INTRASPECIFIC HEIGHT VARIATION OF WHITE SPRUCE PROVENANCES IN ONTARIO

By

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April 2020

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ABSTRACT

Humphrey, J. 2020. Intraspecific height variation of white spruce provenances in Ontario. 53 pp.

Key Words: Climate, environment, genetics, height, population, provenance, variables, variation, white spruce.

Provenance tests in Ontario have been used for decades to evaluate the optimal seed sources for different environments. Understanding the genetics, adaptations and selection pressures of tree species using provenance testing will help determine future favourable planting locations. The growth of many tree species will be adversely affected by climate change, as most woody plant species cannot keep up with the rate of change. White spruce (*Picea glauca* (Moench) Voss) is a widespread, economically important tree species for the Canadian forest industry. Being a widely distributed species, Ontario has many white spruce provenance test trials with sources from across the province and the country. Provenances from across Ontario have been planted at a Kakabeka test site to determine the top performing seed sources. This thesis explores the variation in height between provenances at this test site to determine the climatic variables which are most significantly related to this intraspecific variation. The top performing provenances at the Kakabeka site originated from southern Ontario and Quebec, and the worst performing provenances mostly originated from northwestern Ontario. Provenance and block effects explained a significant portion of variation in mean heights. Growing season climate variables showed a significant relationship to height variation among provenances. The best predicting variables were mean annual solar radiation (MAR) and Hargreaves reference evaporation (Eref). This study provides valuable data to determine the optimal seed sources for current climate conditions.

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ACKNOWLEDGEMENTS

I would like to thank Dr. Ashley Thomson for her continuous guidance, edits, and unparalleled support through the entire duration of this thesis. I would also like to thank my second reader, Paul Charrette, for taking time to introduce me to the Kakabeka provenance site and providing valuable feedback to ensure this thesis is of acceptable quality. Thank you Dr. M. Leitch and Dr. L. Meyer for guiding us through all the formatting and requirements beginning in our first semester class. I would also like to give honourable mentions to David Baehre, Emily Pollington, and James Thordarson who took time to help me with data collection. The continued support from these people and the rest of my friends and family has been deeply appreciated, and I would not have gotten this far along without it.

INTRODUCTION

Tree improvement programs and provenance trials have been used in Ontario for several decades (Lu et al. 2014). Establishing a good genetic basis for selection, breeding, and ensuring local adaptation of native/introduced tree species encompass many of the goals that tree improvement programs aim to achieve (Carlisle 1970). With present climatic changes, the optimal ranges of many Canadian tree species are shifting at rates which many cannot keep up with (Carter 1996, Aitken et al. 2015). Most tree species show genetic variation at a regional scale when responding to environment conditions, making tree plantations comprised of many seed sources suitable to determine individual tree responses to climate change (Andalo et al., 2004, Matyas 1996).

White spruce (*Picea glauca* (Moench) Voss) is a widespread species that is utilized for both pulp and lumber products and has significant economic importance in the Canadian Forest industry (Andalo et al., 2004, Stiell 1976). The range of white spruce encompasses almost all of Ontario and a considerable range of climate conditions. This enables many provenance sites to be utilized for testing across the province. In a study by Lesser et al. (2003), 127 white spruce seed sources were used at six test locations across Ontario to determine optimal breeding zones for white spruce.

The objective of this study was to determine which white spruce provenances are best suited to the current climatic conditions at the Kakabeka, Ontario test location from the 2002 series (Lesser and Parker 2004). I predict that local white spruce provenances will be outcompeted by provenances from south eastern Ontario, as southern seed sources have exhibited superior performance in several previous white spruce provenance studies.

LITERATURE REVIEW

SILVICS OF WHITE SPRUCE

White spruce is a boreal tree species that is naturally widespread and encompasses a significant area across Canada (Stiell 1976). It can perform well across a variety of environmental conditions and soils. Growth can occur in soils with a pH level ranging from 4.7 to 7.0, and with varying fertility and moisture levels (Niensteadt and Zasada 1990). The species can tolerate an extreme range in temperatures; from -54° C in northern ranges to 43° C in southern ranges. Furthermore, white spruce grows in areas which have vast differences in growing season length, ranging from 20 days in Northern Canada to approximately half a year in Maine (Niensteadt and Zasada 1990). It is a shade tolerant species and can survive under moderate brush and hardwood canopies. Forest geneticists recommend the use of white spruce in plantations because of its robust nature and wide range of capabilities (Stiell 1976). It is one of the most important commercial species in Canada and significant efforts have been made to understand how climate change might impact its growth and survival (Azcona et al. 2018).

CLIMATE CHANGE AND PROVENANCE TESTS

With ample evidence of global warming, there has been an increase in attention towards the potential biological responses of forests to climate change (Matyas 1996, Schmidtling 1994). There are three possibilities for the survival of tree species in a rapidly changing climate: adaptation, migration, or extirpation (Aitken et al. 2008, Carter 1996). Tree species may have to adapt to new conditions over time as the climate changes. Migration of species may occur to spatially track the favourable ecological niche for the species. Extirpation will occur if a tree species cannot adapt to the new environmental conditions present, and a local extinction of that species will be imminent. Assisted migration of species from warmer climates to colder ones may be necessary to maintain local adaptation (Azcona et al. 2018). Warm adapted seed sources run a higher risk of being damaged by frost if they are migrated too far northward, or if unexpected colder temperatures persist in spring.

An extensive history of common garden testing has revealed high levels of genetic variation within most boreal conifers for traits related to adaptation and variation along climatic gradients (Aitken et al. 2008). A common garden experiment is a test done by taking populations from different geographical areas into a common environment and observing population response (usually growth) to the common environment. Provenance research is used to analyze common garden plantations of tree populations that are originally from different areas (Matyas 1996). The word 'provenance' means the source of a population sample that represents a defined area. Provenance tests are generally time consuming to establish. Originally, provenance tests were established to identify tree populations that exhibit the fastest growth for a planting area. With more recent concern over shifting environments for tree species, the response of tree growth to climate change has been a central motivation in the establishment and measurement of provenance tests (Carter 1996).

In the past, there have been three main series of white spruce provenance test studies (Lesser 2005). The 93 series, 194 series, and the 410 series encompass experiments and trials covering all of Ontario and parts of Quebec in order to determine the best sources, genetic variation, and within-region variability (Morgenstern and Copis

1999). The 93 series is the oldest of the three series (planted in 1953), where 30 provenances originating across Ontario and western Quebec were planted at three field locations (Morgenstern and Copis 1999). The 194 series was implemented in 1963-65 at nine field test sites with provenances from natural stands ranging from Ontario, Quebec, New Brunswick, and neighbouring states such as New York, Michigan, Minnesota, and Wisconsin. The 410 series were established between 1978 and 1985 at fifteen test trial sites across Ontario (Morgenstern and Copis 1999).

More recently in 2002, provenance trials were set up at six locations for 127 white spruce seed sources that ranged across Ontario and western Quebec (Lesser and Parker 2004). Seeding was done at the Lakehead University greenhouse, and trials were established in Dryden, Kakabeka, Longlac, Englehart, Petawawa, and a greenhouse trial at the university. Each test consisted of 3 blocks with 10 tree repetitions for each of the 127 provenances. The Kakabeka test site from this series is the one used for this study. Over the subsequent field seasons of 2002 and 2003, many growth and phenological variables were measured at each of the test sites for significant differences between provenances.

HOW PROVENANCE TESTS ARE USED TO PREDICT TREE POPULATION RESPONSE TO CLIMATE CHANGE

There are many characteristics of populations that can be measured to examine patterns of local adaptation (Carter 1996, Matyas 1996). Tree height growth is often used as a proxy for fitness, and the plantation-like setting of provenance test sites requires trees to display apical dominance to be competitive (Aitken et al. 2015). Height growth increment and growth rate within populations of a species have high differentiation on average, which suggests that height growth variations in populations are significantly related to local adaptation. Regression models developed to test the relationship between height growth and climate are usually significant, suggesting strong patterns of local adaptation (Andalo et al. 2004). Work on 127 white spruce provenance sites across the entire species range found that traits such as height, bud set/flush and precipitation patterns showed significant amounts of variation (Lesser 2005).

Bud flush occurs in the spring when there is a consecutive amount of warm days which triggers the bud to break open to begin growth (Lu and Man 2011). When bud flushing is not synchronized with a local climate, the vulnerability of trees to damage from late spring frost can increase and result in losses of vigour and growth potential (Lu and Man 2011). White spruce often requires less growing degree days compared to other boreal species for its buds to flush and this can result in heightened mortality to frost damage when seed sources are not optimally matched to their planting location. Observation of the timing of bud set and bud flush is closely related to the cold hardiness of a species, and provenances from differing climates often show significant variance in cold hardiness and height growth.

Seed zones are geographic subdivisions of a species range that are used for the collection of seed for forest regeneration (Morgenstern 1996, Thomson et al. 2010). Seed/breeding zones are regulated to make sure that populations are planted into environments in which they are expected to grow well through adequate adaptation (Thomson et al. 2010). Populations trying to grow from a provenance that is drastically different from the source environment may experience severely reduced growth and survivability. Intense silvicultural activity will not produce acceptable growth if maladapted seed is used, and therefore seed zones have to be developed based upon demonstrated patterns of adaptive variation on a per species level (Parker and Lesser 2004).

To properly understand the various data collected from provenance sites, proper data analysis must be executed. Schmidtling (1994) suggested the use of regression methods to analyze provenance response to temperature differences between the source site and test site. This method was applied to Carter's study (1996) on the provenance test data for 10 forest tree species that are common in Canada. The use of an analysis of variance test (ANOVA) can help to determine whether significant differences in growth and phenology occur between provenances (Lesser and Parker 2004). To identify variables that demonstrate clear geographic or climatic patterns, ANOVA tests in combination with simple linear regressions can be used (Thomson et al. 2010). For testing mean height and mean annual temperature, simple linear regressions are often used (Aitken et al. 2016). With this method of analysis, fine scale patterns of variation in environmental gradients may not be detected.

