Available online at www.sciencedirect.com

ScienceDirect

Forest Ecology and Management 242 (2007) 636–647

Forest Ecology and Management

www.elsevier.com/locate/foreco

Seed transfer and climate change effects on radial growth of jack pine populations in a common garden in Petawawa, Ontario, Canada

Y. Savva[a,*], B. Denneler[a], A. Koubaa[b], F. Tremblay[a], Y. Bergeron[a], M.G. Tjoelker[c]

[a] Chaire Industrielle CRSNG-UQAT-UQAM en Aménagement Forestier Durable, Université du Québec en Abitibi-Témiscamingue, 445 boul. de l'Université, Rouyn-Noranda, Que., Canada J9X 5E4

[b] Chaire de Recherche du Canada en Valorisation, Caractérisation et Transformation du Bois, Université du Québec en Abitibi-Témiscamingue, 445 boul. de l'Université, Rouyn-Noranda, Que., Canada J9X 5E4

[c] Texas A&M University, Department of Forest Science, 2135 TAMU, College Station, TX 77843-2135, USA

Received 28 November 2006; received in revised form 24 January 2007; accepted 29 January 2007

Abstract

The effects of seed transfer and climate change on the width and basal area of tree rings were studied in 21 provenances of jack pine (*Pinus banksiana* Lamb.) grown in a common-garden plantation in Petawawa, Ontario, Canada. Seed-source origin significantly influenced both mean tree-ring width and mean annual basal area increment over a 25-year growth period (1975–1999). Temperature and precipitation transfer functions were developed to predict width and basal area of tree rings of the jack pine populations. The best predictors of growth were the transfer distances of mean annual maximum daily temperature and annual precipitation between the plantation site and the seed origins. Radial growth of the jack pine populations was mainly related to temperature at seed origin and, to a lesser degree, to precipitation at seed origin. Extension of the transfer functions to three sets of independent data revealed significant correlations between estimated and predicted mean radial growth characteristics. Seed sources of jack pine originating from warmer and drier climates than that of the plantation site in Petawawa had slightly higher mean ring widths and basal areas than the local populations. The application of different climate change scenarios derived from general circulation models to the developed transfer functions indicated that radial growth of jack pine may decline only if significant climate changes occur, which might not happen before the mid 21st century. Both a higher radial growth of southern seed sources and a potential negative effect of a significant temperature increase and precipitation decrease in future suggest restricting the northward transfer of southern seed sources to less than 1° latitude. However, provenance specific differences in survivorship, frost- and disease-resistance, and cone serotiny should also be taken into consideration.

Keywords: Adaptation; Climate change; GCM; *Pinus banksiana*; Provenance; Radial growth; Transfer functions

1. Introduction

Jack pine (*Pinus banksiana* Lamb.) is widely distributed across Canada and some northern parts of the USA and is of great economic value (Rudolph and Laidly, 1990). It is one of the least shade-tolerant tree species and typically grows in pure or mixed even-aged stands. Jack pine mainly establishes after fire in boreal forests, tundra transition areas, dry flats, and hills, and grows on poorer soils than its associates red pine (*Pinus resinosa*) and white pine (*Pinus strobus*) (Gauthier et al., 1996; Desponts and Payette, 1993). Its range has changed considerably over the last 10,000 years. From central North America, jack pine migrated north- and westward at the end of the Pleistocene and reached its present distribution limits in northern Canada ca. 5000 years BP in the northwest (Critchfield, 1985; McLeod and MacDonald, 1997) and ca. 3000 years BP in the northeast (Gajewski et al., 1993; Payette, 1993).

Evolutionary processes such as genes flow and selection are responsible for the high genetic variation of jack pine. High genetic variation suggested strong natural selection against self-fertilization and increased homozygosity, and heterozygosity for many alleles (Rudolph and Yeatman, 1982). Several phenotypic traits of jack pine were found to be significantly variable due to geographical origin of the populations. These traits include bark, crown form, wood, foliage (Schoenike,

---

* Corresponding author at: Département des Sciences Biologiques, CP 8888 Succ Centre Ville, Université du Québec à Montréal, Montréal, Qc, Canada H3C 3P8. Tel.: +1 514 987 3000x1908; fax: +1 514 987 4647.

E-mail address: julia.savva@uqat.ca (Y. Savva).

0378-1127/$ – see front matter © 2007 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2007.01.073

1976), cone shape and serotiny, cone volume and length (Rudolf, 1965; Teich, 1970; O'Loughlin, 1973; Gauthier et al., 1996), and seed germination (Greenwood et al., 2002).

To date the literature evidence is contradictory and incomplete with respect to the potential effects of climate change on the growth, survival, distribution, and abundance of jack pine, but knowledge of these effects is crucial for the understanding of the role of climate change in tree species responses. For example, Cantin et al. (1997) studied growth of jack pine seedlings in an elevated CO_2/temperature environment and found significant genotype differences in response of height growth, biomass increment, and water-use efficiency. They suggested that fast-growing jack pine families would show greater growth enhancements in a warmer, higher CO_2 environment during the seedling establishment stage. Other studies showed a possible negative effect of climate change on productivity and growth of jack pine. Kimball et al. (1997), using a process-based general ecosystem model (BIOME-BGC), found a decrease in productivity of old-growth jack pine stands in response to simulated low soil water contents. They concluded that jack pine stands appeared better adapted to conserve soil water through lower daily evapotranspiration losses, but exhibited a narrower margin between daily net photosynthesis and respiration. Brooks et al. (1998) examined annual variations in tree-ring widths and carbon isotope ratios of cellulose and found that increased temperature and spring precipitation increased annual radial growth of jack pine at its southern and northern range limits in central Canada. They concluded that growth of jack pine at its southern range limit could decline due to increasing potential evapotranspiration under climate warming. Several studies reported that forest harvesting and increased fire disturbances due to climate change affected the abundance of jack pine and, hence, forest composition. For example, He et al. (2002) used the spatially explicit landscape model LANDIS to examine jack pine distribution in northern Wisconsin under climate warming. They found that the ecoregion presently dominated by jack pine could transform into grass- and shrubland in about 250 years. Forest harvesting could accelerate the decline of jack pine already suffering from environmental stress. Thompson et al. (1998), however, predicted that the combination of rising temperatures and increasing fire frequency would favor pyrophilic species such as jack pine. Conversely, a prolonged fire cycle due to increased precipitation, as predicted for parts of eastern Canada, might disfavor jack pine (Bergeron et al., 2001).

Provenance plantations, i.e., seeds of the same species from different geographic origins that are planted at the same site, were initially established for the purpose of revealing seed sources with the best survival and growth at a given site and to quantify genetic variation. In recent years, old provenance tests are of increasing interest because they enable predictions of the effects of climate change on tree growth (Matyas and Yeatman, 1992; Matyas, 1994; Schmidtling, 1994; Oleksyn et al., 1998; Rehfeldt et al., 1999a,b; Beaulieu and Rainville, 2005; Chuine et al., 2006). Indeed, northern provenances transferred to southern sites simulate a climate warming and vice versa. Matyas and Yeatman (1992) studied height growth and mortality of jack pine provenances planted at eight sites in Ontario and showed that height-growth responses were shaped by thermo- and photoperiodic effects. The geographic pattern was latitudinally clinal, but weakly expressed. vanNiejenhuis and Parker (1996) studied seedling height, needle flushing date, timing of shoot elongation, fall foliage color change, and drought survival of jack pine seed sources grown at three sites in Ontario. They found a greater growth potential of seedlings from the southwestern portion of the range compared to those from the north shore of Lake Superior and concluded that climate at seed origin should be considered the prime factor in planning seed transfers.

In this study we used a long-term range-wide provenance test in eastern Ontario to quantify the effects of provenance, climate, and climate change on radial growth of jack pine. The objectives were: (1) to compare radial growth of the different provenances and identify the seed sources with the best growth, (2) to identify climatic predictors and develop a model of radial growth of diverse populations of jack pine in a common garden, and (3) to predict growth of the jack pine provenances under projected climate change based on global climate change model scenarios.

