

Potential change in lodgepole pine site index and distribution under climatic change in Alberta

Robert A. Monserud, Yuqing Yang, Shongming Huang, and Nadja Tchebakova

Abstract: We estimated the impact of global climate change on lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) site productivity in Alberta based on the Alberta Climate Model and the A2 SRES climate change scenario projections from three global circulation models (CGCM2, HADCM3, and ECHAM4). Considerable warming is apparent in all three models. On average, the increases in mean GDD₅ (growing degree-days >5 °C) are 18%, 38%, and 65% by the 2020s, 2050s, and 2080s, respectively. Change in precipitation is essentially nil. This results in proportional increases in dryness index. We used the dryness index to predict the potential future range and GDD₅ to predict its potential productivity. Generally, lodgepole pine site index is predicted to increase steadily by 3 m for each 30-year period. Offsetting this increase is a large reduction in suitable area as drying increases. At first, the warming increases the potential range up to 67% by the 2020s but then shrinks from 34% to 58% of its current area by 2080. Such major changes will need to be considered when setting long-term forest management plans. The increased risk of both wildfire and insect outbreaks further compounds this planning problem, especially because these disturbance events can interact and further increase risk.

Resume : Nous avons estimé l'impact des changements climatiques sur la productivité de stations dominees par le pin tordu latifolie (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.), en Alberta, en se basant sur le modele climatique de l'Alberta et les projections du scenario de changements climatiques A2 SRES de trois modeles de circulation globale (CGCM2, HADCM3 et ECHAM4). Un rechauffement considerable est apparent dans les trois modeles. En moyenne, l'augmentation du nombre moyen de degres-jours de croissance au dessus de 5 °C (DJC5) est de respectivement de 18%, 38 % et 65 % pour les annees 2020, 2050 et 2080. Les changements de precipitation sont essentiellement nuls. Cette situation engendre une augmentation proportionnelle de l'indice d'aridite. Nous avons utilise l'indice d'aridite pour prédire l'étendue potentielle future et le DJC5 pour prédire la productivité potentielle. Généralement, l'indice de qualité de station du pin tordu devrait augmenter régulièrement de 3 m pour chaque période de 30 ans. Cette augmentation est compensée par une forte réduction de la superficie productive à mesure que l'aridité augmente. Dans un premier temps, le réchauffement augmente l'étendue potentielle jusqu'à 67 % vers les années 2020, mais la réduit par la suite pour atteindre 34% à 58 % de la superficie actuelle vers 2080. Des changements aussi importants devront être considérés lors de l'élaboration de plans d'aménagement forestier à long terme. L'augmentation des risques de feu et d'épidémie d'insecte complique davantage ce problème de planification surtout parce que ces perturbations peuvent interagir entre elles et augmenter encore davantage les risques.

[Traduit par la Rédaction]

Introduction

Growing concern about global climate change (Houghton 1997; IPCC 2007) has placed greater urgency on understanding the relationship between climate and important management factors such as site productivity, a key component in growth and yield prediction. As an indication of the current rate of change, Menzel and Fabian (1999) found that growing season length across Europe has increased by

11 days since the 1960s. Global average surface air temperature is projected to warm between 1.4 and 5.8 °C by 2100, relative to 1990, which is about 2-10 times as fast as the observed 20th century warming (IPCC 2000). Barrow and Yu (2005) predicted that under several climate change scenarios for Alberta, mean annual temperature is expected to rise 3-5 °C by the 2050s, with degree-days >5 °C increasing 30%-50% and dryness index (DI) increasing 20%-30% (i.e., greater drying). Working in southern Siberia where similar temperature increases are predicted at similar latitudes, Tchebakova et al. (2003) concluded that both the rapid rate of change and the large absolute amount of change are expected to have profound effects on terrestrial ecosystems at all hierarchical levels: from biome-level vegetation zones (Tchebakova et al. 2003) to ecosystems (Guisan et al. 1995) to species composition (Box et al. 1999), and to populations within species (Rehfeldt et al. 1999).

Canada's location in the high latitudes means that it is likely to experience some of the largest changes in climate, in particular changes in temperature (Barrow and Yu 2005). Rising temperatures could increase forest productivity by the direct effect of additional heat and by increasing the length

Received 2 February 2007. Accepted 27 August 2007. Published on the NRC Research Press Web site at cjfr.nrc.ca on 8 February 2008.

R.A. Monserud. PNW Research Station, USDA Forest Service, 620 SW Main Street, Suite 400, Portland, OR 97205, USA.

Y. Yang and S. Huang. Forest Management Branch, Public Lands and Forestry Division, AFB Sustainable Resource Development, 8th Floor, 9920-108 Street, Edmonton, AB T5K 2M4, Canada.

N. Tchebakova. Sukachev Forest Institute, Russian Academy of Sciences (Siberian Branch), 660036 Krasnoyarsk, Russia.

¹Corresponding author (e-mail: rmonserud@fs.fed.us).

of the growing season. Increasing CO₂ could increase productivity by increasing photosynthesis and water use efficiency, although effects vary by species (Vitarshall and Monserud 1996; Monserud and Marshall 2001). Negative effects could result if the increased warming is not offset by a commensurate increase in precipitation, leading to moisture stress and potential shrinking of existing species range distribution (Barrow and Yu 2005; Hamann and Wang 2006). Other negative effects include increased risk of catastrophic losses due to wildfire, insect outbreaks, and disease (IPCC 2001; Soja et al. 2007). Because it is essential to predict future growth and yield for credible long-term forest management (Peng et al. 2004), we seek to examine the potential effect, of such changes in climate on the productivity of lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.), one of the most important commercial species in Alberta (Huang et al. 2004).

The objective of this study was to examine the potential effect of global climate change on the spatial distribution of lodgepole pine site productivity over time in Alberta. We used the A2 SRES climate change scenario projections from three of the major Global Circulation Models (GCMs) for three 30-year time periods over this century. Site index (SI), the most commonly used measure of site productivity in forest management, was chosen for this study. For well over a century, forest mensurationists have successfully used the height and age of dominant trees to index the volume productivity (m³·ha⁻¹·year⁻¹) of a forest stand over time (Assmann 1970; Monserud 1984). Observed SIs (dominant height at an index age) were derived from the large and extensive network of tree sectioning stem analysis plots. Because suitable sites for establishing and growing lodgepole pine are likely to change as climate change occurs, our second objective focused on predicting the future potential distribution range of lodgepole pine across Alberta.

