ADAPTIVE VARIATION OF TREMBLING ASPEN IN NORTHWESTERN ONTARIO

by

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ABSTRACT

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Key words: adaptive variation, trembling aspen, provenance, leaf flushing phenology

To demonstrate the pattern of adaptive variation of *Populus tremuloides* (Michx.) to northwestern Ontario climate conditions, a statistical analysis was completed of growth and phenology variables from 26 provenances. Growth variables included: height measured in 1999, 2000, 2003 and 2004; stem diameter measured in 1999, 2000 and 2002; leader length measured in 2000; and, leaf flushing measured in 2000. Adaptive variation was summarized by four principal component (PC) axes modeled by climate variables at seed origin that explained 41.5, 15.8, 10.0 and 6.3 percent of the growth and phenology variation among provenances. A clinal pattern of adaptive variation in leaf flushing predicted by temperature in the growing season was demonstrated by the first PC axis. The second PC axis was strongly influenced by growth data at one test site (Dog River) and showed a weak latitudinal trend related to winter temperature and precipitation at the start of the growing season. A longitudinal pattern of adaptive variation in growth and chlorophyll florescence variables predicted by July precipitation was demonstrated in PC axis 3. A latitudinal trend was shown for PC axis 4 where adaptive variation was expressed through a combination of winter temperatures and June mean temperature that predicted leader length and height potential together with October frost hardiness. The pattern of adaptive variation indicated significant genetic variation among trembling aspen provenances over a relatively small region.

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INTRODUCTION

Trembling aspen (*Populus tremuloides* Michx.) is the most extensively distributed tree species in North America (Perala 1990). It is an interesting species because of clonal reproduction where a genotype can live almost indefinably as long as the root system continues suckering (Barnes 1966). Due to the clonal nature the trembling aspen genotype is considered more permanent on the landscape than most conifers (Barnes 1966). Hyun et al. (1987) from enzyme studies described trembling aspen as genetically variable and moderately differentiated.

The wide range of trembling aspen requires adaptation to a widely variable environmental gradient (Farmer 1996). Adaptation to climate is important to a species perpetual presence on the landscape and is the basis for species seed transfer zones in Ontario (Ontario Ministry of Natural Resources 1987; Parker and van Niejenhuis 1996). The timing of growth processes (phenology) is highly correlated with climatic patterns and processes such as bud flushing and shoot elongation are considered adaptive traits. Quantitative traits, such as height and diameter, are also considered adaptive traits. A trait is considered adaptive if one or more climate variables can be significantly correlated to that trait (Parker and van Niejenhuis 1996).

Insight into the patterns of adaptive variation of trembling aspen in northwest Ontario is critical to understand the genetic diversity of this species but also to provide a basis for further study regarding climate change in the region. Previous work in northwest Ontario includes description of the patterns of adaptive variation for frost hardiness (Weng 2002; Weng and Parker 2008), and for height and diameter growth (Young 2004). However, to provide an encompassing description of the adaptive variation patterns, phenological variables were important to investigate in combination with growth and hardiness data. Therefore, analysis was undertaken that included height, leader length and stem diameter assessments. Phenological data for leaf flushing stages was also analyzed. These data were combined with previously published data for frost hardiness, provided by Y. Weng (Weng 2002), and 2003 and 2004 height and stem diameter measurements provided by M. Young (Young 2004). The purpose of this study was to comprehensively describe the patterns of adaptive variation expressed among 26 trembling aspen provenances (seed sources) from northwest Ontario.

LITERATURE REVIEW

TREMBLING ASPEN RANGE

Trembling aspen, also referred to as quaking aspen, is the most extensively distributed native tree species in North America covering 111° of longitude and 48° of latitude (Perala 1990). The range extent stretches from northwestern Alaska south into Arizona with pockets in the mountains of Mexico, across Canada from British Columbia to Newfoundland and Labrador, and throughout the US lake states from Missouri east to New Jersey (Perala 1990). Only the shores of Hudson Bay are without aspen in Ontario (Hyun et al. 1987; Perala 1990).

