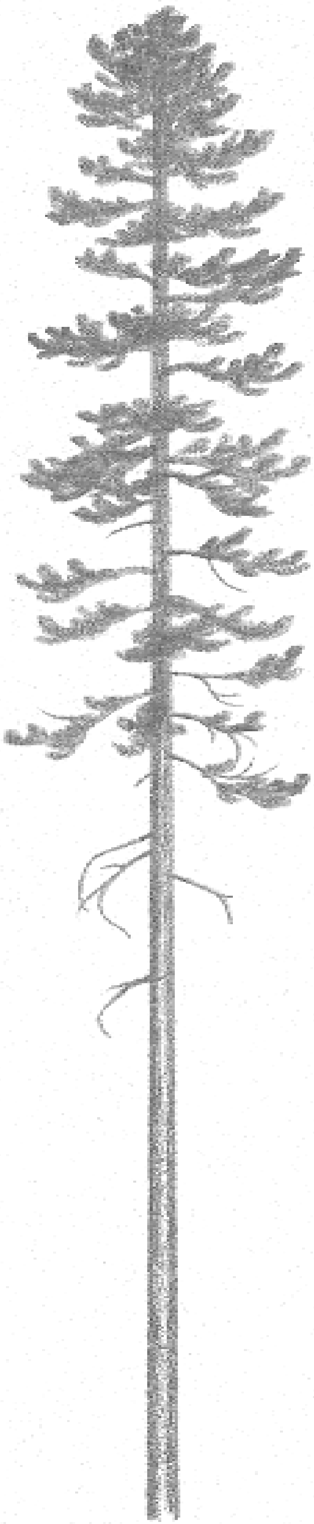

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ALBERTA TREE IMPROVEMENT
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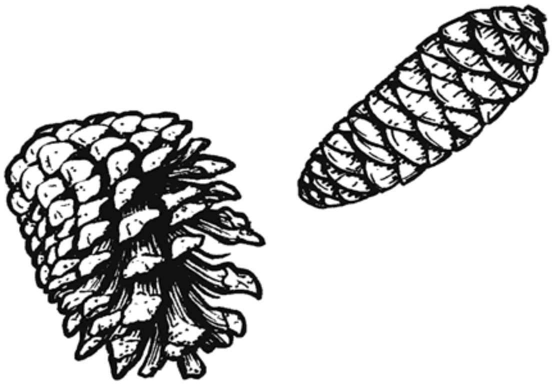

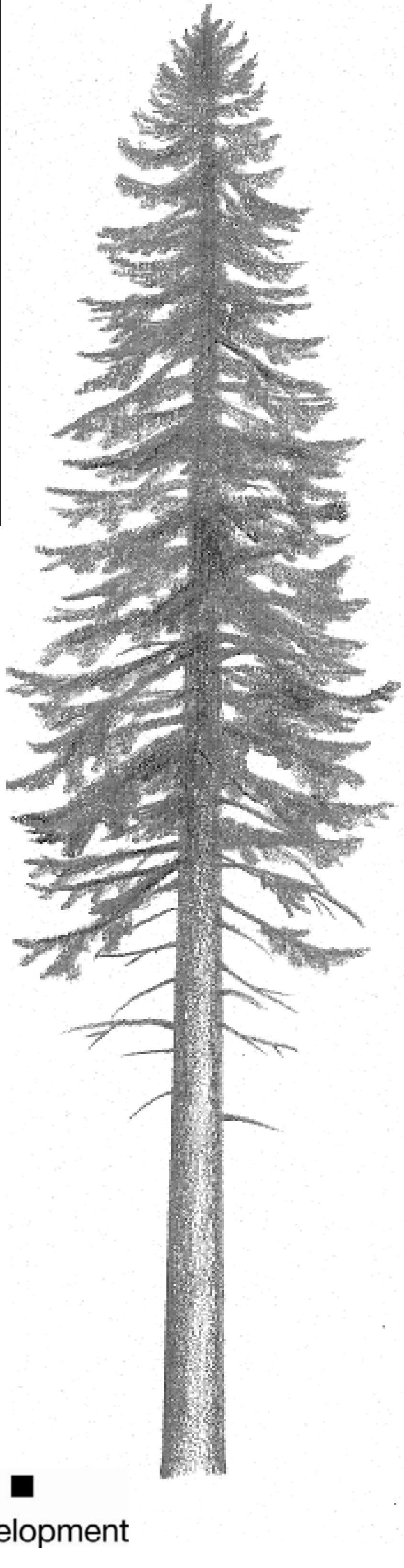

Government of Alberta
Sustainable Resource Development

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SUMMARY

This paper describes the pattern of genetic variation for growth potential among white spruce provenances in Alberta, Canada. It uses total height (H27) and diameter at breast height (D27) at 27-years from seed to identify provenance differences in relation to latitude and elevation of seed origin. Latitude and elevation are the main variables that adequately describe climatic variability in Alberta. Indirectly, latitude also describes regional variation in day length. Climate and day length are the main natural selection pressures governing genetic differentiation among forest tree populations. The regressions of height and diameter on latitude and elevation of seed origin are used to predict the location from which provenances of the highest growth potential on a specified site or environment are expected to originate. This location is referred to as an optimum seed source. By examining the pattern of provenance variation on similar sites and the correlation of provenance ranks among sites (genotype by environment interaction), it is possible to establish seed transfer guidelines that will enhance efficient use of seed while maintaining provenance climatic adaptation. Results from the present analysis are summarized below.

(1) Genetic variation among provenances was strongly related to latitude and elevation of seed origin. Provenances of the highest growth potential on many sites were from mid-latitudes (approximately 55°N to 56°N) and mid-elevations (mainly 600 to 800 m above sea level [asl]). From mid-latitudes, growth potential declined gradually with an increase in latitude of seed origin to approximately latitude 57°N beyond which high latitude provenances began to outgrow mid-latitude provenances in a high latitude region. From mid-elevations, growth potential declined with an increase in elevation of seed origin to the Upper Foothills where white and Engelmann spruce are known to hybridize.

(2) On most sites located at about or below 800 m asl, growth potential was more related to latitude (r^2 = 0.59 to 0.77) than elevation (r^2 = 0.16 to 0.48) of seed origin. In contrast, the relationship between growth potential and elevation of seed origin was strong mainly on sites located in the foothills of the Rocky Mountains region ($r^2 > 0.60$). This suggests that at low and mid-elevations, seed transfer guidelines have to control latitudinal (north-south) seed movement but, in the foothills and other mountainous regions, seed transfer guidelines have to control elevational seed movement.

(3) Analysis of genotype by environment interaction through genetic correlation between test sites showed that the site at the highest latitude (~ 59°N) was not well correlated with sites at mid-latitudes and mid-elevations (r = -0.45 to 0.56). The correlations increased with a decrease in latitudinal differences among sites. Likewise, the site located at 1220 m als in the Upper Foothills was not well correlated with sites located at mid-elevations and high latitudes (r = -0.45 to 0.40) and the correlations increased with a decrease in elevational differences between sites. Sites located at mid-latitudes and mid-elevations were highly correlated (r = 0.79 to 0.99) depending on their latitudinal and elevational proximity. Thus, latitude and elevation that are related to provenance genetic differentiation and climatic differences among sites also appear to explain the pattern of genotype by environment interaction in these trials.

Currently, seed transfer for reforestation in Alberta is regulated through seed zones, which are finer divisions of the Natural Subregions (see FGRMS 2009). With few exceptions, Natural Subregions and their subdivisions generally follow a latitudinal gradient in the boreal forest and an elevational gradient in the foothills and boreal highland regions. It is recommended that a 2° northward latitudinal seed transfer be implemented in the boreal forest to approximate latitude 57°N within elevations not exceeding 800 m asl. In the mountainous areas, a 200 m upward elevational transfer within a narrow latitudinal zone (maximum 2° northward) is recommended. It

is further recommended that such seed transfers be implemented along Natural Subregion divisions, which, in essence, pools together closely related seed zones along latitudinal or elevational gradients. Thus, seed transfers across Natural Subregions and seed zones may be implemented as outlined below.

(1) For seed zones located in the Central Mixedwood (CM) Natural Subregion, seed may be transferred northward from CM3 to CM2 and CM2 to southern areas of CM1 series seed zones. Such transfers should not be extended north of latitude 57^{o}N.

(2) The Dry Mixedwood (DM) Natural Subregion has two major disconnected parts, that is, the southern part (CM2) next to the Parkland Natural Subregion and the north western part (DM1). DM1 is narrow in terms of east-west extension but has a significant north-south extension. Although much of DM is farmland, a 2^o northward latitudinal seed transfer may be implemented in DM1 series seed zones.

(3) The northernmost part of Alberta is mainly comprised of the Northern Mixedwood (NM) Natural Subregion with very cold winters, long warm summer days, low precipitation and extensive wetlands. In addition, because of the extensive nature of the Central Mixedwood, the region north of 58^{o}N includes sections of the CM1 series seed zones. It is recommended that this region (NM and northern sections of CM1 series seed zones) be treated as a separate reforestation zone where regeneration uses locally selected seed sources.

(4) For isolated hill systems in the boreal forest (boreal highlands), seed may be transferred from the LBH to UBH while observing a 200 m upward elevational transfer distance from seed source to planting site.

(5) In the foothills region, seed may be transferred from LF to UF while observing a 200 m upward elevational transfer distance from seed source to planting site.

(6) Limited seed transfer from the UF to higher elevation Natural Subregions (upper Montane, Subalpine and Alpine) is not recommended because no sufficient provenance and progeny testing has been conducted in these areas and because hybridization between white and Engelmann spruce must be limited to levels occurring in nature.

It should be noted that these seed transfer recommendations are intended to preserve regional adaptation that can be inferred from geographic point descriptors (latitude and elevation) as determinants of climate and day length. Any variation in soils that may be recognizable in some of the Natural Subregions or existing seed zones is considered local and discrete and thus beyond the scope of this paper. It is expected that due to cross pollination and long distance pollen and seed dispersal, population differentiation due to soil types is unlikely in conifers such as white spruce. Small-scale patchy variation in soils and moisture regimes tends to affect species dominance (deciduous vs. coniferous on south or north topographic aspects); this is not a subject of this paper.

1.0 INTRODUCTION

White spruce (*Picea glauca* [Moench] Voss) is the most important forest tree species in Alberta accounting for 45.9% of provincial conifer volume and 27.9% of total combined soft and hardwood volume (AFLW 1985). The species has a continuous distribution across the boreal forest in Canada and the northern USA. Its natural range extends from Newfoundland and Labrador to the Bering Sea in Alaska and from 44^{o}N in Wyoming and South Dakota to 69^{o}N in the Arctic. In terms of elevation, white spruce occurs from sea level to 1520 metres (m), although it is occasionally found at a much higher elevation in the Rocky Mountains of western Canada (Nienstaedt and Zasada 1990). In Alberta, white spruce has a nearly continuous distribution in the northern boreal forest. Generally, its southern limit in Alberta occurs at the woodland-grassland transition where mean annual precipitation is between 380 and 510 mm and the mean July temperature maximum is greater than 24^o C. Thus, drought is a limiting factor for white spruce distribution in southern Alberta (Nienstaedt and Zasada 1990). A substantial outlier forest of white spruce occurs in the Cypress Hills of southeastern Alberta. At higher elevations (1200 – 1800 m) in the foothills, white spruce hybridizes with Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) forming a hybrid complex, which is eventually replaced by pure Engelmann spruce forest types at the highest elevations.

The reproductive biology, ecology and silviculture of white spruce were discussed by Nienstaedt and Teich (1971) and Nienstaedt and Zasada (1990). Only a brief review of the genetic variation of the species revealed by provenance trials is discussed in this section. Most emphasis is given to how provenances from other provinces perform in Alberta. Provenance studies have shown that white spruce exhibits high genetic variation among populations. In the eastern part of its natural range, provenances with highest growth potential occur in southeastern Ontario (e.g., Teich et al. 1975; Stellrecht et al. 1974; Li et al. 1997; Tebbetts 1981) and in these eastern studies, growth potential declines with an increase in latitude (e.g., Khalil 1986; Hall 1986; Nienstaedt and Riemenschneider 1985) and longitude (Furnier et al. 1991) of seed origin.

A range-wide trial (Alberta G103RW) with 43 provenances from across Canada was established at Calling Lake in central Alberta (55^{o}17’ N; 113^{o}09’ W and 625 m) in 1982. This trial is part of the white spruce provenance research (series 410) that was coordinated by the Canadian Forest Service at Petawawa National Forestry Institute. Provenances originated from latitudes 44^{o}26’ − 66^{o}02’N, longitudes 57^{o}36’ − 139^{o}00’W and elevations 30 − 1280 m als. At 24 years from seed, a quadratic regression showed that height was related to latitude (R^2 = 0.45) and longitude (R^2 = 0.76) of seed origin (unpublished data). Provenances with the highest growth potential originated from southern Ontario and Quebec and southeastern Manitoba near the Ontario border. The British Columbia, Yukon and Northwest Territory provenances had the lowest growth potential. Provenances from Newfoundland, New Brunswick and Nova Scotia had low growth potential similar to that of high elevation provenances from the Rocky Mountains in southwestern Alberta (unpublished data). The six top ranking provenances exceeded the height of local Alberta provenance (an average of provenances with latitudes and elevations similar to the test site) by about 0.5 – 1.0 m (10 − 18%).

The pattern of provenance variation in G103RW suggests that growth potential is expected to decline westward from Ontario and Quebec. However, the origin of the 43 provenances tested has a northwestern-southeastern orientation that confounds latitudinal and longitudinal effects. The best provenances from Ontario, Quebec and Manitoba were from south of latitude 50^{o}N and below 400 m als. In contrast, slow growing provenances from western Canada were from latitudes 54^o to 66^{o}N and 500 – 1000 m als. The Pearson’s correlation coefficient between 24-year height and longitude of seed origin was -0.52 ($P < 0.0001$), whereas the partial correlation between the two variables while controlling latitude of seed origin was 0.01. Likewise, the correlation between 24-year height and provenance latitude was -0.62, whereas the partial correlation between the two variables while controlling longitude was -0.40. Thus, the observed westward decline in growth potential (longitudinal cline) is a direct consequence of the northward decline in growth potential (latitudinal cline), which has been observed in other studies of white spruce elsewhere in Canada and the USA.

