Genetic Variation in *Picea glauca* for Growth and Phenological Traits From Provenance Tests in Ontario

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Abstract

Ecologically based management of white spruce (*Picea glauca* [Moench] Voss.) requires an understanding of its patterns of adaptive variation. This understanding will become increasingly important under changing climate conditions. Five common garden tests and a greenhouse trial established in 2002 across Ontario were used to assess levels of genetic variation and relate this variation to local climate. Growth and phenological variables, including height, root collar diameter, survival, timing of spring budflush, and timing of fall budset were measured. Intraclass correlation coefficients were calculated for all traits to determine levels of genetic variation. Simple linear regressions were used to relate these differences to local climate conditions.

After two growing season's levels of between-provenance genetic variation ranged from 0 percent for several of the budflush variables to 22 percent for 2003 survival at the Englehart field trial. Overall, growth variables showed higher levels of between-provenance variation than phenological variables. Variation was predominately explained by longitude, a surrogate for precipitation patterns in Ontario, and temperature variables related to the growing season with r^2 values ranging from 0.03 to 0.55. Generally, patterns of adaptive variation followed a southeast to northwest trend across Ontario. Northern sources flushed earlier and set bud earlier, while southern sources demonstrated superior growth. Results support previous white spruce genecology studies showing superior growth of sources from the Ottawa valley region of Ontario and Quebec.

Key words: Picea glauca, white spruce, genetic variation, adaptive variation, provenance trials, intraclass correlation coefficient, climate.

Introduction

White spruce (*Picea glauca* (Moench) Voss.) is an economically important species with a transcontinental boreal range extending from Newfoundland to the Yukon and Alaska (NIENSTAEDT and ZASADA, 1990). To develop an efficient and constructive tree improvement program for this species it is vital to understand its adaptations to the environment that it will be planted in. As climate change progresses, this knowledge will become increasingly important.

Patterns of variation in white spruce have been found to be generally clinal, following climatic and geographic gradients (NIENSTAEDT and TEICH, 1972; MORGENSTERN and COPIS, 1999). Also, evidence supporting ecotypic variation has also been presented by TEICH and HOLST (1974), although this finding was not supported by a more recent study (LESSER *et al.,* 2004). Significant differences have been found among white spruce provenances in terms of phenology, growth, wood density and other traits (NIENSTAEDT and TEICH, 1972; BEAULIEU and CORRIVEAU, 1985; KHALIL, 1986; BLUM, 1988; CORRIVEAU *et al.,* 1987; LI *et al.,* 1992). Differences between provenances have also been shown in allozyme studies although no geographic trend was evident (FURNIER *et al.,* 1991).

Based on the 194 Series of provenance tests TEICH *et al.* (1975) found that non-local sources often performed better than local sources throughout Ontario. Other studies utilizing the 93 and 194 Series of provenance tests have shown superior growth from southern sources across much of the province (FOCKEN, 1992; BROWN, 2001; SARAZIN, 2001). Within Ontario the 410 Series of range-wide white spruce provenance tests has been the most extensive and useful to date in terms of establishing patterns of variation (MORGENSTERN and COPIS, 1999).

For the present study, a series of tests were planted in 2001 that utilized many of the same seed sources from the 410 Series. The goal of this study was to compare the results from the first two years of these tests to those of older tests in Ontario and to general patterns and levels of adaptive variation that have been found elsewhere for white spruce. A further goal was to relate seedling performance in a series of common garden trials to local climate variation.

Materials and Methods

Test Establishment

A total of 127 white spruce seed sources from across Ontario and western Quebec were obtained from several cooperatives and seeded in Jiffy pot 3065-140's between January and March 2002 in the Lakehead University greenhouse. Seed collections came from wild stands and were comprised of five or more open-pollinated families. The sources used in this analysis and the test site locations are shown in *Figure 1*. Detailed location information for each provenance is shown in *Table 1*.

Five field trials and a Lakehead University greenhouse trial were established in June and July 2002. Each test consisted of three blocks, each with 10 single tree plot repetitions of all 127 provenances. Field trial locations are referred to by the town or general area that they are located in. From west to east these trials are Dryden, Kakabeka, Longlac, Englehart, and Petawawa (*Figure 1)*.

Data Collection

Over the course of two field seasons, 2002 and 2003, growth variables were measured at the field trials and greenhouse trial. Growth variables included height for both years and root collar diameter in 2003. Due to hardening off prior to field planting, height measurements for 2002 were not indicative of site location differences. Hence 2002 height for all trials were treated as a single variable. Survival was also determined for both 2002 and 2003.

Phenological variables were measured in 2003. These variables were determined at the onset of spring growth and onset of fall dormancy. Field trial scores were based on the number of days from January 1, 2003. Beginning in early May seedlings were scored for phase of bud flush based on a six stage system described by POLLARD and YING (1979). Field trial and green-