PROVENANCE VARIATION IN WHITE SPRUCE

A study by Lu et al. (2014) analyzed the survival and growth patterns of white spruce across provenance sites. There were 16 trial sites across Ontario, and results showed high survival across all of them. The Thunder bay site was determined to have lowest survivability for white spruce, at 55.8%. Growing season length was shown to have strong correlation to survivability ($P = 0.03$), while mean annual temperature showed a weaker correlation (P = 0.07). Furthermore, the Thunder Bay site had the highest average tree height, at 7.2 meters. A multiple regression analysis was done on average provenance tree height growth across climatic variables, showing the most significant correlation between mean tree height growth and mean annual temperature.

Morgenstern et al (2006) conducted a study of 25 white spruce provenances planted at a site in Petawawa. Measurements were taken when the white spruce were 44 years old, and ANOVA analyses were carried out. Heights and survival rates were measured and tallied when the trees were 15 years old, which provided an additional comparison. The eight provenances with the greatest survival and volume originated from southeastern Quebec and near the Ottawa Valley. The local Chalk River provenance was out competed by most of the more southern provenances. Correlations were shown to be significant between heights recorded at 15 and 44 years for the provenance trees.

Lesser and Parker (2004) measured genetic variation in white spruce by analysing growth and phenological traits in provenance trials around Ontario. Of the 76 variables tested in that study, 41 showed were significantly ($p < 0.05$) related to phenotypic variation among provenances. The Kakabeka test site had the lowest mean height at 137.82 mm. The top five performing provenances at each of the field trials for this study were located from Canton Gaboury, Quebec, and the others are from the Quebec side of the Ottawa Valley. The more north western test sites, Kakabeka and Dryden, displayed earlier bud flush values, while the south eastern sites like Petawawa had a later bud flush.

A study by Andalo et al. (2004) explored the impact of climate change on the growth of white spruce populations in Quebec. White spruce provenances were optimally adapted when current temperatures matched the temperature of the seed source location. Maximum growth occurred in white spruce when the largest precipitation measurement differences were seen between seed sources and planting sites. The largest R-squared values and correlation coefficients were seen when regression models used variables of both temperature and precipitation. Temperature was the largest differentiation between populations in that study. The most significant regression model for height growth had an R-squared value of 0.20 when used with maximum daily temperature.

Lesser (2005) conducted a graduate thesis study on the genecology and adaptive variation of white spruce and focal point seed zone development methodologies. Five field test sites were used across Ontario to examine variation among 127 provenances. This study was based off the series established in 2002. The test locations were Kakabeka, Petawawa, Dryden, Longlac, and Englehart. A variety of survival, phenological, and growth variables were used to test for significance in provenance variation. The top performing provenances at each test site were predominantly southeastern sources. A total of 94 climatic and geographic variables were tested using linear regressions to explain adaptive variations for the provenances. Growing season variables displayed the most significant relationship to provenance variation.

MATERIALS AND METHODS

For this study, two of the three blocks were measured at the Kriekmann white spruce provenance test. The property is located about eight kilometers from Kakabeka, at the end of Holomego Road. The white spruce provenance site consists of three test blocks, of which blocks 1 and 2 were measured for height. Figure 1 below shows the location of blocks 1 and 2, which are adjacent to each other, with block 3 located below them. Each of the blocks has a white spruce planted in a grid-like fashion with a spacing of 2.5m. Each test block is was planted in a configuration of 24 columns and 55 rows, for a total of 1,320 trees per test block. Each tree is marked with a metal pigtail stake and attached metal tag which states the provenance location and repetition for each tree.

Figure 1. Google Earth map display of white spruce provenance test blocks 1 (left), 2 (right), and 3 (bottom) located at the Kreikmann property.

A height pole was used to measure the height of each white spruce tree. The height pole used was a tape-reading height pole manufactured in Japan. When using a height pole on a tree, it is required to get as close to the tree stem as possible; inaccurate heights can be recorded if the pole is held at a large angle towards the tree. To ensure consistency of measurement technique, tree heights were recorded when the tip of the tree was met by the center of the eyelet in the top metal tab of the height pole (Figure 2). The height pole has a minimum height of 1.41 m, so a tape measure was used to measure shorter trees. Tree tags were checked at the beginning and end of each row to make sure that the correct provenance and replicate was measured.

Figure 2. Height pole used to measure tree heights at the Kakabeka white spruce provenance tests.

Two methods were used for data collection; printed tally sheets and an excel spreadsheet via smartphone. A clipboard with extra water-proof tally sheets and writing utensils was also carried in case of rain or low cell-phone battery. After all height measurements were obtained, the data was entered into an Excel spreadsheet for analysis. Before the data was analyzed, provenances 127, 128, 129, 131, and 132 were removed to remain consistent with the study Lesser et al. (2005). A variety of statistical tests were done to examine patterns of intraspecific variation in height growth. Analysis of variance (ANOVA) tests were used to test variables block, height, and provenance in explaining variation in height. Scatter plots with trendlines displaying the R-squared values for each of the variables was done in Microsoft Excel in order to determine which annual climatic variables were most significantly correlated to the height of the white spruce provenances. A multiple linear regression analysis was done on SPSS to determine which of the combinations of climatic variables showed the most significant correlation to the mean height variation between the white spruce provenances. ClimateNA software (Wang et al. 2016) was used to obtain thirty-year climate normal data for each provenance and test location. ClimateNA is a Microsoft Windows-based software application that extracts climate data and calculates over 200 annual or seasonal climatic variables (Wang et al. 2016). For this study, the directly calculated annual variables and the derived annual variables were used, which involved the statistical analysis of 23 variables (see Appendix III). These variables are from the 1961-1990 reference time period. SPSS software was used to compute mean heights for each provenance, test for between subject effects (ANOVA), and conduct linear/multiple linear regressions for the climate NA variables.

RESULTS

BEST/WORST PERFORMING PROVENANCES

Table 1 lists the average heights for each of the top provenances and Figure 3 displays the location of the top 10 performing provenances in terms of total height growth at the Kakabeka site. Nine out of the ten top provenances originated from around the Ottawa Valley area and southwestern Quebec. The one exception is provenance 86, located near Elliot Lake, which originated from about 160 km west of Sudbury. The top performing provenance was number 19, with an average height of 673.42 cm, and originated from Lac Cayamant, located in Southern Quebec.

The worst performing provenances in terms of total measured height growth are listed in Table 2. Provenance 110 located near Parks Lake was determined to be the worst performing provenance, with an average tree height of 409.93 cm at the Kakabeka site. Most of the worst performing provenances originated from Northwestern Ontario, with a few provenances from the Toronto area.

Table 1. The top ten performing provenances, with their average heights and locations.

Provenance	Average Height	Location
19	673.42	Lac Cayamant
49	634.89	Lac Smith
1	626.00	Cornwall
67	622.74	N. Dame des Quinze
50	622.68	Rutherglen
34	618.79	Laurentian Hills
26	617.2	Grove Creek
44	616.95	Canton Sebille
86	616.47	Elliot Lake
59	610.65	Canton Mercier

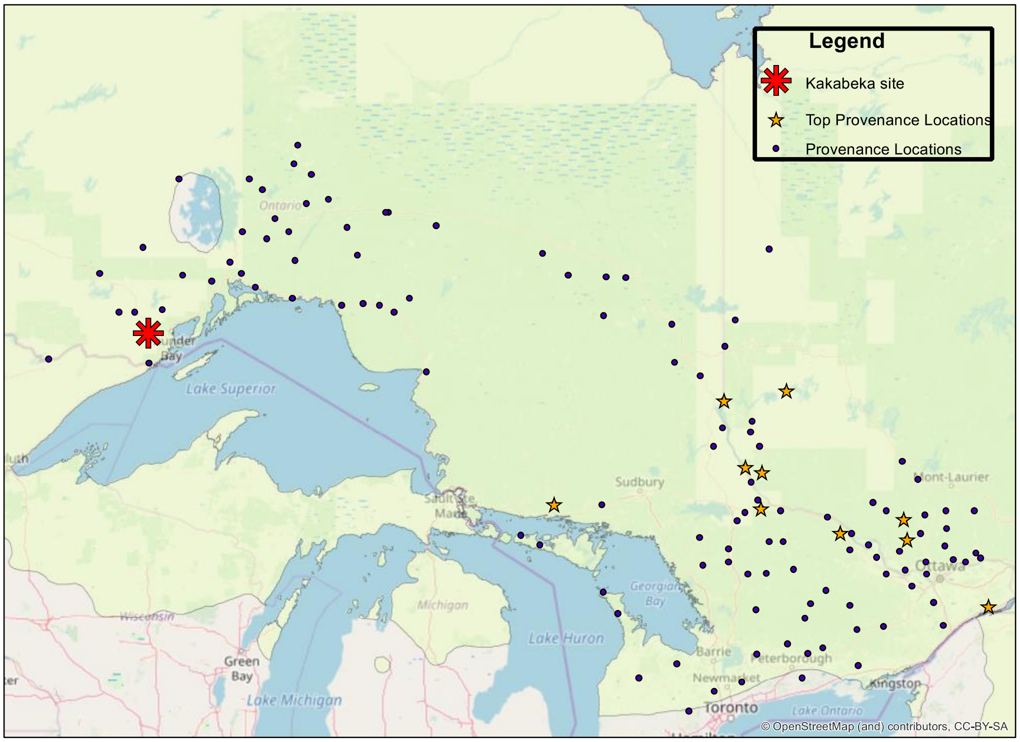

Figure 3. Map displaying provenances tested at the Kakabeka site, including the top 10 provenances for height measurements. The natural range of white spruce is displayed in light green.

