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Pattern of genotype–environment interaction in *Picea glauca* (Moench) Voss in Alberta, Canada

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Abstract

• **Introduction** Genotype-environment interaction (GEI) among 19 white spruce provenances planted on eight sites in Alberta, Canada, was analyzed using type B correlations (r_p) and the additive main effects and multiplicative interaction (AMMI) model. The objectives were to quantify the extent of crossover interaction for height and diameter; evaluate the age-trends in GEI for height and diameter; and examine the role of provenance and test site climate in causing GEI.

• **Results and discussion** A high-latitude ($\sim 59^\circ\text{N}$) site was poorly correlated ($r_p = -0.31$ to 0.56) with sites located south of latitude 56°N ; a high-elevation (1,220 m) site was poorly correlated ($r_p \leq 0.40$) with most of the sites located at medium and low elevations (≤ 800 m); additive main effects and multiplicative interaction analysis revealed a strong association between provenances and sites with similar climate; high-latitude provenances and sites with cool winters and dry summers, and high-elevation provenances and sites with high precipitation and short growing seasons contributed the greatest to GEI.

• **Conclusion** Because the relationship between GEI and climate corresponds well with latitudes and topography, seed transfer in Alberta can be effectively regulated by setting latitude and elevation transfer limits that are periodically adjusted to reflect the changing conditions caused by climate change.

Keywords AMMI · Climate · Provenance trial · Type B correlation · White spruce

1 Introduction

Crossover genotype-environment interaction (GEI) is a major obstacle to reforestation requiring environment-specific provenances to be identified (Falconer 1952; Robertson 1959; Zobel and Talbert 1984). This is a common phenomenon in species with wide geographic ranges or occupying heterogeneous environments whereby provenances adapted to specific sections of the environmental niche inevitably create GEI. Environmental differences in climate, soil types and mineralogy, and stand establishment and management contribute to the GEI observed in forest genetic trials (e.g., Wu and Ying 2001; Xie 2003; St. Clair et al. 2005). Soil-related environmental variation is discrete and often occurs at a micro-scale that is smaller than gene flow distances for wind pollinated conifers. Likewise, short-term silvicultural treatments of provenance trials differ significantly from long-term field conditions in which operational forests grow. In contrast, climate varies at a macro-scale, its pattern is predictable, and selected provenances are likely to grow in a climate similar to that of the provenance trials. Hence, from a predictability point of view, only GEI related to climatic variation among provenances and test sites is important when matching seed sources to planting environments.

White spruce (*Picea glauca* [Moench] Voss) is a major component of the boreal forest ecosystem in Canada (Nienstaedt and Zasada 1990) and commercially, the most important tree species in Alberta (e.g., Rweyongeza et al. 2007a). It is genetically highly variable in terms of growth potential (e.g., Nienstaedt and Riemenschneider 1985; Li et al. 1993, 1997) and well adapted to local climate (Rweyongeza et al. 2007a, 2010). This genetic variation is an opportunity for selecting and deploying superior provenances to maximize growth and yield while preserving the species' adaptation to the environment.

Despite numerous provenance and progeny trials, there is limited information about the extent and nature of GEI for white spruce in Canada. Except the study by Xie (2003) for

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interior spruce (hybrid of *P. glauca* and *Picea engelmannii* Parry ex Engelm) in British Columbia, no substantial analysis has been done to study GEI in white spruce provenances. In Alberta, white spruce occupies a more climatically diverse environment than in other parts of Canada (Rweyongeza et al. 2007a). In addition, Alberta has a 27-year-old series of eight provenance trials that have been measured for height and diameter at short regular intervals. This provides an opportunity for studying the role of climate in generating GEI and how GEI vary with tree age.

This article presents results of a GEI study for height and diameter measured at eight sites in Alberta, Canada. It uses type B correlations to evaluate the extent of crossover GEI, the additive main effects and multiplicative interaction (AMMI) model to reveal the pattern of GEI, and multivariate climatic indices to examine the role of climate in causing GEI.

2 Materials and methods

2.1 Provenances and sites

The Alberta white spruce provenance trials known as G103 series has 46 provenances planted on eight sites as previously described by Rweyongeza et al. (2007a). Nineteen of these provenances (Table 1) were planted at all sites, whereas the rest were selectively planted on specific sites. Nevertheless, the 19 provenances occurring on all sites, which are a subject of the present study span the entire natural range of white spruce in Alberta (Rweyongeza et al. 2007a). Seeds were cold stratified at 2°C for 21 days, sown and seedlings raised for one growing season in the greenhouse followed by three growing seasons in an outdoor nursery. Four-year-old seedlings were planted on eight sites in a randomized complete block design with five replications (blocks) and nine-tree row plots at 2.5×2.5-meter spacing between trees. All trees were measured for total height at ages 12, 15, 21, 24, and 27 years from seeds, whereas diameter at breast height was measured at ages 21, 24, and 27 years. In this article, these traits are identified as H12, H15, H21, H24, H27, D21, D24, and D27, respectively.

