Concluding from these results, it was possible to select yew-clones among a variety of clones of different origin with a high rooting ability and root growth which can be used in ongoing research work for investigations concerning taxol biosynthesis on all levels.

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Genetic Variation in Height Growth among Populations of Eastern White Pine (*Pinus strobus* L.) in Ontario

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Abstract

Provenances of eastern white pine (*Pinus strobus* L.) were sampled from natural populations in Ontario and assessed in a 2-year greenhouse study followed by two 5-year short term field tests to reveal the scale and patterns of genetic variation in growth and adaptation at early ages. Results indicate that considerable genetic variation in growth potential exists among white pine populations in Ontario and that appreciable genetic gain can be realized through seed source selection in reforestation programs. Strong age-age correlation between growth traits at different years and the weak genotype-by-provenance interaction suggested high efficiency in provenance selection at early stage. Due to the latitude predominated clinal pattern of geographic variation and the significant reduction in growth potential when seeds are transferred from north to south, it is recommended not to use seed sources 1.5 to 2.0 degrees (latitude) north of a place where regeneration of eastern white pine occurs. Because of the relatively mild test environments at two sites and the short-term nature of this study, further research is required to investigate differences in cold hardiness among provenances before safe south to north seed transfer distances can be determined.

Key words: Pinus strobus, seed source, genetic variation, growth potential, seed transfer.

Introduction

For forest tree species with large natural distributions, such as the eastern white pine (*Pinus strobus* L.), substantial genetic variation in growth among provenances has been reported from range-wide provenance tests (FOWLER and HEIMBURGER, 1969; GARRETT et al., 1973; GENYS, 1987; ABUAKER and ZSUFFA, 1991). While range-wide provenance tests are valuable for revealing large-scale geographic patterns of genetic variation, as well as in identifying potentially superior provenances, results from these tests with eastern white pine are insufficient to satisfy operational forest regeneration needs, such as seed source selection, in Ontario. The difficulty exists mainly because only a few eastern white pine population samples from Ontario were included in these range-wide provenance tests (FOWLER and HEIMBURGER, 1969) and the test sites were not representatives of the environmental conditions in Ontario where most eastern white pine regeneration takes place. The

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preference of using local provenances and the concerns over maladaptation precipitated by long distance seed transfer require a better understanding of the scale and patterns of genetic variation among populations of eastern white pine in Ontario.

To supplement range-wide provenance tests of eastern white pine established in the USA and Canada, we conducted a short-term regional provenance study in the greenhouse for 2 growing seasons and in 2 short-term field tests for 5 growing seasons after planting. This paper reports the scale and patterns of genetic variation among eastern white pine populations in growth potential.

Material and Methods

Seed collection

Seeds were collected in the fall of 1994 from the natural range of eastern white pine populations in Ontario (*Figure 1*). Populations were sampled more intensely where the species' abundance is high (such as the region from Toronto to Ottawa, the Ottawa Valley, and along the North Bay area). Fewer samples were, however, obtained around the area of Huntsville where the abundance of eastern white pine is historically low. The populations ranged from 42.9° to 48.3°N in latitude, from 74.4° to 84.7°W in longitude, and from 53 to 520 m in elevation (*Table 1*).

At each of the sampling locations, collections consisted of seeds from 10 trees at least 20 m apart or from at least 4 squirrel caches. In some areas seeds were, however, collected from fewer than 10 trees due to the sparse distribution of eastern white pine. All trees used for seed collection were naturally regenerated. Seed weight for each population was determined by weighing 100 seeds. Climatic variables associated with the provenance origins were interpolated using an Ontario climate model based on geographic coordinates (i.e., latitude, longitude, elevation) of each provenance. Weather information was based on 20-year average climate variables (between 1968 and 1988) observed from weather stations across Ontario and surrounding areas (McKenney et al., 1999).

Greenhouse tests

Seeds were doubly sown into 3.8 x 21 cm Ray Leach tubes filled with 1:1 commercial peat moss/vermiculite (v/v) mix between April 12 and 19, 1995, in the greenhouse in Sault Ste. Marie. After germination, seedlings in each tube were thinned to a single stem and supplemental day light was set for 16 h with a temperature regime of 28°C (day)/18°C (night). Seedlings were misted daily at 8, 12, and 16 h. Once the secondary needles were evident, fertilization was applied weekly with a 20-8-20 complete fertilizer solution at 100 ppm nitrogen. The greenhouse environment was designed to give seedlings optimal growing conditions to fully express their growth potential and to maximize differentiation among populations (Eriksson et al., 1993). On August 14, 1995, seedlings were moved from the greenhouse to the holding area for natural hardening. Fertilization was subsequently changed to 8-20-30 at 50 ppm nitrogen applied once a week.