Table 2. The ten worst performing provenances, with their average heights and locations.

Provenance	Average Height	Location
110	409.93	Parks Lake
119	420.2	Waweig Lake
80	437.11	Pagwa
106	446.25	Eastnor
88	454.89	Elizabeth Bay
96	454.9	Hemlo
107	465.61	Terrace Bay
130	466	King
109	473.37	Jellicoe
30	473.58	Barrie

ANALYSIS OF VARIANCE

The ANOVA tests ran for height, block, and provenance showed significant results between them. Table 3 displays the significant difference between the mean provenance heights and the block variable, shown by the sig. value (P value) of 0.000. Differences are not significant when the P value is greater than 0.05. Table 4 also displays the significant difference between mean provenance height and the provenance variable, shown by the sig. value 0.000. Table 5 outlines the between subject effects of the independent variables (block, provenance) and dependent variables (height). Individually, the block and provenance variables both have a low sig. value (0.000 and 0.002 respectively), meaning they have a significant effect on the dependent height variable. The interaction of the two independent variables (block * provenance) were shown to have an effect on height that was not significant, evident by the sig. value of 0.191.

Table 3. One-way ANOVA for the variables height and block.

	Sum of Squares	df	Mean Square	F	Sig.
Block	1392750.27	1	1392750.27	47.708	0.000
Error	69334160.2	2375	29193.331		
Total	70726910.5	2376			

Table 4. One-way ANOVA for variation in height among provenances.

	Sum of Squares	df	Mean Square	F	Sig.
Provenance	6581305.51	131	50238.973	1.758	0.000
Error	64145605	2245	28572.653		
Total	70726910.5	2376			

Table 5. General linear model for effect of independent variables block, provenance, and block*provenance interaction on variation in height.

Source:		Sum of Squares	df	Mean Square	F	Sig.
Intercept	hypothesis	676666047	1	676666047	13196.3	0.000
	error	6810970.6	132.83	51277.168		
Block	hypothesis	1494161.8	1	1494161.84	48.51	0.000
	error	4129158.0	134.06	30800.432		
Provenance	hypothesis	6757056.3	131	51580.583	1.67	0.002
	error	4039980.7	131	30839.548		
Block* provenance	hypothesis	4039980.7	131	30839.548	1.11	0.191
	error	58677924	2113	27769.959		

LINEAR REGRESSION ANALYSIS

Linear regressions were evaluated for each of the Climate NA variables against the average height of each provenance. Table 6 summarizes the top five most and least significant climatic variables in terms of R-squared values. The most significant variable was MAR, which is the mean annual solar radiation (Figure 4). The R-squared value was calculated to be 0.2737 for this variable, which accounts for at least 27% of the variability between the average heights of each provenance. The top five variables had a range of R-squared values from 0.2737 to 0.1609 (Figures 4-8). The least significant climatic variable was PAS (Figure 9), which is the amount of precipitation of snow, measured in mm. The R-squared value calculated for this variable was 0.0009, meaning that PAS accounted for not even 0.1% of variation between average heights across the white spruce provenances. The simple linear regression plots for the rest of the climatic variables can be found in Appendix I.

Table 6. The five best and worst R-squared values for the variables used in the simple linear regressions, with descriptors for each (Wang et al. 2016).

	Climatic variable	Description	R-squared
Top 5:	MAR	Mean annual solar radiation	0.2737
	Eref	Hargreaves reference evaporation	0.1896
	MWMT	Mean warmest month temperature	0.1752
	DD>5	Degree-days above 5°C, growing degree-days	0.1626
	bFFP	Day of year which frost free period begins	0.1609
Bottom 5:	PAS	Precipitation as snow, period between Aug (prev. year) and July (current year)	0.0009
	MSP	May to September precipitation	0.015
	TD	Temperature difference between mean warmest and coldest month	0.0293
	CMD	Hargreaves climatic moisture deficit	0.0367
	SHM	Summer heat-moisture index	0.04

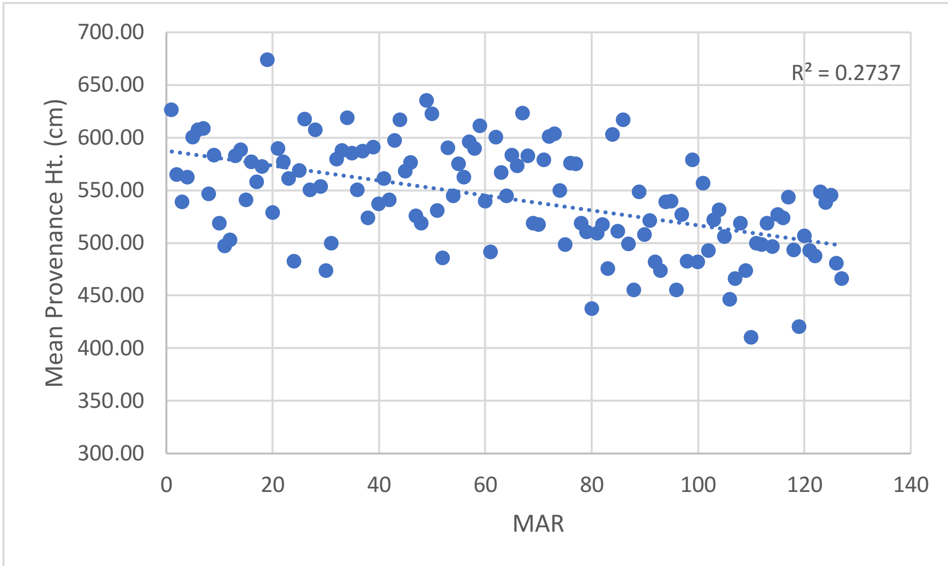

Figure 4. Scatterplot display of the simple linear regression between MAR and the mean provenance heights.

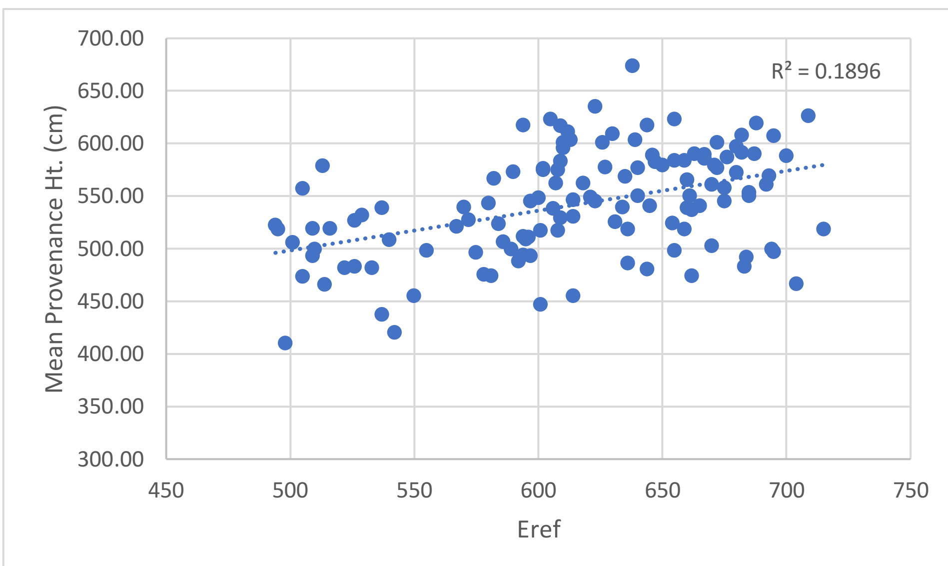

Figure 5. Scatterplot display of the simple linear regression between Eref and the mean provenance heights.

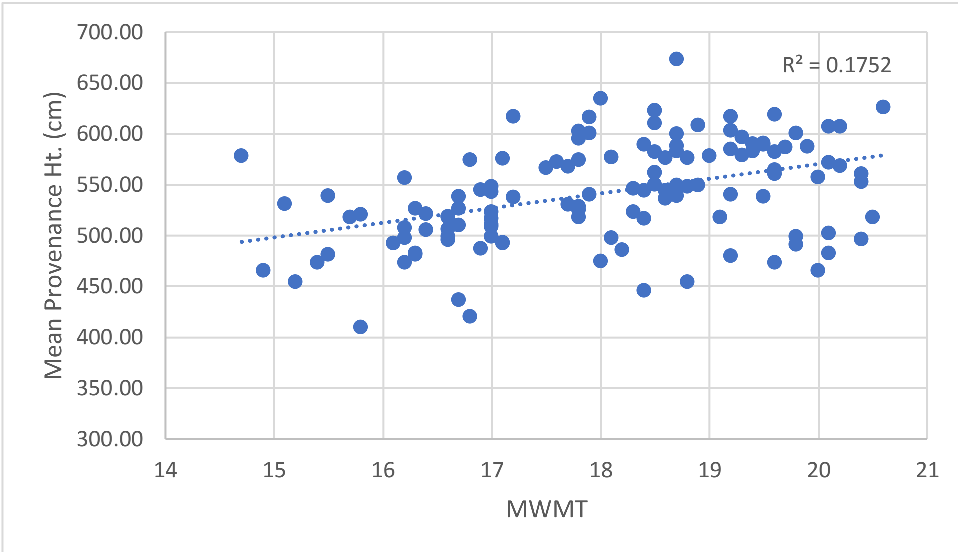

Figure 6. Scatterplot display of the simple linear regression between MWMT and the mean provenance heights.