Early results (15-year height) of the G103RW prompted establishment of six more trials (G276 and G277 series) at different locations in Alberta using provenances tested in G103RW and additional provenances from Alberta, British Columbia, Saskatchewan, Manitoba, Ontario and Quebec. Because of low growth potential in G103RW, provenances from Newfoundland, New Brunswick, Nova Scotia and the Northwest Territory were not included in the new series of trials. The northernmost of these trials (Alberta G277A) is located at latitude 57°47'N, longitude 118°12'W and 500 m als. The location of this trial is interesting because it provides a measure of how far low latitude provenances from Manitoba, Ontario and Quebec can be transferred north without losing growth superiority over local northern provenances. Measurement of 15-year height at this site showed that a provenance from Caramat, Ontario (49°36'N; 89°09'W; 305 m als), exceeded the height of the local provenance (57°36'W; 117°31'W; 460 m als) by 5% and the height of the other three Alberta provenances by 21 – 25% (unpublished data). The quadratic regression showed that in trial G277A, height was significantly ($P < 0.05$) related to latitude ($R^2 = 0.22$) and longitude ($R^2 = 0.21$) of seed origin. Corresponding R^2 values in trial G277B (54°03'N; 115°47'W; 823 m als) were 0.36 and 0.39. In the case of G277A, many Ontario, Quebec, Manitoba and Saskatchewan provenances outgrew Alberta provenances. No Alberta provenance was included in G277B.

The Alberta G276 series contains 12 provenances sampled from Manitoba, Ontario and Quebec and 11 provenances from Alberta. Provenances from outside Alberta originated in regions considered to be potential sources of superior provenances based on G103RW and the G277 series. The G276 series has four trials (A through D) between latitudes 52°37'N and 56°18'N and elevations 495 m and 990 m als. Only subsets of the 23 provenances were tested on each of the four trials. Generally, sites A, B and C are located at middle latitudes and results resemble those described for the G103RW and G277 series. Site G276D (52°37'; 115°05'; 990 m als) allows us to gauge the performance of southern low elevation provenances at a higher elevation site in the foothills of the Rocky Mountains of southwestern Alberta. Measurements of 15-year height showed that three provenances from latitudes 51°00' to 52°00'N and elevation of 224 – 270 m, and two provenances from latitudes 49°26' and 50°05'N and elevation of 1007 to 1100 m had better growth potential than all other provenances. Their growth potential was similar to that of one of the local provenances located at 52°20'N and 1067 m als. Performance of provenances at this site may be difficult to interpret because of large differences in seed source elevations and longitudes.

Generally, the G276 and G277 trials suggest that southern provenances could be transferred considerably northward and maintain growth potential superior to local provenances. However, the risks of frost and winter damage for southern provenances adapted to a relatively warmer and longer growing season would need to be considered in any such proposed seed movement. Although no meaningful correlations between winter related damage incidence and provenance were found in the G276 and G277 trials, it should not be assumed that no significant correlations exist, becauase the southern provenances may not have been transferred far enough north to sustain winter damage.

The recently established white spruce complex genecology and climate change provenance trial series provides an example of the risk associated with moving southern provenances too far north. This trial involves 90 provenances from across western North America from latitudes 35°46'N to 65°16'N, longitudes 105°25'W to 130°16'W and elevations 165 to 2987 m als. Provenances are a mixture of putative white spruce, Engelmann spruce and hybrids of the two species. This provenance trial is replicated at 15 sites in British Columbia, two sites in Alberta and one site in the Yukon Territory. All trials were established in 2005. The Hay River trial (59°08' N, 117°34'W and 370 m als) in northern Alberta has been assessed for height growth, winter-related tissue damages and terminal dieback for two consecutive growing seasons and the results were reported by Dhir et al. (2007) and Barnhardt et al. (2008). There was extensive dieback incidence in the first two growing seasons that was considered to be caused by winter damage to the terminal shoot. In the first growing season (see Dhir et al. 2007), average percentage dieback was the lowest (< 10%) among provenances from northern British Columbia, the Yukon Territory, Northwest Territories and Alberta. Dieback among provenances from low latitudes and elevations in British Columbia and all of the USA ranged from 19.8% to 86%. The amount of terminal shoot killed (dieback severity) also followed the same pattern. Pearson's correlation coefficients between provenance mean and degree days below 0° C (NDD) of seed origin were 0.72 and 0.61 for damage incidence and severity, respectively. Because NDD was entered as negative value, the positive correlation shows that provenances from locations with warmer winters (least negative NDD values) had more diebacks than provenances locations with cooler winters (most negative NDD values). Corresponding correlations for growing degree days above 5° C (GDD) were 0.45 and 0.36. The correlation between provenance means and the continentality index (defined as the difference between mean temperature of the coldest and warmest months) was -0.58 and -0.53 for dieback incidence and severity, respectively. All correlation coefficients were significant at the 0.1% level of probability. The same pattern of provenance differences for dieback incidence and severity was observed in the second growing season (see Barnhardt et al. 2008).

These correlations show that provenances from the continental climate (cold winters and warm dry summers) found at high latitudes in northern British Columbia, the Yukon Territory, Northwest Territories and Alberta are more resistant to cold winter temperatures than provenances from warmer and moister climates in the USA and British Columbia. Thus, if moved further north in Alberta, white spruce provenances from southern Manitoba, Ontario and Quebec are likely to suffer substantial winter-related damages, especially at a young age.

This paper discusses the genetic variation of white spruce provenances originating and tested in Alberta based on 27-year height and diameter at breast height (dbh). It follows the format of a similar paper describing genetic variation of lodgepole pine (*Pinus contorta* Doug.) in Alberta (Rweyongeza et al. 2010a). The objective is to describe the pattern of optimum growth potential among provenances and use this information as a tool in the implementation of seed transfer guidelines defined by the Alberta Forest Genetic Resource Management and Conservation Standards (FGRMS 2009). At 27 years from seed, most white spruce provenance trials covered in this paper are attaining crown closure. This provides an excellent opportunity for describing the pattern of variation at an age where ranking of provenances is expected to stabilize.

2.0 MATERIALS AND METHODS

2.1 Experimental Methodology

The G103 series of white spruce provenance trials consists of 46 provenances representing most of the species' natural range in Alberta (Figure 1).

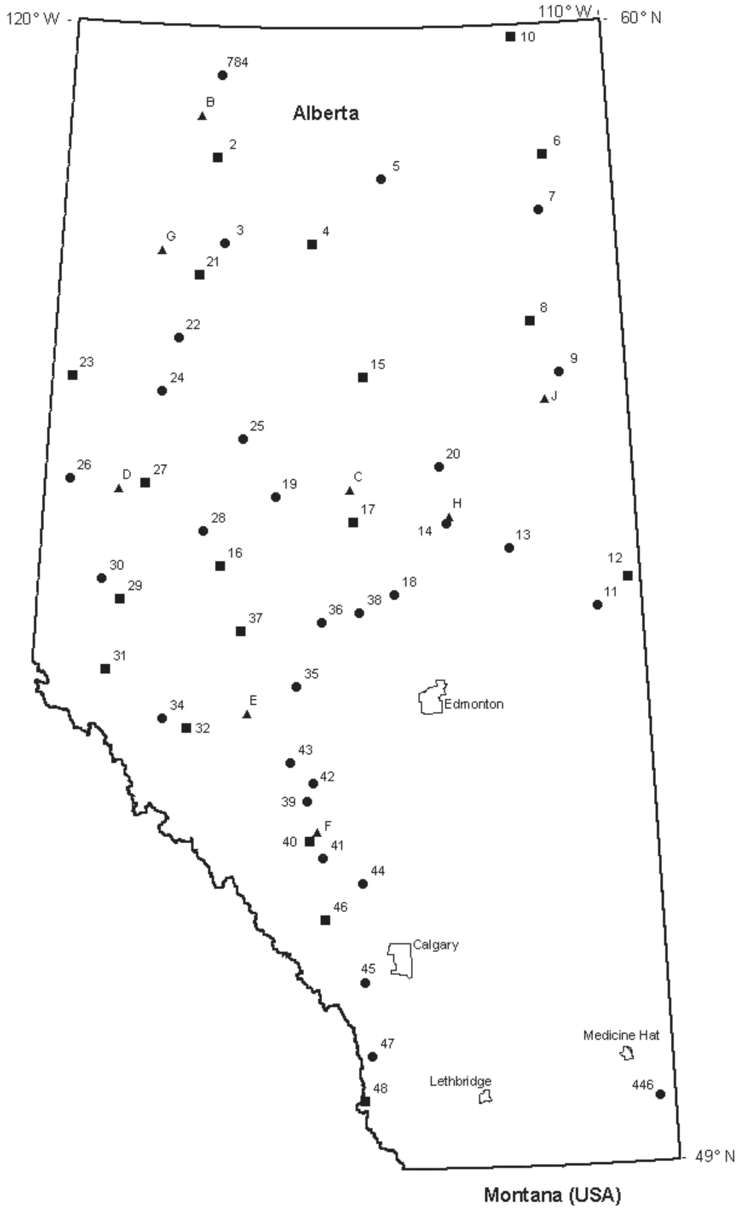

Figure 1. White spruce provenances and test sites in the G103 series. Dot and/or square markers with numeric identifications indicate provenances; triangular markers with character identifications indicate test sites. Only provenances identified by square markers are covered in this paper.

Seeds were collected from natural stands in the period between 1959 and 1976 as operational reforestation and research seedlots. Three of these provenances were Engelmann spruce and the rest were considered putative white or hybrid spruce depending on the elevation of origin in the Rocky Mountains.

In January and February of 1976, seeds were cold stratified at 2° C for 21 days, sown in 65cc Spencer Lemaire containers and grown in the greenhouse for one growing season. Seedlings were then transplanted into nursery beds and grown for three growing seasons before establishment of field trials. Between 1980 and 1983, the 4-year old seedlings were used to establish 12 field sites across Alberta. The number of provenances per site varied between 26 and 30 but a subset of 19 provenances was established at all sites. These provenances are identified by square markers in Figure 1 and their locations are described in Table 1. Because of very low survival in early years of establishment four sites were discontinued. The eight remaining trials, which are covered in this paper, are described in Table 1 and identified by character labels in Figure 1. Extended descriptions of provenances covered in this paper and all others in the G103 series are available in Rweyongeza et al. (2007; 2009b).

Table 1. Locations, Natural Subregions and and climatic description of white spruce provenances and test sites in the Alberta G103 series. The described provenances are those planted on all test sites.

ID	LOCATION	LAT	LONG	ELE	MAT	MTCM	NDD	MTWM	GDD	MAP	MSP	NSR
2	Footner Lake	58°44’	117°15’	335	-1.6	-21.9	-2654	16.0	1197	418	272	Central Mixedwood
4	Footner Lake	57°55’	115°30’	360	-0.4	-20.9	-2344	16.4	1282	435	301	Central Mixedwood
6	Athabasca Forest	58°44’	111°15’	235	-1.8	-23.9	-2738	16.9	1244	397	255	Peace-Athabasca Delta
8	Athabasca Forest	57°08’	111°38’	274	-0.2	-21.1	-2329	16.9	1349	465	309	Central Mixedwood
10	Athabasca Forest	59°53’	111°43’	183	-2.6	-25.2	-2968	16.7	1181	338	212	Northern Mixedwood
12	Lac La Biche	54°38’	110°13’	610	0.6	-18.0	-2009	16.2	1309	490	342	Central Mixedwood
15	Slave Lake	56°38’	114°35’	731	-0.1	-17.5	-2029	14.8	1092	558	378	Central Mixedwood
16	Slave Lake	54°48’	116°59’	731	2.5	-12.7	-1419	15.6	1298	577	391	Central Mixedwood
17	Slave Lake	55°14’	114°46’	610	1.6	-15.0	-1686	15.7	1263	542	381	Central Mixedwood
21	Peace River	57°36’	117°31’	460	-0.5	-20.6	-2320	15.8	1228	449	291	Dry Mixedwood
23	Peace River	56°34’	119°40’	762	-0.2	-18.0	-2077	14.7	1097	466	295	Lower Boreal Highl.
27	Grande Prairie	55°35’	118°18’	640	1.6	-15.7	-1727	15.9	1328	508	325	Dry Mixedwood
29	Grande Prairie	54°27’	118°38’	940	1.8	-12.9	-1459	14.5	1118	646	427	Lower foothills
31	Edson	53°46’	118°48’	1402	0.7	-11.7	-1440	12.1	788	653	389	Subalpine
32	Edson	53°14’	117°48’	1340	1.5	-11.4	-1345	13.3	943	636	436	Upper foothills
37	Whitecourt	54°11’	116°37’	945	2.4	-11.1	-1325	14.8	1167	624	438	Lower Foothills
40	Rocky/Clearwater	52°10’	115°28’	1341	1.4	-11.5	-1353	13.2	923	657	472	Upper Foothills
46	Bow/Crow	51°24’	115°13’	1600	0.8	-11.5	-1431	12.5	811	614	415	Subalpine
48	Bow/Crow	49°39’	114°37’	1585	2.1	-9.3	-1132	13.6	950	763	356	Montane
B	Hay River	59°08’	117°34’	370	-2.3	-23.1	-2862	15.7	1137	410	268	Central Mixedwood
C	Zeidler Mills	55°33’	114°50’	670	1.2	-15.5	-1745	15.5	1219	572	395	Central Mixedwood
D	Sexsmith	55°31’	118°30’	805	1.2	-14.9	-1710	15.1	1209	532	339	Lower foothills
E	Swartz Creek	53°23’	116°30’	990	2.1	-11.6	-1380	14.5	1123	580	432	Lower Foothills
F	Prairie Creek	52°15’	115°21’	1220	1.7	-11.7	-1348	13.5	975	667	479	Upper Foothills
G	Chinchaga	57°50’	118°12’	470	-0.8	-20.8	-2381	15.7	1201	454	298	Central Mixedwood
H	Calling Lake	55°17’	113°09’	625	0.9	-17.5	-1901	15.9	1254	488	359	Central Mixedwood
J	Hangingstone	56°23’	111°26’	550	0.2	-18.7	-2088	16.1	1258	559	371	Central Mixedwood

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°C); NDD –negative degree days (< 0°C); MTCM –mean temperature for the coldest month (°C); MTWM –mean temperature for the warmest month (°C); MSP –mean summer (April-September) precipitation (mm); NSR –Natural Subregion. B and C –established in 1980; D, E and F –established in 1981; G and H –established in 1982; J –established in 1983.

All sites have a randomized complete block design with 5 replications, 9-tree row plots and 2.5 × 2.5 metre spacing between trees. Trials were assessed for survival, climatic-related damages and height growth at 3-year intervals beginning at age 12 years; dbh measurements commenced at age 21 years. Analyses of survival, climatic damage and growth prior to age 27 years appear in Rweyongeza and Yang (2005) and Rweyongeza et al. (2007, 2010). Only 27-year height (H27) and diameter (D27) are covered in the present paper. Figure 1 shows that the 19 provenances covered in the present paper span the entire range of the 46 provenances in the G103 series and much of the latitudinal and longitudinal range of white and hybrid spruce in Alberta, except the Cypress Hills. Therefore, geographic patterns developed in this paper will be adequately generalized across the province.

2.2 Data Analysis

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

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

where Y_{ijn} is H27 or D27 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:

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

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 out of the scope of this paper.

