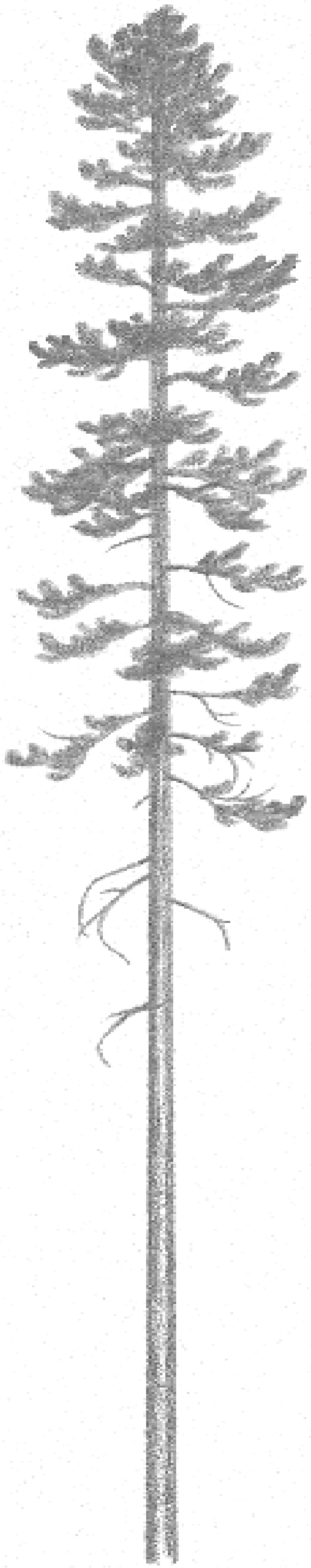

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ALBERTA TREE IMPROVEMENT
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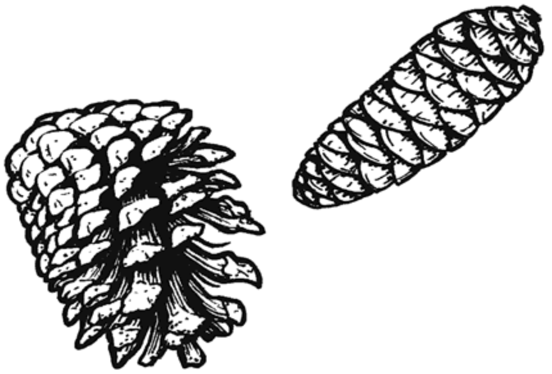

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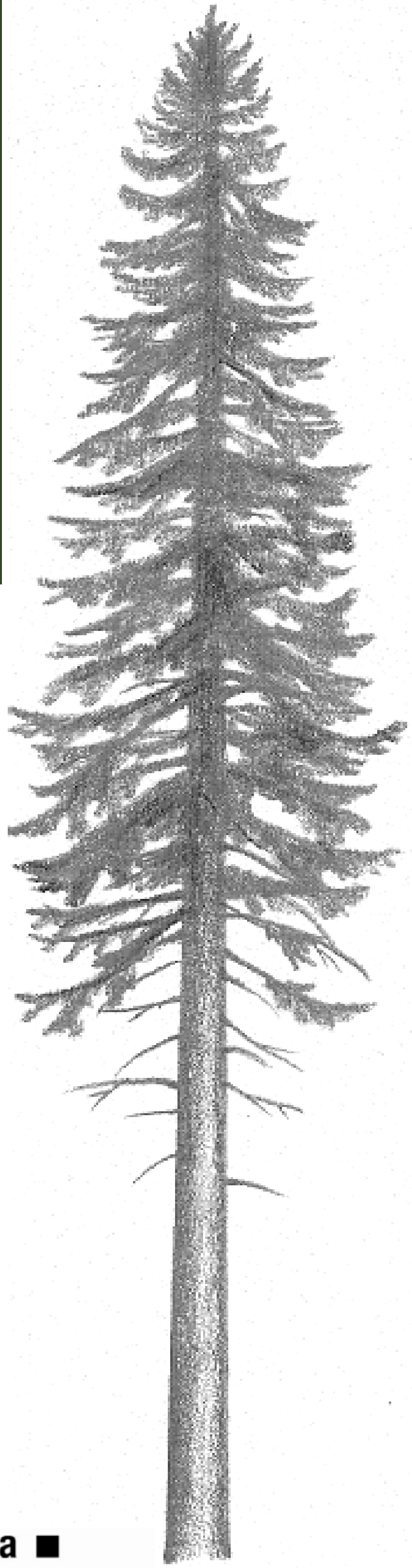

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Deogratias M. Rweyongeza, Leonard K. Barnhardt, Christine Hansen

Alberta Tree Improvement & Seed Centre
Alberta Sustainable Resource Development
Smoky Lake, Alberta Canada

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SUMMARY

Lodgepole pine is ecologically and economically an important species in western North America including Alberta. Provenance and progeny trials both in North America and Europe have shown that the species exhibits high genetic variation, which needs to be considered when choosing seed sources for reforestation and demarcating natural stands for *in-situ* gene conservation. Seed collection for *ex-situ* gene conservation also needs to capture this genetic variation for future forests to maintain adequate evolutionary capacity.

The Alberta Tree Improvement and Seed Centre (Ministry of Alberta Sustainable Resource Development) has been conducting provenance and progeny research for major Alberta conifers for nearly 34 years. As some of these field experiments reach an age where patterns of genetic variation for growth potential can be reliably described, there is a need to transfer the knowledge gained from this research to tree breeders, foresters and educational institutions. This report on the genetics of lodgepole pine in Alberta is the first in a series of technical research papers on conifers that will be produced by the Alberta Tree Improvement and Seed Centre (ATISC).

The report describes results from measurements of 15 year height (H15) and diameter at breast height (D15) made on a series of provenance trials comprised of 23 Alberta populations planted on 9 test sites across the province. Although currently the age of these trials ranges from 19 to 24, only 15 year data for height and diameter are available for all trials. Results from analysis of these data are summarized below.

(1) The study showed that there is high genetic variation for growth potential among lodgepole pine populations in Alberta. The pattern of this variation corresponds to major climatic divisions determined by latitudes and elevation of seed origin whereby,
  (a) Populations with low growth potential on a broad range of environments originated from high latitudes in northern Alberta and high elevations in the Rocky Mountains.
  (b) Populations with high growth potential on a broad range of environments originated from the Lower Foothills (LF) and Lower Boreal Highlands (LBH) between 1000 m and 1100 m above sea level (asl).
  (c) On a test site located at latitude 59^{o}08'N, the local population and those from surrounding northern areas outgrew populations from LF and LBH in the south. This indicates that growth in the extreme north can be maximized only by use of locally selected parent trees.
  (d) Populations from LF between 800 m and 1000 m were among the best populations on a test site located at 1350 m asl in the Montane Natural Sub Region (MO). This suggests that seeds from a hybrid-free zone of the LF can conservatively be transferred to higher elevations in the Upper Foothills (UF) and MO regions to improve growth.

(2) The tendency for genotypes such as populations to be ranked differently on two or more environments is known as genotype by environment interaction (GE). A practically significant GE implies that we cannot use the same seedlots to do reforestation everywhere. In this case, there are specific seedlots for specific planting regions. This study measured GE using a genetic correlation at a population level and results are generalized as follows:

(a) The correlations between Ste B (59°08'N) and all sites located between 49°23'N and 55°17'N ranged from -0.52 to 0.02. This shows that the high latitude region is environmentally very different from the rest of the province and should be reforested only with locally selected trees.

(b) The correlation between Ste I (49°23'N and 1350 m asl) and all sites located in LF and LBH ranged from 0.52 to 0.80. These moderate to high correlations were attributed to better growth of some of the LF populations at sites located in both LF and MO regions. Because none of the UF and MO populations grew well in LF, these correlations show that potential exists in this region for transferring LF seeds upward into UF and MO but not the other way round.

(c) Correlations between sites within LF and LBH ranged from 0.91 to 0.97, which suggests that the test sites represent a broad environmentally similar area that can be treated as one region for reforestation purposes.

The observed pattern of genetic variation and GE has the following practical implications regarding reforestation and conservation of lodgepole pine in Alberta.

(1) Although populations from LF and LBH have high growth potential on a broad range of environments, they cannot be planted north of latitude 57°N to improve height and diameter, because local provenances grew better in this region. Adaptation (survival, growth and reproduction) are governed by environmental extremes and natural cues that follow a regular pattern or occurrence. Thus, growth of high latitude populations is attuned to seasonal changes of winter temperatures and day length also known as photoperiod (e.g., Morgenstern 1996). Theoretically, a warming climate would make northern Alberta warmer in winter allowing vigorous southern populations to be introduced at high latitudes with low risk of late spring or early autumn frosts. Thus, depending on how populations balance their response to extreme winter temperatures that will likely change and a photoperiod that will remain stable, the potential exists for northward movement of seeds. In the meantime, however, it suffices to conclude that maximization of growth at high latitudes is attained through use of local seeds.

(2) At high elevations in the Rocky Mountains in southwestern Alberta, annual growth is constrained by a short growing season and risks of mid-season frosts. Climate change would create longer growing seasons and minimize incidences of mid-season frosts in this region. As the present study shows, this would make it even safer to transfer vigorous populations from LF to higher elevations to improve growth. In the present climate, a conservative upward seed movement of up to 300 m from LF to UF and MO could be permitted. Although few trials have been located at elevations higher than 1400 m, data from progeny trials suggest that as the elevation of the planting site increases, the lower elevation limit for populations that can be suitably transferred upward also increases. For example, whereas UF and MO may be regenerated with seeds from the LF, regeneration of the Subalpine may require seeds from the UF and MO.

(3) This and similar studies have shown that when populations are transferred from high to low latitudes and high to low elevations they attain greater height and diameter growth than growth realized in their native marginal environments. Despite this increase in growth, their

ranking in new environments is still lower than that of local populations. Thus, high latitude or elevation populations cannot be productively transferred to lower or mid latitudes or elevations. Use of these populations in reforestation should be confined to their native environments.

(4) Regional and single-site models developed in this paper are intended to provide a quantitative measure of potential effects on growth of introducing seed from outside the designated reforestation region. When used cautiously, these models should be a useful tool in limiting seed transfer along latitudinal and elevation boundaries to preserve growth potential. Because adaptation is not only limited to growth traits, other potential sources of maladaptation (e.g., frost, drought, insects, diseases and soils characteristics) that would affect survival and reproduction of the species should be considered. In areas where lodgepole and jack pine coexist and hybridize, upward seed transfer should be limited to prevent moving jack pine genes into lodgepole pine areas, which works against conservation objectives by diluting the lodgepole pine gene pool.

The Alberta Forest Genetic Resource Management and Conservation Standards (FGRMS) manual provides guidelines for transferring seeds between seed zones in Alberta. This study and those of other conifers (e.g., Rweyongeza et al. 2007) have shown that seeds can be transferred longer distances across seed zones than previously directed. As a general rule, seed may be transferred by 2^o of latitude from south to north and 200 m from a lower to a higher elevation in the current climate. Seed transfer from north to south by more than 1^o of latitude is expected to cause substantial reduction in growth compared to locally available stands. Likewise, transfer of seed from a higher to a lower elevation by more than 50 m (Figures 15 and 16) is expected to reduce growth compared to locally available stands. At a specified latitude, east-west seed transfer is not considered detrimental to growth, except where such transfer involves a significant change in elevation. Because lodgepole pine is largely a high elevation species, controlling elevation transfer distance will limit the distance with which seed can be transferred from east to west. The need to minimize enhanced hybridization between lodgepole and jack pine will also limit the distance with which seed from the eastern fringe of lodgepole pine natural range can be transferred eastward. It is expected that the results presented in this paper will greatly aid the application and evaluation of lodgepole pine seed transfer variances in Alberta.

1.0 INTRODUCTION

The regeneration of harvested forest lands and conservation of natural tree populations are integral components of sustainable forest management. Although artificial reforestation may be understood merely as a replacement of a predominant pre-harvest species, the type of seeds or vegetative propagules used may be genetically different from those present before harvest. To those individuals not knowledgeable about genetics and the principles of evolutionary biology, reforestation may be as simple as using any available seeds to replant a harvested area. However, according to Dobzhansky (1964), nothing makes sense in biology except in the light of evolution. Here evolution is meant to imply a process whereby a population becomes adapted to its environment by optimizing its survival and reproductive success. Variation in the physical environment the species inhabits, generates genetic variation in the species (e.g., Dobzhansky 1964; Turesson 1923, Langlet 1971). Thus, there is no single seedlot for all cases of reforestation.