2.2 Testing presence of GEI

Before analyzing the pattern of GEI, a combined-site analysis was performed on plot means for individual traits using the model with (model I) and without (model II) the provenance×site interaction effect, described as $Y_{kij} = \mu + S_k + R_{i(k)} + P_j + PS_{jk} + \varepsilon_{kij}$ and $Y_{kij} = \mu + S_k + R_{i(k)} + P_j + \varepsilon_{kij}$, respectively. In both models, Y_{kij} is the plot mean for the j th provenance in the i th replication at the k th test site; μ is the general mean; S_k is the effect of the k th site; $R_{i(k)}$ is effect of

the i th replication at the k th site; P_j is the effect of the j th provenance; PS_{jk} is provenance×site interaction (GEI) and ε_{kij} is the residual. Except μ and S_k , all other effects were considered random. The -2 Res Log Likelihood of the two models from PROC MIXED (SAS Inst. 2004) were used to test the presence of a significant GEI under the following null ($H_0: \sigma_{ps}^2 = 0$) and alternative ($\sigma_{ps}^2 > 0$) hypothesis (Yang 2002; Fry 2004). All traits showed a highly significant ($P < 0.0001$) GEI. Because this analysis only serves to detect the presence or absence of a significant GEI, results are not presented and discussed any further.

2.3 Extent of crossover GEI

Falconer (1952) indicated that the extent of crossover interaction could be estimated by the genetic correlation of the same trait expressed in two environments. This type B genetic correlation (Burdon 1977) measures correspondence in provenance ranking between pairs of test sites. Preliminary analysis by PROC MIXED (Yang 2002; Fry 2004) showed that some of the correlations (r_p) were 1.0 even though corresponding Pearson’s correlations of provenance means were less than 0.7 and crossover interaction was graphically present. Normally, this happens when r_p is greater than 1.0 and PROC MIXED’s REML constrains the estimate within a permissible range (−1.0 to 1.0). To avoid out of range and potentially misleading perfect correlations, r_p was estimated from mean squares of standardized data as described by Robertson (1959).

$$r_p = \frac{ms_p - ms_{ps}}{ms_p + ms_{ps} - 2 \times ms_e} \tag{1}$$

where, r_p is type B provenance correlation; ms_p , ms_{ps} , and ms_e are type 3 mean squares from PROC GLM (SAS Inst. 2004) for the provenance, provenance×site interaction and residual (error) effect, respectively. The model (Model I) and assumptions were the same under PROC MIXED and GLM. The standard error for r_p was also approximated according to Robertson (1959).

$$SE(r_p) \approx \sqrt{\frac{[1 + nt(1 - r_p^2)]^2 + r_p^2}{(N - 1)n^2t^2}} \tag{2}$$

where $SE(r_p)$ is standard error of r_p ; N is the number of provenances; n is the number of trees per provenance; and t is intraclass correlation ($t = \frac{\sigma_p^2}{\sigma_p^2 + \sigma_{ps}^2 + \sigma_e^2}$, where σ_p^2 , σ_{ps}^2 and σ_e^2 are restricted maximum likelihood variance components for the provenance, provenance×site interaction and residual, respectively. Because of data imbalance caused by cumulative mortality, the coefficient for the provenance effect in the expected means squares was used as a substitute for n (Eq. 2).

Table 1 Location and climatic description of provenances (numeric ID) and test sites (character ID) for white spruce in Alberta