Previous work (Rweyongeza and Yang 2005a; Rweyongeza et al. 2007; 2010) showed that height and diameter growth potential followed the quadratic function. Thus, to analyze the pattern of optimal growth potential, provenance means predicted from the individual site model were fitted to the following equation:

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

where Y_i is H27 or D27 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 acts as a surrogate variable for day length, also known as photoperiod. The regression of a biological variable such as height growth 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 provenances 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 quadratic function is sufficient to describe the pattern of genetic variation only when the continuum of the predictor variable (e.g., latitude as a surrogate for temperature) is the only justifiable 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 temperature occurs at the lowest latitude and highest temperature occurs at the highest latitude, then 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 latitudes. This happens when the latitudinal gradient is intersected by another climate-controlling gradient such as elevation. In Alberta, the increase in growing season temperature from high to low latitudes intersects with a southward increase in elevation. Consequently, the north to south increase in the length of the growing season applies only to a section of the Alberta landscape beyond which elevation becomes a major influence on the growing degree days and frost-free period. Thus, the often observed parabolic relationship of the provenance growth potential when latitude and elevation are used individually as predictor variables is a result of both variables limiting growth in the opposite extremes of the species' natural range in Alberta. Therefore, although a single-variable regression (transfer function) may provide adequate predictions of provenance growth, it does not provide an appropriate biological explanation of the underlying cause of low or high growth potential. In this case, combining geographic predictor variables in an easily interpretable regression provides a better explanatory model than a single-variable parabolic regression.

In this report, the factorial regression combining latitude and elevation as surrogates for aggregate climate 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 H27 or D27 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).

Application of 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 the expected H27 or D27 of a provenance from a defined latitude and elevation at a specified test site. When using single-variable quadratic regression models different heights or diameters for the same provenance may be predicted depending on the variable used i.e. latitude or elevation.

3.0 RESULTS AND DISCUSSION

3.1 Mean Survival and Growth

Overall mean survival and range of provenance means are summarized in Table 2. Site mean survival was the lowest at sites B and C, both of which had about 55% mortality after 23 years of field establishment. All other sites had survival higher than 70% and survival of individual provenances on these sites ranged from about 58% to 100%.

Table 2. Site means, range of provenance means for survival, height and diameter at age 27 years.

Site	Survival (%)		Height (m)		Diameter (cm)	
	Mean	Range	Mean	Range	Mean	Range
B	55.3 ± 1.7	31.1 – 84.4	6.05 ± 0.20	4.15 – 6.76	8.63 ± 0.28	6.11 – 9.78
C	54.9 ± 1.7	42.2 – 75.6	5.14 ± 0.35	3.78 – 6.25	7.70 ± 0.76	5.50 – 10.96
D	86.9 ± 1.2	68.9 – 97.8	7.64 ± 0.15	6.73 – 8.37	12.88 ± 0.32	11.68 – 15.49
E	97.1 ± 0.6	91.1 – 100	7.86 ± 0.17	6.48 – 8.78	12.11 ± 0.26	10.39 – 13.35
F	73.8 ± 1.5	57.8 – 91.1	5.95 ± 0.24	4.76 – 6.86	9.65 ± 0.39	8.02 – 11.91
G	83.7 ± 1.3	64.4 – 95.5	7.21 ± 0.29	5.78 – 7.89	9.83 ± 0.49	7.83 – 10.39
H	94.5 ± 0.8	79.5 – 100	6.91 ± 0.24	5.35 – 7.89	11.13 ± 0.32	8.90 – 12.51
J	88.9 ± 1.1	44.4 – 100	7.82 ± 0.23	5.37 – 8.67	13.16 ± 0.44	8.82 – 13.48
All Sites	79.3 ± 0.5	65.2 – 85.3	7.84 ± 0.24	5.67 – 7.33	12.18 ± 0.42	8.57 – 11.54

The high mortality at site B was largely caused by annual spring flooding due to snow melt in two of the five replications. Site C is located on an abandoned sawmill site with substantial soil compaction which may be responsible for the high mortality in the early years of field establishment. Thus, the high mortality on both sites does not indicate poor adaptation of provenances on these sites. While survival differences among provenances were significant on some sites ($P < 0.05$), we did not find meaningful correlations between survival and location of seed origin. This suggests that differential mortality among provenances may have been caused more by test site factors such as stand management and poor planting microsites than environmental attributes of the seed origin. Therefore, variation in survival is not discussed any further in this paper.

Table 2 summarizes height and diameter growth for test sites and provenances. The lowest growth occurred at site C; this was largely expected due to soil compaction. Table 1 shows that this site has among the highest precipitation (MAP) and growing degree days (GDD). Thus, climate was not a likely cause of poor tree growth at this site. On average, the northernmost (B) and highest elevation (F) sites had similar height and diameter growth. However, it will later be shown that ranking of provenances differed between the two sites. Tables 1and 2 show that the highest growth, especially for diameter occurred on sites located in the southern portion of the Central Mixedwood (H and J) and Lower Foothills Natural Subregions (D and E).

3.2 Patterns of Optimal Growth

Table 3 summarises the transfer functions describing the relationship of 27-year height and diameter with latitude and elevation of seed origin. Generally, for white spruce, height and diameter growth potential were more correlated with latitude than they were with elevation of seed origin. Transfer functions relating height and diameter with latitude of seed origin are graphically illustrated in Figure 2. The relationship between latitude and growth potential was strongest on sites located at mid-elevations in the boreal forest (C, G, H and J) and on site E located at a slightly higher elevation in the Lower Foothills. For site C, the regression of D27 on latitude appears weak mainly due to an exceptionally high mean value for provenance 21 located at about 2° north of the test site. Without this provenance, the D27 transfer function at this site has an R^2 of 0.40 ($P < 0.01$). In contrast, Table 3 shows that the relationship between growth potential and elevation of seed origin was strongest on the two high elevation sites (E and F) and on site H located at medium elevation in the boreal forest. Despite minor exceptions, the pattern of provenance variation described by the regressions in Table 3 suggests that at mid-elevations in the boreal forest, growth potential is determined by latitude of seed origin. In contrast, growth potential in the foothills and boreal highlands is determined by elevation of seed origin, as suggested by the significant R^2.

Table 3 also shows that the provenance's expression of growth potential depends on its origin relative to the planting site. For the six sites located between latitudes 53°N and 58°N, the predicted location for provenances of highest growth potential (optimum latitude) lies between 55° and 56°N. Except for site E, the predicted optimum latitude is very similar to the latitude of the test site with the best provenances predicted to originate just south of the test site (Table 3). The best provenances for site E are predicted to originate from about 2° north or 100 m below the test site. At high latitude site B (Table 1), the best provenances are predicted to originate from north of latitude 58°N (Table 3), which indicates that locally selected provenances are the most appropriate for reforestation in this region. The elevation transfer function shows that the best provenances for site F located at 1220 m als would originate from about 1000 m als (Table 3). Therefore, in the current climate, the latitudinal transfer functions suggest that, in the boreal forest region, provenances could be transferred northward by 1° to 2° of latitude. Likewise, elevation transfer functions suggest that in the foothills region, provenances could be transferred upward by 100 to 200 m.

In analysing the 24-year data (ATISC 2008), it was observed that some of the high elevation provenances, especially provenance 48 (elevation 1585 m asl), had unexpected high growth potential at site D (elevation 805 m). Based on the performance of the other provenances in this trial series, on the results of Alberta lodgepole pine provenance trials (see Rweyongeza et al. 2010a) and on an extensive review of the literature on provenance testing, a subalpine provenance outgrowing all local provenances at 780 m below its native elevation is highly unusual. A visit to site D showed that some of the plots of provenance 48 had trees that resembled Engelmann spruce and others had trees that were among the largest and best white spruce in the trial. This suggests that misidentification of this provenance likely occurred during establishment of this trial. Fitting site D regressions with 27-year data and keeping provenance 48 as it is currently designated showed that the best provenances for site D would originate from 53°40'N ($R^2 = 0.37$) and 1011 m ($R^2 = 0.45$) for height and 54°14'N ($R^2 = 0.22$) and 982 m ($R^2 = 0.19$) for diameter. The diameter transfer functions could be ignored, because they explained very little of the variation among provenances at this site. The elevation transfer function for height suggests that the best provenances for site D would originate from about 1000 m asl in an area known to be an origin of poor provenances for other low and mid-elevation sites. Likely, these results are distorted by the misidentified provenance 48.

Table 3. Summary of individual site transfer functions describing the relationship of height and diameter with latitude and elevation of seed origin in Alberta.

SITE	TRAIT	Latitude Transfer Functions						Elevation Transfer Functions						Combined latitude and elevation Functions				
		β_0	β_1	β_2	R^2	Site	Optimum	β_0	β_1	β_2	R^2	Site	Optimum	β_0	β_1	β_2	β_3	R^2
B	H27	-70.485	2.6434	-0.02273	0.49**	59°08’	58°09’	6.6711	-8.17036c	-3.7g	0.34*	370	-	1.6074	0.07925	-5.5130b	1.03334c	0.44*
	D27	-55.094	2.1307	-0.01766	0.38*		60°20’	9.7800	-2.11989b	-6.4f	0.29		-	-3.9429	0.22124	-2.0850b	4.60460d	0.36
C	H27	-152.995	5.7180	-0.05157	0.58**	55°33’	55°26’	4.5372	2.35421b	-1.5e	0.36*	670	784	27.4969	-0.38490	-1.7367a	2.97756c	0.54**
	D27	-245.930	9.1644	-0.08260	0.29		55°28’	6.9018	3.26234b	-2.1e	0.16		771	37.4001	-0.51376	-2.6526a	4.62620c	0.26
D	H27	-190.916	7.1893	-0.06497	0.77***	55°31’	55°20’	6.4768	3.34967b	-1.9e	0.41*	805	875	18.6949	-0.20714	-2.2735a	4.27979c	0.71***
	D27	-343.652	12.8470	-0.11555	0.65***		55°35’	11.4533	4.42904b	-2.7e	0.26		806	26.8071	-0.26600	-3.7999a	7.17078c	0.54*
E	H27	-177.845	6.7776	-0.06170	0.60***	53°23’	54°56’	6.3849	4.61185b	-2.6e	0.64***	990	893	38.6046	-0.53499	-2.3528a	4.10233c	0.76***
	D27	-279.959	10.6577	-0.09700	0.68***		54°56’	9.9397	6.71105b	-3.7e	0.62***		899	54.5921	-0.74342	-3.6063a	6.37944c	0.76***
F	H27	-97.256	3.8398	-0.03560	0.42*	52°15’	53°55’	4.4330	4.17922b	-2.1e	0.64***	1220	980	32.3592	-0.46013	-1.5505a	2.65864c	0.65**
	D27	-136.056	5.4847	-0.05141	0.42*		53°20’	7.1415	6.48372b	-3.1e	0.55**		1037	47.5272	-0.66502	-2.2097a	3.85275c	0.54**
G	H27	-116.202	4.4004	-0.03913	0.69***	57°50’	56°13’	6.9633	1.44718b	-1.1e	0.45**	470	679	12.5234	-0.09483	-1.3314a	2.45196c	0.62**
	D27	-141.617	5.4285	-0.04853	0.63***		55°56’	9.6464	1.17004b	-8.8e	0.23		669	13.4078	-0.06852	-1.4901a	2.81129c	0.50*
H	H27	-222.582	8.3485	-0.07575	0.63***	55°17’	55°06’	5.1151	5.78392b	-3.3e	0.77***	625	874	43.6986	-0.63965	-2.9564a	5.16195c	0.83***
	D27	-346.460	12.9826	-0.11757	0.69***		55°13’	8.6362	8.18181b	-4.7e	0.72***		865	59.9069	-0.85178	-4.4560a	7.88504c	0.80***
J	H27	-203.631	7.5712	-0.06762	0.70***	56°23’	55°59’	7.2471	2.79721b	-1.9e	0.48**	550	722	22.4139	-0.25621	-2.3394a	4.24182c	0.65**
	D27	-255.673	9.5803	-0.08547	0.59***		56°03’	11.5389	3.19636b	-2.3e	0.35*		707	25.6464	-0.24082	-2.9110a	5.35842c	0.53**

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.; *a* = $\times10^{-2}$; *b* = $\times10^{-3}$; c = $\times10^{-4}$; d = $\times10^{-5}$; e = $\times10^{-6}$; f = $\times10^{-7}$; g = $\times10^{-8}$;

APPLICATION: As an example, to estimate 27-year height of provenance 17 from latitude 55°14’ or 55.2333 and elevation 610m als at site D using a model combining latitude and elevation of seed origin, first convert latitudinal minutes to decimals by dividing 14 by 60 (14 ÷ 60 = 0.2333) and add it to 55 to obtain 55.2333. Then notice that $\beta_0 = 18.6948$, $\beta_1 = -0.20714$, $\beta_2 = -2.2735\times10^{-2}$ or -0.022735, $\beta_3 = 4.27979 \times 10^{-4}$ or 0.000427979.
Thus, expected H27 = 18.6848 − (0.20714×55.2333) − (0.022735×610) + (0.000427979×55.2333×610) = 7.798 or approximately 7.80m. The actual observed H27 is 7.95 or approximately 8.0m.