The layout of seedlings in the greenhouse and the holding area for the first year was a randomized complete block design using 10 seedlings per plot with 15 replications. Initially 121 populations were sown, but 9 were subsequently excluded from the experiment either because of low germination rate or the merging of populations, which were from similar geographic locations.

On April 22, 1996, 3 replications were moved back to the greenhouse to start the second growing season in a controlled environment, while the rest were used to establish the two field tests. The greenhouse was maintained at 18°C (day)/13°C (night) temperatures with 16 h photo-period. Seedlings were fertilized weekly with 20-20-20.

Measurements in the greenhouse study included first-year seedling height, needle length, over winter damage, and seedling height increments measured from April 24 (onset of height growth) to June 6, 1996 (end of height growth) at 3-day intervals. From the 3-day height measurement interval we calculated the beginning and end of shoot elongation and the duration of the growth cycle.

Field tests

Field tests were established in the spring of 1996 at Turkey Point and Sault Ste. Marie, Ontario (*Figure 1*). Turkey Point is

Table 1. – Identification, geographic coordinators and elevations of eastern white pine populations sampled in this short-term provenance study.

ID	Longitude (° W)	Latitude (° N)	Elevation (m)	ID	Longitude (° W)	Latitude (° N)	Elevation (m)
1	78.83	44.50	270	212	84.35	46.68	210
2	80.08	44.47	180	213	84.40	46.92	260
3	79.63	44.72	180	215	84.70	47.12	260
13	80.42	42.89	240	216	84.30	46.58	270
17	79.78	43.60	200	217	84.50	46.47	190
31	81.47	42.92	240	218	83.98	46.33	200
32	75.83	44.50	100	220	83.20	47.87	420
33	76.68	44.97	230	221	82.33	48.23	330
34	74.85	45.63	53	222	81.78	48.27	330
35	75.23	45.58	61	223	80.43	47.78	300
36	76.83	45.27	210	224	80.87	47.63	350
37	77.08	45.52	167	225	81.27	47.53	380
38	77.78	45.01	350	226	81.60	47.87	360
39	77.26	45.02	274	227	82.43	47.55	420
40	77.12	45.64	160	228	83.62	46.68	480
41	76.10	44.58	125	229	83.68	47.53	450
42	76.43	44.59	130	230	83.40	46.38	300
43	76.58	44.98	160	231	83.22	46.45	300
44	76.61	45.37	190	233	82.90	46.62	360
45	77.53	44.90	350	234	82.55	46.32	300
47	75.04	44.96	70	235	84.07	46.87	350
50	80.28	45.78	213	238	82.13	46.25	270
57	74.87	45.55	53	239	82.18	46.45	330
58	77.13	44.68	258	240	82.20	46.57	410
59	80.08	43.63	370	241	81.98	46.57	330
64	77.30	45.03	379	242	81.65	47.07	450
68	75.40	44.79	90	243	81.63	46.98	450
69	75.90	45.08	121	244	81.60	46.75	420
70	74.42	45.18	53	245	81.42	46.62	350
71	79.96	44.57	100	246	81.00	46.83	330
72	76.09	44.91	120	247	80.75	46.92	320
73	76.13	45.27	150	248	80.83	46.90	300
74	76.72	44.28	120	249	80.52	46.47	230
75	79.05	43.90	130	250	80.20	46.43	240
76	77.98	44.38	220	251	79.42	46.25	210
77	78.38	44.60	290	252	79.53	46.50	320
101	77.75	45.92	210	253	79.70	46.63	300
102	83.42	46.25	200	254	79.77	46.85	300
103	83.00	46.20	180	255	79.80	47.08	320
104	83.00	46.25	200	256	79.75	47.23	360
105	82.42	46.20	210	257	79.90	47.18	360
106	84.17	47.00	370	258	79.93	46.67	300
107	83.83	47.17	520	259	80.25	46.63	270
108	81.08	46.80	380	260	79.18	46.47	330
109	80.00	47.00	340	261	79.15	46.62	300
110	77.37	44.98	350	262	78.97	46.48	300
111	77.17	45.00	320	263	78.80	46.35	240
201	83.82	46.75	350	264	78.90	46.25	180
202	83.72	46.82	450	265	78.93	46.13	300
203	83.46	46.87	425	266	79.15	46.27	240
205	84.52	47.95	300	267	79.48	46.10	230
206	83.73	46.45	240	268	79.37	46.12	260
207	83.65	46.45	300	269	79.93	46.47	240
208	83.42	46.60	330	270	80.75	46.22	210
209	83.43	46.73	330	271	81.50	46.33	210
210	83.32	46.85	390	272	84.65	47.22	210
211	83.12	46.98	410	273	84.68	47.37	270