ID	Location	Latitude	Longitude	Elevation (m)	MAT (°C)	NDD	GDD	MAP (mm)	CPCA1	CPCA2
2	Footner Lake	58°44'	117°15'	335	-1.6	-2,654	1,197	418	-3.998	-1.382
4	Footner Lake	57°55'	115°30'	360	-0.4	-2,344	1,282	435	-3.361	-0.179
6	Athabasca Forest	58°44'	111°15'	235	-1.8	-2,738	1,244	397	-5.017	-1.335
8	Athabasca Forest	57°08'	111°38'	274	-0.2	-2,329	1,349	465	-3.725	-0.237
10	Athabasca Forest	59°38'	111°43'	183	-2.6	-2,968	1,181	338	-5.792	2.067
12	Lac La Biche	54°38'	110°13'	610	0.6	-2,009	1,309	490	-1.817	-0.622
15	Slave Lake	56°38'	114°35'	731	-0.1	-2,029	1,092	558	-0.346	-1.067
16	Slave Lake	54°48'	116°59'	731	2.5	-1,419	1,298	577	0.947	1.912
17	Slave Lake	55°14'	114°46'	610	1.6	-1,686	1,263	542	-0.034	1.097
21	Peace River	57°36'	117°31'	460	-0.5	-2,320	1,228	449	-2.948	-0.745
23	Peace River	56°34'	119°40'	762	-0.2	-2,077	1,097	466	-1.231	-1.238
27	Grande Prairie	55°35'	118°18'	640	1.6	-1,727	1,328	508	-0.773	1.141
29	Grande Prairie	54°27'	117°38'	940	1.8	-1,459	1,118	646	2.029	0.440
31	Edson	53°46'	118°48'	1402	0.7	-1,440	788	653	3.763	-2.097
32	Edson	53°14'	117°28'	1340	1.5	-1,345	943	636	3.109	-0.225
37	Whitecourt	54°11'	116°37'	945	2.4	-1,325	1,167	624	2.312	1.414
40	Rocky/Clearwater	52°10'	115°28'	1341	1.4	-1,353	923	657	3.088	-0.131
46	Bow/Crow	51°24'	115°13'	1600	0.8	-1,431	811	614	3.326	-1.440
48	Bow/Crow	49°39'	114°37'	1585	2.1	-1,132	950	763	4.485	-0.764
B	Hay River	59°08'	117°34'	370	-2.3	-2,844	1,147	419	-4.272	-2.221
C	Zeidler Mills	55°35'	114°50'	670	1.2	-1,745	1,219	572	0.180	0.481
D	Sexsmith	55°31'	118°30'	805	1.2	-1,710	1,209	532	0.155	0.246
E	Swartz Creek	53°23'	116°30'	990	2.1	-1,355	1,133	614	2.034	1.175
F	Prairie Creek	52°15'	115°21'	1220	1.7	-1,348	975	667	2.893	0.303
G	Chinchaga	57°50'	118°12'	470	-0.8	-2,385	1,201	454	-2.953	-1.038
H	Calling Lake	55°17'	113°09'	625	0.9	-1,879	1,254	512	-1.267	0.623
J	Hangingstone	56°23'	111°26'	550	0.2	-2,088	1,258	559	-1.497	0.019

CPCA1 and CPCA2 are multivariate climatic indices developed by principal component analysis from 11 climatic variables namely: mean annual temperature (*MAT*), mean temperature for the coldest month (*MTCM*), mean daily minimum temperature for the coldest month (*MMIN*), mean temperature for the warmest month (*MTWM*), mean daily maximum temperature for the warmest month (*MMAX*), mean annual precipitation (*MAP*), mean precipitation for the period between April and September (*MSP*), winter precipitation or snow fall (*WP*), degree of continentality (*CI*) expressed as a difference between *MTCM* and *MTWM*, degree days below 0°C (*NDD*), degree days above 5°C (*GDD*)

2.4 Pattern of GEI

To visualize the pattern of GEI, the additive main effects and multiplicative interaction (AMMI) model was fitted to the two-way (provenance × site) data. Briefly, AMMI analysis combines features of the analysis of variance (ANOVA) and principal component analysis (PCA) as follows (Kang et al. 2004; Gauch 2006):

$$\begin{aligned}
 E(Y_{kj}) &= \mu + S_k + P_j + PS_{kj} \\
 &= \mu + S_k + P_j + \sum_l \lambda_l \nu_{lk} \mu_{lj}
 \end{aligned}
 \tag{3}$$

where, $E(Y_{kj})$ is expected value (mean) for the j th provenance at k th site; μ , S_k , P_j , and PS_{kj} are as previously

defined; ν_{lk} and μ_{kj} is an interaction parameter (score) for the k th site and j th provenance, respectively; and λ_l is singular value associated with the l th PCA axis. AMMI is a doubly centered PCA where singular value decomposition is performed on the residual, which is PS_{kj} (Eq. 3) after subtracting the site and provenance effects from the mean of the j th provenance at k th test site. Because type B correlations were very similar among traits, it is expected that AMMI would reveal similar pattern of GEI for all traits. Therefore, AMMI was applied only to H27.

To discern the relationship of GEI with provenance and test site climates, the first (IPCA1) and second (IPCA2) AMMI axes were correlated with two multivariate climatic indices. These climatic indices were developed by principal component analysis (PCA) using PROC PRINCOMP in SAS from

11 variables describing provenance and test site climates. The original input variables were mean annual temperature (MAT), mean temperature for the coldest month (MTCM), mean daily minimum temperature for the coldest month (MMIN), mean temperature for the warmest month (MTWM), mean daily maximum temperature for the warmest month (MMAX), mean annual precipitation (MAP), mean precipitation for the period between April and September (MSP), winter precipitation or snow fall (WP), degree of continentality (CI) expressed as a difference between MTCM and MTWM, degree days below 0°C (NDD), degree days above 5°C (GDD). Climate data were available from the Alberta climate model (Alberta Environment 2005). The first (CPCA1) and second (CPCA2) principal component accounted for 74.8% and 16.9% of the variance in climate, respectively. Because the eigenvalues for the third and subsequent principal components were less than 1.0, they were not considered for further analysis. CPCA1 had high positive loading for winter temperatures and precipitation (MAP and MSP) variables, which indicates that, in Alberta, regions with cold winters have low precipitation. In contrast, CPCA2 had high positive loading for summer temperatures (GDD, MTWM, and MMAX) and negative loading for WP, which indicates that regions with high temperatures during the growing season have low winter precipitation. To preserve space, only MAT, NDD, GDD, and MAP are presented in Table 1 alongside CPCA1 and CPCA2 scores for provenances and test sites. These variables provide a general description of winter and growing season temperatures, and precipitation of provenances and test environments. When performing PCA, provenance and test site climate data were combined into a single dataset so that provenances and test sites with similar climate would have similar CPCA1 and CPCA2 scores.