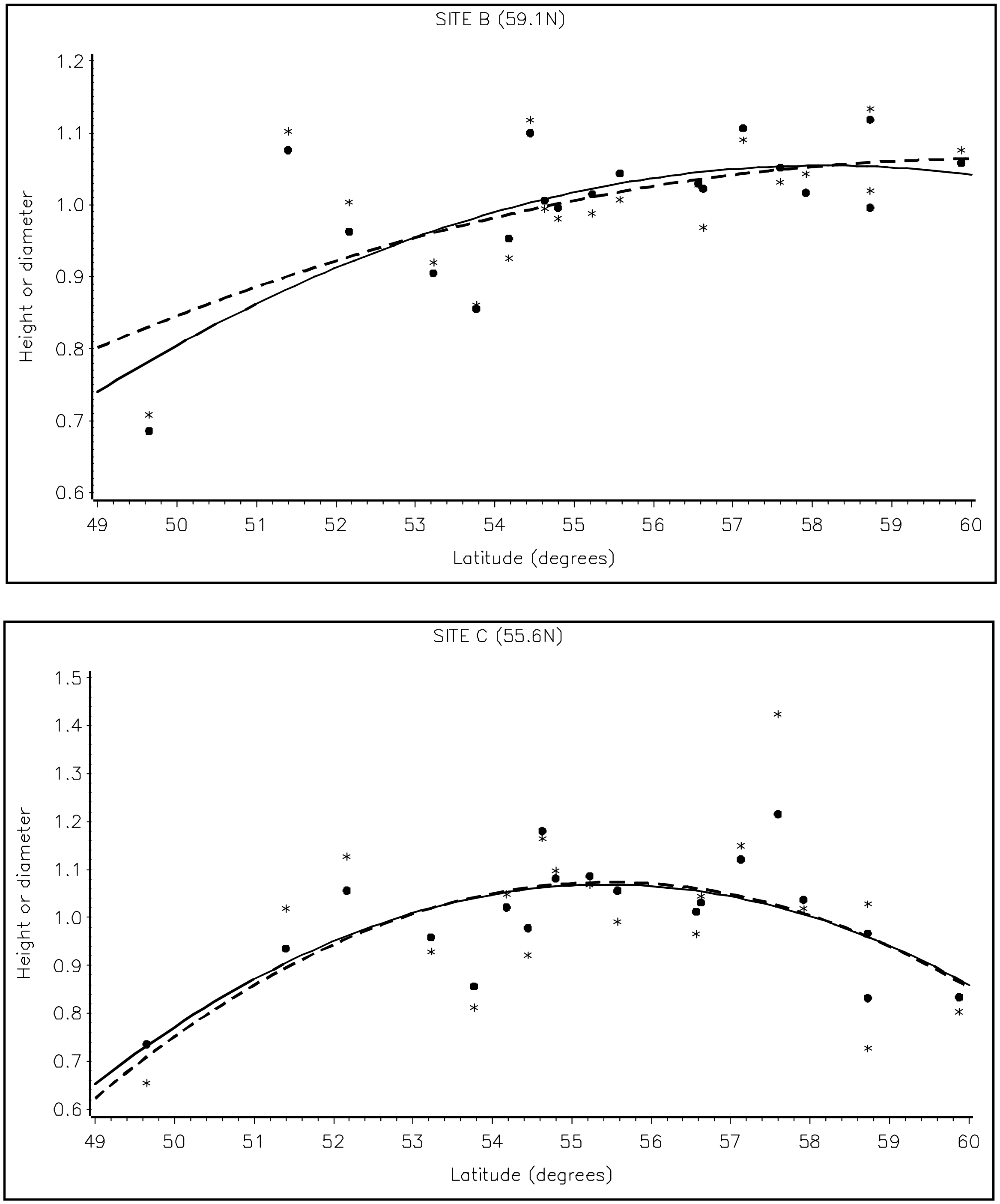

Figure 2. Height and diameter growth potential as related to latitude of seed origin. Provenance height (— •) and diameter (— — *) are scaled relative to the site mean[1].

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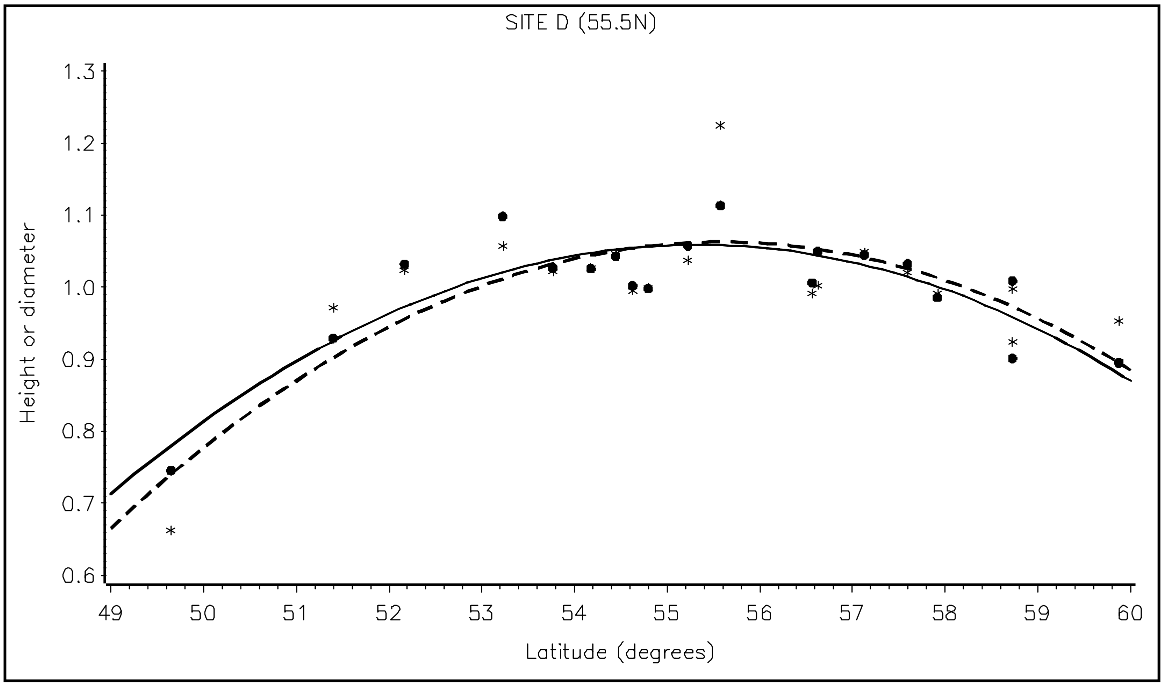
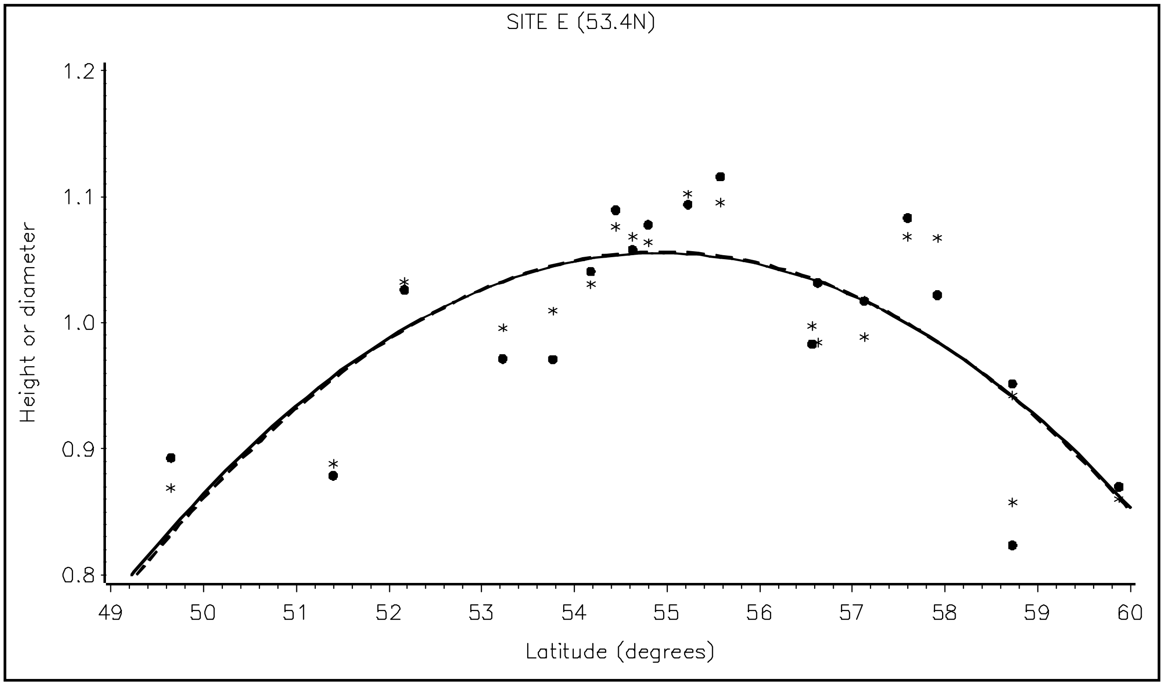
[1] Actual height or DBH can be obtained by multiplying the value on the vertical axis by the site mean from Table 2. For example, a provenance with height value of 1.1 at site B has height of 1.1 × 6.05 = 6.7 m. For the same site, provenance with DBH value of 1.1 on the graph has DBH of 1.1 × 8.68 = 9.5 cm.





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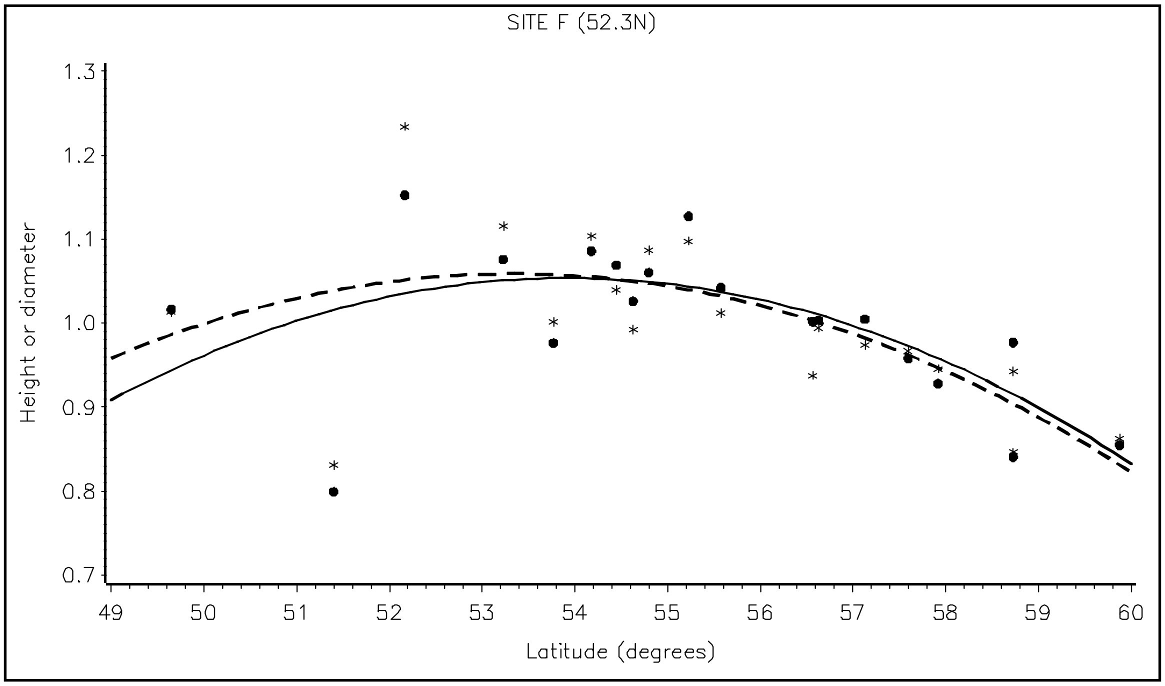

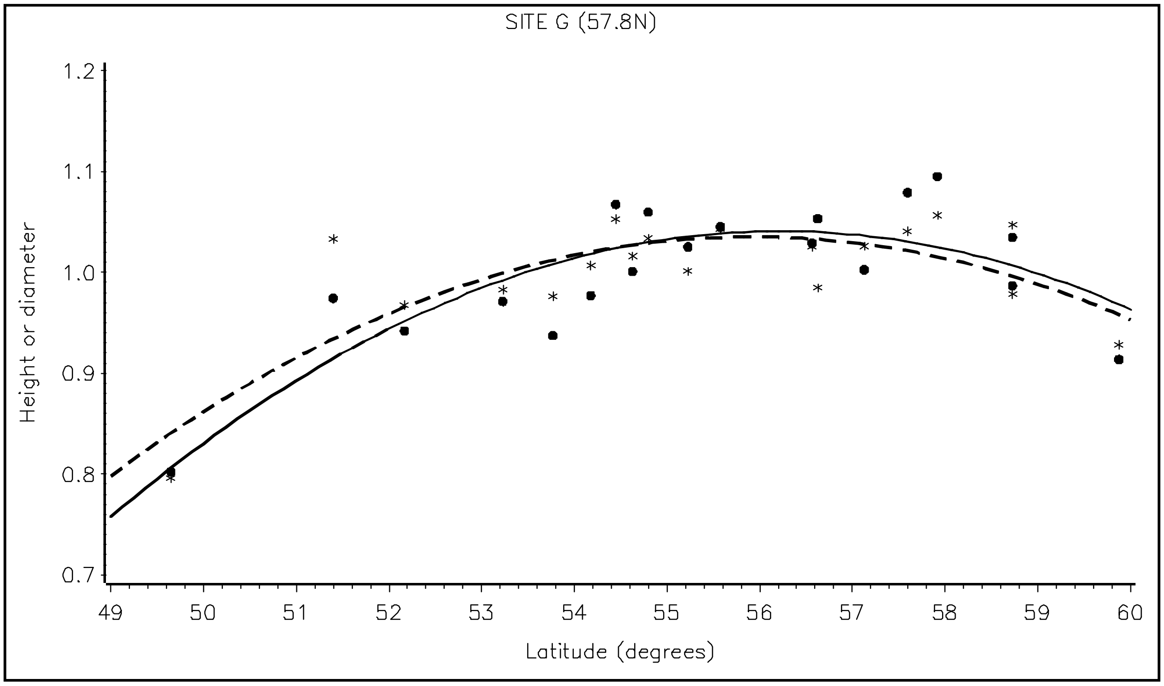

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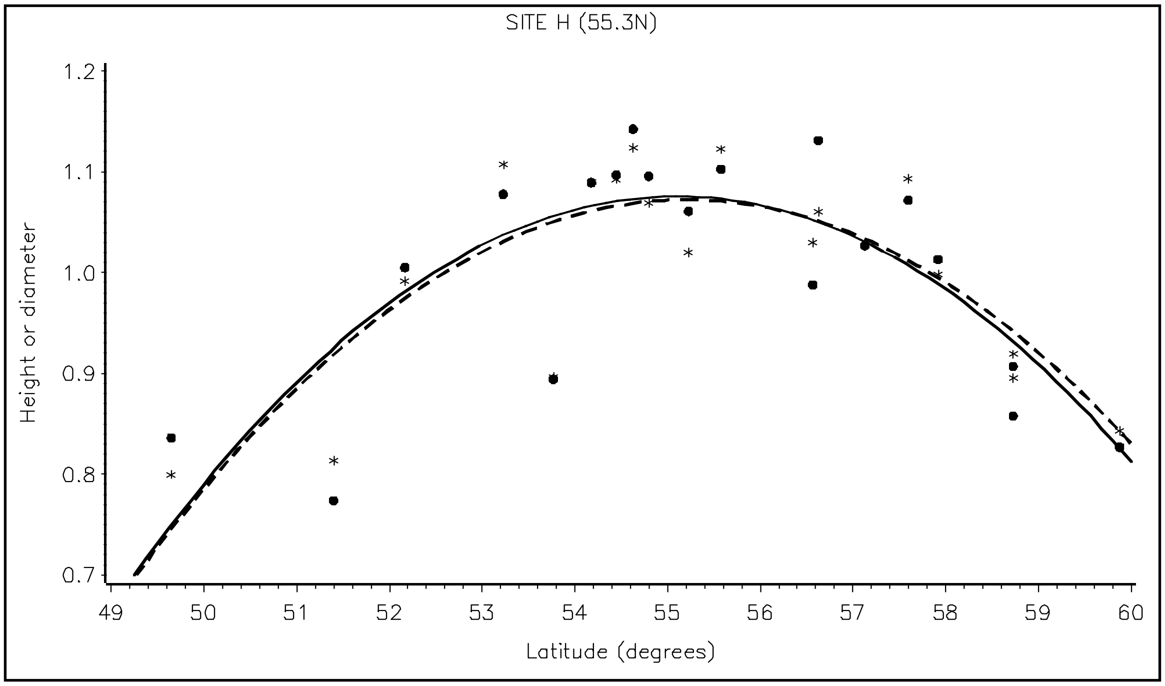