Existing climate-site relationships from Monserud et al. (2006) were used to relate climate to site productivity. The Alberta Climate Model (Alberta Environment 2005) was used to determine the baseline climate. The climate and site productivity data sets were linked via spatial location (latitude, longitude, and elevation), which allowed us to map results across the range of lodgepole pine in Alberta. We used climate change scenario projections from three GCMs to examine variation with respect to space, time, climatic variables, and model (Hulme et al. 1999).

Methods

Data description

Alberta has sectioned thousands of trees and collected a large amount of data on lodgepole pine stand growth and site productivity over the past few decades (Huang et al. 1997). Most sectioned trees were sampled in the buffer zones around permanent sample plots, with the remainder obtained from temporary sample plots. Ring counts and measured lengths of all stain sections (stem analysis) allowed for the reconstruction of the actual height growth curve for each tree's life and the determination of height at age 90 at breast height (see Huang et al. 1997; Monserud and Huang 2003). These stands are predominantly even-aged, both because of shade intolerance of lodgepole pine

and because the most common causes of regeneration are either wildfire or clearcut harvesting, events that introduce a single cohort. Because cross-sectional ring counts were examined in detail in the course of determining age throughout each tree's height growth history, anomalous ring growth patterns indicating earlier suppression would have been detected and the site tree replaced with another with no such ring pattern. This ring and stem analysis procedure greatly reduces a bias due to selecting dominant site trees that were not always dominant (Monserud 1984).

The Alberta Climate Model (Alberta Environment 2005) provided estimates of climatic variables at each plot location. This model is based on 30-year climate normals from the period 1961-1990. A network of between 1260 and 1433 weather stations from Alberta and portions of six adjacent jurisdictions was used in climatic model development, depending on the climatic variable. To produce the climate model, the weather station network was continuously interpolated across Alberta using Hutchinson's (2002) ANUSPLIN, which uses thin-plate smoothing splines for the interpolation. Basically, this is a spatial regression model of a given climatic response as a three-dimensional function of elevation and spatial location (latitude and longitude) across Alberta. Inclusion of weather stations from an additional 2° buffer (latitude and longitude) surrounding Alberta eliminated edge effects during the interpolation.

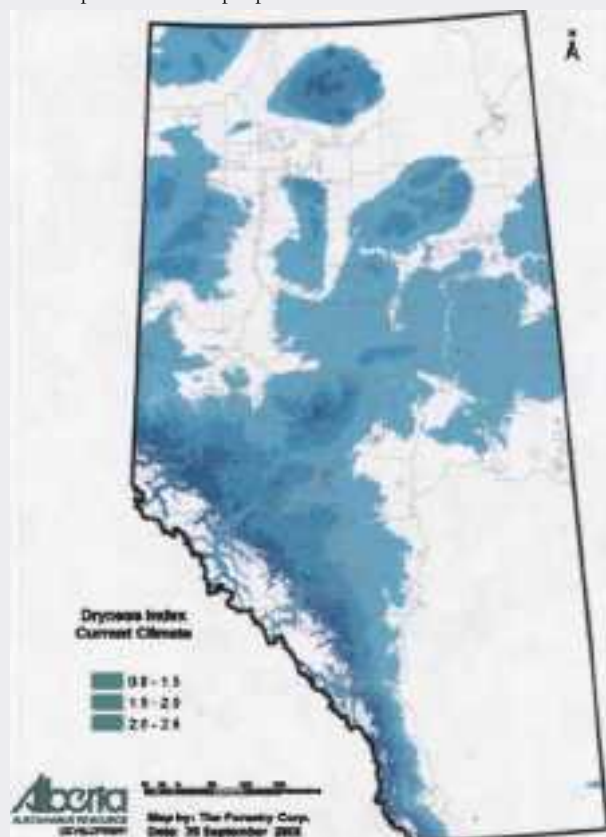
Monserud et al. (2006) used 1145 stem analysis plots for an analysis linking lodgepole pine site index and climatic variables. Working from a suite of 16 climatic variables from the Alberta Climate Model, they found that simple measures of heat explained the most variation in SI (24%-27%). Because most of the climatic variables were highly intercorrelated (especially the various measures of heat, with $r = 0.98$), higher-level combinations of climatic variables explained only a small amount of additional variation over the best one-variable models. For this study, SI was predicted from growing degree days > 5 °C (GDD₅):

$$[1] \quad SI = 2.39 + 0.01214 \times GDD_5$$

This model had a standard error of 2.8 m compared with a mean SI of 14.4 m. Monserud et al. (2006) also found that DI, the ratio of GDD₅ to annual precipitation, was a significant predictor of SI ($R^2 = 0.20$), largely through the effect of GDD₅. Two classes of climatic variables that were essentially uncorrelated with SI were measures of precipitation and winter temperature. This is not to say that precipitation and winter temperatures are not important factors in the fundamental causes of lodgepole pine productivity. Rather, these results indicate that precipitation and winter temperatures simply are not limiting within lodgepole pine's natural range once trees are established.

Next, the natural distribution of lodgepole pine was examined as a function of DI. Based on the data of Monserud et al. (2006), the 1% and 99% limits on DI are 0.9 and 2.6 °C·mm⁻¹, respectively (Fig. 1). We used this range to identify potential future lodgepole pine distributions under various climate change models. Based on the hand-drawn Alberta lodgepole pine distribution map from earlier work (Monserud and Huang 2003), 80% of the pixels (picture elements) were within the DI limits of 0.9-2.6 °C·mm⁻¹. The lodgepole pine distribution map was carefully examined via

Fig. 1. Dryness index using the 1% and 99% empirical limits from the 111.5 permanent sample plots.



extensive field visits to distinguish lodgepole pine from other coniferous species, especially along the edges of the rtdp.

Climate change scenarios

In 1996, the IPCC called for the development of a new set of emissions scenarios, termed **SRES** for the Special Report on Emission Scenarios that described them (IPCC 2000). They included the additional effect of sulfur emissions and revised economic and technological assumptions. We used the A2 **SRES** climate change scenario from the Canadian Climate Centre (CGCM2; Flato et al. 2000), the Hadley Centre in the United Kingdom (HADCM3; Johns et al. 1997), and the Max Planck Institute in Hamburg (ECHAM4; Roeckner et al. 1996). The A2 SRES scenario is basically a storyline that focuses on regional solutions to economic, social, and environmental concerns, with less concern for economic growth and new energy technology than the A1 scenarios (IPCC 2000). In general, both the A1 and A2 SRES scenarios lead to greater cumulative emissions and resultant temperature increase than the B1 and B2 SRES scenarios, and the A2 SRES can be viewed as an approximate upper bound in this small family of available SRES scenarios (IPCC 2000). We used three three-decade time periods that were available from the IPCC Data Distribution Centre (ipcc-ddc.cru.uea.ac.uk): the 2020s (2011–2040), 2050s (2041–2070), and 2080s (2071–2100). We obtained scenario data for our Alberta window from the Canadian Institute for

Climate Studies (University of Victoria, Victoria, British Columbia; www.cics.uvic.ca/scenarios).

