will be driven by migration, gene flow, and selection. Natural processes, however, tend to occur at rates too slow to match the projected speed of global warming. Without the intervention of mankind in the evolutionary processes, accommodating the warming expected by 2100 may require many centuries.

INTRODUCTION

In the preface to his text on climate and plant distributions, Woodward (1987) notes that one of the central theses in plant ecology is that climate is the primary factor controlling the distribution of vegetation but that the relationship, nonetheless, is poorly understood. Forest trees provide a fine example. For at least three centuries, botanists have been aware that widespread tree species are composed of populations that are physiologically attuned to different climates (Morgenstern 1996). Forest managers, therefore, long have known that successful reforestation requires planting stock that is physiologically suited to the climate of the planting

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site. In an effort to provide guidelines to managers, common garden studies have been established for most of the world's widespread trees. By their very nature, common garden studies are controlled experiments in climate change; populations have been transferred from the climate of their provenance to that of the garden (Mátyás 1994).

Studies with forest trees have demonstrated, first with the results of Langlet (1936) and then subsequently in numerous works, that genetic variability among populations tends to be distributed along clines that can be described with models driven by geographic variables (Morgenstern 1996). These studies, therefore, have collectively demonstrated the principles of ecological genetics that are well known for plants in general (Brown and Gibson 1983): widespread species tend to be composed of populations that differ in innate growth potential and cold hardiness, the two of which are negatively correlated. Although involving a suite of traits, adaptation of populations can be viewed simplistically as a balance between selection for growth potential where the climate is mild and selection for cold tolerance where the climate is severe (Rehfeldt 1988, 1989, 1994).

While geographic patterns of genetic variation are invariably interpreted in terms of climate, attempts to substitute climate variables for their geographic surrogates have been hampered by an inability to estimate climate variables at the remote locations where forests typically grow. Recently, however, innovative steps have been taken by Booth (1990) and his colleagues (Booth et al. 1989a, 1989b) who used climate surfaces to guide the intra-specific transfer of seeds for reforestation and to pinpoint foreign climates suitable for the introduction of Australian species. Climate models of this type offer the potential of describing genetic variation with climatic predictors such that the impact of climate, fluctuating climates, and climate change on the distribution, growth, and productivity of forest trees can be assessed.

Advances are taking place on two fronts. One deals with a quantitative description of the clines that occur in response to climate and the second involves ecologic principles governing adaptation of populations. Both require site-specific estimates of climate variables.

CLIMATE ESTIMATES FOR REMOTE LOCATIONS

The historic approach to estimating climate for remote locations used data from the closest weather station to characterize provenance climate. This approach understandably has met with limited success except when applied in regions either covered by a fine network of weather stations or with little topographic relief. Of the exceptions, however, (Langlet 1959**)** demonstrated an R^2 of 0.89 between the 17-year height of 47 Swedish populations of *Pinus sylvestris* and the average Julian date when the mean temperature first reached 6°C.

Another approach (Rehfeldt 1995, Rehfeldt et al. 1999) uses polynomial regression models driven by geographic variables (latitude, longitude, elevation, and various transformations thereof) to interpolate the climate between weather stations. One such model, based on data from about 500 weather stations in western Canada, was found to be well suited to modeling temperature variables (e.g., R^2 for mean annual temperature of 0.90) but became more problematic for precipitation (e.g., R^2 for mean annual precipitation of 0.61) (Rehfeldt et al. 1999). The functions, therefore, seemed reasonably well suited for analyses confined to small geographic regions but were notably incapable of describing abrupt transitions in climate that occur, for example, across rain shadows. The approach, therefore, was less well suited to large regions of diverse topography where extrapolation would be necessary.

A third and more sophisticated approach uses the thin plate splines of Hutchinson (1991, 2000) to fit climate variables to geographic surfaces. The surfaces can be queried to obtain predictions of climate at point locations. While the suitability of the approach has been repeatedly demonstrated (e.g., Hutchinson and Bischof 1983, Booth et al. 1989a, 1989b, Booth 1990), applications aimed toward understanding the relationship between climate and vegetation (Rehfeldt 1994, McKenney et al. 2001, Tchebakova et al. 2003) are only recent. An example of a spline climate surface for degree-days > 5°C of western United States and southwestern Canada is presented in Fig. 1. To generate this figure, tri-variate splines using latitude, longitude, and elevation were fit to climate data from 3 006 weather stations. Predictions were made for each cell of a DEM (digital elevation model) matrix gridded at 0.0083 degrees (GLOBE Task Team 1999). The map is based on estimates for more than six million pixels; in the figure, degree-days are presented for ten classes that range from essentially zero (white) in the highest mountains to 6 700 in the deserts to the southwest (black).

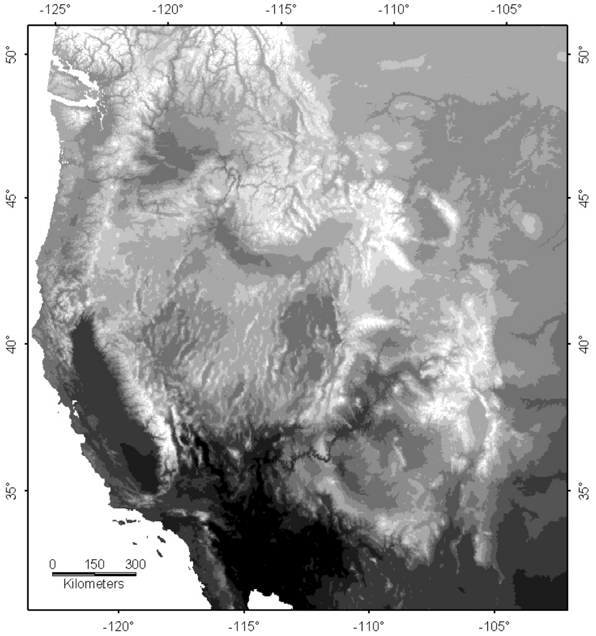

Figure 1. Map of degree-days > 5°C using shades of grey to code 10 classes ranging from zero (white) to 6700 (black) (from Rehfeldt, unpublished).

GEOGRAPHIC VERSUS CLIMATIC DESCRIPTORS OF CLINES

Recent analyses have allowed clines described with geographic variables to be compared with those driven by climate variables. One example involves the 2-year height of *P. sylvestris* populations tested in a common garden in Moscow, Idaho, USA. In Fig. 2, the relationship between genetic variation and the best fitting geographic variable, latitude, can be compared with that for the best fitting climate variable, degree-days > 5°C.The figure shows that clines described by either independent variable are steep, but that the relationship (R^2 = 0.80) between genetic variation and degree-days > 5°C of the provenance is the strongest. In this example, latitude makes a suitable surrogate for degree-days because summer temperatures are strongly correlated with latitude.

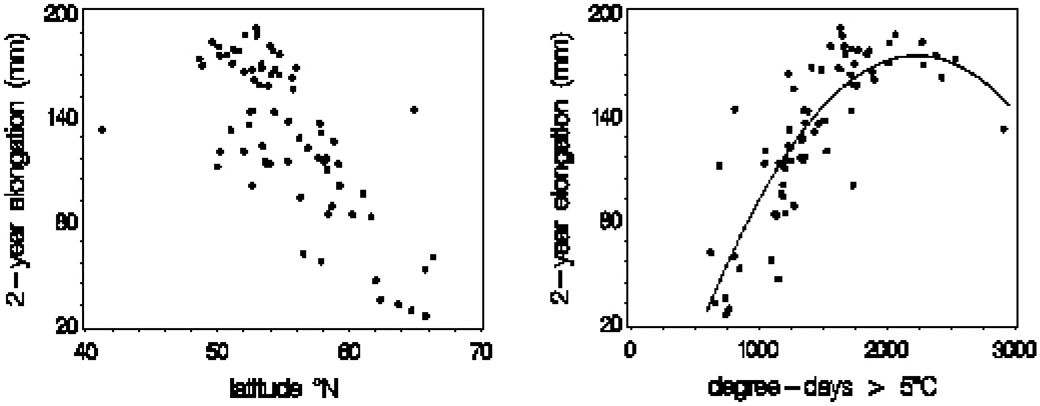

Figure 2. Mean 2-year shoot elongation of *Pinus sylvestris* populations measured in greenhouse-shadehouse studies plotted against the provenance latitude (left) and provenance degree-days > 5°C (right).

Another example (Fig. 3) deals with genetic variation among 215 populations of *Picea engelmannii* from western United States (Rehfeldt 1994). In this case, the best fitting geographic surrogate, provenance elevation, is a weak ($R^2 = 0.07$) but nonetheless statistically significant ($p < 0.05$) predictor of variation among populations. By contrast, the best fitting climate variable, degree-days < 0°C, is closely related ($R^2 = 0.62$) to genetic variation. In this example, geographic variables were poor surrogates for climate and led, therefore, to a fallacious view of the species' genetic structure.

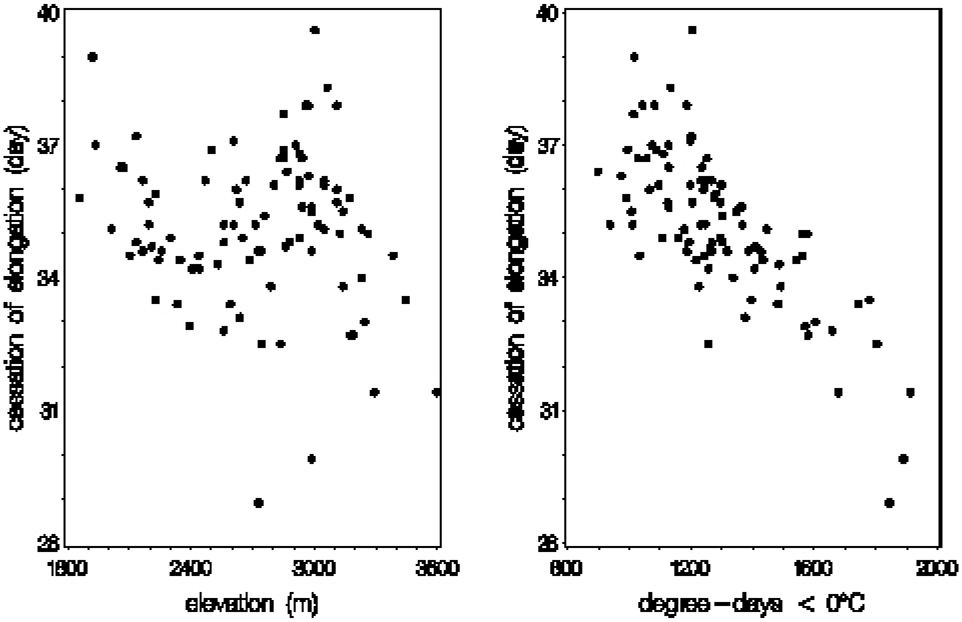

Figure 3. Mean date of the cessation of shoot elongation of 2-year *Picea engelmannii* populations measured in greenhouse-shadehouse studies plotted against the provenance elevation (left) (Rehfeldt 1994) and provenance degree-days < 0°C (right) (Rehfeldt 2004).

These results along with those for *Larix occidentalis* of western North America (Rehfeldt 1995) demonstrate that converting clines with geographic drivers to those with climatic drivers is not only feasible but also may lead to alternative interpretations. Among the climate variables tested to date, those closely linked to genetic differentiation of populations include summer temperatures (degree-days > 5°C and mean maximum temperatures of July), winter temperatures (degree-days < 0°C and mean minimum temperatures of January), and an annual moisture index (ratio of degree-days > 5°C to mean annual precipitation).

Many of the results presented herein involve measurements of juvenile trees made in common gardens far removed from native habitats. The results, nonetheless, are used to assess the adaptedness of natural populations growing in native environments throughout their long lives. To be sure, foresters tend to greet such extrapolations with considerable skepticism. Yet, 2-year shoot elongation measured in a greenhouse in Moscow, Idaho, USA accounts for 80% of the variance among *P. sylvestris* populations for 13-year heights attained in the most optimal of 46 test sites scattered across the former Soviet Union (Fig. 4). These results along with numerous reports of significant juvenile-mature correlations in forest trees support the veracity of short term testing programs for studying ecological genetics.

ECOLOGICAL INTERPRETATIONS OF CLINAL RESPONSES

From Langlet's (1936) demonstrations to the present, clines that parallel geographic gradients tend to be interpreted from the selectionist viewpoint: environmental selection alters gene frequencies to produce local populations physiologically attuned to their environment. Clines (e.g., Figs. 2 and 3), therefore, were thought to reflect optimization of adaptedness via natural selection. However, analyses of two long-term common garden studies of enormous scope have shown that this interpretation needs modification. The studies deal with *Pinus contorta* of western Canada and *P. sylvestris* of Russia. In each, numerous (> 100) populations were planted in designed experiments across a broad range of sites that numbered between 45 and 55. Because of the large number of test sites, data collected from these studies could be used to develop population-specific functions describing height and survival at age 20 for *P. contorta* and at 13 for *P. sylvestris* from climate variables (Rehfeldt et al. 1999, Rehfeldt et al. 2001, Rehfeldt et al. 2002).

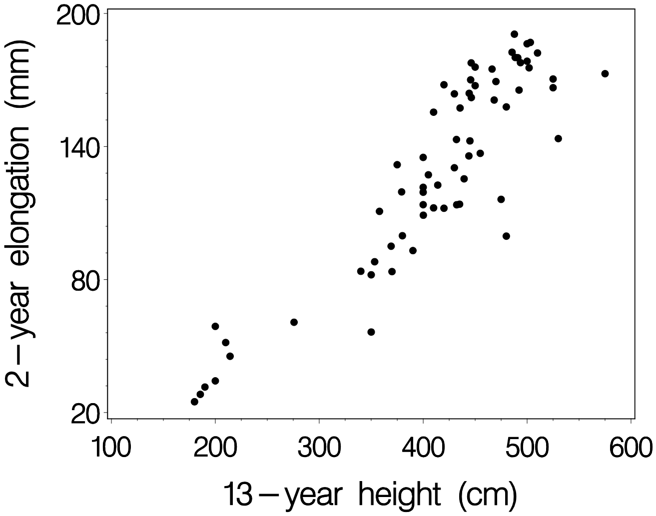

Figure 4. Mean 2-year shoot elongation of *Pinus sylvestris* populations measured in greenhouse-shadehouse studies conducted in Moscow, Idaho, USA plotted against 13-year height at the optimal of 46 test sites scattered across the Soviet Union.

Even though the two studies were planned and implemented independently, their results lead remarkably toward similar conclusions. These same conclusions, moreover, were reached earlier with a disparate series of analyses of populations of *Pinus banksiana* from eastern Canada (Mátyás and Yeatman 1992). In Fig. 5, for example, modeled responses of two populations of each species are compared in relation to the general temperature regime of the provenance. The pair of populations are from either warm or cold provenances. The mean annual temperature at McLeod Lake, for instance, averages 2.1°C while that at Atlin averages -1.5 °C; and degree-days > 5°C at Veshensk average 2 536 days while those at Surgut average 999 days. As one would expect, populations from the mildest climates exhibit a growth potential that is superior to those of populations from severe environments; and populations from cold climates achieve optimal growth in climates that are colder than those in which populations from warm climates attain their optimum.

These relationships are illustrated further in Fig. 6 for several *P. contorta* populations, the sample of which represents the range of responses among the 108 populations that were analyzed. The functions presented in these two figures thus demonstrate principles of ecological genetics that are well known for plants in general (e.g., Brown and Gibson 1983) and for forest trees in particular (e.g., Rehfeldt 1988, 1989, Morgenstern 1996): adaptation of populations appears as a balance between selection for growth potential in mild climates and selection for cold tolerance in severe climates.

If the responses of Figs. 5 and 6, however, develop from a selectionist strategy whereby adaptatedness is optimized, populations should occupy climates that approach their climatic optima. They do not. The Atlin and McLeod Lake populations of Fig. 5 occur in climates that are about 3°C colder than their optima, while the Veshensk and Surgut populations occupy climates that are cooler by about 400 degree-days > 5°C. An examination of all populations in both studies led to the unambiguous conclusion that most populations of these species occupy climates suboptimal for their growth and survival. In addition, disparity between the optimal and inhabited climate unquestionably increases as the climate becomes more severe (Fig. 7).

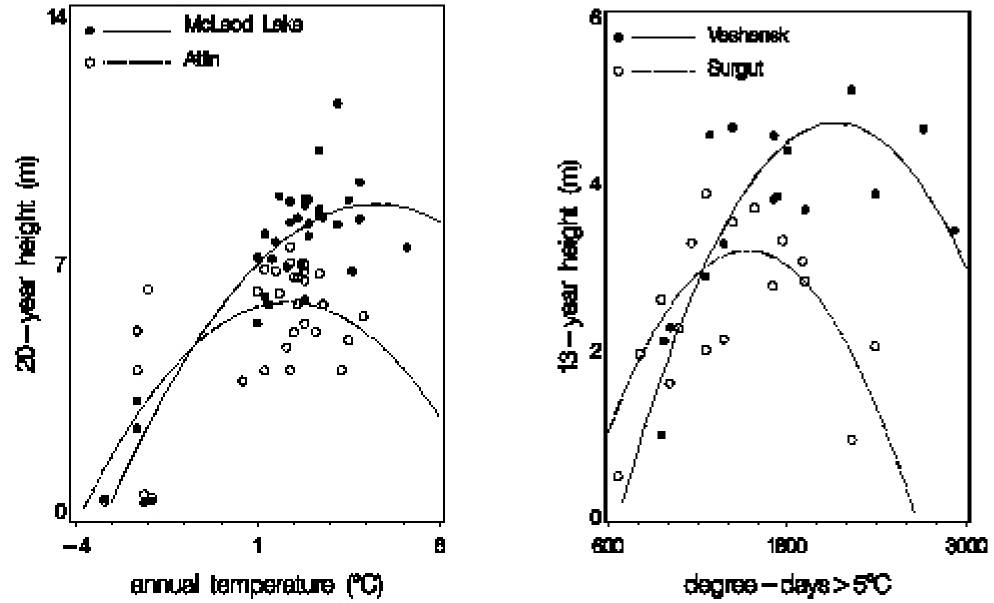

Figure 5. Population-specific response functions plotted in relation to the observed data for predicting the height of two provenances from the climate of the planting site for *Pinus contorta* (left) (Rehfeldt 1995) and *Pinus sylvestris* (right) (Tchebakova et al. 2003).

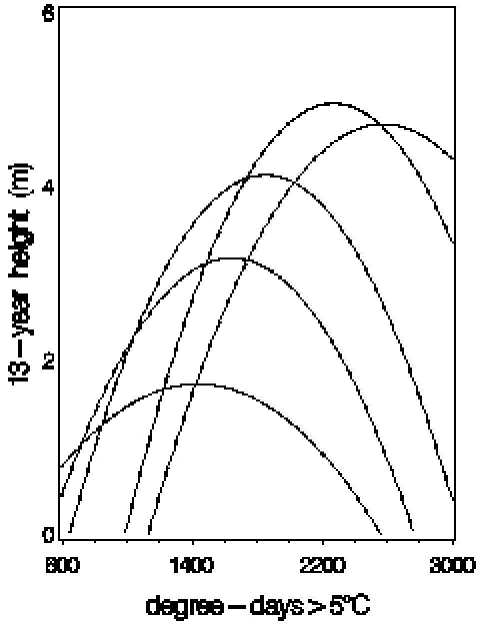

Figure 6. Response functions using degree-days > 5°C as a predictor of height for five populations of *Pinus sylvestris* that represent a variety of responses (Rehfeldt et al. 2001).

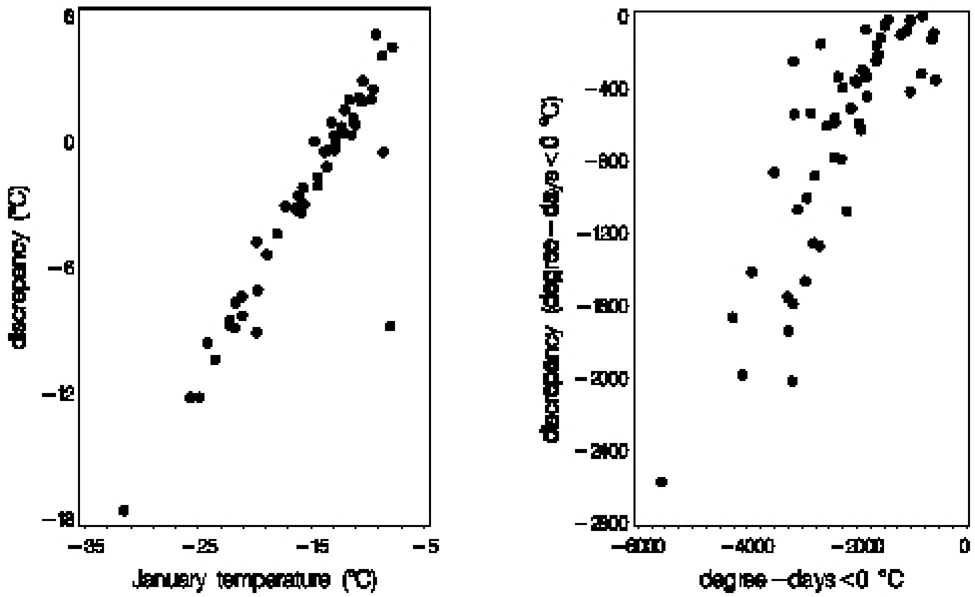

Figure 7. Discrepancy between the inhabited climate and the optimal climate plotted by provenance climate for *Pinus contorta* populations (left) (Rehfeldt 1995) and *Pinus sylvestris* populations (right) (Rehfeldt et al. 2001). Discrepancies are based on response functions that predict height from climate. Negative values occur when the inhabited climate is colder than the optimum.

Although evolutionary processes undoubtedly have produced the climatic clines that characterize the genetic systems of *P. contorta*, *P. sylvestris*, and *P. banksiana*, the results nonetheless lead toward the unambiguous conclusion that natural populations exist in climates that are suboptimal to their growth and survival (Arthur 1987, Mátyás and Yeatman 1992, Rehfeldt 1995, Rehfeldt et al. 2002). The only reasonable explanation for these seemingly antithetical results is for the distribution of genotypes to be determined as much or more by competition than by adaptation to the physical environment. Put simply, as stands of forest trees mature, self-thinning and density-dependent selection regulate densities to levels commensurate with the resources at the site. For these three species, over-reproduction is common and density-dependent selection can be intense. As a result, the distribution of genotypes within species is driven by adaptation to the physical environment (Figs. 2 and 3) and by density-dependent selection (Figs. 5 and 6).

According to this view, therefore, if seeds from Veshensk and Surgut were dispersed across a site with 1 500 degree-days > 5°C, seedlings from both undoubtedly could grow superbly (Fig. 5 right). Yet, genotypes from Veshensk would be 75 cm taller after 13 years than those from Surgut. In time, therefore, density-dependent selection would favor genotypes from Veshensk. Precisely the same argument can be made for *P. contorta* genotypes from Atlin and McLeod Lake (Fig. 5 left). Genotypes from Surgut and Atlin, therefore, would be competitively excluded from their climatic optima. Competitive exclusion would be initiated by the fastest growing genotypes which, by virtue of their high growth potential, would exclude genotypes of other populations from their optima (Figs. 5 and 6). Because genotypes occur where they are competitively exclusive, those populations with the highest growth potential initiate a cascading sequence of effects which ultimately relegate most populations to suboptimal climates (Fig. 6). While some populations are relegated to climates warmer than their optima (see Rehfeldt et al. 2003), most occur in climates that are colder than their optima.

It seems, therefore, that adaptation and competition, the processes controlling the distribution of species (Arthur 1987), also control the distribution of genotypes within species. To be sure, sexual reproduction in the face of the high levels of gene flow that typify many forest tree species disassembles in each generation those genotypes best suited for a given site. Consequently, the balance between high growth potential (competitive exclusiveness) and adaptation to the climate must be re-established each generation. Asymmetric gene flow along a climatic gradient from the center of distribution toward the periphery (Garcia-Ramos and Kirkpatrick 1997, Kirkpatrick and Barton 1997) couples with strong density-dependent selection to prevent populations from inhabiting their ecological optima (Rehfeldt 1995). Toward the periphery of the distribution, therefore, where the climate is most inhospitable, the discrepancy between the optimal and inhabited climates becomes the largest.

GENETIC DIFFERENTIATION ALONG CLIMATIC GRADIENTS

Genetic variation across geographic regions develops in response to multiple climatic gradients. Variation among populations, therefore, is continuous. However, as an aid to visualizing complex multivariate patterns across forested ecosystems and to provide tools to forest managers, continuous variation is frequently classified into climatypes, the climatic ecotypes of Turesson (1925). One means of classifying continuous variation is to equate the breadth of a climatype to the confidence interval surrounding a population mean (Rehfeldt 1988, 1989, 1994). With this approach, therefore, there is a reasonable probability that genotypes from disparate climatypes are genetically different.

This technique was used for mapping climatypes of *P. sylvestris* and *Larix sibirica* (see Fig. 4, left, Tchebakova et al., this proceedings) for the Sayan Mountains of Krasnoyarsk Krai in south-central Siberia (Tchebakova 2003). To produce this map, the climate transfer functions of Rehfeldt et al. (2002) were used to subdivide climate distributions into climatypes. These functions suggested that genetically different populations of *L. sibirica* tended to be separated by at least 650 degree-days > 5°C, 2 200 degree-days < 0°C, or 1.0 units of an annual moisture index (ratio of degree-days > 5°C to mean annual precipitation). Subdividing the climatic distribution of the entire species according to these limits produced three classes for degree-days > 5°C, two for degree-days < 0°C, and eight for the moisture index. In total, therefore, there were 48 possible climatypes for the species, 24 of which were projected for the Sayan Mountains. These 24 occupy 67% (318 586 km^2) of the region, leaving 32% beyond the climatic limits of the species for at least one of the three climate variables. Of the 24 climatypes, most are minor; five, in fact, account for 90% of the species' distribution. Of the five, two are mammoth, occupying about 55 000 km^2.

Note, however, that the map in Fig. 4 of Tchebakova et al. (this proceedings) reflects the potential distribution of climatypes. Although *L. sibirica* can flourish within these climatic zones, about 50% of this region is dominated by dark-needled conifers (e.g., *Pinus sibirica*) which tend to competitively exclude *L. sibirica*. The realized distribution, therefore, is much less than the potential. This discrepancy between potential and realized climatic distributions was addressed for *P. engelmannii* (Rehfeldt 2004). The approach involved mapping limits of distribution according to: 1) the species climatic envelope (Box et al. 1999), defined according to the absolute limits among 315 provenances for 17 climate variables, and 2) the limits determined by a canonical discriminant analysis using the same 17 climate variables from point-locations to separate 9 species. A visual comparison of two-dimensional range maps of Little (1971) with maps developed from these two approaches showed that both overestimated actual distributions but that together, the two methods provided a realistic estimate. A species' distribution prepared in this manner thus seems to provide a reasonable basis for portraying intraspecific variation (Fig. 8). For *P. engelmannii* of Fig. 8, climatypes are based on genetic variation in six variables described by clines driven by the winter temperature regime and summer maximum temperatures.

RESPONSES TO CLIMATE CHANGE

The response functions of Figs. 5 and 6 imply that a directional shift in climate will alter the productivity and adaptedness of individual populations and, therefore, of species as a whole. Because sessile forest trees are unable to track the climate in which they can be competitively exclusive (see Rehfeldt 1995, Rehfeldt et al. 2002), there will be both short- and long-term impacts of a changing climate in general and of global warming in particular. Short-term effects arise as plastic physiological systems respond to the change, while long-term effects encompass the redistribution of genotypes required to realign climatypes within the novel distribution of climates (Rehfeldt et al. 2001). Both effects are complex.

Short-term plastic effects depend on the relationship between the inhabited climate and the optimal climate (Rehfeldt et al. 2001). A warming climate will have a positive effect for populations occupying climates cooler than their optima, but a negative effect on those inhabiting their optima. The relationships in Fig. 6 suggest, therefore, a negative impact in the southern and low altitudinal portions of a species' distribution and a positive effect in the north and high altitudinal portions. Continual warming will push temperatures beyond the climatic optima of an increasing number of populations, with negative impacts accumulating sequentially across the landscape from warm provenances to cool. Extreme warming eventually will push temperatures beyond the ecological tolerances of the population and result, therefore, in extirpation.

Figures 5 and 6 suggest further that thresholds will be reached during warming when genotypes from distant populations become better suited to the new climate than endemic genotypes. At these thresholds, natural selection and migration will begin the long-term redistribution of genotypes required to balance adaptation to the physical environment with competitive exclusiveness (Rehfeldt 1995, Rehfeldt et al. 2002).

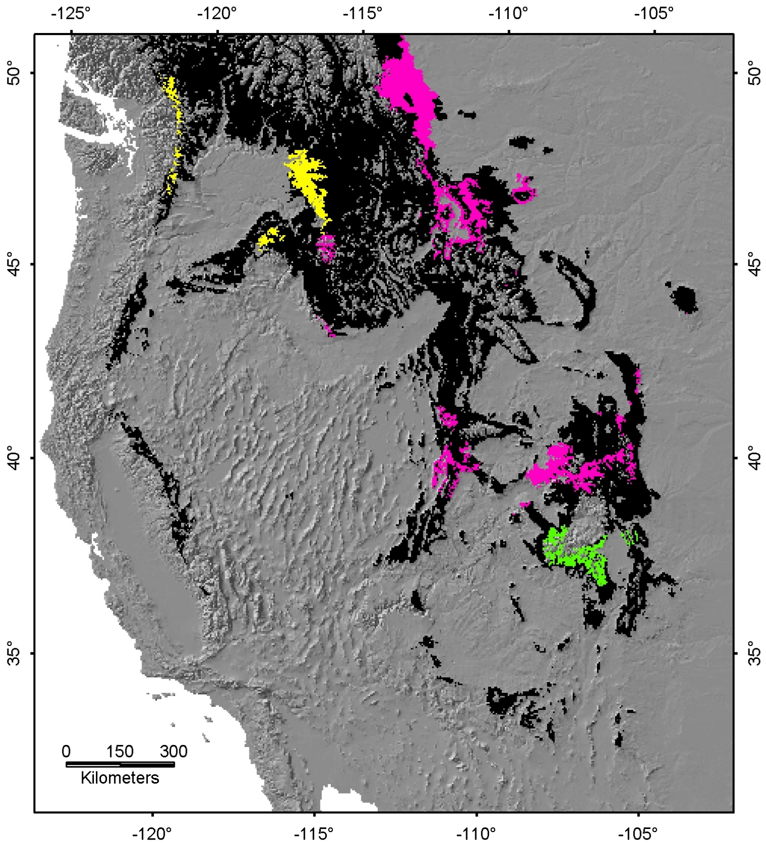

Figure 8. Three climatypes of *Picea engelmannii* superimposed on the species' climatic distribution in western United States and southwestern Canada (Rehfeldt 2004).