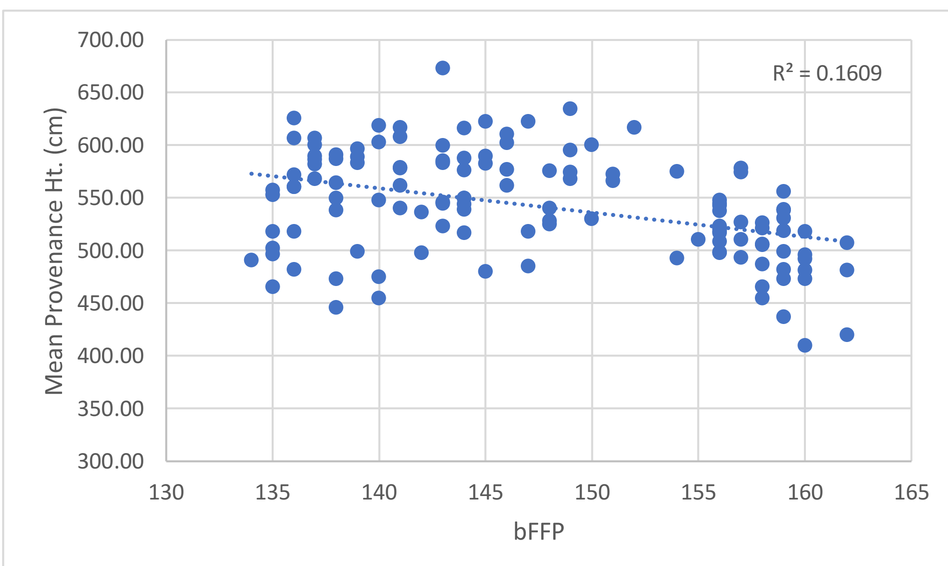

Figure 7. Scatterplot display of the simple linear regression between bFFP and the mean provenance heights.

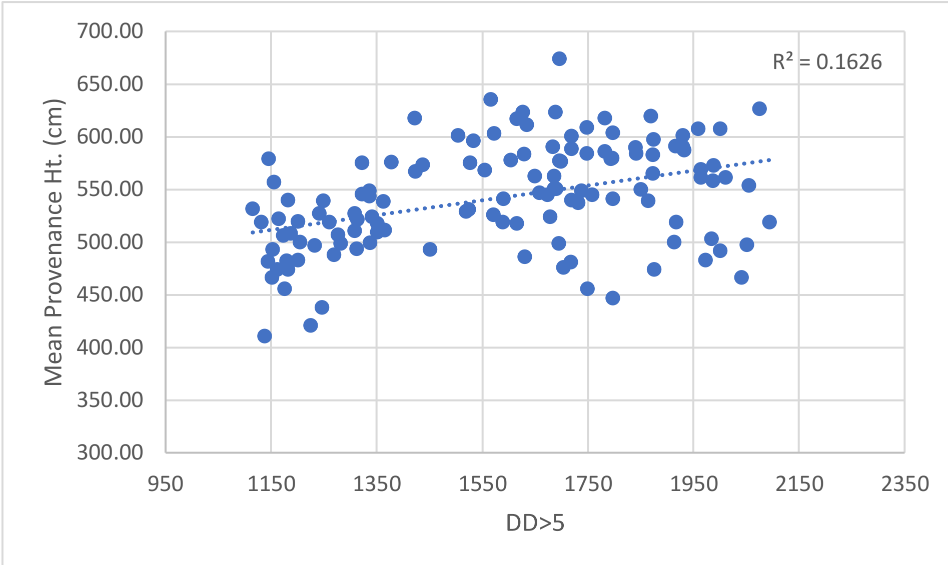

Figure 8. Scatterplot display of the simple linear regression between DD>5 and the mean provenance heights.

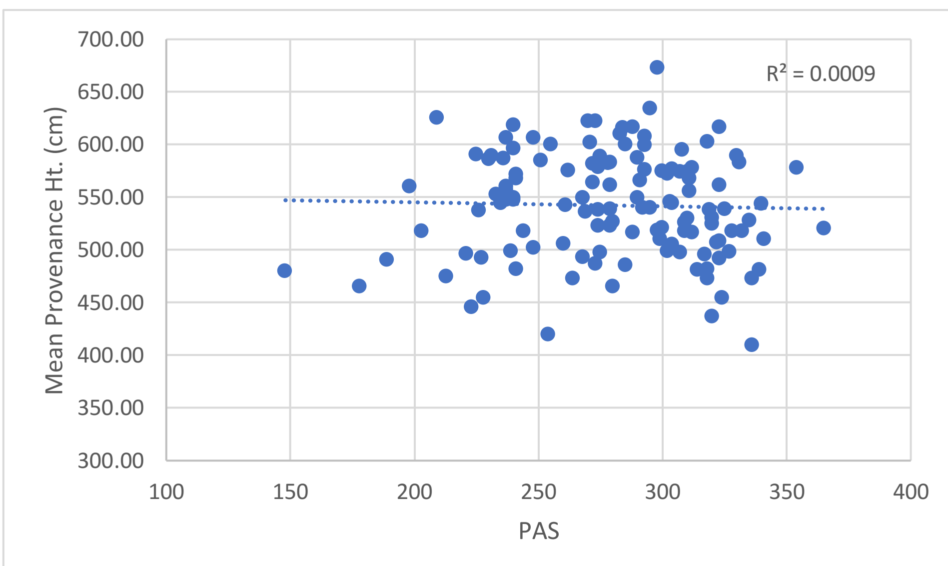

Figure 9. Scatterplot display of the simple linear regression between PAS and the mean provenance heights

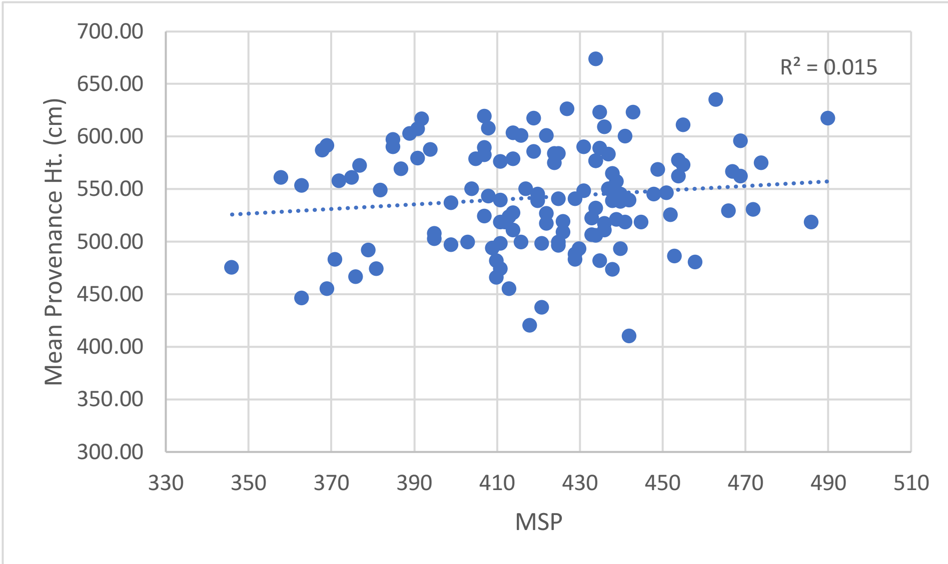

Figure 10. Scatterplot display of the simple linear regression between MSP and the mean provenance heights.

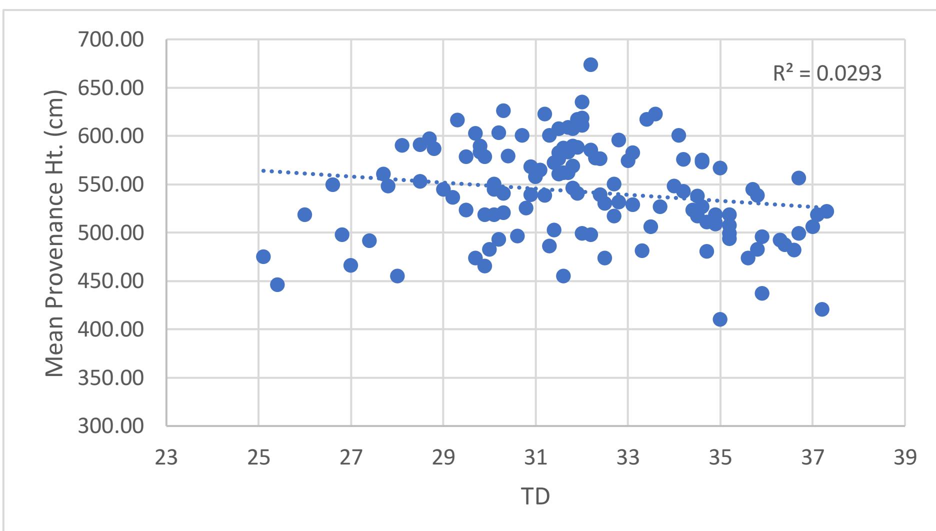

Figure 11. Scatterplot display of the simple linear regression between TD and the mean provenance heights.

