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Genotype by Environment Interaction and Genetic Correlation of Greenhouse and Field Performance in *Pinus contorta* ssp. *latifolia*

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Summary

Family by site interaction from 4 progeny test sites for 9-year height and its impact on estimation of genetic correlation between greenhouse traits and 9-year height were investigated in 110 families of *Pinus contorta* ssp. *latifolia* from Alberta, Canada. Significant family by site interaction, site and family effects were observed in 9-year height among 4 progeny test sites. The estimated narrow-sense heritability was from 0.127 to 0.277 for individuals and was from 0.247 to 0.475 for family means. 25 greenhouse seedling traits (height, diameter, bud, branch and biomass) in 2 growing seasons were jointly studied with 9-year tree height at the 4 progeny test sites. The genotype by site interaction had a significant impact on greenhouse-field family-means and genetic correlations. Only 9-year tree height in the best site (site B), which had more similar growing conditions to the greenhouse, had significant family-mean and genetic correlations with greenhouse seedling traits. Seedling traits of height increment at the dormancy induction period between 2 growing seasons (HG1, $r_g = 0.52$), height at the second growing season (H3, $r_g = 0.36$), and height ($r_g = 0.37$) and diameter ($r_g = 0.42$) at harvest, had the highest and significant family-mean and genetic correlation. The pattern of greenhouse-field family-mean and genetic correlations among 4 sites indicates that early testing should be conducted under simulated field conditions. The implications of genotype by site interaction on early selection were discussed for lodgepole pine.

Key words: Genotype by environment interaction, juvenile-mature correlation, type-B genetic. correlation, early selection, lodgepole pine.

FDC: 165.3; 181.525; 181.65; 232.1; 174.7 *Pinus contorta;* (712.3).

Introduction

Lodgepole pine (*Pinus contorta* ssp. *latifolia* Englm.) is one of the most widely distributed trees in Western Canada, and is a commercially important conifer, native to Alberta. It is valued for its growth potential, good form characteristics, timber quality and relative freedom from major pests. It is the second most important tree species and accounts for 22.3% or 3.37 million hectares of the productive forest in Alberta (Dhir and Barnhardt, 1993). Variability in economic traits such as growth, form and wood quality is expressed both within and among populations (Critchfield, 1980; Rehfeldt, 1985; Yanchuk, 1986; Fries, 1987). Therefore, lodgepole pine is a prime candidate for genetic improvement through selective breeding to increase plantation forest productivity and quality in Alberta.

Improvement of *P. contorta* ssp. *latifolia* in Western Canada has generally included phenotypic mass selection in wild stands and use of this material for seed production in clonal or seedling seed orchards. The selection criteria invariably emphasized height and diameter growth and form traits, and additive genetic effects were assumed (Wheeler, 1979; Fries, 1986, 1989; Carlson, 1990). In Alberta, phenotypic selection for growth and form traits among trees within stands was initiated in the late 70's by the Alberta Forest Service (Dhir, 1983; Dhir and Barnhardt, 1993). Progeny tests of the phenotypic selections were established to select genetically superior families for reforestation and for further breeding purposes.

The lower limit of rotation age of *P. contorta* spp. *latifolia* in Alberta was about 70 years (Smithers, 1961). Waiting for one-half rotation age for final evaluation and selection of families, as commonly recommended (Zobel and Talbert, 1984), would be very inefficient in terms of genetic gain per unit time. Thus, the method of early selection, particularly, early greenhouse

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and nursery screening have been advocated for lodgepole pine selection to accelerate generation turnover and increase genetic gain per decade.