3 Results

3.1 Variation among sites

Because site mean and ranges of provenance means on each site were previously published (Rweyongeza et al. 2010), they are not reproduced in this article. It suffices to say that mean H27 was lowest at site C (mean = 5.14 ± 0.35 m; range 3.78–6.25). On the northernmost site (B), average H27 was 6.05 ± 0.20 (range, 4.15–6.76 m), whereas at the highest elevation site (F) average H27 was 5.95 ± 0.24 (range, 4.76–6.86 m). For all other sites located at mid-latitude and mid-elevation (D, E, G, H and I), average H27 ranged from 6.91 m to 7.86 m with individual provenance means ranging from 5.35 to 8.78 m. Site variation for growth in diameter (D27) followed a pattern similar to H27.

3.2 Type B correlations

Table 2 shows that the correlations depended on the geographic proximity between sites. For example, site B (~59°N) had high H27 correlations ($r_p \geq 0.70$) with sites G and J located north of 56°N and low correlations (–0.31 to 0.56) with all other sites. Likewise, site F (1,220 m a.s.l) was better correlated with sites D and E (>800 m a.s.l) than sites located at lower elevations ($r_p \leq 0.40$), except site H ($r_p = 0.76$). Up to age 24 years, the lowest correlations for height were between site B and F, which in terms of latitude and elevation are the most separated sites. For H27 and diameter growth, correlations between sites B and F were moderately the most negative showing that the greatest divergence in provenance ranking was between the two most distant sites. Crossover GEI between these sites is illustrated in Fig. 1. The highest correlations ($r_p = 0.89$ to 0.96) were between site E and H (Table 2; Fig. 2). With minor exceptions, sites located at mid-latitudes (55°–57°N) and mid-elevations (500–800 m a.s.l) had medium to high correlations with each other (Table 2). Figure 3 shows that, with minor exceptions, height correlations had minor fluctuations between ages. With few exceptions, correlations for height at a specific age were higher than corresponding correlations for diameter.

3.3 GEI pattern by AMMI

The first (IPCA1) and second (IPCA2) interaction principal component axis accounted for 54.5% and 23.6% of the variance in GEI, respectively. Subsequent IPCAs accounted for less than 8% of the variance and were consequently dropped from further discussion. A biplot for IPCA1 and IPCA2 appear in Fig. 4. To aid the choice of other informative biplots, IPCA1 and IPCA2 were correlated with H27 and the first (CPCA1) and second (CPCA2) principal component climatic indices (Table 1). The Pearson's correlation was –0.005 (IPCA1 and H27), 0.49 (IPCA2 and H27), –0.08 (H27 and CPCA1), 0.44 (H27 and CPCA2), –0.67 (IPCA1 and CPCA1), –0.50 (IPCA1 and CPCA2), and 0.53 (IPCA1 and CPCA2). Thus, the biplot of H27 with IPCA2 (Fig. 5) was chosen to illustrate the relationship of GEI with provenance growth potential and test site productivity. In Fig. 4, IPCA1 aligns provenances and test sites from north to south whereby provenances from extreme ends of this geographic continuum contributed more to GEI than provenances from the middle. In contrast, IPCA2 aligns provenances along the gradient of provenance growth potential and site productivity. Site D appears as an exception to this generalization for reasons that will be discussed later. Figure 6 is a biplot of IPCA1 with CPCA1 to illustrate the relationship of GEI with provenance and test site climate.

Table 2 Type B provenance correlations (\pm SE) between pairs of test sites for height and diameter growth