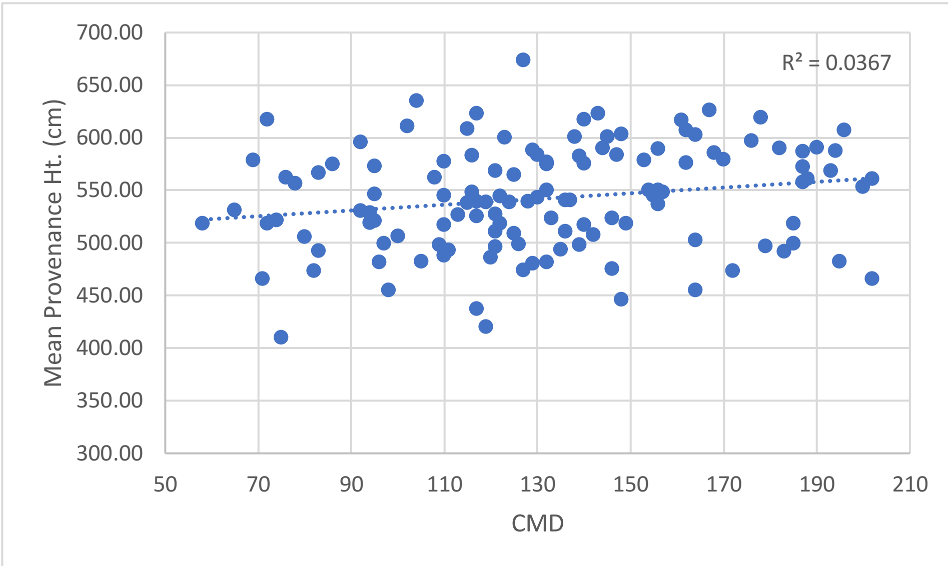

Figure 12. Scatterplot display of the simple linear regression between CMD and the mean provenance heights.

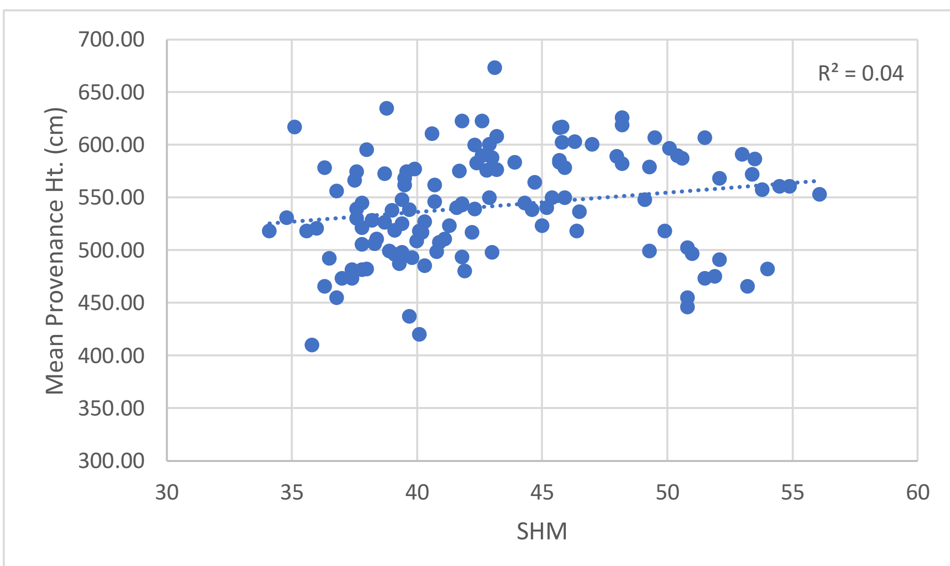

Figure 13. Scatterplot display of the simple linear regression between SHM and the mean provenance heights.

DISCUSSION

The top-performing provenances for height growth at the Kakabeka site predominantly originated in Southeastern Ontario and Southwestern Quebec. Many previous studies have reported similar results for white spruce provenance performance in Ontario (Azcona et al. 2018, Deogratias et al. 2011, Lesser and Parker 2004, Lesser 2005, Lu et al. 2014, Morgenstern 2006, Li et al. 2017, etc). Performance differences between northwestern and southeastern sources in Ontario often reflect a trade-off between growing season traits and cold-tolerance (Mimura and Aitken 2007). Frost damage to southern provenance sources in northern test sites can occur more frequently (Morgenstern and Copis 1999, Deogratias et al. 2011).

Nine out of the top ten performing provenances for height growth were found to be within southeastern Ontario and Quebec, while seven of the ten worst performing provenances were from northwestern sources. Many other studies have shown the occurrence of a latitudinal cline when assessing the genetic variation of white spruce populations (Andalo et al 2004, Azcona et al 2018, Li et al. 1997). A study utilizing the 194 series test near Thunder Bay concluded that southern sources outperformed local sources, in which the same results were found at the Petawawa research forest for the same 194 series tests (Brown 2001, Sarazin 2001). Morgenstern and Copis (1999) found that the top performing provenances from the 410 series at the Petawawa/Chalk River trial were local or from a similar latitude. This trend is not found at the northwestern test sites such as Kakabeka, as the superior provenances are from the same southeastern origins. 401 series trials in Dryden, Kenora, Angus, and Red Lake provide further evidence to the superior growth performance of southeastern sources (Morgenstern and

Copis 1999). Looking specifically at the 2003/3004 height measurements for Kakabeka, three of the top five provenances were shown to be from the northwest (provenances 117, 115, and 101), although when analyzing overall performance (taking into account all field trial locations), the top provenances are from southeastern Ontario and Quebec. In our study, only one of the ten top provenances was not from southeastern Ontario/Quebec (provenance 86) which was located near Elliot Lake, which would be classified as more central Ontario.

White spruce provenances originating from southeastern Ontario and Quebec generally outperform ones from other provinces/states, namely Alberta and western Canada (Deogratias et al. 2011, Lu et al. 2014, Nicholson 1970). Deogratias et al. 2011 outlined in their regression analysis that provenance variation and growth potential in Alberta is very much determined by the latitude of seed origin, which is similar to patterns seen in Ontario. Trial G277A (lat 57°N), the most northern trial from that study (Deogratias et al. 2011) and its location provides examples of how provenances from Ontario and Quebec that occur at lower latitudes exhibit superior performance over local sources from Alberta even though the trial location is at a much higher latitude. The measurements of 15 a year-old white spruce provenance from Caramat, Ontario exceed the heights of local and other provenances around Alberta by up to 25% at trial G277A (Deogratias et al. 2011). Provenances from these lower latitudes may experience increased winter related damages if tested further north, in which local provenances and ones from Northern Ontario may be more suited (Deogratias et al. 2011). In addition, Rweyyongeza et al. (2011) reported white spruce provenances from southern Ontario and Quebec to have the highest growth rate at test trials in central Alberta when compared to other provenances originating from across Canada. Nicholson (1970) reported that 31 provenances tested at in a Newfoundland trial from the 194 series were all from southern Ontario and Quebec, with their average growth outperforming other provenances by 15 percent.

Each of the top five climatic variables that displayed the most significant correlation to mean heights between provenances for our study are directly or closely related to measurements of temperature or precipitation. Mean annual solar radiation (MAR) was the most significant climatic variable in the linear regression test in this study. Annual precipitation and temperature were also found to be significant predictors of intraspecific variation in height in a previous white spruce study (Azcona et al. 2018). In Lesser et al. (2005), intraspecific variation in white spruce height was mainly explained by temperature variables. Azcona et al. (2018) outlines that latitude was the most important predictor variable to explain height differences between provenances. Aitken et al. (2015) found that the variable MAT (mean annual temperature) showed significant relation to height growth potential for white spruce and a variety of other coniferous species. Out of the 23 data sets and 18 species analyzed from the literature (white spruce included), provenance MAT tested to be significant for height growth at the $p<0.05$ level for 14 of the data sets and 13 of the tree species (Aitken et al. 2015). MAT was one of the climatic variables tested in this study, although it was not one of the top five variables for explaining mean provenance height in the linear regression analysis. Many of the variables that were among the poorest predictors of intraspecific variation in height in this study were precipitation or temperatures for specific times of the year, such as MSP and PAS. Azcona et al. (2018) outlines that significant relationships between tree height are usually found with mean annual temperature and precipitation. Therefore, testing variables that look at precipitation for portions of the year will not be as effective.

Block effects in this study showed a significant relationship to mean height variation of the provenances. Many of the trees in the top right corner of block 2 were found to be stunted, dead, or missing due to the excessive long grass and shrub growth. In this area of increased competition, only a select few white spruce trees were able to compete with the grass and shrubs. The surviving trees in these adverse conditions were predominantly stunted, chlorotic, or near dead. This relatively large area of block 2 may have explained some of the significant variation between the two blocks and mean provenance heights. Farm field provenance test sites (like the Kakabeka site) are often visually homogenous but can be substantially heterogenous for provenance performance (Funda et al. 2007). Spatial variation due to underlying soil differences and micro-environmental heterogeneity can be present among and between different blocks (Funda et al. 2007), further contributing to the significance between the blocks and mean provenance heights. For future studies on white spruce at the Kakabeka test site, other measurements should be recorded. This study only used height measurements but utilizing other variables such as diameter growth and cold tolerance traits (bud setting/flushing dates) would provide significant data. The use of only height measurements created many limitations on the statistical analyses that was done. In addition to this, only two of the three blocks were measured in this study, which limits the size of the dataset. With a larger data set, more significant correlations could be made that could better explain provenance variation in white spruce.

CONCLUSION

The top performing provenances at the Kakabeka test trial site for height growth were predominantly from southern Ontario and Quebec, as provenances from these origins are usually top performers across Canada. Growing season variables were significant predictors of intraspecific variation in provenance height. Two of the top variables shown in this study to have a strong correlation to height variation are mean annual solar radiation (MAR) and mean warmest month temperature (MWMT). Block effects were shown to have a significant effect on provenance height, outlining the importance of microclimatic conditions and site heterogeneity.

White spruce is an important tree species to the forest industry in Ontario and needs to be properly managed into the future to ensure that viable populations with superior growth attributes are maintained. Over the past couple decades, growing conditions in northwestern Ontario have become more and more favourable for southern sources (Lesser 2005), and should be used predominantly in further studies. Further studies and analyses like this one and the supporting literatures should be continued on other critically important species across Ontario (black spruce, jack pine, etc.). Developing a thorough understanding of how Canadian tree species adapt to the changing climate through provenance testing will better prepare professionals in the industry to take effective proactive measures.