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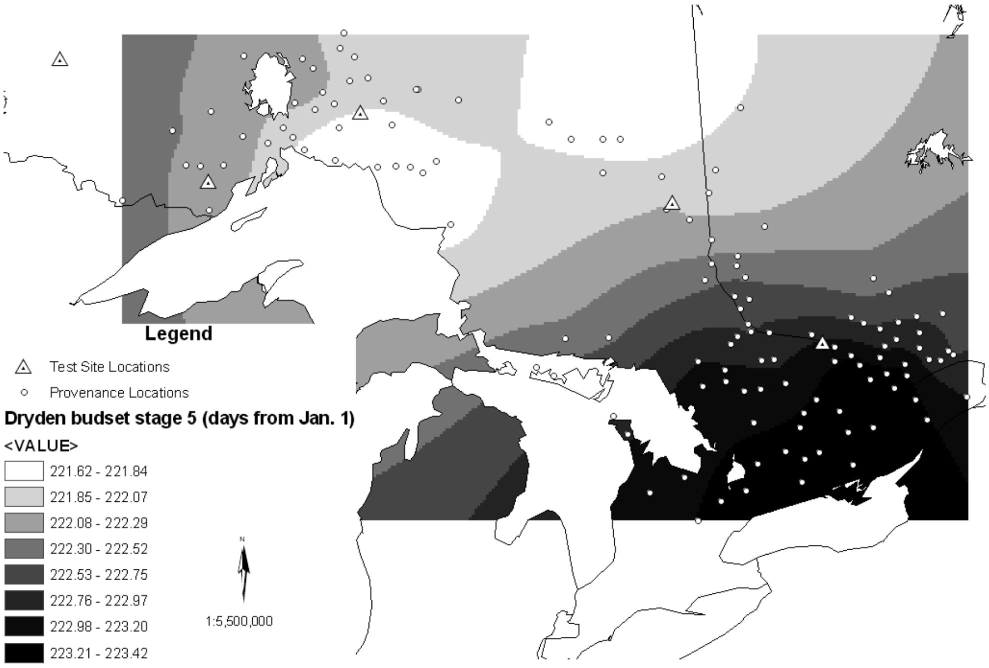

Figure 1. – Contour map of days from January 1, 2003 to reach budset stage 5 at the Dryden field trial.

house seedlings were individually scored every 3 days until elongation began to occur.

Greenhouse scoring was based on days after removal from cold storage, which was April 16, 2003. Shoot elongation increment was measured for the greenhouse trial five times. The first four elongation measurements were made on a four day interval beginning May 3, 2003 (day 18). The final measurement took place on June 24, 2003 (day 70) directly before hardening off was initiated.

Beginning in early August every seedling in each of the five field trials was individually scored for onset of dormancy (budset). The scoring system was based on changes observed in the terminal bud of the seedling. A five stage scoring system was developed: (*i*) no visible terminal bud, (*ii*) terminal bud visible and white, (*iii*) terminal bud fully swollen, (*iv*) terminal bud turning brown in colour, and (*v*) terminal bud brown, bud scales visible (bud in winter condition). Seedlings were scored every three days until the final stage of dormancy was reached.

Climate Data

Climatic data for the period 1961 to 1990 were obtained from Dr. DAN MCKENNEY, Canadian Forest Service, Landscape Analysis and Application Section, Great Lakes Forestry Centre (2004). Canada-wide grids along with point data for the 127 provenance locations were provided for sixty- seven climate variables. Maximum monthly temperature, minimum monthly temperature, and monthly precipitation constituted 36 of these variables. The remaining 34 variables were derived using the BIOCLIM/ANUCLIM and SEEDGROW prediction systems (MCKENNEY, 2004). These variables consisted of growing degree days, temperature and precipitation amounts by quarter and growing period along with growing season length, start time and end time. Variables that were retained by regressions of measured variables against climatic variables are listed in *Table 2*, along with the range for the 127 source points, the units of measure, and the code used in subsequent analysis. Variables pertaining to quarter represent the three month block, starting at January 1, which fits that particular criterion, whether wettest, driest, warmest, or coldest. Variables designated by period are associated with the growing season, with period 3 corresponding to the entire growing season. The growing season is defined as starting at the point that, following March 1, there were 5 consecutive days where the mean daily temperature was greater than or equal to 5 degrees Celsius. The growing season is considered ended when the minimum temperature falls below -2 degrees Celsius following August 1 (MACKEY *et al.,* 1996).

Data Analysis

All 76 growth and phenological variables were tested by analysis of variance (ANOVA) for significant differences between provenances. All dependent variables were treated as random and the analysis was run using the GLM procedure in SAS (SAS INSTITUTE, 2000). Components of variance were calculated using the restricted maximum likelihood method (REML) within the Varcomp procedure in SAS (SAS INSTITUTE, 2000). Based on the components of variance, the intraclass correlation coefficient (ICC) was calculated for each variable. The ICC was calculated as the variation expressed between provenances divided by the total variation expressed for that trait. Total variation is calculated as the additive variation from the between block variation, the between provenance variation, the provenance-block interaction variation, and the error, or within provenance, variation.

Provenance mean values were calculated for each variable that showed significant differences, and simple linear regressions were run on these means against the 67 climatic and 3 geographic variables (longitude, latitude, and elevation). The purpose in calculating these regression models was to determine to what extent the variation being expressed between provenances could be attributed to climatic effects. Longitude, latitude, and elevation were entered into the predictor variable set as surrogates for climatic influences not captured by the actual climate data.

Mapped patterns of growth and climatic variables are useful for comparison purposes to evaluate the utility of the models. To graphically show the observed patterns of variation, grids were produced using GIS tools. The Kriging raster interpola-

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tion method was used to create a sample grid for a budset variable based on the 127 source points using ArcMap 8.3 (ESRI 2002). This grid was compared to a digital climate model for growing degree days (MCKENNEY, 2004).

Results

Significant levels of between provenance differentiation were clearly shown for the majority of the 76 variables tested by ANOVA. Variables and associated levels of significance are

Table 1. – Source, location, and geographic coordinates for 127 white spruce provenances.