Site pair	H12	H15	H21	H24	H27	D21	D24	D27
B,C	0.74±0.15	0.59±0.19	0.50±0.23	0.45±0.24	0.56±0.20	0.36±0.29	0.18±0.40	0.47±0.24
B,D	0.56±0.21	0.69±0.15	0.48±0.22	0.28±0.26	0.12±0.35	0.32±0.27	0.17±0.31	0.29±0.37
B,E	0.22±0.34	0.36±0.25	0.25±0.28	0.16±0.32	0.18±0.30	-0.11	-0.20	0.01±0.47
B,F	-0.03	0.05±0.59	-0.01±0.32	-0.14	-0.31	-0.32	-0.49	-0.45
B,G	0.79±0.13	0.73±0.14	0.85±0.10	0.67±0.17	0.75±0.14	0.65±0.20	0.59±0.22	0.83±0.12
B,H	0.07±0.40	0.19±0.31	0.31±0.27	0.17±0.31	0.13±0.32	-0.19	-0.26	0.05±0.38
B,J	0.78±0.12	0.84±0.09	0.83±0.09	0.72±0.13	0.70±0.14	0.67±0.16	0.63±0.17	0.64±0.17
C,D	0.24±0.39	0.44±0.24	0.60±0.18	0.66±0.17	0.65±0.18	0.39±0.26	0.45±0.24	0.49±0.28
C,E	0.59±0.22	0.76±0.13	0.83±0.10	0.86±0.09	0.86±0.09	0.61±0.19	0.62±0.19	0.70±0.16
C,F	-0.12	0.28±0.34	0.43±0.25	0.51±0.23	0.40±0.27	0.28±0.33	0.32±0.32	0.26±0.34
C,G	0.82±0.12	0.89±0.08	0.81±0.11	0.82±0.11	0.78±0.12	0.87±0.11	0.67±0.19	0.72±0.16
C,H	0.42±0.27	0.58±0.20	0.77±0.12	0.82±0.10	0.82±0.11	0.53±0.22	0.55±0.21	0.66±0.17
C,J	0.66±0.18	0.66±0.16	0.64±0.16	0.74±0.13	0.81±0.10	0.63±0.17	0.62±0.18	0.70±0.15
D,E	0.41±0.27	0.58±0.18	0.80±0.10	0.83±0.09	0.87±0.08	0.75±0.13	0.78±0.11	0.79±0.14
D,F	0.22±0.36	0.35±0.27	0.67±0.16	0.67±0.16	0.82±0.11	0.47±0.23	0.46±0.24	0.41±0.32
D,G	0.50±0.22	0.67±0.16	0.74±0.13	0.79±0.11	0.57±0.20	0.74±0.14	0.82±0.10	0.82±0.17
D,H	0.41±0.25	0.50±0.21	0.80±0.10	0.82±0.10	0.86±0.08	0.72±0.14	0.80±0.11	0.78±0.14
D,J	0.40±0.24	0.56±0.19	0.54±0.19	0.62±0.16	0.42±0.23	0.54±0.19	0.64±0.16	0.43±0.26
E,F	0.49±0.24	0.66±0.17	0.76±0.13	0.81±0.11	0.77±0.12	0.67±0.17	0.64±0.18	0.68±0.16
E,G	0.78±0.12	0.89±0.07	0.67±0.15	0.75±0.13	0.65±0.16	0.73±0.15	0.69±0.16	0.65±0.18
E,H	0.93±0.06	0.93±0.05	0.90±0.06	0.92±0.05	0.96±0.04	0.89±0.08	0.96±0.04	0.93±0.06
E,J	0.48±0.22	0.64±0.16	0.55±0.18	0.63±0.16	0.67±0.15	0.52±0.21	0.56±0.19	0.58±0.19
F,G	0.06±0.59	0.25±0.31	0.20±0.34	0.27±0.30	0.07±0.55	0.07±0.71	-0.02	-0.10
F,H	0.48±0.23	0.64±0.18	0.72±0.15	0.81±0.11	0.76±0.13	0.53±0.22	0.55±0.20	0.58±0.20
F,J	0.01±1.03	0.20±0.32	0.21±0.30	0.31±0.26	0.16±0.33	0.03±1.22	0.00	-0.04
G,H	0.71±0.15	0.75±0.13	0.72±0.14	0.76±0.12	0.65±0.16	0.68±0.17	0.64±0.18	0.63±0.18
G,J	0.93±0.05	0.91±0.06	0.92±0.05	0.87±0.07	0.87±0.08	0.87±0.08	0.88±0.08	0.84±0.10
H,J	0.52±0.20	0.57±0.19	0.64±0.16	0.73±0.13	0.73±0.13	0.57±0.19	0.56±0.19	0.65±0.16

The standard error is not calculated for site pairs where the combined-site provenance variance was negative (assumed to be zero)

H12, H15, H21, H24, and H27: total height at ages 12, 15, 21, 24, and 27 years, respectively; D21, D24, and D27: diameter at breast height at ages 21, 24, and 27 years, respectively

4 Discussion

The eight sites in this study have clear climatic differences stretching from north to south and low to high elevations. This is evident in scores of the CPCA1 climatic index (Table 1) whereby the northernmost lowest elevation site (B) has the strongest negative scores, whereas the southernmost highest elevation site (F) has the strongest positive score. The remaining sites are climatically intermediate between B and F, and their CPCA1 score depends on their geographic distance between B and F. The northern sites and provenances with highly negative scores represent a region with very cold winters, warm long summer days, low precipitation, and high continentality. Highly positive scores represent the Rocky Mountains region in southwestern Alberta. In this region, temperatures are mild in both

winter and summer due to the Pacific Ocean influence, growing degree days ($>5^{\circ}\text{C}$) are few and the frost-free period is short due to high elevation (AARD 2005), precipitation is high relative to the available summer heat, and the region lacks seasonal temperature extremes (continentality). Sites in between B and F (small negative and positive scores) have milder temperatures and higher precipitation than northern Alberta, and longer growing seasons than both northern Alberta and the Rocky Mountains. Climatic differences among provenances follow the pattern similar to test sites.