We hypothesized that radial growth of jack pine differs among geographically diverse seed-source origins of jack pine. We expected to observe tree growth decreases with increasing transfer distance between the seed source and the plantation site. Consequently, we predicted that radial growth of jack pine would decline in response to climate change.

2. Material and methods

2.1. Study material

We studied a common-garden plantation of jack pine in the Petawawa Research Forest, southern Ontario (45.58°N, 77.25°W) that is part of a range-wide provenance experiment established in 1966. For this test, 99 seed sources were collected from native stands throughout the geographic range of the species and planted at sites in Canada and the USA (Holst, 1967). In the Canadian tests, all seeds were sown in nurseries in Petawawa in 1964 and transferred to the planting sites 2 years later. The experimental design of the common-garden plantation in Petawawa is a triple lattice square, which was represented with 10 blocks (replications) and one 'demonstration' block near the edge of the plantation. Every block included one plot per provenance whose position within the block was randomly assigned. Every plot was initially represented by 10 trees of the same provenance in a single row and planted at a 1.8 m × 1.8 m spacing. The mineral soil of the planting site is an acidic, light-textured sandy loam on granite sand and stony till sediments (Wilde, 1946; Hills and Pierpoint, 1960).

2.2. Tree-ring data development

Tree-ring cores of 21 *Pinus banksiana* provenances were collected from 10 blocks in the Petawawa common-garden plantation in the fall of 2005 (Table 1, Fig. 1). One two-radius core per tree was sampled from about 20 trees per provenance randomly chosen in a block from all 10 blocks. Only a few northern provenances with low survivorship were not sampled from all blocks. The number of sampled trees for the two northernmost provenances was restricted to five trees due to the low survivorship. Cores were taken at approximately 50 cm above ground to ensure a maximum number of tree rings. This height above the stem base represented a loss of about 3–5 years of growth relative to total tree age.

The total ring-widths were measured with the QTRS-01X Tree-Ring Scanner (QMS, Knoxville, TN, USA). This scanner utilizes X-ray technology to measure ring-width and wood density characteristics. We used a 0.04 mm linear resolution step size for measurements. The demarcation zone between annual rings was automatically set up at a density level of 450 kg/m^3 and was double-checked manually for every scanned tree-ring profile. In case of manual definition of this zone, we assigned it approximately at the midpoint between the highest and lowest density levels of the two neighboring rings. Also, the raw measurements were cross-dated and quality-checked with the COFECHA software (Holmes, 1983; Grissino-Mayer, 2001). About 5% of the samples were excluded from further analysis because of their poor quality (e.g., fragmented core, rotten wood, measurements not cross-datable).

Annual basal area increment per tree (TRA) in the year n was calculated as a non-linear function of the cumulative tree radius (R) in the year $n-1$ and tree-ring width (TRW) in the year n. We calculated basal tree-ring area increment for each tree ring and for every tree using the following formula:

$$\begin{aligned}\mathrm{TRA} &= 4\pi(R+\mathrm{TRW})^2 - 4\pi R^2\\ &= 4\pi R^2 + 8\pi R \times \mathrm{TRW} + 4\pi\mathrm{TRW}^2 - 4\pi R^2\\ &= 4\pi\mathrm{TRW}(2R+\mathrm{TRW})\end{aligned}$$

For each tree, tree-ring width and annual basal area increment per tree were averaged over the period 1975–1999. The analyzed time window was restricted to this period to (i) avoid the distinct trend related to tree age in the early years, and (ii) allow extension of our growth-seed-source origin models to tree-ring data from other sites that ends in 1999. Further analysis was conducted using the following radial growth characteristics: tree-ring width and tree-ring basal area increment per tree and per year.

2.3. Climate data

The 1971–2000 climate normals of the sites nearest the seed origins and the plantation site in Petawawa, Ontario, Canada were downloaded from the Environment Canada web site (http://www.ec.gc.ca/) for the Canadian seed sources, and from the National Climate Data Center (http://www.ncdc.noaa.gov/oa/ncdc.html) for the American seed sources. We selected the same climate stations as those reported for given seed sources in the initial report on the experiment setup (Holst, 1967), except for a couple of provenances for which the data from the

Table 1
Site-origin description and growth characteristics (for the period 1975–1999) of the 21 jack pine provenances planted in Petawawa

#	Provenance origin[a]	Latitude (N)/ longitude (W)	Elevation (m a.s.l.)	Mean annual temperature (°C)	Mean annual maximum daily temperature (°C)	Total annual precipitation (mm)	Mean tree-ring width[b] (mm)	Mean annual tree-ring basal area increment per tree[b] (cm^2)	Total tree-ring basal area per tree[b] (cm^2)
57	Miller Lake, Ont.	45.1/81.5	198	6.6	10.8	830	2.59 ± 0.78	39.3 ± 19.0	953.9 ± 475.7
75	Gladstone, MI	46.0/86.5	198	5.6	10.4	725	2.51 ± 0.56	37.7 ± 15.0	962.6 ± 375.4
62	Cowganda Lake, Ont.	47.7/80.7	335	2.2	8.2	785	2.47 ± 0.41	36.9 ± 10.7	926.7 ± 267.5
70	Nokomis, WI	45.6/89.8	472	6.4	12.0	847	2.43 ± 0.47	37.4 ± 12.6	944.2 ± 315.1
61	Benny, Ont.	46.8/81.6	396	3.7	8.8	899	2.40 ± 0.54	37.8 ± 14.4	904.5 ± 358.8
47	Harry Lake, Que.	46.4/76.2	183	3.7	9.9	909	2.40 ± 0.55	35.4 ± 11.6	847.7 ± 289.3
48	Baskatong Lake, Que.	46.8/76.1	244	3.3	9.2	1015	2.36 ± 0.42	34.7 ± 11.9	922.5 ± 297.6
79	Cloquet, MN	46.7/92.6	390	4.6	11.2	807	2.29 ± 0.57	34.0 ± 13.0	864.7 ± 326.2
45	York River, Ont.	45.2/77.7	320	4.0	10.5	843	2.29 ± 0.46	35.2 ± 12.7	907.3 ± 317.6
55	Clark Point, Ont.	44.1/81.8	180	6.7	11.8	1121	2.29 ± 0.43	32.3 ± 10.8	856.4 ± 269.1
63	Nellie Lake, Ont.	48.8/80.8	305	0.9	7.4	776	2.24 ± 0.53	31.6 ± 12.1	813.0 ± 303.3
81	Fort Frances, Ont.	48.8/93.5	338	2.9	8.8	721	2.23 ± 0.36	28.9 ± 10.2	744.5 ± 255.5
86	Red Lake, Ont.	51.0/94.1	354	0.9	6.4	640	2.15 ± 0.45	28.1 ± 9.8	714.4 ± 246.2
68	Waupaca, WI	44.3/89.0	290	6.8	12.7	782	2.05 ± 0.36	27.6 ± 5.9	699.1 ± 148.6
18	St. Alexandre, Que.	47.7/69.7	91	3.5	8.7	983	2.02 ± 0.31	23.6 ± 6.2	590.8 ± 101.7
49	Capitachouare River, Que.	47.8/76.7	457	2.8	7.9	950	2.01 ± 0.36	26.1 ± 6.6	617.1 ± 164.0
30	Port Alfred, Que.	48.3/70.9	251	2.3	7.9	951	2.00 ± 0.42	25.2 ± 8.5	631.4 ± 212.8
20	Toulnoustook River, Que.	49.7/68.4	76	1.5	6.3	1014	1.83 ± 0.28	20.5 ± 3.2	516.9 ± 80.7
15	Patapedia Depot, Que.	48.1/67.5	366	2.3	8.0	1027	1.70 ± 0.25	17.5 ± 4.2	424.3 ± 105.6
38	Mistassini Post, Que.	50.4/73.9	390	−1.8	3.9	946	1.57 ± 0.29	11.1 ± 5.1	276.8 ± 126.5
36	Ducharme River, Que.	49.4/74.0	381	0.0	5.2	961	1.55 ± 0.27	18.1 ± 5.4	452.0 ± 135.5

# Indicates the number of provenance. Provenances are ordered from high to low mean tree-ring width.

[a] Michigan (MI), Minnesota (MN), Ontario (Ont.), Quebec (Que.), Wisconsin (WI).