The effectiveness of early selection depends largely on the early-mature genetic correlation and the heritability of juvenile traits. Much efforts has been made in several species to maximize the early-mature genetic correlation by selecting optimal juvenile-test environments and appropriate juvenile traits (LAMBETH, 1983; WILLIAMS, 1987, 1988). To find the proper juvenile traits for efficient early selection, the ontogeny of seedling and components of seedling traits were examined. For example, the shoot/root biomass ratio of *Pinus taeda* L. seedlings grown under unstressed water regime was a better predictor of later performance than seedling height, seedling shoot and root weights (WAXLER and VAN BUIJTENEN, 1981); WILLIAMS, (1987) observed that the length of shoot beyond the first budset was the best juvenile indicator of eight-year tree height in the field; however, seedling shoot dry weight was found to be a very useful early trait in other studies (LOWE and VAN BUIJTENEN, 1989); BRIDGEWATER (1990) found that the annual leader length of second year seedlings was a better predictor of 8-year tree size than other components of shoot growth such as number of stem units and stem unit length. LI et al. (1991) observed that the elongation of cyclic growth, number of growth cycles per year and number of stem units exhibited greater correlation with 12-year field height than seedling height and shoot biomass. On the other hand, LAMBETH et al. (1982) observed that the correlations between seedling dry weight and later performance in 16 full-sib loblolly pine families were higher than between seedling height and later performance. In a study of 36 full-sib families of *Pinus sylvestris* L., JIANG (1988) found the mean length of stem units was more related to the field performance than were seedling height and biomass. In Douglas-fir (*Pseudotsuga menziesii* (MIRB.) FRANCO) seedlings, budset, height and its increment and branch index showed greater correlations with field performance than seedling basal area, dry weight and shoot/root biomass ratio (RIITTERS and PERRY, 1987).

Genotype by environment interaction in the field tests will reduce the effectiveness of early selection and also early-mature genetic correlations. It is well-known that performance of genotypes relative to each other can vary with testing environments. Genotypes that are superior in one environment may not be correspondingly superior elsewhere, or the degree of difference among genotypes may vary according to the test environment. Genotype by environment interaction is important in many aspects of a breeding program (BRIDGWATER and STONECYPHER, 1978). Interaction in field trials affects mature selection and also early selection. Early-selected families may perform differently in one test site than in another when there is strong genotype by environment interaction across sites. Thus, when evaluating the effectiveness of early selection, it is imperative to determine whether the genotype by environment interaction among sites has a meaningful impact on early-mature genetic correlation, what field elements are causing the interaction and how these elements affect early-mature genetic correlation and early selection efficiency. This paper reports genotype by environment interaction in a series of lodgepole pine field tests and its impact on the estimation of greenhouse-field genetic correlations in Alberta, Canada.

Material and Method

1. Field experiment

A series of 4 open-pollinated family field trials was established by the Alberta Land and Forest Service as part of its central region lodgepole pine tree improvement program in 1981. This breeding region is located in central Alberta and is within the boreal foothills ecological zone. A set of 110 families was used in this study from a total of 224 families established in the regional field trials. These families represent a total of 33 natural stands sampled in the breeding region. Geographic range of the stands sampled was: Latitude 53 °58'N to 55 °12'N; Longitude 115 °11'W to 116 °50'W; Elevation 885 m to 1160 m.

Parent trees in each stand from which seeds were collected were phenotypically selected for superior growth, stem straightness, branching, and crown traits. Seeds were sown in Spencer-Lemaire Hillson (150 cc) containers in a greenhouse in March 1981. The seedlings were grown in the greenhouse for 20 weeks and hardened outdoors. Site preparation consisted of windrowing and subsequent burning of slash, brushing and fencing. Seedlings were outplanted at 2.5 m x 2.5 m spacing in 4 field sites (A, B, C and D) in a sets-in-replications randomized complete block design (DHIR, 1983). 110 families were planted in 5 replications of 5-tree row plots at each site with 12 families per set.

The sites were weeded at 2-year intervals to reduce vegetative competition, particularly in site A. All plantings were generally healthy and did not suffer any serious pest damage during the duration of this study. The progeny tests were assessed in October 1990 for 9-year height (measured to nearest cm) and survival.