No.	410 no.	Location	Lat	Long	Elev	No.	410 no.	Location	Lat	Long	Elev
1	\	Cornwall	45.07	74.83	80	65	8167	Armour Tp	45.62	79.42	300
2	\	St-Andre Avellin	45.67	74.97	155	66	\	Lac Labyrinthe	48.22	79.48	289
3	\	St-Andre Avellin	45.73	75.05	152	67	\	N.Dame des Quinze	47.58	79.50	213
4	\	Camp 27	46.25	75.08	259	68	8163	Lorrain Tp	47.25	79.52	240
5	\	Thurso	45.62	75.23	100	69	8165	Peck Tp	45.48	78.75	460
6	\	Poupee	45.65	75.45	15	70	8036	Cobalt	47.03	79.68	306
7	\	Lac Iroquois	46.03	75.57	213	71	8152	McKellar	45.58	79.87	275
8	\	Ruisseau Murphy	46.25	75.58	304	72	8038	Englehart	47.87	79.92	215
9	\	Val-Des-Bois	45.82	75.60	168	73	8189	East Mills	45.92	79.93	245
10	\	Augusta	44.83	75.63	100	74	\	Erin	43.75	80.12	427
11	8209	Marlborough Tp	45.12	75.80	90	75	\	Osprey	44.35	80.33	503
12	\	Breckenridge	45.47	75.92	107	76	8044	Kirkland Lk	48.03	80.37	304
13	\	Wakefield	45.62	75.93	244	77	8187	Bowman Tp	48.48	80.42	290
14	\	Bouchette	46.20	75.95	183	78	\	Bentinck	44.17	81.00	305
15	\	Aylwin	45.97	76.03	152	79	8049	Clute 2	49.02	81.23	289
16	\	Grand-Remous	46.63	76.07	244	80	8043	Pagwa	49.77	85.42	245
17	8032	Antrim	45.32	76.18	121	81	8053	Fraserdale	49.03	81.58	215
18	\	Wyman	45.52	76.30	91	82	8188	Robb Tp	48.58	81.62	290
19	\	Lac Cayamant	46.15	76.33	274	83	\	St. Edmunds	45.25	81.63	206
20	\	Lac Du Faucard	46.85	76.35	305	84	8021	Nairn Tp	46.32	81.65	243
21	\	Ladysmith	45.75	76.40	213	85	8046	Gurney Tp	49.05	82.25	215
22	\	Lac Usborne	46.25	76.63	274	86	\	Proctor	46.33	82.50	249
23	8028	Renfrew	45.47	76.63	121	87	8236	Cargill	49.30	82.70	289
24	8210	Silver Lk	44.82	76.68	180	88	\	Elizabeth Bay	45.83	82.75	191
25	8026	Beachburg	45.68	76.80	137	89	\	Meldrum Bay	45.95	83.08	183
26	\	Grove Creek	45.90	76.27	244	90	8047	Arnott Tp	49.62	84.58	275
27	\	Riviere-Coulonge	46.35	76.87	274	91	8039	Wawa	47.92	84.75	306
28	\	Lac Cranson	45.83	76.95	122	92	8045	Bouchard	48.78	85.05	457
29	\	Tyendinaga	44.33	77.13	107	93	8052	White R	48.62	85.32	305
30	\	Barrie	44.78	77.15	274	94	\	Highway 11	49.77	85.47	236
31	\	Sheenboro	45.97	77.25	152	95	8051	Mobert Tp	48.70	85.58	305
32	\	Denbigh	45.08	77.28	305	96	8067	Strathearn	48.72	85.87	335
33	8161	Alice	45.77	77.28	150	97	8066	Manitouwadge	49.28	85.97	305
34	8024	PNFI	45.98	77.45	160	98	8061	Caramat	49.60	86.15	305
35	\	Rolphton	46.17	77.67	183	99	8063	Pic R	48.70	86.25	240
36	\	Carlow	45.27	77.70	366	100	8083	Kenogami	49.92	86.48	305
37	\	Marmora	44.55	77.75	229	101	8075	Nakina	50.20	86.78	335
38	8025	Bancroft	45.10	77.97	396	102	8081	False Crk	49.87	86.87	365
39	\	Dummer	44.48	78.02	236	103	8065	O'Sullivan	50.53	87.02	335
40	8211	Anstruther Tp	44.92	78.07	365	104	8076	Long Lake	49.22	87.07	335
41	\	Haldimand	44.17	78.12	274	105	\	Maun/Anaconda Rd	50.32	87.09	328
42	8015	Whitney	45.53	78.27	396	106	\	Eastnor	44.98	81.37	191
43	\	Harvey	44.60	78.38	300	107	8064	Terrace B	48.78	87.12	200
44	\	Canton Sebille	47.70	78.40	305	108	\	Grandpa Rd	49.55	87.18	404
45	\	Lister	45.87	78.45	442	109	8079	Jellicoe	49.70	87.42	365
46	\	Canton Cameron	46.25	78.50	183	110	8240	Parks Lk	49.47	87.57	460
47	\	Osler	45.87	78.70	442	111	8077	S Onaman R	50.03	87.65	305
48	\	Lac Wawagosis	49.35	78.70	289	112	\	Mountain Bay	48.91	87.77	195
49	\	Lac Smith	46.72	78.83	335	113	8078	Auden	50.15	87.88	335
50	8019	Rutherglen	46.28	78.85	229	114	8082	Beardmore	49.55	88.00	365
51	\	Baie Kelly	47.03	78.87	335	115	8074	Limestone	49.07	88.02	245
52	8157	Mattawan Tp	46.38	78.90	305	116	8056	Nipigon	49.20	88.22	229
53	\	Eldon	44.47	78.92	280	117	\	Stewart Lake	48.98	88.54	267
54	8164	Hindon Tp	45.03	78.93	335	118	8057	Chief Bay	49.05	89.05	275
55	\	Canton Gaboury	47.33	79.00	305	119	8060	Waweig L	50.15	89.12	305
56	8153	Jocko Tp	46.60	79.02	306	120	\	Lakehead U. Woodlot	48.65	89.41	457
57	\	Lac Guay	47.20	79.03	305	121	8087	Pigeon R	48.02	89.65	306
58	8166	Sinclair Tp	45.47	79.08	370	122	8069	Twist L	49.37	89.75	425
59	\	Canton Mercier	46.78	79.12	305	123	8084	Shabaqua	48.62	89.90	410
60	8186	Bonfield Tp	46.23	79.13	245	124	8088	Shebandowan	48.62	90.18	459
61	\	Scott	44.12	79.18	290	125	8068	Upsala	49.07	90.52	489
62	8168	Chisholm	46.13	79.27	275	126	8089	Eva L	48.07	91.42	428
63	\	Lac Hebecourt	48.53	79.30	224	130	\	King	44.00	79.67	240
64	\	Strong	45.78	79.42	381						