The species' natural range is composed of populations that differ genetically to a varying degree. A given population may survive and reproduce on a given environment better than alternative populations. Adaptation describes possession of hereditary characteristics that enable an organism to survive and reproduce optimally in a given environment (e.g., Futuyma 1979). Although the ability to grow to a reproductive age is a component of adaptation of the organism or population to its environment, the ability to grow rapidly in a given environment is not limited to a local population. Therefore, among populations that are able to survive and reproduce in a given environment, selection could be made for rapid growth to maximize growth and yield.

Tree breeding and silviculture complement each other to increase yield per unit area of land. Using genetics and statistical principles, tree breeders identify genetically fast growing populations and individual trees. Silviculture uses principles of plant physiology and land management to enable genetically superior populations and individual trees to attain their full growth potential. This blend of tree breeding and silviculture is commonly known as tree improvement (Zobel and Talbert 1984). Thus, identification of adapted and superior populations for a specific region is a prerequisite for successful silviculture and reforestation. In addition, for future reforestation to succeed populations adapted to present and future climates have to be identified and conserved.

The Alberta Tree Improvement and Seed Centre, Ministry of Sustainable Resource Development has undertaken conifer provenance and progeny testing for almost 34 years. Results from these studies have been published in many journal articles and internal reports. However, this information is not readily available to most foresters and other practitioners outside the research and academic community. In addition, the scope of journal publications is too narrow to have immediate application by practicing foresters or biologists. Therefore, a readily available and practically oriented technical publication is needed to facilitate knowledge transfer from research to field application. This technical research report is the first in a series of reports to be published and disseminated by ATISC. The target audience is college students, practicing foresters and biologists, and tree breeders. An attempt has been made to simplify the presentation of the methodology, results and their interpretation, while including more information needed for practical use than would be found in a journal article. An extensive, though not exhaustive review of the literature about provenance trials in lodgepole pine (*Pinus contorta* Dougl.) has been included to allow readers to see the consistency in the pattern of population differentiation and adaptation in this species.

2.0 THE SPECIES AND GENETICS

Lodgepole pine has a wide natural range extending from 31°N to 64°N and from sea level along the Pacific coast to 3660 m in the Rocky Mountains. It occupies a diverse climate with the minimum temperature ranging from -57°C in the northern Rocky Mountains to 7°C along the coast, and the maximum temperature ranging from 27°C to 38°C (Lotan and Critchfield 1990).

Lodgepole pine has four taxonomically recognized varieties namely, *P. contorta* var. *contorta* found along the Pacific coast, *P.contorta* var. *murrayana* found in the Sierra Nevada, *P. contorta* var. *bolanderi* found in Mendocino County White Mountains of California, and *P. contorta* var. *latifolia* found in the Rocky Mountains (Lotan and Critchfield 1990).

The variety *latifolia* is the only lodgepole pine variety found in Alberta. It is an early successional and fire adapted cordilleran species, which commonly occurs in pure often extensive even aged stands particularly at higher elevations. At lower elevations, in the transition to boreal, montane and parkland forests, it occurs on mixedwood ecosites as an early successional codominant with trembling aspen (*Populus tremuloides* [Michx.]). In these areas, it tends to dominate on poorer and coarser textured upland soils or along bog margins where both soil drainage and nutrient levels are poor. It is well adapted to the mountains and foothills of Alberta, which have shorter and cooler growing seasons but milder winters than are typical for the province. Although it is tolerant of a wide range of climatic, soil, moisture and nutrient conditions, its best growth occurs in well aerated till soils of loam texture and mixed coarse fragment size.

Genetic variation for growth potential in lodgepole pine has been extensively studied in provenance and progeny (family) trials. The largest of these trials is the Illingworth test series in British Columbia (BC) that was established in 1974 (see Ying *et al*. 1985). This series consisted of 140 provenances distributed among varieties *contorta*, *latifolia* and *Murrayana* from across the entire natural range of lodgepole pine. Subsets of these provenances were planted at 60 field sites across 8 BC biogeoclimatic zones. The number and type of provenances shared among sites varied depending on regional site classification, and only 10 of the 140 provenances were planted at all 60 sites (see Wu and Ying 2004).

Early results of the Illingworth tests were published by Ying *et al*. (1985). For example, 13 year height at 11 test sites was negatively correlated with latitude (r = -0.49 to -0.03), longitude (r = -57 to -0.19) and elevation (r = -0.48 to -0.05) of seed origin. The north-south trend shows that northern provenances had lower growth potential than southern ones. The east-west trend in this trial most likely was due to differences in growth potential between the coastal variety *contorta* and inland variety *latifolia*. The low to high elevation trend indicates that high elevation provenances have lower growth potential than low elevations.

Genetic variation for height growth after 20 years of field growth was analyzed and published by Wu and Ying (2004). Combined-site analysis of the 10 provenances common to 57 sites showed that variation among provenances accounted for 52% of the total variance in height growth. This provenance variance was probably inflated by growth differences among varieties, which were not considered in the model.

Wu and Ying (2004) regressed height on the model containing the first degree, second degree, and cross product terms of provenance latitude, longitude and elevation. The coefficients of determination (r^2) ranged from 0.63 to 0.92. At 51 of the 53 sites where regressions permitted estimation of the optimum provenance location, the local provenances were found to be the optimal ones. The degree of optimality described by Wu and Ying (2004) as the difference between predicted height of the local provenance and height at the predicted optimum location decreased from southwest to northeast. This indicates that the likelihood of a local provenance to be optimal was higher at high latitudes and continental environments than at lower latitudes and maritime environments. Along an elevation gradient, optimum provenances were found to originate at a lower elevation than elevation of the test sites for most sites. This suggests that, within a reasonable distance, seeds could be transferred from lower to higher elevation to improve growth. For sites located at elevations below 1000 m, local provenances were the optimum ones.

Studies of genetic variation in lodgepole pine using seedlings and younger trees showed that height growth potential declined linearly with an increase in elevation of seed origin with r^2 of -0.75 (e.g., Rehfeldt 1985). The results of a study of 30 provenances planted at Cluculz and Negro Creek, BC, Ying *et al*. (1989) showed that, based on 18 year height, provenances could be grouped into coastal, coastal-interior transition and central-southern interior sources. The coastal and central-southern interior provenances exhibited the lowest and highest growth potential, respectively. Within the southern-central interior group, regression of height on geographic coordinates had a r^2 of 0.29 (Cluculz) and 0.60 (Negro Creek), and generally, provenances from high latitudes and high elevations exhibited the lowest growth potential. Similar patterns of genetic variation were observed for volume and survival after 20 years in the field (Xie and Ying 1995).

Lodgepole pine is a widely domesticated species in mainland Europe and the United Kingdom. Provenance trials of lodgepole pine in Europe predate those in North America. Only a limited review of European studies is included in this paper. Fletcher (1993) discussed a series of local and International Union of Forest Research Organizations (IUFRO) sponsored lodgepole pine provenance trials in Scotland, which involved many seed sources and test sites. The best provenances for 10 and 15 year height and diameter at breast height (DBH) originated from Vancouver Island, Puget Sound, south coastal BC and the Oregon coast. Provenances with the lowest growth potential originated from the Yukon and Alaska.

Since 1960, a total of 151 lodgepole pine seed sources have been tested in German provenance trials including those organized by IUFRO. These trials included all varieties of lodgepole pine from across the species natural range. Stephan *et al*. (1993) discussed results for two sites each with 100 provenances. For both variety *contorta* and *latifolia*, 7 year height and 20 year DBH declined linearly with an increase in latitude of seed origin. Southern provenances of the variety *contorta* from Washington State and Oregon, and the variety *latifolia* from southern BC had the highest height growth. Northern provenances of the *latifolia* variety from Alberta, Yukon, northern BC and Alaska were slow growing.

Hagner (1993) described survival and growth of provenances of the *latifolia* variety from Canada planted in provenance trials in northern Sweden. On climatically mild sites, provenances from southern BC and Alberta ranked the highest for 7 year height. For sites located further north in harsh climates, provenances from high latitudes in northern British Columbia and Alberta ranked the highest. Generally, high elevation provenances had poorer growth than low elevation provenances from similar latitudes. In addition, northern and high elevation provenances survived much better than southern ones on climatically harsh sites located further north.

Lindgren (1993) examined variation in 42 Canadian provenances of lodgepole pine from north of latitude 50^{o}N (excluding coastal provenances) planted at 10 sites in Sweden. Regression of 18 year height, diameter and volume/ha on latitude of seed origin showed that (1) on marginal sites at high latitudes, northern provenances grew better than provenances from further south; and (2) on mild sites at lower latitudes, southern provenances grew better than high latitude provenances. Using cluster analysis to group provenances based on growth potential, it was shown that (1) northern BC and Yukon provenances were similar even though the environment appears to be different; and (2) other observed groups including northwestern (outside the northern BC-Yukon region) and southwestern with some similarity overlaps between provenances from the Yukon and southwestern Alberta. According to Lindgren (1993) variation appeared to follow a northwest-southeastern direction parallel to the mountain chains, and that this variation was explained by latitude and distance from the coast.

These few reviewed studies illustrate the following frequently observed general trends in boreal coniferous species: (1) when planted in a warm climate, populations from cold regions (high latitudes, high elevations) exhibit lower growth potential than populations from warm regions; (2) when planted at high latitudes, high latitude populations exhibit higher growth potential than populations from warmer regions (low latitudes); (3) the tendency for locally adapted populations to be optimal in their native environments is higher at high latitudes than it is at high elevations; (4) populations from climatically mild environments (low latitudes or low elevations) can be productively moved outside their native environments more than populations from cooler climates (high latitudes or elevations).

Wu and Ying (2001) studied how the ranking of provenances on one site may change substantially on other sites, a phenomenon known as genotype by environment (GE) interaction. They used 10 provenances common to 57 sites in the Illingworth series in British Columbia and the additive main effect and multiplicative interaction (AMMI) technique to establish a relationship between 20 year field height and climate. Their analysis revealed a close association between provenance performance and test sites of similar climate defined by mean annual temperature (MAT), mean annual precipitation (MAP), and frost free period (FFP). Climate (e.g., Rehfeldt *et al*. 1999) has been shown to be the main factor governing genetic variation among tree populations. For provenances from high latitudes, adaptation to day length (photoperiod) is also a major factor governing genetic variation among tree populations (e.g., Vaartaja 1959; Morgenstern 1996).

In the next sections, we discuss the results of a series of lodgepole pine provenance trials in Alberta. We develop models that may be used to predict 15 year height and DBH when a provenance is planted at a specified location. Where similarity exists between sites, data from these sites are combined to develop a regional model.

3.0 MATERIALS AND METHODS

3.1 Experimental Methodology

This report involves the 23 provenances planted on all sites in the Alberta-wide provenance trial series G134 (Table 1; Fig. 1). These include 18 provenances from natural stands of lodgepole pine outside the hybridization zone and 5 provenances from the region where hybridization between lodgepole and jack pine is known to occur. Seedlots were collected as open-pollinated bulk populations or single-tree families from across Alberta in the period between 1976 and 1988. Seedlots collected as single-tree families from specific stands were later bulked in equal proportions to create populations for provenance trials.

In the period between 1985 and 1990, provenances were planted at 9 trial sites (Table 1; Fig. 1) using one-year old seedlings. These seedlings had been grown a year earlier at Pine Ridge Forest Nursery, near Smoky Lake, Alberta. Prior to conversion to experimental stands, the natural vegetation at the test sites was aspen/poplar for Sites A, B, D and F, aspen-spruce mixture for Sites E and H, paper birch-spruce-pine mixture for Site G, poplar-pine-spruce for Site I, and farmland for Site J. Site J has sandy-loam soils and has a long history of agricultural farming including the use of fertilizers and herbicides. Although Site B has the lowest MAP of all sites (Table 1), it has poor drainage and some sections are frequently flooded during spring thaw. All the original vegetation on all sites was cleared and burned. The sites were then disced prior to planting. Field trials were planted in 1985 (A, B and D), 1986 (E and F), 1989 (J) and 1990 (G, H and I).

On all sites the experimental layout was a randomized complete block design with 4 replications and row plots. At Sites D, E and J five-tree plots were used. Elsewhere provenance plots had 9 trees. Except for Site J (3 × 3 metre spacing), trees are spaced 2.5 m apart. Prior to measurement at age 15 years from seed, much of Site F was destroyed by fire. Therefore, in this report, Site F is treated differently due to data limitations.

Table 1. Location and climatic (1961 – 1990) description of lodgepole pine provenances and test sites in the Alberta G134 series of provenance trials.