Data are given in terms of anomalies, which are deviations from the baseline period of 1961–1990 (Smith and Hulme 1998). We added these anomalies to the corresponding baseline climatic maps for Alberta using the Alberta Climate Model (Alberta Environment 2005). Because the GCMs are rather coarse resolution (between 2.5 and 3.75° latitude and longitude) relative to the Alberta Climate Model (we used 2 km x 2 km resolution), we interpolated the anomalies for each pixel by using an inverse-distance-squared weighting method. We overlaid the GCM anomaly grid (4 x 4 cells for CGCM2, 5 x 5 cells for ECHAM4, and 6 x 4 cells for HADCM3) onto the Alberta climate map and calculated the weighted average of the nearest five anomalies for each of the 165 860 pixels. This interpolation step is also called downscaling.

After interpolation of the anomalies, we used mean monthly temperatures to calculate mean annual temperature and mean monthly precipitation to calculate total annual precipitation. We then calculated GDD₅ using the month-specific relationships between degree-days and mean monthly temperature used to develop the Alberta Climate Model (see appendix 1 in Alberta Environment 2005). *(Note: an error in the GDD calculations in Alberta Environment (2005) was recently found and corrected. The formula on pp. 87–28 of appendix 1 in Alberta Environment (2006) for the normalized average monthly temperature (T) for a given station should be $T = (T + 13)/24$.)* After GDD₅ was determined, we calculated DI as the ratio of GDD₅ to annual precipitation.

Results

All 165 860 pixels (2 km x 2 km) were used to calculate mean climatic values for Alberta (Table 1). Mean annual temperature was predicted to increase between 0.9 °C (Hadley) and 1.7 °C (Hamburg) by the 2020s. The increases were from 1.9 °C (Hadley) to 2.9 °C (Canadian and Hamburg) by the 2050s and from 4.0 °C (Hadley) to 4.8 °C (Canadian and Hamburg) by the 2080s. Because the Hadley model predicted the coolest temperatures, it was the overall coolest of the three scenario projections.

When we focused on growing season temperatures (GDD₅), considerable warming was apparent in all three GCMs (Table 1; Fig. 2). The increases in mean GDD₅ were from 16% (Hadley) to 20% (Hamburg) by the 2020s, from 37% to 38% (all three models) by the 2050s, and from 62% (Canadian) to 68% (Hadley) by the 2080s. That is an increase in GDD₅ of 750–840 °C over the current-climate mean of 1224 °C by the 2080s. Under current climate, GDD₅ is <1500 °C across Alberta except for the Prairie lands in southeastern Alberta (Fig. 2a). Using the Canadian CGCM2 model as an example, this picture switches dramatically by the 2080s. GDD₅ is >1500 °C across Alberta by the 2080s, except for the Canadian Rocky Mountains on the southwestern border and the Caribou Mountains in the far north (Fig. 2b).

Corresponding to this overall warming, change in precipitation is essentially nil, at most 9% (45 mm·year⁻¹) of the baseline (Canadian and Hadley). The Hamburg model pre-

Climatic variable	Mean climatic value		
	U	(si)	U
January temperature (°C)	17.0	17.3	17.0
July temperature (°C)	17.3	17.3	17.3
Mean annual temperature (°C)	16.6	16.6	16.6
GDD ₅ (°C)	1419.2	1419.2	1419.2
Precipitation (mm)	508.6	508.6	508.6
Dryness index (°C·mm ⁻¹)	3.0	3.0	3.0

dicts a reduction in total precipitation of 13-25 mm year⁻¹. This overall small change in precipitation leads to a strong increase in DI (Table 1). For the 2020s, mean DI ranges from 3.0 to 3.5 °C·mm⁻¹, an increase of 0.3 °C·mm⁻¹ (Hadley) to 0.7 °C·mm⁻¹ (Hamburg). By the 2050s, mean DI ranges from 3.5 to 3.8 °C·mm⁻¹, an increase of 0.7 °C·mm⁻¹ (Hadley) to 1.1 °C·mm⁻¹ (Hamburg). By the 2080s, DI ranges from 4.0 to 4.7 °C·mm⁻¹, an increase of 1.3 °C·mm⁻¹ (Canadian and Hadley) to 2.0 °C·mm⁻¹ (Hamburg).

Because of the predicted increase in growing season temperatures in all three GCMs and for all three time periods, potential SI is predicted to increase over the current-climate pixel mean of 13.5 m (Table 2) using eq. 1. For the 2020s, the predicted increase in SI ranges from 2.9 m (Hadley) to 3.4 m (Hamburg). By the 2050s, the increase in SI is predicted to range from 5.5 m (Canadian) to 5.8 m (Hadley). By the 2080s, the increase in SI is predicted to range from 8.3 m (Canadian) to 9.9 m (Hadley), with an increase of 9.5 m with the Hamburg scenario (Table 2). This amounts to a steady 1 m increase per decade.

Table 3 lists total area by predicted SI class for each model and each year. By the 2020s, the Canadian model shows an expansion of the climatically suitable area of 37%, the Hadley model shows an even larger expansion of 67%, while the Hamburg model shows no expansion. The mean SI is relatively similar across the three GCMs, ranging from 16.8 m (Hamburg) to 17.3 m (Hadley). Note that this potential range expansion into northeastern Alberta includes areas currently occupied by the closely related jack pine (*Pinus banksiana* Lamb.) as well as lodgepole pine - jack pine hybrids. By the 2050s, the expansion in area suitable for lodgepole pine (0.9 < DI < 2.6) has been reversed (Table 3). The Canadian model has lost 59000 km² of suitable habitat over the 2020s expansion, which is a drop of 12% over the current-climate land area. The Hamburg model in the 2050s has lost 44 000 km² of suitable climatic habitat, a drop of 34% over the current-climate land area. By the 2050s, the Hadley model has lost 89 000 km² of climatically suitable habitat, a drop of 6% over the current-climate land area. Because of increases in GDD₅ by the 2050s, potential SI continues to increase (Table 2), from a mean of 18.1 m (Canadian and Hamburg) to 18.8 m (Hadley). By the 2080s, suitable area continues to shrink with all three models (Table 3). The Canadian model shows a drop of 42% over the current-climate land area, the Hamburg model a drop of 67% over the current-climate land area, and the Hadley model a drop of 59% over the current-climate land area. By the 2080s, potential SI continues to increase (Table 2), from 19.3 m (Hamburg) to 20.2 m (Hadley).