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Table 2. – Geographic and climatic variables with study area ranges and measured units[a].

Definition	Range Min	Range Max	Units	Code
longitude	-101	-74	decimal degrees	long
mean temperature wettest quarter	-6	19	C°	mtempwetq
mean temperature warmest quarter	13	19	C°	mtempwarmq
Julian day number of start of growing season	105	135	julian day	daystart
Julian day number of end of growing season	285	325	julian day	dayend
number of day in growing season	157	217	days	daygrow
gdd above base temp for period 3	946	1895	degree days	gddp3
Temperature range for period 3	21	28	C°	tempranp3
February mean monthly minimum temperature	-26	-11	C°	febmintemp
June mean monthly minimum temperature	5	11	C°	junmintemp
May mean monthly maximum temperature	13	19	C°	maymaxtemp
August mean monthly maximum temperature	19	25	C°	augmaxtemp
September mean maximum temperature	13	20	C°	sepmaxtemp
November mean monthly maximum temperature	-4	6	C°	novmaxtemp
June mean monthly precipitation	64	107	mm.	junprecip
August mean monthly precipitation	68	105	mm.	augprecip

[a] All values supplied by Dr. D. McKenney (2004)

shown in *Table 3*. Of the 76 variables, 41 showed significant differences at the $p < 0.05$ level. The variables that did not show significant differences were all phenological stage and survival variables. All growth variables (height, root collar diameter, and greenhouse elongation) at all tests showed significant differences at the $p < 0.05$ level.

Trial means, standard deviations and least significant differences are presented in *Table 3*. Mean heights in 2003 were similar at Dryden, Petawawa and Englehart, ranging from 156.75 to 152.66 mm. The Longlac trial had a mean height of 146.14 mm, and Kakabeka had the lowest mean height at 137.82 mm. This last value is most probably a result of very low snowfall amounts in the Thunder Bay area during the 2002–2003 winter resulting in severe tip burning at the Kakabeka trial. The 2003 diameter means ranged from 4.01 mm at Englehart down to 3.51 at Kakabeka.

Budflush values were consistently later at the Longlac, Englehart, and Petawawa trials through the beginning stages; however, for stage 6, Longlac (142 days) was similar to the other two northwest trials, Dryden and Kakabeka, ranging from 140 days in Dryden to 143 in Kakabeka. Englehart and Petawawa remained later at 145 and 147 days respectively. Early budset stages occurred at all trials within a four day period; however, most of these differences were not significant. This result was partly due to the fact that many of the seedlings had already passed the initial stages of budset when scoring commenced. Later stages of budset, which showed high levels of significant differences, indicated that the Dryden trial reached winter bud condition the earliest (223 days) and that budset came later to the east and south with the mean budset stage six value at Petawawa being 229 days.

ICC values are also shown in *Table 3*. Values ranged from zero percent for Kakabeka budflush stage 2 and 5, Longlac budset stage 2, Petawawa budset stage 2, and Dryden 2003 survival up to 21.64 percent for Englehart 2003 survival. Generally, ICC values were higher for growth variables compared to phenological variables. Greenhouse budflush values, ranging from 0.99 to 8.73 percent, were considerably higher than field trial budflush results which range from 0 to 3.21 percent. Overall, budflush ICCs were generally higher for the middle stages than beginning or end stages.

Budset ICC results ranged from 0 percent for Longlac stage 2 and Petawawa stage 2 to 10.41 percent for Kakabeka stage 4. Budset results showed higher ICC values in later stages, with stages 4 or 5 showing the highest values at every trial except Englehart where stage 3 showed the highest value (5.64%). ICC values for height ranged from 6.2 percent in Dryden for 2003 to 16.68 percent in Englehart for 2003. The 2002 height variable which reflects greenhouse growth showed a similarly high ICC (16.51%). Root collar diameter ICC values showed a

Table 3. – Mean, standard deviation, least significant difference and Intraclass Correlation Coefficiant for 19 measured variables across 6 white spruce provenance trials.