ID	Location	LAT	LONG	ELEV	MAT	MAP	GDD	NDD	MTCM	MTWM	MSP	NSR
1956 (1)	Cypress Hills	49^{o}30'	110^{o}15'	1160	2.9	421	1372	-1366	-12.2	16.7	288	MO
2163 (2)	Grande Prairie	54^{o}38'	119^{o}07'	1100	1.4	647	1017	-1506	-12.5	13.8	436	UF
2164 (3)	Grande Prairie	54^{o}39'	119^{o}06'	1065	1.4	636	1039	-1504	-12.6	14.0	429	UF
2165 (4)	Fox Creek	54^{o}17'	116^{o}53'	950	2.3	611	1159	-1336	-11.2	14.8	444	LF
2177 (5)	Grande Prairie	54^{o}32'	117^{o}49'	825	2.2	646	1170	-1392	-12.1	14.8	440	LF
2235 (6)	Pelican Mts.	55^{o}38'	113^{o}27'	915	0.1	634	1065	-1986	-17.0	14.7	462	LF
2237 (7)	Cameron Hills	59^{o}42'	117^{o}59'	730	-3.7	489	893	-3066	-23.6	14.2	299	SAT
2238 (8)	Watt Mountain	58^{o}42'	117^{o}23'	590	-2.3	487	1034	-2740	-21.8	14.9	322	LBH
2285 (9)	Virginia Hills	54^{o}28'	115^{o}52'	1127	1.2	642	1009	-1553	-12.5	13.9	467	UF
2286 (10)	Swan Hills	54^{o}44'	115^{o}18'	1064	1.2	640	1023	-1564	-12.7	14.1	460	UF
2287 (11)	Swan Hills	54^{o}42'	115^{o}30'	1130	1.1	646	987	-1548	-12.3	13.8	459	UF
2288 (12)	Judy Creek	54^{o}26'	115^{o}35'	1097	1.3	612	1034	-1554	-12.6	14.1	440	UF
2312 (13)	Blue Ridge	54^{o}06'	115^{o}32'	978	1.5	596	1102	-1560	-13.1	14.5	447	LF
2313 (14)	Chickadee Ck	54^{o}13'	115^{o}54'	829	1.9	573	1188	-1504	-13.0	15.0	428	LF
2314 (15)	Virginia Hills	54^{o}16'	116^{o}13'	978	1.8	603	1111	-1468	-12.2	14.5	447	LF
2494 (16)	Hotchkiss Rd.	57^{o}14'	118^{o}16'	792	-1.2	513	1025	-2348	-19.7	14.5	344	LBH
2497 (17)	Clear Hills	56^{o}36'	119^{o}42'	960	-0.7	513	977	-2142	-17.7	15.6	325	LBH
2504 (18)	Saddle Hills	55^{o}44'	119^{o}40'	825	0.7	522	1109	-1812	-15.4	14.6	331	LF
2505 (19)	Fallen Timber Ck.	51^{o}29'	115^{o}11'	1650	1.1	576	839	-1396	-11.2	12.7	417	UF
2506 (20)	Prairie Ck.	52^{o}16'	115^{o}13'	1175	1.8	626	1002	-1357	-11.7	13.8	476	LF
2507 (21)	Colt Creek	52^{o}38'	116^{o}05'	1520	1.0	629	851	-1452	-11.3	12.9	464	UF
2508 (22)	Hinton	53^{o}12'	117^{o}32'	1360	1.4	594	920	-1382	-11.5	13.2	424	UF
2509 (23)	Edson River	53^{o}44'	116^{o}35'	1080	1.9	599	1073	-1399	-11.3	14.2	450	LF
A	Calling Lake (A)	55^{o}17'	113^{o}09'	625	0.9	488	1254	-1901	-17.5	15.9	359	CM
B	Hay River (B)	59^{o}08'	117^{o}34'	370	-2.3	410	1137	-2862	-23.1	15.7	268	CM
D	Swartz Ck. (D)	53^{o}23'	116^{o}30'	990	2.1	580	1123	-1380	-11.6	14.5	432	LF
E	Hangingstone (E)	56^{o}23'	111^{o}26'	540	0.3	531	1255	-2114	-18.7	16.1	368	CM
F	Mitsue South (F)	55^{o}06'	114^{o}32'	762	1.1	566	1176	-1753	-15.1	15.2	413	LF
G	Carson Lake (G)	54^{o}24'	115^{o}34'	1006	1.4	594	1087	-1547	-12.8	14.5	433	LF
H	Diamond Hills (H)	52^{o}37'	115^{o}05'	990	2.5	585	1224	-1357	-12.2	15.1	437	LF
I	Castle River (I)	49^{o}23'	114^{o}20'	1350	3.6	776	1156	- 946	-8.1	14.9	396	MO
J	Pine Ridge (J)	54^{o}04'	112^{o}12'	610	1.5	442	1340	-1806	-16.2	16.1	338	DM

Numeric and character ID represent provenance and test site, respectively. LAT. –latitude; LONG. Longitude; ELEV. Elevation; MAT –mean annual temperature, MAP –mean annual precipitation (mm); GDD –growing degree days (> 5^{o}C); NDD –negative degree days (< 0^{o}C); MTCM –mean temperature for the coldest month (^{o}C); MTWM –mean temperature for the warmest month (^{o}C); MSP –mean summer (April-September) precipitation (mm); NSR –Natural Subregion. MO –Montane; CM –Central Mixedwood; LF –Lower Foothills; UF –Upper Foothills; LBH –Lower Boreal Highlands; SAT –Subarctic; DM –Dry Mixedwood.

Field assessments made at ages 5, 10 and 15 years from seed included scores for survival, physical and climatic damages, insect damage, incidence of western gall rust damage, and measurement for height and DBH. This report covers only provenance variation for height (H15) and DBH (D15) at age 15 years from seed. Earlier analyses indicated that provenance survival did not follow any specific geographic pattern (see Rweyongeza and Yang 2005a). Consequently, survival data are only tabulated along with height and DBH in this report without further discussion. The objective is to allow readers to gauge growth superiority of the provenance against its survival expectation on a given site.

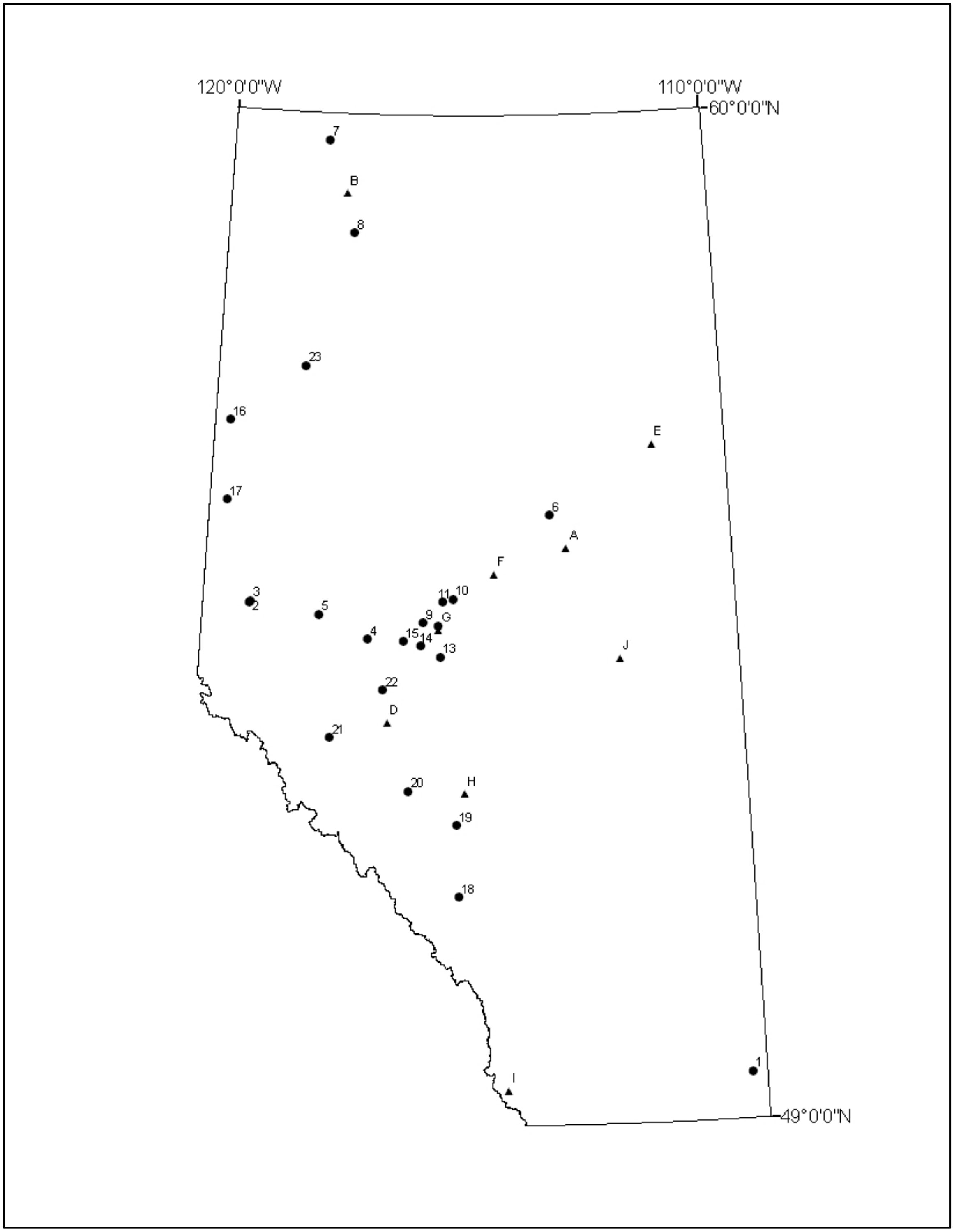

Fig. 1 Location of lodgepole pine provenances (numeric ID) and test sites (character ID) in Alberta.

3.2 Data Analysis

Data was analyzed on an individual site basis and then combined and analyzed across sites. The single-site analysis of variance model is described as follows:

$$Y_{ijn} = \mu + \alpha_i + \beta_j + \alpha\beta_{ij} + \varepsilon_{ijn} \qquad [1]$$

where Y_{ijn} is height (H15) or diameter (D15) for tree n of provenance j in replication i; μ is the general site mean; α_i is the replication effect; β_j is the provenance effect; $\alpha\beta_{ij}$ is the interaction effect of replication and provenance (experimental error); and ε_{ijn} is the residual. Except μ, all effects on the right side of the model were considered random with zero expectation and respective variance components. The combined site model is described as follows:

$$Y_{kijn} = \mu + \gamma_k + \alpha_{i(k)} + \beta_j + \gamma\beta_{kj} + \alpha_{ik}\beta_j + \varepsilon_{kijn} \qquad [2]$$

where γ_k is the effect of test Site K and $\gamma\beta_{kj}$ is the provenance × site interaction (also known as genotype × site interaction). All other terms correspond to those defined earlier for the single site model. Except μ and γ, all terms on the right side of the model were considered random with zero expectation and respective variance components. Both models were fitted with the mixed models procedure in SAS (SAS Inst 2004). Although variance components and their proportions as percentages of the total variance were predicted, reporting and discussion of these statistics is considered out of scope for this paper.

Previous work (see Rweyongeza and Yang 2005a; Rweyongeza et al. 2007) showed that height and DBH growth potential followed the following polynomial function. Thus, to analyze the pattern of optimal growth potential, provenance means predicted from the individual site analysis of the variance model were fitted to the following regression model:

$$Y_j = \beta_0 + \beta_1 X_j + \beta_2 X_j^{\ 2} + \varepsilon_j \qquad [3]$$

where Y_i is H15 or D15 for provenance j; X_j is latitude or elevation for provenance j; β_0, β_1 and β_2 are regression coefficients; and ε_j is the residual.

Used in this manner, latitude and elevation are surrogate variables for climate (especially temperature) of the seed origin. Moreover, latitude is a surrogate variable for day length, also known as photoperiod. The regression of a biological variable such as growth potential on a location or environmental variable of seed origin (e.g., latitude, temperature) is called a transfer function. It expresses the degree to which growth potential of the provenance is affected when trees are planted outside their native location. Although exceptions may be found, the strength of the regression depends on the extent with which individual populations have been environmentally displaced from their location of origin. The greater the environmental difference between provenance and test site location, the greater the transfer distance.

The single-variable second-degree polynomial regression is sufficient to describe the pattern of genetic variation only when the continuum of the predictor variable such as temperature for which latitude or elevation are surrogates is justifiably the only cause of the increase, levelling and subsequent decline in growth potential. For example, if variation in temperature along a latitudinal gradient is such that the lowest and highest temperature occurs at the lowest and highest latitude, respectively, a curvilinear transfer function in growth potential is justified. In this case, growth increases with an increase in temperature to reach the maximum growth at the optimum temperature and thereafter growth declines as the optimum temperature is exceeded. More often, however, low temperatures or a short growing season may occur at both the lowest and highest latitude. This happens when the latitudinal gradient is intersected by another climate-controlling gradient such as elevation. This is particularly true for Alberta where the southward increase in spring and summer temperatures, and thus the length of the growing season is interrupted by the south westward increase in elevation. Consequently, the growing season, and specifically the frost free period is short in northern Alberta due to high latitude, and in the southwest due to high elevation (see AARD 2005). In this case, the single-variable second-degree polynomial transfer function shows that growth potential is controlled by more than one predictor variable jointly determining provenance climate. Thus, a combination of predictor variables in an easily biologically interpretable regression provides a better explanation of the genetic variation in growth potential than a single-variable quadratic regression.