[b] Mean ± S.D.

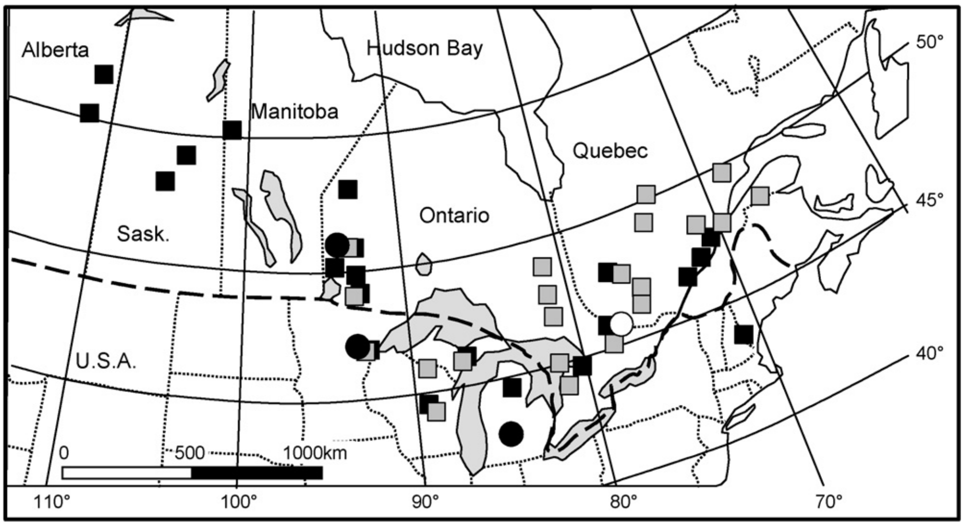

Fig. 1. Map of the geographical locations of jack pine seed sources and plantation sites. The symbols represent the study site Petawawa (empty circle), the validation sites Cloquet (Minnesota), Allegan (Michigan), and Red Lake (Ontario) (black circles), the 21 provenances studied in Petawawa (grey squares) and the 21 provenances used in the validation sites (black squares). The provenances refer to the descriptions in Table 1.

indicated climate stations were not available. Therefore, for those seed sources we used other closest climate stations. The most remote climate station used in the study was located within the area of 1° by 1° latitude and longitude from the seed source. For the plantation site, we used the climate station Petawawa National Forestry, Ontario, which was nearby the plantation.

2.4. Temperature/precipitation transfer functions

To assess the growth-seed origin relationships, we developed general regression models, i.e. transfer functions, with predictors expressed as distances between plantation site and seed sources in climatic units. These transfer functions were developed using relative values of mean tree-ring width and mean tree-ring basal area increment per year of the jack pine provenances in Petawawa as dependent variables. For each provenance, relative values of mean tree-ring width and mean annual basal area increment were calculated as a percentage of the site mean, i.e., as the ratio of the provenance mean values, calculated and averaged for the period of 1975–1999, over the site mean. Based on a literature review, we chose seven temperature and two precipitation variables, which are often used to model radial growth of trees and might serve as predictors. They included the following: mean annual temperature, mean annual maximum and minimum daily temperature, degree-days above 5 °C, number of days with maximum temperature above 0 °C, number of days with maximum temperature above 10 °C, summer–winter temperature differential (defined as the difference between mean monthly temperatures in January and July), total annual precipitation, and total summer precipitation (June–August). For each climate variable and provenance, we calculated the transfer distances as the difference between the values at the plantation site and those at the seed source origin. Many studies showed that transfer functions usually have a quadratic shape (Matyas and Yeatman, 1992; Rehfeldt et al., 2002; Andalo et al., 2005, Saenz-Romero et al., 2006). Therefore, we tested about 140 linear and quadratic models with different combinations of the seven predictors. Adjusted R^2, Mallow's C_p statistics, and the significance of the model's coefficients served as criteria to select the best subset model among the tested models. We used statistical software Statistica 6.0 (Statsoft.com) to estimate the model parameters as well as the statistics used to select the best models.

We used mean tree-ring width and mean annual basal area increment data from three other common-garden plantations that are part of the same range-wide provenance test, to extend our transfer models to independent data from other sites (Table 2) (Savva et al., unpublished data). This will indicate whether or not the results can be extended to other sites. We consider positive correlations among sites as evidence of confidence in the generality of the models. These three plantations are located along a latitudinal gradient in Allegan, Michigan (42.5N, 85.9W), Cloquet, Minnesota (46.7N, 92.6W), and Red Lake, Ontario (51.0N, 94.1W) (Fig. 1). In this separate study, tree-ring cores from about six trees for several provenances were collected in 1999 in Cloquet and Red Lake and in 2001 in Allegan. For this validation exercise, we used data for 17 provenances in Allegan, 21 provenances in Cloquet, and 20 provenances in Red Lake. Only a few provenances used in our study in Petawawa were the same as those sampled in Red Lake, Cloquet, and Allegan. For each site and each provenance, relative values of mean tree-ring width and mean annual basal area increment were calculated as a percentage of the site means, i.e., as the ratio of the provenance mean values, calculated and averaged for the period of 1975–1999, over the site means. To test our transfer models, we calculated Pearson's correlation coefficients between the predicted growth based on the transfer functions and the observed growth at the three independent sites with use of statistical software Statistica 6.0 (http://statsoft.com). We used these three sites separately to validate the models because we

Table 2
Geographical and climatic parameters of the four common-garden plantations of a range-wide jack pine provenance study established in 1966 that were used to develop (Petawawa) and validate (Red Lake, Cloquet, and Allegan) the transfer functions of radial growth of jack pine

Site	Petawawa	Red Lake	Cloquet	Allegan
State or province	Ontario	Ontario	Minnesota	Michigan
Number of provenances	21	20	21	17
Latitude (N)	45.6	51.0	46.7	42.5
Longitude (W)	77.3	94.1	92.6	85.9
Mean annual temperature (°C)	4.3	0.9	4.6	7.9
Mean annual maximum temperature (°C)	9.9	6.4	11.2	13.6
Total annual precipitation (mm)	853.3	640.2	807.2	1025.9
Total summer precipitation (June–August) (mm)	254.6	214.4	305.1	295.9
Mean tree-ring width ± S.D. (mm)	2.25 ± 0.51	1.39 ± 0.40	2.25 ± 0.54	2.14 ± 0.67
Mean basal tree-ring area increment ± S.D. (cm^2)	31.75 ± 12.27	11.45 ± 57.2	31.80 ± 14.46	27.00 ± 14.91

Values of mean tree-ring width and mean tree-ring basal area were calculated for the period of 1975–1999.

expected that the validation correlation coefficients would differ among sites due to a significant effect of genotype × environment interaction on radial growth of jack pine provenances revealed earlier for these sites (Savva et al., unpublished data).

2.5. Growth response to climate change

The transfer functions were used to simulate the effect of climate change on growth of jack pine, assuming no changes in biotic and non-climatic, abiotic factors. Tree-ring widths and annual basal area increments of jack pine in Petawawa were predicted by replacing the present transfer distances of mean annual maximum daily temperature and total annual precipitation, i.e., zero transfer distance, by the expected changes in these climate variables in future. We used maximum annual temperature and precipitation data projected for 2020, 2050, and 2080 for the region including Petawawa, Ontario based on the two SRES climate scenarios A2a and B2a of the Canadian Global Coupled Model (CGCM2) of the Canadian Centre for Climate Modeling and Analysis (McFarlane et al., 1992; Flato et al., 2000; Flato and Boer, 2001) and the six SRES climate scenarios A1F, A2a, A2b, A2c, B2a and B2b of the general circulation model of the Hadley Center (HADCM3) (Cullen, 1993; Gordon et al., 2000) (The IPCC Data Distribution Center, http://ipcc-ddc.cru.uea.ac.uk/). We built the 95% confidence interval for predicted ring width responses at given levels of independent variables using statistical software Statistica 6.0. The confidence interval for a predicted value of the dependent variable gives a range of values around which the "true" population mean (of the dependent variable for given levels of the independent variables) can be expected to be located with a given level of certainty.