Measured Variable[a]	Greenhouse				Test: Dryden				Kakabeka				Longlac				Englehart				Petawawa			
	Mean	Std. Dev.	L.S.D.	I.C.C.(%)	Mean	Std. Dev.	L.S.D.	I.C.C.(%)	Mean	Std. Dev.	L.S.D.	I.C.C.(%)	Mean	Std. Dev.	L.S.D.	I.C.C.(%)	Mean	Std. Dev.	L.S.D.	I.C.C.(%)	Mean	Std. Dev.	LS.D.	I.C.C.(%)
Ht02	110.97	34.12	6.25	16.51**	\	\		\	\	\		\	\	\	\	\	\	\	\	\	\	\	\	\
Ht03	\	\	\	\	156.75	55.45	48.59	6.20**	137.82	52.86	25.77	8.07**	146.14	44.30	26.51	14.17**	152.66	48.12	45.76	16.68**	156.28	58.64	33.70	8.65**
Dia03	\	\	\	\	3.69	1.12	0.98	7.35**	3.51	1.36	0.67	5.90**	3.87	1.28	0.79	7.40**	4.01	1.26	0.73	11.36**	3.88	1.37	0.78	7.56**
Surv02	\	\	\	\	87.64	6.35	10.10	2.12	86.52	7.58	11.96	1.97	88.75	4.76	7.24	9.26**	76.26	12.60	17.43	18.14**	54.21	20.42	16.78	3.57**
Surv03	\	\	\	\	83.35	9.62	15.68	0.00	84.52	9.33	14.72	3.77	67.69	12.29	19.26	4.82	57.89	12.34	17.18	21.64**	59.41	16.68	18.14	0.73
Budflush																								
stage 2	7.68	1.37	0.74	4.30**	122.68	7.53	3.89	1.49**	123.88	4.88	2.51	0.00	129.14	3.99	2.08	1.31**	129.81	9.36	5.85	0.38	130.02	11.94	7.04	1.64*
stage 3	10.1	1.75	0.85	8.79**	127.10	8.91	4.70	0.77**	126.99	5.32	2.84	0.20	132.31	3.95	2.06	3.11**	133.27	7.91	5.13	0.79	133.68	12.35	7.56	0.92
stage 4	12.34	1.72	0.84	8.73**	129.68	7.27	4.05	1.33**	129.32	4.86	2.63	0.49	134.70	3.60	1.93	3.21**	135.66	6.91	4.55	0.19	135.63	11.46	7.17	0.92
stage 5	14.86	1.52	0.77	1.46**	133.59	5.81	3.31	2.42**	133.59	4.35	2.40	0.00	138.31	2.89	1.71	2.41**	139.37	5.64	3.78	0.68	139.54	9.45	6.15	0.59
stage 6	17.57	2.54	1.28	0.99**	140.02	4.91	2.91	3.05**	143.10	4.80	2.75	1.01*	141.98	2.83	1.76	1.29**	147.09	4.68	3.34	1.47	145.26	6.85	5.15	0.38
Budset																								
stage 2	\	\	\	\	221.51	1.49	3.23	3.43	219.12	0.65	0.62	0.11	222.38	2.34	1.78	0.00	220.24	1.36	2.66	1.19	222.37	1.52	2.89	0.00
stage 3	\	\	\	\	222.22	2.01	3.66	1.11	220.38	1.79	1.04	3.50**	224.56	3.00	1.95	0.66	221.91	3.01	2.61	5.64**	223.29	2.42	1.99	2.64**
stage 4	\	\	\	\	222.63	2.39	2.60	1.67	223.03	3.02	1.47	10.41**	226.51	3.64	2.22	2.58**	224.19	4.99	3.10	4.66**	225.91	3.95	2.38	6.54**
stage 5	\	\	\	\	222.54	2.58	1.31	5.02**	227.42	3.55	1.84	6.65**	227.92	4.05	2.65	2.94**	228.60	4.07	3.22	2.27**	229.36	3.17	3.86	1.25
Greenhouse Elong.																								
Day 18	20.28	5.9	3.03	5.80**	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\
Day 22	38.31	11.06	5.47	4.98**	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\
Day 26	54.76	13.94	6.96	3.75**	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\
Day 30	72.73	17.51	8.66	2.43**	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\
Day 70	269.1	61.8	28.67	13.61**	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\

** – statistically significant at 0.05 level.

* – statistically significant at 0.1 level.

[a] Ht02 (height 2002), Ht03 (height 2003), and Dia03 (diameter 2003) measured in millimetres; Surv02 (survival 2002) and Surv03 (survival 2003) measured as percentage of surviving trees; field trial budflush and budset measured as number of days from Jan.1, 2003; Greenhouse budflush and elongation (in mm.) measured as number of days from cold storage thawing.

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similar pattern with Englehart having the highest value (11.36%). Kakabeka showed the smallest amount of explained variation for the root collar diameter variables with 5.9 percent. ICC values for survival ranged from 0 percent for Dryden 2003 up to 21.64 for Englehart 2003. Similarly, Englehart 2002 survival variable also showed a high amount of genetic variation at 18.14 percent.

Greenhouse elongation ICC values ranged from 2.43 percent for shoot length on day 30 up to 13.61 for shoot length on day 70. Values dropped off from beginning dates and then increased dramatically between the last two dates.

Simple regression results of the 42 variables that showed significant regressions ($p < 0.05$) against geographic and climatic predictor variables are shown in *Table 4*. Coefficients of determination (r^2) values for significant regressions ranged from 0.55 for Kakabeka budset stage 4 down to 0.03 for Dryden and Kakabeka 2003 height.

Height, root collar diameter and survival variables were explained by longitude, which strongly influences precipitation patterns in Ontario, and a mixture of temperature related variables (*Table 4*). Growth and survival variables gave relatively lower r^2 values compared to phenological traits, with the highest being 0.17 for the Longlac 2003 root collar diameter variable.

Table 4. – Simple regression results of 42 measured variables against geographic and climatic predictor variables.