2. Greenhouse experiment

Seeds of the 110 families tested in field trials had been stored for 9 to 12 years at low temperature (–20 °C). In 1989, seeds of each family were imbibed in tap water for one day before sowing and then 30 seeds per family were sown into individual plastic cells filled with peat moss during the fourth week of February, 1989. The 30 cells from each family were grouped together on a bench in a greenhouse at the University of Alberta. The seedlings were transplanted in the middle of June into 5.6 litre plastic pots filled with a mixture of peat moss and sand to allow for accelerated free growth through artificial photoperiod extension. The transplanted seedlings were studied for 2 growing periods with daylength shortened to induce dormancy of seedlings between the growing seasons. The greenhouse regime was selected based on the optimal growth conditions of lodgepole pine in the Prairie provinces (CARLSON, 1983; DYMOCK and WILSON, 1986). A randomized complete block design with 20 replications of single-tree plots was used in greenhouse. The detailed procedure for greenhouse experiment, measurement of seedling growth, bud and branch traits, and genetic parameters for a larger population (116 families) were reported elsewhere (WU et al.,1995).

Besides periodic measurements of seedling height, diameter, bud and branch traits, seedlings were individually harvested, separated into parts and oven-dried at 80 °C for 48 hours at the end of 2 growth periods. Weights of the stem, branches, needles and roots were recorded. In addition, 3 ratio traits: HI, harvest index (i.e. stem/above-ground biomass) (KARKI and TIGERSTEDT, 1985); SR, ratio of above-ground (shoot) to root biomass (THOMPSON, 1985); HD, ratio of height to basal diameter at the end of second growth period were studied. These ratio traits are important for early seedling assessment, and also in relation to mature selection. Harvest index reflects allocation of biomass to bole versus other above-ground parts of the tree. Higher harvest index suggests greater amount of photosynthetic products are being allocated into the tree bole. SR and HD are important nursery traits which have commonly been referred to as the shoot-root ratio and sturdiness quotient, respectively. SR reflects allocation of above-ground and below-ground biomass and may be related to adaptation such as tolerance to water stress (CANNELL et al., 1978). The HD is related to tree taper and reflects tree bole quality. HD also is a good indicator of the ability to withstand physical damage due to wind, drought, and frost (THOMPSON, 1985). Genetic effect on biomass partition and tree architecture has been reported (WU and YEH, 1997). Total 25 greenhouse traits were jointly studied with traits based on the 4 field trials.

3. Statistical analyses

A preliminary analysis indicated that stand effects were insignificant in the field experiments and in the greenhouse experiment, and thus the following model was used for analysis of combined field data

$$Y_{ijkl} = \mu + S_i + R_{j(i)} + F_k + S*F_{ik} + E_{ijkl} \text{ ,}$$

where μ is grand mean, S_i is i^th^ site effect, $R_{j(i)}$ is j^th^ replication effect within i^th^ site, F_k is k^th^ family effect, $S*F_{ik}$ is interaction effect between i^th^ site and k^th^ family, and E_{ijkl} represents residual. All effects except the overall mean were considered random. For analysis of individual site data, the model was the form

$$Y_{jkl} = \mu + R_j + F_k + R*F_{jk} + E_{jkl} \text{ ,}$$

where $R*F_{jk}$ is interaction effect between j^th^ replication and k^th^ family.

To investigate which site would have more impact on total genotype and environment interaction, the magnitude of interaction between each pair of four sites was investigated by type-B genetic correlation (BURDON, 1977).

The analyses of variance for greenhouse data were conducted using the following linear model:

$$Y_{jk} = \mu + R_j + F_k + E_{jk} \text{ .}$$

The least square solution was used to estimate variances in both field and greenhouse traits (MILLIKEN and JOHNSON, 1984; SEARLE, 1987). SATTERTHWAITE's approximate test (1946) was used for significant testing of variance components in field data analysis. Genetic variance components were estimated on a half-sib families basis (WU et al., 1995). Family variance approximately estimated one-quarter of the additive genetic variance.