Using the Canadian CGCM2 model, we illustrate the changing distribution of both lodgepole pine predicted SI over time and its potential range of occurrence (Fig. 3). We use the 1% and 99% DI limits to determine the species range. As GDD₅ increases over time under the climate change scenario, SI is predicted to steadily increase. However, this increase must be considered in relation to locations with suitable DI values. In the 2020s, the area suitable for lodgepole pine establishment and growth expands greatly (+37%) (Table 3), primarily in the Lower Foothills subregion in central Alberta (Fig. 3b). This increase in potential

Fig. 2. Growing degree-days >5 °C under (a) current climate (Alberta Environment 2005) and (b) using the Canadian Climate Centre CGCM2 model for the 2080s.

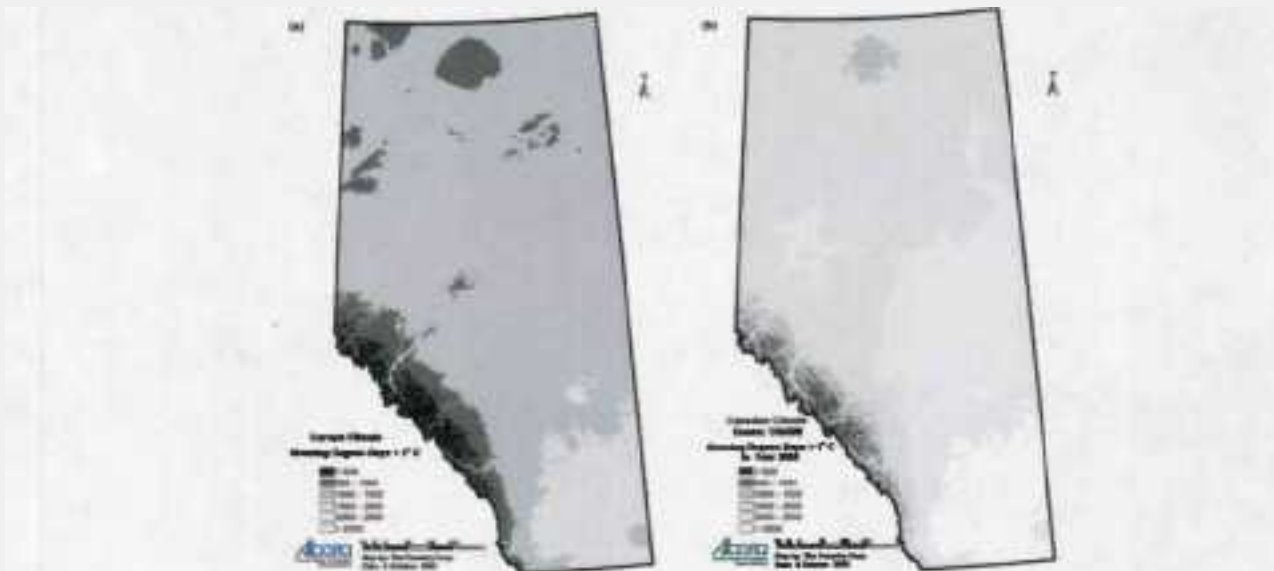


Table 2. Predicted site index statistics by GCM and year.

Model	Year	Variable	N	Mean	SD	Min.	Max.
Current climate	2000	SI_00	24909	13.5	2.3	4.6	20.3
CGCM2	2020s	SI_20	41443	17.0	2.4	9.4	23.1
	2050s	SI_50	26739	18.2	2.9	10.1	25.6
	2080s	SI_80	1573	19.6	3.5	11.3	30.1
ECHAM4	2020s	SI_20	31071	16.8	2.2	10.7	23.1
	2050s	SI_50	20081	18.1	2.5	11.7	26.1
	2080s	SI_80	11139	19.3	2.9	13.2	30.7
HADCM3	2020s	SI_20	50767	17.3	2.1	10.5	22.7
	2050s	SI_50	28611	18.8	2.5	11.6	25.9
	2080s	SI_80	12405	20.2	3.0	13.7	31.4
CGCM2	2020s	SI_20-SI_00	24549	3.2	1.7	-3.4	10.3
	2050s	SI_50-SI_00	20123	5.5	1.7	-0.9	12.1
	2080s	SI_80-SI_00	12460	8.3	1.9	2.3	15.9
ECHAM4	2020s	SI_20-SI_00	22455	3.4	1.7	-2.8	10.8
	2050s	SI_50-SI_00	16011	5.6	1.8	-0.1	12.6
	2080s	SI_80-SI_00	5125	9.5	2.0	4.0	17.1
HADCM3	2020s	SI_20-SI_00	24790	2.9	1.7	-3.8	9.9
	2050s	SI_50-SI_00	21179	5.8	1.7	-0.7	12.1
	2080s	SI_80-SI_00	7632	9.9	2.0	4.0	17.3
CGCM2	2020s	SI_50-SI_20	25677	2.4	0.2	1.6	3.5
	2050s	SI_80-SI_50	16560	3.0	0.3	2.2	4.9
	2080s	SI_80-SI_20	15493	5.4	0.5	4.2	8.3
ECHAM4	2020s	SI_50-SI_20	18846	2.5	0.3	2.0	3.7
	2050s	SI_80-SI_50	8247	4.0	0.3	3.3	5.3
	2080s	SI_80-SI_20	7011	6.6	0.5	5.4	9.0
HADCM3	2020s	SI_50-SI_20	27010	3.0	0.2	2.5	4.1
	2050s	SI_80-SI_50	10490	4.5	0.4	3.8	5.9
	2080s	SI_80-SI_20	8889	7.5	0.6	6.3	9.9

Note: N is the number of 2 km x 2 km pixels that had a DI between the limits of 0.9 and 2.6. Change in predicted SI between periods was also calculated but using only pixels that were both within the DI limits in both periods. SI_00 is SI under current climate (2000) and SI_20, SI_50, and SI_80 are predicted SI for the 2020s, 2050s, and 2080s, respectively.

Table 3. Total area (1000 km²) by SI class for each model and each year.