Measured Variable	R^2	Sig.	Retained Independent Variables[a]
Budflush			
Dryden stage2	0.06	0.0044	junmintemp
Dryden stage3	0.12	<0.0001	junmintemp
Dryden stage4	0.15	<0.0001	long
Dryden stage5	0.12	<0.0001	long
Dryden stage6	0.15	<0.0001	daygrow
Longlac stage2	0.14	<0.0001	long
Longlac stage3	0.18	<0.0001	long
Longlac stage4	0.17	<0.0001	long
Longlac stage5	0.13	<0.0001	long
Longlac stage6	0.05	0.0102	long
greenhouse stage2	0.10	0.0003	long
greenhouse stage3	0.14	<0.0001	long
greenhouse stage4	0.11	0.0002	long
greenhouse stage5	0.08	0.0011	junprecip
greenhouse stage6	0.06	0.0058	augprecip
Budset			
Dryden stage5	0.50	<0.0001	gddp3
Kakabeka stage3	0.45	<0.0001	gddp3
Kakabeka stage4	0.55	<0.0001	mtempwarmq
Kakabeka stage5	0.51	<0.0001	augmaxtemp
Longlac stage4	0.22	<0.0001	daygrow
Longlac stage5	0.29	<0.0001	tempranp3
Englehart stage3	0.33	<0.0001	novmaxtemp
Englehart stage4	0.44	<0.0001	gddp3
Englehart stage5	0.17	<0.0001	junmintemp
Petawawa stage3	0.18	<0.0001	dayend
Petawawa stage4	0.40	<0.0001	daystart
Height			
ht2002	0.05	0.0159	mtempwetq
Dryden ht2003	0.03	0.0356	mtempwetq
Kakabeka ht2003	0.03	0.0389	tempranp3
Longlac ht2003	0.08	0.0010	long
Englehart ht2003	0.05	0.0127	mtempwetq
Petawawa ht2003	0.09	0.0007	maymaxtemp
Diameter			
Dryden dia2003	0.07	0.0038	long
Longlac dia2003	0.17	<0.0001	long
Englehart dia2003	0.11	0.0002	long
Petawawa dia2003	0.07	0.0027	sepmaxtemp
Survival			
Englehart surv2003	0.08	0.0013	febmintemp
Greenhouse Elongation			
greenhouse elong.1	0.24	<0.0001	long
greenhouse elong.2	0.28	<0.0001	long
greenhouse elong.3	0.32	<0.0001	long
greenhouse elong.4	0.27	<0.0001	long
greenhouse elong.5	0.04	0.0351	tempran3

Table 5. – Top 5 performing provenances at each field trial based on 2003 height measurements.

Trial	Prov. No.	Mean ht. (mm)	Trial	Prov. No.	Mean ht. (mm)
Dryden	18	213.90	Englehart	55	225.00
	117	210.40		49	217.75
	12	204.20		7	209.00
	21	202.60		66	202.43
	66	202.00		86	199.78
Kakabeka	101	180.59	Petawawa	74	219.48
	117	179.87		1	205.74
	53	175.03		53	202.86
	115	173.72		49	197.25
	55	170.73		55	194.43
Longlac	55	189.95			
	63	188.18			
	7	182.41			
	32	179.59			
	115	178.76			

Budflush r^2 values ranged from 0.05 for Longlac stage 6 up to 0.18 for Longlac stage 3. Generally, middle budflush stages showed the highest values within each trial location. Budflush variables were explained predominately by longitude. Budset variables were explained predominately by variables associated with the growing season. Late stage budset variables, which were best predicted by climate (r^2 of 0.55 for Kakabeka stage 4 to 0.29 for Longlac stage 5), all were related to growing season and summer month variables. These variables included growing degree days in period three (entire growing season), starting and ending date of the growing season, the number of days in the growing season, the temperature range during the growing season, and mean temperature in the wettest quarter (July, August, and September). August maximum temperature and June minimum temperature were also indicated.

Greenhouse elongation regressions had relatively high r^2 values for the first four measurements (0.24–0.32). Longitude was selected for all four of these variables. Temperature range during the growing season was indicated for the fifth measurement time, but with a much lower r^2 value (0.04).

Two contour maps are shown here for demonstration purposes (*Figures 1* and *2*). The contour map of the Dryden budset stage 5 variable (*Figure 1*) shows a strong north-south trend through western Quebec and adjacent Ontario. Moving westward the trend shifts to east-west around Lake Nipigon. Earliest budset in Dryden occurred for sources from the far northeast and off the eastern shore of Lake Superior. Budset occurred latest as one moves into southern Ontario and the Ottawa valley. The western extent of the study area, moving west of Lake Nipigon, shows similar budset timing as south-central Ontario. Figure 2, which shows number of growing degree days in period three bears a strong resemblance to *Figure 1*. The same north-south trend through the eastern portion of the study area is evident as is the east-west trend west of Lake Nipigon.

Table 5 lists the top 5 performing provenances at each of the field trials based on 2003 height measurements. Provenance 55, from Canton Gaboury, Quebec, is the best performing provenance at both the Longlac and Englehart trials, and is in the top 5 at the Kakabeka and Petawawa trials. Three of the 5 best performing provenances at the Dryden test site occur on the Quebec side of the Ottawa valley (12, 18, and 21). The second tallest provenance (117) is from the northwest part of the