Genetic correlation (r_g) between a greenhouse trait (x) and 9-years tree height (y) in the progeny tests was estimated by the following equation:

$$r_g = \frac{cov(f_x\ f_y)}{\sqrt{\sigma^2_{f_x}\ \sigma^2_{f_y}}}$$

where cov(f_x f_y) is the family covariance between x and y, and $\sigma_{fx}{}^2$ and $\sigma_{fy}{}^2$ are family variances of x and y, respectively. The estimate of cov(f_x f_y) was derived from the family-mean covariance. Since TAYLOR's expansion method (KENDALL et al., 1987) to estimate standard error for this type of genetic correlation is unsatisfactory, no standard error for type-B genetic correlation was estimated.

Results

Mean survival of the 110 families at age 9 years was 83.6% across the 4 sites. It varied from a low of 79.4% at site A to a high of 85.5% at site C (*Table 1*). Mortality was primarily the result of poor microsites or excessive vegetative competition. Differential survival of the saplings attributable to family effects was not apparent.

Table 1. – Location of four lodgepole pine progeny testing sites and their average height and survival at nine-year age.

Site	Latitude	Longitude	Elevation (m)	Survival	Height (cm)
A	54°26'N	115°35'W	1097	79.4%	194.4
B	54°28'N	115°51'W	1127	85.0%	261.3
C	54°40'N	115°30'W	1143	85.5%	204.5
D	54°41'N	115°18'W	1064	84.5%	207.5

The site B was by far the most productive. This site is relatively less wind-exposed and its soil is a well drained sandy-loam characterized by a lower level of vegetative competition. The average height of site B (261.3 cm) was 34.4%, 27.8% and 26.0% better than site A (194.4 cm), C (204.5 cm) and D (207.5 cm), respectively (*Table 1*). The fact that the site A had the most severe vegetative competition (mainly by *Calamagrostis canadensis*) and sites C and D are more wind-exposed and stony are probably reasons for relatively slower growth on these sites.

1. Genotype by site interaction

The analyses of variance indicated a significant family by site interaction at the 1% probability level for 9-year tree height (*Table 2*). Significant differences were also observed for sites, replications, and families. The family and site interaction variance was equivalent to 117% of the size of the family variance component.

Table 2. – Analyses of variance for nine-year tree height of lodgepole pine from four progeny test sites (the percentage of variance PV is also presented).

Source of variation	DF	MS	EMS [a]	PV	F	Pr.>F [b]
Site	3	1560405	$\sigma_e{}^2+16.20\sigma_{s*f}{}^2+356.28\sigma_{r(s)}{}^2+1781.4\sigma_s{}^2$	32.8	34.5	0.0001
Replication(site)	16	44918	$\sigma_e{}^2+362.8\sigma_{r(s)}{}^2$	4.6	30.0	0.0001
Family	109	6493	$\sigma_e{}^2+16.51\sigma_{s*f}{}^2+66.06\sigma_f{}^2$	2.3	2.5	0.0001
Site*family	327	2635	$\sigma_e{}^2+16.63\sigma_{s*f}{}^2$	2.6	1.8	0.0001
Residual	6890	1496	$\sigma_e{}^2$	57.7		
Total	7345					

[a] DF, MS and EMS are degree of freedom, mean squares and expected mean squares. $\sigma_e{}^2$-residual variance, $\sigma_{s*f}{}^2$-variance of site by family interaction, $\sigma_f{}^2$-variance of family effect, $\sigma_{r(s)}{}^2$-variance of within-site replication, and $\sigma_s{}^2$-variance of site. [b] Pr. > F is probability of a larger F value.