SI class (m)	Total area by site class (1000 km ²)									
	CGCM2				ECHAM4			HADCM3		
	Current climate, 2000	2020s	2050s	2080s	2020s	2050s	2080s	2020s	2050s	2080s
6-9	15									
9-12	37	9	5	1	3			4		
12-15	47	22	11	9	24	10	3	25	10	3
15-18	19	69	26	11	56	28	11	85	26	10
18-21	3	65	49	20	40	35	13	88	56	15
21-24		1	16	26	1	8	12	1	21	18n
24-27				3			1			3
>27										1
Total area (1000 km ²)	121	166	107	70	124	80	41	203	114	50

range is coupled with a 3.2 m increase in SI due to greater warming (Table 2). By the 2050s, this potential range has receded to 12% less than the current range area (Fig. 3c). Increasing GDD₅ continues to increase potential productivity by 5.5 m (Table 2), but the heating is not offset by a commensurate increase in precipitation. The result is that the potential species range is shrinking. By the 2080s, the area with suitable DI conditions has shrunk considerably to levels much less (42%) than the present species distribution (Fig. 3d). Productivity has greatly increased (mean SI = 19.6 m), but this increase is spread over a shrinking landbase. Climatically suitable lodgepole pine areas are predicted to nearly disappear from the northern half of Alberta due to increased drying. Offsetting this shrinking range area somewhat is an expansion into the Subalpine and Alpine subregions, with warming coming to the higher mountain locations with adequate precipitation provided by orographic lifting of air masses.

Similar results were obtained using the Hadley HADCM3 model (Figs. 4a-4c), except that the potential species range expands even greater (+67%) than with the Canadian model in the 2020s. The expansion is strong into the plateaus and discontinuous hill systems in northern Alberta. Suitable habitat also expands to the northeast of the current Lower Foothill/Tubregion (Figs. 4a-4c). By the 2080s, the potential species range has shrunk considerably (-59%), even more so than with the Canadian model. By the 2080s, the Lower Foothills predicted range has nearly disappeared, with lodgepole pine confined almost entirely to the Rockies and the Upper Foothills. Across the entire northern half of Alberta, only isolated pockets in the Caribou Mountains are predicted.

The Hamburg ECHAM4 model showed the greatest drying (Figs. 4d-4f), with almost no range expansion in the 2020s. By the 2080s, lodgepole pine is predicted to disappear from northern Alberta almost completely (Fig. 4f). Suitable DI species limits are only found in the Rockies and the nearby Upper Foothills.

Discussion

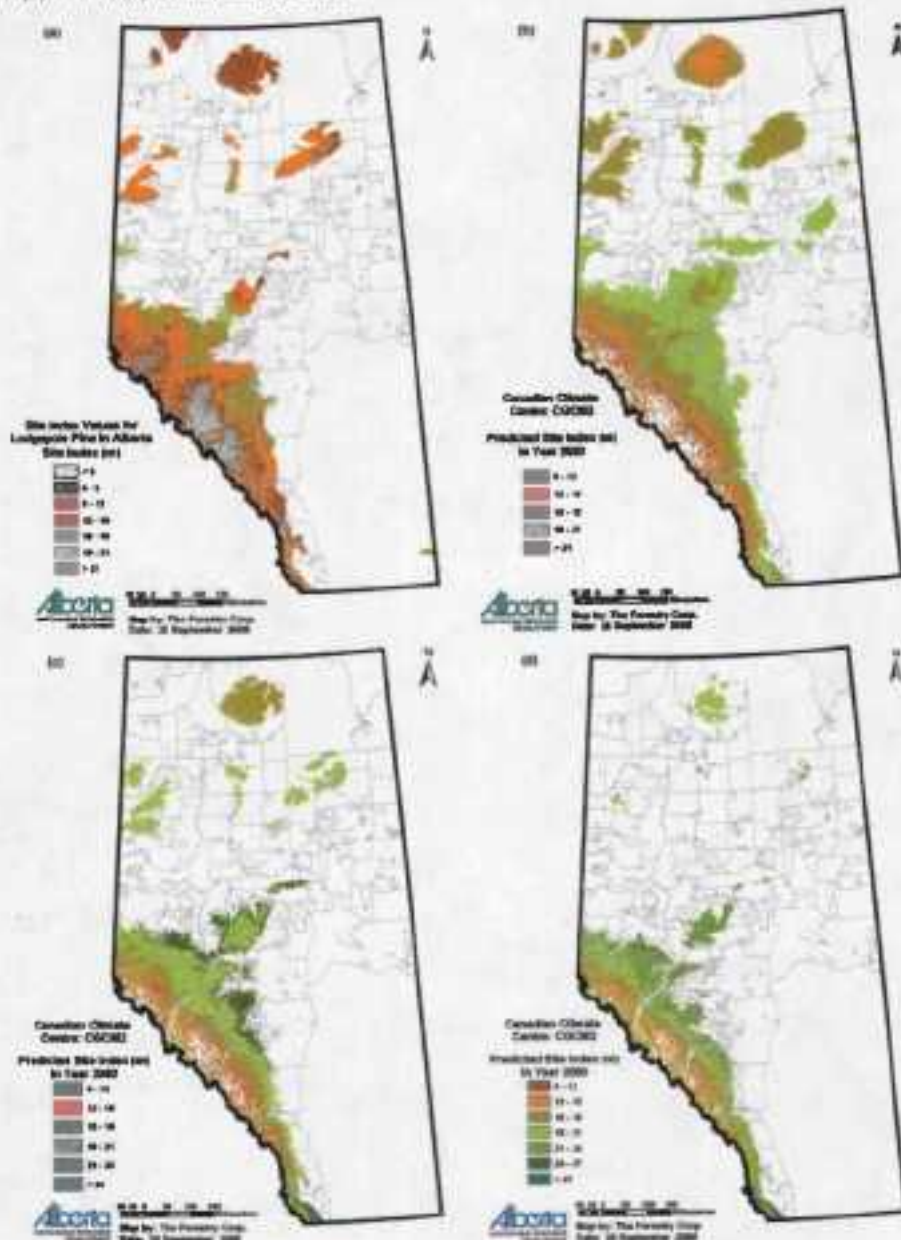
Although individual GCM model variation is apparent in Figs. 3 and 4 and Tables 1-3, the three models project a similar story. On the positive side, the steady increase in heating (e.g., GDD₅) indicates large increases in the potential SI. These expected increases average 3 m in the 2020s,

almost 6 m by the 2050s, and about 9 m by the 2080s (Table 2). A study conducted in southern Siberia, an area of similar latitude to southern Alberta, showed that dominant tree height growth may increase up to 5 m in the mountains, where precipitation is sufficient (Tchebakova and Parfenova 2003). Generally, this increase in productivity is offset by a shrinking landbase of suitable sites due to increasing DI, creating moisture stress limiting the establishment and survival of lodgepole pine. The potential lunge at first expands greatly by the 2020s (except for ECHAM4, which remains constant), begins to recede to present-day limits by the 2050s, and continues to shrink by the 2080s (Table 3). As heating increases, drying and moisture stress continue to increase proportionately because precipitation is predicted to remain relatively constant.