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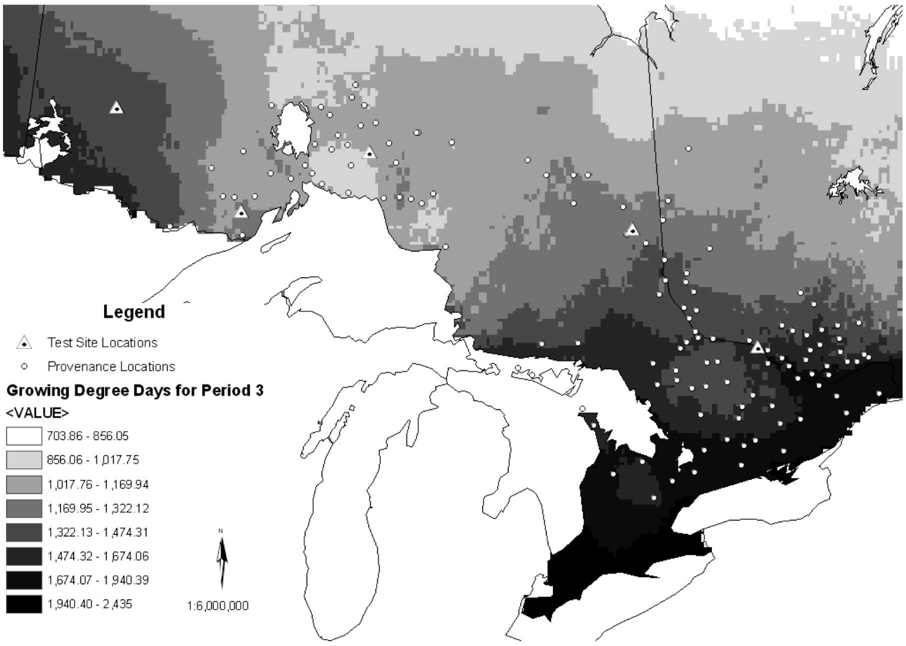

Figure 2. – Contour map of growing degree days above base temperature (5 °C) in period 3, the entire growing season.

study area, and is also in the top five at the Kakabeka trial. Along with provenance 117, provenances 115 and 101 are also from the northwest region and performed in the top five at Kakabeka. Provenance 115 is the only northwestern source in the top five at the Longlac trial. The other 4 top sources are from western Quebec and south eastern Ontario. The Englehart and Petawawa trials both show the same trend with best performing sources extending across western Quebec and through eastern and southern Ontario. No sources from the northwestern region of the study area are in the top five at either of these trial locations.

Discussion

Significant differences were found for most of the growth and phenological variables at each of the trial locations. Overall growth variables showed the highest levels of among provenance variation, with phenological traits generally lower. On average the amount of variation attributable to provenances was 4.25% of the total variation. The remaining variation could be attributed to block effects, environmental effects, and within-provenance differences which may reflect among-family variation. Although each provenance was made up of, on average, 4 to 5 wind-pollinated families, these were not tracked and therefore the actual amount of family variation could not be calculated. However, large family differences have been reported for many traits from multiple studies (Li *et al.,* 1993), and are therefore a probable source of experimental error variation in this study as well.

A study utilizing 57 provenances of white spruce from Quebec and Ontario showed similar levels to ours for among provenance variation (average 3.1%) for growth and phenological traits (Li *et al.,* 1993). The same study showed no significant differentiation among provenances for budburst at year 3. Our results differed somewhat with more than half of the measured budflush variables being significant.

Another study on budflush timing of white spruce in Ontario showed no significant variation amongst provenances (Pollard and Ying, 1979). That study dealt with a far more localized area than ours, dealing with only the south-eastern portion of Ontario. Our study's results taken for the same geographic area showed that 6 of the 15 significant budflush variables were still significant within that area (results not shown), suggesting that fairly localized differentiation does occur for white spruce. In a study conducted in Maine, it was found that significant differences did occur amongst provenances in number of days until bud flush (Blum, 1987) Results from that study showed a slight geographic trend with sources from higher latitudes flushing earliest. Similar geographic trends in budflush timing were expressed in our data, with northern sources generally flushing earlier than southern sources.

In another study conducted on white spruce provenance tests in Newfoundland, Khalil (1986) found significant differences amongst provenances for seed weight, germinative capacity, hypocotyl length, and 4-month seedling height. Regression analysis results showed both northsouth and east-west trends were evident in the majority of these traits.

Regressions mainly showed correlations to longitude, a surrogate for precipitation patterns in Ontario, and temperature variables related to the growing season. Nienstaedt and Teich (1971) reported similar findings, stating that precipitation, temperature regime and photoperiod have all acted as important selective pressures on white spruce. Overall, regressions point to clear geographic trends for patterns of adaptation within the study area. Height and diameter growth are greatest from south eastern areas and decrease with movement north and west. In terms of phenological variables, sources from more northern locations flushed and set buds earliest, while southern sources flushed later and set bud later in the fall (*Figure 1*).

Top performing provenances in terms of 2003 height growth were generally from the southeast region of the study area. Only two of the top performing provenances in our study are 410 Series sources (101 and 115), neither of which were in the top performing provenances reported by Morgenstern and Copis (1999). However, many are in close proximity, and general trends are in keeping with previous studies where it was found that Ottawa River Valley sources showed superior growth at many trial locations (Morgenstern and Copis, 1999).

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MORGENSTERN and COPIS (1999) looked at 410 Series provenance performance at test locations by HILLS' site regions (HILLS, 1961). Although our test locations are not identical, with the exception of Chalk River/Petawawa, we do have tests in 4 of the same site regions as 410 series tests, and comparisons can be made. Tree ages at the 410 series tests, at the time of measurement ranged between 10 at Chalk River, to 18 at Kenora. Comparisons show that results are similar in all four of the site regions. For site region 5E, located in the south-east area of Ontario local provenances performed best. For site regions 3E (north-eastern Ontario) and 4S (north-western Ontario) a combination of local provenances and more southern provenances were in the top five in both studies. Site region 3W, in the north-central region of Ontario does show differences between our study and the 410 Series results. Three of the five top provenances at our Longlac test were from more southern origins, compared to the 410 results which showed all top provenances as boreal origin, coming from a fairly narrow latitudinal band (MORGENSTERN and COPIS, 1999).