3. Results

3.1. Seed source effect on growth

Mean tree-ring width for the period of 1975–1999 ranged from 1.55 mm of the Ducharme River provenance in northern Quebec to 2.59 mm of the Miller Lake provenance in southern Ontario (Table 1). Mean annual basal area increment for the same period, which is a function of annual radial growth and tree diameter, varied from 11.1 cm^2 in the Mistassini Post provenance in northern Quebec, to 39.3 cm^2 in the Miller Lake provenance. Mean ring width and mean tree-ring basal area increment of the provenance closest to the plantation site, Harry Lake, were about 7% and respectively 8% lower than those of the best performing provenance (Miller Lake). The mean total tree-ring basal area accumulated over the period of 1975–1999 also showed a strong seed source effect (Table 1). Compared to the provenance with the highest value (Miller Lake: 954 cm^2), the northernmost provenance, Mistassini Post, was 70% lower (277 cm^2) and that of Harry Lake 11% lower (848 cm^2).

Mean ring width and mean annual tree-ring basal area increment were significantly related to climate and latitude at the seed-source origin (Fig. 2). Quadratic functions best described the relationships between the ring-width characteristics and latitude as well as the climate variables, such as the annual mean of the daily maximum temperatures and the degree-days above 5 °C. The climate variables explained between 60% and 64% of the growth variations and latitude explained between 39% and 45%.

3.2. Transfer models

The best subset model was selected using adjusted R^2, Mallow's C_p statistics, and the significance level of the model's coefficients (Table 3). The transfer model of ring width based on the transfer distances in annual mean maximum daily temperature between the plantation site and each provenance site explained 56% of the variation in the ring-width data (Table 3). This temperature-transfer model is well supported using relative ring-width data for jack pine populations in the independent common-garden plantations of Red Lake ($r = 0.65$, $p = 0.002$), Allegan ($r = 0.75$, $p = 0.002$), and all three validation sites together ($r = 0.42$, $p = 0.001$), but not for the Cloquet site ($r = 0.35$, $p = 0.112$). If annual total precipitation is added as a predictor along with temperature, the transfer model explained 65% of the variance, but the validation correlation coefficients decreased, particularly when the transfer functions were applied to the Red Lake dataset.

The best subset temperature-transfer model for mean annual tree-ring basal area increment included annual mean maximum

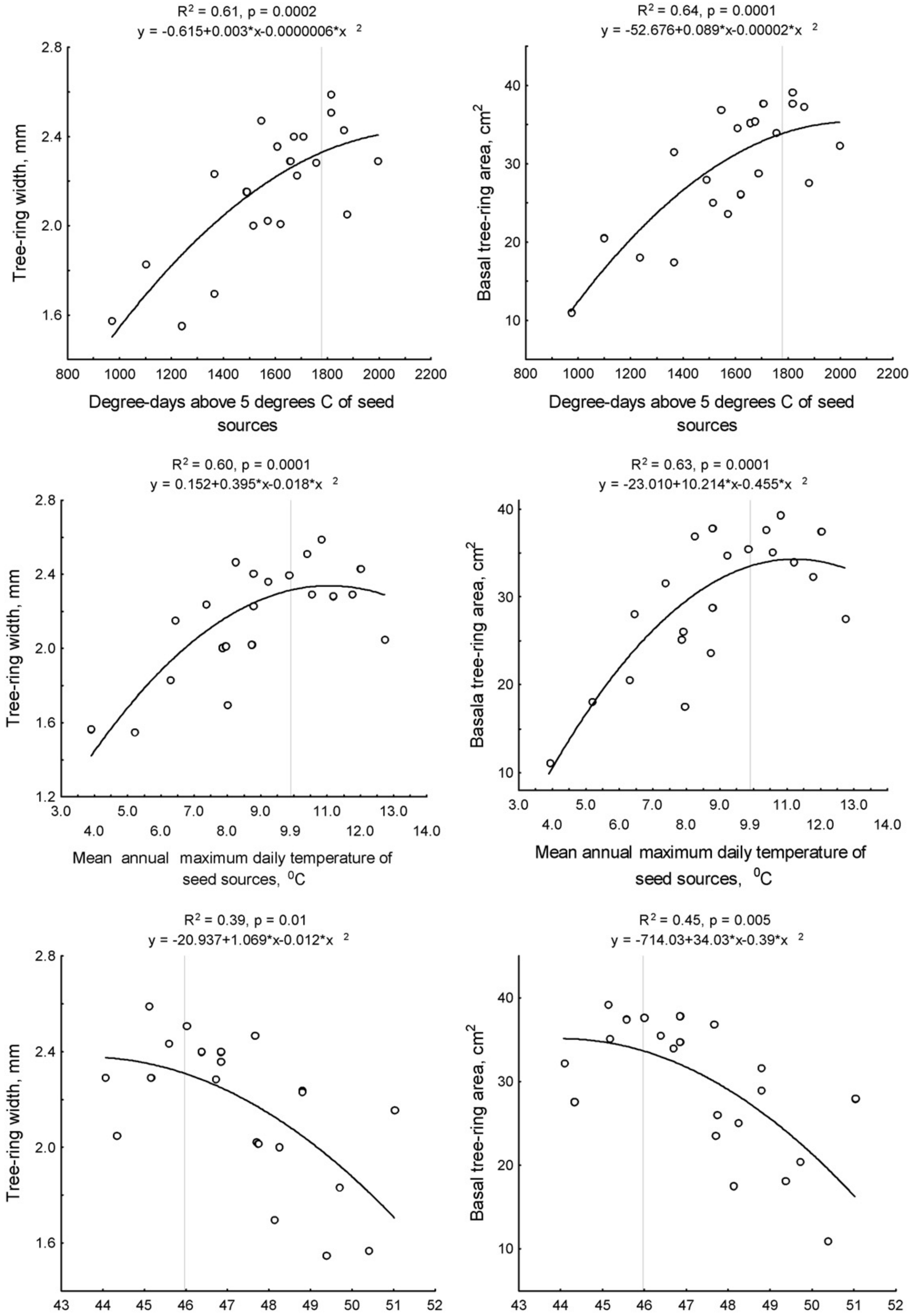

Fig. 2. Mean tree ring-width and mean annual tree-ring basal area increment averaged over the 25-year period 1975–1999 for the jack pine provenances planted in the common-garden experiment in Petawawa in relationship to degree-days above 5 °C, mean annual maximum daily temperature, and the latitude of the seed origin. The solid lines show the quadratic functions fitted to the data and the thin vertical lines indicate mean annual maximum daily temperature and latitude of the plantation site in Petawawa.

Table 3
Transfer models developed for tree-ring width and annual tree-ring basal area increment of jack pine populations in Petawawa, Ontario

Trait	Transfer model[a]	Adjusted R^2	Mallow's C_p	Validation correlation coefficient[b]			
				Red Lake, Ont.	Cloquet, MN	Allegan, MI	All three sites
Mean tree-ring width[c]							
Temperature-transfer model	$0.99_{(0.02)} - 0.018\text{MAXT}_{(0.01)} - 0.008\text{MAXT}^2_{(0.003)}$	0.558	3.0	0.65 (0.002)	0.35 (0.112)	0.75 (0.002)	0.42 (0.001)
Temperature/precipitation transfer model	$0.99_{(0.021)} + 0.00033P_{(0.0001)} - 0.017\text{MAXT}_{(0.011)} - 0.007\text{MAXT}^2_{(0.002)}$	0.645	4.0	0.14 (0.549)	0.34 (0.132)	0.70 (0.002)	0.39 (0.003)
Mean annual tree-ring basal area increment[c]							
Temperature-transfer model	$0.99_{(0.041)} - 0.037\text{MAXT}_{(0.020)} - 0.0136\text{MAXT}^2_{(0.005)}$	0.585	3.0	0.66 (0.002)	0.51 (0.018)	0.76 (0.001)	0.45 (0.001)
Temperature/precipitation transfer model	$1.01_{(0.040)} + 0.003\text{SP}_{(0.001)} - 0.062\text{MAXT}_{(0.015)}$	0.617	3.0	−0.46 (0.040)	0.08 (0.717)	0.41 (0.115)	0.01 (0.962)

Note. Validation was carried out from correlation analysis between the estimated values at Petawawa and the observed values of the three common-garden plantations at Red Lake ($n = 105$), Cloquet ($n = 110$), and Allegan ($n = 77$). MAXT: the difference in annual mean maximum daily temperature between the plantation site and the seed source site. P: the difference in total annual precipitation between the plantation site and the seed source. SP: the difference in total summer precipitation (June–August) between the planting site and the seed source.