The extent of these long-term effects is illustrated in Fig. 3 of Tchebakova et al. (this proceedings) for *P. sylvestris* climatypes of the Sayan Mountains. In the contemporary climate of Siberia, these climatypes occupy climates much colder than their optima (Rehfeldt et al. 2003). It is not surprising, therefore, that Tchebakova et al. (2003) show that the climate of 2090 in the Sayan Mountains should be more amenable for *P. sylvestris* than at present. Indeed, the areal distribution of climates potentially suitable for the pine should increase from 71 to 91%. This increase is expected to accompany a warming of about 6 to 8°C according to the greenhouse gas scenario (1% increase per year in greenhouse gases) of the Hadley Centre (Gordon et al. 2000). As the acreage suitable for the pine increases, the number of climatypes suitable for the region should increase from 25 to 35. Of these, most are small: two, for example, account for about 50% of the area suitable for the species, while 12 account for less than 1%; in 2090, three should account for about 42%, while 17 would account for less than 1%. By 2090, however, the climate suitable for one of the two largest contemporary climatypes should disappear, while that suited for the second should become reduced by 38%. Of the three largest climatypes of the future, two are absent in the region today, while the third occupies only 3.3%. Twelve climatypes that occur in the region today are not expected to be present in the future and 23 expected in the future do not occur there today. Only 13 climatypes should be present throughout the century, but all are expected to be displaced altitudinally. This analysis shows clearly, as did similar analyses for *L. sibirica*, that the adjustment to global warming in species of the Sayan Mountains will require a complete redistribution of genotypes.

These long-term effects are illustrated further in Fig. 9 for climatypes of *P. sylvestris* currently inhabiting the Minusinsk Valley. As the climate warms, the climates sutiable for this climatype are displaced southward toward higher altitudes. While the contemporary altitudinal distribution of this climatype is from about 800 to 1 000 m, the altitudinal range of future climates for which this climatype is suited should be from 1 800 to 2 200 m.

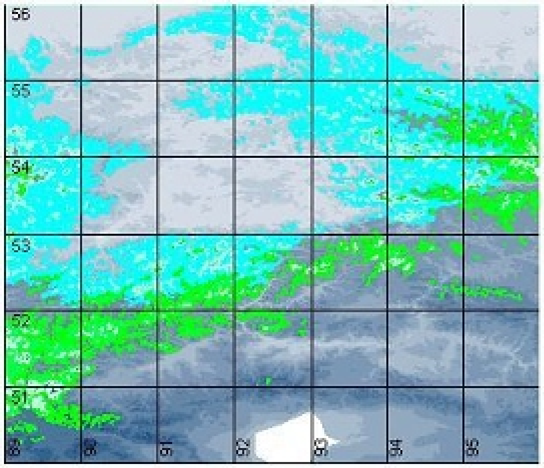

Figure 9. Climatype of the Minusinsk Valley in Siberia for the contemporary climate (blue) and the 2090 distribution of its climate (green) superimposed on altitude (white, < 200 m; black, 3 500–4 000 m) (Tchebakova et al. 2003).

The impact of global warming is expected to be much different for *P. engelmannii* of western North America than for species of the Sayan Mountains of Siberia. *Picea engelmannii* is a species of the subalpine forests that reaches the southern limits of its montane distribution in western USA. Many populations, therefore, occupy climates that approach their ecological optimum. Consequently, global warming of 2 to 3°C projected for this region (Gordon et al. 2000) should have a devastating impact on *P. engelmannii* on both the short- and long-term (Rehfeldt 2004). By 2090, the species' distribution is expected to shrink by 89% as distributions are forced upwards (Fig. 10) by as much as 1 000 m; climates suitable for the climatypes of Fig. 8 are expected to be lost by 2060; and the future number of climatypes that occur in the region should be approximately one-half of those that occur today and much reduced in size (Fig. 10).

These analyses indicate that the impact of global warming will be large and quite complex. While extirpation and immigration are expected at the margins of distributions (see Thompson et al. 2002, Davis and Shaw 2001) warn that the impact of a changing climate encompasses much more than shifts in the distribution of species. Indeed, intra-specific adjustments should produce a wholesale redistribution of genotypes across the landscape to realign climatypes with the distribution of new climates and thereby to maintain growth, productivity and survival (Rehfeldt 1995, Rehfeldt et al. 2002).

Nonetheless, there seems little doubt that natural processes are capable of accommodating global warming; adjustments during the Pleistocene glacial epic, for instance, accommodated temperature shifts of nearly 7°C in the western United States (Betancourt 1990). Migration and selection undoubtedly are the processes that will control the evolutionary adjustments (see Rehfeldt 1995). While seed-dispersed migration is the only feasible means by which genotypes can immigrate, natural selection coupled with gene flow undoubtedly will be the primarily processes acting to restore adaptedness. Yet, rates of migration tend to be slow (Davis 1989), and although responses to selection can be rapid, genetic gains per generation are limited by additive genetic variances, heretabilities, and selection differentials. Calculations for *P. contorta* (Rehfeldt 1995, Rehfeldt et al. 2001) and *P. sylvestris* (Rehfeldt et al. 2002) suggest that genetic responses to global warming may require as many as 10 generations. Analyses of migration rates (Davis 1989) coupleed with these estimates of genetic response suggest that in some regions, natural systems may require as many as 10 centuries to adjust to global warming.

Consequently, to biologists, the most daunting aspect of global warming is the projected speed rather than the absolute amount. Quite obviously, restoring and maintaining forest growth and productivity in the face of global warming will require the participation of mankind (Rehfeldt 1995, Rehfeldt et al. 2002, Rice and Emery 2003). Man's role will be to assist the natural processes using guidelines such as Fig. 10 as a blueprint.

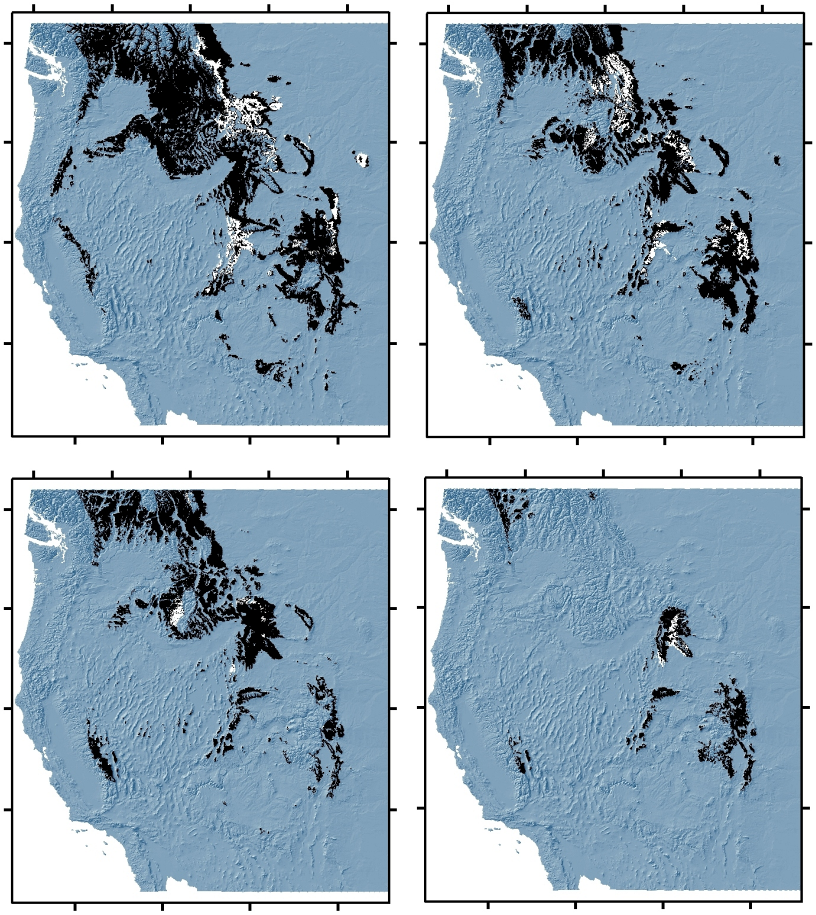

Figure 10. Distribution of a *Picea engelmannii* climatype superimposed on the climatic distribution of the species for the contemporary climate (upper left) and the distribution of future climates suitable for the climatypes in the decades beginning in 2030 (upper right, 2060 (lower left), and 2090 (lower right) (Turesson 1925). Future climates are based on a global warming scenario of the Hadley Centre of 1% (Gordon et al. 2000) increase in greenhouse gasses per year.

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REDISTRIBUTION OF VEGETATION ZONES AND POPULATIONS OF *Larix sibirica* Ledeb. AND *Pinus sylvestris* L. IN CENTRAL SIBERIA IN A WARMING CLIMATE[1]

Nadezda M. Tchebakova[2], Gerald E. Rehfeldt[3] and Elena I. Parfenova[2]

[2] Sukachev Institute of Forest
Siberian Branch
Russian Academy of Sciences
Akademgorodok
Krasnoyarsk
660036
Russia
E-mail: ncheby@forest.akadem.ru

[3] USDA Forest Service
Rocky Mountain Research Station
1221 S. Main
Moscow, ID
83843

INTRODUCTION

Evidence for global warming over the past 200 years is overwhelming (Hulme et al. 1999), 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). Recent GCM projections of the Hadley Centre (Gordon et al. 2000) for Siberia show an increase in temperature of 4 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 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 plants of the boreal forests at all hierarchial levels: from forest zones (Monserud et al. 1993), to ecosystems (Guisan et al. 1996), 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, first, at the highest level of organization and second, at the lowest. The first considers the effects of global warming as zonal vegetation shifts across the plains and plateaus of central Siberia and the second considers intraspecific effects within the mountains of southern Siberia. For the second objective, we invoke Turesson's concept of climatypes, the climatic ecotypes that comprise species, and illustrate intraspecific effects for *Pinus sylvestris* and *Larix sibirica*.

METHODS

Study Area

Our studies of the effects of global warming on vegetation zones deal with the plains and tablelands of central Siberia, roughly 90–120°E longitude and 50–75°N latitude. Studies of the effects of global warming on climatypes deal with the southern mountains, the Sayan Mountains, bounded by 89–96°E longitude and 50–56°N latitude. Our base map for this region was a 1 km grid (GLOBE 1999) which contained 5 600 000 pixels for the plains and tablelands and 420 000 pixels for the southern mountains.

Mapping Current Climates

January and July temperatures, growing degree-days, base 5°C (GDD_5); negative degree-days, base 0°C (NDD_0); and an annual moisture index (AMI), the ratio of GDD_5 to mean annual precipitation were proven to

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be useful in previous analyses addressing plant responses to climate (Tchebakova et al. 1994; Rehfeldt et al. 1999a, 2002). We assembled these data normalized for the period 1900–1964 from 200 weather stations across Siberia, 60 of which were in the Sayan Mountains (Reference books, 1967–1970). We used Hutchinson's (2000) thin plate splines to produce climatic surfaces of these variables on our base map using the 1 km grid. 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.

Mapping Future Climates

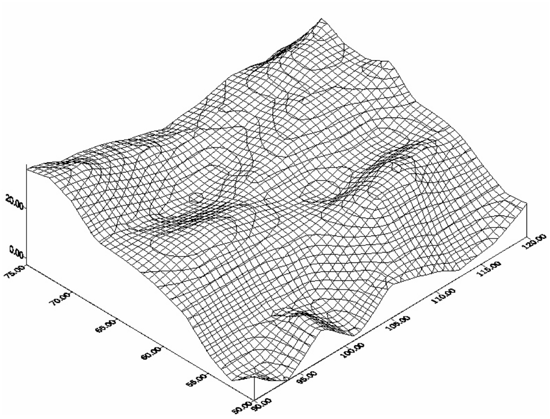
For predictions of global warming, we used the greenhouse gas scenario from the Hadley Centre, HadCM3GGa1 (Gordon et al. 2000) for the decade beginning in 2090. This scenario estimates winter temperature increases of 3 to 9°C, summer temperature increases of 4 to 6°C, and annual precipitation changes (in percentage) between -4 and +25% over the study area (Fig. 1). Future January and July temperatures and annual precipitation for each pixel were calculated from the change in monthly means for temperature and annual average for precipitation between the normalized period and the future decade (Fig. 1). Future values of GDD_5 and NDD_0 were calculated using the following linear regressions: GDD_5 was calculated from mean July temperature (R^2= 0.90), NDD_0 from January temperature (R^2=0.96). Future values of AMI were directly calculated dividing the future GDD_5 image by the future annual precipitation image.

Vegetation Zones

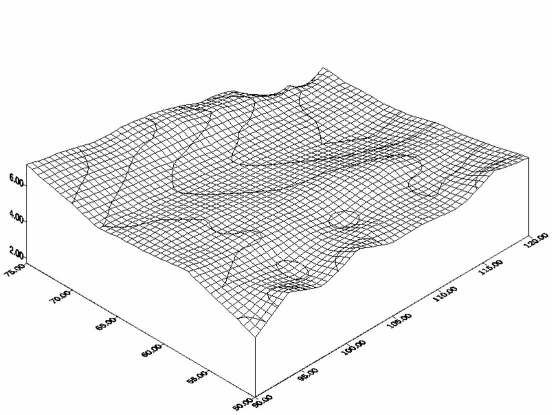
The Siberian bioclimatic model of Tchebakova et al. (1994) was modified to predict vegetation zones (types) from three bioclimatic parameters: GDD_5, NDD_0, and AMI. From the physiologic viewpoint, GDD_5 represents the plant's requirements for warmth; NDD_0 characterizes the plant's cold tolerance and AMI representing a ratio of GDD_5 to annual precipitation characterizes plants' drought tolerance (Rehfeldt et al. 2002).

Seven major vegetation types are recognized by geobotanists on the plains of central Siberia: 1) Tundra, 2) Forest-tundra and sparce forest, 3) Dark-needled (*Pinus sibirica, Picea obovata,* and *Abies sibirica*) taiga (northern, middle, southern) on elevated tablelands, 4) Light-needled (*L. sibirica* and *L. gmelinii,* and *P. sylvestris*) taiga (northern, middle, southern), 5) Birch (*Betula pendula* and *B. pubescens*) and light-needled (*L. sibirica* and *P. sylvestris*) subtaiga, 6) Birch (*B. pendula* and *B. pubescens*) and light-needled (*L. sibirica* and *P. sylvestris*) forest-steppe, and 7) Steppe (Shumilova 1964, Isachenko 1988).

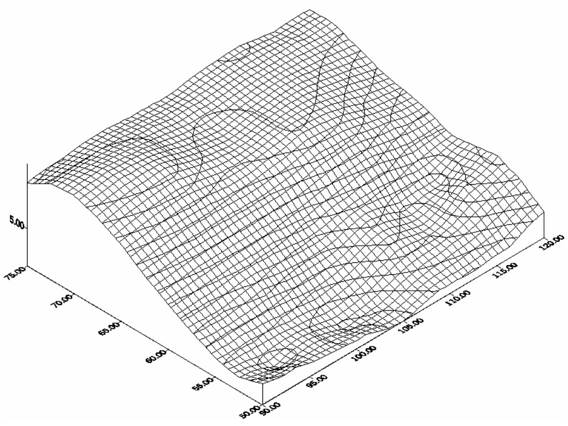
In our bioclimatic model, the annual moisture index separates vegetation into two large types**,** arboreal and non-arboreal (forests and steppes), and further subdivides the former type into dark-needled and light-needled forests. The cold parameter, NDD_0, also tends to separate dark-needled and light-needled tree species. In Siberia, permafrost prevents dark-needled species from spreading eastward across Asia (Shumilova 1964), although summers are sufficiently warm to allow them to survive as far east as Yakutia. The dark- and light-needled forest zones are further separated into latitudinal subzones (e.g., forest-tundra and sparse forests, northern, middle and southern taiga, forest-steppes) by GDD_5. Because southern taiga and subtaiga are not separated by GDD_5 these two types were combined into one zone. Although steppe, semidesert-desert, broadleaf forest, and temperate forest-steppe types are not found under current Siberian climate, these four classes are included into our model because of their potential importance under a warming climate. In total, therefore, our model considers 13 vegetation types, each of which can be defined climatically (Table 1).



a. Precipitation difference (%) between current and future climates in central Siberia



b. July temperature difference (°C) between current and future climates in central Siberia



c. January temperature difference (°C) between current and future climates in central Siberia

Figure 1. Climate differences by 2090 according to the Hadley climate change scenario (2001).

Table 1. Climatic limits for the modified Siberian model of Tchebakova et al. 1994

Vegetation type	GDD_5		AMI		NDDo	
	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	> -4500	None
Northern light-needled taiga	500	800	> 1.5	None	None	< -4500
Middle dark-needled taiga	800	1050	None	< 1.5	> -3500	None
Middle light-needled taiga	800	1050	> 1.5	None	None	< -3500
Southern dark-needled taiga and birch subtaiga	1050	1250	None	< 2.25	None	None
Southern light-needled taiga and subtaiga	1050	1250	> 2.25	None	None	None
Forest-steppe	1250	1650	None	< 3.25	None	None
Steppe	1250	1650	> 3.25	None	None	None
Semi desert/Desert	> 1650	None	None	None	None	None
Broadleaf forest	1250	1650	None	< 1.5	None	None
Temperate forest-steppe	> 1650	None	1.5	3.25	None	None

Climatypes

The distributions of *P. sylvestris* and *L. sibirica* were subdivided into climatypes using the results of Rehfeldt et al. (in press). 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 were 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 among populations 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 limits for a group of populations whose individuals are adapted to same or similar climate.

The analyses of Rehfeldt et al. (in press) 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, those driven by GDD_5, NDD_0, and AMI are used herein.

The transfer functions showed that height and survival decrease as transfer 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 (see Rehfeldt et al. 1999a) the climatic distance separating genetically different populations. For *P. sylvestris,* the limits were 240 GDD_5, ±575 NDD_0, and ±0.6 units of AMI and for *L. sibirica* ±325 GDD_5, ±1150 NDD_0, and ±0.5 units of AMI. Because these limits reflect the distance that seeds can be moved from their provenance before growth and survival begin declining, they also reflect the climatic breadth of a climatype.

Climatypes were defined by subdividing the climatic distribution of the species into classes bounded by these limits. Because the 313 pine provenances used in these tests ranged from 626 to 2 916 GDD_5, 5 classes, 480 degree-days in breadth were required to encompass the species distribution. Six classes were needed for both NDD_0 and AMI. All possible combinations of these classes produced an upper limit to the number of pine climatypes at 180. For the larch, there were 8 classes for moisture index, 3 for GDD_5, and 2 for NDD_0 which produced a maximum of 48 climatypes.

Climatypes defined in this manner must be considered as potential climatypes because many may not exist (e.g., high GDD_5 coupled with low NDD_0). Other combinations may exist, but the landscape may be occupied by species that have competitively excluded either *P. sylvestris* or *L. sibirica.* In the Sayan Mountains, for instance, the pine and larch rarely occur in climates inhabited by the dark-needled conifers even though they are capable of growing there (Ermolenko 2001). Nonetheless, for our analyses of intraspecific effects of a changing climate, we will assume that all climatypes exist.

Climatypes of both species were mapped for the Sayan Mountains using the climate maps of GDD_5,NDD_0,and AMI produced above. Mapping was done for the contemporary climate and for the climate expected by the Hadley GCM for the decade beginning in 2090.

RESULTS

Vegetation Zones

Estimates of the area occupied by zonal vegetation types in current and future climates of central Siberia are given in Table 2.

In the contemporary climate east of Yenisei River, light-needled taiga prevails, with *L. sibirica* and *L. gmelinii* being the domimant species. *Pinus sylvestris* can also dominate these forests in the warmer climates of the south or on sandy soils wherever they may occur. Dark-needled species appear in moist and warm climates, such as those along of the Yenisei Ridge at the mid-latitudes (60°E), in the Sayan Mountains in the south, and in the West Siberian Plain which is west of Yenisei River and south of 64°N. At the high latitudes of the Putoran Mountains (north of the the Arctic Circle), only larch taiga can withstand the cold climate and permafrost, although *P. obovata* and *Pinus sibirica* may be mixed with *Larix* in the large river valleys which tend to be warmer than the surrounding landscape. In the current climate, northern vegetation types like tundra, forest-tundra, and northern taiga cover about 60% of the landscape. About a quarter of the territory is under middle taiga, most of which is light-needled. Only 10% of the region is occupied by a southern taiga, in which dark and light taiga and subtaiga are equally represented. No grasslands are shown by our model north of 56°N (Fig. 2a).

Enormous changes in the vegetation cover of central Siberia are projected for a warmed climate (Table 2, Fig. 2b). Southern vegetation types such as southern taiga, subtaiga, and forest-steppe are expected to expand from about 10 to 70% coverage. This increase in coverage would be largely at the expense of northern and middle taiga each of which would then occupy less than 20%. Forest-tundra and sparse forests would nearly dissappear, while tundra and bare lands should disappear completely. These latter types would be replaced primarily by forest-tundra and dark-needled taiga in the Putaran Plateau and by dark-needled taiga in the Anabar Plateau. In a warmed climate, the forest-tundra which currently surrounds both of the northern plateaus should be replaced by light-needled taiga and even forest-steppe. Forest-steppe also is expected to reach the Putoran Plateau which is more than 1 000 km north of the contemporary distribution of this vegetation type.

Although forest-steppe, steppe, and semidesert do not exist in the current climate of central Siberia, these vegetation types are expected to occupy 50% of the study area in the climate of 2090. Large areas of steppe are projected for the central Yakutian Plain and the Tungus Plateau, while semi-desert should cover a significant area on the Angar Plain.

Table 2. Areas (10^4 km^2) of vegetation zones in Siberia in current and warmed climates

Vegetation zone	Current climate	Proportion (%)	Warmed climate	Proportion (%)
Bare land	3.6	1.3	-	-
Tundra	35.8	12.5	0.1	0.0
Forest-tundra and sparse taiga	54.3	19.0	1.6	0.6
Northern dark-needled taiga	22.5	7.9	17.8	6.2
Northern light-needled taiga	62.5	21.9	3.2	1.1
Middle dark-needled taiga	3.1	1.1	12.6	4.4
Middle light-needled taiga	75.3	26.4	17.0	6.0
Southern dark-needled taiga and birch subtaiga	13.1	4.6	9.2	3.2
Southern light-needled taiga and subtaiga	15.2	5.3	56.1	19.6
Forest-steppe	0.3	0.1	99.0	34.7
Steppe	-	-	22.6	7.9
Semi-desert/Desert	-	-	19.4	6.8
Temperate Broad-leaf forest	-	-	0.6	0.2
Temperate Forest-steppe	-	-	26.5	9.3
Total	285.7	100	285.7	100

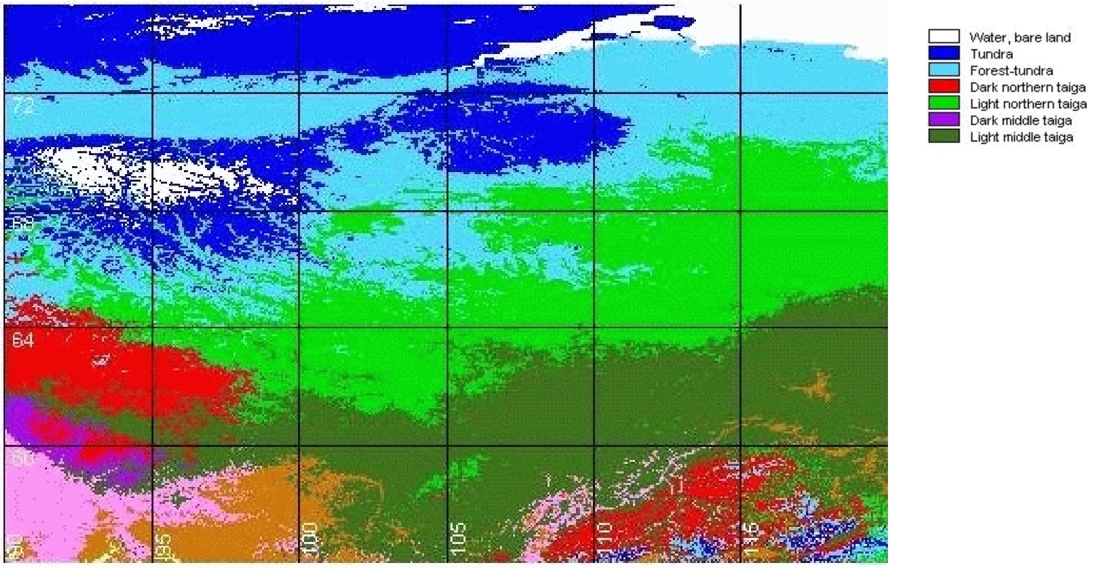


Figure 2a. Vegetation distribution in central Siberia in current climate.

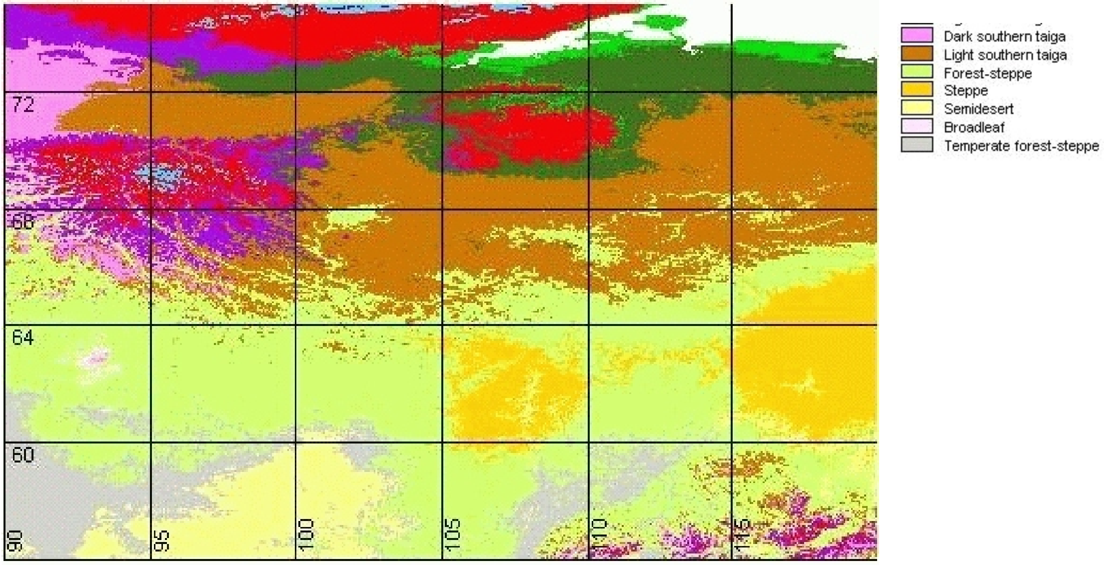


Figure 2b. Vegetation distribution in central Siberia by 2090 in a warmed climate.

Our model also shows that two additional vegetation types that currently do not exist in Siberia should occur there in a warmed climate. One is the temperate forest-steppe, found by analogy from our global vegetation model (Tchebakova et al. 1994). This type should cover a large area on the plains and tablelands where mainly dark-needled taiga occurs today (between latitudes 56°N and 60°N and longitudes 90°E and 100°E). The second novel type is the temperate broad-leaved forest which is expected to appear in the small valley of the Velmo River (about 93°E and 63°N). Because the climate change scenario we are using predicts a high degree of warming for Siberia, the concomitant invasion of broadleaved species into central Siberia seems reasonable. This is supported further by Khotinsky (1977) who reconstructed past 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.

Climatypes

Pinus sylvestris Of the 180 possible climatypes (Table 3), 26 were found for the contemporary climate in the Sayan Mountains (Fig. 3a and b). These 26 occupy 71% of the region, leaving 29% (class # 0) beyond the climatic limits of distribution of the pine for at least one of our three climate variables. Note, however, that these results do not imply that pine occurs across 71% of the region; in fact, cover types show that the pine in reality occupies only about 10%, with much of the region inhabited by dark-needled species which competitively exclude the pine. Of the 26 climatypes of today, most are minor (Table 3); twelve, in fact, account for less than 0.5% of the total area (< 1 575 km^2). Only five climatypes cover more than 5% (15 750 km^2), and of these, # 4 and # 46, are mammoth, accounting for 16 and 20% of the total area, respectively (Table 4).

Figure 3b shows the distribution of climatypes expected in the Sayan Mountains for the projected climate of 2090 according to the Hadley GCM. This figure suggests that the future climate should become more amenable for the pine, with *P. sylvestris* climatypes then encompassing all but 9% of the region (Table 4, Fig. 3b). The increase amounts to 20% of the total land area (about 63 000 km^2) climatically suitable for the pine. Likewise, the number of climatypes suitable for the region should increase from 26 to 35 (Table 4), but again, many (18) of these should account for < 1% of the area. Of the 35, three (# 40, # 82, and # 88) are, accounting for 12 to 15% of the total area.