While not as useful as the 410 Series in terms of statistical reliability coupled with less than optimal site maintenance (MORGENSTERN and COPIS, 1999), results from the 194 and 93 series of white spruce provenance tests also show the same trend as the 410 Series and our results. FOCKEN (1992) reports that provenances from the Beachburg area of the Ottawa Valley in the 410, 194 and 93 Series of provenances tests all showed consistently superior height growth throughout the central region of Ontario. A 2001 study of the 194 Series test in Pearson Township, 50 km. southwest of Thunder Bay, found that southern sources on average outperformed local sources (BROWN, 2001). This result is further supported by a second 2001 study of the two 194 Series tests located at the Petawawa Research Forest (SARAZIN, 2001). Overall, our results strengthen the conclusion that southern sources are outgrowing local sources in many cases suggesting the possibility of northward shifts to increase growth potential.

Maternal effects, most notably seed weight, can have a significant impact on seedling performance at early ages (PERRY, 1976); however, the high degree of similarity between our results and those from older previous studies suggests that maternal effects are having a minimal influence on our results. Furthermore, these similarities indicate that despite the early age of the seedlings, our results are demonstrating true patterns of adaptive variation.

Later flushing in white spruce can be a useful strategy in avoiding spruce budworm (*Choristoneura fumiferana* Clemens) predation (POLLARD and YING, 1979; BLUM, 1987). Early flushing in white spruce can be a source of spring frost damage, with later flushing being used as a strategy to avoid this (BLUM, 1987). Coupled with greater growth performance and later budset timing in the fall giving a longer growing season, sources from south-eastern Ontario and western Quebec should yield greater productivity when planted throughout the study area. Although this strategy may be advisable in order to optimize fibre production it goes against the philosophy that local sources are better adapted to their environment. Planting of non-local sources may result in maladaptation, but resulting losses have not been demonstrated in numerous provenance trials. Also anticipated temperature increases resulting from climate change may lower the risks of northward transfers.

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Genetic Variability and Early Growth Performance of *Eucalyptus tereticornis* Sm. in Provenance cum Progeny Trials in India

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Abstract

Results of provenance cum progeny trials of *Eucalyptus tereticornis* Sm. laid out in 2002 at three sites viz. FRI Campus (Uttaranchal), Chiryanpur (Uttaranchal) and Midnapore (West Bengal) located in tropical region of India are reported and discussed. Thirteen provenances representing 91 families from Australia and Papua New Guinea (PNG) viz. Oro bay to Emo, PNG; Sirinumu Sogeri Plat, PNG; Warwick, QLD; Yurammie, SF, NSW; Buckenbowra SF, NSW; Selection flat SF559, NSW; Credition SF, QLD; Cardwell, QLD; Mitchell River MT Molloy, QLD; Mill stream archer creek, QLD; Helenvale, QLD; Walsh River, QLD; Burdekin River, QLD were evaluated from nursery stage to field performance (age 21months). As a local seed source open-pollinated seeds collected from selected interspecific Eucalyptus F1 hybrid trees of FRI-4, FRI-5 and Mysore gum (*Eucalyptus teretirornis*) were used to serve as check material (control). Significant differences between the provenances and families at age 21 months were observed for height, clean stem length, collar diameter and field survival. Significant provenance x site interaction was observed for height. In general the north Queensland provenances performed better and in particular two provenances viz. Walsh River, QLD and Burdekin River, QLD ranked the best in comparison to others at this age. Results indicate that significant genetic differences exist between the families and provenances of *E. tereticornis*. The growth traits were inter-correlated with each other. Geographic clinal variation pattern was observed in some of the growth traits viz. height, clean stem height and collar diameter. There were fair differences between phenotypic and genotypic coefficient of variability. Heritability (narrow sense) values were fairly good for height and clear stem length in comparison to collar diameter. The relative performance of the provenances was fairly consistent throughout test sites.

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Key words: Eucalyptus tereticornis, variation, provenance, genetic improvement, productivity, heritability, progeny, provenance x site interaction.

Introduction

Eucalyptus tereticornis Sm. commonly known as forest red gum is native to Papua New Guinea and Victoria, New South Wales and Queensland of Australia. It has a very extensive natural distribution in a long narrow strip from southern Papua New Guinea to Victoria, Australia (ELDRIDGE *et al.,* 1994), thus facing wide climatic variation of dry summer and winter seasons. The altitudinal range of its occurrence varies from sea level to about 1000 m with remarkable variation in annual rainfall from 500–1500 mm (ELDRIDGE *et al.,* 1994). Hence populations of eucalyptus both natural and planted contain considerable amount of genetic variation. This species has been introduced for production of wood for fuel, poles, construction and pulp in many parts of the world and ranks among the most extensively planted Eucalyptus in the tropics and subtropics (ZOBEL *et al.,* 1987; EVANS, 1992). It's popularity, as that of other widely planted eucalypts is attributed to its rapid growth and production of desirable wood when grown in a wide range of environmental and soil conditions (ZOBEL *et al.,* 1987; LAMPRECHT, 1989).

Populations of Eucalyptus in India are highly inbred and the existing variability of Eucalyptus has been over exploited through intensive selection of promising trees and their multiplication for commercial plantation. The Eucalyptus hybrid also known as "Mysore gum" represents about half of the eucalypts planted in many parts of India (JACOBS, 1981), which is believed to be derived from one small stand of the early introductions in Nandi Hills (PRYOR, 1966; CHATURVEDI, 1976). Lack of sufficient genetic variability is one of the important reason for low productivity of Eucalyptus plantations in India as compared to other countries because this restricts the intensity of selection in insufficient base population. In order to broaden

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