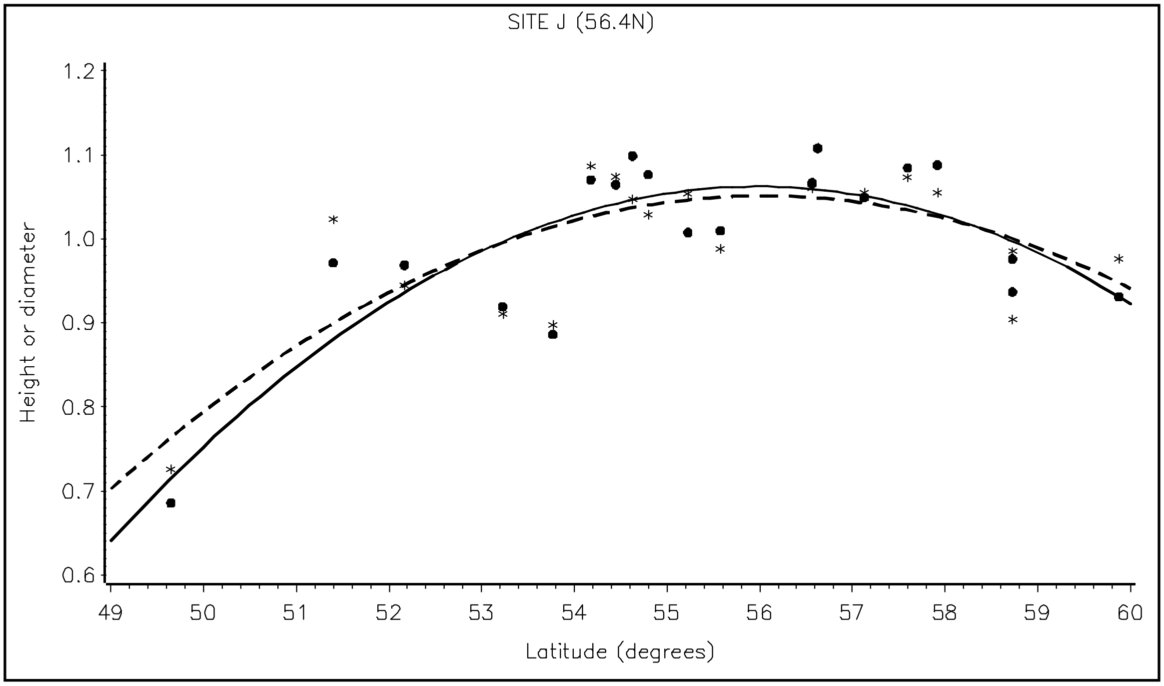

Figure 2. continued.

Instead of dropping provenance 48 from site D transfer functions, we chose to estimate its height and diameter at site D based on its performance at the other seven sites (B, C, E, F, G, H, and J). To do this, we disregarded all the data of provenance 48 at site D as if it was not planted at this site. We then developed a single-provenance transfer function for provenance 48 similar to a response function (see Rweyongeza et al. 2007) but employing a transfer distance between the location of provenance 48 and the location of each of the seven test sites. The model was the same as equation 3, except that in this case X_i is the provenance latitude or elevation minus the test site latitude or elevation. Four models were fitted, that is, H27 with latitude, H27 with elevation, D27 with latitude and D27 with elevation. Each regression had seven data points corresponding to mean H27 or D27 of provenance 48 at each of the seven test sites. Expected mean H27 or D27 of provenance 48 at site D was then calculated by inserting the latitudinal (-5.87°) and elevational (780 m) transfer distances between the origin of provenance 48 and the location of site D into the provenance 48 transfer function. Two values of H27, one predicted by the latitude model and the other by the elevation model were then averaged to obtain a single H27 mean for provenance 48 at site D. The same procedure was used to obtain mean D27 for provenance 48 at site D. The two estimated values of provenance 48 at site D were then combined with the observed means of all other provenances at site D to fit the site D transfer function (see Table 3; Figure 2). Because of these estimated values, one error degree of freedom was dropped when testing the statistical significance of site D transfer functions.

Table 3 and Figure 2 show that the mean height and diameter of provenance 48 at site D estimated on its response to latitudinal and elevational displacement and independent of the performance of other provenances at site D significantly improved site D transfer functions, especially for latitude. The R^2 for H27 and D27 increased from 0.37 to 0.77 and from 0.45 to 0.65, respectively. More importantly, the predicted optimum source of the best provenances is around the test site, which is consistent with predictions for all other sites in the mid-latitude zone. Although the improvement in the elevation transfer function was moderate, it also shows that the best provenances would originate from an elevation similar to that of the test site (Table 3).

Table 3 summarizes the relationships of height and diameter with location of seed origin using a factorial regression on latitude and elevation of seed origin. The negative regression coefficient for latitude (β_1) shows that, at a constant elevation, genetic growth potential is expected to decrease with an increase in latitude of seed origin. With positive β_1, site B appears to be an exception in that growth at this site generally increased with an increase in the latitude of seed origin. However, it should be noted that site B is at the northern end of the sampled latitudinal range with only provenance six originating 45' north of the test site. Figures 2 and 3 suggest that provenances from further north of latitude 60°N would be expected to exhibit low growth potential at site B.

The negative regression coefficient for elevation (β_2) Table 3 also shows that, at a given latitude, genetic growth potential is expected to decrease with an increase in elevation of seed origin. Provenances from high elevations are expected to have lower growth potential than those from low elevations (Figure 3).

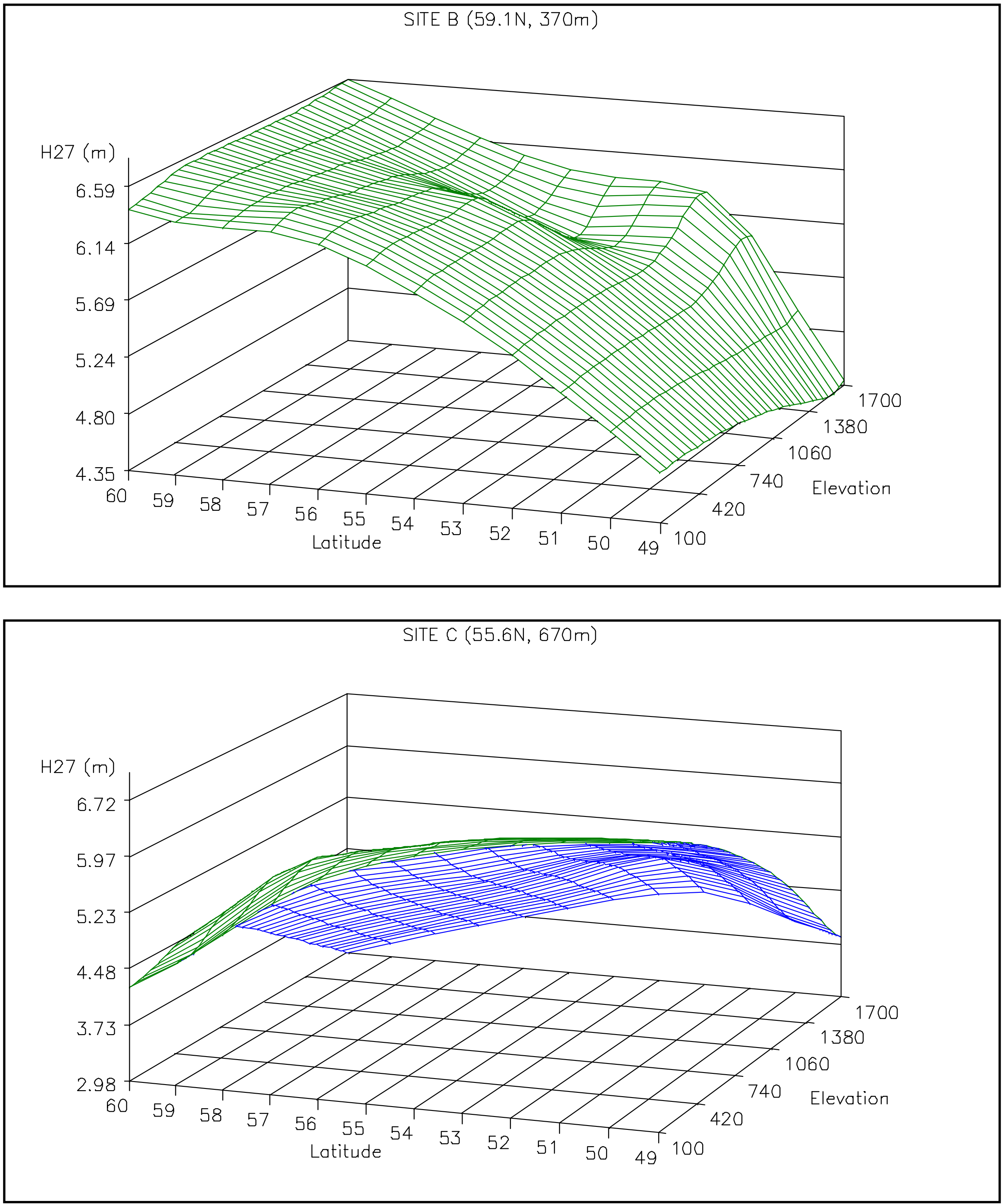

Figure 3. Height growth potential as related to latitude and elevation of seed origin[2].

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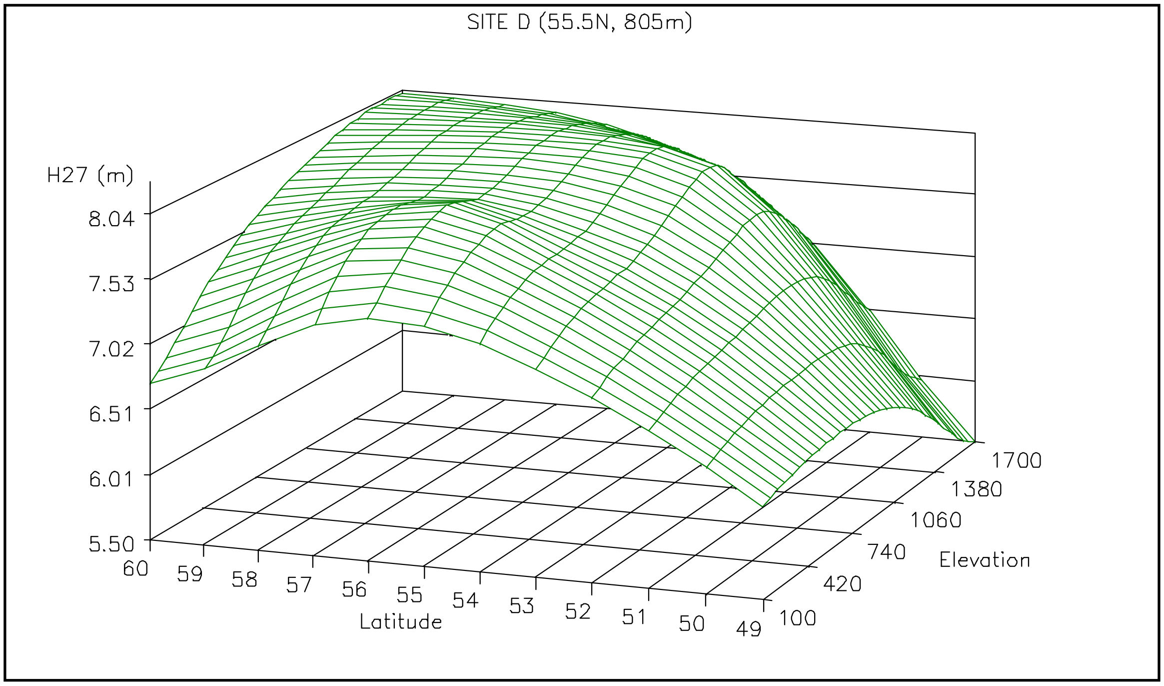
[2] To create a continuous response surface, the computer program uses observed sample data points to generate intermediate points within a specified range and intervals. Thus, a response surface may indicate expected provenance heights in a region that was not actually sampled but fits a trend set by the observed data.