Using DI limits of 1% and 99% (0.9-2.6 °C mm⁻¹) to determine the potential species distribution of lodgepole pine appeared to work well. Tchebakova and Parfenova (2003) pointed out that heat supply is a primary determinant of productivity and that DI is a determinant of species range. If temperature increase is not balanced by sufficient additional precipitation, the DI would increase (as predicted under all three GCMs; see Table 1) and the moisture stress would have a negative effect on growth and productivity as well as survival rate. At the northern border (and at high elevations) of a species' range, DI operates through a shortage of heat, and at the southern border, it operates through a shortage of water with respect to the heat available to support tree occurrence. The primary effects of climate on plants are determined by the interactions of energy and water (Stephenson 1998). Other DIs using different formulations of moisture parameters also work well for determining species ranges (Tchebakova et al. 1993; Hogg 1991; Stephenson 1998). However, many of those moisture parameters are not typically recorded in most weather stations. We avoided this problem by only using *vasinnhi stisat* are direct functions of observed temperature and precipitation, thus arriving at a straightforward DI.

Increasing moisture stress is a factor that could limit the potential increase in height growth due to a warming climate. Barrow and Yu (2005) found that changes in precipitation are predicted to be between -10% and +15% by the 2050s and that DIP is projected to increase by the 2080s, driven primarily by large increases in GDD₅. They concluded that moisture stress is likely to occur because the

Fig. 3. Potential size index predictions and species distribution range under (a) current climate and using the Canadian Climate Centre CGCM2 model for the (b) 2020s, (c) 2050s, and (d) 2080s.



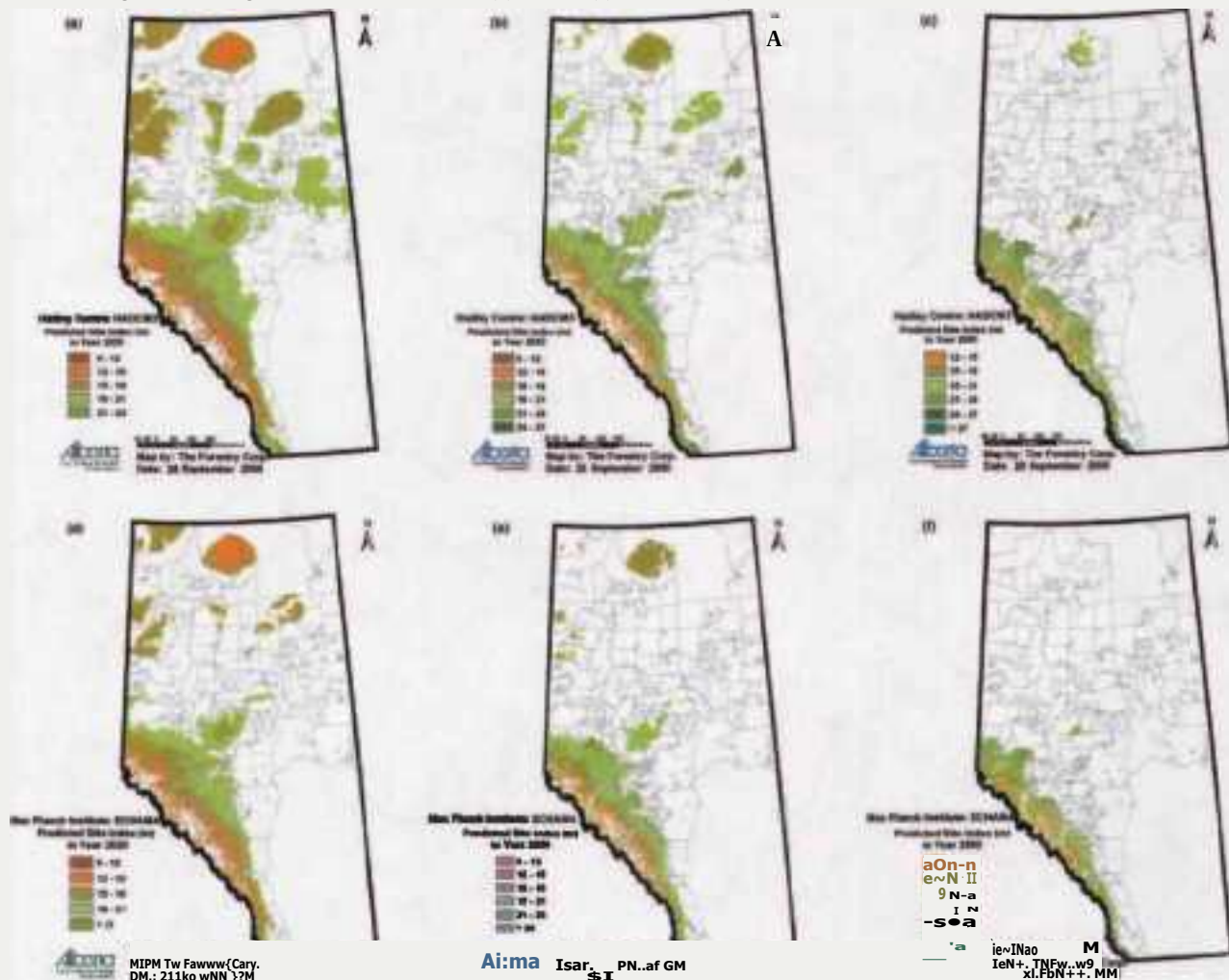
largest decreases in precipitation occur during the summer season, which is also the season when most degree-day units are accrued. Our analysis of DI under climate change confirmed this increase in moisture stress.

The warming predicted through the 2020s is balanced by enough precipitation that DI does not increase greatly, resulting in large expansions of the potential range of lodgepole pine. The increases in growing degree-days will not be offset by greater precipitation, resulting in increasing DI, greater drying, and increasing moisture stress in trees. By the 2080s, the drying in northern Alberta is so thorough under all three CGMs that potential lodgepole pine locations have nearly disappeared entirely, save only for isolated hills in the far north. Even greater reduction in the range of

lodgepole pine in Alberta and British Columbia was predicted due to climate change by Hamann and Wang (2006).

Iverson and Prasad (2001) pointed out that many species distribution models also assume that tree species occur in all environments where it is possible for them to survive. The opposite is probably true (Loehle and LeBlanc 1996), leading to the difference between a species' realized and potential fundamental niche (Rehfeldt et al. 1999). Within the potential range of suitable lodgepole pine habitats, colonization success will depend on a suite of additional variables, such as edaphic barriers, landscape connectivity, seed dispersal distances and fates, population adaptability, winter temperature extremes, interspecific competition, and agricultural activity (Iverson and Prasad 2001). A climatic change

Fig. 4. Potential site index predictions and species distribution range using the Hadley HADCM3 model for the (a) 2020s, (b) 2050s, and (c) 2080s and using the Hamburg ECHAM4 model for the (d) 2020s, (e) 2050s, and (f) 2080s.