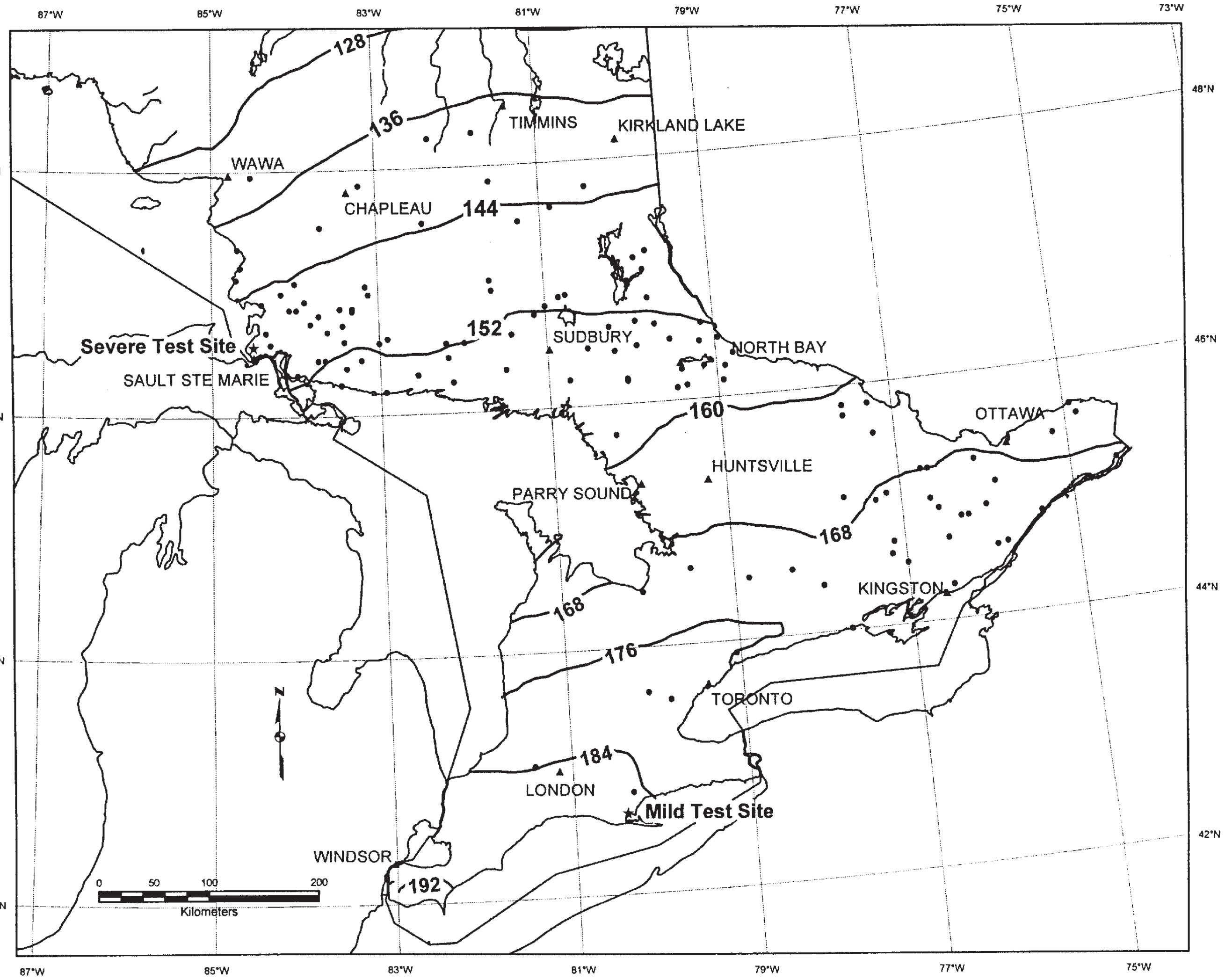

Figure 1. – Distribution of seed sources of eastern white pine used in the study and the predicted provenance height growth at age 5 in Sault Ste. Marie. Note that field test site is indicated by a star, provenance origins are given by solid dots, and predicted provenance height growth potential at Sault Ste. Marie is presented with lines of a 8 cm interval.

a south site with higher annual mean temperature and longer growing season than Sault Ste. Marie, which has a relatively harsher environment with heavy snowfall in the winter. Environmental conditions for the sites are summarized in *Table 2*.

Table 2. – Summary of environmental conditions of the field provenance tests.