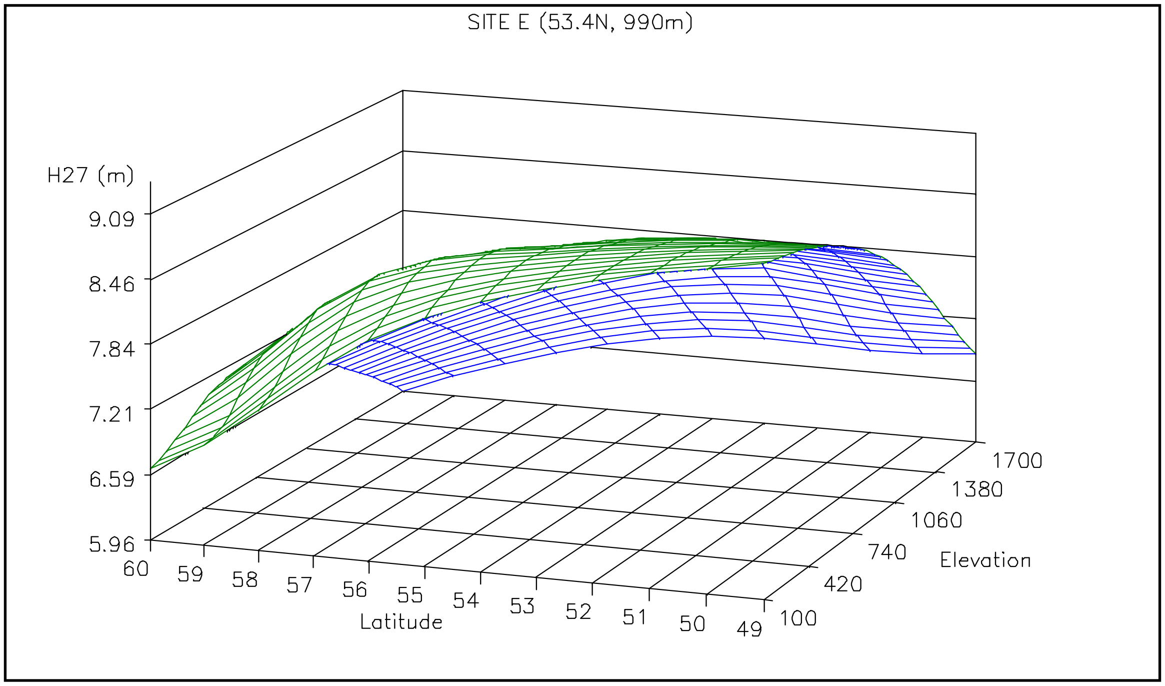
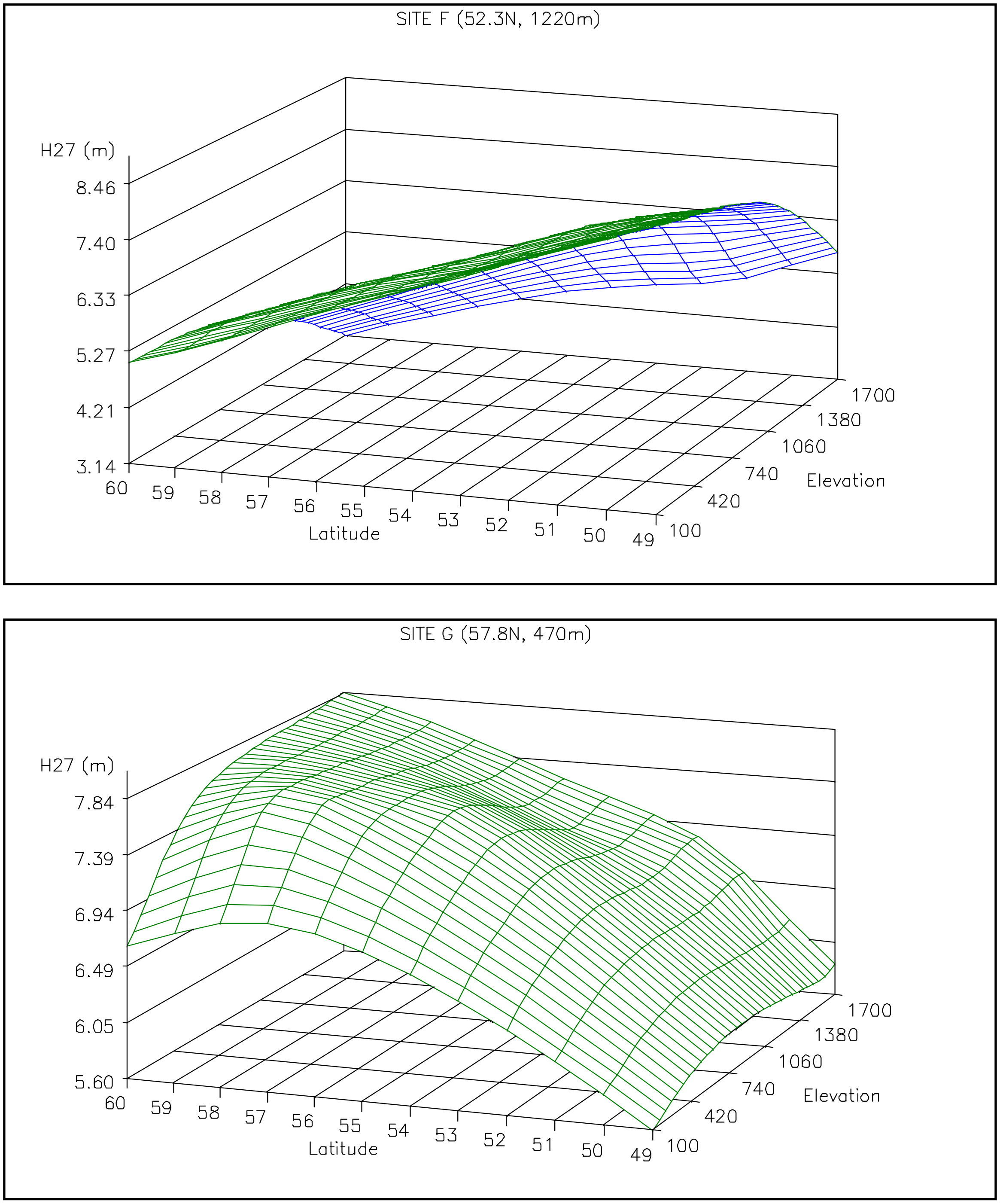


Figure 3. continued.



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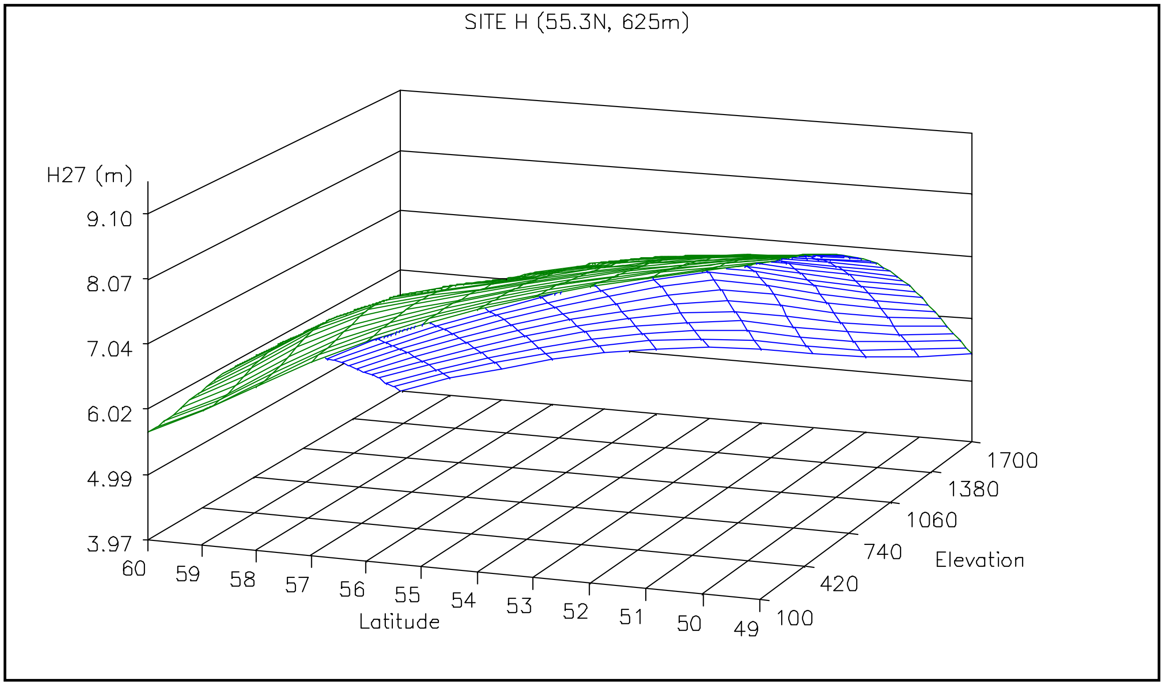

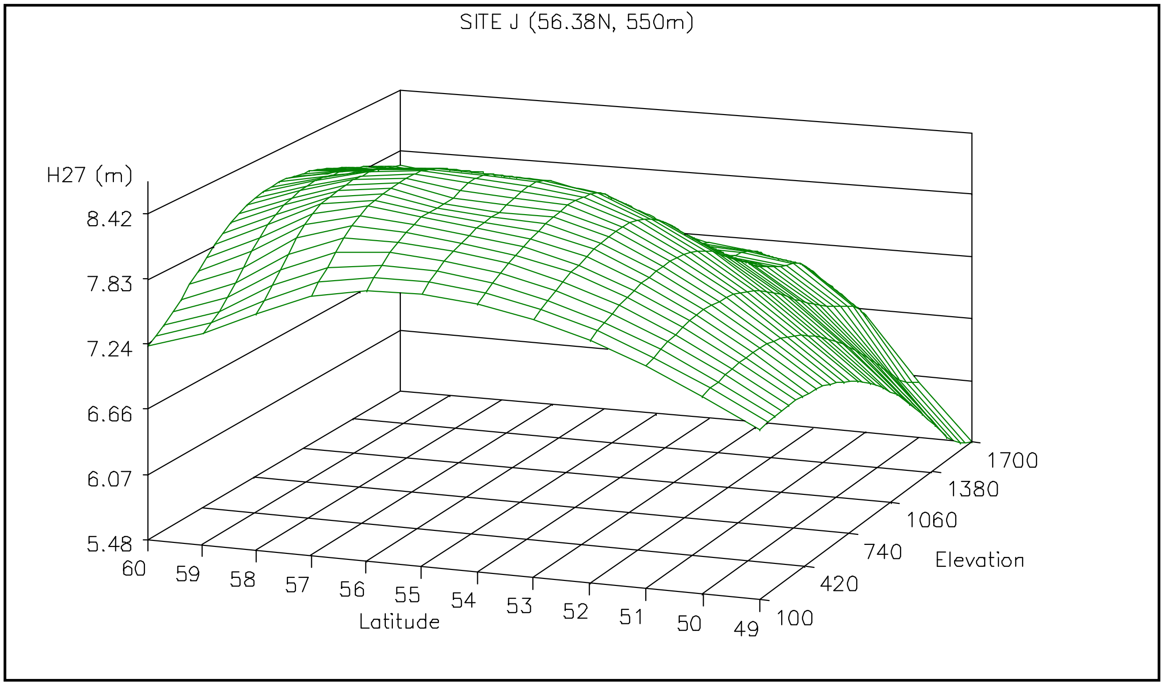

Figure 3. continued.

Table 4 shows superior provenances defined as provenances with an observed mean H27 greater than two standard errors above the site mean. For site B, provenances 2 and 8 are considered local due to their proximity to the test site. In contrast, provenances 29 and 46 are from more than 4^{o} south of the test site and their elevations of origin are more than 500 m higher than the test site elevation. Therefore, their superior performance at this site is unexpected.

Table 4. Provenances with observed or predicted mean height greater than two standard errors above the site mean.

Observed height and diameter growth								Height and diameter predicted by LAT-ELEV model^{++}							
SITE	PROV	H27 (m)	D27 (cm)	SITE	PROV	H27 (m)	D27 (cm)	SITE	PROV	H27 (m)	D27 (cm)	SITE	PROV	H27 (m)	D27 (cm)
B	2	6.76	9.78	G	4	7.89	10.39	D	15	8.06	13.65	H	29	7.50	12.00
	8	6.69	9.41	H	12	7.89	12.51		16	7.87	13.18		37	7.53	12.02
	29	6.65	9.96		15	7.82	11.80		23	8.10	13.71	J	15	8.36	12.91
	46	6.51	9.51		16	7.57	11.90		27	7.86	13.21		23	8.38	12.94
C	12	6.07	9.97		21	7.41	12.17		29	7.95	13.31		27	8.29	12.69
	21	6.25	10.96		27	7.62	12.49		31	7.95	12.29				
D	8	7.86	13.26		29	7.58	12.16		37	7.90	13.20				
	15	7.89	12.68		32	7.45	12.32	E	12	8.70	13.24	B^{+}	2	6.45	9.26
	17	7.95	13.12		37	7.53	12.13		16	8.52	13.05		4	6.37	9.08
	27	8.37	15.49	J	4	8.51	12.83		17	8.53	13.03		6	6.39	9.20
	29	7.84	13.23		15	8.67	13.48		27	8.40	12.89		10	6.48	9.43
	32	8.26	13.36		16	8.42	12.51		29	8.35	12.87		15	6.34	8.97
E	12	8.32	12.94		21	8.49	13.05		37	8.39	12.90		21	6.37	9.06
	16	8.48	12.88		23	8.35	12.90	F	12	6.62	10.56		23	6.34	8.97
	17	8.60	13.35		29	8.33	13.06		16	6.46	10.36	C^{+}	12	5.80	8.57
	21	8.52	12.94		37	8.38	13.22		17	6.45	10.30		16	5.64	8.39
	27	8.78	13.27					H	12	7.92	12.47		17	5.68	8.43
	29	8.57	13.03						16	7.71	12.24		27	5.58	8.32
F	17	6.71	10.60						17	7.73	12.25	G^{+}	15	7.57	10.28
	37	6.46	10.65						27	7.59	12.09		23	7.58	10.30
	40	6.86	11.91												

+ -predicted values for these sites are for provenances that are greater than one standard error above the site mean.

++ -predicted from a factorial regression of latitude and elevation (Eq. 4).

Because of the demonstrated low growth potential of high elevation provenances in this and other studies (e.g., Rweyongeza et al. 2007), the superior growth of provenance 32 at site D is also unexpected given that its elevation of origin is about 500 m above the elevation of site D. All other superior provenances at site D are from relatively small latitudinal and elevational distances from the site. The three superior provenances at site F (17, 37 and 40) are remarkably different in terms of elevation ranging from about 600 m asl to 1300 m asl. Provenance 17 is 3^{o} north of and about 600 m lower than site F but provenances 37 and 40 are relatively closer to site F. Except for provenance 32 at site H, superior provenances at sites G, H and J have similar latitudes to those of the test sites; however, elevations of the superior provenances vary substantially from the test site elevation.

Large elevational and latitudinal differences among provenances and test sites and the tendency for elevation and latitude to be negatively correlated make it difficult to determine a criterion to describe the relationship between provenances and test sites. Use of multivariate climatic indices as described by Rweyongeza et al (2009b) may help to resolve this problem. However, a climatic description of provenance variation is out of the scope of the present paper.

Also shown in Table 4 are the provenances with expected H27 greater than two standard errors above the site mean. The expected height and diameter of these superior provenances were predicted from the factorial regression model (Eq. 4) which describes provenance growth potential based on provenance latitude and elevation. Conceptually, the predicted height and diameter in Table 4 identify provenances that are expected to show the highest growth potential on a given site based on the observed relationship between growth potential and location of seed origin. Because this relationship is mainly a function of latitudinal and elevational transfer distances between the provenance and the test site, it should resolve most of the observed provenance rank inconsistencies such as those described for site B. For predicted height, the best provenances for site B are northern provenances in closer proximity to the test site and mid-latitude provenances between about 56.5°N and 57.5°N latitude. Even in this group, there is a clear trend that provenances closer to the test site have better predicted height and diameter than those farther away (Table 4). For all other sites, the best provenances are expected to originate from between latitudes 54°N and 57°N. Provenances in this group are mainly from between 600 and 950 m asl. Predicted growth of provenance 31 at site D is an exception in that it originated from 1402 m asl, about 600m above the test site. Expression of such high growth potential for a high elevation provenance at lower latitudes is generally unexpected.