In this report, the factorial regression combining latitude and elevation of seed origin was fitted to the data to describe provenance variation in growth potential. This regression is described as follows:

$$Y_j = \beta_0 + \beta_1 X_j + \beta_2 Z_j + \beta_3 X_j Z_j + \varepsilon_j \qquad [4]$$

where Y_i is H15 or D15 for provenance j; X_j is latitude for provenance j; Z_j is elevation for provenance j; β_0, β_1 β_2 and β_3 are regression coefficients; and ε_j is the residual. All regressions were fitted in PROC REG (SAS Inst. 2004).

This regression recognizes that, for Alberta, a change in latitude involves a reciprocal change in elevation of seed origin. When used as a predictive model, this regression provides a single estimate of H15 or D15 a provenance from defined latitude and elevation is expected to attain at a specified test site. When using single-variable polynomial regression models, latitude and elevation may individually predict different heights or diameters for the same provenance.

4.0 RESULTS AND DISCUSSION

4.1 Mean Survival and Growth

Site means and range of provenance means on individual sites and combined-sites are summarized in Table 2. After 14 years in the field, overall mean survival remained high (> 80%), except for Sites B and I, which had about 45% and 40% mortality, respectively. High mortality at both sites occurred during early stages of field establishment. High mortality at Site B is probably due to a combination of cold winters, periodic drought and localized flooding due to poor drainage. Mortality at Site I could have been caused by frosts.

Table 2. Site means, range of provenance means for growth and survival for height and DBH at age 15 years.

Site	Survival (%)	Height Growth (m)	DBH Growth (cm)
Calling Lake (A)	90.8 ± 1.5 (75.0 – 96.9)	4.44 ± 0.30 (3.56 – 5.34)	7.06 ± 0.57 (4.87 – 9.33)
Hay River (B)	55.0 ± 3.8 (3.1 – 93.8)	3.65 ± 0.19 (3.02 – 4.46)	6.14 ± 0.25 (5.56 – 7.35)
Swartz Creek (D)	83.5 ± 2.2 (65 0 – 100)	5.75 ± 0.21 (4.50 – 6.55)	9.99 ± 0.36 (5.96 – 11.47)
Hangingstone (E)	91.3 ± 1.6 (75.0 – 100)	6.27 ± 0.33 (5.60 – 6.70)	9.84 ± 0.40 (7.99 – 11.11)
Carson Lake (G)	89.2 ± 1.2 (71.9 – 100)	5.43 ± 0.11 (4.54 – 6.06)	8.62 ± 0.21 (6.50 – 9.66)
Diamond Hills (H)	91.7 ± 1.1 (84.4 – 100)	5.04 ± 0.13 (3.65 – 5.95)	8.42 ± 0.28 (5.08 – 10.33)
Castle River (I)	59.7 ± 2.2 (40.6 – 81.3)	3.14 ± 0.09 (2.36 – 3.74)	4.61 – 0.18 (3.20 – 5.82)
Pine Ridge (J)	91.5 ± 1.3 (60.0 – 100)	3.99 ± 0.07 (3.48 – 4.49)	8.31 – 0.22 (6.93 – 9.71)
Combined-Sites	81.5 ± 0.9 (74.8 – 90.3)	4.62 ± 0.31 (3.88 – 5.05)	7.65 ± 0.61 (5.52 – 8.90)

Height and diameter differences among sites are partly due to site differences in precipitation, length of the growing season as defined by growing degree days (GDD), and probably site productivity related to soil characteristics. The lowest growth occurred at Sites B and I (Table 2), which have the least favourable growing conditions. Site B has the lowest precipitation relative to GDD, which is an indicator of drought stress during the growing season. While its GDD is generally high (Table 1), the number of days with a temperature greater than 5°C is low (see AARD 2005) suggesting that active growth processes may be confined to a short period. Incidence of mid-season frosts is probably responsible for low tree growth at Site I. At Site J where sandy soils, low precipitation and high GDD translate to low moisture availability, low growth potential is largely attributed to drought, even though the trial was watered during the first five years to ensure adequate survival.

Sites located in the Lower Foothills (D, G and H) had relatively similar growth potential with a site mean for H15 ranging from 5.04 m to 5.75 m. Although Site F (Lower Foothills) had low survival due to fire damage, its mean H15 (4.99 m) is consistent with growth at the other Lower Foothills sites. Mean D15 at Site F was 9.87 cm, which is also consistent with D15 for other Lower Foothills sites (Table 2).

4.2 Patterns of Optimal Growth

Table 3 contains regression coefficients, coefficients of determination (R^2) and a predicted optimum source of provenances of highest growth potential on specific test sites. Single-variable transfer functions are also plotted in Figures 2 and 3.

Table 3. Coefficients of determination, predicted optimum latitude and elevation of seed origin, and regression coefficients for the factorial model for lodgepole pine in G134 trials.

Site	Trait	Latitude		Elevation		Latitude and Elevation				
		R^2	Optimum	R^2	Optimum	Intercept	LAT	ELEV	LAT × ELEV	R^2
A	H15	0.30*	54°17’	0.21	1094	29.922	-0.4599	-0.02302	0.0004179	0.37*
	D15	0.30*	53°48’	0.21	1117	63.794	-1.0168	-0.04648	0.0008356	0.40*
B	H15	0.18	-	0.26*	-	-10.018	0.2598	0.01291	-0.0002472	0.25
	D15	0.08	-	0.10	-	-2.414	0.1714	0.01072	-0.0002118	0.13
D	H15	0.56***	54°44’	0.25	1020	41.223	-0.6348	-0.03273	0.0005891	0.55**
	D15	0.73***	54°31’	0.27*	1074	108.348	-1.7770	-0.09148	0.0016630	0.62***
E	H15	0.41**	56°19’	0.11	-	10.220	-0.0742	-0.00772	0.0001444	0.25
	D15	0.46**	55°07’	0.10	1017	40.705	-0.5682	-0.03516	0.0006514	0.27
G	H15	0.51***	54°46’	0.50**	1029	40.433	-0.6237	-0.03186	0.0005706	0.75***
	D15	0.46**	54°11’	0.45**	1064	76.049	-1.1938	-0.05477	0.0009699	0.76***
H	H15	0.58***	54°46’	0.41**	1041	47.778	-0.7682	-0.04056	0.0007337	0.68***
	D15	0.54***	54°28’	0.38**	1061	100.234	-1.6412	-0.08089	0.0014524	0.66***
I	H15	0.42**	53°15’	0.23	1186	21.460	-0.3318	-0.01444	0.0002626	0.43*
	D15	0.41**	52°34’	0.23	1229	37.769	-0.6009	-0.02402	0.0004366	0.41*
J	H15	0.21	54°18’	0.13	1083	12.886	-0.1594	-0.00774	0.0001395	0.24
	D15	0.17	52°39’	0.05	1394	20.359	-0.2178	-0.00713	0.0001288	0.12

* -$P < 0.05$; ** -$P < 0.01$; *** -$P < 0.001$

Generally, height and diameter were correlated more with latitude than elevation of seed origin. The lodgepole pine variety *latifolia* found in Alberta is predominantly a high elevation variety. Of the provenances covered in this report, only three provenances (19, 21 and 22) originated above 1200 m, whereas only two provenances (7 and 8) originated below 800 m. All other provenances are from between 800 m and 1200 m. Thus, lack of a strong elevation (Table 1) trend is probably due to limited sampling along the elevation gradient.

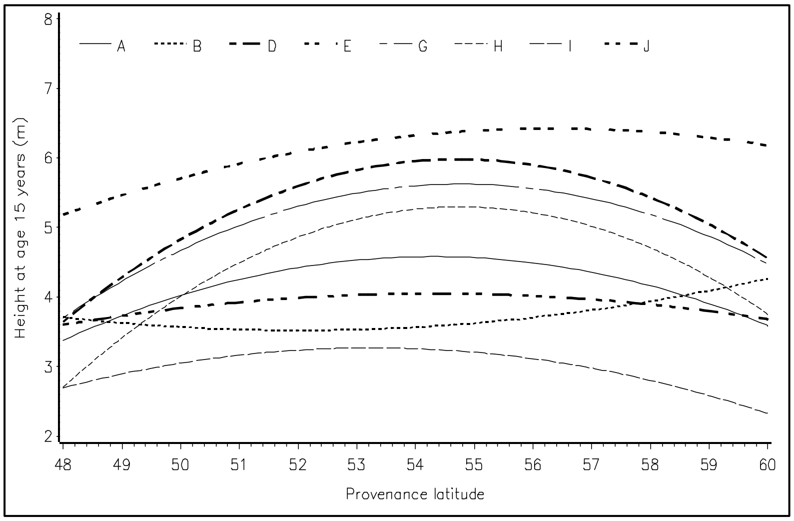

Fig. 2 Height growth potential in latitude of seed origin.

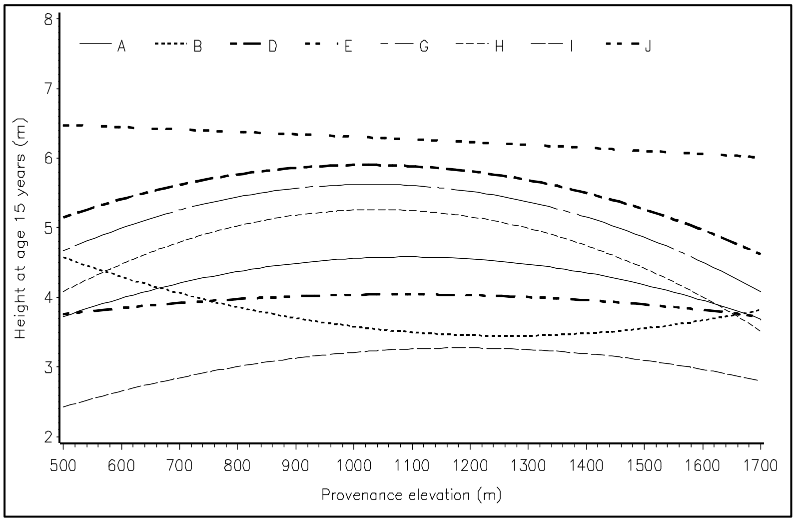

Fig. 3 Height growth potential in relation to elevation of seed origin.
(see Table 3 for details).

The transfer functions for Site B were concave with the minimum instead of maximum stationary point (Figures 2 and 3). The latitudinal transfer function shows that the best provenances for Site B and similar latitudinal regions are expected to originate from high latitudes. This is in sharp contrast with transfer functions of other sites where except for Site E, the optimum latitudinal source lies south of 55^{o}N (Table 3).

The pattern of variation at Site B illustrates the strength of local adaptation at high latitudes and elevations. Site B is located at 59^{o}08'N with negative degree days (NDD) of -2862 and mean temperature of coldest month (MTCM) of -23^{o}C (Table 1). Provenances with winter conditions similar to Site B are 7 and 8, which originated north of latitude 58^{o}N (Table 1). Although these provenances originated from relatively higher elevations than Site B, they are the most local to Site B, and like Site B have a more boreal climate. Table 4 shows provenances whose H15 was greater than two standard errors from the site mean. For Site B, these provenances include 7 and 8. This is in sharp contrast with performance of these provenances at other sites. Provenance 7 was ranked last at 6 of the remaining 7 sites and 21 at Site I.

Table 4. Mean height, diameter and survival for provenances whose 15 year height was greater than the site mean plus two standard errors.