The climatic similarity between sites and provenances and its relationship with latitudes and elevation dictates the strength of crossover interaction. With minor exceptions, the larger the difference in climate between sites the larger the crossover interaction (Table 2). The association between

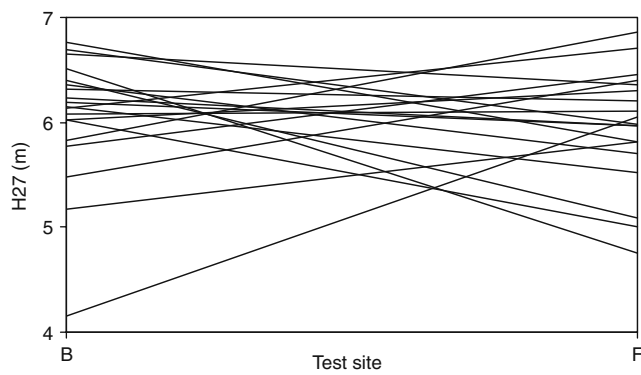


Fig. 1 GEI between the northernmost and southernmost sites which also represent the lowest and highest elevation sites ($r_p = -0.31$)

provenances and test sites is also closely tied to their climatic similarities. For example, except provenance 46, the northernmost provenances (2, 6, and 10) are associated with the northernmost sites (B and G) along an IPCA1 continuum (Fig. 4). Likewise, high elevation provenances (e.g., 31, 32, and 40) are associated with a high elevation site (F). Provenances from extreme ends of CPCAI exhibited the lowest growth potential on sites other than their native environments, thus contributing the greatest to GEI (Figs. 5 and 6). This association of provenances and sites with similar climate explains negative correlations between site B and F (Table 2). The positive but predominantly low correlations of sites C, D, E, H, and J with B or F indicate a tendency for some provenances from the intermediate climatic region to grow well at site B or F depending on climatic similarity and geographic (latitudinal or elevation) proximity between sites and provenances.

The association of site D (805 m a.s.l) with provenances from much higher elevations (Table 1; Fig. 4) is an exception. Provenances such as 32 and 48 from between 1,300 m and 1,600 m a.s.l grew better than local

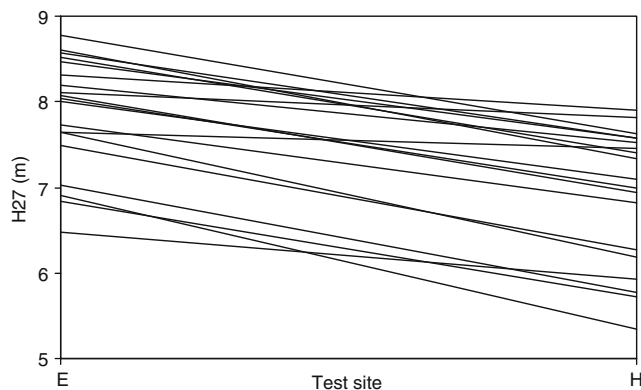


Fig. 2 Provenance height growth between sites E and H exhibiting the lowest GEI in this series of trials ($r_p = 0.96$)

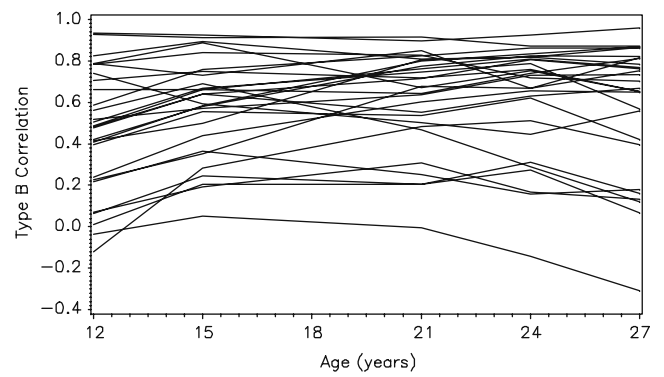


Fig. 3 Age trend in Type B correlation for height illustrating the fluctuation of GEI with the change in tree size

provenances at site D. Based on performance of these provenances elsewhere and results of similar studies in other species (e.g., Rweyongeza et al. 2007b), it is unusual for a high-elevation population to outgrow local populations at an elevation of about 500 to 800 m below its origin. Thus, possible mislabelling for some of high elevation provenances at site D during site establishment was suspected but could not be corroborated from the establishment records.