Third, our 2 km × 2 km grid does not afford fine-scale topographic features such as slope and aspect. A variable such as DI cannot distinguish between different vegetation on north- versus south-facing slopes at a given location. The Cypress Hills in southeastern Alberta are an example of one of the driest areas supporting lodgepole pine stands (DI between 2.0 and 2.6), which are mostly confined to the cooler and moister north-facing slopes. One way that we got around this limitation was by using on-the-ground knowledge of the distribution of lodgepole pine to intentionally set the DI upper limit at 2.6, even though an upper limit of DI = 2.0 provides a better fit to the natural distribution map. This meant that the Cypress Hills would be included in the current climate potential distribution map (Fig. 1).

Fourth, although the climate - site productivity relationship was based on a large network of plots, only one quarter on the variation in productivity was due to climate. The sources of variation in site productivity are twofold: genetic and environmental. Monserud and Rehfeldt (1990) found that a genetic index (a standardized 3-year seedling weight in genetic trials) explained 42% of the variation in SI of Rocky Mountain Douglas-fir (*Pseudotsuga menziesii* var. *glomifolia* (Beissn.) Franco) in the northern Rocky Mountains. Like Douglas-fir, lodgepole pine is a genetic specialist with steep adaptive clines. Therefore, the correlation between genotype and environment could be strong, and both genetic and environmental effects should contribute to variation in SI (Monserud and Rehfeldt 1990). In general, environmental sources of variation include climate (primarily heat and precipitation), soil (both moisture regimes and nutrient availability), and perhaps some measure of the climax vegetation (Monserud 1984). Finally, unexplained sources of variation can be due to sampling error, measurement error, and microsite and microclimatic differences among sites.

If currently observed climate trends continue or accelerate, major changes to management of natural resources will become necessary (Hamann and Wang 2006). Thorpe et al. (2006) adopted a proactive response to potential climate change. They eschewed the common forest management assumption of a forest in equilibrium with its climate and instead recommended increasingly intensive management policies. These could include deliberately assisting the movement of species (or populations within species) to suitable new habitats. This issue is particularly acute for forest systems, where natural migration (for example, of new tree species or of climatically more suitable genetic populations of locally extant tree species) may not be possible without human intervention (Rehfeldt et al. 1999; Thorpe et al. 2006). Finally, future analysis based on other emission scenarios is needed to confirm the climate trends and guide forest management practices.

Acknowledgments

We thank Brian Maier of The Forestry Corp. for his tremendous help at various stages, especially generating maps. We appreciate the contributions of Hinton Wood Products Ltd., Weyerhaeuser Canada Ltd., Sunpine Forest Products Ltd., and Canadian Forest Products Ltd. for providing the underlying site productivity data. The Forest Resource Improvement Association of Alberta and Alberta Sustainable

Resource Development provided funding and logistic support necessary to carry out this research. Special thanks to Narinder Dhir and Christine Hansen for making the Alberta Climate Model available and for help in running the model. TN Hogg, Dave Morgan, and Leonard Barnhardt provided constructive suggestions and helpful review comments. We also thank the anonymous reviewers and Associate Editor for their review comments. R.A. Monserud was supported by the Pacific Northwest Research Station (USDA Forest Service) for his contribution to this research.

References

- Alberta Environment. 2005. Alberta Climate Model (ACM) to provide climate estimates (1961-1990) for any location in Alberta from its geographic coordinates. Publ. T/749. Alberta Environment, Edmonton, Alta.
- Assmann, E. 1970. The principles of forest yield studies. Pergamon Press, Oxford, U.K.
- Barrow, E., and Yu, G. 2005. Climate scenarios for Alberta. Prairie Adaptation Research Collaborative, Regina, Sas. (www.parc.ca/research_pub_scenarios.htm).
- Box, E.O., Crumpacker, D.W., and Hardin, P.S. 1999. Predicted effects of climatic change on distribution of ecologically important native tree and shrub species in Florida. *Clim. Change*, **41**: 213-248. doi:10.1023/A:1005483507351.
- Flannigan, M.D., Logan, K.A., Amiro, B.D., Skinner, W.R., and Stocks, B.J. 2005. Future area burned in Canada. *Clim. Change*, **72**: 1-16. doi: 10.1007/s10584-005-5935-y.
- Flato, G.M., Boer, G.J., Lee, W.G., McFarlane, N.A., Ramsden, D., Reader, M.C., and Weaver, A.J. 2000. The Canadian centre for climate modelling and analysis global coupled model and its climate. *Clim. Dyn.* **16**: 451-467. doi:10.1007/s003820050339.
- Gill, N.P., Weaver, A.J., Zwiers, F.W., and Flannigan, M.D. 2004. Detecting the effect of climate change on Canadian forest fires! *Geophys. Res. Lett.* **31**(18): L18211. doi:10.1029/2004GL020876.
- Guisan, A., Holten, J.I., Spichiger, R., and Tessier, L. 1995. Potential ecological impacts of climate change in the Alps and Fennoscandian Mountains. *Mount. Res. Dev.* **16**: 182-183.
- Hamann, A., and Wang, T. 2006. Potential effects of climate change on ecosystem and tree species distribution in British Columbia. *Ecology*, **87**: 2773-2786. doi:10.1890/0012-9658(2006)87[2773:PEOCCO]2.0.CO;2. PMID:17168022.
- Hogg, E.H. 1997. Temporal scaling of moisture and the forest-grassland boundary. *Agric. For. Meteorol.* **84**: 115-122. doi:10.1016/S0168-1923(96)02380-5.
- Hogg, E.H., and Bernier, P.Y. 2005. Climate change impacts on drought-prone forests in western Canada. *For. Chron.* **81**: 675-682.
- Hogg, E.H., Brandt, J.P., Kochubajda, B., Michaelian, M., and Frey, B.R. 2006. Impact of the 2001-2003 drought on productivity and health of western Canadian aspen forests. In *Proceedings of the 53rd Western International Forest Disease Work Conference*. USDA Forest Service, Intermountain Region, Ogden, Utah.
- Houghton, J.T. 1997. *Global warming: the complete briefing*. 2nd ed. Cambridge University Press, Cambridge, U.K.
- Huang, S., Titus, S.J., and Koppstein, G. 1997. Development of a subregion-based compatible height-site index-age model for young and mature lodgepole pine in Alberta. *Res. Note 6*. Publ. T/353. Alberta Environment, Edmonton, Alta.
- Huang, S., Monserud, R.A., Braun, T., Loughheed, H., and Bakowsky, O. 2004. Comparing site productivity of fire-origin and