Table 3. 180 possible combinations of climatic indices (GDD$_5$, AMI, and NDD$_o$) for pine climatypes in Russia

Annual moisture index/Growing degree-days, 5°C	Negative degree-days, 0°C					
	-6000 – -4850	-4850 – -3700	-3700– -2550	-2550 – -1400	-1400 – -250	-250 – 0
0.6–1.8/ 600–1080	1	2	3	4	5	6
1.8–3.0/ 600–1080	7	8	9	10	11	12
3.0–4.2/ 600–1080	13	14	15	16	17	18
4.2–5.4/ 600–1080	19	20	21	22	23	24
5.4–6.6/ 600–1080	25	26	27	28	29	30
6.6–7.0/1080–1560	31	32	33	34	35	36
0.6–1.8/1080–1560	37	38	39	40	41	42
1.8–3.0/1080–1560	43	44	45	46	47	48
3.0–4.2/1080–1560	49	50	51	52	53	54
4.2–5.4/1080–1560	55	56	57	58	59	60
5.4–6.6/1080–1560	61	62	63	64	65	66
6.6–7.0/1080–1560	67	68	69	70	71	72
0.6–1.8/1560–2040	73	74	75	76	77	78
1.8–3.0/1560–2040	79	80	81	82	83	84
3.0–4.2/1560–2040	85	86	87	88	89	90
4.2–5.4/1560–2040	91	92	93	94	95	96
5.4–6.6/1560–2040	97	98	99	100	101	102
6.6–7.0/1560–2040	103	104	105	106	107	108
0.6–1.8/2040–2520	109	110	111	112	113	114
1.8–3.0/2040–2520	115	116	117	118	119	120
3.0–4.2/2040–2520	121	122	123	124	125	126
4.2–5.4/2040–2520	127	128	129	130	131	132
5.4–6.6/2040–2520	133	134	135	136	137	138
6.6–7.0/2040–2520	139	140	141	142	143	144
0.6–1.8/2520–3000	145	146	147	148	149	150
1.8–3.0/2520–3000	151	152	153	154	155	156
3.0–4.2/2520–3000	157	158	159	160	161	162
4.2–5.4/2520–3000	163	164	165	166	167	168
5.4–6.6/2520–3000	169	170	171	172	173	174
6.6–7.0/2520–3000	175	176	177	178	179	180

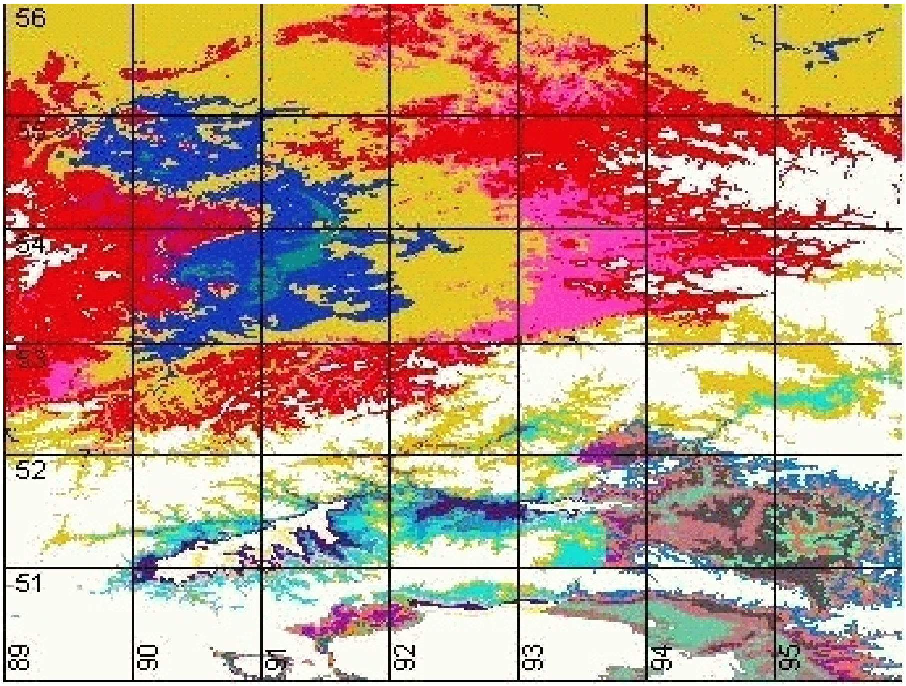


Figure 3a. Distribution of *Pinus sylvestris* climatypes in the Sayan Mountains in the current climate.

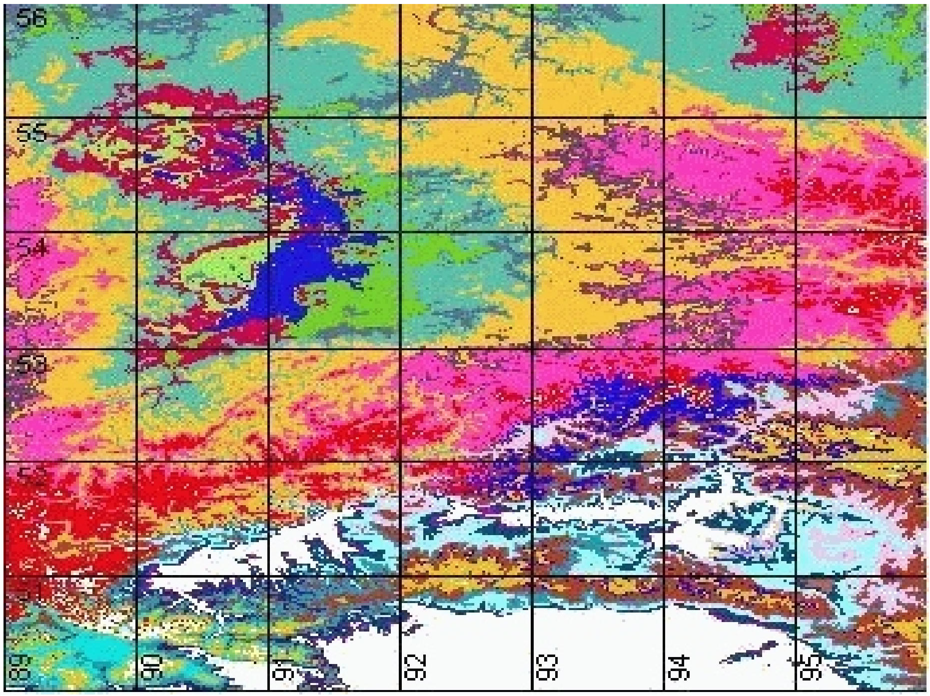


Figure 3b. Distribution of *Pinus sylvestris* climatypes in the Sayan Mountains in a warm climate. Different colors are 180 climatypes according to Table 3. Not all climatypes are realized in actual climatic space. White means that pine does not occur in a given climate.

Table 4. Areas (km^2) of seed zones for *Pinus sylvestris* in current and warmed climates in the Sayan Mts

Climatype number	Current climate	Proportion (%)	Warmed climate	Proportion (%)
0	93 383	29.16	29 282	8.90
2	5 565	1.72		
3	21 556	6.79	8 676	2.67
4	47 974	15.76	18 293	5.77
5			0.7	0.00
8	6 618	2.03		
9	7 985	2.47	4 331	1.31
10	6 004	1.99	67	0.02
14	1 743	0.53		
15	1 652	0.51	64	0.02
20	525	0.16		
21	253	0.08		
26	309	0.09		
32	70	0.02		
39	113		6 884	2.16
40	13 993	4.60	37 131	11.99
44	1 715	0.53		
45	798	0.25	19 729	6.11
46	59 278	19.87	12 181	
50	6 250	1.93		
51	2 406	0.74	8 779	2.69
52	16 900	5.55	46	0.01
56	4 592	1.41		
57	2 835	0.87	2 060	0.63
58	1 625	0.53		
62	4 020	1.22		
63	2 143	0.66	617	0.19
68	1 112	0.34		
69	495	0.15	86	0.03
76			9 033	2.94
81			1 201	0.38
82			44 558	14.70
87			8 522	2.64
88			43 240	14.46
92			5	0.00
93			9 929	3.06
94			12 455	4.14
98			315	0.10
99			7 367	2.27
100			3 511	1.16
104			34	0.01
105			1 610	0.49
106			72	0.02
118			35	0.01
124			8 003	2.70
130			7 914	2.62
134			24	0.01
135			453	0.14
136			4 876	1.60
140			51	0.20
141			465	0.14
142			20	0.01

A comparison of the current and future distribution of climatypes (Fig. 3) shows that by the end of this century, there should be a complete redistribution of climatypes across the entire region. Two of the three most important climatypes of the future, # 82 and # 88, do not exist in the region today (Table 3). The third, # 40, which is expected to cover 12% of the region in the future, currently occupies only 4.6%. The two huge contemporary climatypes, # 4 and # 46, should still be present in the future but are expected to occupy only about 5% of the total area. Twelve climatypes that occur in the region today are not expected to be present in the future, and 23 that should be present in the future do not occur in the region today. Even though contemporary and future climates are expected to have only 13 climatypes in common, their geographic locations should change greatly. Indeed, except for their physiognomic basis, Figs. 3a and b have very little in common.

Larix sibirica Of the 48 possible combinations of our climate classes (Table 5), 24 occur today within the Sayan Mountains (Table 6, Fig. 4a). These climatypes cover approximately 67% or the region, thus suggesting that 33 % lie outside the climatic limits of *L. sibirica*. Of the 24 climatypes, 11 cover < 1% or the area and only 5 cover more than 5%. Two of the climatypes, # 1 and # 3, are huge, covering 19 and 17 % of the total area, respectively. These two, therefore, account for almost one-half of the area that is climatically suitable for larch (Fig. 3a).

The climate in the decade beginning in 2090 is expected to become more amenable to larch, with about 92% of the land then lying within the species climatic limits (Fig. 4b, Table 6). This represents an increase of 24%, or about 75 500 km^2. This greater suitability for larch in the future climate is also reflected by the presence of 34 climatypes, an increase of 10. As a result, 71% of all of the potential larch climatypes should be found within the Sayan Mountains. As before, however, only six of the climatypes should occupy more than 5% of the region, and of these, only one, # 20, is huge.

Figure 4a and b, illustrates the change in the distribution of climatypes that would be expected for the decade beginning in 2090. While the present and future climates should have 20 climatypes in common, their relative importance (Table 6) and geographic positions (Fig. 3b) change greatly. Climatypes # 1 and # 3, which are huge in the contemporary climate, should occupy < 5% of the area in the future. Likewise, climatype # 20, which should dominate in the future climate, covers < 1% of the area today. In total, 7 climatypes that occur in the region today are not expected in the future and 14 that should be present in the future do not occur in the region today. As for *P. sylvestris*, the changing climate will have far reaching effects on the distribution of *L. sibirica* climatypes in the Sayan Mountains.

DISCUSSION

Climate change obviously will alter the adaptedness of forest tree species that are composed of climatypes. Genotypes of sessile forest trees simply cannot track their optimal climate as it changes. Our results join with those on *Pinus contorta* (Rehfeldt et al. 1999b, 2001) and *P. sylvestris* (Rehfeldt et al. 2002) to illustrate that intraspecific adjustment to change will not be trivial. Adjusting to global warming will require a wholesale redistribution of genotypes across the landscape to re-align climatypes in the novel climates and thereby maintain optimal forest growth and productivity (Rehfeldt et al. 2001). 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 re-shuffled across the landscape (Rehfeldt et al. 1999b, 2002).

Our analyses suggest that by 2090, the climate of the Sayan Mountains should be more amenable for both *P. sylvestris* and *L. sibirica* than it is today. Nonetheless, the distribution of climatypes is expected to undergo a complete overhaul. The prominent climatypes of today should either be absent from or minor in the future forests. Likewise, the most prominent climatypes expected in the future are either absent or minor today. Even those climatypes that should remain in the landscape throughout the present century are expected to change in position and importance. To be sure, climate change as predicted by the Hadley GCM, should have widespread effects on the distribution of genotypes within these species.

Table 5. 48 possible combinations of climatic indices (GDD_5, AMI and $NDD_{o)}$) for *Larix sibirica* climatypes in Russia

Annual moisture index/Growing degree-days, 5°C	Negative degree-days (0°C)	
	-4500 – -2200	-2200 – -1200
0.8–1.8/ 650–1300	1	2
1.8–2.8/ 650–1300	3	4
2.8–3.8/ 650–1300	5	6
3.8–4.8/ 650–1300	7	8
4.8–5.8/ 650–1300	9	10
5.8–6.8/ 650–1300	11	12
6.8–7.8/ 650–1300	13	14
7.8–8.5/ 650–1300	15	16
0.8–1.8/ 1300–1950	17	18
1.8–2.8/ 1300–1950	19	20
2.8–3.8/ 1300–1950	21	22
3.8–4.8 / 1300–1950	23	24
4.8–5.8/ 1300–1950	25	26
5.8–6.8/ 1300–1950	27	28
6.8–7.8/ 1300–1950	29	30
7.8–8.5/ 1300–1950	31	32
0.8–1.8/ 1950–2350	33	34
1.8–2.8/ 1950–2350	35	36
2.8–3.8/ 1950–2350	37	38
3.8–4.8 / 1950–2350	39	40
4.8–5.8/ 1950–2350	41	42
5.8–6.8/ 1950–2350	43	44
6.8–7.8/ 1950–2350	45	46
7.8–8.5/ 1950–2350	47	48

Table 6. Areas (km^2) of seed zones for *Larix sibirica* in current and warmed climates in the Sayan Mts

Climatype number	Current climate	Proportion (%)	Warmed climate	Proportion (%)
0	103 636	32.53	26 043	7.96
1	58 330	18.84	26 741	8.33
2	14 945	4.95	19 482	6.27
3	50 777	16.68	12 845	3.94
4	15 064	5.03	142	0.04
5	20 351	6.52	2 325	0.70
6	2 501	0.83		
7	6 179	1.92	667	0.20
8	46	0.02		
9	2 753	0.84	154	0.05
11	1 355	0.41	3	0.00
13	552	0.17		
15	286	0.09		
17	261	0.08	5 532	1.76
18	93	0.03	24 060	7.85
19	4 276	1.40	14 863	4.65
20	2 376	0.78	39 466	12.97
21	4 855	1.60	14 191	4.40
22	4 009	1.29	22 296	7.41
23	5 923	1.89	10 619	3.27
24	1 117	0.36	7 489	2.48
25	3 420	1.05	7 789	2.39
26			1 583	0.52
27	3 755	1.15	4 397	1.35
28			264	0.09
29	3 264	0.99	2 657	0.81
30			3	0.00
31	175	0.54	1 167	0.36
36			3 127	1.02
38			20 078	6.76
39			0.8	0.00
40			23 130	7.77
41			1 020	0.31
42			8 339	2.75
43			2 207	0.68
44			4 484	1.47
45			2 700	0.83
46			4.4	0.00
47			2 053	0.63

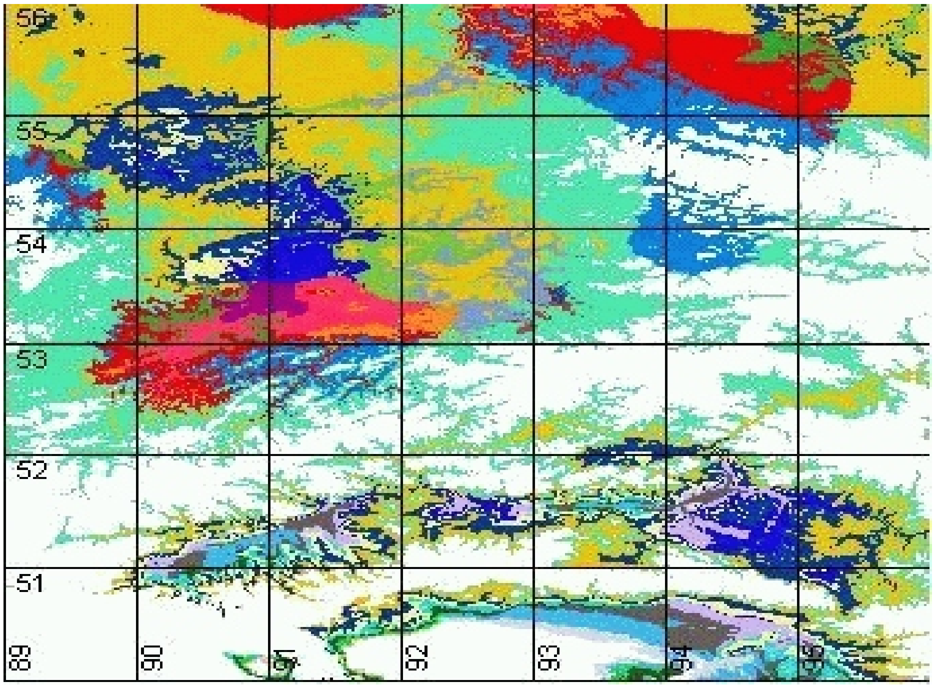


Figure 4a. Distribution of *Larix sibirica* climatypes in the Sayan Mountains in the current climate.

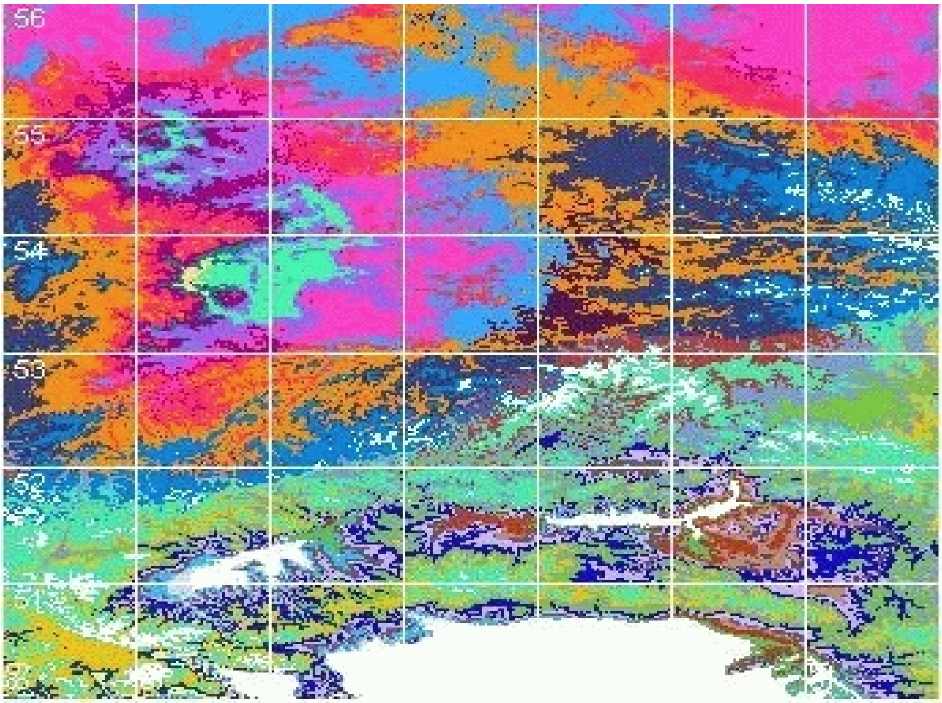


Figure 4b. Distribution of *Larix sibirica* climatypes in the Sayan Mountains in a future warm climate. Different colors are 48 climatypes according to Table 5. Not all climatypes are realized in actual climatic space. White means that larch does not occur in a given climate.

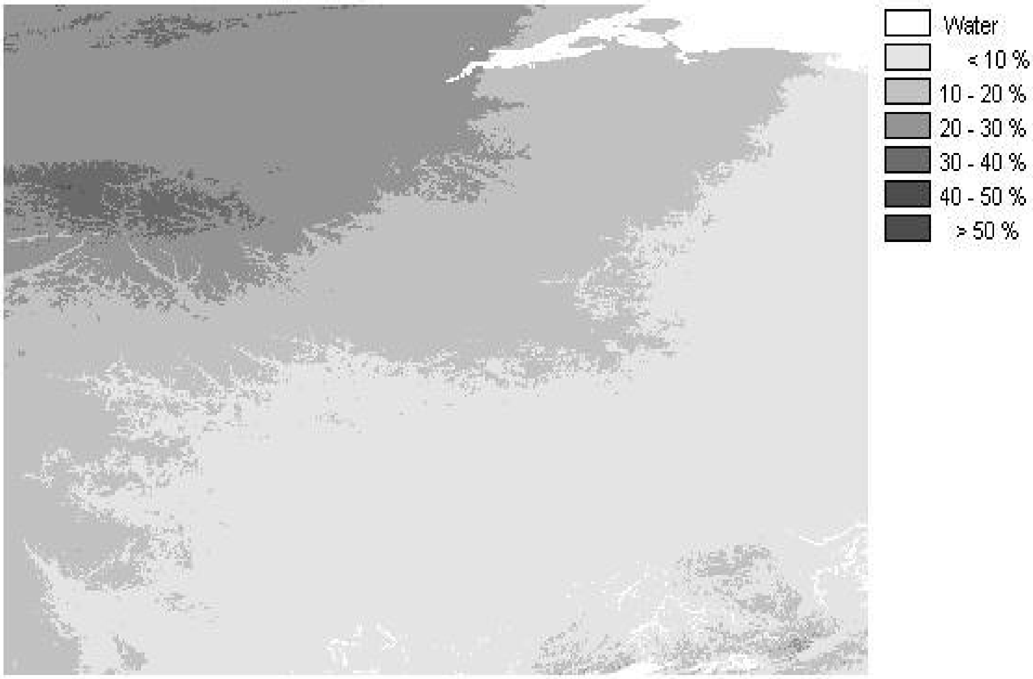


Figure 5a. Percentage of the freezing layer decrease by 2090 with respect to the current climate.

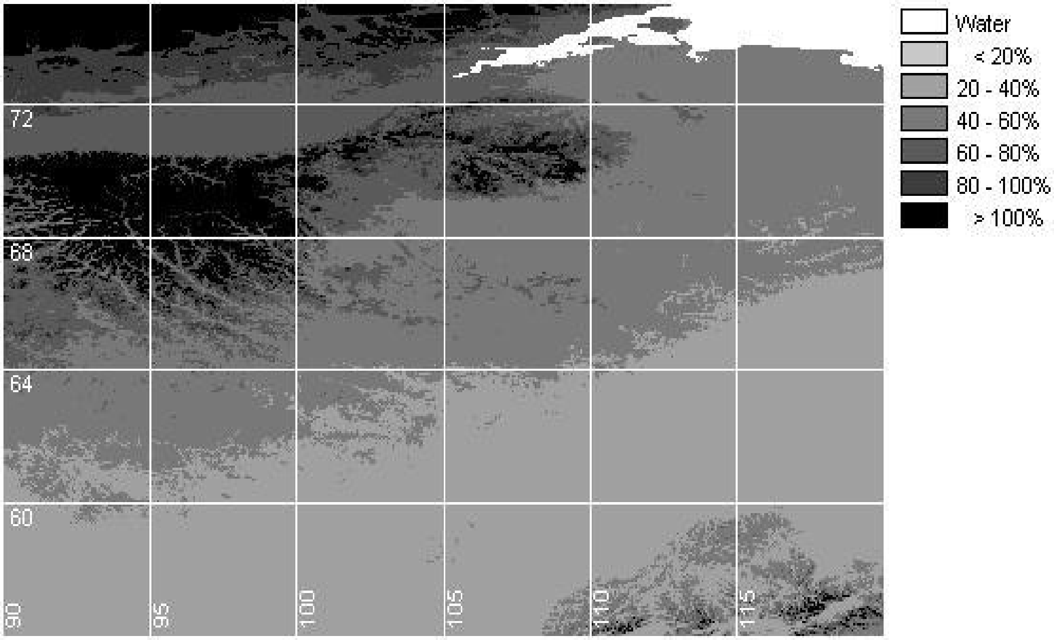


Figure 5b. Percentage of the thawing layer increase by 2090 with respect to the current climate.

As an indication of the scope of these intraspecific effects, it is instructive to assess the contemporary location of the climatypes expected to be of future importance in the Sayan Mountains. Of the three *P. sylvestris* climatypes expected to dominate future forests, one, # 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. Climatypes # 82 and # 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 degrees of longitude to the west. Climatype # 20, for *L. sibirica*, which is to be of future importance, also is present today in the Altai Republic. However, the climatic conditions with which this climatype is associated also can be found west of the Ural Mountains in European Russia. Because the dominant larch west of the Ural Mountains is *L. sukaczewii,* it is possible that the future climates of the Sayan Mountains may be suited to a mixture of larch species and their hybrids. Regardless, it is clear that the genotypes expected to be of importance to the future vegetation of the Sayan Mountains currently reside at long distances from their future habitat. 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.

Migration and natural selection undoubtedly are the processes that will control the evolutionary adjustments necessary for plants to accommodate a changing climate. While migration is the only feasible means by which genotypes can invade and become established in climates beyond their contemporary distributions, natural selection is the process by which genotypes change when exposed to novel climates. Although rates of migration tend to be slow (Davis 1989), responses to selection can be rapid. Nonetheless, there is a limit 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 for Siberia, 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.

Migration becomes even more problematic when dealing with the vegetation shifts illustrated in Fig. 2. Obviously, vegetation zones of either the plains or mountains will not shift as a unit. Individuals migrate, and, as a result, contemporary plant associations may or may not re-assemble in the novel climates. Nonetheless, the paleogeographic record demonstrates that the process by which migrants adjust to novel climates is complex and slow, requiring millenia. Because ongoing climate warming (3–6°C) is predicted to occur for 50–100 years, changes in vegetation due to migration should, first, lag far behind the climatic shifts (see Tchebakova et al. 1994) and, second, disrupt vegetation zones. Only seven species can withstand the severe contemporary climates of Siberia: five conifers (*P. sibirica*, *P. obovata, P. sylvestris, Larix* spp., and *A. sibirica*) and three broadleafs (*B. pendula*, *B. pubecens*, and *Populus tremulus*). Until natural selection adjusts the available genetic variability, it is concievable that none of the available genotypes of these species would be suited to the novel climate. If a species occurs under conditions beyond its climatic optimum it declines. For example, the southern tree border of species distributions are expected to shift northwards because moisture stresses will increase. A favorable climate, moreover, would promote competetive abilities of species inhabiting their climatic optima and these species may become dominating. For example, the growth of dark-needled species like *P. sibirica* and *A. sibirica* is expected to be enhanced in the middle taiga in a warmed climate. So, vegetation redistribution would depend on the joint actions of seed dispersal and environmental selection, with the latter determining which genotypes of which species become, first, established and, second, competitively exclusive. However, in the mountains vegetation redistribution due to tree migration seems feasible over short periods of 50–100 years. This is because migration of adapted genotypes across mountainous landscapes only needs to occur across a few hundred meters in order for genotypes to track the climate to which they are adapted optimally. For this reason, mountains readily serve as refuges during times of extripation.

Fire is another factor that is capable of influencing the speed by which vegetation adjusts to climate change. In the short term, fire will aid the redistribution of vegetation by opening sites for colonization that were previously occupied. In fact, forest fire succession is predicted to dominate central Siberia (Furyaev et al. 2001), and in doing so should increase the abundance of *Betula* spp. in warm zones and *Larix* spp. in cold zones.

In accounting for the effects of climate change on the vegetation, permafrost cannot be ignored. To be sure, permafrost is the principal factor controlling the distribution of vegetation in central Siberia and Yakutia. First, it allows forests to develop in areas where otherwise semi deserts would occur (Shumilova 1964). Second, it limits the eastward spread of dark-needled species (*P. sibirica*, *P. obovata*, and *A. sibirica*) in Siberia. Inside the permafrost zone, these dark-needled species can reach high latitudes only on sandy soils along river valleys and benches where permafrost may thaw as deep as 1–1.5 m (Shumilova 1964). *Larix gmelini* and *L. cajanderi*, by contrast, may grow on soils which thaw only about 10–30 cm in summer (Abaimov et al. 1999). Under the climate change scenario we used in this study, the heat resources will be available for melting permafrost. From Stefan's formula (Dostavalov and Kudriavtsev 1967), we estimated the ratio of the depth of the freezing layer during contemporary winters and those expected under a changing climate (Fig.

5a) and the ratio of the depth of the thawing layer during contemporary summers and those expected under a changing climate (Fig. 5b). The depth of the freezing (or thawing) layer is proportional to the square root of the ratio NDD_0 (or GDD_5) in future to current climates. At the highest latitudes, much milder winters and warmer summers should promote a rapid demise of the permafrost, especially in mountains. As a result, dark-needled species would be expected to track the retreating permafrost and thereby invade the Taymyr Peninsula and the Putoran and Anabar Plateaus, which are currently dominated by tundra and forest-tundra. The presence of dark-needled species at these locations during warm epocs is supported by pollen spectra (Khotinsky, 1977) from the mid-Holocene. In the middle latitudes covering about 65% of our area, the depth of thawing should increase by 40–60%. This amount of thawing most likely is not sufficient for allowing dark-needled species to become established. As a result, light-needled taiga would dominate this area. In the south, the thawing layer is predicted to increase only 20–40%, an amount that should allow forest-steppes and steppes to develop.

A tremendous amount of water stored in the permafrost of the northern plains and mountains is expected to be released under rapid warming. The release of this water undoubtedly will have a large impact on the Siberian landscapes. A part of this water collected from the basins of two big rivers, Lena and Khatanga, will flow directly into the Arctic ocean and may flood the coastal area between Khatanga and Olenek Bays. Another part of the water collected from the basins of the other two big rivers, Nizhniaia Tunguska and Kureika, will flow into the Yenisei River near the Arctic Circle. Our rough estimates of the possible flooding of its lower left bank occurring in the West Siberian Plain show that it may cover at least 1–2 km.

All together, our analyses 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 within species. Because analogs to the future forests of Siberia exist within the present-day distributions, there is no doubt that the vegetation is capable of adjusting to the predicted changes. Current estimates, however, suggest that redistribution of forest zones and 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. Indeed, the lag in vegetal response to rapid change suggests that if the climate does not stabilize, the vegetation may never be able to approach equilibrium. From the practical viewpoint, therefore, it seems obvious that maintaining optimal levels of productivity in Siberian forests will require the participation of mankind in the natural processes to assure that the appropriate species and genotypes appear in the appropriate climates in a timely manner.