Linking GEI to predictable indicators of environmental variation is essential in matching seed sources to planting environments. Studies show that spatial variation in climate is the major natural selection pressure in temperate and boreal conifers (Matyas and Yeatman 1992; Morgenstern 1996; Rehfeldt et al. 1999; Rweyongeza et al. 2007a) and a cause for GEI. Variation in climate and its relationship with GEI may be expressed either indirectly through location

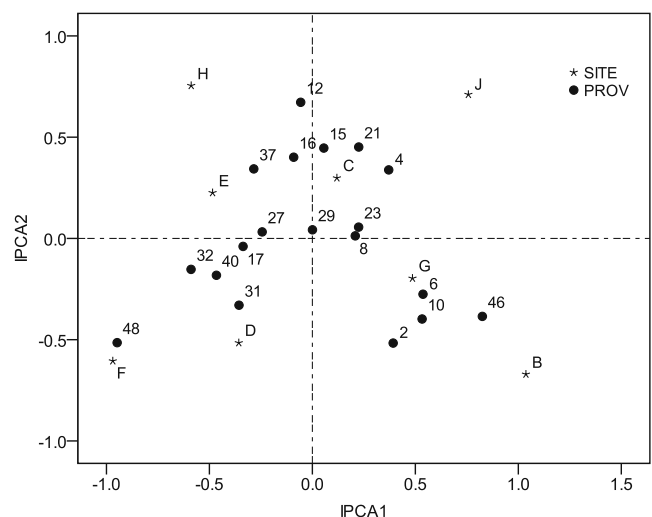


Fig. 4 Biplot for the first and second interaction principal component axes illustrating the association of test site with provenances of similar origin

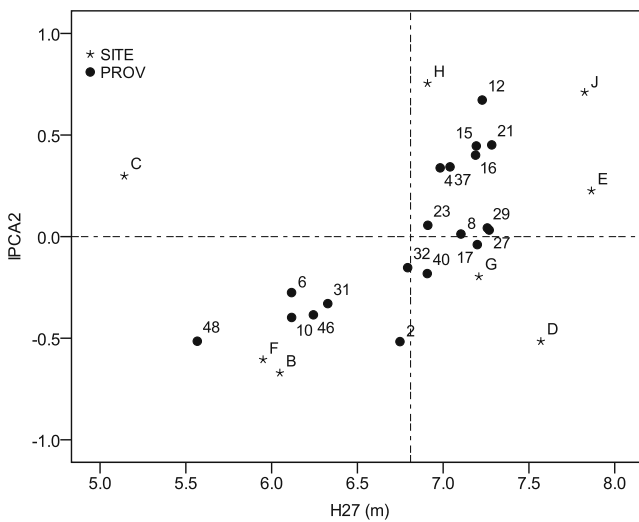


Fig. 5 Biplot for height growth and second interaction principal component axes illustrating the association of GEI with provenance growth potential and site productivity

(latitude, longitude, and elevation) or directly through temperature and precipitation variables. For example, using AMMI, Wu and Ying (2001) identified mean annual temperature, mean annual precipitation, and frost-free period as major causes of GEI for height growth of *Pinus contorta* Dougl in British Columbia. In a cluster analysis of interior spruce height growth in British Columbia, Xie (2003) showed that sites with similar biogeoclimates were grouped together and type B correlation among them averaged 0.97. The correlation decreased with an increase in latitude differences between pairs of sites. Hamann et al. (2000) found that provenance differences in length of

growing season, average temperature, precipitation, and continentality caused GEI for height in *Alnus rubra* Bong. Latitude explained 60% of provenance variation in provenance climate. In *Pseudotsuga menziesii* (Mirb) Franco, provenance variation was more related to winter temperatures and frost dates than precipitation and summer temperatures (St. Clair et al. 2005). While Krakowski and Stoehr (2009) found no strong correlation between volume growth and provenance climate in Douglas-fir, high-elevation provenances were ranked higher than low-elevation provenances at high-elevation sites and vice versa, which indicates an association between provenances and sites of similar climates that may not have been captured by the climatic variables used in the analysis.

Although shoot growth occurs in spring and summer, annual height increment is limited by anticipation of winter (Howe et al. 2003). In boreal and temperate conifers, there is a tradeoff between maximization of annual growth and avoidance of frost damage (Loehle 1998, 2000; Howe et al. 2003). This tradeoff between growth and survival is mediated through photoperiodism and sensitivity to seasonal temperatures (Kramer 1936; Taiz and Zeiger 2006). Because of photoperiodism and temperature-sensitivity, tree populations vary genetically in the timing of initiation and cessation of shoot growth (Vaartaja 1959; Morgenstern 1996; Howe et al. 2003). Photoperiodic sensitivity, which triggers cessation of growth (Kramer 1936; Howe et al. 2003), is highest among subarctic provenances (Vaartaja 1954, 1959). High-latitude and high-elevation provenances are more sensitive to changes in seasonal temperature than provenances from lower latitudes and elevations (Loehle 1998, 2000; Howe et al. 2003). Because photoperiod vary along latitudes (Morgenstern 1996), north-south clines of growth potential that is often observed in trees is due to adaptation to photoperiod in addition to temperature (Matyas and Yeatman 1992). For example, in the first growing season of *Picea abies* (L.) Karst, growth cessation was delayed, and growth significantly improved at a 24-h photoperiod for provenances from north of latitude 61°N compared with those from 47°N (Heide 1974a). However, growth in subsequent seasons was related to both temperature and photoperiod suggesting that the interaction between temperature and photoperiod was probably more important in explaining provenance variation in growth potential than the two variables individually (Heide 1974b).