[a] Mean tree-ring width and mean annual tree-ring basal area increment were calculated over 25-year period 1975–1999 and expressed as a proportion (of 1.0) of that of the local populations.

[b] p-Values of the correlation coefficients are shown in parentheses.

[c] Standard errors associated with estimates are shown in parentheses.

daily temperature transfer distance as a predictor (adjusted $R^2 = 0.59$) (Table 3).

The model was well extended to three independent sites; the correlation coefficients between observed and estimated values of annual basal tree-ring area increment ranged between 0.45 and 0.76 and were all statistically significant. Including total summer precipitation in the model only slightly improved the model (adjusted $R^2 = 0.61$) and the correlation failed for all sites but Red Lake. Therefore, we used the temperature/precipitation transfer model to predict tree-ring width and the temperature transfer model to predict tree-ring basal area increment for the seed sources at the Petawawa plantation site in the climate change models described in the next section.

Populations originating from slightly warmer and drier climates than Petawawa had slightly higher mean tree-ring width and mean tree-ring basal area increment compared to local populations (Fig. 3). Mean tree-ring width of the local provenances (i.e. with a temperature and precipitation transfer distance of zero) was 2.33 mm and mean annual tree-ring basal area 33.48 cm^2 (or 1.0) (Fig. 4A–F). The transfer model also

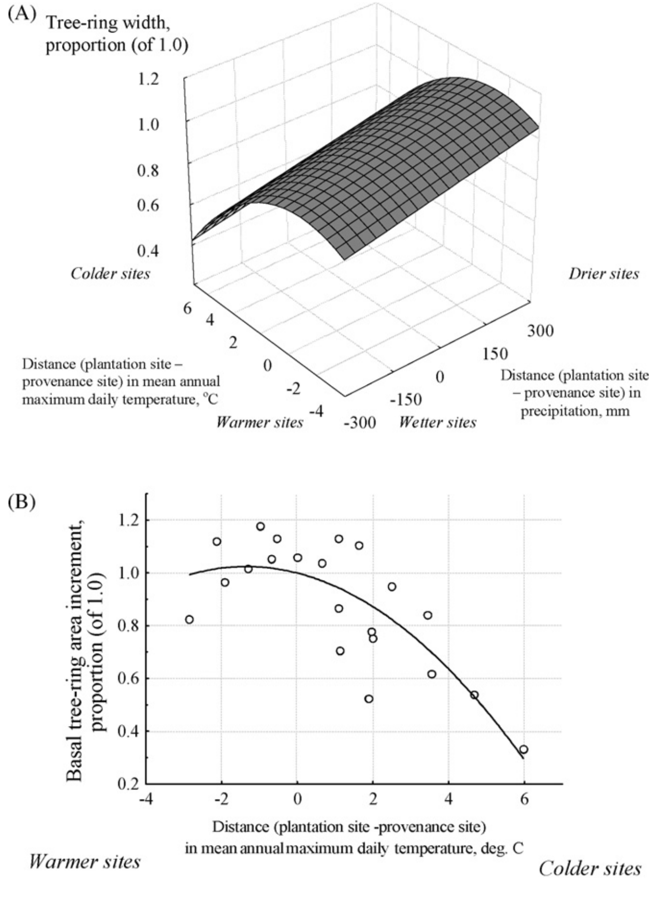

Fig. 3. Transfer functions of mean tree-ring width (A) and mean annual tree-ring basal area increment (B) expressed as the differences between the plantation site (Petawawa) and the provenance origins for annual total precipitation and/or mean annual maximum daily temperature. Positive values indicate seed sources that originated from drier/colder climates than that of the common-garden (Petawawa), and hence, were transferred to a wetter/warmer climate. Mean tree-ring width and mean annual tree-ring basal area increment were calculated over the 25-year period 1975–1999 and expressed as a proportion of 1.0 of those for the local populations.

shows that maximum mean ring width (2.52 mm, which is equivalent to 8% from the local mean) is attained by provenances transferred from origins with 1.3 °C higher mean annual maximum daily temperature and 213.7 mm/year lower precipitation than in Petawawa (Fig. 4B). Also, the highest tree-ring basal area of 34.30 cm^2, which is about 2% higher than that of the local seed sources, could be reached if seeds are transferred from warmer sites with mean annual maximum daily temperature higher by 1.3 °C relative to Petawawa (Fig. 2).

3.3. Application to climate change

We used the developed transfer functions to simulate the effect of predicted climate change on tree-ring width and mean annual basal area increment of jack pine populations in Petawawa (Fig. 4C–F, Table 4). Changes in tree-ring width and mean basal area increment depended upon climate scenario and climate model applied to the developed transfer functions. The smallest changes in mean annual maximum daily temperature for the next several decades among the tested climate models were predicted by the B2a scenario of the Canadian Global Coupled Model CGCM 2, whereas the largest changes were predicted by the general circulation model of the Hadley Center HADCM 3, especially by the A1F climate scenario. These models predicted rises in mean annual maximum daily temperature of 1.00 and 1.07 °C in 2020, 1.83 and 3.15 °C in 2050 and 2.45 and 5.77 °C in 2080 in the Petawawa, Ontario region. The same scenarios also predicted increases in mean annual precipitation of 50 and 6 mm/year through the 2020s, 74 and 23 mm/year through the 2050s, and 65 and 27 mm/year through the 2080s. The rising temperatures and increased precipitation under these climate change scenarios all resulted in predicted decreases in radial growth of jack pine. Thus, the application of our transfer models showed that the mean ring width would decline to 2.22–2.31 mm, depending upon climate model (−1% to −5% relative to the reference period 1975–1999) by the 2020s, decline to 2.05–2.26 mm (−3% to −12%) by the 2050s, and decline to 1.55–2.18 mm (−6% to −33%) by the 2080s. The rising temperatures and increased precipitation also predicted a decrease in mean annual basal area increment of jack pine. Application of the transfer models showed that the mean annual tree-ring basal area increment would decrease to 29.8–31.8 cm^2 depending upon climate model (−5% to −11% relative to the reference period 1975–1999) by the 2020s, to 25.1–29.7 cm^2 (−11% to −25%) by the 2050s and to 27.8–11.2 cm^2 (−17% to −66%) by the 2080s.

4. Discussion

4.1. Seed source transfer effects

Our study showed a significant effect of seed-source origin on radial growth of jack pine populations grown in a common-garden plantation in Petawawa, Ontario. Provenances originating from slightly warmer and drier climates than that prevailing at the plantation site showed higher long-term radial growth compared to the northern provenances. The better growth performance of the southern populations in Petawawa might be the result of their genetic adaptation to a longer growing season in their native environment, where bud burst starts earlier in spring and bud setting occurs later in fall (O'Neill and Yanchuk, 2005). The transfer of southern seed sources to moderately colder climate increases summer day-length, which may enhance photosynthesis and growth. However, despite the better growth performance of southern populations transferred to a northern climate, they are often subjected to maladaptation and affected by frosts injuries, pest attacks, and disease that can cause high mortality rates (Campbell, 1979; Zobel and Talbert, 1984).