- regenerated lodgepole pine stands in Alberta. *Can. J. For. Res.* **34**: 1181-1191. doi:10.1139/x04-009.
- Hulme, T.I., Sheard, N., and Markham, A. 1999. Global climate change scenario* Climatic Research Unit, Norwich, U.K.
- Hutchinson, M.F. 2002. ANUSPLIN. Version 4.2. Centre for resource and environmental studies, The Australian National University, Canberra (cres.anu.edu.au/outputs/anusplin.html).
- IPCC. 2000. Emissions scenarios. Cambridge University Press, Cambridge, U.K.
- IPCC. 2001. Climate Change 2001. The scientific basis (Working Group I). Impacts, adaptation, and vulnerability (Working Group II); Mitigation (Working Group III). Cambridge University Press, Cambridge, U.K.
- Iverson, L.R., and Prasad, A.M. 2001. Potential changes in tree species richness and forest community types following climate change. *Ecosystems* (N.Y. Print), **4**: 186-199. doi:10.1007/s10021-001-0003-6.
- Johns, T.C., Clnnell, R.E., Crossley, J.F., Gregory, J.M., Mitchell, J.F.B., Senior, C.A., Tett, S.F.B., and Wood, R.A. 1997. The second Hadley centre coupled ocean-atmosphere GCM: model description, spinup and validation. *Clim. Dyn.* **13**: 103-134. doi: 10.1007/s003820050155.
- Loehle, C., and LeBlanc, D. 1996. Model-based assessments of climate change effects on forests: a critical review. *IBES Model.* **90**: 1-31. doi:10.1016/0304-3800(96)83709-4.
- Logan, J.A., and Powell, J.A. 2001. Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). *Am. Entomol.* **47**: 160-172.
- Marshall, J.D., and Monserud, R.A. 1996. Homeostatic gas-exchange parameters inferred from $\delta^{13}C$ in tree rings of conifers during the twentieth century. *Oecologia*, **105**: 13-21. doi:10.1007/BF00328786.
- Menzel, A., and Fabian, P. 1999. Growing season extended in Europe. *Nature (Lond.)*, **397**: 659. doi:10.1038/17709.
- Monserud, R. 1984. Height growth and site index curves for inland Douglas-fir based on stem analysis data and forest habitat type. *For. Sci.* **30**: 943-965.
- Monserud, R., and Huang, S. 2003. Mapping lodgepole pine site index in Alberta. In *Modelling forest systems*. Edited by A. Amaro, D.D. Reed, and P. Soares. CABI Publishing, Wallingford, U.K. Chap. 2. pp. 23-30.
- Monserud, R.A., and Marshall, J.D. 2001. Time-series analysis of $\delta^{13}C$ from tree rings: I. Time trends and autocorrelation. *Tree Physiol.* **21**: 1087-1102. PMID:11581016.
- Monserud, R.A., and Rehfeldt, G.E. 1990. Genetic and environmental components of variation of site index in inland Douglas-fir. *For. Sci.* **36**: 1-9.
- Monserud, R.A., Huang, S., and Yang, Y. 2006. Predicting lodgepole pine site index from climatic parameters in Alberta. *For. Chron.* **82**: 562-571.
- Peng, C., Zhav, L., Zhou, X., Dang, Q., and Huang, S. 2004. Developing and evaluating tree height-diameter models at three geographic scales for black spruce in Ontario. *North. J. Appl. For.* **21**: 83-92.
- Rehfeldt, G.E., Ying, C.C., Spittlehouse, D.L., and Hamilton, D.A. 1999. Genetic responses to climate in *Pinus contorta*: niche breadth, climate change, and reforestation. *Ecol. Monogr.* **69**: 375-407.
- Roeckner, E., Arpe, K., Bengtsson, L., Christoph, M., Claussen, M., Dumenil, L., Esch, M., Giorgetta, M., Schlese, U., and Schulzweida, U. 1996. The atmospheric general circulation model ECHAM4: model description and simulation of present-day climate. Rep. 218. Max Planck Institut für Meteorologie, Hamburg, Germany.
- Smith, J.B., and Hulme, M. 1998. Climate change scenarios. In *UNEP handbook on methods for climate change impact assessment and adaptation studies*. Edited by J.F. Feenstra, I. Burton, J.S. Smith, and R.S.J. Tol. United Nations Environment Programme, Nairobi, Kenya, and Institute for Environmental Studies, Amsterdam, the Netherlands. pp. 3-1-3-40.
- Soja, A.J., Tchebakova, N.M., French, N.H.F., Flannigan, M.D., Shugart, H.H., Stocks, B.J., Sukhinin, A.I., Parfenova, E.I., Chapin, F.S., and Stackhouse, P.W. 2007. Climate-induced boreal forest change: predictions versus current observations. *Global Planet. Change*, **56**: 274-296. doi:10.1016/j.gloplacha.2006.07.028.
- Stephenson, N.L. 1998. Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. *J. Biogeogr.* **25**: 855-870. doi:10.1046/j.1365-2699.1998.00233.x.
- Tchekalova, N.M., and Parfenova, E.I. 2003. Stand growth and productivity of mountain forests in southern Siberia in a changing climate. Edited by A. Amaro, D.D. Reed, and P. Soares. CABI Publishing, Wallingford, U.K. Chap. 17. pp. 189-197.
- Tchekalova, N.M., Monserud, R.A., Leemans, R., and Golovanov, S. 1993. A global vegetation model based on the climatological approach of Budyko. *J. Biogeogr.* **20**: 129-144. doi:10.2307/2845667.
- Tchekalova, N.M., Rehfeldt, G.E., and Parfenova, E. 2003. Redistribution of vegetation zones and populations of *Larix sibirica* Ledeb., and *Pinus sylvestris* L. in Central Siberia in a winning climate. *Sib. Ecol. J.* **10**: 677-686. [In Russian.]
- Thorpe, J., Henderson, N., and Vandall, J. 2006. Ecological and policy implications of introducing exotic trees for adaptation to climate change in the western boreal forest. SRC Publ. No. 11776-1E06. Saskatchewan Research Council, Saskatoon, Sask.
- Westerling, A.L., Hidalgo, H.G., Cayan, D.R., and Swetnam, T.W. 2006. Warming and earlier spring increase western U.S. forest wildfire activity. *Science (Washington, D.C.)*, **313**: 940-943. doi: 10.1126/science.1128834. PMID: 16825536.