Parameter	Turkey Point	Sault Ste. Marie
Latitude	42° 41'	46° 31'
Longitude	80° 21'	84° 27'
Soil	Deep fine sand	deep loamy sand
Growing season length	218 days	185 days
Growing season precipitation	599 mm	511 mm
Growing degree days	2195	1592
Annual mean temperature	8°C	4.4°C
January mean minimum temperature	-10.3°C	-16.2°C

A randomized complete block design with 10-tree row plots and 4 blocks were used at each site. 92 provenances were planted at Turkey Point site while 112 provenances were planted at Sault Ste. Marie. To maintain homogeneous environment, narrow spacing of 1.0 x 0.5 m between rows and columns was used in the field tests to minimize block sizes. During the first year and at the beginning of the second year, both trials were kept competition free through hand hoeing. In subsequent years, each site was treated with a 20 cm band of Simazine (pre-emergent herbicide at 2.5 kg/hectare) supplemented by hand weeding and spot applications of glyphosate. Fertilizer (10-10-10) was applied at 2.0g/tree at Turkey Point. Methoxychlor was sprayed in the spring of 1999 and 2000 to prevent white pine weevil damage. Observations in the field included annual assessment of height, height increment, tree health status, and stem form.

Statistical analysis

Mixed linear models were used to analyze the data. Before each pooled analysis of field and greenhouse experiments, data were standardized by block to reduce variance heterogeneity caused by scale effects (WHITE, 1996). For a pooled analysis involving 2 or more experiments, the mixed linear model used was:

$$y_{ijkl} = u + t_i + b_{j(i)} + s_k + ts_{ik} + p_{ijk} + e_{ijkl} \qquad (1)$$

where,

y_{ijkl} is the lth tree of the kth provenance growing in the jth block of the ith test,

u is the overall mean,

t_i is the fixed effect of the i[th] test location,

$b_{j(i)}$ is the random effect of the j[th] block within the i[th] test,

s_k is the random effect of k[th] provenance,

ts_{ik} is the random effect of the k[th] provenance by the i[th] test interaction,

p_{ijk} is the random k[th] plot effect within the j[th] block of the i[th] test,

e_{ijkl} is the random residual effect.

SAS Mixed Procedure (SAS® 1996) was used to estimate variance components. Variance components were partitioned into provenance (σ_s^2), test-by-provenance interaction (σ_{ts}^2), plot effect (σ_p^2), and residual (σ_e^2). The proportion of total phenotypic variance contributed by each variance component was calculated to indicate their relative significance.

Provenance stability across environments was evaluated using the concept of type B genetic correlation (BURDON, 1977) with the formulae (YAMADA, 1962):

$$r = \frac{\sigma_s^2}{\sigma_s^2 + \sigma_{ts}^2} \quad (2)$$

where, σ_s^2 is the variance component for provenance and σ_{ts}^2 is the variance component for test-by-provenance interaction.

Least significant differences for multiple comparisons were calculated at the significance levels of $\alpha = 0.05$ for growth traits to determine at what point provenances should be considered significantly different in seed source planning. Mean provenance height growth was then regressed against geographic or/and climatic variables using the PROC REG with stepwise/rsquare selection options (SAS® 1996) to detect clinal patterns of genetic variation (PARKER et al., 1994; XIE and YING, 1995; LI et al., 1997; REHFELDT et al., 1999). Equations fitted at each test were validated using independent measurements of the same traits at the other test site after adjusting for population differences in means and variances between the tests. For example, to use data from test A to validate a fitted equation for a trait at test B, provenance means at test A were adjusted using the formula:

$$y_{a'} = \bar{y}_b + (y_a - \bar{y}_a)\frac{s_b}{s_a} \quad (3)$$

where, $y_{a'}$ is the adjusted provenance mean height at test A, y_a is the observed provenance mean height at test A, y_b is observed provenance mean height at test B, s_a is the standard deviation among observed provenance mean heights at test A, and s_b is the standard deviation among observed provenance mean heights at test B, and $\bar{y}_b$ and $\bar{y}_a$ are the grand means at test A and B, respectively. The relative importance of environmental variables that predict significant growth differences among provenances were determined by their partial regression coefficients on the prediction variables. Finally, appropriate information was integrated into a GIS-based climate model to produce a visual presentation of the patterns of genetic variation.

Results

Greenhouse traits

Significant differences in height growth were detected among populations of eastern white pine in the greenhouse. Populations differed significantly in first-year seedling height, needle length, initiation of shoot elongation, date of shoot growth cessation, length of shoot elongation period, and the second year seedling height. There was no significant difference among populations in over winter damage on first-year seedlings at Sault Ste. Marie since the seedlings were stored in a freezer at –2°C. Genetic variation among populations accounted for 17% to 19% of the total phenotypic variation in seedling height, while accounting for less than 5% of the phenotypic variation for other greenhouse traits (*Table 3*). The first- and second-year provenance mean seedling heights were significantly correlated with seed weight (i. e., r = 0.25** and r = 0.20*, respectively), but seed weight effects explained less than 6% of the phenotypic variation of height growth and decreased as seedling size increased.