Table 4 shows that provenances 17, 37 and 40, which have an observed H27 greater than two standard errors above the site F mean, originated from between 610 and 1341 m als. Likewise, the three best provenances (12, 16 and 17) based on expected H27 predicted by the latitude-elevation model are from 610 to 731 m als. The elevation at site F is 1220 m. These data suggest that seed may be transferred upward by as much as 600 m. For example, seed could be transferred from the boreal and Lower Foothills to the Upper Foothills. However, the risk of climatic maladaptation is likely too great with this elevational transfer distance, especially for provenances from the boreal forest. For sites such as F located in the higher elevation and lower latitude periphery of the sampled region of the species' range in Alberta, additional provenances tested at this site (not tested on all sites) may provide additional information about the transferability of seeds. When known Engelmann spruce provenances are excluded, site F has a total of 25 provenances. These include the 19 provenances tested at all sites and 6 provenances that were selectively tested. Of the additional 6 provenances, 4 are from 1036 to 1280 m in the Lower and Upper Foothills, one is from the Cypress Hills (1310 m) and one is from northern Alberta (59°32'N and 305 m als). These provenances provide additional data from the upper end of the sampled elevational range. The elevational transfer function for site F with 6 additional provenances appears in Figure 4.

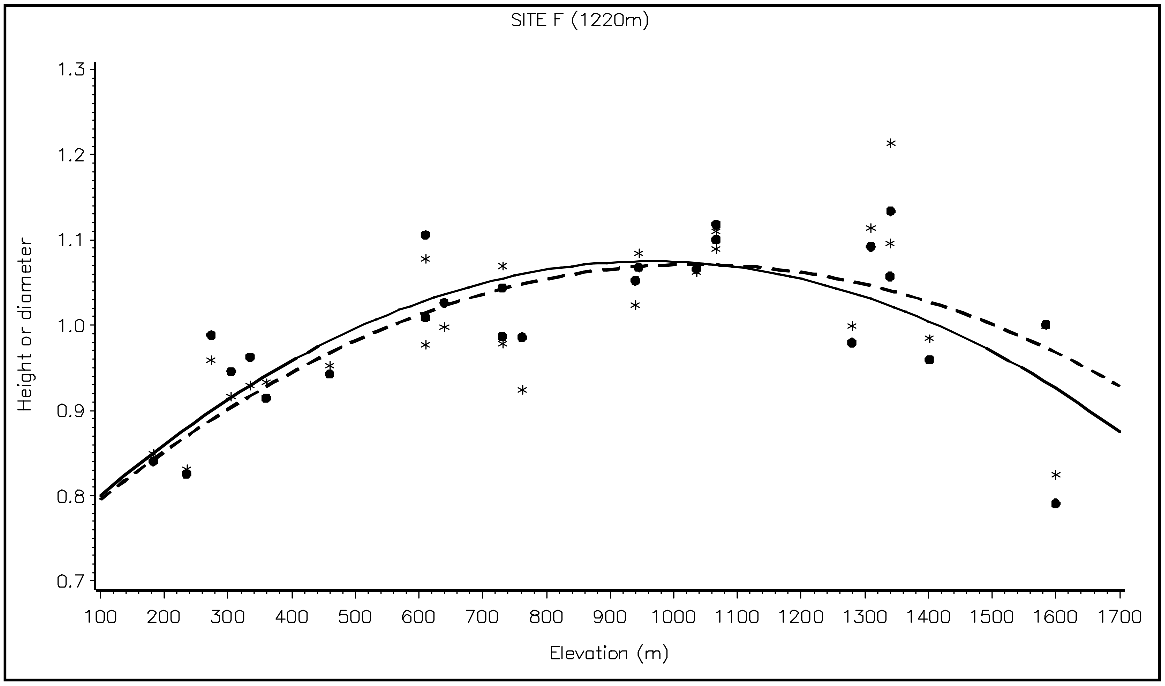

Figure 4. Height and diameter growth potential at site F as related to elevation of seed origin. Provenance height (— •) and diameter (— — *) are scaled relative to the site mean.

The new latitudinal transfer function for H27 including the six additional provenances had a R^2 of 0.38 (*P = 0.0052*) and a predicted optimum seed source of 52°57'N. The new latitudinal transfer function for D27 had a R^2 of 0.45 (P = 0.0015) and an optimum seed source location of 52°05'N. The elevational transfer function for H27 had a R^2 of 0.59 (*P < 0.0001*) and an optimum seed source location of 963 m als. The new elevational transfer function for D27 had a R^2 of 0.54 (*P = 0.0002*) and an optimum seed source location of 1031 m als. Thus, the six additional provenances did not alter the results in terms of predicted optimum elevation. In both cases (see Table 3), the predicted optimum elevation is approximately 1000 m als. With 25 provenances, the 10 provenances with the highest observed H27 at site F include 16 (731 m) and 17 (610 m); the remaining provenances originate from between 940 and 1341 m als. Figure 4 shows that most of the provenances from mid-elevations where provenance 16 and 17 originate had average performance at site F. Better performing provenances appear to originate from just below 1100 m and slightly above 1300 m als. Thus, it can be generalized that the region around 1200 m als could be reforested with seeds from between 1000 and 1300 m als within a narrow latitudinal band similar to that of the planting site.

3.3 Genotype-Environment Interaction

Genotype by environment interaction (GE) describes a statistical concept whereby ranking of genotypes, such as provenances, differs between sites, or the magnitude of their absolute differences varies between sites. When the ranking of genotypes differs between sites, GE is referred to as crossover interaction. GE due to varying differences of genotypic means between sites without altering genotype rankings leads to differences in the size of the genetic variance among sites and is called a scale effect. With the scale effect, genotypes selected in the two interacting environments are the same. In contrast, with crossover interaction, genotypes selected in the two environments differ substantially (see Falconer and Mackay 1996). According to

Falconer (1952), the extent of the crossover interaction can be estimated by the genetic correlation of the same trait measured in two environments. In forestry, this type of correlation has come to be known as a Type B correlation (Burdon 1977). It is a correlation of the same trait (e.g., height at the specified age) measured on different individuals of the same provenance or family raised in different environments. This distinguishes it from a Type A correlation, which is the correlation of two different traits or same trait at different ages measured on the same individual in the same environment.

In this paper, the extent of GE interaction was estimated using the Type B genetic correlation calculated according to Robertson (1959). This method calculates the genetic correlation from the mean squares after standardizing the data. The 28 site-pair correlations for height and diameter are not tabulated here but general correlation patterns are discussed below.

(1) The correlations between sites B and G were 0.84 and 0.75 for H27 and D27, respectively; the corresponding correlations between sites B and J were 0.64 and 0.70, respectively. In terms of latitude, sites G and J are geographically the closest to site B (Table 1). The correlations between site B and the other sites declined southward from 0.47 (H27) and 0.56 (D27) between sites B and C to -0.45 (H27) and -0.30 (D27) between sites B and F.

(2) The correlations between sites F and E were 0.68 (H27) and 0.77 (D27); similarly, the correlations between sites F and H were 0.58 and 0.76 for H27 and D27, respectively. The moderate to high correlations between sites F and H, which are significantly different in elevation, are directly attributable to the high correlation between sites E and H ($r > 0.90$). The correlations between sites F and D were 0.41 (H27) and 0.64 (D27) and the correlations between site F and all other sites, including B, ranged from 0.41 to -0.45. Thus, the strong correlations between site F and H are exceptions. The general trend in the correlations involving site F is for a decline with increased elevational difference between site F and the other site. Site F, located in the Upper Foothills at 1220 m als, is expected to exhibit greater similarity with site E in the Lower Foothills at 990 m als than with sites located at lower and medium elevations in the boreal forest.

(3) Within the mid-latitude and mid-elevation zone, including sites C, D, G, H and J, all sites except G are approximately within 1^{o} of latitude and 255 m in elevation of each other (Table 1). In contrast, site G is about 2^{o} 27’ from site H, the greatest distance between site G and the other sites in terms of latitude, and 335 m from site D, the greatest distance between site G and the other sites in terms of elevation. The correlations between site C and the other sites in this zone ranged from 0.66 to 0.82, except for a low correlation ($r = 0.49$) for H27 between sites C and D. Except for moderate correlations of 0.43 (H27) and 0.58 (D27) between sites D and J, the correlations between site D and the other sites in the mid-latitude and mid-elevation zone ranged from 0.70 to 0.84. The correlations among sites G, H and J ranged from 0.63 to 0.87. Despite minor exceptions, it could be generalized that the correlations among sites C, D, G, H and J for height and diameter are between 0.60 and 0.90.

GE interaction may result from differential genotypic response to differences in climate, soil characteristics, site management practices and other sources of environmental variation. Spatial variation in soil physical and chemical characteristics and occurs more often and is less predictable than climatic variability. In the continental interior, variability in climate is often determined by changes in latitude and elevation, and where applicable, by aspect. Thus, GE interaction among sites located in a narrow latitudinal and elevational band is likely caused by variation in soil characteristics, by site-specific microclimates such as frost pockets, and by site management practices during stand establishment. The potential for edaphic ecotypes of white spruce to evolve is lessened by continuous gene flow resulting from wide spread seed and pollen dispersal which is characteristic of wind-pollinated species. Because gene flow and reforestation take place on a scale larger than individual patches of differing soils and test site microclimates, a selected population or genotype is normally deployed on lands that may be substantially different in terms of soils and other factors of micro-environmental variation. Thus, when regulating seed transfer, GE caused by unknown and unpredictable variation in soils, site-specific microclimates and stand management practices is generally ignored. Only GE interaction due to predictable climatic differences between sites will influence the choice of seed sources.

In this study, there are strong climatic similarities among sites C, D, H and J, with differences between sites gradually increasing with latitudinal separation. All four sites have negative degree days (NDD) between -1700 and -2100, and growing degree days above 5^{o} C (GDD) between 1200 and 1250. The multivariate climatic index developed by Rweyongeza et al. (2009b) shows that these sites are similar in terms of winter temperatures, precipitation and continentality. Site G, on the other hand, is located at the northern edge of what would be considered a mid-latitude zone. Thus, it has much cooler winters than the other four sites (NDD ~ -2400), reflecting a transition from a mid-latitude to a high-latitude climate. Local site differences in soils contribute to lower Type B correlations between sites with similar climates. The differences would be minimized by correlating the provenance means predicted by the regression models described earlier. Conceptually, such correlations indicate the similarity in provenance rankings between sites based on observed provenance responses to geographic transfer. Because latitude and elevation are surrogates for climate, sites with similar geography and thus climate should exhibit consistent provenance rankings based on predicted rather than observed growth potential. The concept is that predicted provenance means are less influenced by non-climatic site factors than are observed means.

To further examine the relationship between sites in the mid-latitude and mid-elevation zone, H27 and D27 predicted by the factorial model combining latitude and elevation (Eq. 4) on each site were used to generate the Pearson's correlation coefficients between pairs of test sites. Except for a slightly lower correlation between sites G and H for H27, all other correlations among sites C, D, G, H and J for both height and diameter ranged from 0.79 to 0.99 ($P < 0.0001$). This consistency in ranking of provenances among sites in the mid-latitudinal zone is illustrated by the similarity of superior provenances among sites as shown in Table 4. Generally, these high correlations suggest that provenances could be transferred northward by 2^{o} because the five sites all fall approximately within a 2^{o} latitudinal band. For example, it should be safe to move seed from latitude 55^{o}N to 57^{o}N. However, because isolated hill systems exist in this region, this seed movement should be confined to elevations below 800 m als. In Alberta, moving seed northward indirectly implies transferring provenances from a higher to a lower elevation. However, 800 m asl represents the region within which most provenances originated and test sites are located. As stated earlier, geographic trends in this region are more related to latitude than to elevation. Thus, outside the boreal highlands, the primary consideration for seed transfer in Alberta's boreal forest is latitudinal displacement. In this region, elevational displacement is secondary and may be considered along with other physical factors that distinguish seed sources.

(4) The Type B correlations between site E located at 990 m als and sites at mid-latitudes and mid-elevations (470 – 805 m als) were moderate to high. Except for a correlation of 0.86 between sites E and C for H27, the correlations between site E and sites C, G and J ranged from 0.58 to 0.70. Correlations between sites E and D were 0.82 (H27) and 0.79 (D27) and the correlations between sites E and H were 0.95 (H27) and 0.93 (D27). Exceptionally high correlations between site E and H are difficult to explain considering differences of about 2^{o} of latitude, 360 m of elevation and -520 units of NDD between the sites. However, the general pattern of Type B

correlations for site E suggests that, at least within a narrow latitudinal band, upward seed transfer of 200 to 300 m could be permitted in a region between 600 and 1000 m als. Specifically, this would involve seed movement from the upper portion of the Central Mixedwood to the Lower Foothills. In any case, a narrower upward seed transfer of about 200 m would be preferred in the current climate.

(5) Type B correlations between site E in the Lower Foothills and site F in the Upper Foothills provides a measure of provenance transferability in the upper slopes of the Rocky Mountains. The correlations were 0.76 for H27 and 0.58 for D27. The corresponding Pearson's correlations for H27 and D27 predicted by a regression model (Eq. 4) were 0.90 and 0.78. These high correlations indicate that some of the provenances that grew well at site E also do well at site F. None of the provenances from the Upper Foothills grew better at site E. This suggests that selected superior provenances could be moved from about 1000 to 1200 m als. However, because the region in the upper slopes includes a hybrid zone, such seed transfers should be permitted only when a risk for enhanced hybridization between white and Engelmann spruce is negligible.

4.0 PRACTICAL IMPLICATIONS

The outlined patterns of optimal growth potential and GE for white spruce in Alberta result from latitudinal and topographic variation in the province. The current forest seed zones in Alberta (see FGRMS 2009) are subdivisions of Natural Subregions, which, with the exception of the Dry Mixedwood (DM), are vegetation and climatic divisions mainly along latitudinal and elevational gradients (see Natural Regions Committee 2006). Thus, the pattern of genetic variation discussed in the present paper has practical application on the movement of seed across seed zones within major Natural Subregions. Although white spruce is a component of the natural vegetation in most of the forested Natural Subregions of Alberta, most harvesting and regeneration occurs in the Central Mixedwood (CM) and foothills and lower slopes of the Rocky Mountains. There is large climatic variation within the CM mainly due to its north-south orientation that spans 8^{o} of latitude (Natural Regions Committee 2006). From north to south, the CM is divided into CM1, CM2 and CM3, and each is further subdivided to form seed zones (FGRMS 2009). In the foothills, climatic and vegetation types are largely determined by changes in elevation. The region is divided into Lower Foothills (LF) at lower elevations and Upper Foothills (UF) at higher elevations. Both Natural Subregions are further subdivided to form seed zones in the foothills region. Within the boreal forest, there are foothills-type highlands where climate is determined by a combination of high elevation and northerly latitude. At lower elevations is the Lower Boreal Highlands (LBH), analogous to the LF and, at higher elevations, is the Upper Boreal Highlands (UBH), analogous to the UF. Subdivisions of LBH and UBH form seed zones within the major foothills outliers and hill systems of the boreal forest (see Appendix 1).