The extensive range of trembling aspen over a variety of climatic conditions as well as elevation changes suggest the inherent ability of this species to adapt to a wide range of environmental conditions within the parameter that annual precipitation exceed evapotranspiration (Perala 1990). Trembling aspen is found in an elevational range from sea level to 3,700m (Mitton and Grant 1996), but in mountainous areas, such as the central Rocky Mountains, the lower limit in the distribution of aspen is associated with an approximate mean annual temperature of 7°C (Perala 1990). January average temperatures have been reported from a low of -30°C (interior Alaska) to -3°C (Fort Wayne Indiana) with July average temperatures in these same locations as 16°C and 23°C respectively; and with the southern limit of the range at approximately 24°C mean

July temperature in the eastern United States (Perala 1990). Precipitation has been reported to range from 180mm per year in Interior Alaska to 1,020mm in Gander Newfoundland (Perala 1990). Annual surface water runoff has been noted as a limiting factor to influence the range of trembling aspen from the southern limits in the prairie provinces moving east to northwestern Minnesota and down to southern Iowa (Perala 1990).

For comparison of the range values noted above with the study area, Environment Canada reports climate normal conditions (1971-2000) at the airport in Thunder Bay, Ontario, at 199m elevation, $48^{o}22'$ north latitude and $-89^{o}19'$ west longitude, having mean annual values for temperature of 2.5^{o}C, precipitation of 711mm, and degree days above 0^{o}C of 2,424 per year (Anonymous 2014). January mean temperature is reported as -14.8^{o}C and July mean temperature at 17.6^{o}C (Anonymous 2014). The climate in the study area is strongly influenced by two bodies of water, Lake Superior and Lake Nipigon, creating strong climate gradients in the area (Weng and Parker 2008; Parker et al. 1994).

GENETIC VARIATION

Genetic System and Genetic Process

A species ‘genetic system’ includes a species mating and reproduction systems as well as population size and chromosome factors (Darlington 1958). Genetic system components describe the patterns of genetic recombination that result in genetic variation verses genetic uniformity as Morgenstern (1996) notes. The components of trembling aspen’s genetic system are described by Morgenstern (1996) as: 1) having a large population size with great genetic variability across a transcontinental distribution; 2) reproducing through both sexual and asexual means; 3) having an outbreeding mating system with dioecious flowering and wind as the pollination vector; and 4) diploid with polyploid also possible.

There are a number of genetic processes that can influence gene and genotype frequencies and hence the magnitude and expression of genetic diversity (Morgenstern 1996). Mutation is a genetic process that results in new genetic variability (Morgenstern 1996). Independent assortment results in genetic recombination, and occurs during sexual reproduction (Morgenstern 1996). Seed and pollen dispersal change gene frequencies through the process of gene flow (Morgenstern 1996). Gene flow can connect populations within a species and is considered a hindrance to local adaptation (Kawecki and Ebert 2004) and reduces genetic diversity (Morgenstern 1996). Natural selection directly affects phenotypes during each stage of development, including reproduction, and as such indirectly affects genotypes (Morgenstern 1996). Natural selection results in gene frequencies changes through unequal reproduction and survival and is the strongest driver of adaptation (Morgenstern 1996).

Reproductive Strategies and Genetic Diversity

Trembling aspen reproduces sexually and asexually (Perala 1990). Trembling aspen seed and pollen are capable of long distance dispersal influencing the extensive range of trembling aspen and the high levels of both among- and within-population genetic variation (Morgenstern 1996; Mitton and Grant 1996; Long and Mock 2012). Sexual reproduction provides the genetic variation required for adaptation to climate changes over millennia and enhances the ability of the species to colonize new sites

(Long and Mock 2012). The ability to propagate through suckering also ensures persistence in a specific place for long periods of time when conditions are not favourable for seed germination and establishment (Mitton and Grant 1996) and results in an accumulation of genetic variation (Cheliak and Dancik 1982). However, Mock et al. (2008) reported for Utah sources of trembling aspen that recent sexual reproduction contributed to genetic diversity at the population level to a greater extend than did the accumulation of somatic mutations from vegetative reproduction.