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CLIMATE CHANGE: IMPACTS AND ADAPTATION IN FORESTRY

David L. Spittlehouse

BC Ministry of Forests
Research Branch
PO Box 9519, Stn. Prov Govt
Victoria, BC
V8W 9C2
E-mail: dave.spittlehouse@gems4.gov.bc.ca

ABSTRACT

Current changes in climate are already affecting forest species. Future climate change will bring greater changes in range of occurrence, forest disturbance, and growth rates. These changes in turn will affect society's ability to use forest resources. We already take account of climate in forest management; in the future we will have to apply these techniques with a greater intensity and in different areas. Climate change adaptation strategies for the forest management sector should be based on the application of vulnerability assessment or risk management concepts. An adaptation plan must address biophysical and socio-economic impacts and include policy and institutional considerations. We will need to evaluate current vulnerability, speed recovery after disturbance, and reduce vulnerability to further climate change. The adaptation plan should include monitoring the state of the forest to detect change to aid determining when to intervene. An example of using this framework to adapt to changing forest productivity is presented. Many forest ecosystems and species will have to adapt autonomously because management can only influence the timing and direction of forest adaptation at selected locations. In general, society will have to adjust to how forests adapt. Sustainable forest management already embodies many of the activities that will be required to respond to the effects of climate change on forests. Including adaptation to climate change, as part of forest planning, does not necessarily require a large financial investment now with an unknown future payback time.

INTRODUCTION

By the end of the 21st century, the mean annual temperature for western North America could be 2–5°C above the range of temperatures that have occurred over the last 1 000 years (Houghton et al. 2001). An increase in winter precipitation and a decrease in summer precipitation may also occur. These changes would significantly affect forest ecosystems and their utilization by society (McCarthy et al. 2001, Spittlehouse and Stewart 2003). Predicted changes include the movement of species ranges northward and up in elevation with new assemblages of species occurring in space and time (Hebda 1997, Kirschbaum 2000, Hansen et al. 2001). Forest management decisions are usually based on the assumption that the climate will remain relatively stable throughout a forest's life. This may have worked well in the past, but future climate change challenges this assumption. Canada's natural resources and associated industries and communities are vulnerable to climate change and there is a need for the forestry community to be proactive in adapting to climate change (Davidson et al. 2003, Standing Senate Committee on Agriculture and Forestry 2003, Spittlehouse and Stewart 2003).

Adaptation to climate change refers to adjustments in ecological, social, and economic systems in response to the effects of changes in climate (Smit et al. 2000, Smit and Pilifosova 2001, Davidson et al. 2003). The development of adaptation measures for some time in the future, under an uncertain climate, in an unknown socio-economic context is bound to be highly speculative (Burton et al. 2002). Some people may view responding as a greater risk than doing nothing, or that adaptation is not a feasible option. Although forest ecosystems will adapt autonomously, their importance to society means that we may wish to influence the direction and timing of this adaptation at some locations. In other cases, society will have to adjust to whatever change brings.

This paper is based on Spittlehouse and Stewart (2003). My objective is to encourage the forestry community to begin assessing its vulnerability to climate change and develop adaptation strategies. I will present a brief summary of current and possible future changes in the environment and forest ecosystems and then present a framework for determining options to adapt to climate change.

CURRENT AND FUTURE CHANGES IN BC

Globally, there has been an increase in mean annual air temperature of over 0.5°C in the last 100 years. British Columbia has seen similar or greater changes, particularly in winter minimum temperatures, and with the increase being greatest in northern regions (Anon. 2002). There has not been a consistent long-term change in precipitation. Possible responses to these changes in temperature include retreating of glaciers, shift in the annual hydrograph, permafrost melt and increase in landslides in the north, and changes in fire occurrence (Leith and Whitfield 1998, Anon. 2002, Clague 2003, Gillet et al. 2004). There are no long-term measurements to allow assessment of biological response in British Columbia (BC)'s forest ecosystems to these changes. However, world-wide there are reports of an earlier start to the growing season, earlier arrival of migratory birds, increase in boreal forest productivity, earlier breeding of animals and genetic adaptation in resident populations (Stewart et al. 1998, Climate Change Impacts and Adaptation Directorate 2002, Stenseth et al. 2002, Walther et al. 2002, Reale et al. 2003).

Possible future climates for BC are presented in Table 1. The range of values reflects the uncertainty in future greenhouse gas emissions and differences in how the various models simulate the climate. All projections show a warming that tends to be greater in northern areas and larger in winter and spring. Winter precipitation is expected to increase and summer precipitation may increase or decrease. A number of factors will control biological responses to these climate changes. They include the rate and magnitude of climate change, species and population sensitivity to climate, fecundity, life span, habitat requirements, current distribution, frequency, timing and size of disturbance (fire, disease, insects, harvest), competition, barriers to movement and human adaptive actions. Climate change impacts for BC include: species ranges moving northward and up in elevation (Hebda 1997), increase in the frequency, intensity, and timing of disturbances such as fire (Stocks et al.1998) and pests (Sieben et al. 1997, Carroll 2003), change in forest productivity (Spittlehouse 2003) and change in biome distribution (Scott et al. 2002). For example, by 2080 there could be a significant expansion of true grassland and the forest/grassland transition climates in southern BC (Hebda and Spittlehouse, unpublished data); though how rapidly such changes may translate into movement of species is uncertain (Loehle 2003). Species ranges may be reduced if the current warmer/drier end of a range becomes unsuitable and species are unable to move into areas where the climate is suitable because of slow migration rates, unsuitable growing substrate or lack of habitat (Stewart et al. 1998). Some species will adapt better than others. Harding and McCullum (1997) suggested that in BC and Yukon about 70% of the bird and ungulate species and 20% of fish species would have an increase in habitat under climate change, while the remainder would have a loss.

Table 1. Future climate scenarios for 2020 and 2080 for southern and northern British Columbia presented as changes from current conditions. Data encompass predictions from eight global climate models, though there are outliers outside the ranges presented. Data are available from the Canadian Institute for Climate Studies (http://www.cics.uvic.ca/scenaros/index.cgi?Scenarios).

	2020		2080	
	Temp. (°C)	Precipitation (%)	Temp. (°C)	Precipitation (%)
Southern				
Winter	0 to 2	-5 to 15	2 to 6	0 to 25
Spring	0.7 to 1.7	-3 to 10	2 to 6	-5 to 15
Summer	1 to 2	-25 to 5	3 to 7	-45 to 5
Fall	0.7 to 1.5	-5 to 5	2 to 6	-5 to 15
Northern				
Winter	0 to 2	0 to 15	3 to 10	5 to 45
Spring	0.5 to 2.5	2 to 20	2 to 8	5 to 50
Summer	0.5 to 1.5	-10 to 17	2 to 6	-10 to15
Fall	0.5 to 2	-5 to 10	2 to 6	10 to 25

Forest management activities will not be immune to the effects of climate change. We already take account of climate in forest management; in the future we will have to apply these techniques with a greater intensity and in different areas. Fire management is an obvious example and we may need to focus on the protection of areas with high economic or social value, while in other areas fire is allowed to run its course (Stocks et al. 1998, Parker et al. 2000). Increasing winter precipitation will affect water management in forests. An increased risk of sediment transport to streams threatens water quality and fish spawning habitat. Warmer winters will reduce the opportunities for winter logging in areas where the frozen surfaces of forest roads and ice bridges are essential for site access, and where a snow pack is necessary to protect the land during harvesting (Pollard 1991). Harvesting restrictions could increase due to the increased risk of landslides under heavy rainfall. There will be changes in wood quality and timber supply locally and globally, and market impacts will not be uniformly distributed (Perez-Garcia et al. 2002). A changing climate means that the geographic extent of seed transfer zones will change. Thus we need to determine the limits of transferability of species and genotypes and develop new regeneration strategies (Ledig and Kitzmiller 1992, Rehfeldt et al. 1999, Parker et al. 2000). We will need to re-evaluating conservation and recovery programs because rare and endangered plant species usually have specialized environmental requirements and low genetic diversity (Peters 1990, Hansen et al. 2001). Attributes that parks and wilderness areas were designed to protect may no longer exist within the protected area (Halpin 1997, Scott et al. 2002) and a ‘hands-off” approach to wilderness management may not be an appropriate response.

ADAPTATION TO CLIMATE CHANGE IN FORESTRY

Forecasting impacts is difficult because of our limited knowledge about the vulnerability of ecosystems and species, and the poor spatial and temporal resolution of the future climate. Although we do not have a clear view of the future climate and forest, it is critical to begin the process of developing adaptation strategies now. Adaptation to climate change in forest management requires a planned response well in advance of the impacts of climate change. Evaluating vulnerability is critical for developing adaptation strategies. Vulnerability is the degree to which a system (organism, ecosystem, company, or community) is susceptible to, or unable to cope with, adverse effects of climate change. It depends on the magnitude and rate of climate change, sensitivity to climate, and the system’s adaptive capacity. Adaptive actions reduce the risks (decrease vulnerability) by preparing for adverse effects and capitalizing on the benefits. However, intervention will be selective and there will be impacts that cannot be prepared for or anticipated. Spittlehouse and Stewart (2003) presented an extensive list of adaptive actions proposed in the literature for forest management.

Adaptation requires (Dale et al. 2001, Spittlehouse and Stewart 2003) that the forestry community:
1) Establish objectives for the future forest under climate change.
2) Increase awareness and education within the community about adaptation to climate change.
3) Determine the vulnerability of forest ecosystems, forest communities, and society.
4) Develop present and future cost-effective adaptive actions.
5) Manage the forest to reduce vulnerability and enhance recovery.
6) Monitor to determine the state of the forest and identify when critical thresholds are reached.
7) Manage to reduce the impact when it occurs, speed recovery, and reduce vulnerability to further climate change

I focus here on a framework for planning adaptive actions. It is a format for risk analysis of which there are many examples in the literature (Kelly and Alger 2000, Davidson et al. 2003, Spittlehouse and Stewart 2003, Turner et al. 2003). A plan for facilitating adaptation in forestry must address biophysical and socio-economic impacts and will include policy and institutional considerations. First we need to identify the issue of concern. Next comes the assessment of the vulnerability (sensitivity, adaptive capacity) of the forest, forest dependent communities, and society in general to climate change. This assessment facilitates the development of adaptive actions to be taken now and those required for the future as change occurs. Current activities include those that facilitate future responses to reduce vulnerability. Adaptation options must include the ability to incorporate new knowledge about the future climate and forest vulnerability as they are developed. Until climate change has had sufficient impact to warrant intervention it is likely that in many situations there is a not much that is to be done ‘on the ground, in the forest’ for a few decades. However, we need to have a suite of options ready to go when we do wish to intervene; thus there is work to do now.

The following is an example of using the framework noted above on the effect of climate change on a managed forest. Other examples can be found in Spittlehouse and Stewart (2003). This example is not in the detail required for a full analysis but is presented to show how the risk analysis might take place.

Issue: A managed forest under climate change.
Vulnerability: Lower summer precipitation and increased temperature – reduce growth rates, change wood quality, increase the risk of disturbance by fire, insects and disease, change in species suitability, change in wildlife habitat, loss of recreational opportunities.
Increased winter precipitation and temperature – increase risk of erosion, increase in streamflow, reduced winter logging opportunities
Options for the future: Adjust rotation ages, utilise small logs, increase salvage after disturbance by fire and insects, modify seed transfer zones, upgrade culverts.
Actions to do now: Replace geographically defined seed transfer zones with zones defined by climate, identify policy and knowledge barriers to implementation, develop harvesting and wood processing technology to meet the future fibre supply.

Climate change adaptation strategies can be viewed as the risk management component of sustainable forest management plans. Actions can be taken that are useful now, but would also reduce the risk of unacceptable losses in the future. As can be seen in the above example, many actions required in adapting to climate change benefit the present as well as the future. Spittlehouse and Stewart (2003) proposed a number of questions that need to be addressed to facilitate adaptation planning. These included: what are the research and educational needs; what are barriers to the implementation of adaptation in forest management; what forest policies need to be in place to facilitate adaptation; and are current monitoring systems adequate to spot problems induced by climate change soon enough to allow implementation of an acceptable response?

CONCLUSIONS

Current forest utilization and preservation is based on how forests developed under past climatic conditions. Policy-makers and forest managers must accept that climate change in the near term is probable and that forests and forest dependent communities face significant challenges. Planned adaptation will reduce the vulnerability of commercial tree species at selected sites. However, many forest species will have to adapt autonomously and society will have to adjust to the result. Until climate change has had sufficient impact to warrant intervention it is likely that in many situations there is not much that can be done in the forest at present. However, it is necessary to start assessing forest vulnerability to climate change and developing adaptation strategies. Sustainable forest management already embodies many of the activities that will be required to respond to the effects of climate change on forests. Including adaptation to climate change as part of forest planning does not necessarily require a large financial investment now with an unknown future payback time.

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VOLUNTEER PAPER ABSTRACTS

TOWARDS THE DEVELOPMENT OF A COMPOSITE GENETIC MAP IN WHITE SPRUCE

Stéphanie Beauseigle[1], Betty Pelgas[1], Isabelle Gosselin[1], Manuel Lamothe[2], Jean Bousquet[1] and Nathalie Isabel[2]

[1] Canada Research Chair in Forest and Environmental Genomics
Université Laval
Pavillion C-E-Marchand
Sainte-Foy, QC
G1K 7P4
E-mail: stephanie.beauseigle@rsvs.ulaval.ca

[2] Natural Resources Canada
Canadian Forest Service
Laurentian Forestry Centre
PO Box 3800
Sainte-Foy, QC
G1V 4C7

Comparative mapping is an alternative method for non-model species to better understand their genome organization and highlight homeologous chromosomic segments involved in adaptative and economical traits. Recently, (Pelgas et al. 2004, Mol. Breed.), we developed over one hundred multiallelic ESTP anchor markers for comparative mapping between *Picea mariana* (Mill.) BSP and *P. glauca* (Moench) Voss, two evolutionarily distant species in the genus *Picea*. Among these, more than 50 ESTP markers were identified as potential candidate genes involved in abiotic stresses and/or wood formation, and polymorphisms (either SNPs or indels) were detected for all of them. All ESTP markers were used in combination with AFLPs and microsatellite markers to generate a composite map for *P. glauca*. Two crosses were selected with one parent in common to maximize the number of segregating ESTPs. Up to now, four individual linkage maps have been constructed from these crosses, with a length ranging from 2 045 cM to 2 801 cM and a marker density of about 8.4 cM. The use of two pedigrees in *P. glauca* resulted in 25% additional anchor markers useful for interspecific comparison with *P. mariana*.

ECOLOGICAL GENETICS OF WHITEBARK PINE

Andrew Bower and Sally Aitken

Department of Forest Sciences
University of British Columbia
3401–2424 Main Mall
Vancouver, BC
V6T 1Z4
E-mail: adbower@interchange.ubc.ca

Whitebark pine (*Pinus* albicaulis) is considered a keystone species in the subalpine ecosystems where it occurs. It has been severely impacted throughout its range by the introduced disease white pine blister rust (caused by the fungus *Cronartium ribicola*) and by successional replacement. There is much concern about local extirpation in some areas and restoration efforts may be needed to maintain this species in areas where it is most vulnerable. Marker studies have indicated that whitebark pine populations are not well differentiated, however the level of differentiation based on quantitative traits was previously unknown. Seed collected throughout the range of whitebark pine has been grown in a common garden test on the University of British Columbia campus, to study the level of genetic differentiation among seed sources in quantitative traits. Seed weight and germination, phenology, growth, and cold hardiness have been assessed for a total of 157 open-pollinated families from 18 populations across the range of whitebark pine. The influence of various climatic and geographic variables on these traits has been examined to determine the degree and pattern of genetic differentiation among seed sources. There appears to be clinal variation for the timing of needle flush and cold hardiness in fall, spring, summer, with temperature of the parent tree location having the greatest influence on these traits. The clinal pattern of variation in these adaptive traits suggests that populations are adapted to their local environment; in which case, movement of seed should be carefully considered in order to minimize maladaptation of planting stock. The potential affects of climate change on whitebark pine will also be discussed.

EFFECTS OF GENOTYPE AND SILVICULTURE ON WESTERN HEMLOCK DIAMETER GROWTH AND WOOD DENSITY

Charlie Cartwright[1] and Mathew Koshy[2]

[1] **BC Ministry of Forests**
Research Branch
7060 Forestry Road
Mesachie Lake, BC
V0R 2N0
E-mail: Charlie.Cartwright@gems1.gov.bc.ca

[2] **Department of Forest Sciences**
University of British Columbia
4343 West Mall
Vancouver, BC

Wood quality is clearly responsive to genetics, with most traits having high heritabilities relative to growth traits. It is also apparent that site has a strong influence. It follows from this that silvicultural treatments might have an effect, and it is possible that there could be interactions between genotypes and silvicultural treatments. Seventy open-pollinated hemlock families in a progeny trial were thinned to two densities and aspects of cell morphology measured for the growth ring of the year before treatment, the year of treatment, and the year after. Similarly, on a separate site in the same series, the families were fertilized with either 300 or 600 kg/ha. In both studies the treatments resulted in improved growth, yet wood density was not diminished as might be anticipated. Family by treatment interactions were statistically significant in both investigations, however this result is rendered difficult to interpret because the treatment by family by year (growth ring) effect was not significant. Several possible explanations and some details of the results are rendered.

CLIMATE-CHANGE RESPONSE STRATEGIES AMONG THREE CO-OCCURRING, ECOLOGICALLY DISTINCT NORTHERN CONIFEROUS TREE SPECIES

D. Scott Green

Ecosystem Science and Management
University of Northern British Columbia
3333 University Way
Prince George, BC
V2N 4Z9
E-mail: greens@unbc.ca

There remains considerable uncertainty about predicting the responses of trees and forests to climate change in Northern and high-elevation regions, where we anticipate the greatest future climate fluctuations. No general theory describing climate-driven responses among disparate tree species currently exists, owing to the diversity of ecological niches and growth strategies found among co-occurring species. Comparing species-specific tradeoffs in competition-survival traits across climate gradients (e.g., latitude, elevation) offers a systematic basis to characterize the response capacities of ecologically distinct tree species.

Inherent clinal responses for four quantitative traits thought to be adaptive in cold-limited environments were characterized in a controlled greenhouse study for three ecologically distinct and co-occurring Northern tree species: lodgepole pine (*Pinus contorta* Dougl. ex. Loud. var. *latifolia*, interior spruce *Picea glauca* (Moench) Voss x *Picea engelmannii* Parry ex Engelm., and subalpine fir *Abies lasiocarpa* (Hook.) Nutt.). For each species, clinal trends were quantified among populations adapted to increasingly cold-limited climates across a severe elevational gradient approaching the treeline.

Tradeoffs between competitive capacity and survival capacity across the climate gradient differed markedly among these tree species. Strong clinal trends observed in subalpine fir for all the quantitative traits indicated a highly conservative approach to climate response. Phenotypic plasticity in traits may be low among subalpine fir populations in severe climates and we might anticipate a limited capacity to express competitive responses to improving growing conditions under a warming climate. Trends in lodgepole pine and interior spruce suggested a more plastic strategy, favoring competitive traits across a wide range of climate conditions. These species might exhibit pronounced competitive responses to warming conditions, particularly near the cold extreme in the species climate ranges where high growth potentials are muted. Study findings suggest that it may be useful to characterize general differences among ecologically distinct species, such as early- and late-successional positions, in predicting forest responses to climate change.

POTENTIAL IMPACT OF CLIMATE CHANGE ON ECOSYSTEMS, SPECIES DISTRIBUTIONS, AND GENETIC RESOURCE MANAGEMENT IN BRITISH COLUMBIA

Andreas Hamann[1], Tongli Wang[1], Sally N. Aitken[1] and Alvin D. Yanchuk[2]

**[1] Department of Forest Sciences
University of British Columbia
3401–2424 Main Mall
Vancouver, BC
V6T 1Z4**
E-mail: hamann@interchange.ubc.ca

**[2] BC Ministry of Forests
Research Branch
PO Box 9519 Stn Prov Govt
Victoria, BC
V8W 9C2**

One way to investigate whether expected global warming is likely to threaten forest ecosystems, tree species, or their genetic resources is through bioclimate envelope studies. We use canonical discriminant analysis to determine current climatic envelopes and subsequently a mahalanobis-distance based matching procedure to predict future distributions of various spatial units (ecological zones, species ranges, seed zones).

Ecological zones that are partially or entirely in mountainous areas have their climate envelope shifting upward. Most vulnerable is the Mountain Hemlock and Montane Spruce zone. Other large impacts are the initial expansion of the climatic envelope for Interior Coastal Hemlock and the rapid reduction of the Alpine Tundra and Spruce Willow Birch climates by 2025. Subsequently, Interior Douglas-Fir and Ponderosa Pine climate regions expand throughout the interior plateau replacing current climate envelopes of sub-boreal and boreal ecosystems between 2055–2085.

Tree species that have their current northern range limit within BC gain large amounts of new potential habitat, and increase in frequency where they already occur (e.g., *Pseudotsuga menziesii*). Hardwoods that already occur throughout British Columbia appear to be unaffected by climate change in their overall frequency but could potentially occupy higher elevations (e.g., *Betula papyrifera*). Some of the most important conifer species in British Columbia are expected to significantly decrease in frequency and loose a large portion of their suitable habitat (e.g., *Abies lasiocarpa*, *Picea glauca*, P. *engelmanii*, *P. mariana*, and *Pinus contorta*).

In British Columbia, transfer of seed and the use of planting stock from seed orchards is designed to match planting stock with climatic conditions where genotypes perform best. Using the same bioclimate envelope approach, coastal Seed Planning Units (SPUs) are predicted to shift upward in elevation by approximately 50 m per decade. Interior SPUs also shift northward at a rate of approximately 50–100 km per decade. SPUs currently covering the south (particularly NE) may provide suitable planting material for an extended portion of BC in the future.

More information: http://genetics.forestry.ubc.ca/hamann/climate

MODELLING FROST RISK IN NORWAY SPRUCE

Mats Hannerz[1], Ola Langvall [2] and Urban Nilsson[3]

[1] Skogforsk
Uppsala Science Park
SE-751 83
Uppsala, Sweden
E-mail: mats.hannerz@skogforsk.se

[2] Swedish University of Agricultural Sciences
Asa Forest Research Station
SE-360 30
Lammhult, Sweden

[3] Swedish University of Agricultural Sciences
Southern Swedish Forest Research Centre
PO Box 49
SE-230 53
Alnarp, Sweden

Norway spruce is most susceptible to frost injury from the time of budburst till the end of shoot elongation. Accumulated temperature sum can be used to predict the time of budburst for a defined genetic origin with relatively high precision. Thus, it is also possible to predict frost risk during the critical period of budburst and shoot elongation.

The purpose was to model the risk of frost occurrence during the critical period for Norway spruce of different genetic origins, i.e., for different critical temperature sums for budburst, for a reforestation site with defined geographic coordinates adjusted for local-scale topography. Effects of silvicultural practices on microclimate and time of budburst were also included in the model, e.g., shelterwood of various density and height, site preparation, seedling age, and seedling type. Long-term temperature records from a network of 357 climate stations throughout Sweden were used. The model can be used for predicting the effects of genetic origin and silvicultural practices both in large-scale at the national level and as an evaluation of a specific reforestation site. As an example of a large-scale output of the model, we found that the frost risk shifted from 20–30% to less than 10% throughout most of southern Sweden, if seedlings of Belarusian late-flushing provenances were chosen instead of the local provenance.

INITIATION OF STEM INFECTION IN WESTERN WHITE PINE BY BLISTER RUST

R.S. Hunt

Natural Resourses Canada
Canadian Forest Service
Pacific Forestry Centre
506 W. Burnside Road
Victoria, BC
V8Z 1M5

The majority of early produced needle infection spots caused by a September inoculation of *Cronartium ribicola* were small and sectioning showed that the fungus readily gained access to the vascular cylinder of *Pinus monticola* by penetrating the endodermis. By inoculating only a portion of the foliage of *Pinus monticola* in September with *C. ribicola* and removing it at monthly intervals, it was determined that stem infection was initiated a month, or more, earlier than if seedlings had been classified as “cankered” by observing discoloured stems. Consequently, the majority of the reported “needle shedding resistance responses” in *Pinus monticola* seedlings to *C. ribicola* would be ineffective because they occurred after stem infection had already been initiated. Placing potted *P. monticola* seedlings beneath *C. ribicola* infected *Ribes nigrum* plants for weekly intervals resulted in infection from June through October in the interior of British Columbia. Because natural infections can occur earlier than September, stem canker initiation and development would be more advanced under natural conditions, than that determined from only a September inoculation, thus a “needle shedding resistance response” would be even less effective as a resistance response. These data are consistent with the notion that *P. monticola* lacks a “needle shed resistance response”.

GENETIC VARIATION IN TOLERANCE TO SWISS NEEDLE CAST IN COASTAL DOUGLAS-FIR

Randy Johnson[1], Fatih Temel[2] and Keith Jayawickrama[3]

[1] **USDA Forest Service**
3200 SW Jefferson Way
Corvalis, OR
97331
E-mail: randyjohnson@fs.fed.us

[2] **Kafkas Universitesi**
Artvin Orman Fakultesi
08000 Artvin
Turkey

[3] **Northwest Tree Improvement Cooperative**
Department of Forest Science
Oregon State University
Corvalis, OR
97331-5752

Swiss needle cast (SNC) is impacting Douglas-fir (*Pseudotsuga menziesii*) in coastal Oregon and Washington and is reaching epidemic proportions along the north coast of Oregon. The genetic variation in tolerance to this disease has been investigated over the past 7 years. Foliage color and retention traits exhibit low to moderate heritabilities and tend to be less than heritabilities for growth traits assessed in the same trials. Foliage traits are correlated with subsequent growth in SNC areas, but selection on diameter growth seems to be the best single selection trait to obtain tolerance. Early selection for foliage traits is possible, but the economic benefits of early selection are not clear. Because we did not find family differences in the amount of fungus in needles, we propose that Douglas-fir exhibits tolerance, the ability to continue growth in the presence of the disease, as opposed to resistance, i.e., actively resisting the fungus. The tolerance mechanism is not completely understood, but some aspect appears to be associated with the tree's ability to shed unproductive needles. Although provenance variation has been shown for SNC tolerance, there is very little association between the climate of a seed source location and its tolerance level when examined within a seed zone. Breeding programs are actively underway to develop SNC tolerance and seed resulting from our most recent orchards should be appropriate for use in areas with moderate SNC symptoms.

EFFECT OF THERMAL CLIMATIC CHANGES ON VOLUME GROWTH RESPONSE IN SITKA SPRUCE

Jodie Krakowski[1], Ping Xu[1], Cheng C. Ying[2] and Yousry A. El-Kassaby[1]

[1] **Department of Forest Sciences**
University of British Columbia
2424 Main Mall
Vancouver, BC
V6T 1Z4
E-mail: jodiek@interchange.ubc.ca

[2] **BC Ministry of Forests**
Research Branch
PO Box 9519 Stn Prov Govt
Victoria, BC
V8W 9C2

The potential impacts of anticipated temperature increases due to climate change within the next century were modelled on population-level Sitka spruce (*Picea sitchensis*) volume growth. Twenty-year growth data from the series of IUFRO provenance trials planted throughout British Columbia, comprising 43 provenances representing the entire range of the species and replicated over 12 sites, were analyzed and used to predict volume responses. Data were corrected to remove potentially confounding effects of photoperiod change caused by latitudinal seed transfer. Projected increases in yield, primarily due to the longer growing season, will only result where summer precipitation is > 500 mm. In the maritime seed planning zones (approximately congruent with the moist and wet maritime and the hypermaritime subzones of the Coastal Western Hemlock biogeoclimatic zone) where summer precipitation is > 700 mm, up to 20% volume gain was predicted using the model. Results indicate that Sitka spruce will respond with a linear, rapid volume gain to increased precipitation and is less sensitive to rapid warming. Volume response due to more rapid accumulation of heat sum (4.3%) was approximately double that due to fewer frost free days (2.3%), given a mean annual temperature increase of 5°C. The actual impacts will be tempered by moisture availability, which current models can predict with only low certainty. Summer drought will likely be more prevalent, resulting in lower gains than predicted based on temperature alone.

GLOBAL WARMING AND THE CHILLING REQUIREMENT OF SOME CONIFERS

Denis P. Lavender

3925 Fairhaven Drive SW
Corvalis, OR
97333–1431
E-mail: denis.lavender@oregonstate.edu

The existence of a chilling requirement of some perennial, woody temperate zone plants has been recognized for over a century and has limited the areas suitable for establishment of non-indigenous trees. More recently, with the possibility of a general global warming, it may result in dramatically reduced survival and growth of both native and introduced plants. The term chilling requirement refers to the requirement of vegetative buds of some trees to be exposed for a period of at least several weeks to temperatures of about 5°C to prepare them for resumed growth in the spring. It may be considered analogous to the stratification requirement of some seeds.

Populations of potted 2-1 Douglas-fir (*Pseudotsuga menziesii*) seedlings, all in a receptive physiological state, were exposed for periods up to fifteen weeks to one of the following temperatures: 5, 7, or 9°C with an 8-hour daily photoperiod. During the subsequent 9-week growth period (15°C, 12-hour daily photoperiod) the incidence of bud break and new growth was recorded. Seedlings which had been exposed to five-degree temperature for thirteen weeks produced significantly faster bud break, had greater numbers of active buds, and weight of new growth.

A second study of grafted 2-1 Douglas-fir seedlings planted south of San Francisco was exposed to mean winter temperatures of 9–12°C. All seedlings and grafts had anomalous break the year after planting and most died within two years.

A third study of Douglas-fir seedlings grown under natural conditions in the Corvallis area but with mean temperatures raised 3½°C demonstrated reduced bud break and poor growth.

Accordingly, if the mean temperature of elevations below 300 m in the Willamette–Puget Sound–Gulf of Georgia Trench were to rise about 4°C between November and February we could expect to lose Douglas-fir and its associates.