At first sight, it may be surprising that the northern populations did not benefit more from transfer to a warmer climate at the plantation site. But, northern populations transferred to a warmer climate were found to be more conservative (genetically constrained) in their growth cycle phenology than the local populations, and may be predisposed to being overtopped and suppressed by local populations when grown together (Davis and Shaw, 2001; O'Neill and Yanchuk, 2005). Therefore, an inherent earlier onset of growth cessation of northern populations transferred southwards may lead to a lower radial growth despite improved temperature conditions. Our findings are supported by other studies of radial and height growth of seeds of *Pinus* species transferred to a warmer climate (Matyas and Yeatman, 1992; Rehfeldt et al., 2002; Savva et al., 2002).

Our study showed that the radial growth of jack pine populations was arrayed along climatic and geographical clines. However, climatic and environmental factors of the plantation site also play an important role in radial growth differentiation among intraspecific populations through environmental effects and genotype by environment interaction effects (Zobel and van Buijtenen, 1989; Matyas, 1999). The validation procedure used in this study showed that the correlation coefficients differed among independent sites, which is probably due to a significant effect of genotype × environment interactions on radial growth (Savva et al., unpublished results). Absolute values of radial growth of the provenance differed among the three validation sites. Therefore, the effect of site differences were minimized by using relative growth characteristics of the provenances calculated as a percentage of the site mean. Our objective was to test if radial growth of jack pine provenances followed a general pattern of decreasing growth with increasing distance between seed-source origin and common planting site. Two sites out of three supported our model and showed positive significant correlations with the developed transfer models, but the intermediate site in Cloquet, MN did not. However, the three sites combined extended the range of transfer distances and encompassed the genotype × environment interaction effect on radial growth of provenances and showed a significant correlation coefficient with the transfer models. This result suggests that the pattern of the relationships of tree growth and seed-source origin depends upon genotype, environment, and genotype × environment interactions.

The developed transfer models revealed that the differences in radial growth of the diverse jack pine provenances grown in

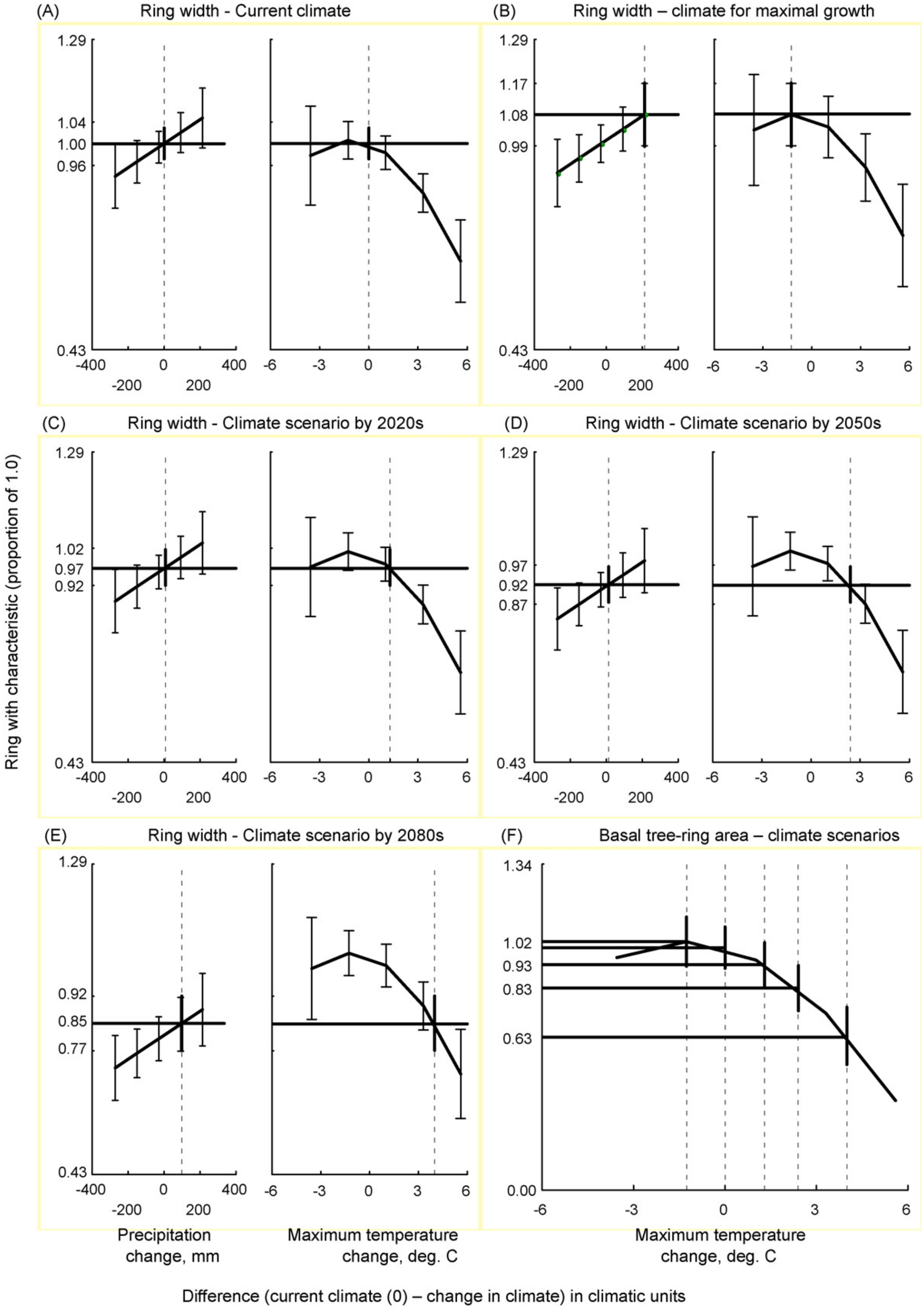

Fig. 4. Values of mean tree-ring width (A, B, C, D and E) and mean annual tree-ring basal area increment (F) at given levels of changes in mean annual maximum daily temperature and/or annual total precipitation in Petawawa, Ontario, predicted from the developed transfer models (see Table 3). The vertical lines can be interpreted as levels of both: (1) the distances (provenance site–plantation site) expressed in the indicated climatic units; (2) the changes in annual total precipitation and/or mean annual maximum daily temperature predicted from the climate scenario A2a of the Canadian Global Coupled Model CGCM2 by 2020s, 2050s and 2080s for the region including Petawawa, Ontario (see Table 4 for the derived changes in climatic characteristics for the study area). The graphs C–F are based on the application of this climate change scenario for the 2020s, 2050s and 2080s to the developed transfer models and show the predicted mean ring-width characteristics at

Table 4
Predicted values of mean tree-ring width (TRW) and mean annual tree-ring basal area increment (TRA) calculated from application of the different climate scenarios of the general circulation models to the transfer functions