Patterns of Genetic Variation

Morgenstern (1996) states that a species genetic system influences the range and population size of the species, while evolution is driven by environmental conditions, and the raw material of evolution is genetic variation. Environmental factors, such as climate conditions, interact with the components of a species genetic system and result in the development of geographic patterns of variation (Morgenstern 1996). It is important to note that studies of adaptive variation along clinal patterns are observation of the product of natural selection pressures, not observation of the process of selection itself (Farmer 1996).

Phenotypic variation in leaf size, shape and tooth number demonstrated a clinal pattern of variation from southern Utah to northern Montana and Idaho and the differences in morphology suggested a genetic basis for such marked variation among populations (Barnes 1975). Variation in wood specific gravity demonstrated a clinal pattern which decreased from south to north in natural populations in Wisconsin and Upper Michigan (Einspahr and Benson 1966). However, in the same study no geographic pattern for growth and form traits or for other wood properties such as, fiber length and strength, and pulp yield was demonstrated (Einspahr and Benson 1966).

High levels of within population phenotypic variation were demonstrated in quantitative traits to have a significant heritable genetic basis in a population located in southern Utah (Kanaga et al. 2008). The coefficient of genetic variation was high for all growth traits (12.5 initial height, 19.3 total height and up to 41.1 relative growth rate) and some leaf traits (leaf number 18.3 and leaf area 24.2) (Kanaga et al. 2008). Broad sense heritability ranged from 0.17 to 0.56 and was significantly different from zero for all growth, leaf and physiological (UV-A transmittance and water use) traits (Kanaga et al. 2008).

Brissette and Barnes (1984) studied phenology of leaf flushing (bud burst) of open-pollinated seedlings sourced from Michigan, Alaska, Alberta and Utah and planted in Michigan. Results indicated that leaf flushing occurred earliest for the Alaska sources, followed by Utah sources, then those from Alberta and finally the local sources flushed last (Brissette and Barnes 1984). Flushing dates ranged from April 5th for Alaska sources to past May 2nd for the Michigan sources (Brissette and Barnes 1984). Height growth cessation followed a similar pattern with Alberta and Alaska ceasing in mid- to late June followed by Utah and finally local Michigan sources in mid-August to early September (Brissette and Barnes 1984). This broad geographic pattern for leaf flushing was attributed to accumulated degree-days with less required for northern sources to initiate flushing. Patterns of growth cessation were attributed to the influence of photoperiod changes with latitude and also changes with elevation of the seed source with northern sources stopping growth first when planted in Michigan (Brissette and Barnes 1984). As was shown in Pauley et al. (1963), western sources moved east performed poorly compared to the local eastern sources in terms of height growth (Brissette and Barnes 1984).

Spring budbreak phenology was studied in Alberta for an extensive range of seed sources (43 half-sib families) from Minnesota to British Columbia planted in common garden trials (Li et al. 2010; Schreiber et al. 2013). Seed sources demonstrated a northeastern to southwestern cline in heat sum requirements for budbreak (Li et al. 2010). Lower heat sums were required in the northern and high elevation seed sources from British Columbia and higher heat sums were required for more southern sources from the central boreal plains in Saskatchewan and Alberta (Li et al. 2010). However, the clinal pattern did not extend across the entire range of sources studies by Li et al. (2010), instead, Minnesota sources demonstrated similar heat sum requirements as those for Northern Alberta sources; they were moderate compared to the lower heat sum required in the northeast and the higher heat sums required for budbreak in the central boreal plains. Li et al. (2010) attributed the clinal northeast to southwest pattern that resulted in budbreak phenogy as partly attributed to adaptation that balances frost risk verses growing season utilization where moisture was not limited at seed source for the British Columbia and northern Alberta sources. However, Li et al. (2010) also described adaptation to winter precipitation and dryness demonstrated by the central boreal plans provenances that broke bud last despite a higher latitude than sources from Minnesota but where Minnesota sources had a higher winter and spring precipitation.