Site	Prov	H15 (m)	D15 (cm)	S15 (%)	Site	Prov	H15 (m)	D15 (cm)	S15 (%)
A	3	5.09 ± 0.33	8.54 ± 0.65	87.5	H	3	5.50 ± 0.25	9.36 ± 0.57	93.8
	9	5.19 ± 0.33	8.59 ± 0.64	90.2		4	5.91 ± 0.24	10.24 ± 0.57	96.9
	13	5.34 ± 0.33	9.33 ± 0.65	87.5		6	5.36 ± 0.26	9.14 ± 0.59	84.4
						9	5.55 ± 0.24	9.25 ± 0.56	96.9
B	5	4.28 ± 0.35	6.65 ± 0.57	93.8		12	5.35 ± 0.25	8.99 ± 0.58	90.6
	7	4.41 ± 0.37	6.71 ± 0.60	81.3		13	5.42 ± 0.24	9.71 ± 0.56	96.9
	8	4.30 ± 0.62	6.84 ± 0.84	37.5		14	5.95 ± 0.25	10.33 ± 0.58	90.6
	13	4.46 ± 0.55	7.35 ± 0.80	40.6		23	5.43 ± 0.25	9.13 ± 0.57	93.8
D	4	6.55 ± 0.28	11.44 ± 0.55	80.0	I	3	3.33 ± 0.28	4.85 ± 0.52	56.3
	5	6.43 ± 0.26	11.12 ± 0.52	95.0		4	3.49 ± 0.28	5.24 ± 0.51	56.3
	6	6.18 ± 0.27	10.46 ± 0.53	90.0		5	3.55 ± 0.28	5.70 ± 0.53	50.0
	14	6.37 ± 0.27	11.47 ± 0.54	85.0		15	3.64 ± 0.26	5.78 ± 0.49	65.6
	18	6.38 ± 0.26	11.41 ± 0.51	100		17	3.45 ± 0.31	5.13 ± 0.57	40.6
	23	6.44 ± 0.26	11.30 ± 0.52	95.0		20	3.43 ± 0.26	5.29 ± 0.47	71.9
						23	3.74 ± 0.27	5.82 ± 0.49	62.5
G	2	5.90 ± 0.23	9.45 ± 0.49	84.4					
	4	6.06 ± 0.23	9.60 ± 0.48	87.5	J	3	4.24 ± 0.21	9.13 ± 0.62	90.0
	5	5.98 ± 0.23	9.66 ± 0.48	87.5		9	4.19 ± 0.25	8.88 ± 0.73	60.0
	9	5.69 ± 0.23	9.24 ± 0.48	87.5		11	4.22 ± 0.22	8.88 ± 0.63	85.0
	13	5.70 ± 0.22	9.42 ± 0.46	100		13	4.49 ± 0.21	9.71 ± 0.61	95.0
	14	5.83 ± 0.23	9.49 ± 0.48	87.5					
	15	5.85 ± 0.23	9.52 ± 0.48	87.5	E^+	8	6.70 ± 0.37	10.10 ± 0.64	85.0
	18	5.93 ± 0.24	9.26 ± 0.50	78.1		9	6.64 ± 0.34	11.11 ± 0.60	96.7
	23	5.86 ± 0.22	9.17 ± 0.47	93.8					

+ -Data for Site E are for provenances whose H15 was greater than the site mean plus one standard, since no provenance exceeded the site mean plus two standard errors.

Although provenance 8 was ranked 1 and 8 at Sites E and J, respectively, it was ranked between 17 and 22 at all other sites. This shows that provenances from cold boreal regions are not suitable for reforestation in warm environments, but they are the most suitable seed sources in their native environments.

The better growth potential of provenance 8 at Sites E and J could also be explained in terms of climatic similarity between the provenance and the test site. Of the 8 test sites used in this study, Site E has the second coldest winters with NDD of -2114 and MTCM of -18.7^{o}C. Thus, provenance 8 is climatically more similar to Site E than most provenances. This analogy could be extended to explain the better performance of provenance 8 at Site J as well.

Another group of provenances whose growth potential needs to be discussed includes provenances 16 and 17. These provenances are of mid-northwestern origin with cooler winters than most provenances (Table 1). Because of their mid-northern origin, these provenances from the Lower Boreal Highlands have cooler winters than Sites A, E and J located in the mixedwood boreal forest. At the time of seed collection and in our previous work (e.g., Rweyongeza et al. 2007), these provenances were treated as putative hybrids. Height growth ranking of these provenances varied on different sites with provenance 17 growing better than 16 on most sites. On cooler sites (E and J), these provenances had above average heights. This suggests that climatic similarity between provenances and test sites played a role in the observed growth potential of these provenances. Provenance 16 originates from a more northern and boreal climate than 17. This would partly explain its better height growth potential than 17 at northernmost Sites A, B and E.

The other provenances (13, 14 and 15) previously treated as hybrids originated from around latitude 54^{o}N and elevations between 800 m and 1000 m in the Lower Foothills. Their geography and climate are so similar that they would be expected to have similar growth potential on the same sites. However, the three provenances showed contrasting growth potential at many of the test sites. For example, provenance 13 was ranked first on continental sites (A, B and J). In contrast, provenance 15 was ranked 20 at Sites B and J. Height (H15) of provenance 13 exceeded that of 15 by 119 cm and 45 cm at Sites B and J, respectively. Likewise, DBH of provenance 13 exceeded that of 15 by 1.65 cm and 1.85 cm at Sites B and J, respectively. At Site I, provenance 15 and 13 were ranked 2 and 17, respectively. Provenance 15 exceeded 13 by 87 cm (H15) and 1.58 cm (D15). Elsewhere, 15 appeared to be an average provenance ranked between 6 and 9. Provenance 14 was ranked 1 at Site H (5.95 m) and 22 at Site E (5.89 m), even though it attained almost the same height at both sites. Elsewhere, 14 was an average provenance ranked between 4 and 12. On test sites located in the Lower Foothills (D, G and H), 13 was an average provenance ranked between 6 and 9.

4.3 Genotype-Environment Interaction

Genotype × environment interaction (GE) describes a statistical condition whereby genetic entities such as provenances are ranked differently in different environments or the magnitudes of their differences differ between environments (see Falconer and Mackay 1996). In other words, provenances may be superior in terms of growth potential in some environments and inferior in others. This crossover interaction affects the choice of provenances for reforestation in different environments. Alternatively, the absolute differences in size attained by a pair of provenances may be large on some sites and small on others while the ranking of the provenances among environments remains unchanged. This scale effect does not affect choice of provenances for reforestation in different environments.

At a provenance level, GE interaction is expressed as the provenance × site interaction. Because provenances are normally adapted to their natural environments, GE interaction is frequently observed in range-wide provenance trials (e.g., Wu and Ying 2001). For reforestation, provinces or regional areas are divided into seed zones and breeding regions. These land divisions are either demarcated based on vegetation, soil and climatic information or provenance test results. They are designed to be climatically similar so that reforestation can be undertaken with minimum risk of genetic maladaptation. This implies minimizing GE interaction within a seed zone or breeding region.

Although there are different ways of quantifying GE interaction, their review is considered out of the scope of this report. Among other methods, the extent of the crossover interaction can be expressed as a genetic correlation of the same trait between pairs of test sites (see Falconer and Mackay 1996). In this case, a trait such as height at a specific age attained in two environments is considered to represent two potentially different traits. The genetic correlation between these two traits measures the similarity of the two environments. In forest genetics, this type of correlation has come to be known as Type B correlation (see Burdon 1977), because it is a correlation between measurements taken from different individuals of the same family or provenance raised in different environments. Its opposite is the Type A correlation, which is the standard correlation coefficient between two different traits or the same traits but at different ages measured on the same individual in the same environment.

In the present trials, the combined-site analysis revealed a significant ($P < 0.0001$) GE interaction for both H15 and D15. Compared with the variance among provenances, the provenance × site interaction variance component was 87.4% and 64.1% of the provenance variance component for H15 and D15, respectively. This shows that GE interaction is of practical significance in the artificial regeneration of lodgepole pine in Alberta (e.g., Shelbourne 1972). The Type B correlation between pairs of test sites was estimated according to Robertson (1959). The total of 56 pairs of correlations (both H15 and D15) revealed the following general patterns.

(1) The correlations between Site B, the most northern and lowest elevation site, and all other sites were very low and predominantly negative for both H15 and D15. Except for a 0.41 correlation (D15) between Sites B and J (boreal mixedwood lowland sites), correlations between Site B and all other sites ranged from -0.52 to 0.02. Site B represents the cold, high latitude part of the province where local provenances grew better than provenances from the south, but grew poorly when planted outside the region. This pattern of variation in growth potential is the cause of the negative Type B correlations.

(2) The correlations between Site I (most southern and highest elevation site) and other sites had two general patterns. First, correlations between Site I and sites located in the boreal forest region (A, E and J) were low ranging from 0.04 to 0.46, the lowest being between Sites I and J. These correlations show that optimizing growth and yield in the boreal region and Montane (MO) region similar to Site I would require different suites of provenances. Second, the correlations between Site I and sites located in the Lower Foothills (D, G and H) were generally moderate ranging from 0.52 to 0.80 for both H15 and D15. These correlations are due to the fact that some of the best provenances at Site I originated from the Lower Foothills (LF). This suggests that provenances could be conservatively transferred from lower elevations (LF) to higher elevations in the Montane and Upper Foothills to improve growth and yield.

(3) The correlations of sites located in the boreal forest region (A, E and J) with sites located in the LF (D, G and H) were moderate ranging from 0.34 to 0.79, the highest being those involving Site A ($r = 0.56$ to 0.79). The boreal region represented by Sites A, E and J (elevation 540 to 625 m) is more continental with colder winters (NDD = -1806 to -2114) and warmer summers (GDD = 1254 to 1340) than most provenances that are largely from the Foothills area (Table 1). Because none of the tested provenances originated from this part of the boreal forest, the moderate correlations observed in this study may be difficult to interpret. As it will be shown later, the response surface for Site A (Fig. 10) is similar to those of LF sites.

(4) The correlations between sites within the boreal forest (A, E and J) were mixed. The correlation between A and E for D15 was 0.53, whereas all other correlations (A & E, J & E)

ranged from 0.07 to 0.25. This shows that Sites A and J were generally not correlated with Site E. This is also clearly visible from the differences of the Site E response surface (Fig. 11) with response surfaces of Sites A and J (Figures 10 and 12). The correlations between Sites A and J were 0.93 and 0.98 for D15 and H15, respectively, although no significant provenance variation was observed at Site J (Table 3). Thus, these near perfect correlations are most likely associated with high standard errors. Pearson's correlations for family means between Sites A and J were 0.72 (H15) and 0.69 (D15).

(5) The correlations among sites within the LF were high for both H15 and D15 ranging from 0.91 to 0.97. The corresponding Pearson's correlations for provenance means ranged from 0.83 to 0.88. Both types of correlations show a consistent pattern of provenance ranking among sites within the Lower Foothills region.

4.4 Prediction Models

The pattern of optimal growth potential and GE interaction discussed in earlier sections show that regional generalizations could be made about the optimality of lodgepole pine provenances in Alberta. These generalizations could then serve as criteria for developing guidelines for seed movement within the province. Because of terrain heterogeneity, especially in the western part of the province, movement of seeds in Alberta should guard against adversely displacing the seed in terms of both the latitude and elevation. In other words, there has to be guidelines regarding movement of seeds northward or southward and from low to high elevation or vice versa from their origin. Considering the pattern of optimum growth and GE interaction regional generalizations have been developed.

4.4.1 Lower Foothills

Table 1 shows that although Sites D, G and H differ in terms of latitudes, they are located at approximately the same elevation. The sites are highly correlated genetically and phenotypically and the regression coefficients from their factorial regressions (Table 3) and response surfaces (Figures 4, 5 and 6) are very similar. Thus, data for the three sites were combined to fit a single factorial regression representing the LF region (n = 69) described by the following equation:

$$Y_{(H15)} = \beta_0 - \beta_1 \times lat - \beta_2 \times elev + \beta_3 \times lat \times elev \qquad \text{[Model 1]}$$

where

$Y_{(H15)}$ = Expected provenance mean height in metres at age 15 years,

β_0 = 43.14451,

β_1 = 0.67555,

β_2 = 0.03505,

β_3 = 0.00063113,

lat = latitude (^{o}N) at a place of seed origin with minutes expressed as decimals, and

$elev$ = provenance elevation in metres.

This model has R^2 of 0.49 ($P < 0.0001$). However, Table 3 shows that individual site regressions had R^2 of 0.55 to 0.75. Table 2 shows that total heights attained at the three sites whose data were combined differ. Because the extent with which the model fits the data (R^2) depends on the vertical distance from the observed data to the fitted common regression ($y_i - \hat{y}_i$ or residual), the scale difference between sites is the cause of the reduction in R^2. Dividing each data point by its site mean [$t(y) = \bar{y}_i / \bar{y}_s$], where $t(y)$ is partially standardized height, $\bar{y}_i$ is mean height for provenance i, and $\bar{y}_s$ is site mean], to harmonize the scale among sites before fitting the regression results in an R^2 of 0.64 ($P < 0.0001$), which is approximately the same as the average individual site regression R^2s (Table 3).