Years	General circulation model	Climate change scenario	PRC (mm/year)	MAXT (°C/year)	TRW, proportion (of 1.00)	95% confidence interval TRW, proportion (of 1.00)	TRA, proportion (of 1.00)	95% confidence interval TRA, proportion (of 1.00)	ΔTRW[a], proportion (of 1.00)	ΔTRA[b], proportion (of 1.00)
2020	CGCM2	B2a	50.1	1.00	0.99	(0.94;1.04)	0.95	(0.86;1.04)	−0.01	−0.05
	HADCM3	A1F	5.7	1.07	0.97	(0.93;1.02)	0.95	(0.85;1.04)	−0.03	−0.05
	CGCM2	A2a	8.1	1.26	0.97	(0.92;1.02)	0.93	(0.84;1.02)	−0.03	−0.07
	HADCM3	A2a	18.6	1.44	0.97	(0.92;1.02)	0.92	(0.83;1.01)	−0.03	−0.08
	HADCM3	B2b	3.0	1.35	0.97	(0.92;1.01)	0.93	(0.83;1.02)	−0.03	−0.07
	HADCM3	B2a	15.6	1.46	0.97	(0.91;1.01)	0.92	(0.83;1.01)	−0.03	−0.08
	HADCM3	A2b	12.6	1.36	0.97	(0.92;1.02)	0.92	(0.83;1.02)	−0.03	−0.08
	HADCM3	A2c	24.3	1.80	0.95	(0.90;1.00)	0.89	(0.80;0.98)	−0.05	−0.11
2050	CGCM2	B2a	74.4	1.83	0.97	(0.91;1.03)	0.89	(0.79;0.98)	−0.03	−0.11
	HADCM3	B2b	7.2	2.1	0.94	(0.88;0.98)	0.86	(0.77;0.96)	−0.06	−0.14
	HADCM3	B2a	25.8	2.53	0.92	(0.87;0.97)	0.82	(0.73;1.03)	−0.08	−0.18
	CGCM2	A2a	13.2	2.41	0.92	(0.87;0.97)	0.83	(0.74;0.93)	−0.08	−0.17
	HADCM3	A2a	26.7	2.72	0.91	(0.85;0.96)	0.80	(0.71;0.89)	−0.09	−0.20
	HADCM3	A2c	26.1	2.91	0.90	(0.85;0.95)	0.78	(0.68;0.87)	−0.10	−0.22
	HADCM3	A1F	23.4	3.15	0.88	(0.83;0.94)	0.75	(0.65;0.85)	−0.12	−0.25
2080	CGCM2	B2a	65.1	2.45	0.94	(0.88;0.99)	0.83	(0.74;0.92)	−0.06	−0.17
	HADCM3	B2b	21.6	3.10	0.88	(0.83;0.94)	0.76	(0.66;0.85)	−0.12	−0.24
	HADCM3	B2a	25.5	3.44	0.86	(0.81;0.92)	0.71	(0.61;0.82)	−0.14	−0.29
	CGCM2	A2a	98.0	4.00	0.85	(0.77;0.92)	0.64	(0.52;0.75)	−0.15	−0.36
	HADCM3	A2b	29.7	4.64	0.77	(0.69;0.85)	0.54	(0.39;0.69)	−0.23	−0.46
	HADCM3	A2a	29.1	4.66	0.77	(0.69;0.85)	0.53	(0.38;0.68)	−0.23	−0.47
	HADCM3	A2c	34.2	5.05	0.74	(0.64;0.83)	0.47	(0.29;0.64)	−0.26	−0.53
	HADCM3	A1F	27.3	5.77	0.67	(0.54;0.79)	0.34	(0.10;0.57)	−0.33	−0.66

General circulation models used in the study are: (i) general circulation model of the Hadley Center (HADCM3) and (ii) Canadian Global Coupled Model (CGCM2) of the Canadian Centre for Climate Modeling and Analysis. Values of mean tree-ring width and mean tree-ring basal area were calculated as a proportion of 1.0 relative to the current climate. Tree-ring width is arranged in descending order for 2020, 2050 and 2080. MAXT and PRC indicate changes in mean annual maximum temperature and mean annual precipitation, respectively.

[a] Change in TRW relative to TRW in current climate.

[b] Change in TRA relative to TRA in current climate.

Petawawa were mainly explained by the mean annual daily maximum temperature at the seed-source origins and, to a much lesser degree, by the total annual precipitation at seed-source origin. Our results are consistent with those of Andalo et al. (2005), which is one of very few studies of the effects of both temperature and precipitation at seed-source origin on growth of provenances in common gardens. That study showed that temperature rather than precipitation at seed-source origins explained height growth of white spruce populations in Quebec.

Including 30 or more provenances would perhaps be ideal for development of the regression-based transfer functions described in this study. However, the population pool of northern provenances was limited by low survivorship at this site. In spite of this, we collected a sufficient number of trees per provenance (about 20 two-radius cores) that resulted in a representative sample size for estimation of means of almost all of the 21 studied populations. We also verified that we had enough data points to avoid overfitting. Additionally, the extension of our models to three independent sites proved the robustness of the models.

4.2. Climate change effects

The high genetic differentiation of jack pine has allowed this species to adapt genetically and physiologically to climate of seed-origin with high survivorship and resistance to frost and diseases. We showed that slight changes in climate such as projected for the 2020s would not result in a significant growth decline of jack pine in Petawawa in central Ontario, Canada. However, the climate changes predicted for the 2050s and 2080s could cause a significantly reduced radial growth of jack pine, assuming other biotic and abiotic factors and their interactions do not change. This adverse impact of global warming is most probable because jack pine will likely not be able to naturally migrate northward fast enough to compensate for the temperature increase unless genotypes are redistributed

these levels of climatic changes. The graph A shows the mean ring width (1.0) predicted at current climate (or that of the local populations of jack pine, i.e. when the transfer distance between the plantation site and provenance site is zero). The graph B shows the maximal predicted mean ring width at the optimal climate (also interpretable as that of the provenance with the best radial growth performance at the study site). Mean tree-ring width and mean annual basal tree-ring area increment are expressed as a proportion of 1.0 of those in the current climate (or of those of the local populations). The vertical error bars show the 95% confidence intervals for the predicted tree-ring characteristics.

through seed transfer and planting. Such an adaptation lag to climate change (Matyas and Yeatman, 1992) might result in negative impacts on tree growth and stand development of jack pine.

5. Conclusion

This study is one of few studies of long-term radial growth characteristics of forest tree provenances in a common-garden experiment. Many studies are traditionally focused on height growth and survival and do not include characteristics of long-term growth. Radial growth represents actual, integrated measures of tree and stand wood production, and studies of this characteristic over long periods of time increases the reliability of modeling efforts and conclusions. Our radial growth models of older trees over a long period of time as well as studies on height growth of jack pine populations in young stands (e.g., Matyas and Yeatman, 1992) showed that the southern seed sources could out-perform local populations in diameter and height growth. Southern seed sources might also be better adapted to the warming climatic conditions predicted for the future. Seed transfer could serve in forest management as a silvicultural tool to minimize the adaptation lag and therefore counteract future climate change effects on growth reductions. Yet, the seeds should be transferred northward only for moderate distances to avoid potential maladaptation under current climate conditions. In addition, other factors such as survivorship, disease- and frost-resistance, and the role of fire disturbance should be taken into consideration before using non-local provenances in plantations.

Acknowledgements

This research was supported by the Grants from the Chaire de recherche du Canada en écologie et aménagement forestiers and the Chaire de recherche du Canada sur la valorisation, la caractérisation et la transformation du bois, and the Fondation de l'Université du Québec en Abitibi-Témiscamingue. We thank Steve D'Eon, Professor William Parker and Hugues Laberge for help and technical support. For providing some of the material used in this paper the authors thank Jacek Oleksyn and Peter B. Reich.

References

Andalo, C., Beaulieu, J., Bousquet, J., 2005. The impact of climate change on growth of local white spruce populations in Quebec. Canada. For. Ecol. Manage. 205, 169–182.

Beaulieu, J., Rainville, A., 2005. Adaptation to climate change: genetic variation is both a short- and a long-term solution. Forest. Chron. 81, 704–709.

Bergeron, Y., Gauthier, S., Kafka, V., Lefort, P., Lesieur, D., 2001. Natural fire frequency fort the eastern Canadian boreal forest: consequences for sustainable forestry. Can. J. For. Res. 31, 384–391.

Brooks, J.R., Flanagan, L.B., Ehleringer, J.R., 1998. Response of boreal conifers to climate fluctuations: indications from tree-ring widths and carbon isotope analyses. Can. J. For. Res. 28, 524–533.

Campbell, R.K., 1979. Genecology of Douglas-fir in a watershed in the Oregon Cascades. Ecology 60, 1036–1050.

Cantin, D., Tremblay, M.F., Lechowicz, M.J., Potvin, C., 1997. Effects of CO_2 enrichment, elevated temperature, and nitrogen availability on the growth and gas exchange of different families of jack pine seedlings. Can. J. For. Res. 27, 510–520.

Critchfield, W.B., 1985. The late Quaternary history of lodgepole and jack pines. Can. J. For. Res. 15, 739–772.

Chuine, I., Rehfeldt, G.E., Aitken, S.N., 2006. Height growth determinants and adaptation to temperature in pines: a case study of *Pinus contorta* and *Pinus monticola*. Can. J. For. Res. 36, 1059–1066.