Injury from ozone was significantly less in populations most polluted with ozone in a study conducted in US national parks, and clonal variation in damage was greatest in the least polluted parks suggesting adaptation to ozone as a selection pressure by eliminating or reducing vigor to favour more productive ozone tolerant clones (Berrang et al. 1986; Berrang et al. 1989; Berrang et al. 1991; Farmer 1996). Also, annual precipitation and minimum temperature were negatively correlated with leaf injury which demonstrated areas with greater winter precipitation and a warmer minimum winter temperature were the most ozone tolerant (Berrang et al. 1991).

However, considering CO_2 responses Liu et al. (2006) found no significant difference among or within four seed sources of trembling aspen grown from seed in northwestern Ontario indicating no significant influence of CO_2 in modifying the distribution or genetic structure of trembling aspen in the small study area (Liu et al. 2006). What is interesting, however, is that the two more western sources had significantly greater biomass than the two more eastern sources despite no significant difference in CO_2 responses (Liu et al. 2006).

Adaptive Variation Reported in Northwestern Ontario

The four seed sources studied for CO_2 responses by Liu et al. (2006) were also represented in the trials planted for this study, as well as for Weng (2002) and Weng and Parker (2008) who investigated adaptive variation in cold hardiness and Young (2004) who studied adaptive variation in height and stem diameter.

Young (2004) investigated two years of height data in 2002 and 2003 as well as stem diameter (at the root collar) in 2002 at two test sites in northwestern Ontario (Dog River and Camp 45), and related these data to climate variables associated with each seed source. After demonstrating significant among provenance variation, regression analysis indicated that, in general, summer temperature variables, together with mainly fall precipitation and growing degree days, were significantly related to height in 2003 at Camp 45, and height in 2002 and 2003 at the Dog River site. Spring temperature and growing degree days significantly predicted stem diameter (Young 2004). The pattern of variation was reported generally south to north; however, there was some evidence of a genotype by environment action at one of the test sites where the local sources performed better than southern sources (Young 2004).

Adaptive variation in cold hardiness was extensively investigated in 12 to 26 trembling aspen provenances in northwestern Ontario using three methods, electrical conductivity of tissue diffusates (EC), chlorophyll fluorescence (CF) and visual scoring (VS) by Weng (2002) and Weng and Parker (2008). Provenance accounted for greater than 40% of the total variation for frost hardiness using the EC method (Weng and Parker 2008). Hardiness data from the EC method were related to climate with the following key findings as summarized in Weng (2002) and Weng and Parker (2008): absolute degree of cold hardiness (PC1) was significantly related to heat sums in early summer along with late summer precipitation; onset of cold hardiness (PC2) was significantly predicted by mid- to late summer temperature; and site related differences in cold hardiness (PC3) was related to February maximum temperature. Cold hardiness development in trembling aspen followed the same general trend as EC data for CF data and VS data for the provenances tested (Weng 2002; Weng and Parker 2008).

METHODS

SEED SOURCES AND TEST ESTABLISHMENT

Trembling aspen seed was collected from 26 locations in Northwestern (NW) Ontario (Figure 1). At each location seed was collected from five dominant trees that were spaced well apart to avoid collection from the same clone. These sources ranged from 48°18’20” to 49°45’42” north latitude and 87°58’13” to 90°48’57” west longitude. Seed source and test information is presented in Table 1.

Seedlings were grown as container stock at Hills Greenhouses, Thunder Bay ON in the summer of 1997. The stock was sorted to the experimental test design in the fall of 1997, and the seedlings were over-wintered in cold storage. In May, 1998, the seedlings were brought out of cold storage three weeks before planting. The stock was then pruned to 10 cm in preparation for planting to reduce moisture deficit stress.