WHITE SPRUCE LIMESTONE ECOTYPES: DO THEY REALLY EXIST?

M.R. Lesser[1], M. Cherry[2] and W.H. Parker[1]

[1] Lakehead University
Faculty of Forestry
955 Oliver Road
Thunder Bay, ON
P7B 5E1
E-mail: mrlesser@lakeheadu.ca

[2] Oregon State University
321 Richardson Hall
Corvallis, OR
97331

Previous laboratory and field studies have presented evidence for the existence of limestone ecotypes in white spruce (*Picea glauca* [Moench] Voss) from southern Ontario. Remeasurements made in 2001 of the range-wide 410 series of provenance trials were used for further evaluation of the existence of these ecotypes. Height measurements from 23 provenances grown at four test sites in Ontario, all located south of 46°N were used for the analysis. Digital coverage of the 1993 Ontario Geological Survey data set was used to classify test sites and provenances as occurring on either limestone or non-limestone parent material. While analysis of variance revealed significant differences among test sites and provenances, no significant interactions consistent with the existence of limestone ecotypes were detected. This finding is in contrast to that of an earlier field study that detected a strong interaction between test site and provenance bedrock type ($P < 0.001$). Examination of the relative performance of individual provenances from limestone and non-limestone bedrock types, revealed differences in performance at the four different test sites but few instances supporting the existence of limestone ecotypes. Results found in this study generally support a pattern of between-stand variation in southern Ontario. Although these results offer no support for the existence of limestone ecotypes in Ontario, they do not disprove their existence owing to the limitations of the 410 Series test design and the possible misclassification of provenances according to bedrock type.

APPLICATIONS OF SEED TRANSFER EXPERT SYSTEMS IN REFORESTATION AND RESTORATION

Mary F. Mahalovich

USDA Forest Service
Forestry Sciences Lab.
1221 S. Main St.
Moscow, ID
83843
E-mail: mmahalovich@fs.fed.us

There is an evolution of developing seed transfer guidelines from a two-dimensional zone approach to more sophisticated applications modeling patterns of genetic variation for adaptive traits in three dimensions. These models of continuous variation can utilize elevation, latitude, and longitude as independent variables or more recently, can focus on climatic variables. A natural extension of well designed genecological research is seed transfer expert systems. Based on 30 years of research by Dr. Gerald Rehfeldt of the USDA Forest Service in the Inland West has expert systems for *Pinus ponderosa* var. *scopulorum*, *Picea engelmannii*, and in cooperation with the Inland Empire Tree Improvement Cooperative for *Pinus ponderosa* var. *ponderosa*, *Larix occidentalis*, and *Pseudotsuga menziesii*. An expert system for *Pinus contorta* is under development. Adaptive traits or dependent variables typically consist of phenology, cold hardiness, and disease tolerance data. The basic approach to each model is as follows: a series of equations for each user query are satisfied and evaluated against each species' distribution, where coefficients of prediction do not exceed a least significant difference of 20%. Output can either be viewed as to where a particular seed lot can be planted, or given a parcel of land, where suitable cone collections can be made or existing seed lots utilized. Seed transfer expert systems are showing great promise in finding adapted planting stock following catastrophic fires in Montana, Arizona, Colorado, and New Mexico and on a more routine level, managing seed bank inventories on a regional basis.

SELFING RESULTS IN INBREEDING DEPRESSION OF GROWTH BUT NOT OF GAS EXCHANGE

Kurt Johnsen[1], John E. Major[2] and Chris Maier[1]

[1] USDA Forest Service
Southern Research Station
3041 Cornwallis Road
Research Triangle Park, NC
27709

[2] Natural Resources Canada
Canadian Forest Service
Atlantic Forestry Centre
PO Box 4000
Fredericton, NB
E3B 5P7
E-mail: jmajor@nrcan.gc.ca

In most tree species, inbreeding greatly reduces seed production, seed viability, survival, and growth. In a previous large-scale quantitative analysis of a black spruce (*Picea mariana* [Mill.] BSP) diallel experiment, selfing had large deleterious effects on growth but no impact on stable carbon (*C*) isotope discrimination (an indirect measure of the ratio of net photosynthesis (*A*) to stomatal conductance ($g_{wv)}$)). It was hypothesized that selfing did not impact carbon gain via leaf level gas exchange but it did impair subsequent utilization of *C*. Alternatively, both *A* and g_{wv} may each have been impacted by selfing to the same extent. However, no gas exchange data were ever collected to further test these hypotheses. Here we present photosynthetic gas exchange data collected from three selfed families and three out-crossed families (all the result of controlled pollination) from the same diallel experiment. Photosynthetic responses to intercellular CO_2 concentration (A/C_i curves) were generated from four replicates per family, one block per day, over a four-day period in July. Results indicate no differences between selfed and out-crossed families in maximum carboxylation rate, maximum electron transport, (*A*) and g_{wv} (both estimated at 370 ppm CO_2 concentration), or the ratio A:g_{wv}. Selfed trees had higher mortality during the experiment thus it is possible that there were potential negative impacts on gas exchange of previously living selfed progeny. However, we clearly show that inbreeding can result in trees that have low productivity despite retaining high levels of leaf level A. Results are consistent with the hypothesis that gas exchange was similar between selfed and outcrossed progeny trees, thus subsequent utilization of *C* in selfed progeny must have been modified.

SELECTION, GENE FLOW, AND ADAPTATION IN SITKA SPRUCE: LIFE ON THE EDGE

M. Mimura and S.N. Aitken

Department of Forest Sciences
University of British Columbia
3041–2424 Main Mall
Vancouver, BC
V6T 1Z4
E-mail: mimura@interchange.ubc.ca

Understanding evolutionary population dynamics is essential to predict population fates in changing environments. Long-term population dynamics depend on spatial and temporal distribution of species across environments, which are influenced by a balance among selection, gene flow, and genetic drift. Adaptation to local environments of populations at the edges of their range may be limited by gene flow from central populations which are adapted to different environmental conditions. More restricted gene flow could accelerate local adaptation at the periphery.

Adaptation of populations in similar climates was investigated, but with different levels of gene flow, to determine the degree to which gene flow limits adaptation, and thus species range expansion, using *Picea sitchensis* as a model. The objectives are: to estimate tradeoffs between gene flow and adaptation and to reconstruct range expansion and impacts on genetic relationships during the last deglaciation. Three environmentally controlled growth chambers were used to simulate various environments. Some fitness-related traits showed physiological adaptations to local environments. Peripheral, isolated populations appear better adapted to local environments than peripheral disjunct populations for some phenological and growth traits. Mother-offspring genotyping is proceeding with microsatellite markers to estimate relative gene flow levels for continuous and disjunct populations.

BRAVE NEW BREEDING ZONES

Greg A. O'Neill[1], Andreas Hamann[2], Tongli Wang[2] and Sally N. Aitken[2]

[1] BC Ministry of Forests
Kalamalka Research Centre
3401 Reservoir Road
Vernon, BC
V1B 2C7
E-mail: Greg.Oneill@gems6.gov.bc.ca

[2] Department of Forest Sciences
University of British Columbia
3041–2424 Main Mall
Vancouver, BC
V6T 1Z4

As climate changes, seed from breeding programs will have to be deployed to new areas to ensure that it is adapted to the climate in which it is planted. To examine the direction and extent of these changes, lodgepole pine (*Pinus contorta*) provenance test data were used to develop genetic maps based on current climate. Eleven breeding zones were delineated from the genetic maps in a manner that is expected to minimize maladaptation. The 'climate envelop' of each current breeding zone was defined and used in conjunction with future climate maps to map the location of future breeding zones.

Comparisons of current and future locations of breeding zones indicate that some zones will shift substantially northward within 50 years. In addition, several zones will change significantly in spatial extent, with implications for future seed demand and conservation needs.

COMPARISON OF SEED TRANSFER FUNCTION AND FOCAL POINT SEED ZONE APPROACHES REGARDING PRESENT AND FUTURE CLIMATES

W.H. Parker[1], M. Cherry[2] and M.R. Lesser[1]

[1] **Lakehead University**
Faculty of Forestry
955 Oliver Road
Thunder Bay, ON
P7B 5E1
E-mail: bill.parker@lakeheadu.ca

[2] **Oregon State University**
321 Richardson Hall
Corvallis, OR
97331

The Cauchy function was used to model height growth of white spruce (*Picea glauca* [Moench] Voss) based on data from a 25-year-old range-wide provenance test series. Transfer functions were produced for 3 test site locations from eastern Ontario based on late summer temperatures and predicted height of all sources at each test site was mapped. Data from a recently established greenhouse and 5 common garden trials were used to generate focal point seed zones for the same locations. Results for present-day (1961–1990) climate normals were compared with those determined for a future climate scenario (GCM1 2040–2069). Seed transfers for best present-day growth based on the Cauchy models are differentially compatible with predicted climate change depending on latitude. The use of focal point seed zone models forecast into the future provides an additional and more robust means to evaluate the adaptive suitability of potential seed transfers.

TECHNIQUES AND PRELIMINARY RESULTS FROM FOUR GENERATIONS OF SELFING WESTERN REDCEDAR

John Russell and Craig Ferguson

BC Ministry of Forests
Research Branch
7060 Forestry Road
Mesachie Lake, BC
V0R 2N0
E-mail: John.Russell@gems1.gov.bc.ca

Western redcedar (*Thuja plicata* D.Don) has many of the biological attributes that make it an ideal model species for genetic selection experiments. These include early flowering, ability to self, low inbreeding depression, and ease of vegetative propagation. A study was initiated 10 years ago with the objective of studying response to selection and inbreeding depression in western redcedar. F1 seedlings derived from single-pair matings from a base of 30 wildstand parents (F>0), were grown under accelerated conditions. Two seedlings were selected from each full-sib family based on early height growth, as well as two random seedlings. From these 60 lines (F=0 at initiation), four generations of selfing have been accomplished in eight years (F=0.938 in absence of selection).

In this talk, we will describe the techniques employed that have enabled us to turn over five generations in 10 years, some preliminary results from selection, and finally, future direction.

SURVEY OF GENE CONSERVATION REQUIREMENTS FOR FOREST TREE AND SHRUB SPECIES IN CANADA

J.D. Simpson[1], T. Beardmore[1], J. Loo[1] and B. McAfee[2]

[1] Natural Resources Canada
Canadian Forest Service
Atlantic Forestry Centre
PO Box 4000
Fredericton, NB
E3B 5P7
E-mail: Dale.Simpson@nrcan.gc.ca

[2] Natural Resources Canada
Canadian Forest Service
580 Booth Street
Ottawa, ON
K1A 0E4

Determining gene conservation needs across the country will provide important information to ascertain the role that the Canadian Forest Service can play. A survey was conducted to identify priority native tree and shrub species requiring gene conservation. The survey included shrubs greater than 1 m in height and those shorter than 1 m but belonging to a genus that includes trees. Species that may require gene conservation measures were identified on the basis of a set of criteria. If one or more of the criteria were judged to apply, the species was assigned a rating ranging from attention may be needed but current knowledge is inadequate, to specific gene conservation measures are required. The resulting lists were sent to people, known to have expertise, in each province and territory. The data from each province and territory were amalgamated into a single data set and sorted by genus. This allowed us to evaluate the frequency with which a given species was given a rating. Species were often assigned different ratings in different jurisdictions depending on their status for a particular province or territory. To simplify summarizing the survey, we only considered the highest rating value which is indicative of the worst case scenario for that species.

A total of 57 tree species (12 coniferous and 45 deciduous), including 2 varieties, and 107 shrub species (including 9 varieties) were identified as requiring some level (*in situ* and/or *ex situ*) of gene conservation in at least one province or territory. The large number of tree species is influenced in particular by the 25 or so of these species unique to the Carolinian forest of Ontario. *Salix* species were identified in each province and territory. Forty-two of the 56 *Salix* species and varieties require gene conservation measures. Twenty-six of the 29 species and varieties of *Crataegus* growing in Alberta and Ontario east to Newfoundland and Labrador require some form of gene conservation. Three dwarf species within the *Betula* genus were identified to be in need of conservation efforts in the Atlantic provinces as well as four *Betula* tree species in three provinces. *Ulmus* was another genus consistently identified throughout its range, in 7 provinces, as requiring specific gene conservation measures.

The results of the survey provide a basis for identifying gene conservation priorities for tree and shrub species in Canada but there are other considerations such as: 1) geographic distribution of species is important for setting priorities for conservation work and supporting research, 2) determining the need to work on species with populations threatened in part of its range but under no threat throughout the remainder of the range, 3) prioritizing efforts on threatened, outlying populations of species with known information on economic, ecological, and genetic parameters vs. those where these parameters are unknown, and 4) difficulties in taxonomic identification of some species and varieties.

CLIMATE MODELS AND GENETIC APPLICATIONS FOR LODGEPOLE PINE IN BRITISH COLUMBIA

Tongli Wang[1], Andreas Hamann[1], Sally N. Aitken[1], Alvin Yanchuk[2] and Greg A. O'Neill[3]

[1] Department of Forest Sciences
University of British Columbia
3041–2424 Main Mall
Vancouver, BC
V6T 1Z4
E-mail: tlwang@interchange.ubc.ca

[2] BC Ministry of Forests
Research Branch
PO Box 9519 Stn Prov Govt
Victoria, BC
V8W 9C2

[3] BC Ministry of Forests
Kalamalka Research Centre
3401 Reservoir Road
Vernon, BC
V1B 2C7

Maps of interpolated climate normals have recently become essential tools for many types of forestry research, such as studying genetic adaptation of trees to local environments, modeling species range shifts, or forest productivity under climate change scenarios. In this paper we evaluate two widely used climate models (i.e., polynomial functions of Rehfeldt and others (1999) and the PRISM climate model) for British Columbia, and improved the PRISM model through an elevation adjustment for temperature variables. Both models accurately predicted temperature variables; however, the PRISM model had a greater ability to predict local variation in precipitation.

We applied the improved climate model to develop climatic response functions of growth for lodgepole pine (*Pinus contorta*) provenances from each Seed Planning Unit (SPU) using new methodology. The climatic response functions were improved by using predicted anchor points of the quadratic curves. Productivity maps were produced for current and predicted future climatic regimes using Geographic Information Systems in British Columbia. We found that overall productivity of lodgepole pine will increase with increases in mean annual temperature (MAT) up to 2°C over current. Further warming will result in productivity declines and a northward shift in the productive range of the species. Some areas in southern BC will be beyond the species' climatic tolerance if MAT increases by 5°C. Optimization of seed source selection for reforestation will not only dramatically increase productivity if mild global warming continues, but facilitate increases in productivity with moderate warming (up to current MAT +3.5°C) and partially mitigate declines in productivity for warming beyond this level.

HOLOCENE CLIMATE CHANGE AND ITS IMPACT ON GENETIC STRUCTURES

Robert D. Westfall and Constance I. Millar

USDA Forest Service
Sierra Nevada Research Center
PSW Research Station
PO Box 245
Berkeley, CA
94701
E-mail: bwestfall@fs.fed.us

Widely used measures of population structure assume equilibrium conditions and most simulations of genetic structure are run over hundreds of generations and under constant background conditions. However, recent advances in climate science indicate that climatic variability since the late Glacial Maximum has been substantial. We first review climatic cycles from interannual to millennial periodicities, focusing here on those from centennial to millennial scales. We then review Holocene climatic periods in the Great Basin, USA and consequent vegetation changes, drawing on some of our own data from the Eastern Sierra Nevada. From data on fine-scale genetic structures in whitebark pine (*Pinus albicaulis*) and coast redwood (*Sequoia sempervirens*), we argue that these structures are the consequence of climatic changes over the past 600 years. Such structures are consistent with theoretical analyses of climate change and evolution (Pease et al. 1989, Garcîa-Ramos and Rodrîguez 2002). These studies also predict that evolution will lag climate change, empirically illustrated by data in Rehfeldt et al. (1999).

RECONSTRUCTING A PAST CLIMATE USING CURRENT MULTI-SPECIES' CLIMATE SPACES

Robert D. Westfall[1], Constance I. Millar[1] and John C. King[2]

[1] USDA Forest Service
Sierra Nevada Research Center
PSW Research Station
PO Box 245
Berkeley, CA
94701
E-mail: bwestfall@fs.fed.us

[2] Lone Pine Research
2604 Westridge Drive
Bozeman, MT
59715

We present an analysis of a ghost forest on Whitewing Mountain at 3 000 m in the eastern Sierra Nevada, southeast of Yosemite National Park. Killed by a volcanic eruption about 650 years ago, the deadwood on Whitewing dates by standard tree-ring analysis to 800–1330 CE, a period known as the Medieval Warm Anomaly. Individual stems have been identified as *Pinus albicualis*, *P. monticola, P. jeffreyi*, *P. contorta*, *P. lambertiana*, and *Tsuga mertensiana*. With the exception of *P. albicualis*, which is currently in krummholz form at this elevation, the other species are 200 m or more lower in elevation. One, *P. lambertiana*, is west of the Sierran crest and 600 m lower in elevation. Assuming that climatic conditions on Whitewing during this period were mutually compatible with all species, we reconstructed this climate by the intersection of the current climatic spaces of these species. We did this by first generating individual species' ranges in the Sierran ecoregions through selecting vegetation GIS polygons from the California Gap Analysis database (UCSB) that contain the individual species. Climatic spaces for each species were generated by the GIS intersection of its polygons with 4 km gridded polygons from the PRISM climatic estimates (OSU); this was done for annual January and July maximum and minimum temperature and precipitation and merged together for each species. Climatic intersections of the species were generated from the misclassified polygons of a discriminant analysis of species by the climatic data. The average data from these misclassified polygons suggest that the climate on Whitewing during the existence of this forest community was 230 mm, 1°C, and 3°C greater than present in precipitation, and maximum and minimum temperature, respectively.

DOTHISTROMA NEEDLE BLIGHT OF LODGEPOLE PINE IN NORTHWEST BRITISH COLUMBIA

Alex Woods

BC Ministry of Forests
Bag 6000
Smithers, BC
V0J 2N0
E-mail: Alex.Woods@gems8.gov.bc.ca

Dothistroma needle blight caused by the fungus *Mycosphaerella pini* is causing severe damage to managed and natural stands of lodgepole pine in northwest BC. There appear to be two principle causes behind the damage occurring in this specific area, at this time. First, forest management policy and practice has lead to an unprecedented amount of young lodgepole pine hosts on the landscape. Second, the weather of the past decade appears to be changing resulting in more frequent events of consistent days of warm rain during summer months. The weather events coinciding with a previous outbreak of Dothistroma in the study area were investigated. The weather events that possibly lead to the decline in this previous Dothistroma outbreak, two consecutive years of dry conditions, have not reoccurred during the current epidemic.

GENETIC VARIATION IN BLACK COTTONWOOD, *Populus trichocarpa*

Cheng C. Ying and Diane Holowachuk

BC Ministry of Forests
Research Branch
PO Box 9519 Stn Prov Govt
Victoria, BC
V8W 9C2
E-mail: Cheng.Ying@gems9.gov.bc.ca

A genecology study of black cottonwood was initiated in the mid-1990s. Cuttings were collected from over 1 000 trees throughout the major drainage along the coast of British Columbia, and Washington and Oregon, USA. Two common-garden tests were established in 1999 at two contrasting sites, Surrey Nursery (south coast) and Terrace (north coast). About 900 clones were tested. Stem elongation was measured every two weeks from April till elongation ceased. Bud flushing in 2001 and 2002 was assessed at weekly intervals from late February till leaflets were fully extended. The north coast test suffered extensive damage caused by moose. As a result, data were collected primarily from the south coast test. Data analyses focussed on parameter estimates from fitting growth curves and vegetative cycles, and their variation associated with drainage, stands (provenance) within drainage, and trees within stands. Preliminary results indicate an ecotypic pattern of geographic variation with a division along the Skeena and Nass Drainage. Substantial variation exists also among and within stands.

TREE SEED WORKING GROUP

WORKSHOP ABSTRACTS

QUALITY ASSURANCE IN THE SEED HANDLING SYSTEM

Dave Kolotelo

BC Ministry of Forests
Tree Improvement Branch
18793 32nd Avenue
Surrey, BC
V4P 1M5
E-mail: Dave.Kolotelo@gems7.gov.bc.ca

INTRODUCTION

What is Quality Assurance? Why do I need it? There are at least as many answers to these questions as people in this room. It is a 'concept' that is linked to the **continuous improvement** of activities you are involved with. As a starting point, I'll define Quality Assurance [QA] for our purposes as "the evaluation, monitoring, and management of information and practices related to activities within the Seed Handling System". It is a wide definition, but several concepts are apparent:

1) There is a need or desire to **improve** or better understand (evaluate) our practices.
2) This is not a one-time event, but a '**continuous**' process.
3) Change, especially constant change, is not something everyone is comfortable with.

Quality assurance has evolved from the manufacturing sector with the goal of reducing or eliminating product variability. When we are dealing with tree seeds the variability present in a seedlot will serve to insure our future forests against insects, diseases and yes even climate change. There is an intrinsic value in the variation present in our tree seed to ensure the resulting forest can survive until rotation age (if applicable). The common concept of reducing 'product variability' may not always be applicable and I'd like to emphasize the reduction in process variability (=standardization) in the Seed Handling System instead. I'm not saying we should encourage variation in our products, but that we need to recognize and not select against the genetic variation present in our seedlots.

For those producing a product it is more efficient to have cones, seed or seedlings all the same size and/or shape. The variability around these products is the cost of maintaining genetic variation in our products. Our closest seed industries (agriculture, bedding plants) do not have these same costs as they produce short-term crops with a relatively narrow genetic base. We often look to these industries for advancements in seed science and rightly so, but we must appreciate that these technologies will work more efficiently under the background of relatively little genetic variation. In these industries variation is frowned upon (i.e., if you pay for deep purple double petunias, you should get 100% deep purple double petunias). These industries are closer to classical QA as they truly wish to reduce and even eliminate variation. The distinction between our closest industries is important and needs to be appreciated.

I am not an expert on Quality Assurance, but it is something I truly believe is required to be efficient in our operations. It isn't very sexy, doesn't attract funding, and probably hasn't been a buzzword for several decades. Out of the reading I've done I'd like to present 7 'truisms' for QA before specifically discussing this mornings session.

QUALITY ASSURANCE "TRUISMS"

1) Focus on customer satisfaction (*understanding what they need*).
2) Concentrate on reducing variability.
3) Decisions should be based on data.
4) Root causes for problems should be sought out by disciplined investigation.
5) Data recording must be performed consistently.
6) Barriers between departments need to be broken down.
7) QA needs to provide significant added value and it needs to demonstrate it effectively to management.

The workshop is intended to be an opportunity to hear various people speak about QA and how it may be implemented in the Seed Handling System. Different speakers will approach the topic differently and no one will entirely cover their topic of discussion. There is no QA system recipe and system development can vary greatly between similar facilities. In order to obtain more comprehensive information I'm going to try and invoke some audience participation following each of our talks this morning. You participation will determine how successful this session is – please participate and speak your mind.

The Seed handling System can be broken down into discrete components, but it is a continuous chain of activities from reproductive bud development to the production of seedlings for reforestation. Following each of our talks I'd like to spend approximately 10 minutes discussing QA at this stage of the Seed handling System. Please comment freely indicating other QA activities your facilities may implement (QA - things you do / things you monitor). To ensure some feedback I'm going to pose two discussion questions.

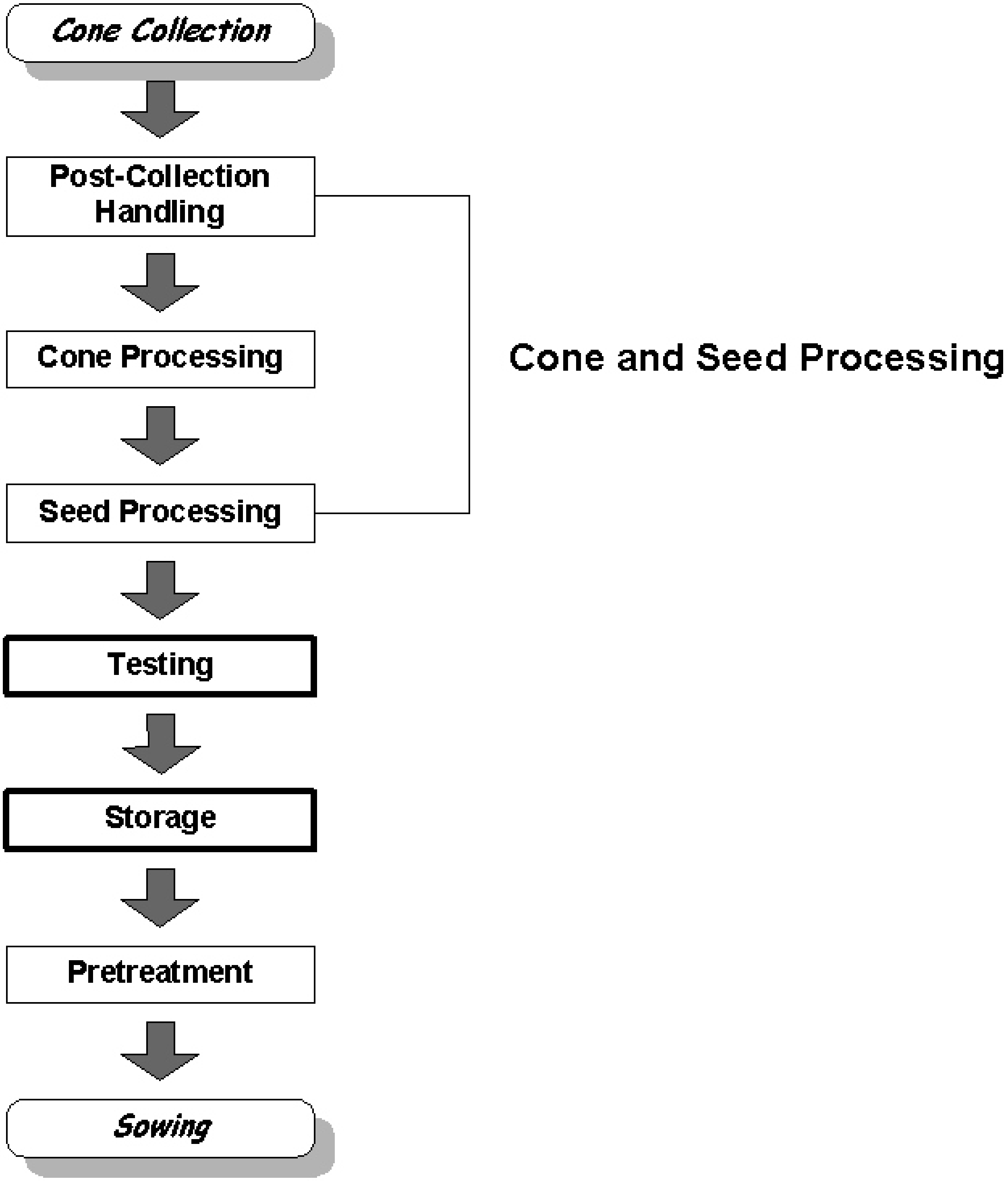
1. What is the largest source of variability at this stage going from the inputs to outputs?
I believe that by identifying the largest source(s) of variability one can go a long way to targeting QA points and improving efficiency (i.e., reducing process variability).

2. What step is most critical to delivery of the output?
The most variable stage may not be the most critical to product delivery. Is there one stage that can make or break your product?

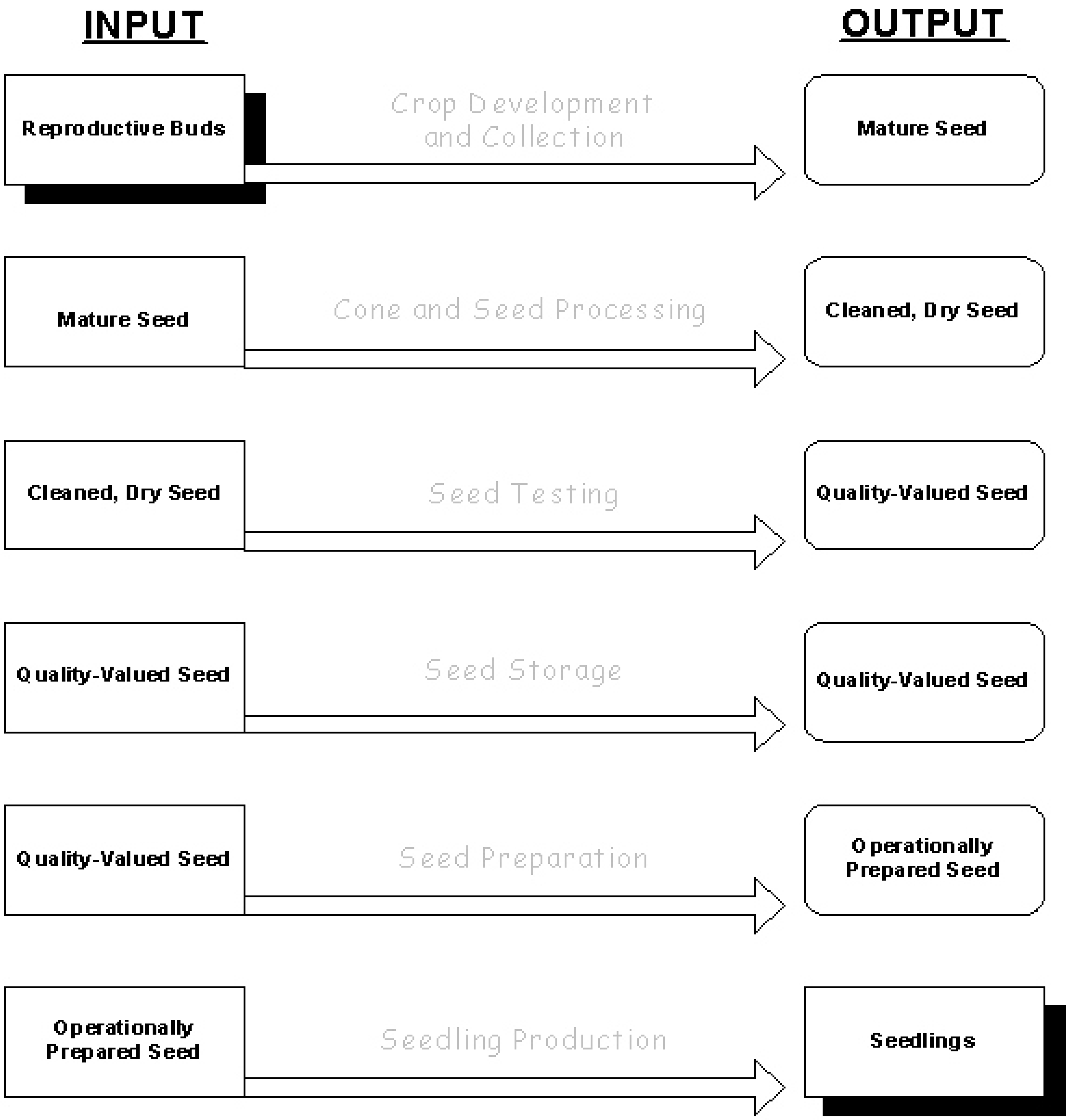
I hope you enjoy the session this morning. I think it is important to us running efficient operations, being good stewards and making advances in our understanding of tree seed biology. Thank you for your interest. Just one final thought as it is very important that you actually use the information you generate through your QA program.