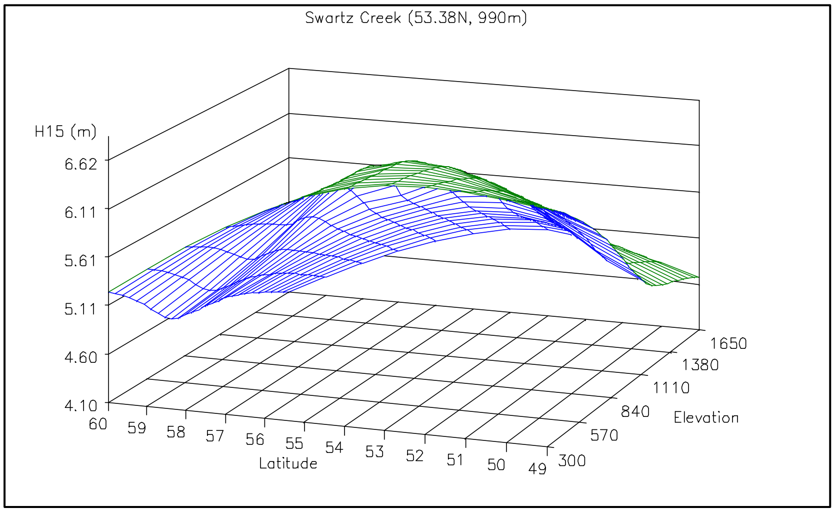

Fig. 4 Pattern of height growth at Site D.

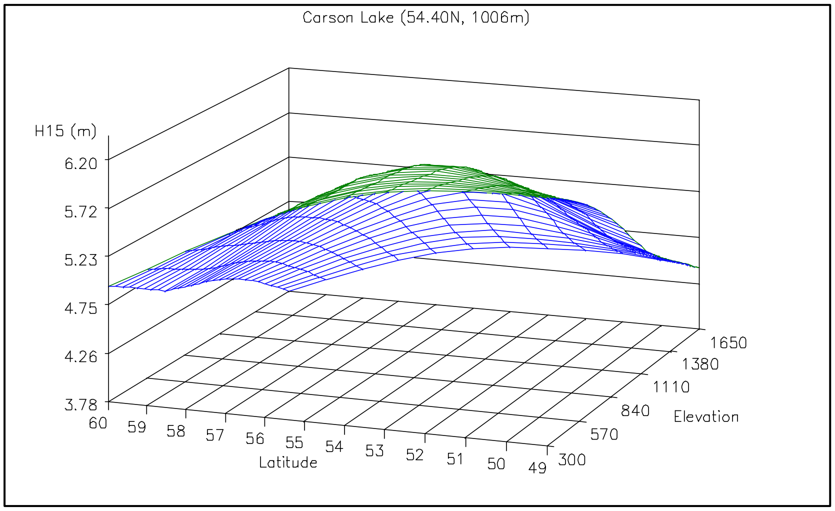

Fig. 5 Pattern of height growth at Site G.

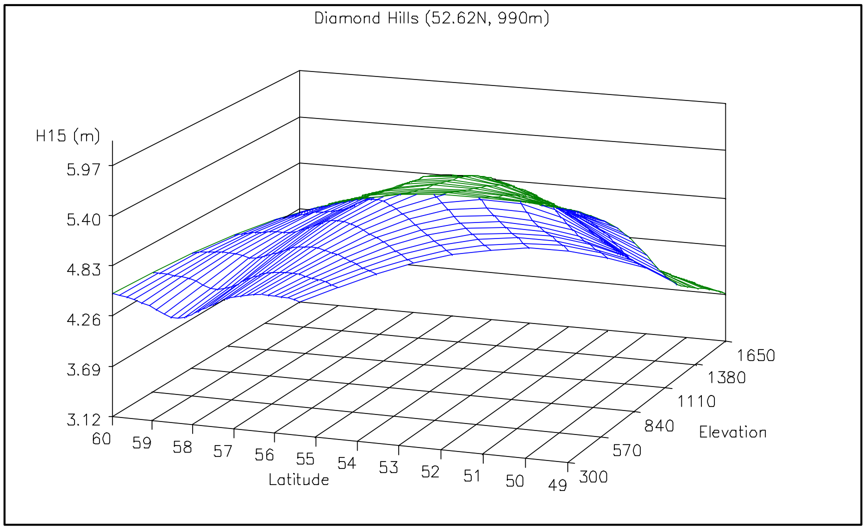

Fig. 6 Pattern of height growth at Site H.

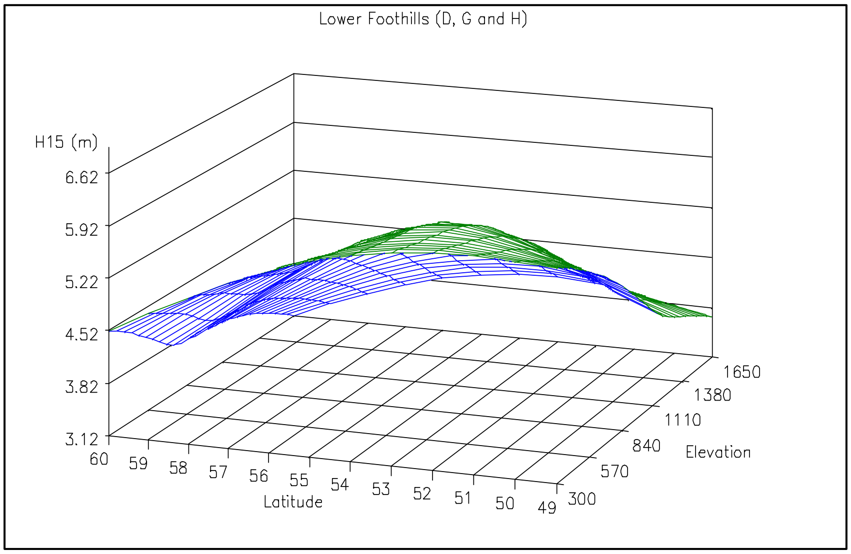

Fig. 7. Pattern of height growth in Alberta's Lower Foothills (D, G and H combined).

The model describing 15 year DBH in the Lower Foothills region is described as follows:

$$Y_{(D15)} = \beta_0 - \beta_1 \times lat - \beta_2 \times elev + \beta_3 \times lat \times elev \qquad \text{[Model 2]}$$

where

$Y_{(D15)}$ = Expected provenance mean DBH in centimetres at age 15 years,

β_0 = 94.87767,

β_1 = 1.53732,

$\beta_2 =$ 0.07571, and
$\beta_3 =$ 0.00136.

The regression has R^2 of 0.47 ($P < 0.0001$). When the effect of scale is corrected as shown for height, R^2 for the diameter model is 0.65.

As stated earlier, the Mitsue South (F) site was largely destroyed by fire. Thus, 15 year height and DBH data are available only for approximately 30% of the original trial. Ecologically, this site is also characterized as Lower Foothills. However, its elevation is lower and it is located a little further north than Sites D, G and H. Consequently its winters are cooler than the other three Lower Foothills sites. Its age 10 and 15 year height response surfaces appear in Figures 8 and 9, respectively.

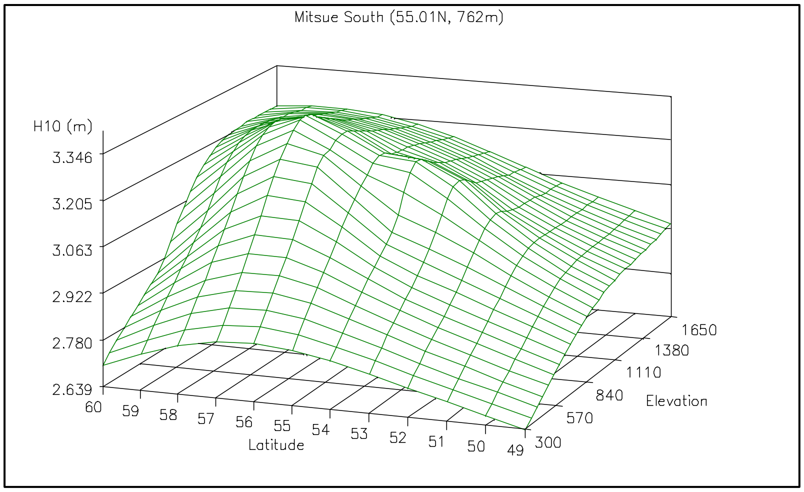

Fig. 8 Pattern of height growth at Site F.

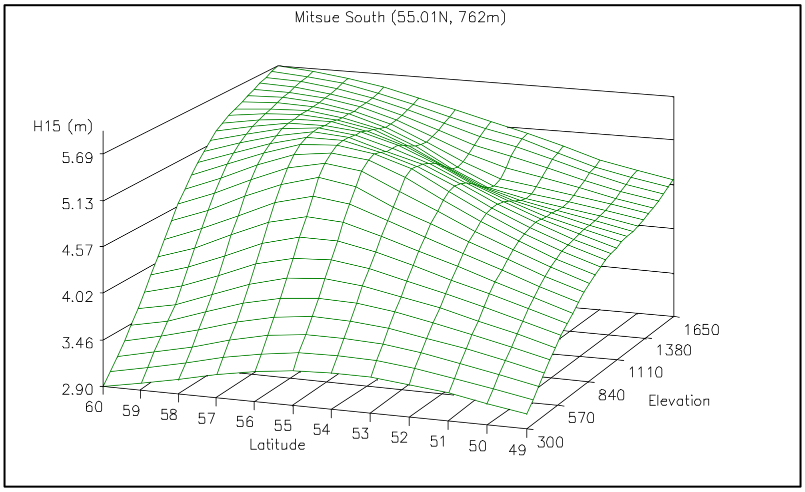

Fig. 9 Pattern of height growth at Site F.

The factorial regressions for 10 and 15 year height for this site had a R^2 of 0.24 ($P > 0.05$) and 0.36 ($P = 0.0428$). This model fit is much weaker than that of the three Lower Foothills sites (Model 1) discussed earlier. Using the same expression described for the Lower Foothills model the model for 15 year height at Site F had the following coefficients:

β_0 = 34.931057,
β_1 = 0.564943,
β_2 = 0.0337089,
β_3 = 0.00063735.

In can be seen that, except for the intercept (β_0), the regression coefficients for Site F resemble closely those of the three-site Lower Foothills model described earlier. Thus, in the absence of good data for the northern low elevation portion of the Lower Foothills, the three site models could be cautiously extended to Mitsue South and other similar areas in the Swan Hills and Pelican Mountain Region.

4.4.2 Southern Boreal Region

The southern boreal is the region represented by Sites A, E and J. The response surfaces for sites in the southern boreal are depicted in Figures 10, 11 and 12.

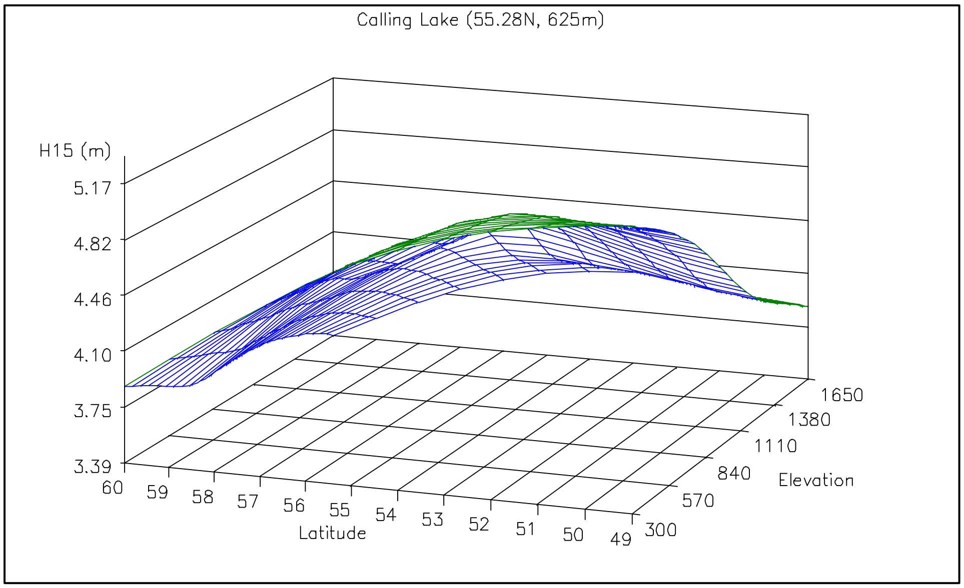

Fig. 10 Pattern of height growth at Site A.