Three parallel provenance tests were established in NW Ontario that included the 26 northwest Ontario sources (Table 1). The three test sites were prepared during the winter and early spring of 1998. Table 1 describes the test site locations. Two of the locations were harvested forest sites: Camp 45 (C45) and Dog River (DR). Trembling aspen, white spruce, black spruce and jack pine were the predominant tree cover at DR and C45 prior to harvest. The third location, Kreikmann (KRM) was formally a sod farm. Both C45 and DR sites were prepared using a bull dozer to shear-blade material from the site. Rocks and debris were then picked up by hand and a small excavator. Finally the sites were disked with farm machinery. The Kreikmann site had heavy sod and required plough work before the site was disked.

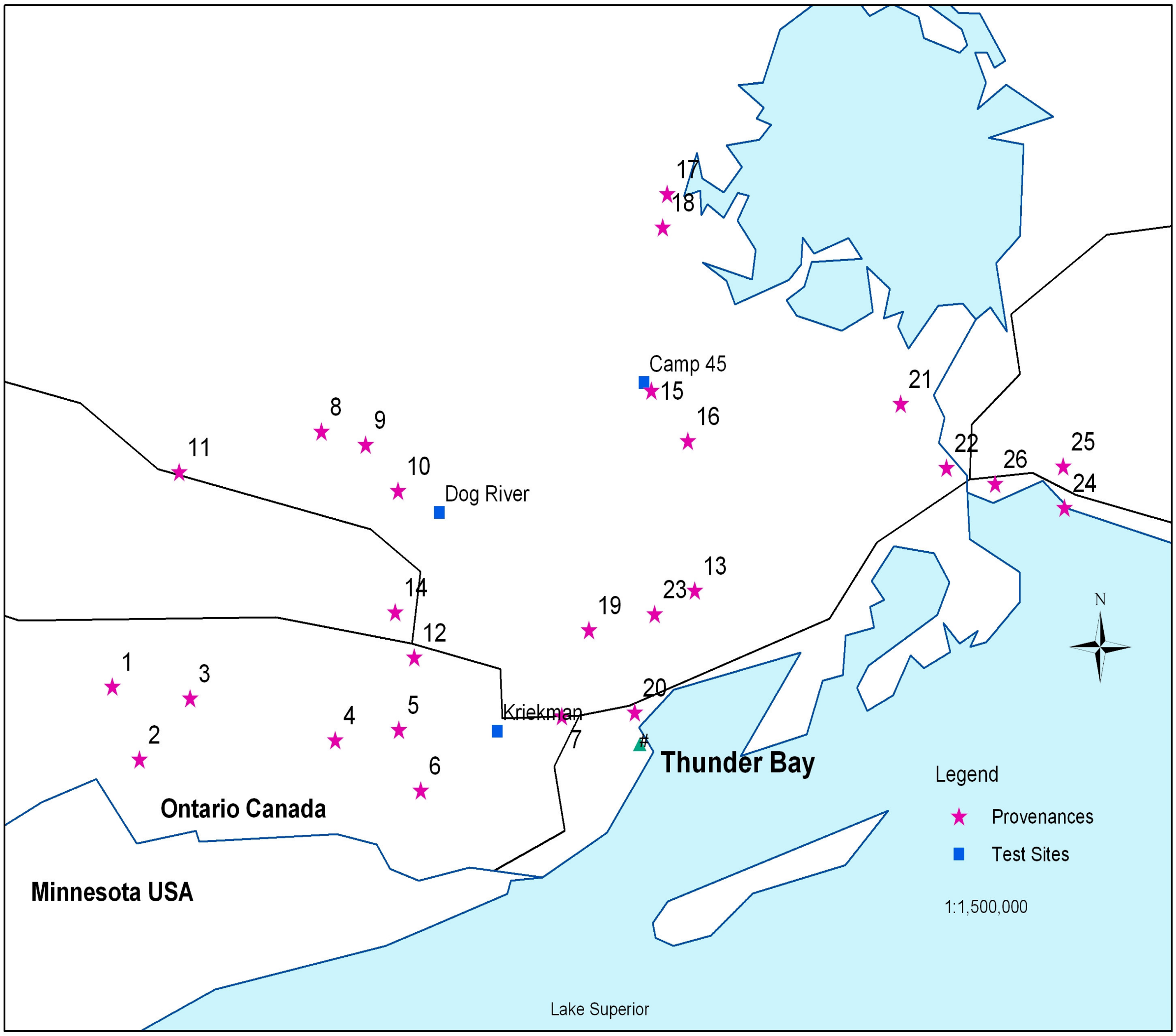

Figure 1: Location of test sites and provenances of trembling aspen in Northwestern Ontario, Canada