Table 3. – Mean height growth, coefficient of variation (C.V.), and the contributing variance components to phenotypic variation in short-term eastern white pine provenance tests †.

Trait‡	Mean*	C.V. (%)	σ_s^2 (%)	σ_{ts}^2 (%)	σ_p^2 (%)	σ_e^2 (%)
Grh_ht1	9.34	17.64	18.91	--	9.03	72.05
Grh_ht2	16.70	17.62	17.22	--	6.19	76.58
Needle length	10.08	10.30	3.21	--	6.44	90.35
Growth period (day)	25.68	14.38	4.35	--	4.36	91.29
Growth start (day)	11.23	31.38	2.05	--	4.66	93.29
Growth end (day)	8.142	50.69	3.02	--	6.51	90.46
TP_ht1	14.78	24.01	13.53	--	10.63	75.84
TP_ht2	30.46	23.84	18.34	--	6.15	75.51
TP_ht3	60.79	30.30	14.75	--	10.17	75.08
TP_ht4	107.06	27.97	10.80	--	14.50	74.70
TP_ht5	174.26	19.70	12.14	--	11.43	76.44
Arb_ht1	12.20	25.71	16.83	--	13.70	69.47
Arb_ht2	26.36	24.29	21.16	--	6.07	72.77
Arb_ht3	55.59	23.15	22.48	--	7.70	69.82
Arb_ht4	98.20	21.31	19.51	--	7.19	73.30
Arb_ht5	156.06	19.43	14.99	--	6.69	78.32
Pooled ht1	13.35	26.71	14.62	0.67	12.36	72.35
Pooled ht2	28.17	25.18	18.98	0.95	6.10	73.97
Pooled ht3	57.80	27.13	16.96	2.33	8.76	71.96
Pooled ht4	101.94	25.02	13.87	1.96	10.30	73.87
Pooled ht5	160.58	20.13	12.11	2.31	11.96	73.62

Measurement in cm unless otherwise indicated. † Variance components were estimated using standardized data to reduce variance heterogeneity due to scale effects with σ_s^2 being among provenance variance, σ_{ts}^2 being test-by-provenance interaction variance, σ_p^2 being plot variance and σ_e^2 being error variance; C. V. $=\sigma_s$/mean 100%. ‡ Grh --greenhause, TP --Turkey Point, Arb --Sault Ste Marie (arboretum), ht x— height growth at the end of year x.

Population mean seedling heights at the end of first and second year, mean needle length, and length of the growing period were all negatively correlated with latitude of provenance origins at the probability level $\alpha = 0.01$ (r = –0.44, –0.50, – 0.30 and –0.29 respectively). The shorter growing period for northern populations seemed mainly due to the early cessation of shoot growth as indicated by the significant negative correlation between growth cessation date and latitude (r = –0.28). No significant correlation between the starting date of shoot elongation or early growth (up to May 21) and the geographic/climate variables was detected, which was probably affected by the greenhouse environmental conditions.

Field growth

Survival averaged 94.6% for the farm-field tests at year 5 for trees that were alive at the end of the first growing season in the field. Almost all mortality was caused by white pine blister rust (*Cronartium ribicola* FISCH.). There were no statistically significant differences among provenances in survival rate, suggesting none of these populations are more resistant or susceptible to the disease. The two field tests, however, showed significant differences among provenances in consecutive 5 year height measurements. At year 5, the top 10 provenances averaged 202 cm in height at Turkey Point and 179 cm at Sault Ste. Marie. In contrast, the bottom 10 provenances averaged 151 cm and 134 cm, respectively, or about 25% smaller. The Turkey Point test had larger average annual height increment than the Sault Ste. Marie test because of higher annual mean temperature and longer growing season (*Table 2*). However, provenance variation in height growth was larger at the Sault Ste. Marie test, where variation among provenances accounted for 15% to 22.5% of total phenotypic variance in 5 consecutive years, versus 10.8% to 18.3% at Turkey Point (*Table 3*). These results were partially due to the more uniform environment and higher intensity of trial maintenance, resulting in higher experimental precision of the trial at Sault Ste. Marie. Across two tests, about 70% to 78% of the phenotypic variation resided among trees within provenance.

Similar to greenhouse results, seed weight effects on field height growth were significant during the first 2 years after planting, but were insignificant by the end of the third season. No information on genetic differentiation among populations in terms of cold hardiness was determined from the field tests because winter damage was negligible.