Except for the residual, sites accounted for the largest variance component, which was 32.8% of the total variance (*Table 2*). Replication within sites also accounted for a considerable proportion of total variance (4.6%). Family and family by site interaction, respectively accounted for 2.3% and 2.6% of the total variance. Estimated individual heritability for overall sites was 0.144 ± 0.031 and family heritability was 0.393 ± 0.112.

Both linear and rank correlation of family-mean among four sites indicates substantial rank change among family means of four sites (*Table 3*). Particularly, there was no family-mean correlation between site B and D. Family mean correlations among other site pairs were also low, from 0.19 for sites A and D to 0.38 for sites C and D. Genetic correlations varied from a minimum of 0.20 for site pair B and D to a maximum of 1.08 for site pair A and C. It was observed that genetic correlations were substantially higher than family-mean correlations. In general site D was less correlated with sites A and B, and site C also had a relatively lower genetic correlation with site B.

Table 3. – Estimates of family-mean (r_f), Spearman rank (r_s) and genetic (r_g) correlation for nine-year tree height on each pair of four lodgepole pine progeny test sites.

	Site pair					
	AB	AC	AD	BC	BD	CD
r_f	0.26**	0.37**	0.19*	0.24**	0.07	0.38**
r_s	0.26**	0.36**	0.20*	0.22*	0.03	0.37**
r_g	0.90	1.08	0.62	0.60	0.20	0.89

* significant at 5%,
** significant at 1%.

Thus, it is expected there would be larger interaction between site D and sites A, B, and between sites B and C.

2. Individual sites

Analysis of variance indicates that replication, family and interaction effects between replication and family were all significant at the 1% probability level at 4 field sites (*Table 4*). Replication variances varied from 3.9% for site C to 10.4% for site A. The percentage of family variance was from 3.7% for site A to 6.8% for site C. There was considerable family by replication interaction at all four sites. The percentage variances of the interaction varied from 13.5% to 24.7%, which were larger than main effect of family and replication. Narrow-sense heritability for 9-year height varied from 0.127 ± 0.033 of site A to 0.277 ± 0.056 of site C. Heritability for family-mean was from 0.247 ± 0.045 to 0.475 ± 0.081 (*Table 5*).

Table 4. – Results of analyses of variance presented as percentage of total variance for nine-year tree height at four lodgepole pine progeny test sites [a].

	Site			
Sources of variation	A	B	C	D
Replication	10.4**	6.4**	3.9**	5.7**
Family	3.7**	4.3**	6.8**	3.9**
Replication*family	19.0**	24.7**	13.5**	14.4**
Residual	67.4	64.6	75.8	76.0

** significant at 1%.

Table 5. – Estimates of individual (h_i^2), family (h_f^2) heritabilities, and their standard error (s.e.) of nine-year tree height at the four lodgepole pine progeny test sites.

	Site			
	A	B	C	D
h_i^2	0.127	0.191	0.277	0.197
s.e.	0.033	0.048	0.056	0.043
h_f^2	0.247	0.337	0.475	0.380
s.e.	0.045	0.057	0.081	0.059

3. Greenhouse-field site correlation

Estimates of family-mean and genetic correlations between 25 greenhouse traits and 9-year tree height of 4 lodgepole pine trials are given in *table 6*. None of the greenhouse traits were significantly correlated with 9-year tree height on sites A, C and D based on family-mean. Only at site B, 9-year tree height correlated significantly at the 5% probability level with 4 greenhouse traits: height at second growing season (H3, r_f = 0.18), height (H6, r_f = 0.18) and basal diameter (D6, r_f = 0.20) at harvest and height increment during the dormancy induction period between 2 growing seasons (HG1, r_f = 0.21). In addition, 5 correlations between greenhouse traits (H4, H5, DG, BRN1, BRN2) and 9-year tree height on site B were significant at the 10% probability level.