Provenances and sites in this study have wide latitude and elevation ranges (Table 1) making thermo- and photoclimate the most likely cause of the observed GEI. While the role of photoperiod cannot be tested in this study, climate derived from latitude, longitude, and elevation coordinates should indirectly account for photoperiodic effects. Lack of perfect correlations between sites with similar climate and geographically close may be explained

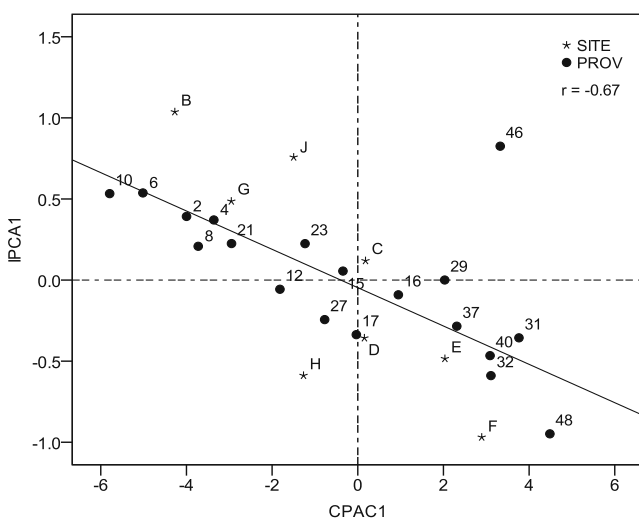


Fig. 6 Biplot for IPCA1 and CPAC1 illustrating the relationship of GEI with provenance and site climate characterized by winter temperatures and precipitation

by differences in microsites related to variation in soils and site managements.

The pattern of GEI observed in this study may be used to develop seed transfer guidelines along latitudinal and elevation boundaries. For example, the area north of 57°N where site B is located may be treated as a separate region to be regenerated using local seeds. Likewise, the Rocky Mountains area above 1,000 m represented by site F could be treated as a separate region regenerated by local seeds but also with a potential for upward seed movement from medium elevations (≥ 800 m) depending on the evaluated risk of frost damage. At medium latitudes (54°–57°N) and elevations (500–800 m) in the boreal forest where most of the sites are located, northward seed movement can be implemented by setting a maximum permissible latitudinal transfer distance, because only a gentle latitudinal cline of growth potential exist in this region (Rweyongeza et al. 2007a). Consistent with the pattern of type B correlations and provenance–site association in AMMI, 2° northward and 200 m upward seed transfers would improve productivity while remaining conservative enough to maintain adaptation to the current climate.

Generally, the observed pattern of GEI describes provenance adaptation to the present climate whereby provenances of high growth potential from mid-latitudes and mid-elevation are not suitable at higher latitudes compared with local provenances. If low temperature at higher latitudes is the main limitation to superior growth of provenances from mid-latitudes, climate change would potentially alter this balance. Climate change predictions show that northern Alberta will increasingly become warmer and drier throughout this century (Barrow and Yu 2005). Warmer winters and longer growing seasons at high latitudes will reduce the risk of frost damage for mid-latitude provenances and also allow them to generate larger preformed shoots from which subsequent year height growth increment arise. Thus, if the observed pattern of GEI reflects provenance adaptation to temperature more than precipitation, provenances from mid-latitudes will be deployable at high latitudes in future climates. If precipitation has a significant role in determining the pattern of GEI, such deployment will not be feasible due to intensification of drought in northern Alberta.

Burrow and Yu (2005) also shows that the Rocky Mountains region in southwestern Alberta will become warmer in a changing climate. In the present climate, this region has high precipitation, short growing season (low GDD), and high incidence of mid-growing season frosts (Alberta Environment 2005; AARD 2005). Because climate change does not pose imminent risk of drought in this region, deployment at a higher elevation of fast growing mid-elevation provenances will be feasible in future climates. In Table 2, moderate correlations of sites D and

E with F suggest a tendency for mid-elevation provenances to grow relatively well at higher elevations. In the medium term, this would be strengthened by climate change.

The mid-latitude and mid-elevation region in Alberta is predicted to become drier due to a rapid increase in GDD and low change in MAP (Barrow and Yu 2005). Because high latitude and high elevation provenances may not be productively introduced in this currently optimal region for white spruce, local provenances will increasingly become genetically maladapted due to moisture stress with no potential replacement by provenances from other regions within Alberta. In this case, maintaining productivity will require (1) introducing drought-hardy white spruce provenances from elsewhere in Canada and USA, (2) breeding local provenances for drought tolerance, or (3) introducing drought-hardy non-native species.

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