Provenances of eastern white pine exhibited consistent height growth in both environments and time. Variance components attributable to provenance-by-environment interaction accounted for less than 2.5% of the total phenotypic variation for height growth traits for the 5 consecutive years. Estimates of type-B genetic correlation between the two field tests ranged from 0.84 to 0.96 for the 5-year consecutive height measurements. Genetic correlation between greenhouse seedling heights and field tree heights was greater than 0.7. Provenance rankings between the two field trials were also consistent, with Spearman's ranking correlation coefficients ranging from 0.7 to 0.8. Age-age correlation between first year and fifth year field measurements were greater than 0.95 across two tests.

Pattern of genetic variation

Geographic patterns of genetic variation in height growth among populations of eastern white pine were clinal. Except for a few deviations, provenances from warmer areas grew faster than those did from colder areas. Of 18 geographic and climate variables generated from the climate model, 15 to 17 were significantly linearly correlated with the first- to fifth-year height growth measurements.

In the multiple regression analyses with stepwise/r-square option (SAS® 1996), 2 to 4 climatic and geographic variables were able to explain 50%–65% of the fifth-year mean height growth differences among provenances at the field tests. Slightly different sets of prediction variables were, however, selected for other individual years due to strong auto-correlations among geographic and climatic variables (data not shown). These variables were reflective of, in different ways, the temperature and moisture conditions at the provenance's origins. Using principal component analysis (PCA) to summarize the growth differences among populations on traits of the first- to fifth-year height growth at the two field sites, the first principal component (PC1) explained 86.81% and 91.50%, respectively, of the variation at Turkey Point and Sault Ste. Marie. Regression of the first principal component against climate and geographic variables produced even stronger linear relationships (*Table 4*). R^2 values for fitted prediction equations were always higher for the Sault Ste. Marie site than for the Turkey Point site likely due to more controlled conditions as previously discussed.

Among the prediction variables, latitude could account for a large proportion of mean growth differences among provenances because of the strong correlations it has with many other variables. For example, in the reduced models, latitude alone accounted for 36.7% to 63.6% of the variation in fifth-year mean height and 49.9% to 67.7% variation in PC1 among provenances at Turkey Point and Sault Ste. Marie, respectively (*Table 4*). In addition, latitude was the primary variable to be consistently selected in almost all fitted prediction equations. After latitude, aggregated-degree-days (ADD) above a biological base temperature (≥5 °C) in the first 6 weeks of the growing season seemed to be the climate variable that slightly increased the precision of prediction equations. A reduced model using latitude and ADD could considerably simplify the interpretation of revealed pattern of genetic variation while ensuring more than 80% prediction accuracy as compared with the full models (*Table 4*). At Sault Ste. Marie, the average prediction of these two variables on provenance mean height growth at age 5 are represented by the equation:

Table 4. – Competitive models for main environmental factors determining the patterns of genetic variation of eastern white pine in Ontario

Model	R^2	C_p	C.D.[a]	S(δ)[b] %	Dependent Variable[c]	Independent Variable*	Model improvement (%)¶
1	0.508	4.78	0.564	6.57	Ht5_tp	lat, tp, add, mtrp†	3.3
2	0.492	---	0.644	5.97	Ht5_tp	lat, add‡	9.8
3	0.448	---	0.636	6.06	Ht5_tp	lat‡	
4	0.656	2.56	0.409	5.89	Ht5_arb	lat, add†	3.1
5	0.636	---	0.367	6.12	Ht5_arb	lat‡	
6	0.624	5.84	0.657	---	PC1_tp	tp, add, mt, maxt, mtrp†	12.2
7	0.556	---	0.684	---	PC1_tp	lat, add‡	11.2
8	0.499	---	0.677	---	PC1_tp	lat‡	
9	0.717	2.55	0.547	---	PC1_arb	lat, long†	2.4
10	0.700	---	0.544	---	PC1_arb	Lat add‡	3.4
11	0.677	---	0.499	---	PC1_arb	lat‡	

[a] C.D. is the coefficient of determination in model validation and all values are significant at the probability level of $\alpha = 0.0001$; [b]S(δ) is the square-root of regression-mean-square-error expressed as the percentage to the mean population height; [c] PC1 is the first principle component that summaries the first to fifth year field height growth at each location; * Independent variables are: lat --- latitude (°), long --- longitude (°), add --- aggregated-degree-day above 5°C in the first 6 weeks of growing season, mt --- annual mean temperature (°), mint --- annual mean minimum temperature (°), mtrp --- mean temperature range for the growing season (°), and tp---mean temperature in the first 6 weeks of growing season; † Full models selected based on R^2 and Mellows' Cp statistics. ‡ A reduced model; ¶ relative improvement on R^2 by adding an variable.