The values of genetic correlations between 25 greenhouse traits and 9-year tree height at site B were almost double those of family-mean correlations. The greenhouse traits which were most highly correlated with 9-year tree height for site B were HG1 (r_g = 0.52), SR (r_g = 0.44), D6 (r_g = 0.42), BRN1 (r_g = 0.41) and DG (r_g = 0.40). For site B, genetic correlations with field height were very similar for seedling heights (H1 – H6); the genetic correlation varied from 0.21 (H1) to 0.37 (H6) with the majority of r_g values around 0.35. Genetic correlations between biomass traits and 9-year tree height (around 0.25, except 0.09 for BB) were lower than that of height and diameter measurements. Genetic correlations between branch (BRN1, BRN2 and RBS), bud characteristics (BUDN and BUDS) and 9-year tree height were also similar to those for seedling biomass measurements. However, branch number after the first growing season (BRN1) had a higher r_g (0.41) and relative branch strength (RBS) showed near zero correlation with 9-year tree height (–0.01). Among the 3 ratio traits, shoot/root ratio (SR) had the highest correlation with 9-year tree height (r_g = 0.44).

Table 6. – Estimated family-mean (r_f) and genetic (r_g) correlations between greenhouse juvenile traits and nine-year tree height at four lodgepole progeny test sites.

	Site							
Trait	A		B		C		D	
	r_f	r_g	r_f	r_g	r_f	r_g	r_f	r_g
H1	0.01	0.03	0.11	0.21	-0.07	-0.11	-0.07	-0.14
H2	0.03	0.07	0.16	0.32	-0.05	-0.07	-0.05	-0.10
H3	0.02	0.06	0.18*	0.36	-0.05	-0.08	-0.04	-0.08
H4	0.02	0.06	0.17	0.34	-0.04	-0.06	-0.03	-0.05
H5	0.03	0.08	0.16	0.32	-0.04	-0.06	-0.04	-0.08
H6	0.06	0.15	0.18*	0.37	-0.03	-0.04	-0.03	-0.06
D2	0.06	0.16	0.15	0.31	0.02	0.03	0.02	0.05
D6	0.04	0.10	0.20*	0.42	-0.06	-0.11	-0.01	-0.01
HG1	0.03	0.09	0.21*	0.52	0.04	0.09	0.05	0.11
HG2	0.09	0.25	0.15	0.35	0.03	0.05	0.03	0.06
DG	-0.02	-0.05	0.16	0.40	-0.05	-0.10	0.03	0.08
SB	0.01	0.04	0.13	0.28	-0.03	-0.06	-0.01	-0.02
BB	-0.03	-0.09	0.04	0.09	-0.03	-0.06	0.06	0.14
NB	0.03	0.09	0.12	0.26	-0.01	-0.02	-0.01	-0.02
RB	0.01	0.01	0.09	0.21	-0.01	-0.02	0.03	0.07
TB	0.02	0.05	0.12	0.25	-0.01	-0.02	0.01	0.01
GB	0.03	0.07	0.12	0.26	-0.01	-0.02	-0.01	-0.02
HI	0.05	0.14	0.09	0.21	-0.05	-0.09	-0.01	-0.01
SR	0.17	0.59	0.16	0.44	0.05	0.11	0.06	0.15
HD	0.06	0.17	0.06	0.14	-0.02	-0.04	-0.06	-0.14
BUDN	0.08	0.28	0.09	0.24	-0.01	-0.03	-0.11	-0.30
BUDS	0.07	0.20	0.12	0.26	0.05	0.09	0.08	0.17
BRN1	0.10	0.29	0.17	0.41	-0.01	-0.03	0.02	0.04
RBS	-0.01	-0.02	-0.01	-0.01	-0.04	-0.09	0.09	0.20
BRN2	0.09	0.24	0.12	0.26	0.02	0.04	0.02	0.04

* significant at 5% for family-mean correlation.