Cullen, M.J.P., 1993. The unified forecast climate model. Meteorol. Mag. 122, 81–94.

Davis, M.B., Shaw, R.G., 2001. Range shifts and adaptive responses to quaternary climate change. Science 292, 673–679.

Desponts, M., Payette, S., 1993. The Holocene dynamics of jack pine at its northern range limit in Québec. J. Ecol. 81, 719–727.

Electronic Statistics Textbook Statsoft, 2007. StatSoft Inc. (http://www.statsoft.com).

Environment Canada, 2007. Database of the National Climate Data and Information Archive (http://www.ec.gc.ca/).

Flato, G.M., Boer, G.J., Lee, W.G., McFarlane, N.A., Ramsden, D., Reader, M.C., Weaver, A.J., 2000. The Canadian centre for climate modelling and analysis global coupled model and its climate. Clim. Dynam. 16, 451–467.

Flato, G.M., Boer, G.J., 2001. Warming asymmetry in climate change simulations. Geophys. Res. Lett. 28, 195–198.

Gajewski, K., Payette, S., Ritchie, J.C., 1993. Holocene vegetation history at the boreal forest–shrub-tundra transition in northern Québec. J. Ecol. 81, 433–443.

Gauthier, S., Bergeron, Y., Simon, J.P., 1996. Effects of fire regime on the serotiny level of Jack pine. J. Ecol. 84, 539–548.

Gordon, C., Cooper, C., Senior, C.A., Banks, H., Gregory, J.M., Johns, T.C., Mitchell, J.F.B., Wood, R.A., 2000. The simulation of SST, sea ice extents and ocean heat transports in a version of the Hadley Centre coupled model without flux adjustments. Clim. Dynam. 16, 147–168.

Greenwood, M.S., Livingston, W.H., Day, M.E., Kenaley, S.C., White, A.S., Brissette, J.C., 2002. Contrasting models of survival by jack and pitch pine at a common range limit. Can. J. For. Res. 32, 1662–1674.

Grissino-Mayer, H.D., 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree-Ring Res. 57, 205–221.

He, H.S., Mladenoff, D.J., Gustafson, E.J., 2002. Study of landscape change under forest harvesting and climate warming-induced fire disturbance. For. Ecol. Manage. 155, 257–270.

Hills, G.A., Pierpoint, G., 1960. Forest site evaluation in Ontario. Ont. Dep. Lands, For. Res. Branch, Toronto. Ont. Res. Rep. 42, p. 64.

Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bull. 43, 69–75.

Holst, M.J., 1967. All-range jack pine provenance experiment. Petawawa For. Expt. Sta., Internal Report PET-PS6.

Kimball, J.S., Thornton, P.E., White, M.A., Running, S.W., 1997. Simulating forest productivity and surface-atmosphere carbon exchange in the BOREAS study region. Tree Physiol. 17, 589–599.

Matyas, C., Yeatman, C.W., 1992. Effects of geographical transfer on growth and survival of jack pine (*Pinus banksiana* Lamb.) populations. Silvae Genet 43, 370–376.

Matyas, C., 1994. Modelling climate change effects with provenance test data. Tree Physiol. 14, 797–804.

Matyas, C., 1999. Forest Genetics and Sustainability. Kluwer Academic Publishers, Dordrecht, Boston.

McFarlane, N.A., Boer, G.J., Blanchet, J.P., Lazare, M., 1992. The Canadian climate center second-generaion general-circulation model and its equilibrium climate. J Climate 5, 1013–1044.

McLeod, T.K., MacDonald, G.M., 1997. Post glacial range expansion and population growth of *Picea mariana*, *Picea glauca* and *Pinus banksiana* in the western interior of Canada. J. Biogeogr. 24, 865–881.

National Climatic Data Center, 2007. Climate data, NOAA (http://www.ncdc.noaa.gov/oa/ncdc.html).

Oleksyn, J., Tjoelker, M.G., Reich, P.B., 1998. Adaptation to changing environments in European Scots pine populations across a latitudinal gradient. Silva Fenn. 32, 129–140.

O'Loughlin, T.C., 1973. Cone characteristics and seed yield in a jack pine breeding orchard. Thesis (M.S.). University of Mossouri, School of Forestry, Columbia.

O'Neill, G., Yanchuk, A., 2005. Climate change and forest genetics. Summary of the 29th Biennial Meeting of the Canadian Tree Improvement Association and the Western Forest Genetics Association, Kelowna, BC, July 27–29, 2004, Forest. Chron. 81, 18–19.

Payette, S., 1993. The range limit of boreal tree species in Québec-Labrador: am ecological and palaeoecological interpretation. Rev. Palaeobot. Palyno. 79, 7–30.

Rehfeldt, G.E., Tchebakova, N.M., Barnhardt, L.K., 1999a. Efficacy of climate transfer functions: introduction of Eurasian populations of Larix into Alberta. Can. J. For. Res. 29, 1660–1668.

Rehfeldt, G.E., Ying, C.C., Spittlehouse, D.L., Hamilton, D.A., 1999b. Genetic responses to climate in *Pinus contorta*: Niche breadth, climate change, and reforestation. Ecol. Monogr. 69, 375–407.

Rehfeldt, G.E., Tchebakova, N.M., Parfenova, Y.I., Wykoff, W.R., Kuzmina, N.A., Milyutin, L.I., 2002. Intraspecific responses to climate in *Pinus sylvestris*. Glob. Change Biol. 8, 912–929.

Rudolf, P.O., 1965. Jack pine (*Pinus banksiana* Lamb.) Silvics of forest trees of the United States. Washington, DC In: Fowells, H.A. (Ed.), U.S. Department of Agriculture, vol. 271. Agriculture Handbook, pp. 338–354 (Comp.).

Rudolph, T.D., Yeatman, C.W., 1982. Genetics of Jack Pine. USDA Forest Service, Research Paper WO-38, Washington, DC.

Rudolph, T.D., Laidly, P.R., 1990. Jack pine. In: Burns, R.M., Honkala, B.H. (Eds.), Silvics of North America, vol. 654USDA Agriculture Handbook, pp. 280–294 (Tech. Coords.).

Saenz-Romero, C., Guzman-Reyna, R.R., Rehfeldt, G.E., 2006. Altitudinal genetic variation among *Pinus oocarpa* populations in Michoacan, Mexico—implications for seed zoning, conservation, tree breeding and global warming. For. Ecol. Manage. 229, 340–350.

Savva, Y., Schweingruber, F., Milyutin, L., Vaganov, E., 2002. Genetic and environmental signals in tree rings from different provenances of *Pinus sylvestris* L., planted in the southern taiga, Central Siberia. Trees Struct. Funct. 16, 313–324.

Schmidtling, R.C., 1994. Use of provenance tests to predict response to climatic-change loblolly pine and Norway spruce. Tree Physiol. 14, 805–817.

Schoenike, R.E., 1976. Geographic variation in jack pine. University of Minnesota Agriculture Experiment Station, vol. 304. Technical Bulletin, St. Paul, MN, p. 49.

Teich, A.H., 1970. Cone serotiny and inbreeding in natural populations of *Pinus banksiana* and *Pinus contorta*. Can. J. Botany 48, 1805–1809.

Thompson, I.D., Flannigan, M.D., Wotton, B.M., Suffling, R., 1998. The effects of climate change on landscape diversity: an example in Ontario forests. Environ. Monitor. Assess. 49, 213–233.

vanNiejenhuis, A., Parker, W.H., 1996. Adaptive variation in jack pine from north central Ontario determined by short term common garden tests. Can. J. For. Res. 26, 2006–2014.

Wilde, S.A., 1946. Forest Soils and Forest Growth. Chronica Botanica Co., Walthan, MA.

Zobel, B.J., Talbert, J.T., 1984. Applied Tree Improvement. John Wiley and Sons, New York.

Zobel, B.J., van Buijtenen, J.P., 1989. Wood Variation: Its Causes and Control. Springer, Berlin.