Table 5. – Effects of provenance origins on 1 to 5 year height growth of eastern white pine in Ontario.

	Reduced model using geographic/climate variables						Effects on growth potential[a]			Population differentiation[b]		
	Intercept	latitude	ADD¶	$R^{2\dagger}$	C.D.*	$s(\bar{\delta})$ (cm)‡	Mean	Latitude (%)	ADD (%)	LSD (cm)	Latitude (degree)	ADD
TP_ht1	65.7883	-1.1815	0.013	0.562	0.595	0.95	14.78	-7.99	0.09	2.16	1.83	166.15
TP_ht2	128.5357	-2.5167	0.0665	0.555	0.686	1.94	30.46	-8.26	0.22	3.68	1.46	55.34
TP_ht3	283.0447	-5.8072	0.1753	0.554	0.634	4.81	60.79	-9.55	0.29	11.13	1.92	63.49
TP_ht4	409.0424	-8.0268	0.2621	0.486	0.633	7.17	107.06	-7.50	0.24	19.80	2.47	75.54
TP_ht5	578.379	-10.5548	0.3133	0.492	0.628	9.71	174.26	-6.06	0.18	31.43	3.00	100.32
Arb_ht1	55.608	-1.00116	0.01298	0.554	0.573	1.40	12.20	-8.21	0.11	2.02	2.02	155.62
Arb_ht2	133.2441	-2.5341	0.03968	0.692	0.549	2.17	26.36	-9.61	0.15	3.45	1.36	86.95
Arb_ht3	275.0077	-5.16	0.07363	0.676	0.550	4.48	55.59	-9.28	0.13	7.21	1.40	97.92
Arb_ht4	415.2627	-7.6728	0.1459	0.661	0.489	7.41	98.20	-7.81	0.15	11.63	1.52	79.71
Arb_ht5	587.7783	-10.2113	0.1632	0.656	0.494	9.47	156.06	-6.54	0.10	17.08	1.67	104.66
PC1#	34.2438	-0.8439	0.0176	0.741	--	--	7.96	-10.60	0.22			

Note: a. percent of height growth change per unit increase of predictor variable; b. Units required on predictor variable to reach the required least square difference(LSD) at the probability level of $\alpha = 0.05$. † regression r-square values are significant at the probability level of $\alpha = 0.0001$; * C. D. is the coefficient of determination in model validation and all values are significant the probability level of $\alpha = 0.0001$; ¶ ADD is the, aggregated-degree-day above 5°C in the first 6 weeks of the growing season; ‡ $s(\bar{\delta})$is the square-root of mean square error prediction (MSEP) in model validation; # PC1 is the first principal component summarizing 10 field height measurements from year 1 to year 5 at 2 sites, accounting for 80% of the total variation.

$$Mean\_height\ (cm) = 587.78 + 0.1632^{*} ADD - 10.211^{*} latidude\ (R^2 = 0.656) \quad (4a)$$

in real scales of climate/geographic variables, or in standardized scales (i.e., mean = 0 and variance = 1.0) of climate/geographic variable as:

$$Mean\_height\ (cm) = 158.14 + 17.4677^{*} ADD - 102.077^{*} latidude\ (R^2 = 0.656) \quad (4b)$$

where, latitude ranges from –2.453 to 2.214 and ADD ranges from –2.812 to 1.672.

Latitude and ADD are not correlated ($r = -0.087$, $p = 0.237$) at these provenance origins with unknown reasons, possibly due to the effects of the Great Lakes on climate. Latitude has larger effect in the models than ADD as indicated by partial regression coefficients. From these equations, it was predicted that at Sault Ste. Marie, a change in provenance location northward by one degree of latitude would cause fifth-year mean height growth (156 cm) to decrease by about 6.5%, and an increase of 10 aggregated-degree-days would increase fifth year height by only 1.0%. An increase of latitude by 2 degrees in seed source location would significantly reduce height growth potential (20.4 cm or 13%) at the probability level of $\alpha = 0.05$ (*Table 5*).

Discussion

Our results indicate that there are considerable growth differences among provenances of eastern white pine in Ontario. Between 11% and 22.5% of phenotypic variation in height growth was attributable to provenance effects in different years and locations. This is less than that reported in range-wise provenance tests in southern Ontario, where 52% of the variation in height and 34% of diameter were attributed to among-provenance variation at plantation age 28 (ABUAKER and ZSUFFA, 1991). Population samples covering the full range of the eastern white pine distribution and the advanced age contributed to increased population differentiation in that study. Results from the current study were, nevertheless, comparable to those from a regional provenance test in Quebec (LI et al., 1997), which reported that 20% of the total variation in the fourth-year height growth was attributable to provenance. Our results suggest that within Ontario there is a considerable genetic variation among populations of eastern white pine, which could be exploited through seed source selection and tree improvement programs.