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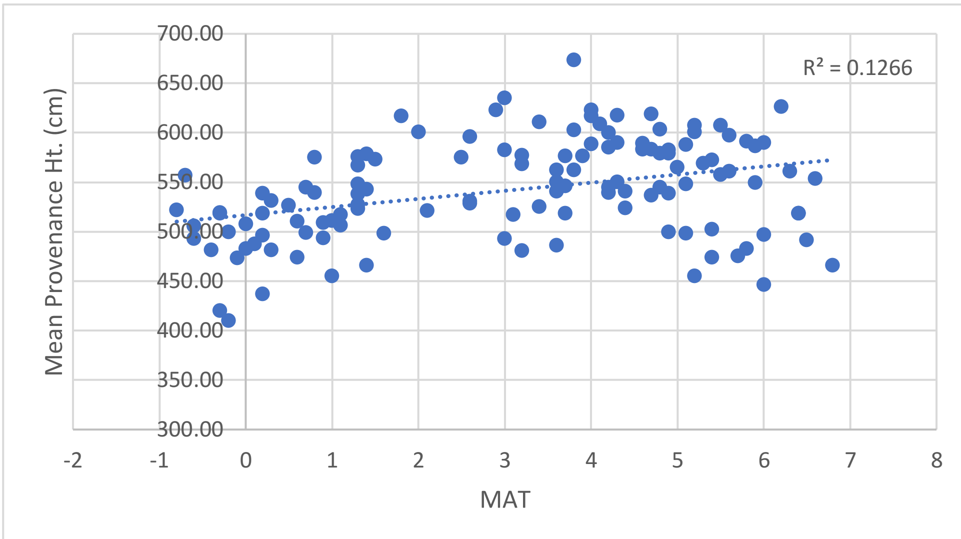
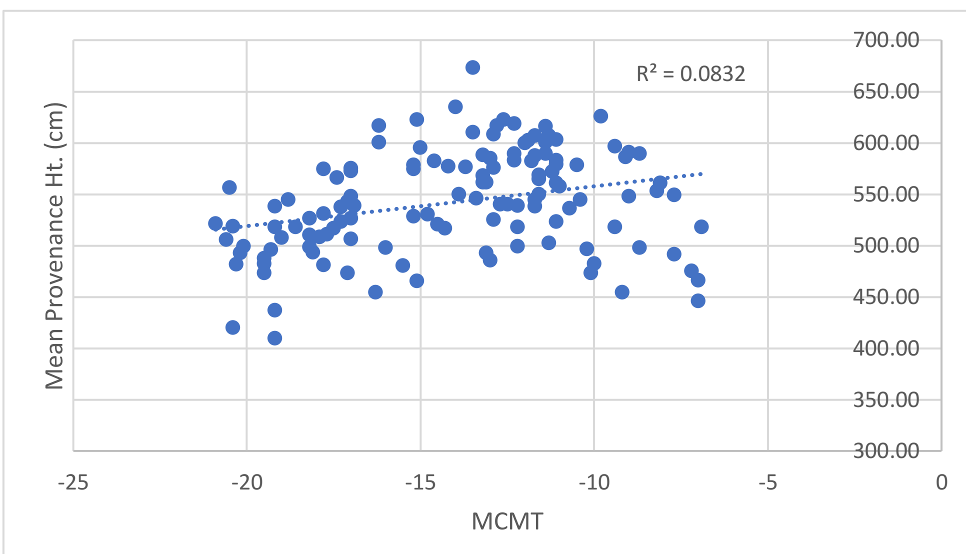
APPDENDICES

APPENDIX I

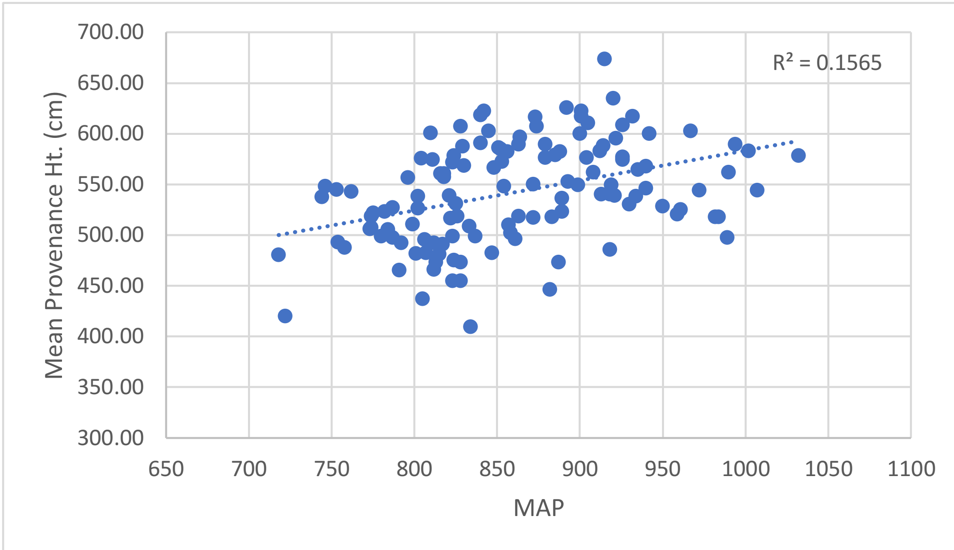
SIMPLE LINEAR REGRESSIONS OF CLIMATE VARIABLES



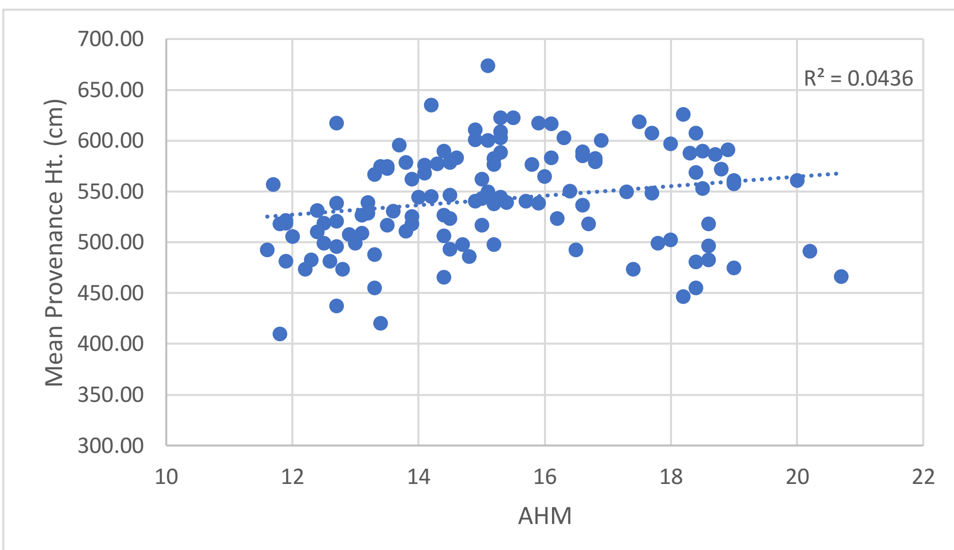
Appendix 1-1. Scatterplot display of the simple linear regression between MAT and the mean provenance heights.



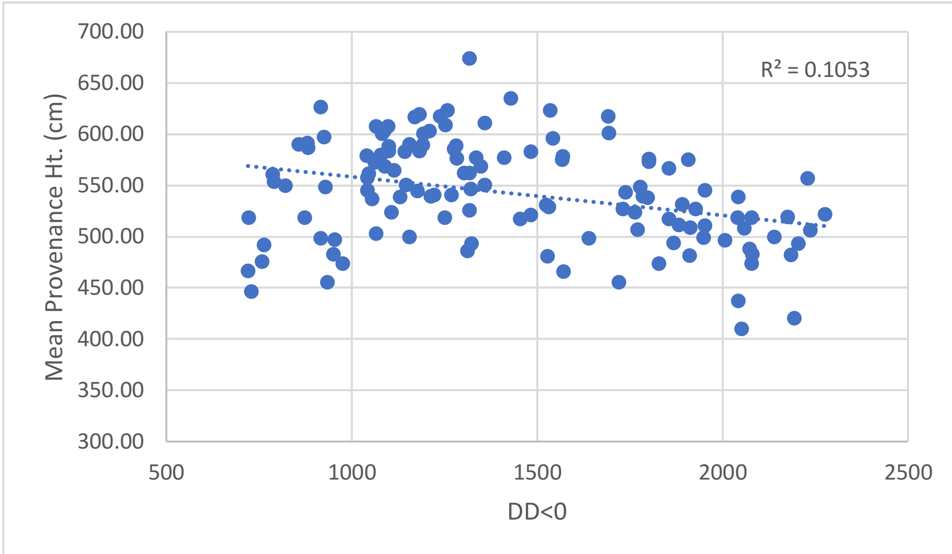
Appendix 1-2. Scatterplot display of the simple linear regression between MCMT and the mean provenance heights.