Table 1: Trembling aspen test and provenance locations

Test Site	Latitude (N)	Longitude (W)	Elevation (m)
Camp 45	49° 16’ 33”	89° 13’ 36”	360
Dog River	48° 56’ 28”	89° 50’ 19”	455
Kreikmann	48° 22’ 41”	89° 39’ 56”	350
Provenance	Latitude (N)	Longitude (W)	
1	48° 29’ 35”	90° 48’ 57”	
2	48° 18’ 20”	90° 44’ 05”	
3	48° 27’ 45”	90° 35’ 02”	
4	48° 21’ 20”	90° 09’ 00”	
5	48° 22’ 55”	89° 57’ 35”	
6	48° 13’ 30”	89° 53’ 40”	
7	48° 25’ 03”	89° 28’ 23”	
8	49° 09’ 02”	90° 11’ 29”	
9	49° 07’ 00”	90° 03’ 34”	
10	48° 59’ 49”	89° 57’ 44”	
11	49° 02’ 45”	90° 37’ 00”	
12	48° 34’ 05”	89° 54’ 50”	
13	48° 44’ 24”	89° 04’ 33”	
14	48° 41’ 47”	89° 58’ 13”	
15	49° 15’ 20”	89° 12’ 16”	
16	49° 07’ 34”	89° 05’ 47”	
17	49° 45’ 42”	89° 09’ 26”	
18	49° 40’ 34”	89° 10’ 17”	
19	48° 38’ 19”	89° 23’ 29”	
20	48° 25’ 35”	89° 15’ 18”	
21	49° 13’ 19”	88° 27’ 37”	
22	49° 03’ 23”	88° 19’ 24’	
23	48° 40’ 47”	89° 11’ 43”	
24	48° 57’ 13”	87° 58’ 13”	
25	49° 03’ 38”	87° 58’ 28”	
26	49° 00’ 57”	88° 10’ 38”	

The tests were laid out in early May, 1998, and planting occurred from May 26th to the 29th. The seedlings were well watered prior to planting. The Dog River test suffered minor frost damage within a week of planting. Seedlings at the Kreikmann test were severely damaged or killed by the forest tent caterpillar (*Malacosoma disstria* Hübner) in July of 2000 and this trial was then abandoned.

Three tests were planted in a randomized complete block design. Each test had 3 blocks with 15 seedlings per provenance per block planted in single tree plots.

GROWTH AND PHENOLOGY ASSESSMENT

Leaf Flushing

The phenology of leaf development was scored using the index of Brissette and Barnes (1984) during the early growing season of 2000. The variable used for analysis was the number of days to reach stage 2 through 6 of leaf flushing (Table 2). Leaf flushing scores were recorded at four to five day intervals at each of the three test sites beginning May 1, 2000. Leaf development stages were scored according to Brissette and Barnes (1984) with one modification: stage 6 was the final stage scored when the leaves had unfolded but were still succulent. The cycle of test site measurements throughout the spring had the Dog River test measured first followed by Kreikmann and then Camp 45.

The scoring data were used to calculate the number of days until each flushing stage was reached for each tree. The numbers of days to reach each flushing stage were recorded from May 1, 2000 until the first occurrence of each stage score for each tree (e.g. days to leaf stage 2 (LS2)). Where more than one stage was surpassed between visits, the average number of days between each visit was considered the stage date for the missed stage. When a stage was missed at the first measurement, the stage was recorded as missing data.

Table 2: Leaf flushing development stages adapted from Brissette and Barnes (1984).