Our study indicates strong stability of provenance performance at young ages. Although growing conditions between the greenhouse and the 2 field tests were diverse in terms of temperature regimes, moisture conditions, length of growing season, soil types, and fertility, there was little provenance-by-environment interaction detected in measurements of height growth over 5 consecutive years. Provenance rankings were highly consistent among the greenhouse and the 2 field tests and age-age genetic correlation between heights measured in different years were nearly perfect. This suggests that greenhouse selection of white pine provenance would be equivalent to field selections up to 5 year after planting. The high stability of provenance performance in eastern white pine was consistent with results from some range-wide provenance tests. For example, GENYS (1987) found significant correlations among provenance performances at different locations and ages. ABUAKER and ZSUFFA (1991) found that evaluation of eastern white pine provenances for height differences was accurate at 7 to 12 years of age.

This study revealed a strong clinal pattern in variation among populations of eastern white pine in Ontario, which is consistent with a larger geographic variation pattern as revealed in previous range-wide provenance tests (FOWLER and HEIMBURGER, 1969; GARRETT et al., 1973; GENYS, 1987). A prediction equation using a geographic and a climatic variable effectively quantified the effects of provenance location on height growth differences, suggesting that temperature conditions at the provenance's origin might play the most important role in affecting growth potential. Latitude and thermal variables were also found to influence the pattern of geographic genetic variation of jack pine (*Pinus banksiana* LAMB) in Ontario (MATYAS and YEATMAN, 1992). Latitude explained the largest proportion of growth variation among provenances, probably because of its high correlation with many other climate variables, such as the growing season length, annual mean, maximum and minimum temperature (data not shown). In addition, latitude is closely associated with photoperiod to which eastern white pine populations may have adapted with different growth rhythms. At a given latitude, provenances having larger aggregated degree days in the first 6 weeks in the growing season tended to have greater height growth potential. This is consistent with the positive effects of warmer weather conditions on height growth, because for most coniferous species, especially pines, shoot elongation occurs during the first few weeks of the growing season (REHFELDT et al., 1995).

Implications of the results in this study are significant for seed transfer guidelines and tree improvement activities in Ontario. Since there are currently no seeds available from genetically improved seed orchards, provenance selection would be the fastest and most economical approach to increase forest productivity in many regions. Based on the prediction equation developed in this study, the fifth-year height growth could decrease by approximately 6.5% as compared with the mean of all populations for site conditions similar to those in Sault Ste. Marie when seed sources are moved from north to south by one degree of latitude, and moving southward by two degrees of latitude would cause significant loss in height growth potential (*Table 5*). As a tentative rule, it would be wise not to use provenances 1.5 to 2.0 latitude degrees north of the planting sites. The distance that a provenance can be moved northward to increase productivity is, however, the subject of a separate study because frost hardiness could become a major concern as indicated in other boreal species (MATYAS and YEATMAN, 1992). Since there was no observed difference among provenances in cold hardiness in the field tests in this study, no direct information was available on the susceptibility of provenances to severe frost damages. The results from two 28-year-old range-wide white pine provenance tests in southern Ontario, in which provenances from Tennessee and Georgia were included (FOWLER and HEIMBURGER, 1969) may provide some relevant information. There were significant differences in growth among the provenances but no significant differences in cold damage, which may suggest some degree of cold tolerance capacity for the species as a whole. However, due to the short-term nature of our study, caution must be used when interpreting provenance cold hardiness from the results.

Aside from the general growth variation trend, there were provenances from northern Ontario (such as provenance 102 and 103) that performed better than expected. And there were a few provenances in the south (for example a provenance near London) that grew slowly. Several factors could have contributed to these results, including sampling errors, genetic variation between populations within a region, and inbreeding. These results indicate that there are opportunities to find locally superior provenances from northern Ontario to use where frost hardiness is a major concern limiting the use of provenances from the south.

Conclusion

Short-term provenance tests with intensive collection of populations of eastern white pine in Ontario have shown that there is considerable genetic variation in height growth among provenances, which could be exploited in tree improvement programs. Strong genetic correlation between growth traits at different years and the weak genotype-by-provenance interaction suggested high efficiency in provenance selection at early stage. Based on the latitude predominated clinal pattern of geographic variation and the significant reduction of growth potential when seeds are moved from north to south, it is recommended that seed not be transferred more than 1.5 to 2.0° (latitude) south of its origin. Further studies on cold hardiness are required to assess the geographic interval within which seeds can be safely transferred northward before frost damage occurs.

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