Data are not Information
Information is not knowledge
Knowledge is not Wisdom

The Seed Handling System



Quality Assurance in the Seed Handling System



1. What is the largest source of variability at each stage going from the inputs to outputs?

2. What step is most critical to delivery of <u>each</u> output?

CROP MAINTENANCE AND COLLECTION IN SEED ORCHARDS

Chris Walsh

BC Ministry of Forests
Tree Improvement Branch
Kalamalka Seed Orchards
3401 Reservoir Road
Vernon, BC
V1B 2C7
E-mail: Chris.Walsh@gems4.gov.bc.ca

Regular orchard maintenance is important for producing a quality crop. Healthy trees are more likely to produce healthy seeds. The trees' needs are provided for through appropriate irrigation, fertilization, general pest protection and site maintenance. Orchard tree identities must be maintained to allow pickers to find the right trees.

Protect the developing crop from cone and seed pests. Regular, diligent monitoring is essential. Some pests dealt with at Kalamalka include *Leptoglossus, Cydia, Strobilomyia,* and *Dioryctria*

Harvest timing can have a significant effect on seed quality. Cones collected too early may contain seed that will germinate poorly or not store well. Cones left too late can open and shed valuable seed. Strategies to help achieve optimum timing include factors such as an experienced labour supply, crew safety, and motivation. The seed cutting test is the final word in determining seed maturity but to judge cone ripeness on a large scale we use the cone cutting test: the cone is cut in half longitudinally and the cut surface examined, paying particular attention to the cone axis. We prioritize picking throughout the harvest using this method.

Safe cone storage and shipping to the extractory ensure that the quality of a well cared for crop is preserved. Ventilation, temperature control, pest protection, and maintaining room for cone expansion are all addressed.

QUALITY ASSURANCE IN SEED TESTING

J.D. Simpson

Natural Resources Canada
Canadian Forest Service
Atlantic Forestry Centre
PO Box 4000
Fredericton, NB
E3B 5P7
E-mail: Dale.Simpson@nrcan.gc.ca

Seed testing is conducted according to international standards such as the International Seed Testing Association’s “International Rules for Seed Testing.” Obtaining a random, representative sample of seed is the starting point for testing. The working sample is used to determine moisture content, purity, 1000-seed weight, and germination. The oven method is typically used to determine moisture content. Purity analysis is conducted to determine the percentage, by weight, of pure seeds of the crop species, seed of other species, and inert matter. Thousand-seed weight is determined by counting and weighing eight replicates of 100 seeds each, calculating the mean, and multiplying by ten. Germination tests are the most important assessment of a seedlot’s quality. It is important that standards be adhered to in order for the results to be as repeatable as possible. Dormancy is commonly encountered with a number of species and is usually alleviated by a period of moist chilling. Seeds are considered to have successfully germinated when all essential structures necessary for continued normal development can be evaluated (radicle, hypocotyl/epicotyl, cotyledons). Viability tests are useful to quickly indicate if seeds are capable of germinating.

QUALITY ASSURANCE OF SEED STORAGE

Donna Palamarek

Alberta Sustainable Resource Development
Tree Improvement and Seed Centre
Smoky Lake, AB
T0A 3C0
E-mail: Donna.Palamarek@gov.ab.ca

The Alberta Tree Improvement and Seed Centre (ATISC) is a Government of Alberta Sustainable Resource Development facility located 150 kilometres northeast of Edmonton. ATISC manages two seed programs both of which have their own storage facility and database management system. The Reforestation Seed Program is responsible for the registration, storage, distribution and tracking of all operational tree seed used for public land reforestation. Currently there are about 42 000 kg of seed of which about ⅔ is owned by forest industry and oil sands companies with the remaining ⅓ belonging to the government. The majority of seed is from wild collections with improved seed accounting for about 2% of the inventory. Average lot size is 25 kg. The Research Seed Program is responsible for the processing, testing, storage, and maintaining pedigree records of research and conservation seedlots in support of the provincial tree improvement program. There are presently about 5 500 seedlots about 4 800 of those being single tree collections. Average lot size is 20 g.

Three functions of seed storage are to: 1) provide storage conditions to minimize loss of seed quality, 2) maintain correct seedlot identity, inventory, and location, and 3) protect seed from harm and/or loss.

Reforestation seed is stored in an underground storage facility built in 1979. Being underground aids in maintaining low temperatures in case of mechanical failure and reduces energy costs. Because the facility is apart from the rest of ATISC's infrastructure and made of concrete there is added protection from fire. Storage temperature is maintained at -18ºC except during defrost cycles when the temperature rises to -16ºC. The bunker has four individual walk-in freezers and has a storage capacity of 84 000 kg of seed. Seed is stored in plastic bags inside waxed cardboard boxes. The 5 mil plastic bags are expelled of excess air and heat-sealed to prevent moisture absorption and spillage if boxes are dropped. The bags are replaced every 10 years. Withdrawals are carried out in the anteroom where temperature is +5ºC which minimizes temperature fluctuations in the seed and excessive moisture absorption.

Because of small lot size, research seed is stored in either glass or high-density polyethylene bottles and sealed with electrical or Teflon tape. The research storage facility is a -18ºC walk-in freezer located in the technical building where seed processing and testing take place. Seedlots are held at +2˚C for two hours and then at room temperature for two hours prior to withdrawal to minimize moisture absorption. Where amounts allow, portions of seedlots are withdrawn and held in the underground bunker for duplicate storage protection.

ATISC has on-site staff that maintain the storage facilities on a day-to-day schedule. Both facilities have back-up power generators and both are monitored 24 hours a day, seven days a week for temperature fluctuations. Should temperatures rise above or fall below the desired set points, a call-out system notifies an ATISC staff member of the situation.

All reforestation seedlots are initially tested for germination, moisture content, purity, and 1000-seed weight prior to storage. Proper moisture content is critical for long-term storability and the desired moisture content range is between 4 and 8%. Government seedlots are retested for germination every 4 to 5 years. Every tenth seedlot that is selected for germination testing is tested for moisture content as well. Industry clients are advised to retest their seed every five years. Because of small lot size, research seed quality is monitored through a reference seedlot testing program where 2% of the total seedlots are selected and tested annually (deciduous) or biennially (conifers).

Reforestation seedlot bags are tagged inside and out with the seedlot number. All boxes are labelled with the seedlot number and the current amount. Seed is stored by company by collection year. A new storage system is currently under review that will allow a company's seed to be stored throughout the four freezers instead of being concentrated in one freezer and will prevent seedlots with similar numbers from being stored adjacent to each other. Reforestation seedlots are inventoried annually to reconcile seed amounts with record amounts. Research seedlot bottles are labelled inside and out with assigned accession numbers and are arranged in numerical sequence.

The ATISC work site is fenced and gates are locked after hours and on weekends. Both storage facilities are locked and the reforestation seed bunker is equipped with an intrusion alarm system.

QUALITY ASSURANCE IN SEED PREPARATION

Dave Kolotelo

BC Ministry of Forests
Tree Improvement Branch
18793 32nd Avenue
Surrey, BC
V4P 1M5
E-mail: Dave.Kolotelo@gems7.gov.bc.ca

Operational seed preparation is concerned with overcoming dormancy (or improving germination characteristics) and facilitating sowing. The treatments are intended to mimic lab testing procedures that determine the quantity of seed required. Four Quality Assurance (QA) foundations are the main supports for seed preparation and all services at the BCMoF Tree Seed Centre: 1) Avoid Physical Contamination (i.e., avoid introduction of debris = **cleanliness**), 2) Avoid Seedlot Contamination (i.e., avoid mixing of seedlots = labelling + attention), 3) Information Management (**organization**), and 4) Handling a perishable product (**exercise due care**).

The last foundation is especially important with imbibed seed as seed can be more easily damaged at elevated moisture contents. The first step for all BC species (except western redcedar that is pellet-coated) is to soak the seed. A minimum amount of moisture must enter the seed before dormancy can be overcome and/or germination initiated. A running water soak is used to reduce the quantity of seed-borne pathogens. Surface drying is subsequently employed to provide a free flowing product that can be easily mechanically sown and not promotive to fungal growth. It is critical that only surface moisture is removed and that internal moisture is not removed during this process. Optimum moisture contents appear to vary by species, but most appear to fall within the 30–35% window. Moisture content can be calculated non-destructively if one knows the storage moisture content, storage weight and hydrated weight of the seed.

The second critical step following appropriate hydration is to provide the correct duration of stratification. Most conifers have some degree of physiological dormancy, but mechanical dormancy is also implicated in western white pine and yellow cedar. Species requirements range from no stratification (western redcedar) to 98 days for western white pine. Naked stratification (i.e., no moisture-retaining media is involved) is conducted at our facility in 4 mil (0.1 mm) polyethylene bags. This thin material allows some gas exchange, but the bags should also have approximately a 4 cm opening at top to allow additional exchange. It is important to perform some germination testing to evaluate the effectiveness of your operational treatments.

Some species have specialized pretreatment methods. In subalpine, Amabilis, and Noble fir we are usually using a split stratification system in which a high moisture content is maintained for 28 days, the seed is then dried back to 30–35% moisture content at this stage and then placed back into stratification for an additional 56 days. In yellow cedar, an imbibed warm period (28 days) precedes cold stratification. In western white pine a 14-day soak is used and in western redcedar no soaking or stratification is performed, but the seed is pellet-coated due to difficulties in mechanically sowing the light-weight winged seed.

Some additional keys to successful seed preparation involve periodic inspection of seed condition and the mixing of seeds within a request to ensure uniform distribution of moisture and access to oxygen. Problems such as mold growth can usually be easily resolved if caught early enough. A well documented set of procedures and troubleshooting processes can be extremely helpful during the hectic sowing season. Tools should be in place to deal with potential problems. At shipping the seed bags need to be closed to avoid contamination and should be performed using an overnight courier service.

SEED QUALITY ASSURANCE IN THE NURSERY

Fernando Rey

Pelton Reforestation Ltd.
12930 – 203rd Street
Maple Ridge, BC
V2X 4N2
E-mail: frey@pelton.com

A seed handling protocol has been developed at Pelton Reforestation Ltd. to ensure the efficient use of seed in seedling production. All the procedures undertaken during seedling production are documented and tracked using an "order"-based Management Information System (PREMIS). Seed information on arrival date, amount, cleanliness, presence of insect/disease damage, stratification, seed treatment, and seeding factor, among others, is incorporated into a database for future reference. Different seed handling procedures were described and discussed in relation to "seed/seedling use efficiency".

THERMO-KINETICS OF WATER ABSORPTION, WITH SPECIAL REFERENCE TO NOBLE FIR SEEDS

D. George W. Edwards

FTB Forest Tree Beginnings
4018 Cavallin Court
Victoria, BC
V8N 5P9
E-mail: dgwe@shawcable.com

The role of imbibition in water uptake by tree seeds is discussed. Emphasis is placed on the effect of temperature on the rate and, more importantly, the completeness of imbibition. A theory is presented to show how the weak attractive force between water molcules and particles of the absorbing substrate (the seed coat), and the kinetic energy of the water molecules, are altered by changes in temperature. Based on this theory it is concluded that, as all text books state, imbibition occurs more slowly at lower temperature than at higher temperatrure. However, to date, no text book has been found that states that given suffcient time, the amount of water absorbed at low temperature is significantly higher than that absorbed at high temperature. Data from a study on noble fir seeds are used to support the theory and the conclusion.

EFFECT OF MOISTURE CONTENT DURING PRE-TREATMENT OR STORAGE ON THE GERMINATION RESPONSE OF ALDER, BIRCH AND OAK SEEDS

Conor O'Reilly, Norberto De Atrip and Colin Doody

University College of Dublin
Dept. Crop Science, Horticulture and Forestry
UCD Belfield
Dublin
Ireland
E-mail: conor.oreilly@ucd.ie

Alder (*Alnus glutinosa* [L.] Gaertn.), birch (*Betula pubescens* Ehrh.), and pedunculate oak *(Quercus robur* L.) now form an important part of the planting program in Ireland. However, seed germination in the nursery bed is often low and/or slow. To this end, the effect of seed moisture content (MC) during pre-treatment on the germination performance of these species was investigated. Alder and birch have orthodox seed characteristics (easy to store at MC < 12%), whereas oak is difficult to store successfully (relatively high MC levels must be maintained during storage). Seeds of each species were adjusted to various MC levels and stored at 4 C for various periods. Acorns were also stored at -3 and 1 C. The optimum or target MC (TMC) during prechilling was about 30% in alder and 35% in birch. Germination increased following up to 24 weeks of prechilling for seeds at TMC levels in alder and 12 weeks in birch, significantly better than achieved using the standard method (fully imbibed for shorter periods). Thereafter, germination remained almost unchanged for seeds that received up to 36 weeks of prechilling, whereas the fully imbibed seeds deteriorated or germinated prematurely. In oak, acorns adjusted to the highest MC level (46%) and stored for 4–6 months at -3 C had the highest germination (76%) while the non-soaked controls and those adjusted to 37% MC has the lowest values (17% for both treatments). Interestingly, the control acorns had significantly lower germination than seeds that were soaked and then dried back to similar levels.

IUFRO UNIT 7.01.14

RESISTANCE BREEDING WORKSHOP

ABSTRACTS

EFFECTS OF GENOTYPE AND SILVICULTURE ON EXTENT OF TERMINAL WEEVIL DAMAGE TO JUVENILE SITKA SPRUCE

Charlie Cartwright[1] and John King[2]

[1] **BC Ministry of Forests**
Research Branch
7060 Forestry Road
Mesachie Lake, BC
V0R 2N0
E-mail: Charlie.Cartwright@gems1.gov.bc.ca

[2] **BC Ministry of Forests**
Research Branch
PO Box 9519 Stn Prov Govt
Victoria, BC
V8W 9C2

Provenance-based resistance to terminal weevil damage was noticed in IUFRO spruce trials that were established by the BC Ministry of Forests in the 1970's. Subsequently, parent trees were selected from resistant sources and areas of similar climate, then screened at disease garden sites. Extra plants from these open-pollinated progeny tests were used to investigate the effects of silvicultural treatments and establish if they supported or detracted from the genetic effects. In 1994, resistant and susceptible families of Sitka spruce (*Picea sitchensis*) were inter-planted with western hemlock (*Tsuga heterophylla*) at rates of 10, 50, and 100% spruce. The following year similar genotypes were planted at 1, 2, and 3 m spacing. Lastly spruce differing in resistance were deployed to 10 sites that varied in weevil hazard (degree-days). Results from the spacing and inter-planting experiments are reported, and the weevil hazard series is described.

MAJOR AND 'R' GENE RESISTANCE – POSSIBILITIES AND PARALLELS BETWEEN PATHOGENS AND INSECTS

John N. King and Peter Ott

BC Ministry of Forests
Research Branch
PO Box 9519 Stn Prov Govt
Victoria, BC
V8W 9C2
E-mail: John.King@gems7.gov.bc.ca

Large gene effect resistance including ‘R’ gene resistance is noted widely in resistances to pathogens and an extensive literature has developed for this. In forest trees the resistance to white pine blister rust (*Cronartium ribicola*) by both western white pine (*Pinus monticola*) and sugar pine (*P. lambertiana*) provide classic examples of this type of resistance. These large gene effect resistances have not been as widely reported in insect resistance and entomologists have concentrated their efforts in describing the mechanisms of resistance rather than investigating such gene effects. One noted exception has been with wheat resistance to the Hessian fly (*Mayetiola destructor*). Large gene effects though do appear to be present in the resistance of Sitka spruce (*Picea sitchensis*) populations to the white pine weevil (*Pissodes strobi)* as indicated by some large phenotypic effects in our data investigations. We report here this evidence from our phenotypic data investigation and look at some of the techniques that can be used in detecting genes of large effects from such phenotypic data.

OVERVIEW OF *Phytophthora lateralis* RESISTANCE PROGRAM IN PORT-ORFORD-CEDAR

R.A. Sniezko[1], S. Kolpak[1], E.M. Hansen[2], L. Elliott[1] and D. Goheen[3]

[1] USDA Forest Service
Dorena Genetic Resource Center
Cottage Grove, OR
97331
E-mail: sekolpak@fs.fed.us

[2] USDA Forest Service
SW Oregon Insect and Disease Center
Central Point, OR
97502

[3] USDA Forest Service
J. Herbert Stone Nursery
Central Point, OR
97502

Phytophthora lateralis is a non-native, invasive root pathogen that has infected 8% of federal lands throughout the range of Port-Orford-cedar (*Chamaecyparis lateralis*) in southwest Oregon and northwest California. Some local populations have had very high mortality and riparian communities on ultramific soils are at risk. An operational program to develop populations of Port-Orford-cedar that are resistant to *P. lateralis* is underway. Phenotypic selections from forest stands are screened using a stem dip test and the top 10% are re-tested using a root dip technique. Over 11 000 field selections have been tested since 1997. Thus far, approximately 100 selections with strong resistance have been identified in the root test. Full-sib families (including selfs) are generated to characterize resistance mechanisms and enhance resistance. Several types of resistance appear to be present in seedling testing: 1) high survival and 2) slower rates of mortality. A single dominant resistant gene is suggested by mendelian segregation ratios for the high survival families. Work is underway to further characterize the slow dying families and to pyramid with the high survival resistance. A Fain's test suggests a single dominant resistant gene is influencing lesion length in the stem dip test.

The phenotypic correlation between stem dip and root dip resistance is moderate, while the genetic relationship is low suggesting the traits are unlinked. Early results from field studies show good survival of resistant families relative to susceptible controls. An important component of the resistance program is maintaining high genetic diversity in the Port-Orford-cedar populations. Genetic studies are underway to characterize genetic structure and diversity in pre-epidemic, post-epidemic, and *P. lateralis* resistant orchard populations. Initial efforts to map resistant genes using an outbred F2 mapping population is in preparation.

EARLY SURVIVAL, HEIGHT, AND BLISTER RUST PERFORMANCE OF *Pinus albicaulis* SEED SOURCES FROM THE INLAND NORTHWEST

Mary F. Mahalovich

USDA Forest Service
Forestry Sciences Lab
1221 S. Main St.
Moscow, ID
83843
E-mail: mmahalovich@fs.fed.us

One hundred ten populations from eastern Washington, Idaho, and Montana from 1 900–3 300 m in elevation, were sown in a common garden study (nursery rust screening) in 1999 to evaluate genetic differentiation. First-year survival varied from 0.4 to 93.4% with a mean of 37.7%, with no differentiation based on geography or elevation. Third-year baseline measurements were obtained (survival, height, and presence of *Fusarium* spp.) prior to artificial inoculation with *Cronartium ribicola* in September 2001. Approximately half of the seedlings of each population were uninoculated to serve as controls. Inoculation efficiency as measured by percent spotting (82.7%) and spots per meter (0.37) was comparable to *Pinus monticola*; however, average number of spots per meter (0.37) typically should be higher (5–20) to accurately assign resistance traits to individual trees. Percent resistant *P. alibcaulis* seedlings (57.3%) is within the range of those reported for *P. monticola*. Preliminary analysis of individual-tree traits is showing low percent bark reaction (3.1%) and needle shed (8.8%) and similar no-spot (17.3%) and short shoot (28.1%) seedlings as compared to *P. monticola*. The majority of the horizontal traits (spot frequency, early stem symptoms, canker alive (tolerance)) are significant ($p < 0.0001$) among all populations except for adjusted bark reaction ($p < 0.6659$). Unlike *P. monticola*, four-year height was significant ($p < 0.0001$) among populations, and *P. albicaulis* is showing both longitudinal and elevation gradients, which likely follow the distribution of mountain ranges in the Inland Northwest. Following the final rust inspection later the fall of 2004, the rust resistance index will be finalized and populations will be ranked by performance. Based on the outcome of regression models, seed transfer guidelines may need to be updated. Survivors of the study will be planted in a long-term performance test in northern Idaho and scion collections will begin from above-average populations to establish seed orchards for the Bitterroots-Idaho Plateau, Selkirk-Cabinets, and Central Montana seed zones. Seed orchards will be located in *P. alicaulis* habitat types rather than low elevation tree improvement areas in an effort to promote flowering.

THE BASIS FOR SELECTION OF PARASITE-SPECIFIC, NON-HOST RESISTANCE

George Newcombe

Department of Forest Resources
University of Idaho
Moscow, ID
83844-1133
E-mail: georgen@uidaho.edu

Related plants host related fungal parasites, many of which are narrowly specialized. So plants can be nonhosts to many specialized parasites of congeners. According to theory, plants owe this general, nonhost resistance to genes that are not parasite-specific. It is presumably only when a parasite of a congener overcomes basic, non-host resistance that a coevolutionary arms race ensues. The initial, extreme susceptibility is thought to spark many generations of selection in both host and parasite, that ultimately results in parasite-specific, gene-for-gene interactions. But, evidence from many studies of resistance in *Populus* suggest that nonhost resistance is parasite-specific. This, and other evidence to be discussed, leads away from the accepted explanation for the existence of parasite-specific, major genes for resistance.

TRAUMATIC RESINOSIS IN SITKA SPRUCE – A RESISTANCE MECHANISM AGAINST ATTACK BY THE WHITE PINE WEEVIL?

Aine Plant

Biological Sciences
Simon Fraser University
8888 University Drive
Burnaby, BC
V5A 1S6
E-mail: aplant@sfu.ca

White pine weevil (*Pissodes strobi* Peck) is a serious pest of Sitka (*Picea sitchensis*) and interior spruce (*P. glauca* x *engelmannii*) in BC. This pest damages the terminal leader causing growth loss and stem deformities that severely impact tree value. Thus far there are no effective methods to control the white pine weevil. As a result, selection and breeding for weevil resistant genotypes hold promise to minimize weevil damage associated with reforestation programs.

In spruce, weevil attack induces a traumatic resinosis response that is characterized by the *de novo* synthesis of oleoresin that is sequestered in newly formed resin canals. Oleoresin is a complex mixture of monoterpenes, sesquiterpenes, and diterpene resin acids that provide chemical and physical protection against herbivores and pathogens. To determine whether traumatic resinosis is an important determinant of resistance we have examined this response in Sitka spruce genotypes that are resistant or susceptible to weevil attack. To achieve this we undertook molecular, histological, and chemical approaches to examine: 1) the expression of genes that encode enzymes responsible for terpenoid formation, 2) the formation of resin canals in the xylem, and 3) qualitative and quantitative changes in resin profiles. The data are presented and discussed as they relate to the response of susceptible and resistant Sitka spruce to artificial (achieved by stem drilling) and real weevil attack.

RESISTANCE BREEDING IN SITKA SPRUCE AGAINST THE GREEN SPRUCE APHID – RESULTS FROM THE DANISH BREEDING PROGRAM

Hans Roulund[1], Susanne Harding[2], Hubert Wellendorf[1],
Mogens L. Jørgensen[2] and Elise Skov[1]

[1] Royal Veterinary and Agricultural University
Forest and Landscape
DK-2970
Denmark
E-mail: hro@kv.dk

[2] Royal Veterinary and Agricultural University
Institute of Ecology
Denmark

The paper summarizes a joint European project: Improving protection and resistance of forests to the spruce aphid (*Elatobium abietinum*), with special reference to the Danish investigations and their consequences for the Sitka spruce (*Picea sitchensis*) breeding program in Denmark. Factors investigated were needle loss, needle anatomy, content of phenols and terpenes, and RAPD markers linked to major genes behind field resistance.

The needle loss was studied in a 20-year-old open-pollinated progeny test from 15 selected clones. The ortets were selected in a heavily attacked Danish stand of Washington origin as healthy escapes, i.e., not attacked and included in a clonal seed orchard. Attacks were recorded in the progeny trial in three separate years 1990, 1992, and 1999, in which the progenies developed from a juvenile to a more mature stage with flowering, seed set, and closed canopy. There were significant difference between progenies demonstrating family heritabilities of 0.6–0.7, but all progenies showed a degree of resistance. The seed orchard offspring showed 50% less needle loss, compared to a commercial standard. In conclusion this investigation showed a consistency in resistance to *Elatobium abietinum* over generations and through different onthogenetic stages.

The possibility to characterise resistant trees by needle anatomy or content of phenols or terpenes was tried, but results were not clear. Two intermediate attacked families were used in the search for RAPD markers co-segregating with field resistance. Three markers co-segregated with needle loss, one in one family and two in the other. In the family in which two markers co-segregated with field resistance, apparent epistatic gene effects on field resistance were observed.

Selection for aphid resistance, either direct phenotypic or marker aided, appears to result in persistent gains throughout the entire rotation of Sitka spruce.

IDENTIFICATION OF GENES INVOLVED WITH WEEVIL RESISTANCE IN SPRUCE

**D. Rungis, Y. Bérubé, J. Wilkin, J. Zhang, S. Ralph, C. Douglas, B.E. Ellis,
J. Bohlmann and K. Ritland**

**Department of Forest Sciences
University of British Columbia
2424 Main Mall
Vancouver, BC
V6T 1Z4**

Forest health is one of the main areas of interest for the GenomeBC forestry project. We have utilised various approaches to further basic understanding of the genetic mechanisms involved and to develop tools for use in forest health improvement. These approaches include the use of microarrays to identify the genes involved in resistance and the use of DNA markers for genetic mapping and genetic variation surveys. The microarray and marker development has been based on a spruce Expressed Sequence Tag (EST) sequencing project that has identified over 20 000 unique genes expressed in various spruce tissues. Development of highly informative DNA markers in conifers has been viewed as a formidable task due to the large, highly repetitive, and mostly uncharacterized genome. Using our EST database and through the integration of bioinformatic and genetic tools we have developed informative markers that will be highly transferable both within spruce species and among other conifers. The combination of information from a wide variety of sources will expedite the development of molecular genetic tools for use in spruce.

BREEDING WESTERN REDCEDAR FOR HERBIVORE RESISTANCE

John Russell

BC Ministry of Forests
Research Branch
7060 Forestry Road
Mesachie Lake, BC
V0R 2N0
E-mail: John.Russell@gems1.gov.bc.ca

Deer and elk browsing on western redcedar (*Thuja plicata* Donn) in the Pacific Northwest can result in delayed regeneration, and in severe cases, plantation failure. In addition, it can cost up to $6 CAN per tree to protect seedlings from browse and bring a plantation to free-to-grow. We are in the process of developing populations of deer resistant and deer preferred trees to help alleviate this problem.

Foliage samples from over 2 000 trees in a western redcedar genetic trial composed of 60 open-pollinated families from 14 populations on southern Vancouver Island were analyzed for 22 monoterpene compounds. In addition, browsing pressure (percent and intensity) and height growth were measured in the field. Browsing pressure was high with approximately 22% of the trees browsed with a mean family range from 5 to 40%. Narrow-sense heritabilities of the seven most prevalent monoterpenes varied from 0.33 to 0.56 and additive CV from 21 to 31%. Genetic correlations among these seven compounds were all positive and most were greater than 0.80. Genetic correlations with total and individual terpene content with growth were all not significantly different from zero.

A combined family within-family index, adjusted for replication effects, was constructed for total foliage terpene concentration. Individuals have been selected for two divergent populations: 1) deer resistance, selected for both absence of deer browse and high needle monoterpenes and 2) deer preferred, selected based on both heavy browse and minimal or no needle monoterpenes. We are currently testing foliage from these putatively resistant trees by feeding them alongside the preferred foliage to penned deer in feeding choice experiments. This will help to explain if specific needle monoterpenes alone result in resistance to deer browsing or if other factors such as primary sugars are also involved. Selections will then be bred for increased resistance based on the above feeding choice experimental results.

Once we are confident in calling these selections deer resistant, the next step is to outplant seed lot mixtures of varying levels of resistance in different percentages in operational trials. If deer pressure is high mixtures of deer resistant with wildstand seed lots would give the deer something to eat and perhaps the resistant trees will be left alone. The preferred trees, which taste just like lettuce, would most likely be gone the day they were planted, leaving the deer no choice but to eat the bitter resistant trees. Although they are high in toxic chemicals, the deer will make a choice on the balance between energy input and cost of detoxification. If deer pressure is moderate but still present, and volume production is a goal, then mixtures of deer preferred seed lots with elite growth seed lots may give the deer enough foliage to browse on and the elite trees may be left alone or browsed minimally.