Leaf Flushing Stage	Description of Leaf Flushing Stage
1	winter condition, tight buds no green colour visible
2	buds swelling, scales tight but some green visible under scales
3	leaves breaking out of the bud, scales still tight
4	leaves clustered and expanding past the bud scale
5	bud scales falling away, leaves separated but still curled
6	leaves unfolded

Growth Variables

Measurements for height were completed at all three test sites in 1999, but only for the two forest sites, Dog River and Camp 45, in 2000, 2002 and 2003 due to the insect damage at the Kreikmann site. Stem diameter was measured in 1999 at all three tests, at the two forest sites in 2000 and only at the Dog River test in 2002. Leader elongation was measured during the 2000 growing season at four to five day intervals. Data from 2002 and 2003 were obtained from Young (2004) and were reanalyzed along with the other mentioned data for consistency in analysis and reporting. A summary of data variables and measurement resolution are presented in Table 3.

Total tree height was measured using a height pole from the base of the stem to the base of the bud of the tallest branch (Brissette and Barnes 1984). The aspen seedlings did not always have a single stem leader with obvious laterally flattened branches. If a few of the top lateral branches all grew sharply upwards, the tallest one was considered the leader. Stem diameter was measured just above the root collar using digital callipers.

The highest branch identified in the 1999 height measurement was used for elongation length measurements. The measurements were first recorded when the leaves were considered at leaf stage 6 (Table 2). This highest branch was measured each visit regardless of other branches overtaking it as the leader by the end of the 2000 growing season. Survival was assessed from the measurement data during analysis.

Damage to the leaders by a shepard's crook fungal pathogen, *Venturia macularis* [(Fr.) Müeller & Arx] first appeared at C45 and DR in late June, 2000 and caused extensive damage through early July. Therefore, data collected for shoot length after July 1, 2000 were dropped from any analysis due to the volume of missing data. The leader length data variables for each site are identified as the number of days from May 1, 2000 (as was the leaf stage data).

Table 3: Summary of biological variables measured at NW Ontario trembling aspen provenance tests.

VARIABLE	CAMP 45 CODE	DOG RIVER CODE	KREIKMANN CODE	ACCURACY	COLLECTION DATE
height 1999	CHT99	DHT99	KHT99	nearest 0.5 cm	before bud flush, 2000
height 2000	CHT00	DHT00	-	nearest 0.5 cm	September 2000
height 2002	CHT02	DHT02	-	nearest cm	before bud flush, 2003
height 2003	CHT03	DHT03	-	nearest cm	September 2003
stem diameter 1999	CSD99	DSD99	KSD99	nearest 0.1mm	before bud flush, 2000
stem diameter 2000	CSD00	DSD00	-	nearest 0.1mm	September 2000
stem diameter 2002	-	DSD02	-	nearest 0.1mm	before bud flush, 2003
leader length day 28[a]	CLL28	-	-	nearest mm	May 28-30, 2000
leader length day 31	CLL31	-	KLL31	nearest mm	May 31 to June 2, 2000
leader length day 36	CLL36	DLL36	KLL36	nearest mm	June 5-7, 2000
leader length day 41	CLL41	DLL41	KLL41	nearest mm	June10-12, 2000
leader length day 46	CLL46	DLL46	KLL46	nearest mm	June 15-17, 2000
leader length day 51	CLL51	DLL51	KLL51	nearest mm	June 20-22, 2000
leader length day 56	CLL56	DLL56	-	nearest mm	June 25-27, 2000
leader length day 61	-	DLL61	-	nearest mm	June 30, 2000
days to leaf stage 2	CLS2	DLS2	KLS2	number of days[b]	May and June 2000
days to leaf stage 3	CLS3	DLS3	KLS3	number of days	May and June 2000
days to leaf stage 4	CLS4	DLS4	KLS4	number of days	May and June 2000
days to leaf stage 5	CLS5	DLS5	KLS5	number of days	May and June 2000
days to leaf stage 6	CLS6	DLS6	KLS6	number of days	May and June 2000

[a] leader length measurements variables named as the number of days from May 1, 2000

[b] leaf stage unit is the number of days from May 1, 2000 to reach the specified stage