H1-Height at the end of the first growth period, H2-Height at the end of first dormancy period, D2-Basal diameter at the end of first dormancy period, BUDN-Bud number at the end of dormancy, BUDS-Bud size at the end of dormancy (small, medium and large), BRN1-Branch number at the end of dormancy, RBS-Relative branch strengh at the end of dormancy (small, average and large), H3-Height of seedlings at three weeks in the second period, H4-Height of seedlings at six weeks in the second period, H5-Height of seedlings at nine weeks in the second period, H6-Height at the end of second growth period, D6-Basal diameter at the end of second growth period, BRN2-Branch number at the end of second growth period, SB-Stem biomass, BB-Branch biomass, NB-Needle biomass, RB-Root biomass, HG1-Height growth in the dormancy induction period (i.e., H2-H1), HG2-Height growth in the second growth period (i.e., H6-H2), DG-Diameter growth in the second growth period (i.e., D6-D2), TB-Total biomass (i.e. SB+BB+NB+RB), GB-Above ground biomass (i.e. SB+BB+NB), HI-Harvest index (i.e., SB/GB), SR-Shoot-root ratio (i.e., GB/RB), HD-Sturdiness quotient (i.e., H6/D6).

Discussion

Site effects on height growth at age 9 were significant at the 1% probability level and were a major influence on the growth of lodgepole pine families in this study. Mean heights after 9-years at the poorest-growth site (site A) and the best-growth site (site B) were 89.8% and 120.3% of the grand mean, respectively (*Table 1*). The effect of sites on 9-year height is not surprising because of the wide range of physiography, soil type and vegetative competition in this breeding region. The environmental factors responsible for genotype environment interaction could be divided into cultural and natural environmental categories (SHELBOURNE, 1972). We may rule out any cultural factors for the genotype by site interaction in this study since all treatments (site preparation, slash burning, planting, fencing and use of herbicide) were the same in these 4 sites. Among natural environmental factors, the climatic differences among the 4 sites in this study are probably not major contributors to genotype by site interaction because the 4 sites are located within less than half degree of latitude, 1 degree of longitude, and within 80 m elevation. These 4 sites are also located within the same ecoclimatic zone according to ecoclimatic classification (STRONG, 1992). Most likely, the wide range of physiographic, soil and vegetative competition effects among the sites contributed to the apparent genotype by site interaction in this study. Despite similar soil texture (sandy loam) of sites A and B, the site A had more severe vegetative competition from *Calamagrostis canadensis* than site B. This may be the major reason why site A showed the poorest survival rate (79.4%) and growth rate. In contrast with sites A and B, sites C and D had a large stone component in the soil and this may have reduced height growth relative to site B.

Greenhouse seedling traits were correlated genetically with 9-year tree height only on site B. Growth at site B was the best of the 4 sites. Apparently, the growth conditions in site B are closer to optimal growth conditions for lodgepole pine in the greenhouse since (1) the culture media (mixture of sandy loam and peat moss) in the greenhouse was similar to sites A and B, and (2) competition regime in the greenhouse was more similar to site B (no competition among seedlings in greenhouse and less competition from vegetation in site B). We suspect that the greater similarity of soil type and vegetative competition level between site B and the greenhouse than with other sites could results in higher correlations with site B. This might indicate that the juvenile selection environment is critical for maximizing gain in juvenile traits as well as correlations between field and greenhouse for effective early selection in lodgepole pine. Our finding also supports the observation from several other juvenile testing studies, that early tests should be conducted under simulated field conditions (LAMBETH, 1983; CANNELL et al., 1978).

The observation of genotype by site interaction among the field sites and varied greenhouse-field genetic correlations among sites in this study has significant implications for implementing early selection through greenhouse or nursery screening in tree improvement of lodgepole pine. This indicates early selection should be used with caution when mature tests show genotype by site interaction. In our lodgepole pine case, early selection of families on greenhouse juvenile traits may not be appropriate for planting in other sites than site B.