WEEVIL RESISTANCE OF PROGENY DERIVED FROM PUTATIVELY RESISTANT AND SUSCEPTIBLE INTERIOR SPRUCE PARENTS

René Alfaro[1], Lara vanAkker[1], Barry Jaquish[2] and John King[3]

[1] Natural Resources Canada
Canadian Forest Service
Pacific Forestry Centre
506 W. Burnside Road
Victoria, BC
V8Z 1M5
E-mail: Rene.Alfaro@nrcan.gc.ca

[2] BC Ministry of Forests
Research Branch
3401 Reservoir Road
Vernon, BC
V1B 2C7

[3] BC Ministry of Forests
Research Branch
PO Box 9519 Stn Prov Govt
Victoria, BC
V8W 9C2

The white pine weevil, (*Pissodes strobi*), has a major impact on spruce regeneration in western North America. Silvicultural, chemical, and biological controls have proven to be inadequate or impractical and genetic resistance is now being considered as a promising tool for weevil management. A collaborative program (Canadian Forest Service and BC Ministry of Forests) to screen BC spruce for resistance to white pine weevil is described. The results of screening controlled-cross progeny derived from weevil resistant and susceptible parents are presented and bark resin canal characteristics of three cross types of differing weevil resistance status are described.

NATIONAL SURVEY OF FOREST GENETIC RESOURCES MANAGEMENT WORKSHOP

A SURVEY OF FOREST GENETIC RESOURCES MANAGEMENT PROCESSES AND PRACTICES IN CANADA

Donald T. Lester

Genetic Resource Management Consulting
Saltspring Island, BC
V8K 1B2
E-mail: dlester@saltspring.com

BACKGROUND

In 2002, the Alberta Forest Genetic Resources Council proposed a study to review how the management of genetic resources of forest trees in the province compared with that of other provinces and to learn from the experience of others. To initiate a comparison, a sub-committee developed a list of topics chosen for relevancy to the management of forest genetic resources and forwarded that list to other Councils in Canada (British Columbia, New Brunswick, and Ontario). The Councils expressed interest in a comparative study and requested additional details. The Alberta Council then assigned a committee to develop a survey that would include the specified topics.

The potential for a survey was explored further at a meeting of representatives from the Alberta Council and the Forest Genetics Council of British Columbia. Two issues were immediately apparent: 1) the operating environment of each Council was poorly understood by the other Council and 2) differences in operating environments would be likely to pose challenges to the comparison of specific operations for some topics. The challenges were expected to increase if some topics were expanded to include technical details.

Despite the expected difficulties, it was deemed useful to recommend a proposal to the Alberta Council. That proposal was as follows:

> *To circulate a very general survey of topics focused at the policy and planning level. The intent of the survey would be to prompt an exchange of ideas and discussion of issues both at the level of policy and, if desired, at more technical levels.*

The Alberta Council accepted the recommendation and directed that all Canadian provinces and territories with forests, regardless of whether a council was in place, should be invited to participate. A survey was developed and all provinces and territories, except Nunavut, were contacted.

Initial responses to the Survey showed that several of the questions were open to different interpretations. Most respondents attached comments to clarify their responses and correspondence with them provided additional information.

At an October 2003 meeting of representatives from the Alberta and British Columbia Councils, it was decided to contact respondents again with a note having the following objectives: 1) distribute an initial, general summary of results, 2) provide an opportunity to change responses (especially those of “not sure”), 3) obtain additional information (number of seed zones, average annual planting numbers, percentage of reforestation by planting) as rough measures of the complexity of forest genetic resource management in each jurisdiction, and 4) indicate the possible extent of public distribution of Survey results and determine whether jurisdictions would choose to have their responses identified.

APPROACH

Completed surveys were received from 11 of 12 jurisdictions. All surveys included comments that helped to clarify responses about specific topics.

The 11 surveys were numerically summarized by the process outlined below:

1. Tally survey responses in 8 classes. The initial tally represented only entries provided by respondents.
    a. Yes
    b. Yes with attached comment

   c. No
   d. No with attached comment
   e. Respondent is "not sure"
   f. Item is being developed
   g. Submitted response is unclear
   h. Topic is not applicable

2. Identify contradictions and uncertainties.

3. Contact respondents for clarification of items under 1.g above.

4. Revise survey tally and array by jurisdiction as "Yes" or "No".

5. For each Survey question, consolidate the tally as follows:

   a. For jurisdictions choosing to be identified, present all "Yes" and "In Progress" responses (Appendix I)

   b. For jurisdictions choosing anonymity, present sums of "Yes" and "In Progress" responses (Appendix I)

6. List some apparent contradictions:

   a. The interpretation of whether policies and plans exist varied because the Survey did not specify whether policies and plans must be written. Therefore, a response of "No" to the query "Does the province have…." is not necessarily contradictory to a response of "Yes" to implementation of a plan.

   b. Similarly, a response of "Not Applicable" might or might not be appropriate when applied to a topic whose apparent prerequisite was tallied as non-existent.

INTERPRETATION

The following interpretations were made from Appendix I. Note that the proportion of "Yes" replies would be increased if the uniformly negative responses from one jurisdiction were omitted. In that jurisdiction, there is virtually no commercial timber harvest at present.

Section 1.1 Seed Transfer – Most jurisdictions have policies and plans for seed transfer. Seed transfer rules are generally implemented and implementation is monitored. The two jurisdictions reporting an absence of policy have guidelines. On questions of implementation, attached comments indicate that control of seed transfer is lacking in three jurisdictions, one of which has legally binding rules under development.

Note that the number of seed zones per jurisdiction (see Program Statistics at the end), as one measure of the complexity of gene resource management, varies widely.

Section 1.2 Conservation – Jurisdictions are fairly evenly split between those that have formal provincial activity in conservation of forest genetic resources and those that do not. Attached comments, however, including responses to question 1.2d suggest that conservation is a neglected topic in only two jurisdictions. Responsibility for gene conservation is vested in Parks Ministries in some provinces.

Section 1.3 Genetic Diversity – Planning for maintenance of genetic diversity is, or will be, in place for about half of the jurisdictions. Implementation and monitoring, however, are much less common.

Section 1.4 Tree Improvement – Planning has been accomplished in most jurisdictions and standards are in place. Less attention has been given to issues of estimation and verification of genetic gain.

Section 2.0 Genetically-modified Organisms – Less than one-third of jurisdictions have a policy on GMOs. The federal government has the responsibility for testing GMOs to determine whether operational use can be allowed. A rigorous protocol for testing is in place.

Section 3.0 Non-native Tree Species – About half of the jurisdictions have a policy but few cover ecosystem impacts. Response to proposals for introduction of non-native species on public lands often seems to be handled on a case-by case basis. Monitoring plans are not generally required.

Section 4.0 Education in Forest Genetics and Tree Improvement – Education in forest genetics and tree improvement is not generally required at the undergraduate level. Graduate-level training is available in about one-half of the jurisdictions. Continuing education for practitioners and extension information are available in most jurisdictions. Communication with the general public is less common.

Section 5.0 Forest Genetic Advisory Council/Board – Formal advisory organizations exist in about one-half of the jurisdictions. Topical focus is somewhat more on tree improvement than on seed transfer, conservation, and use of GMOs. The apparent lack of interest in seed transfer is less apparent when it is recognized that some jurisdictions have decided that one seed zone is adequate.

Representation of primary stakeholders in advisory organizations is common, even without a formal plan for representation. The opportunity for public involvement is less common, however, and this raises the question of who is defined as a primary stakeholder.

SUMMARY

In summarizing the results of the Survey, three points need to be kept in mind. First, the Survey questions reflected, to some extent, a lack of expertise on the part of the authors in developing surveys. Responses, therefore can be open to interpretation. Second, there is a wide range among jurisdictions in the need for and in the complexity of, formal approaches to gene resource management of forest tree species. Third, the existence of a policy or plan might be considered to be a “first level” measure that a given issue has been addressed in some fashion. Whether the details of that policy or plan would be considered to be adequate at a technical level cannot be determined here.

The Survey reveals a general appreciation of issues in forest genetics and tree improvement although several of the respondents have job titles that emphasize silviculture or ecology. The actualization of that appreciation in organizational structures and formal plans varies widely among jurisdictions.

As might be expected, jurisdictions in which the implementation of tree improvement is shared in public/private cooperative formats have the most codified activities. Where implementation of tree improvement is an exclusively governmental function, written standards are less common and, perhaps, viewed as unnecessary or undesirable.

Even where written policies and standards are in place, the resources and commitment to implement and monitor seem rarely to be available.

Possibly the most surprising results from the Survey are the responses of “Not sure”.

At a minimum, the Survey results offer a preliminary “directory” of identified jurisdictions where specific issues have been addressed.

ACKNOWLEDGMENTS

Following is a list of respondents to the Survey. Thanks to each respondent for participating.

Robert Decker, Forest Management Division; Resources, Wildlife and Economic Development, NT
Narinder K. Dhir, Forest Management Branch, Sustainable Resource Development, AB
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Gordon Falk, Foresty Branch – Manitoba Conservation, MB
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Dennis G. Joyce, Genetics Resource Management Program, ON
André Rainville, Ministère des ressources naturelles, QC
Kathy Tosh, New Brunswick Tree Improvement Council, NB
John D. Thompson, Forest Ecosystems Branch, Saskatchewan Environment, SK
Jack Woods, Forest Genetics Council of BC, BC
Debra Wortley, Forest Management Branch, Energy, Mines and Resources, YK

POSTSCRIPT

This report was presented at an informal workshop of interested persons at the 29th Meeting of the Canadian Tree Improvement Association (CTIA), July 26, 2004, in Kelowna, BC. The following points were abstracted from the discussion following that meeting:

1. The fulfillment of national and international requirements for surveying and monitoring natural resources is a federal responsibility.

2. Provincial activities in management of genetic resources of forest trees could be coordinated with federal activities but that would require a lot of work. The amount of work required would arise from differences among provinces and from the distribution of responsibility among several federal agencies.

3. There is no current cooperative effort on the topic at the federal level that corresponds to activity by the Canadian Council of Forest Ministers.

4. Activities in forest certification may move toward standards for gene resource management but that process is slow.

5. In addition to discussing technical issues of gene resource management, exchange of information on administration of Councils could be useful.

6. A Council of Councils might fill a role similar to that of provincial councils providing advice to a Chief Forester.

7. A resolution proposing formation of a Working Group to meet on issues in gene resource management of forest trees will be developed and presented at the CTIA Business Meeting.

Editors Note: Following is the motion that was accepted at the CTIA Business Meeting:

> *That the CTIA endorse a committee of representatives from all provinces and territories, including reps from existing Councils, to be known as the Canadian Forest Genetics Councils Working Group of the CTIA and that this working group advocate and communicate, as needed, on matters related to federal-provincial/territorial policy interactions regarding the management of forest gene resources.*

Appendix I. Summary of "Yes" responses “Y” from 11 jurisdictions. "IP" represents "In Progress". Where sums of "Yes" responses are less than 11, actual responses were mostly "No", a few were "Not sure", and some were "Not applicable".

		Provinces/Territory						Remainder
1.0 Native Species		AB	BC	QC	NB	ON	YK	Yes
1.1 Seed Transfer								
	a. Does the Province have a policy on seed transfer?	Y	Y	Y	Y	Y	Y	3
	b. Does the Province have a plan for seed transfer issues?	Y	Y	Y	Y	Y	Y	2
	c. Has the plan been implemented?	Y	Y	Y	Y		Y	1
	d. Has significant progress been made on implementation?	Y	Y	Y	Y	Y	Y	1
	e. Is implementation monitored?	Y	Y	Y	Y		Y	1
1.2 Conservation								
	a. Does the Province have a policy on conservation?	Y	Y	Y	Y		Y	2
	b. Does the Province have a plan for conservation?	IP	Y	Y	Y	IP	Y	2
	c. Does the plan include coordinated *in situ* and *ex situ*	Y		Y	Y	Y		1
	d. Does the plan include protection for threatened species/populations?	Y	Y	Y	Y	Y	IP	2
	e. Has the plan been implemented?	Y	Y	IP	Y			2
	f. Has significant progress been made on implementation?		Y		Y		Y	2
	g. Is implementation monitored?	Y	Y		Y		Y	2
1.3 Genetic Diversity								
	a. Does the Province have a policy on genetic diversity?	Y	Y	Y	Y			2
	b. Does the Province have a plan for maintenance of genetic diversity?	Y	Y	Y	Y	IP		0
	c. Does the plan include both improved and unimproved species?	Y	Y	Y	Y	Y		0
	d. For improved material does the plan cover both stand-level and landscape-level diversity?	Y		Y		Y		0
	e. Has the plan been implemented?	Y	Y	Y				0
	f. Has significant progress been made on implementation?		Y		Y			0
	g. Is implementation monitored?	Y	Y		Y			0
1.4 Tree Improvement								
	a. Is there a long-term provincial improvement plan?	Y	Y	Y	Y	Y		2
	b. Are written breeding plans required?	Y	Y		Y	Y		2
	c. Are there standards for breeding-plan development?	Y	Y		Y	Y		2
	d. Does the Council monitor progress?	Y	Y		Y	Y		3
	e. Does the Council make recommendations on technical protocols?		Y		Y			3
	f. Is there a protocol for estimation of genetic gain including timber supply modeling?	Y	Y	Y	Y			2
	g. Is there a protocol for monitoring and verifying genetic gain?	Y	Y	Y	Y			2

		Provinces/Territory						Remainder
		AB	BC	QC	NB	ON	YK	Yes
2.0 Genetically-modified Organisms								
	a. Does the Province have a policy on the use of GMO's?	Y	Y	IP				0
3.0 Non-native Tree Species								
	a. Does the Province have a policy on use of non-native species?	Y	Y		Y			2
	b. Does the policy cover ecosystem impacts of non-native species?	Y						0
	c. Does the Province require monitoring plans for non-native species?	Y			Y			0
4.0 Education in FG and TI								
	a. Is education required at the undergraduate level in the Province?		Y	Y		?		0
	b. Is education available at graduate level in the Province?	Y	Y	Y	Y	Y		1
	c. Is continuing education available to practitioners?	Y	Y	Y	Y	Y		2
	d. Is extension information available to practitioners?	Y	Y	Y	Y	Y		3
	e. Is information communicated to the general public?	Y	Y	Y	Y			1
5.0 Forest Genetic Advisory Council/Board								
	a. Does the Province have a Forest Genetic Council?	Y	Y		Y	Y		3
	b. Does Council make recommendations on seed transfer issues?							
	seed transfer issues		Y		Y			2
	conservation	Y	Y		Y			1
	genetic diversity	Y	Y		Y			2
	use of GMO's	Y	Y					1
	tree improvement objectives	Y	Y		Y			3
	tree improvement planning		Y		Y			3
	c. Does Council include representation from primary stakeholder groups?	Y	Y		Y	Y		2
	d. Does Council have a formal plan for sectoral representation?	Y	Y					1
	e. Is there an opportunity for public involvement in planning for forest genetics resources management?	Y			Y			1
	Program Statistics							
	Number of Seed Zones (Number)	74	80	*a*	1	38	13	
	Average Annual Planting (Million)	65	220	130	60	120	0.5	
	Percent of Reforestation by Planting	80	80	18	50	50		

a Quebec uses transfer zones (distance from origin) rather than seed zones

AB - Alberta, BC - British Columbia, QC - Quebec, NB - New Brunswick, ON - Ontario

POSTER ABSTRACTS

IS BRITISH COLUMBIA’S SILVICULTURE PPLICY FRAMEWORK ADEQUATE FOR RESPONDING TO CLIMATE CHANGE?

Brian Barber

BC Ministry of Forests
Tree Improvement Branch
P.O. Box 9518 Stn Prov Govt
Victoria, BC
V8W 9C2
E-mail: Brian.Barber@gems4.go.bc.ca

The Government of British Columbia recently revamped its *Forest Practices Code* by introducing new results-based forest management legislation. In this simplified regulatory model, government establishes objectives for conserving and protecting forest values. Forest licensees are responsible for developing and implementing results and strategies that will achieve those objectives. With the exception of a few default environmental standards (e.g., riparian areas, soil disturbance, and seed use) forest practices are to be prescribed by professionals.

Climate change has not been considered in establishing these objectives and environmental standards. Furthermore, licensees and foresters are not required to incorporate climate change scenarios into their forest management plans; nor would they necessarily have the expertise or resources to do so if they were obligated.

Scientists have suggested a number of adaptive management strategies to reduce the vulnerability of managed forests to climate change. These strategies include planting different species, modifying the seed transfer protocols, increasing the number of genotypes and seedlots used to reforest an area, and higher stocking densities.

This poster is intended to stimulate discussion regarding the adequacy of British Columbia’s silviculture policy framework for responding to climate change. For example, will forests managed under today’s policies be more or less at risk to climate change than unmanaged forests? What are the current opportunities and barriers to implementing the aforementioned silviculture strategies? What adaptation policies could be undertaken today at a reasonable cost that provide benefits under the present climate as well as the future? Will professional reliance be sufficient to implement these changes?

This poster and discussion will be used in refining the topic for a Master of Arts thesis in Environment and Management.

Ex situ CONSERVATION STRATEGY FOR BUTTERNUT (*Juglans cinerea* L.)

T. Beardmore, K. Forbes, J. Loo and D. Simpson

Natural Resouces Canada
Canadian Forest Service
Atlantic Forestry Centre
PO Box 4000
Fredericton, NB
E3B 5P7
E-mail: Tannis.Beardmore@nrcan.gc.ca

Butternut (*Juglans cinerea* L.) survival is threatened in North America by the fungus *Sirococcus clavigignenti-juglandacearum*. To date, control for this fungal disease does not exist and long-term seed storage, as a means to assure survival of the species, is not a viable option. For these reasons, there is a requirement to develop *ex situ* conservation strategies for butternut. One such strategy involves developing storage using embryonic axes from seed collected from non-infected butternut. Embryonic axes, when excised from the nut with approximately 3 mm of cotyledonary tissue, will tolerate exposure to -196°C and subsequently germinate, forming a viable seedling. Water content of 4.8% appears to be a threshold below which some of the axes will germinate following cryopreservation. These results suggest that ultra low temperature storage of embryonic axes may be a viable method for butternut *ex situ* conservation. The use of other *ex situ* conservation methods such as the cryopreservation of apical and lateral buds, and somatic embryogenesis are presented.

GENETIC STRUCTURE AND MATING SYSTEM OF ARBUTUS (*Arbutus menziesii*)

Jaclyn Beland, Carol Ritland, Kermit Ritland and Yousry El-Kassaby

Department of Forest Sciences
University of British Columbia
2424 Main Mall
Vancouver, BC
V6T 1Z4
E-mail: jbeland@interchange.ubc.ca

Arbutus (*Arbutus menziesii* Pursh) is the only broadleaved evergreen tree native to Canada. It belongs to four red- or blue-listed plant communities. Primary threats are urban encroachment, fire suppression, grazing, and exotic invasive species. Its growth is highly sensitive to environmental conditions; therefore more severe summer drought due to future climate change could further threaten this species. No data are available on pollination biology or population genetics of arbutus. Amplified fragment length polymorphisms (AFLPs) were used for the first genetic examination of *A. menziesii* in BC. Ten populations were studied throughout its range and one in Washington, USA. Genetic diversity estimates within populations were low (mean $H = 0.094$) relative to other long-lived perennials (0.25); there were no significant differences among populations. Genetic variation among populations ($F_{ST} = 0.15$) was comparable to the average in long-lived perennials and frugivore-dispersed species ($F_{ST} = 0.19$ and 0.16, respectively). The Gold River, BC population differed the most from other populations, but not significantly. Isolation by distance was significant based on kinship coefficients ($p < 0.01$); half-sibs were ~3 m apart. Mating system analysis of one BC island population revealed high outcrossing ($t = 0.97$); 10–20% of mating was biparental inbreeding. Conservation strategies and future research directions are presented.

EFFECTS OF FRAGMENTATION ON GENETIC STRUCTURE AND INBREEDING IN BIGLEAF MAPLE POPULATIONS

Mohammed N. Iddrisu and Sally Aitken

Department of Forest Sciences
University of British Columbia
2424 Main Mall
Vancouver, BC
V6T 1Z4
E-mail: middrisu@interchange.ubc.ca

Some plant populations including forest tree species have small geographical populations. As land use by man increases, the distribution of several tree species has become fragmented. In fragmented populations, the overall numbers of individuals are drastically reduced and remaining forest populations are restricted to small forest patches. Population genetic theory predicts that habitat fragmentation will result in an erosion of genetic variation in small remnant populations through the combined effects of genetic drift, inbreeding, and random extinctions of local populations. Almost all investigations of habitat fragmentation have used habitats that have been fragmented for close to a century or less. This study uses populations from habitats that have been naturally fragmented throughout the species history to examine the effects of fragmentation on a much longer time scale. Using isozyme markers, two questions were addressed:
1) What are the effects of forest fragmentation on the genetic structure of these populations?
2) Are changes in mating systems the mechanisms through which fragmentation is affecting bigleaf maple populations?

To address these questions, genetic variation and structure of continuous populations were compared to genetic variation and structure of fragmented populations.

Results for genetic diversity indicate that bigleaf maple (*Acer macrophyllum*) exhibits similar levels of genetic diversity as other maple species.

GENETIC GAIN AND GENE DIVERSITY UNDER THINNING SCENARIOS IN A SEEDLING SEED ORCHARD OF *Quercus accutissima*

K.S. Kang[1], Y.A. El-Kassaby[2], S.-U. Han[1], C.-S. Kim[1] and W.-Y. Choi[1]

[1] Forest Genetic Resources Department
Tree Breeding Division
Korea Forest Research Institute
44-3 Omokchun, Kwonsun, Suwon
Kyonggi, 441-350
Republic of Korea

[2] Department of Forest Sciences
University of British Columbia
2424 Main Mall
Vancouver, BC
V6T 1Z4
E-mail: yelkassaby@interchange.ubc.ca

Genetic gain and gene diversity were estimated in a 12-year-old *Quercus accutissima* seedling seed orchard under three thinning scenarios. Both genetic gain and diversity of each scenario were estimated and compared to those of before thinning. These scenarios were based on genetic, systematic, and truncation thinnings. Gene diversity was assessed utilizing the status number concept (i.e., accumulation of coancestry). Genetic thinning involved the removal of individuals within families and the removal of entire families. Genetic thinning was based on the utilization of the family genetic values (GCA) generated from conventional progeny test trials. Truncation thinning produced the highest genetic gain that was coupled with the lowest gene diversity, while genetic thinning produced the optimum balance between genetic gain and diversity. Systematic thinning, on the other hand, produced the lowest genetic gain and the highest diversity. Under the genetic thinning option, the number of families completely removed was intentionally minimized to maintain higher gene diversity and to maintain options for further genetic evaluation and selection. Genetic thinning was accomplished by applying a within-family thinning regime that was proportional to the reverse of every family's genetic gain (i.e., low numbers of trees removed from high genetic gain families and higher numbers from trees from lower genetic gain families). Additionally, the effect of genetic relatedness among families and possible pollen contamination on both genetic gain and diversity, although not studied, their impact, is presented.

GIS-BASED SEED ZONES FOR WHITE SPRUCE IN ONTARIO

W.H. Parker and M.R. Lesser

Faculty of Forestry
Lakehead University
955 Oliver Road
Thunder Bay, ON
P7B 5E1
E-mail: mrlesser@lakeheadu.ca

To properly match seed sources to planting sites according to expressed patterns of adaptive variation, a focal point seed zone methodology was developed for white spruce (*Picea glauca* [Moench] Voss.) in Ontario. One hundred thirty-two provenances from Ontario and western Québec were established at a greenhouse and five field trials throughout Ontario. Growth and phenological variables were measured over two growing seasons and variables expressing variation among provenances were regressed individually against geographic and climate variables to assess whether they exhibited adaptive variation. Principal components (PC) analysis was used to summarize the main components of variation. The first PC axis mainly represented growth potential. PC axes 2 and 3 were strongly determined by phenological traits. PC axis scores for the provenances were regressed against climate variables and the resulting equations were used to model the PC axes. These models were converted to spatial data and reproduced as contoured grids using GIS. For any given point in Ontario the 3 PC axis grids are standardized and intersected, creating zones of adaptive similarity to that point. Focal point seed zones created for 9 example points selected from across the province show strong latitudinal trends and more regional longitudinal trends. Seed transfer for white spruce across traditional site region boundaries may be possible in most of north-central and north-eastern portions of Ontario.

MICROSATELLITE ANALYSIS OF GENETIC EFFECTS OF DOMESTICATION IN LODGEPOLE PINE

Cherdsak Liewlaksaneeyanawin, Yousry A. El-Kassaby, Carol Ritland and Kermit Ritland

Department of Forest Sciences
University of British Columbia
2424 Main Mall
Vancouver, BC
V6T 1Z4
E-mail: yelkassaby@interchange.ubc.ca

Genetic diversity along the domestication process of lodgepole pine (*P. contorta* spp. *latifolia*) was investigated using microsatellite (SSRs) genetic markers. Genetic variability of 10 natural populations, each with 30 individuals, from the Prince George Breeding Zone provided the benchmark for comparison. The genetic diversity of the breeding (92 parents) and production (44 parents) populations as well as a representative seed crop was assessed. It was hypothesized that the domestication process may cause a gradual reduction of genetic diversity through several bottlenecks starting with phenotypic selection followed by the production population and the production of seed crops caused by the steady reduction of individuals included in each population. The number of alleles observed in natural, breeding, and production populations and the seed lot was 195, 166, 150, and 146, respectively. Alleles were grouped into four classes based on their frequencies (high: $P > 0.75$, intermediate $0.25 \leq P < 0.75$, low: $0.01 \leq P < 0.25$, and rare: $P < 0.01$). The majority of alleles fall into the low and rare frequency classes. A small amount of genetic variability was observed among the 10 natural populations studied ($F_{ST} = 0.008$), thus allowing using their collective genetic diversity as a benchmark for comparison. The total number of alleles (A_T) showed a steady reduction along the domestication process; however, most of the alleles lost were rare ($P < 0.01$) and expected heterozygosity (H_e) did not change substantially among the studied populations (range: 0.757 – 0.783). This was expected due to the minuscule effect of the rare allele's contribution to overall diversity. The results from the present study demonstrate that lodgepole pine has not experienced any major reduction of genetic diversity along the domestication process. However, more intensive breeding practices can result in a further erosion of genetic variability, especially the rare alleles.

INTER- VS. INTRA-PROVENANCE CROSSES IN *Pinus monticola*: EARLY PLANTATION RESULTS, WITH RECOMMENDATIONS FOR SEED TRANSFER IN BRITISH COLUMBIA

Michael D. Meagher

MDM Forgene
666 Jones Terrace
Victoria, BC
V8Z 2L7
E-mail: mikebirgitte@shaw.ca

Intra- and inter-provenance crosses of western white pine (*Pinus monticola*), using pollen mixes, were planted on two sites in British Columbia. Age 7 heights (five-years after planting) were analysed for the effect of seed tree, pollen source, and plantation. Although planting site affected population height and rank, interior seed parents and pollens generally produced trees 2–4% taller and Oregon, USA (Cascade Mountains) pollen reduced mean height of crosses consistently by 3–7%. Both positive and negative heterosis among crosses and significant genotype X environment interaction were found. Tentative recommendations for seed and pollen transfer are made.

REPRODUCTIVE AND GENETIC CHARACTERISTICS OF RARE, DISJUNCT PITCH PINE POPULATIONS AT THE NORTHERN LIMITS OF ITS RANGE IN CANADA

A. Mosseler[1], O.P Rajora[2] and J.E. Major[1]

[1] Natural Resources Canada
Canadian Forest Service
Atlantic Forestry Centre
PO Box 4000
Fredericton, NB
E3B 5P7
E-mail: amossele@nrcan.gc.ca

[2] Faculty of Forestry and Environmental Management
University of New Brunswick
PO Box 44555
Fredericton, NB
E3B 6C2

Pitch pine (*Pinus rigida* Mill.) is a rare species in Canada, existing as a disjunct population in the St. Lawrence River Valley in eastern Ontario and as two northern outlier stands in southern Québec along Canada's southern border with the United States. Reproductive and genetic characteristics of these small, scattered stands were investigated to develop a foundation for management and restoration in the event of a northward range expansion under anticipated climate warming. Seed yields and seed quality appeared to be comparable to other eastern conifers, and to pitch pine at the center of its geographic range. For seed and seedling growth traits, most of the variation was attributable to differences among trees within stands and, to a lesser extent, among stands within a population. The population effect was non-significant. For reproductive traits, such as numbers of filled and empty seeds per cone, reproductive efficiency, and inbreeding estimates, high levels of variation (ranging from 26–33%) were found among stands, suggesting that stand structural features, such as stand size and tree density within stands, play an important role in pollination environment and overall reproductive success. Estimates of genetic diversity at 32 allozyme gene loci indicate that these small, isolated stands have maintained high levels of genetic diversity compared to populations at the center of the geographic range and also relative to other widely dispersed eastern conifers. Such comparatively high levels of genetic diversity suggest that Canada's extant pitch pine population may represent a remnant of a much wider distribution during warmer climates of the present interglacial period, rather than a population expanding its range northward. The relatively high levels of viable seed production and genetic diversity in native pitch pine populations indicate that native Canadian populations may be suitable seed sources for species restoration and expansion in Canada. Representative samples of these native Canadian populations have been established in New Brunswick, Prince Edward Island, and Nova Scotia to assess potential environmental limitations to the introduction of pitch pine across the Maritimes. The first series of such tests was established in 1996 and has demonstrated the excellent growth potential of this species for both industrial wood supply and ecological restoration in eastern Canada.

GENE RESOURCE INFORMATION MANAGEMENT IN BRITISH COLUMBIA – BUILDING A RESOURCE INFORMATION STRATEGY FOR GENETIC RESOURCE MAPPING, LAND-BASED STRATEGIC AND OPERATIONAL PLANNING AND EFFECTIVENESS MONITORING

Leslie McAuley and Ron Planden

BC Ministry of Forests
Tree Improvement Branch
PO Box 9513 Stn Prov Govt
Victoria, BC
V8W 9C2
E-mail: Leslie.McAuley@gems9.gov.bc.ca

Gene resource information management (GRIM) forms a critical link to the long-term stewardship and sustainable resource management of the province's forest tree gene resources. GRIM goals and objectives will be met through the development of a Gene Resource Information Strategy. The Strategy will set direction and information management priorities over the next 2 to 5 years.