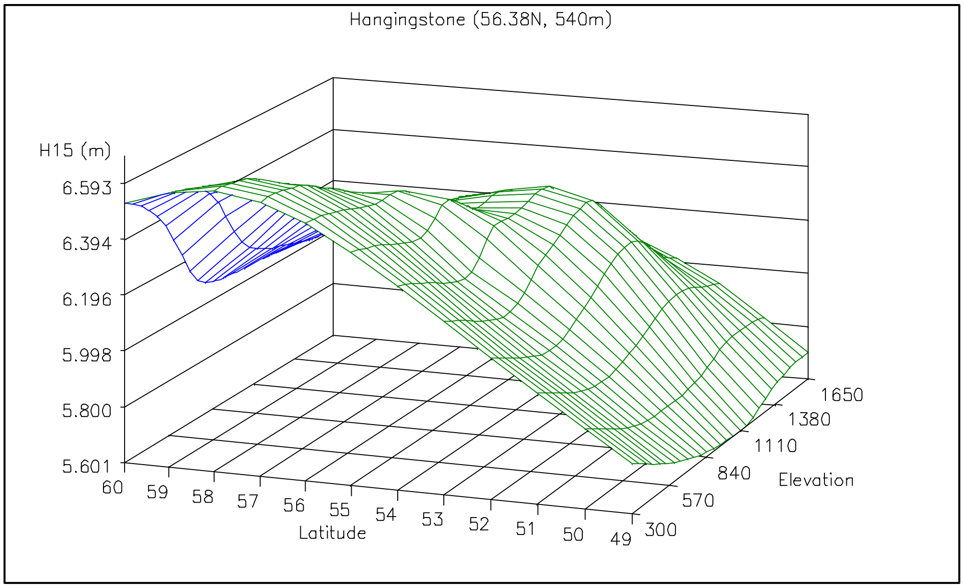

Fig. 11 Pattern of height growth at Site E.

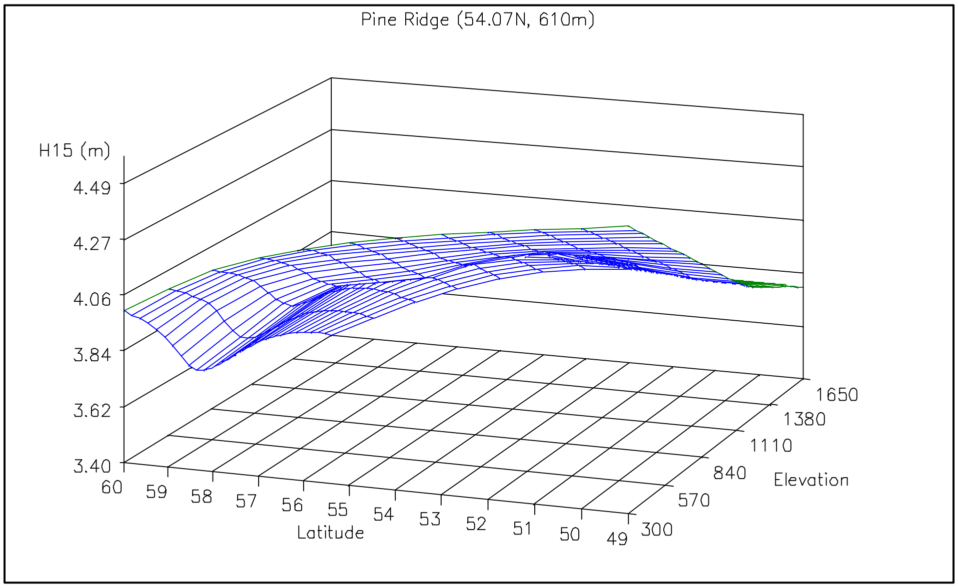

Fig. 12 Pattern of height growth at Site J.

There are clearly large differences among the response surfaces of these sites. The pattern of provenance variation at Site E is opposite that of Sites A and J. In addition, there was only limited population differentiation expressed at Site J. Thus, a single model for the southern boreal sites would not be useful at this age. However, it is important to note that the three sites are geographically and climatically similar. They are located approximately in a two degree latitudinal band (54° – 56°N) and similar elevations (540 – 625 m). They have similar cool winters (NDD = -1806 – 2114) and warm summers (GDD = 1254 – 1340). However, their moisture could be considered substantially different given the relatively lower MAP and higher GDD at Site J. Figures 10 and 12 show that, although the amount of genetic variation expressed at Sites A and J was different, the pattern of variation was the same. The predicted optimum latitude and elevation for the most adapted provenances at both sites were the same (Table 3). For Site E, the most adapted provenance would originate from around the site itself (local provenance). The site location is 56°23'N (Table 1) and predicted optimum seed source location is 56°19'N (Table 3). Thus, as trees grow older and genetic differentiation becomes better expressed, it may be possible to develop a single model for the southern boreal forest using Sites A and J.

4.4.3 Northern Boreal Region

The northern boreal forest region could be defined to cover the high latitude part of the province represented by Site B. ATISC provenance and progeny trials for pine and other conifers such as white spruce (*Picea glauca* [Moench] Voss), black spruce (*Picea mariana* [Mills] BSP) and tamarack (*Larix laricina* [Du Roi] K. Koch) have shown that provenances and families from north of latitude 57°N grow better at high latitudes than provenances from south of 57°N (e.g., Rweyongeza at al. 2007; Rweyongeza and Yang 2005a, 2005b, 2005c, 2005d). The response surface for lodgepole pine populations covered in this report is shown in Fig. 13.

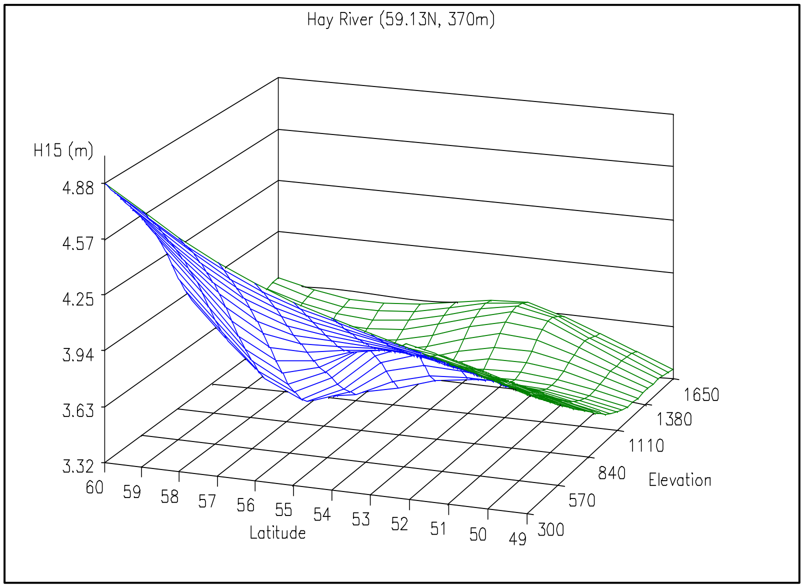

Fig. 13 Pattern of height growth at Site B.

Although the high latitude region is represented by a few provenances and test sites in the ATISC provenances and progeny trial program, results from provenance and progeny trials are consistent across species and support treating the northern boreal forest north of 57°N as a distinct reforestation region. Thus, the single-site regression for Site B (Table 3) is considered sufficient to guide decisions about seed transfer in the northern boreal region.

4.4.4 Upper Foothills and Montane

The Lower Foothills, Upper Foothills, Lower Subalpine and Montane are the main Natural Subregions where lodgepole pine management will likely be concentrated. Because of the well established decline in genetic growth potential with an increase in elevation (see The Species and Genetics section), there is a need to establish geographic limits for seed transfer within the mountainous regions in western Alberta. The Alberta lodgepole pine range-wide provenance trial series has only one site in a high elevation region outside the LF. Its response function appears in Fig. 14.

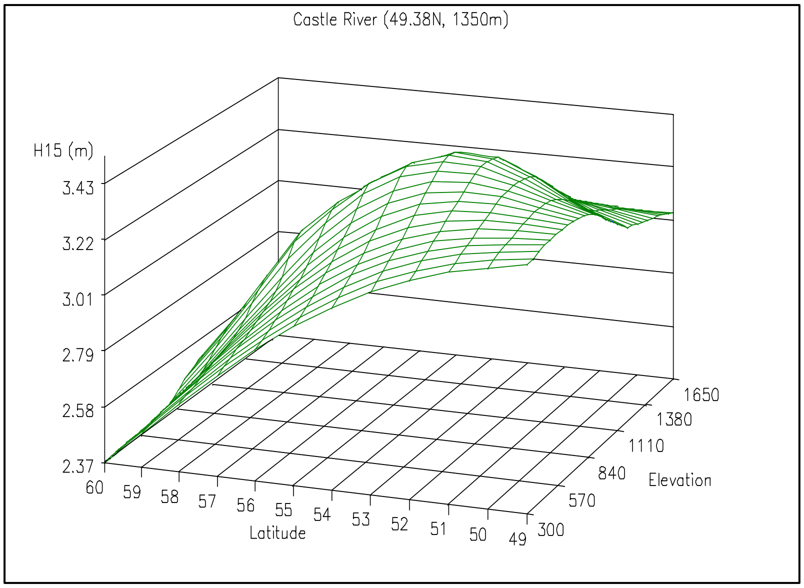

Fig. 14 Pattern of height growth at Site I.

Ranking of provenances for H15 at Site I showed that 7 of the 10 top ranking provenances originated from between 950 m and 1200 m. A provenance from the Diamond Hills area at $52^{o}37'$N and 976 m that was tested only at Sites G, H and I (not listed in Table 1) ranked 2 for H15 and 1 for D15 at Site I. Provenances 5 and 14, which were among the 10 top ranking provenances for H15, originated from 825 m and 829 m, respectively (Table 1). The 9 ranking provenance 21 originated at 1520 m. This provenance is 170 m displaced in elevation from the test site and could therefore be considered local. Its 15 year height was 3.20 m. A provenance from Blairmore at $49^{o}35'$N and 1584 m (not listed) had a similar growth potential (H15 = 3.14 m) at Site I. Performance of this provenance could credibly be evaluated only at a few sites. A provenance from Highwood at $50^{o}40'$N and 1860 m (not listed), which was tested only at Sites G, H and I, had the second lowest height and DBH at Site I. The most northern provenances, 7 and 8, had the lowest height and DBH growth potential at Site I.

Generally, the growth pattern at Site I suggests that provenances from high elevations in the Upper Foothills and Montane regions have lower growth potential than provenances from lower elevations in the LF. In this regard, provenances from 900 m to 1200 m in the LF could be cautiously transferred to the 1300 m to 1400 m zone to improve growth. However, care would be needed when performing such seed transfer to avoid areas of localized frosts and other microclimatic extremes in this mountainous terrain. The poor performance of a provenance from 1860 m suggests that seed from elevations higher than 1600 m is not suitable for reforestation at lower elevations even in the Montane region. Likewise, provenances from high latitudes in northern Alberta are not suitable for planting at high elevations in the south. These general inferences are clearly illustrated by the shape of the response surface for Site I (Fig. 14).

As stated earlier, the high elevation (Upper Foothills and higher) region is poorly represented both in terms of provenances and test sites in the Alberta lodgepole pine provenance trials. Thus, better decisions about the movement of seeds in this region would require adequate testing. In the meantime, data from lodgepole pine progeny trials located in the region may be used to supplement provenance trial information. The G154B trial located at 54^{o}24'N and 1440 m has 125 stands comprised of 456 open-pollinated families and 11 bulk seedlots. These stands are from 53^{o}10' – 54^{o}30'N, 117^{o}00' – 120^{o}00'W and 1200 – 1600 m. A quadratic transfer function for 14 year height at this site is illustrated in Fig. 15.

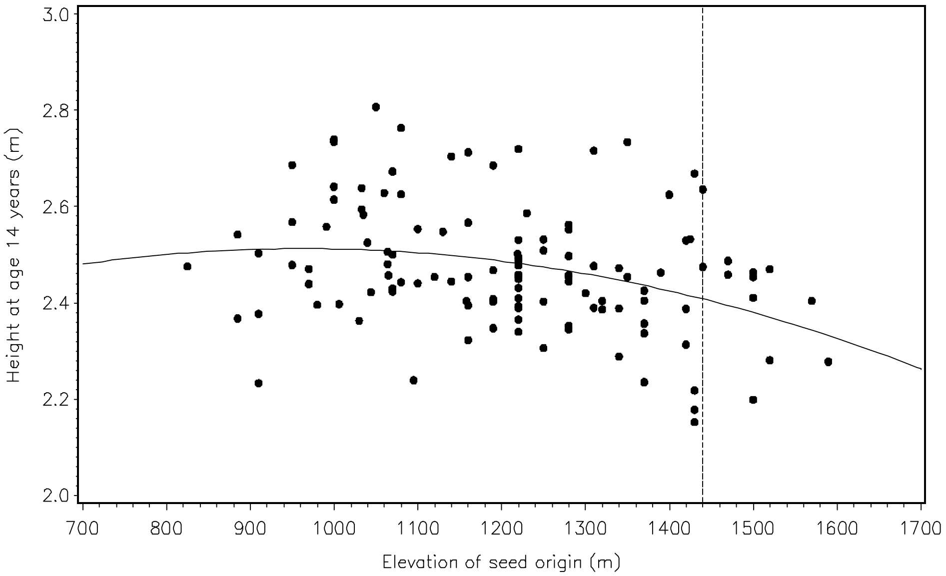

Fig. 15 Height growth in relation to elevation of seed origin at site G154B.
(R^2 = 0.11; *P = 0.0011*). Vertical dashed line indicates the elevation at the test site (1440 m).