Between-sites genetic correlations are always higher than family-mean correlations as long as heritabilities are not perfect (BURDON, 1977). The observation of genetic correlation estimates greater than family-mean correlations has also been reported in many other age-age correlation studies (LAMBETH, 1983; LOO et al., 1984; COTTERILL and DEAN, 1988; RIEMENSCHNEIDER, 1988). However, because between-sites genetic correlation is a highly derivative statistic, there is no statistically-satisfactory way to test this type of genetic correlation (BURDON, 1977) and thus a high between-sites genetic correlation does not necessarily have significant meaning. Such is the case for genetic correlation between shoot/root biomass ratio (SR) and 9-year height at site A. The r_g was 0.59, but family-mean correlation for this trait was not significant. Thus, control of environmental errors in the field and greenhouse tests and large sample size is crucial for an effective estimation of between-sites genetic correlation.

One objective in an early selection study is to find the best early traits for predicting later field performance. The results from many early selection studies are inconclusive (CANNELL et al., 1978; WAXLER and VAN BUIJTENEN, 1981). In loblolly pine (LAMBETH, 1983) and in an earlier retrospective study with lodgepole pine (JIANG, 1988), dry weight of seedlings was correlated better with field performance than seedling height or diameter. But in our study, seedling height and diameter were correlated better with 9-year tree height than biomass traits. Also in lodgepole pine, FRIES (1989) did not observe any rank correlation between 2-year nursery height and 10-year field height in Sweden. These results suggest that population parameters such as genetic correlations should always be interpreted with caution because they are applicable only to the defined base population and reference testing environments.

Increasing correlation between successive seedling heights and field tree height was observed in jack pine (CARTER et al., 1990), loblolly pine (WILLIAMS, 1987; LI et al., 1992) and Scots pine (ERIKSSON et al., 1993) retrospective studies. Such a pattern is not clear in this lodgepole pine study, and we only observed significant family-means correlation at the end of the second growing seasons (H6 and D6) and one height measurement in the second growing season (H3). The significant family-mean correlation in the second growing season, but not in the first season, is comparable with the same observation in an early testing study in loblolly pine conducted by WILLIAMS (1987). She observed that height growth in the second growth period was well correlated with field height, but seedling height prior to first budset was negatively correlated with field height. This was explained as seedlings requiring a minimum phenological development (transition from free growth to cyclic growth) before juvenile traits become reliable selection criteria.

One interesting correlation is between height increment during dormancy induction period (HG1) and 9-year tree height, which was the highest of all greenhouse-field correlations at site B. HG1 may be an indicator of growth cessation characteristics, or merely reflect growth potential of seedlings, since families with high HG1 either had high growth potential before the dormancy condition was imposed or had a longer growing season due to a slow response to the dormancy induction condition. This possibility may explain the high correlation with later field performance if excellent growth of certain families in the field was mainly due to a longer growing season. If HG1 is closely associated with growth potential at later ages, HG1 may be valuable to either early prediction of 9-year tree height or enhancing selection precision of 9-year height when included in an index. If selection for HG1 results in longer growing seasons, HG1 should be used with caution since selection for HG1 might lengthen growing season and make trees more susceptible to early fall frost in Alberta. Therefore, the traits reflecting growth potential are safer to use for early selection in lodgepole pine in Alberta than traits reflecting longer growing season.

Conclusions

From this lodgepole pine study, we can draw following conclusions:

1. There was considerable and significant genotype by environment interaction in 4 progeny test sites in central Alberta in 9-year lodgepole pine height. The interaction was mainly due to the rank change of family-means among sites.

2. Family effects were significant among the 4 lodgepole pine progeny sites, with individual heritability varying from 0.127 to 0.277 and family-mean heritability from 0.247 to 0.475 within sites.

3. Correlation between greenhouse and 4 field trials in lodgepole pine indicates early testing should be conducted under simulated field conditions.

4. Height and diameter may be better indicators of later field performance than biomass and height increment in the dormancy induction period has potential for early selection in lodgepole pine.

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