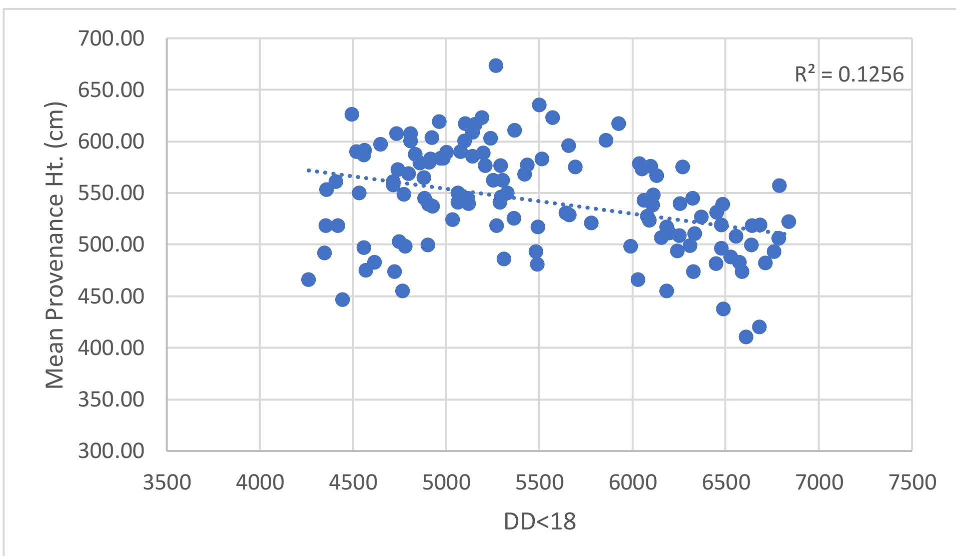
Appendix 1-3. Scatterplot display of the simple linear regression between MAP and the mean provenance heights.



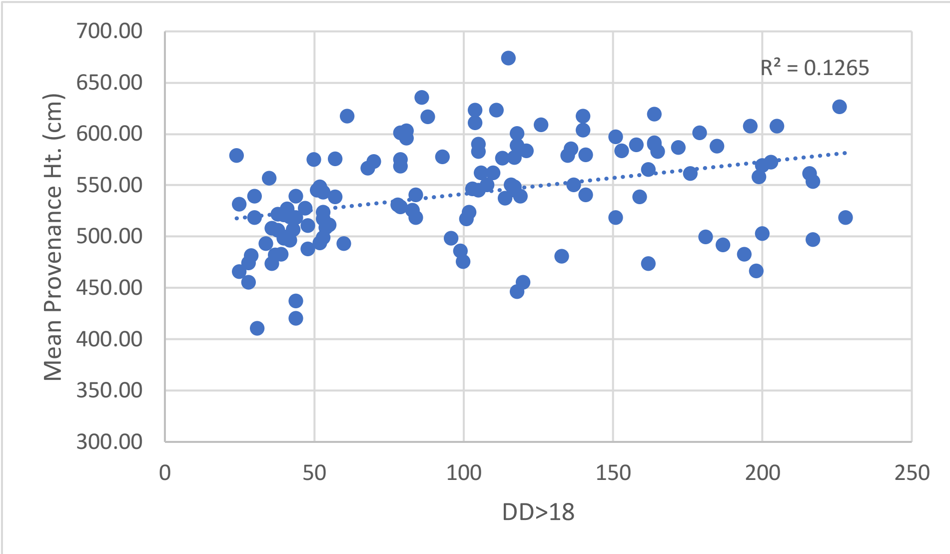
Appendix 1-4. Scatterplot display of the simple linear regression between AHM and the mean provenance heights.



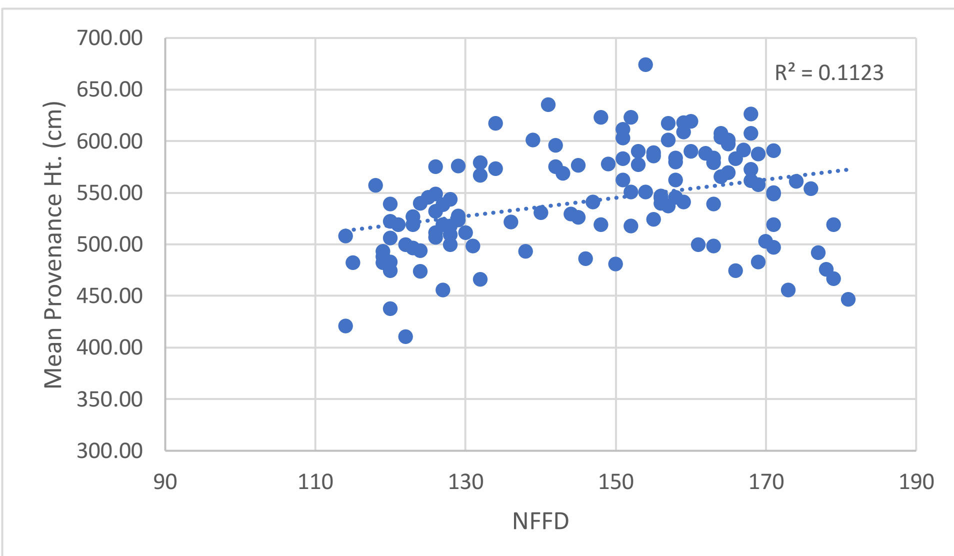
Appendix 1-5. Scatterplot display of the simple linear regression between DD<0 and the mean provenance heights.



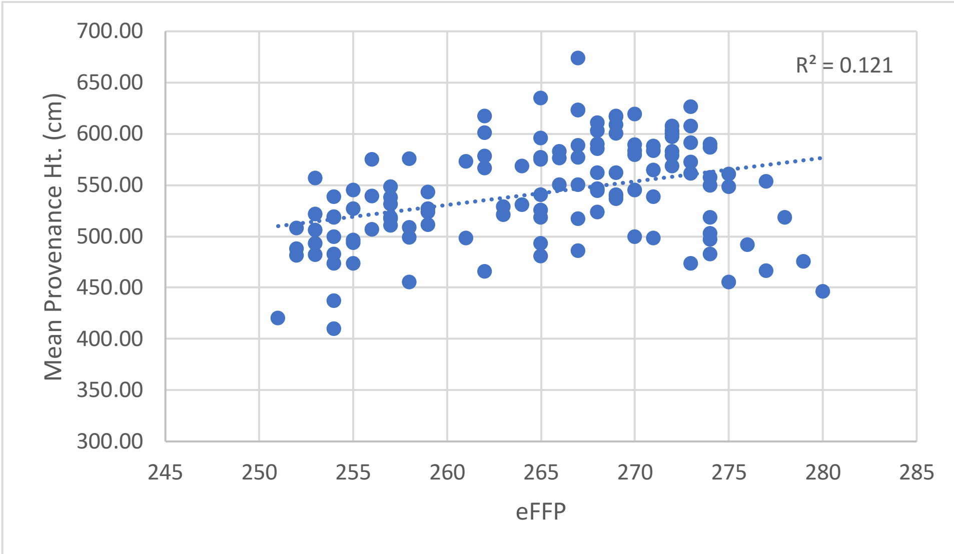
Appendix 1-6. Scatterplot display of the simple linear regression between DD<18 and the mean provenance heights.



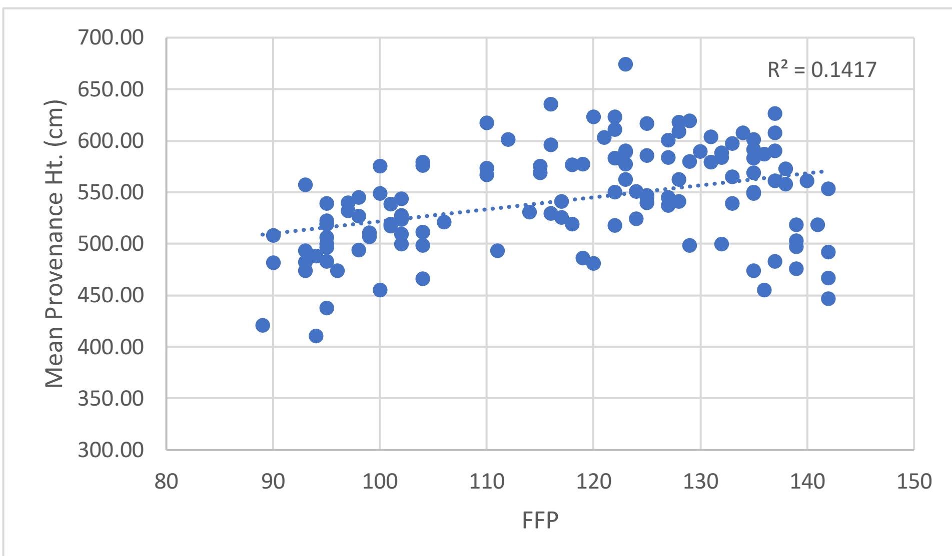
Appendix 1-7. Scatterplot display of the simple linear regression between DD>18 and the mean provenance heights.



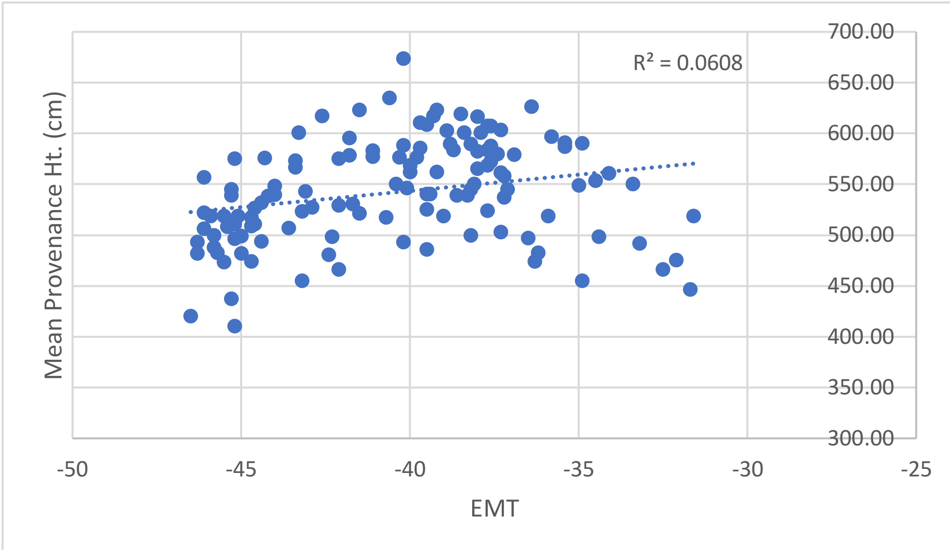
Appendix 1-8. Scatterplot display of the simple linear regression between NFFD and the mean provenance heights.