Although this transfer function has a low R^2 (0.11), it suggests that appropriate seedlots for this test site and the region it represent would originate from between 1000 m and the location of the site itself (1440 m). Seedlots from elevations higher than the test site are likely to have lower growth potential than seedlots from lower elevations.

The G293B progeny trial located at 52^{o}11'N and 1464 m has 115 open-pollinated seedlots 12 of which are bulk seedlots. All seedlots originate from between 50^o and 56^{o}N, 114 and 120^{o}W and 700 m and 1700 m. The transfer function for 11 year height at this site appears in Fig. 16. Despite a low R^2 (0.24), Fig. 16 suggests that appropriate seedlots for this site and the region it represents would originate from between 1200 m and just below 1600 m.

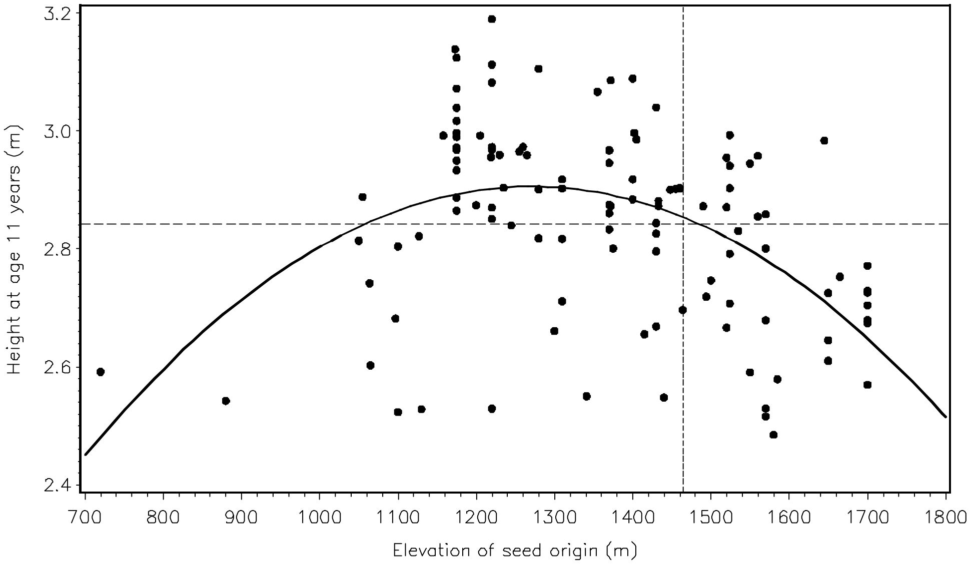

Fig. 16 Height growth in relation to elevation of seed origin at site G293B. ($R^2 = 0.24$; $P = 0.0001$). The vertical dashed line indicates the elevation of the test site (1464 m above sea level). The horizontal dashed line indicates the site mean (2.84 m).

Unlike provenance trials, the seedlots in progeny trials such as G154B and G293B are from superior trees selected within and slightly outside specific breeding regions. Growth variation among families selected from the same stand masks geographic trends making it difficult to establish limits of seed transfer with certainty. However, the trend suggests that as the elevation of the planting site increases, the lower elevation boundary for families/stands suitable for that site also increases. This shows that there is a limit to which lower elevation (e.g., LF) seedlots can be transferred upward while retaining superiority over local high elevation seed sources. Therefore, with a cautious approach, data from progeny trials in places not covered by provenance trials can provide additional guidance to seed transfer decisions.

4.5 Model Applications

Individual site models developed in this report predict a site-specific 15 year height or DBH for a population of trees regenerated by seeds from a defined latitude and elevation. Thus, the potential gain or loss of productivity that may be incurred on a specific site if non-local seeds were used can be evaluated by simply comparing predicted height or DBH of the local provenance with height or DBH of the provenance that could potentially be introduced.

With the recognition of ecological and climatic similarities among sites, the regional models extend the site-specific model concept to cover a broader region that, for practical purposes, could be treated as a single site. However, unlike individual site models, regional models cover large regions where infinite values of expected height and DBH could be calculated. Thus, the use of regional models to assess the benefit of planting non-local provenances would involve comparing height or DBH of provenances at the edges of the target planting region, with height or DBH of provenances that can be potentially introduced into the region. Given that L_U and E_U are, respectively, latitude and elevation at the upper boundary of the target planting area (e.g., LF), and L_L and E_L are latitude and elevation at the lower boundary of the planting area in the same region, we can use a regional model (e.g., LF) for the region where the target planting area belongs to calculate the following values:

H_L = height or DBH for the provenance from the lower boundary of the target planting area; H_U = height or DBH for the provenance from the upper boundary of the target planting area; H_{XL} and H_{XU} = height or DBH for a provenance from outside the lower and upper boundary of the planting area, respectively, which can potentially be introduced from outside the area. Using these expected growth performance values, the potential consequence of introducing a provenance from outside the lower boundary of the planting zones can be calculated as

$$\Delta_L = \frac{H_{XL} - H_L}{H_L} \times 100,$$

where Δ_L is the percentage gain (or loss) due to planting seeds from outside the lower boundary of the target planting region. Likewise, the consequence of planting seeds from outside the upper boundary of the planting area can be calculated as

$$\Delta_U = \frac{H_{XU} - H_U}{H_U} \times 100,$$

where Δ_U is the percentage gain (or loss) due to planting seeds from outside the upper boundary of the target planting region.

In both cases, negative Δ_L or Δ_U indicates that an outside provenance has lower predicted growth potential than provenances from within the boundary of the planting area. Thus, an outside provenance cannot be introduced in the region as a whole. On the other hand, a positive Δ_L or Δ_U implies that an outside provenance has a higher predicted growth potential than provenances from the margins of the planting region. Thus, such a provenance can be introduced into the planting area, if the possibility for other forms of maladaptation (e.g., climatic, edaphic, pests and diseases) is considered negligible. For lodgepole pine, the risk for assisting hybridization between lodgepole and jack pine that would occur as a result of moving hybrids into pure lodgepole pine or lodgepole pine into jack pine areas should be considered alongside environmental maladaptations.

We should caution that the decision to introduce a provenance from outside the region should be supported by high values of Δ_L or Δ_U, especially when potential provenances are located at higher elevations or higher latitudes than the planting area. As discussed in the introductory section, provenances from high latitudes and elevations have low growth potential. Broadly defined, adaptation of an individual or population involves all the genetically determined traits that enable it to survive, grow and reproduce in the existing environment (see Futuyma 1976).

Because the genetics of most adaptive traits of forest trees are yet to be studied, higher thresholds should be placed on the known traits to offset the unknowns. In other words, the unknown risks of introducing a distant provenance should be offset by a promise for a much higher gain in productivity.

It should be noted that topographic patterns do not necessarily follow a consistent trend along a latitudinal gradient. Isolated high elevation landscapes may occur at high latitudes (e.g., the Caribou Mountains in northern Alberta) and low latitudes (e.g., Rocky Mountains in southwestern Alberta). The occurrence of isolated high elevations at latitudes where provenances of high growth potential appear to originate would complicate the use of the latitude-elevation models in the manner described above. However, this can be resolved by considering results of single variable (in this case elevation) regressions. From Table 3, the optimum elevation for most sites lies below 1100 m above sea level. Thus, 1100 m would be considered the highest permissible source of seeds when applying regional latitude-elevation height and DBH models.

5.0 CONCLUSIONS

The current study of lodgepole pine in Alberta indicates that the species is highly variable genetically. The highest genetic variability was expressed on sites located in the Lower Foothills Natural Subregion where most of the provenances originated, and lowest on sites located in the Boreal Forest Region where the dominant pine species is jack pine. Better expression of genetic variability in the Foothills (and possibly in high elevation regions as a whole) where reforestation is concentrated would a enable better selection of provenances and control of seed movement. In contrast, poor expression of genetic variability in the Boreal Forest Region may not have immediate practical consequences, because the region is not a target for artificial regeneration with lodgepole pine. The value of testing lodgepole pine provenances in the boreal forest where the environment is drier and more continental than the species' main natural range (Foothills, Montane and Subalpine) is in simulation of climate change; lodgepole pine provenances with better performance in the current continental environment of the boreal forest may be better suited for survival and growth in the future climate of the Lower Foothills.

Six major conclusions are as follows.

(1) Provenances from high latitudes in northern Alberta and those from high elevation in the Rocky Mountains have low growth potential.

(2) Provenances from medium latitudes between 54° and 56°N and medium elevation between 900 m and 1100 m have high growth potential.

(3) At high latitudes in northern Alberta, local provenances outgrew those from outside the region, which shows that maximization of growth in this region requires use of local seed. However, seed from high latitudes is not appropriate for planting south of latitude 58°N.

(4) Seeds from elevations between 900 m and 1200 m could be planted at a higher elevation between 1300 m and 1400 m to increase productivity. In the current climate this region has warm winters, cool summers and high precipitation, although mid-season frosts occur in some areas. Thus, with adequate care to avoid known frost pockets, an upward seed movement of 300 m should not pose a significant risk of climatic-related injuries.

(5) Despite these generalizations, the optimum seed source for most sites is located very close to the test site (Table 3). Hence, when choosing the seed source for a limited reforestation objective, local seed is generally the best for productivity, climatic adaptation and possibly, pest and disease resistance which are beyond the scope of this paper.

(6) Type B and Pearson’s correlation coefficients between pairs of test sites clearly indicate strong GE interaction between climatically and ecologically dissimilar sites. This suggests a need for restricting seed movement between regions roughly generalized along whole or sections of Natural Subregions instead of seed zones. Because the current Alberta seed zones are subdivisions of the Natural Subregions, relaxation of seed movement restrictions among some of the seed zones may be appropriate. Relaxation of seed movement rules would serve to reconcile seed zone boundaries with the observed patterns of genetic variation.

This paper illustrates the procedure and precautions to be taken when choosing a lodgepole pine seed source for reforestation in Alberta. Although the data were from a series of young provenance and progeny trials, results were consistent with what has been observed in older trials of lodgepole pine and other species in and outside Alberta. Choice of seeds for reforestation affects both the productivity of future forests and their adaptation to a changing environment. Forest trees are long-lived perennial species whose annual growth and reproductive cycle follows natural rhythms of seasonal weather and day length. A healthy and productive forest must have a high annual growth potential while maintaining the ability to respond genetically (evolve) to a changing climate. Future forests can maintain the ability to evolve only when appropriate seed sources for the area are used with sufficient genetic variability. Appropriate seed sources for the area can be identified through range-wide provenance trials. However, as shown in this report, genetic variation among tree populations follows a predictable pattern along latitude and elevation gradients, which are surrogates for climate and/or photoperiod (day length). Climate varies along latitudinal and altitudinal gradients, although local modifications exist due to air mass, ocean currents and proximity to the sea (continentality). In contrast, day length varies exclusively along latitudes. Thus, with minor exceptions, latitude and elevation are reliable surrogate variables that can be used to describe the climate of the seed source and planting site. Therefore, in the absence of provenance test information, matching seed source to planting site by placing limits on the latitude and elevation of the seed source will ensure that climatic adaptation of the planting stock is preserved.

Although the pattern of genetic variation supports movement of seed from a lower to a higher elevation for improving growth potential, upward seed transfer carries a risk of assisting hybridization between lodgepole and jack pine. Thus, in a region where hybridization is known to occur, caution must be exercised when transferring seed to limit the possibility of enhancing hybridization beyond that occurring in nature. Studies have shown that there is an east-west cline of lodgepole pine resistance to the western gall rust disease caused by *Endocronartium* *harknessii* (J. P. Moore) Y. Hiratsuka whereby resistance declines westward from the region of lodgepole-jack pine contact (e.g., Wu et al. 1996). Through coevolution, lodgepole pine populations may also be resistant only to specific rust strains (e.g., Yang et al. 1999; Li et al. 2001). Thus, disease and possibly insect resistance should also be considered when transferring seed from its native environment. Because resistance to fungi and insects is a function of coevolution between the host and parasite, limiting the distance seed can be transferred should reduce the possibility of moving a provenance to an area with fungal or insect strains to which it may be susceptible.

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