This study showed that provenances from mid-latitudes between 55^{o}N and 56^{o}N (approximately between 600 and 800 m als) are expected to grow better than local provenances at about 2^{o} north of their origin. Because of the northward decline in elevation, a northward transfer of seed could also be interpreted as transfer of seed from high to low elevations. Nevertheless, as previously stated, provenance variation outside the foothills region is governed by latitude more than elevation, except in the LBH and UBH Natural Subregions. Thus, the recommendation for seed transfer in the CM and DM Natural Subregions is for northward latitudinal transfer within specified regions. In the foothills region, provenance variation is governed by change in elevation and provenances are expected to grow better than or the same as the local provenances 200 to 300 m above their origin. Thus, the recommendation for seed transfer in the foothills is to transfer seed from a lower to a higher elevation within a narrow latitudinal band. To be consistent with latitudinal transfers, elevational transfers should be restricted to a 2° northward latitudinal band. For example, seed could be transferred from 1000 m als at 53°N to 1200 m als at 55°N; this combines a 2° northward latitudinal transfer and a 200 m upward elevational transfer. Because seed transfers from higher to lower latitudes and higher to lower elevations are not permissible, a reverse transfer is not applicable. The same rule applied in the foothills would apply to seed transfers in the boreal highlands (LBH and UBH).

Overall, a 2° northward or 200 m upward elevational transfer is recommended in the present climate. Integrating this rule into the Alberta Natural Subregions, the following seed transfers are recommended.

(1) In the Central Mixedwood (CM) Natural Subregion, seed may be transferred from CM3 to CM2 and CM2 to CM1 provided that elevation of seed origin does not exceed 800 m als. The climate predicted by the Alberta climate model (Alberta Environment 2005) shows that large temperature and precipitation changes within CM occur at latitude 57°N (Natural Regions Committee 2006), thus climatically separating the boreal forest into a northern part with very cold winters, warm summers and low precipitation, and a southern part with milder winters, warm summers and moderate precipitation. This distinction between the southern and northern boreal forest is generally supported by provenance variation in the white spruce trials presently under study (see Rweyongeza et al. 2007, 2009b). Provenances from north of 57°N appear to exhibit low growth potential at mid-latitudes and high growth potential at high latitudes. Thus, the recommended incremental northward seed transfer within CM allows for a relaxation of seed movement restrictions across existing seed zones while recognizing a gradual northward cline of declining growth potential (see Rweyongeza et al. 2007; ATISC 2008). In the southernmost part of CM3 bordering the LF where elevations exceed 800 m (see Natural Regions Committee 2006) the 200 m upward elevation transfer would apply provided the same latitudinal zone is maintained.

(2) The northernmost part of Alberta is mainly comprised of the Northern Mixedwood (NM) Natural Subregion. It is the coldest portion of the boreal forest in the province, has the lowest elevation, except for isolated hills, and, although precipitation is generally low, much of the subregion is in wetlands (Natural Regions Committee 2006). Because of these unique features, it is recommended that regeneration in the NM be from seed originating within the subregion. In the event of future climate change, it may be possible to transfer seed from CM1 to NM as part of northward seed transfer. The rationale here is that because of limited provenance and progeny testing, a marginal climate (cold and dry) and widespread wetlands, it is safer to assume that local seed is best until relevant testing is performed.

(3) In the boreal highlands, seed may be transferred from the LBH to UBH while observing a 200 m elevational transfer distance from source to planting site. The boreal highlands are isolated hill systems within the boreal forest that do not span more than 1° of latitude; thus, latitudinal transfer restrictions in LBH and UBH are not applicable.

(4) In the foothills region, seed may be transferred from LF to UF while observing a 200 m upward transfer limit from seed source to planting site. While the UF and LF do not differ substantially in terms of NDD, the frost-free period declines and incidence of mid-season frosts increases with an increase in elevation within the Rocky Mountains (see AARD 2005). Thus, a limited upward transfer reduces the risk of deploying LF provenances that may not be frost-hardy enough to withstand frosts at much higher elevations in UF. Consideration is also given to the white-Engelmann spruce hybrid swarm in the UF; the recommended seed transfers are meant to assist seed movements using the knowledge gained from provenance testing in a way that

maximizes growth potential while keeping the two species separate. Thus, upward seed transfer is not applicable if it is likely to enhance hybridization between species.

5.0 OTHER CONSIDERATIONS

White pine weevil (*Pissodes strobi* [Peck]) is the major insect pest attacking young white spruce trees in Alberta. Studies in British Columbia have shown that white pine weevil in white and Sitka (*Picea sitchensis* [Bong.] Carr) spruce is more prevalent among populations with low growth potential (Kiss and Yanchuk 1991; Alfaro et al. 1996) from high latitudes and high elevations (Alfaro et al. 1996). Localized evolution of Sitka spruce populations resistant to white pine weevil was also reported in inoculation studies by Alfaro et al. (2008). These studies also showed that, although the level of infestation may differ between test sites and replications within test sites, there are moderate consistencies in genotypic ranking for resistance among sites (e.g., Kiss and Yanchuk 1991). In Alberta, Dhir et al. (2005) reported an east-west trend in family variation for white pine weevil incidence in an 18-year old white spruce progeny trial at Hay River ($r^2 = 0.45$). Infestation was much higher among families from between longitude 119°W and 120°W than between 110°W and 118°W. In the G103 series of provenance trials, the subject of this paper, assessment of weevil attack has been recorded at 3-year intervals beginning at age 15 years. A preliminary analysis of cumulative infestation between field planting and age 27 years showed that provenances from high elevations had higher incidences of white pine weevil than those from low elevations ($r^2 = 0.22$ to 0.59; $P < 0.05$). In the G103RW Canada range-wide provenance trial at Calling Lake, Alberta, analysis of cumulative infestation between field planting and age 27 years showed higher incidence among populations of low growth potential from Atlantic Canada, Northern British Columbia and the Yukon Territory. It appears that mild climates favouring the evolution of high growth potential in trees may also favour the growth of white pine weevil populations; as the tree and insect populations interact, weevil resistant tree populations may evolve.

The geographic distribution of white pine weevil resistance in white spruce in Alberta is currently being researched to provide concrete measures of the potential impact that seed transfers among regions may have on weevil incidence, and to provide data for resistance breeding. In the meantime, consideration of weevil incidence is not expected to have significant affect on the seed transfer recommendations outlined earlier because provenances of low growth potential, which appear to be susceptible to weevil, will not be transferred to mild climates where weevil populations may be larger and the period of infestation longer than in their native environments. In the long-term, however, climate change may create environments favourable to the rapid growth of insect populations that endanger forest health. Therefore, it is expected that in the future, insect and disease resistance will have to be considered when developing guidelines for seed transfer to improve growth and yield.

6.0 CONCLUSIONS

In this paper, we have examined the genetic differentiation of white spruce populations in Alberta using 27-year height and dbh. At 27 years, most of the plantations have reached crown closure and the pattern of variation for growth potential is similar to that observed at earlier ages (e.g., Rweyongeza et al. 2010b). Although trees have grown larger and the ratio of the provenance variance to environmental variances has fluctuated over time, the landscape pattern of genetic variation is the same. Before crown closure, trees are free growing and the potential for changes in provenance ranking is large. After crown closure, competition within and among provenances will mask genetic variation by increasing the proportion of environmental causes of provenance variability. Because genetic variation for height and diameter at crown closure are good indicators of variation for growth and yield, the 27-year data provide appropriate information for modifying existing white spruce seed transfer guidelines in Alberta.

The general pattern of genetic variation for height and diameter in these trials is that growth potential is highest at mid-latitudes (approximately 55^{o}N to 56^{o}N) and mid-elevations (largely 600 to 800 m als). For the purpose of this paper, we call this region central Alberta. From central Alberta, growth potential declines with an increase in elevation of seed origin to high elevations in the Rocky Mountains where hybridization between white and Engelmann spruce occurs. Likewise, from central Alberta, growth potential declines gradually with an increase in latitude of seed origin to approximately latitude 57^{o}N, beyond which provenances from high latitudes begin to surpass in their native environments. This latitudinal trend is important because it shows that the generalization that high latitude provenances exhibit low growth potential compared to low latitude provenances depends on the location of the test site. When the test site is located at lower latitudes, higher latitude provenances grow poorly. In contrast, when the test site is located at higher latitude, high latitude provenances outgrow low latitude provenances. This reverse ranking of provenances suggests that some environmental conditions necessary for high latitude provenances to attain their full growth potential is lacking at lower latitudes. Adaptation to a critical photoperiod (day length) is considered one of the major cause of genetic differences in growth potential between high and low latitude provenances when the two groups of provenances are tested over a wide range of environments (e.g., Vaartaja 1954, 1959). A discussion on photoperiod is out of the scope of this paper. However, the latitudinal transfer functions explaining provenance variation may indirectly incorporate photoperiod because day length varies with latitude.

The pattern of provenance variation shows that seed collected in a specified location can be planted at a significantly distant location by regulating latitudinal and elevational transfer distances. In this paper, a 2^{o} northward seed transfer in the mid-latitudes zone not exceeding 800 m als is recommended. For foothills regions where change in elevation is the major determinant of provenance variation, an upward seed transfer by 200 m is recommended. It is suggested that these recommendations be implemented through seed transfers between Natural Subregions or primary seed zone levels (e.g., CM1, CM2 and CM3) instead of seed zones (e.g., CM1.1 or CM1.2). Alberta seed zones are finer subdivisions of Natural Subregions. In the Central Mixedwoods, seed zones are large and have in imbedded north to south latitudinal trend. In the foothills and boreal highlands, the seed zones are relatively small and have an imbedded low to high elevational trend. Therefore, the recommended changes in seed transfer guidelines can be easily integrated into the existing seed zones. Although the primary seed zone divisions in the Dry Mixedwood (DM) deviate from the latitudinal pattern, the 2^{o} northward latitudinal seed transfer guidelines should be applied in DM to provide consistency in implementation of the guidelines and for aligning seed transfer rules with the observed pattern of genetic variation.

Seed transfer in the Montane, Subalpine and Alpine Natural Subregions is not discussed in this paper because there is no white spruce provenance or progeny testing in these areas and, for the Rocky Mountains region, Engelmann and hybrids instead of white spruce are the major components of the vegetation. Thus, seed transfer recommendations in this region require information on genetic variation in Engelmann spruce and a clear distinction between pure and hybrid spruces. Nevertheless, there is pure white spruce in the Montane Natural Subregion in the Cypress Hills in southeastern Alberta. The G103 series tested only one population from the Cypress Hills at selected sites. Earlier analyses of white spruce (e.g., ATISC 2008) and lodgepole pine (e.g., Rweyongeza and Yang 2005b) showed that provenances from Cypress Hills have growth potential similar to provenances from the Upper Foothills in southwestern Alberta. Recently, ATISC established two white spruce progeny trials, one in the Cypress Hills and one at Calling Lake in central Alberta to test open-pollinated families from the Cypress Hills. These trials will provide data for assessing genetic variation and developing seed transfer guidelines for this region. In the interim, a 200 m upward elevation seed transfer rule should be implemented on expectation that the pattern of genetic variation in the Cypress Hills will likely be similar to that observed in other mountainous regions of Alberta.

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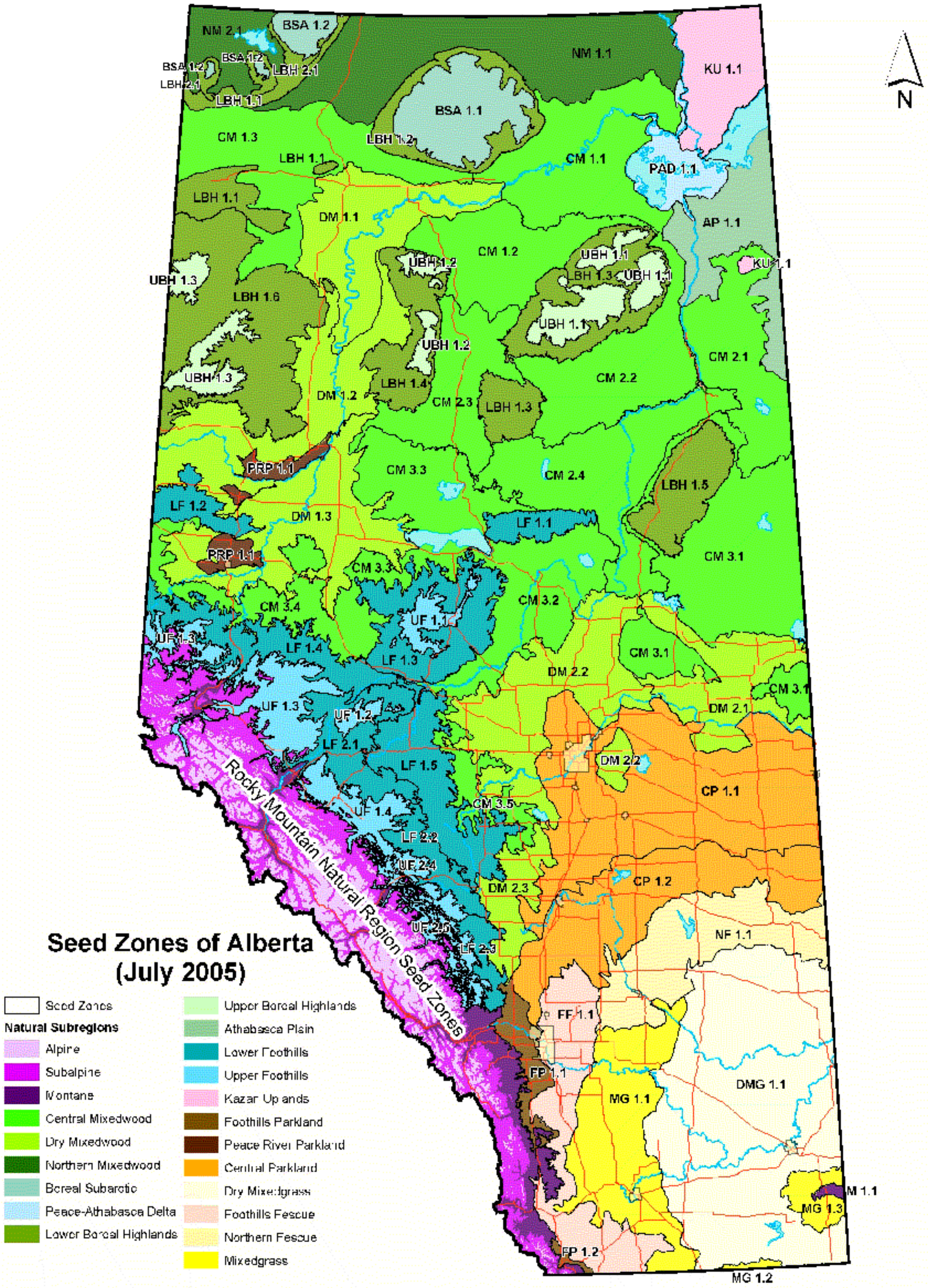

Appendix A: Alberta forest tree seed zones outside the Rocky Mountains. (Source: FRGMS 2009)