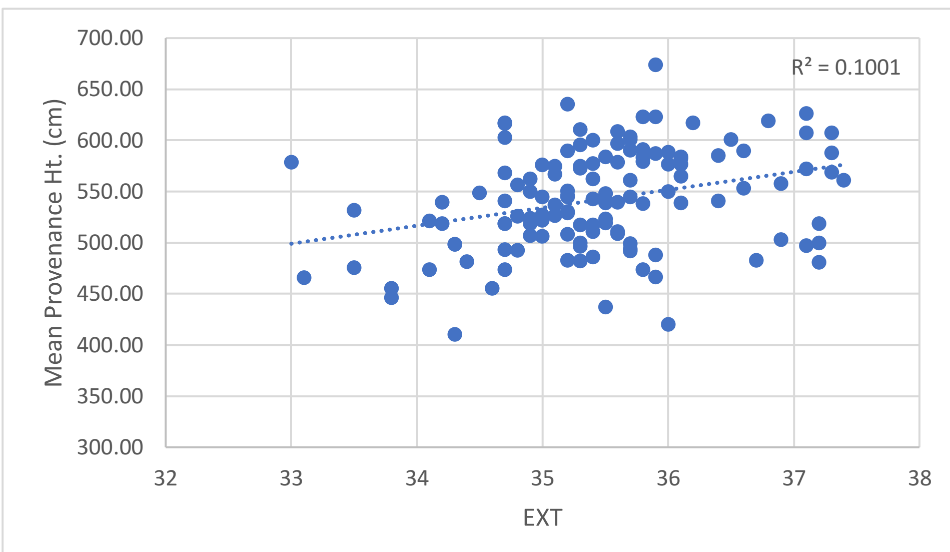
Appendix 1-9. Scatterplot display of the simple linear regression between eFFP and the mean provenance heights.



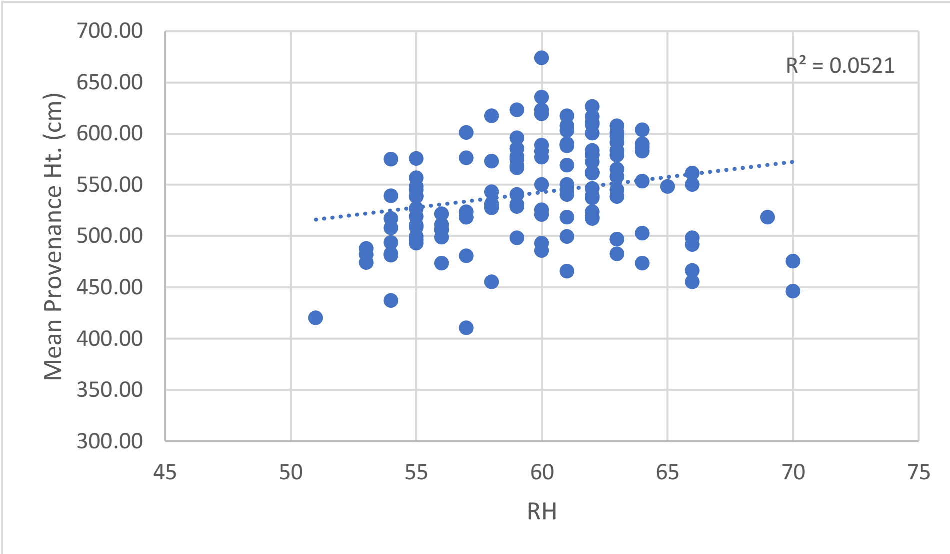
Appendix 1-10. Scatterplot display of the simple linear regression between FFP and the mean provenance heights.



Appendix 1-11. Scatterplot display of the simple linear regression between EMT and the mean provenance heights.



Appendix 1-12. Scatterplot display of the simple linear regression between EXT and the mean provenance heights.



Appendix 1-13. Scatterplot display of the simple linear regression between RH and the mean provenance heights.

APPENDIX II

TEST OF NORMALITY

Appendix 2-1. Test of normality for height at the Kakabeka test site

		Kolmogorov-Smirnov			Shapiro-Wilk		
	block	Statistic	df	Sig.	Statistic	df	Sig.
Ht (2019)	1	0.056	1234	0.000	0.968	1234	0.000
	2	0.089	1143	0.000	0.749	1143	0.000

APPENDIX III

CLIMATE VARIABLE DEFINITIONS

Appendix 3-1. Climate variable definitions.

Directly calculated annual variables	
MAT	mean annual temperature (°C)
MWMT	mean warmest month temperature (°C)
MCMT	mean coldest month temperature (°C)
TD	temperature difference between MWMT and MCMT, or continentality (°C)
MAP	mean annual precipitation (mm)
MSP	May to September precipitation (mm)
AHM	annual heat-moisture index (MAT+10)/(MAP/1000))
SHM	summer heat-moisture index ((MWMT)/(MSP/1000))
Derived annual variables	
DD<0	degree-days below 0°C, chilling degree-days
DD>5	degree-days above 5°C, growing degree-days
DD<18	degree-days below 18°C, heating degree-days
DD>18	degree-days above 18°C, heating degree-days
NFFD	the number of frost-free days
FFP	frost-free period
bFFP	the day of the year on which FFP begins
eFFP	the day of the year on which FFP ends
PAS	precipitation as snow (mm). For individual years, it covers the period between August in the previous year and July in the current year.
EMT	extreme minimum temperature over 30 years
EXT	extreme maximum temperature over 30 years
Eref	Hargreaves reference evaporation (mm)
CMD	Hargreaves climatic moisture deficit (mm)
MAR	mean annual solar radiation (MJ m -2 d -1)
RH	mean annual relative humidity (%)

APPENDIX IV

MEAN PROVENANCE HEIGHTS

Appendix 4-1. Mean provenance heights at the Kakabeka test site.

Provenance	Mean height	N	Std. Deviation
1	626.00	20	162.317
2	564.75	20	154.416
3	538.57	14	216.086
4	561.94	17	110.712
5	600.40	15	153.559
6	607.26	19	127.335
7	608.50	14	128.388
8	546.11	19	211.671
9	583.35	20	146.641
10	518.17	18	157.821
11	496.69	16	163.299
12	502.47	17	143.239
13	582.42	19	184.418
14	588.25	20	155.677
15	540.42	19	195.930
16	577.05	19	139.288
17	557.53	19	189.070
18	572.16	19	159.092
19	673.42	19	99.448
20	528.67	18	160.431
21	589.32	19	132.782
22	576.47	19	120.876
23	560.89	18	148.822
24	482.44	18	137.899
25	568.63	16	201.902
26	617.20	20	144.057
27	549.89	19	173.494
28	607.16	19	93.717
29	553.13	16	140.288
30	473.58	19	213.728
31	499.32	19	216.439
32	579.26	19	130.129

33	587.53	19	147.698
34	618.79	19	98.216
35	585.21	19	119.874
36	550.06	18	195.355
37	586.63	19	174.301
38	523.59	17	216.373
39	590.84	19	122.064
40	536.68	19	136.350
41	560.75	20	130.031
42	540.40	20	200.968
43	596.88	17	157.600
44	616.95	20	124.083
45	568.06	17	106.801
46	576.25	20	155.988
47	525.33	18	204.620
48	518.44	18	151.499
49	634.89	19	125.841
50	622.68	19	125.146
51	530.31	13	113.056
52	485.75	16	206.394
53	589.95	20	203.078
54	544.64	14	149.166
55	574.67	18	164.726
56	561.89	19	157.818
57	595.58	19	119.576
58	589.68	19	167.926
59	610.65	20	155.778
60	539.13	16	199.438
61	491.39	18	178.648
62	600.21	14	144.348
63	566.56	18	153.175
64	544.58	19	153.385
65	583.32	19	153.773
66	572.72	18	138.665
67	622.74	19	110.700
68	582.68	19	167.051
69	518.29	17	187.685
70	517.11	19	174.066
71	578.69	16	81.831
72	600.72	18	175.043
73	603.05	19	156.290

74	549.69	16	181.111
75	497.89	19	130.319
76	575.59	17	123.977
77	574.72	18	147.971
78	518.20	20	146.979
79	510.47	19	175.376
80	437.11	18	147.971
81	508.68	19	126.560
82	516.89	19	118.290
83	475.06	16	91.208
84	602.76	17	113.257
85	510.85	20	153.520
86	616.47	19	130.337
87	498.94	18	155.036
88	454.89	19	148.348
89	548.33	18	124.930
90	507.72	18	111.444
91	520.78	18	123.673
92	481.37	19	146.513
93	473.68	19	140.308
94	538.65	20	98.237
95	539.25	20	132.072
96	454.90	20	132.968
97	526.42	19	78.584
98	482.50	20	104.516
99	578.38	16	112.133
100	481.63	19	134.992
101	556.56	18	126.665
102	492.60	15	111.676
103	521.69	16	104.427
104	531.26	19	97.525
105	505.72	18	135.548
106	446.25	16	105.358
107	465.61	18	63.319
108	518.40	20	114.808
109	473.37	19	98.185
110	409.93	14	128.860
111	499.19	16	173.848
112	497.88	17	147.293
113	518.74	19	125.342
114	496.00	19	160.455

115	526.94	18	161.905
116	523.28	18	101.628
117	542.84	19	151.403
118	493.39	18	166.001
119	420.20	20	154.867
120	506.39	18	142.907
121	492.74	19	121.238
122	487.63	16	158.139
123	548.00	15	110.620
124	538.00	17	148.659
125	544.76	17	140.003
126	480.37	19	115.203
130	466.00	19	158.095