GRIM objectives include: 1) development of a provincial GRM framework (GRM-based Seed Planning Zones) to support forest stewardship plans, silviculture regeneration (seed deployment) strategies, forest tree genetics research, and gene conservation strategies; 2) development and support of forest tree genetic resource mapping, registries, and data warehouse repositories; 3) increased access to tree improvement program products (seed and vegetative material for operational use); 4) development of an integrated GRM effectiveness monitoring program linked to broader forestry initiatives (criteria and indicators, climate change) and land-based resource management issues (species conversion); and 5) incorporation of genetic gain into timber supply analyses through forest inventory updates and the use of GIS-ready spatial and attribute GRM data sets.

VEGETATIVE PROPAGATION OF *Fagus grandifolia* Ehrh. (AMERICAN BEECH) RESISTANT TO BEECH BARK DISEASE

Marianela Ramirez

Faculty of Forestry and Environmental Management
University of New Brunswick
PO Box 44555
Fredericton, NB
E3B 6C2
E-mail: nela.ramirez@unb.ca

American beech (*Fagus grandifolia*) is an important tree species in eastern North America that has been severely affected by beech bark disease (BBD), a complex disease that involves the interaction of a scale insect (*Cryptococcus fagisuga* Lind.) and a *Nectria* fungus. While many trees have been killed, some show resistance to the disease. Resistance is believed to be of genetic origin and this provides an opportunity to propagate disease-free trees, introduce them to natural forests, and increase resistance levels. The purpose of this project is to use vegetative propagation on mature beech trees that appear resistant to BBD and test if the resistance is due to genetic factors. Three propagation techniques are being applied: micropropagation of buds, root sprouts and epicormic roots from branches, and grafting. Due to the difficulty of propagating this species in the past, a pilot study was carried out in 2003 to determine the feasibility of different propagation methods. It was determined that grafting success was low (30%) and was related to diameter of the rootstock. Contamination of *in vitro* cultured buds was high for some genotypes (more than 50% for 45% of the genotypes), and rooting of plantlets was low (less than 25%). Cuttings of root sprouts and shoots induced from branches were unsuccessful and epicormic shoots induced from branches were not vigorous and didn't survive *in vitro*. The grafted material is currently being tested for resistance by inoculating the scale insect on the bark of the seedlings.

DEFINING BLACK SPRUCE GROWTH OPTIMA IN ONTARIO: PRESENT AND FUTURE

W.H. Parker, C.L. Riddell and M.R. Lesser

Faculty of Forestry
Lakehead University
955 Oliver Road
Thunder Bay, ON
P7B 5E1
E-mail: clriddel@lakeheadu.ca

Height data from 19 range-wide black spruce (*Picea mariana* [Mill.] BSP) provenance trials were regressed against monthly minimum and maximum temperatures and monthly precipitation using the Cauchy function. Response functions were developed for individual populations to predict the climate value that will maximize performance for each source. Transfer functions were developed for individual test sites to predict climate values of populations that maximize performance at each of the test locations. Mid-spring and mid-to late-winter temperature data generally yielded the best fitting response and transfer functions. For each population/climate variable combination, a grid was developed to map predicted height growth of that population at all points within the region. Likewise, for each test site/climate variable combination, a grid was developed to predict height growth of all potential seed sources planted at that test site. Contours indicating maximal height growth for present and predicted 2040–2069 climate variables were added to these grids. Excluding the southern part of its range, black spruce seed sources produce better growth when moved south and should achieve better growth under warmer predicted future temperature regimes provided that other factors are not limiting. The incorporation of more southerly seed sources into today's northerly reforestation efforts will result in more rapidly growing trees today, and will also yield trees better adapted to predicted future temperatures.

RESPONSE FUNCTIONS OF LODGEPOLE PINE TO TEMPERATURE AND CO_2

Pia Smets[1], Sally Aitken[1], Robert Guy[1] and Alvin Yanchuk[2]

[1] **Department of Forest Sciences**
University of British Columbia
3401–2424 Mail Mall
Vancouver, BC
V6T 1Z4
E-mail: psmets@interchange.ubc.ca

[2] **BC Ministry of Forests**
Research Branch
PO Box 9519 Stn Prov Govt
Victoria, BC
V8W 9C2

This project-in-progress is a short-term growth chamber experiment to establish norms of reaction to temperature and carbon dioxide. Seedlings of ten populations of lodgepole pine are being subjected to four temperature regimes and two CO_2 levels (ambient and elevated). Each population is represented by open-pollinated families, B+ seed lots, control-pollinated families, and seed orchard seed lots. The four temperature regimes correspond to the growing season of 4 locations with mean annual temperatures (MAT) of 1, 4, 7, and 10°C. Two of these regimes, MAT 4 and 10, receive both ambient and elevated CO_2 concentrations. Daylength is the same for all chambers, but varies from week to week as the season progresses. Water and nutrients are provided in excess. Height is measured periodically, while dry mass, allocation, photosynthetic rate, and water-use efficiency will be measured at the end of the season. Genotypes will be compared in order to determine which populations perform best in future climate scenarios and if there is rank change of genotypes among the scenarios. Differences between natural populations and improved seed lots, if any, will be identified. Gas exchange measurements will reveal whether photosynthetic acclimation to enriched CO_2 (downscaling) occurs. The underlying aim is to understand the physiological basis of these response functions and to determine if norms of reaction in growth chambers resemble those found in long-term field trials in different climates, such as the large-scale Illingworth lodgepole pine trials in BC.

CLIMATE CHANGE AND FORESTRY IN SWEDEN – A LITERATURE REVIEW

J. Sonesson[1], J. Bergh[2], C. Björkman[2], K. Blennow[2], H. Eriksson[3], S. Linder[2], K. Rosén[1], M. Rummukainen[4] and J. Stenlid[2]

[1] The Forestry Research Institute of Sweden
Science Park
75183 Uppsala
Sweden
E-mail: Johan.Sonesson@Skogforsk.se

[2] Swedish University of Agricultural Sciences

[3] National Board of Forestry

[4] Swedish Meteorological and Hydrological Institute

The scope of the study was to review the relevant literature regarding the impact of climate change on forestry in Sweden, to synthesise the current knowledge, to draw conclusions on likely effects of climate change, and to identify the need for new research and knowledge. We have limited the study to the effects on a short and medium time span (20–100 years). We focused on the impact on the trees, both direct and indirect, through the climatic impact on soils, herbivores, insects, pests, and diseases. We made sharp delimitations to other aspects of forests and climate change.

This literature review has revealed major shortcomings in our knowledge about impacts that climate change will have on the forest ecosystems. Not only are the nature and magnitude of climate change uncertain, but even more its potential effects on the structure and processes of forest ecosystems.

However, the most likely effects of climate change can be predicted. They generally include an increase in potential biomass production, possibilities to grow new species commercially, and increased risk for damage of several kinds. It seems that climate change offers new opportunities to forestry in Sweden. At the same time the risk for calamities increases. This calls for demanding new approaches to forest- as well as risk-management.

Future research on the effects of climate change on forestry and forest ecosystems has to take account of a broad spectrum of scientific fields, but most important is probably the need for a multidisciplinary, scientific approach.

INTRASPECIFIC RESPONSES TO CLIMATE IN *Pinus albicaulis*

Marcus Warwell

USDA Forest Service
Rocky Mountain Research Station
Forest Sciences Laboratory
1221 S. Main St.
Moscow, ID 83843
E-mail: mwarwell@fs.fed.us

Provenance tests of 42 populations of *Pinus albicaulis*, originating from inland northwestern United States revealed genetic differentiation for growth potential and phenology in relation to climate. The provenance tests were established at Priest River Experimental Forest, Idaho in 2000 using 2-year-old seedlings. Patterns of shoot elongation were recorded beginning in the second growing season. Hutchinson's thin plate splines were used to make point predictions for climate at each provenance. These climate predictions were then used to describe genetic variation. Genetic variation was significantly correlated with climate effects derived from temperature. Correlations were strongest for degree days > 5°C and timing of last spring frost. The relationship between growth potential and degree days > 5°C was negative. The analyses suggest that genetic differentiation for growth potential and phenology is controlled by the relative mildness of climate in relation to temperature.

POPLAR LEAF RUST CAUSED BY *Melampsora* SPECIES IN KOREA

**Kwan-Soo Woo, Yeong-Bon Koo, Young-Joung Kim,
Jin-Kie Yeo and Tae-Su Kim**

**Department of Forest Genetic Resources
Korea Forest Research Institute
Suwon, 44-3
Korea**

The severity of poplar leaf rust caused by *Melampsora* species on 15 poplar clones was investigated to select resistance in clones to the pathogens and to see whether the pathogens exhibit specificity toward the poplar clones. Cuttings of 15 poplar clones were planted at a nursery bed in Suwon, Korea, in March of 2003. Three rusted leaves per clone were collected from each of the 15 clones, and 10 urediniospores per leaf were observed with both scanning electron microscopy (SEM) and light microscopy (LM). Rust severity was rated on September 2 and 27 and October 20, 2003, using the Schreiner scale (0–100).

Urediniospores from all clones except 72-30, 72-31, Bong-wha 1, and Hyunsasi 3 were oval and tended to be clavate to broadly ellipsoid. Both apices and bases were mostly rounded, but the wall surface of the urediniospore was echinulate except for a smooth patch on the apex. However, urediniospores from the rest of the 4 clones had uniform echinulation. The size of the spores from two groups was also different from each other. The former (11 clones) measured 24-46 X 13-23 ìm, and the latter (4 clones) measured 20-29 X 13-20 ìm. On September 2, 2003, the first rust severity rating date, only two clones, 97-17 and Eco 28, rated a Schreiner score of 100. However, by October 20, 2003, a total of 12 clones rated 100. Bong-wha 1, Dorskamp, and Hyunsasi 3 were only lightly rusted (all 20 on October 20, 2003). All of the leaf rust samples taken from the 11 clones were identified as *M. larici-populina*; however, samples from the 4 clones were not exactly identified. It seems that they belong to the difficult species complex of *Populus* section *Populus.*

ATTENDEES OF THE
29th CTIA/ACAA MEETING

Sally Aitken
University of British Columbia
Faculty of Forestry
3401-2424 Main Mall
Vancouver, BC
V6T 1Z4

Michael Albrecht
Roseburg Forest Products
34937 Tennessee Road
Lebanon, OR
97355

Adriana Almeida-Rodriguez
University of Alberta
Dept. of Renewable Resources
444-Earth Sciences Building
Edmonton, AB
T6G 2E3

Cecilia Alstrom-Rapaport
University of Northern British Columbia
3333 University Way
Prince George, BC
V2N 4Z9

Doug Ashbee
BC Ministry of Forests
Research Branch
PO Box 9519 Stn Prov Govt
Victoria, BC
V8W 9C2

Val Ashley
BC Ministry of Forests
Research Branch, Kalamalka
3401 Reservoir Road
Vernon, BC
V1B 2C7

Brian Barber
BC Ministry of Forests
Tree Improvement Branch
PO Box 9518 Stn. Prov Govt
Victoria, BC
V8W 9C2

Leonard Barnhardt
Alberta Tree Improvement & Seed Centre
PO Box 750
Smoky Lake, AB
T0A 3C0

Tannis Beardmore
Natural Resources Canada
Canadian Forest Service
PO Box 4000
Fredericton, NB
E3B 5P7

Jean Beaulieu
Natural Resources Canada
Canadian Forest Service
PO Box 3800
Sainte-Foy, QC
G1V 4C7

Stéphanie Beauseigle
Université Laval
Pavillion C-E-Marchand local 2167
Québec, QC
G1K 7P4

Robb Bennett
BC Ministry of Forests
Tree Improvement Branch
7380 Puckle Road
Saanichton, BC
V8M 1W4

Henry Benskin
BC Ministry of Forests
Research Branch
PO Box 9519 Stn Prov Govt
Victoria, BC
V8W 9C2

Vicky Berger
BC Ministry of Forests
Research Branch, Kalamalka
3401 Reservoir Road
Vernon, BC
V1B 2C7

Andrew Bower
University of British Columbia
Faculty of Forestry
3401-2424 Main Mall
Vancouver, BC
V6T 1Z4

Kathleen Brosemer
Forest Genetics Ontario
510 Queen Street East
Sault Ste Marie, ON
P6A 2A1

Jean Brouard
Isabella Point Forestry Ltd.
331 Roland Road
Salt Spring Island, BC
V8K 1V1

Patti Brown
Canfor
4858 Skylark Road
Sechelt, BC
V0N 3A2

Mitchell Bumgarner
Quinault Indian Nation
1214 Aalis
Taholah, WA
98587

Betsy Byrum
PRT Oregon
31783 S Meridian Road
Hubbard, OR
97119

Mike Carlson
BC Ministry of Forests
Research Branch, Kalamalka
3401 Reservoir Road
Vernon, BC
V1B 2C7

Charlie Cartwright
BC Ministry of Forests
Research Branch
7060 Forestry Road
Mesachie Lake, BC
V0R 2N0

Paul Charrette
Superior-Woods Tree Improvement Assoc.
Lakehead University
Faculty of Forestry
955 Oliver Road
Thunder Bay, ON
P7B 5E1

Marilyn Cherry
Oregon State University
Pacific Northwest Tree Imp. Research Coop.
321 Richardson Hall
Corvallis, OR
97331

Isabelle Chuine
CEFE-CNRS
1919 route de Mende
34293 Montpelier
France

Louise Corriveau
Weyerhaeuser
PO Box 1720
Prince Albert, SK
S6V 5T3

Jessica Courtier
106 Old Scott Road
Saltspring Island, BC
V8K 2L6

Keith Cox
BC Ministry of Forests
Tree Improvement Branch
Site 13 Comp 5 RR#1
Tappen, BC
V0E 2X0

Tim Crowder
Mount Newton Seed Orchard
1450 Mt Newton Cross Road
Saanichton, BC
V8M 1S1

Bruce Dancik
Devonian Botanic Garden
University of Alberta
Edmonton, AB
T6G 2E1

Gaetan Daoust
Natural Resources Canada
Canadian Forest Service
PO Box 3800
Sainte-Foy, QC
G1V 4C7

Jeff DeBell
Washington State Dept. Nat. Res.
PO Box 47017
Olympia, WA
98504

Howard Dew
Cascade Timber Consulting Inc.
PO Box 446
Sweet Home, OR
97386

Ron Dinus
2490 Goshen Road
Bellingham, WA
98226

David Doede
USDA Forest Service
Mt Adams Ranger District
2455 HWY 141
Trout Lake, WA
98650

Diane Douglas
BC Ministry of Forests
Tree Improvement Branch
PO Box 9518 Stn. Prov Govt
Victoria, BC
V8W 9C2

Dale Draper
BC Ministry of Forests
Tree Improvement Branch
PO Box 9518 Stn. Prov Govt
Victoria, BC
V8W 9C2

Joan Dunlap
USDA Forest Service
2375 Fruitridge Road
Camino, CA
95709

Duane Ecker
Ochoco National Forest
PO Box 490
Prineville, OR
97754

Gordon Falk
Manitoba Conservation
PO Box 27 Grp 8 RR #2
Dugald, MN
R0E 0K0

Al Foley
Ministry of Natural Resources
Ontario Tree Seed Plant
141 King Street, PO Box 2028
Angus, ON
L0M 1B0

Randy Ford
NE Seed Management Association
PO Box 730
Englehart, ON
P0J 1H0

George Foster
USDA Forest Service
1601 N Kent Street
Arlington, VA
22209

George Franssen
BC Ministry of Forests
Research Branch Kalamalka
3401 Reservoir Road
Vernon, BC
V1B 2C7

Terry Garren
BLM
27004 Sheckley Road
Colton, OR
97017

Dan Gaudet
Vernon Seed Orchard Company
6555 Bench Row Road
Vernon, BC
V1H 1G2

Gary Giampa
BC Ministry of Forests
Research Branch, Kalamalka
3401 Reservoir Road
Vernon, BC
V1B 2C7

Grant Glessing
Tolko Industries
1879 Brownmiller Road
Quesnel, BC
V2J 6R9

Alfred Golnick
Huallen Seed Orchard Company
R R #2
Wembley, AB
T0H 3S0

Gloria Golnick
Huallen Seed Orchard Company
R R #2
Wembley, AB
T0H 3S0

Al Gordon
131 Meadow Park Crescent
Sault Ste. Marie, ON
P6A 4H1

Scott Green
University of Northern British Columbia
3333 University Way
Prince George, BC
V2N 4Z9

Mark Griffin
BC Ministry of Forests
Research Branch
PO Box 3536 Stn Prov Govt
Victoria, BC
V8W 9C4

Tim Gylander
Weyerhaeuser
PO Box 7739
Drayton, AB
T7X 2N7

Andreas Hamann
University of British Columbia
Faculty of Forestry
3401-2424 Main Mall
Vancouver, BC
V6T 1Z4

Mats Hannerz
Forest Research Institute of Sweden
Uppsala Science Park
Uppsala, Sweden
75183

Christine Hansen
Alberta Tree Improvement & Seed Centre
PO Box 750
Smoky Lake, AB
T0A 3C0

Dave Hodgin
Weyerhaeuser
7935 Hwy 12 SW
Rochester, WA
98579

Clint Hollefreund
BC Ministry of Forests
Research Branch
4300 North Road
Victoria, BC
V8Z 5J3

Bonnie Hooge
BC Ministry of Forests
Research Branch
17000 Domano Blvd
Prince George, BC
V2N 5M2

Glenn Howe
Oregon State University
Pacific Northwest Tree Imp. Research Coop.
321 Richardson Hall
Corvallis, OR
97331

Dana Howe
Oregon State University
Dept. of Forest Science
321 Richardson Hall
Corvallis, OR
97331

Liang Hsin
USDI BLM
333 SW 1st Avenue
Portland, OR
97204

Rich Hunt
Natural Resources Canada
Canadian Forest Service
506 W Burnside Road
Victoria, BC
V8Z 1M5

Mohammed Iddrisu
University of British Columbia
Faculty of Forestry
3401-2424 Main Mall
Vancouver, BC
V6T 1Z4

Steve Jackson
University of Wyoming
Laramie, WY
82071

Barry Jaquish
BC Ministry of Forests
Research Branch, Kalamalka
3401 Reservoir Road
Vernon, BC
V1B 2C7

Sally John
Isabella Point Forestry Ltd.
331 Roland Road
Salt Spring Island, BC
V8K 1V1

Randy Johnson
USDA Forest Service
Forestry Sciences Lab
3200 SW Jefferson Way
Corvallis, OR
97331

Dennis Joyce
Ontario Ministry of Natural Resources
70 Foster Drive, Suite 400
Sault Ste. Marie, ON
P6A 6V5

Kyu-Suk Kang
Korea Forest Research Institute
44-3 Omokchen, Kwonsun
Suwon, Kyonggi
Korea
441-350

Wayne Kelly
Department of Forestry
Cornerbrook, NL
A0L 1K0

John King
BC Ministry of Forests
Research Branch
PO Box 9519 Stn Prov Govt
Victoria, BC
V8W 9C2

Harvey Koester
USDI - BLM
3040 Biddle Road
Medford, OR
97504

Dave Kolotelo
BC Ministry of Forests
Tree Improvement Branch, Tree Seed Centre
18793 32nd Avenue
Surrey, BC
V4P 1M5

Scott Kolpak
USDA Forest Service
34963 Shoreview Road
Cottage Grove, OR
97424

Jodie Krakowski
University of British Columbia
Faculty of Forestry
2424 Main Mall
Vancouver, BC
V6T 1Z4

Sylvia L'Hirondelle
BC Ministry of Forests
Research Branch
PO Box 9519 Stn Prov Govt
Victoria, BC
V8W 9C2

Chal Landgren
Oregon State University
18640 NW Walker Road # 1400
Beaverton, OR
97006

Denis Lavender
3925 Fairhaven Drive SW
Corvallis, OR
97333-1431

Tim Lee
Vernon Seed Orchard Company
6555 Bench Row Road
Vernon, BC
V1H 1G2

Mark Lesser
Lakehead University
Faculty of Forestry
955 Oliver Road
Thunder Bay, ON
P7B 5E1

Cherdsak Liewlaksaneeyanawin
University of British Columbia
Faculty of Forestry
2424 Main Mall
Vancouver, BC
V6T 2G9

Carolyn Lohr
BC Ministry of Forests
Tree Improvement Branch, Saanich
7380 Puckle Road
Saanichton, BC
V8M 1W4

Pengxin Lu
Ministry of Natural Resources
Ontario Forest Research Institute
1235 Queen Street East
Sault Ste Marie, ON
P6A 2E5

Mary Frances Mahalovich
USDA Forest Service
Forestry Sciences Lab
1221 S Main St
Moscow, ID
83843

John Major
Natural Resources Canada
Canadian Forest Service
PO Box 4000
Fredericton, NB
E3B 5P7

Craig Marbet
Green Diamond Resource Co.
PO Box 9001 Third & Franklin
Shelton, WA
98584

Heather May
USDA Forest Service
34963 Shoreview Road
Cottage Grove, OR
97105

Leslie McAuley
BC Ministry of Forests
Tree Improvement Branch
PO Box 9518 Stn Prov Govt
Victoria, BC
V8W 9C2

John McClarnon
BC Ministry of Forests
Forest Production Branch
PO Box 9513 Stn Prov Govt
Victoria, BC
V8W 9C2

Lesley McKnight
BC Ministry of Forests
Research Branch
PO Box 9519 Stn Prov Govt
Victoria, BC
V8W 9C2

Michael Meagher
MDM Forgene
666 Jones Terrace
Victoria, BC
V8Z 2L7

Helga Mehl
BC Ministry of Forests
Research Branch
4300 North Road
Victoria, BC
V8Z 5J3

Glenn Miller
Bureau of Land Management
PO Box 21
Lorane, OR
97451

Makiko Mimura
University of British Columbia
Faculty of Forestry
3041-2424 Main Mall
Vancouver, BC
V6T 1Z4

Alexander Mosseler
Natural Resources Canada
Canadian Forest Service
PO Box 4000
Fredericton, NB
E3B 5P7

John Murphy
BC Ministry of Forests
Research Branch, Kalamalka
3401 Reservoir Road
Vernon, BC
V1B 2C7

Greg O’Neill
BC Ministry of Forests
Research Branch, Kalamalka
3401 Reservoir Road
Vernon, BC
V1B 2C7

Conor O'Reilly
University College of Dublin
Dept. Crop Sci. Hort. & For. Faculty of Agriculture
UCD Belfield
Dublin
Ireland

Roger Painter
BC Ministry of Forests
Tree Improvement Branch
PO Box 9518 Stn Prov Govt
Victoria, BC
V8W 9C2

Donna Palamarek
Alberta Tree Improvement & Seed Centre
PO Box 750
Smoky Lake, AB
T0A 3C0

William Parker
Lakehead University
Faculty of Forestry
955 Oliver Road
Thunder Bay, ON
P7B 5E1

Giselle Phillips
BC Ministry of Forests
Research Branch, Kalamalka
3401 Reservoir Road
Vernon, BC
V1B 2C7

Don Pigott
Yellow Point Propagation Ltd.
PO Box 669
13735 Quennell Road
Ladysmith, BC
V9G 1A5

Ron Planden
BC Ministry of Forests
Tree Improvement Branch
PO Box 9518 Stn Prov Govt
Victoria, BC
V8W 9C2

Debbie Poldrugovac
BC Ministry of Forests
Tree Improvement Branch, Saanich
7380 Puckle Road
Saanichton, BC
V8M 1W4

John Quinn
Alberta Tree Improvement & Seed Centre
PO Box 750
Smoky Lake, AB
T0A 3C0

Om Rajora
University of New Brunswick
Faculty of Forestry and Environ. Management
PO Box 44555
Fredericton, NB
E3B 6C2

Marienela Ramirez
University of New Brunswick
Faculty of Forestry and Environ. Management
PO Box 44555
Fredericton, NB
E3B 6C2

Jerry Rehfeldt
USDA Forest Service
1221 S. Main
Moscow, ID
83843

David Reid
BC Ministry of Forests
Tree Improvement Branch, Saanich
7380 Puckle Road
Saanichton, BC
V8M 1W4

Spencer Reitenbach
BC Ministry of Forests
Tree Improvement Branch, Tree Seed Centre
18793 32nd Avenue
Surrey, BC
V4P 1M5

Jim Reno
Weyerhaeuser Co.
PO Box 9777
Federal Way, WA
98063

Claire Riddell
Lakehead University
Faculty of Forestry
955 Oliver Road
Thunder Bay, ON
P7B 5E1

Heather Rooke
BC Ministry of Forests
Tree Improvement Branch, Tree Seed Centre
18793 32nd Avenue
Surrey, BC
V4P 1M5

Hans Roulund
Royal Veterinary & Agriculture University
Arboretum Kirkegaardsvej 3a
Horsholm, Denmark
DK-2970

John Russell
BC Ministry of Forests
Research Branch
7060 Forestry Road
Mesachie Lake, BC
V0R 2N0

Marc Rust
University of Idaho
College of Natural Resources
Moscow, ID
83844

Deogratias Rweyongeza
University of Alberta
Faculty of Agric., Food and Nutritional Sciences
Edmonton, AB
T6G 2P5

Salim Silim
Agriculture Canada
Prairie Farm Rehabilitation Administration
PO Box 940
Indian Head, SK
S0G 2K0

Dale Simpson
Natural Resources Canada
Canadian Forest Service
PO Box 4000
Fredericton, NB
E3B 5P7

Pia Smets
University of British Columbia
Faculty of Forestry
202-4574 Main Mall
Vancouver, BC
V6R 2J1

Dave Spittlehouse
BC Ministry of Forests
Research Branch
1st floor, 722 Johnson St.
Victoria, BC
V8W 1N1

Michael Stoehr
BC Ministry of Forests
Research Branch
P O Box 9519 Stn Prov Govt
Victoria, BC
V8W 9C2

Ward Strong
BC Ministry of Forests
Tree Improvement Branch, Kalamalka
3401 Reservoir Road
Vernon, BC
V1B 2C7

Dawn Stubley
BC Ministry of Forests
Tree Improvement Branch, Tree Seed Centre
18793 32nd Avenue
Surrey, BC
V4P 1M5

Don Summers
D W Summers and Company
518 -13501 96th Avenue
Surrey, BC
V3V 1Y8

Cheri Tayler
BC Ministry of Forests
Tree Improvement Branch, Saanich
7380 Puckle Road
Saanichton, BC
V8M 1W4

Nadja Tchebakova
Forest Institute
Russian Academy of Sciences (Siberian Branch)
Krasnoyarsk
Russia

Susan Thorpe
Canfor
JD Little Forest Centre
PO Box 9000
Prince George, BC
V2L 4W2

Kathy Tosh
NB Dept. Of Natural Resources
3732 Route 102
Island View, NB
E3E 1G3

Nicholas Ukrainetz
1381 Heathdale Dr.
Burnaby, BC
V5B 3N9

Annette van Niejenhuis
Western Forest Products
8067 East Saanich Road
Saanichton, BC
V8M 1K1

Rita Wagner
BC Ministry of Forests
Tree Improvement Branch
17000 Domano Blvd.
Prince George, BC
V2N 5M2

Chris Walsh
BC Ministry of Forests
Tree Improvement Branch, Kalamalka
3401 Reservoir Road
Vernon, BC
V1B 2C7

Tongli Wang
University of British Columbia
Faculty of Forestry
3401-2424 Main Mall
Vancouver, BC
V6T 1Z4

Marcus Warwell
USDA Forest Service
1221 S Main Street
Moscow, ID
83843

Andrew Weaver
University of Victoria
PO Box 3055
Victoria, BC
V8W 3P6

Robert Westfall
USDA Forest Service
Sierra Nevada Research Center
PO Box 245
Berkeley, CA
94701

Bevin Wigmore
Mount Newton Seed Orchard
1450 Mt Newton Cross Road
Saanichton, BC
V8M 1S1

Jack Woods
Forest Genetics Council of BC
3370 Drinkwater Road
Duncan, BC
V9L 5Z2

Alex Woods
BC Ministry of Forests
Bag 6000
Smithers, BC
V0J 2N0

Chang-yi Xie
BC Ministry of Forests
Research Branch
1st floor, 722 Johnson St.
Victoria, BC
V8W 9C2

Alvin Yanchuk
BC Ministry of Forests
Research Branch
PO Box 9519 Stn Prov Govt
Victoria, BC
V8W 9C2

Cheng Ying
BC Ministry of Forests
Research Branch
PO Box 9519 Stn Prov Govt
Victoria, BC
V8N 4V1

PHOTOS

Andreas Hamman, Isabelle Chuine, and Makiko Mimura with empty plates at the ice breaker.

Kathy Tosh says "When you've got the "best", who needs the "rest?"

"We'll drink to that!" A jovial table enjoying the festivities at Summerhill Winery. Seated are Louise Corriveau, Tannis Beardmore, Kathy Tosh, Dale Simpson, Dana Howe, and Marilyn Cherry

Marilyn Cherry congratulates Cherdsak Liewlaksaneeyanawin for best student poster

Marilyn Cherry congratulates Mark Lesser for best student oral presentation.

Invited symposium speakers. From left to right, Jerry Rehfeldt, Isabelle Chuine, Steven Jackson, Dave Spittlehouse, Nadja Tchebakova, Andrew Weaver.

CTIA sponsored students: Nicolas Ukrainetz (UBC), Marienela Ramirez (UNB), Adriana Almeida-Rodriguez (UA), Stéphanie Beauseigle (ULaval), Jessica Courtier (UNBC), Jean-François Carle (UdeM), Claire Riddell (Lakehead U).

BC Ministry of Forests, Tree Improvement Branch. Left to right. Bottom row: Chris Walsh, Leslie McAuley, Ron Planden, Rita Wagner. Second row: Dale Draper, Dave Kolotelo. Third row: Cheri Tayler, Heather Rooke, Carolyn Lohr, Don Summers. Fourth row: Robb Bennett, Dawn Stubley, David Reid. Fifth row: Penny Draper, Debbie Poldrugovac, Spencer Reitenbach, Brian Barber, Roger Painter.