CLIMATE DATA

Climate data for 64 variables were derived from the first version of the Ontario Climate Model (Mackey et al. 1996). Mean, minimum and maximum temperature and precipitation data were collected from 471 weather stations in and surrounding Ontario for the period 1968 to 1988 (Mackey et al. 1996). Thin-plate smoothing splines were used to fit interpolation surfaces to each data variable for each month (Mackey et al. 1996). This iterative procedure allowed for the generation of mean, minimum and maximum temperature and precipitation estimates for any point in the province of Ontario (Mackey et al. 1996). From the primary data a number of derived variables were also generated for each location (Mackey et al. 1996).

Using the location information for each seed source, values for the 64 climate variables were generated for each site using GIS Arc/Info (Environmental Systems Research Institute 1987) software. The 'cellvalue' function of Arcplot in the Arc/Info software was used to estimate the climate variable values for each provenance location. A summary of the data is provided in Appendix 1.

STATISTICAL ANALYSIS

Variation

To demonstrate adaptive variation the data must show, 1) a significant component of variation expressed among provenances in the biological variables examined, and 2) those data must also be significantly related to at least one climate variable. A number of analysis steps were preformed with SAS (SAS Institute 2000) software according to methodology described in Parker and van Niejenhuis (1996).

First, the growth and phenology data were tested for homogeneity and normality, and descriptive statistics were generated. Untransformed data, due to normal distributions, were used for all variables. SAS procedure GLM (SAS Institute 2000) was then used to perform analysis of variance (ANOVA). A three-way ANOVA was done to investigate the combined site data. The ANOVA model was:

$Y_{ijk} = \mu + t_i + b_j + tb_{ij} + p_k + tp_{ik} + tbp_{ijk} + \varepsilon_{ijkl}$ where:

μ = mean
t_i = the random effect of test *i*, where *i* = 1 - 3
b_j = the random effect of block *j*, where *j* = 1 - 3
tb_{ij} = the interaction effect of block *j* with test *i*
p_k = the random effect of provenance *k*, where *k* = 1 -26
tp_{ik} = the interaction effect of provenance *k* with test *i*
tbp_{ijk} = the interaction effect of provenance *k* in block *j* with test *i*
ε_{ijkl} = the error term associated with the seedling from provenance *k* in block *j* and test *i*

Two-way ANOVAs were also done by site on the growth and phenology data to better examine the components of variation expressed among provenances. For each ANOVA, variance components were calculated using the Restricted Maximum Likelihood procedure in SAS procedure Varcomp (SAS Institute 2000). As well, the percent variation expressed among provenances (intraclass correlation coefficient) for each component of variation was calculated. Variables from each test that showed no significant ($p \leq 0.05$) variation among provenances were dropped from further analysis. The model for the two-way ANOVA was:

$Y_{ijk} = \mu + b_i + p_j + bp_{ij} + \varepsilon_{ijk}$ where:

μ = mean

b_i = the random effect of block *i*, where *i* = 1 - 3
p_j = the random effect of provenance *j*, where *j* = 1 - 26
bp_{ij} = the interaction effect of provenance *j* with block *i*
ε_{ijk} = the error term associated with the seedling of provenance *j* in block *i*

Adaptive Variation

Cold hardiness data (Appendix II) for the 26 NW Ontario provenances from Weng (2002) were combined with the growth and phenology data for analysis and description of the patterns of adaptive variation. Weng (2002) presented results describing significant provenance variation in cold hardiness (collected in the fall of 2000) for the 26 trembling aspen sources included at the C45 field test. Significant among provenance variation was demonstrated for both the chlorophyll florescence and cambium visual scoring data (Weng 2002). Chlorophyll florescence data included in this work is represented by the mean percent reduction in the Fv/Fm ratio relative to the control at specific temperatures in September and October, while cambium visual damage was represented as percent damage for specific temperatures in October (Weng 2002).

Growth, phenology and cold hardiness variables that demonstrated significant variation among provenances were then related to climate values through simple regression using the SAS regression procedure (SAS Institute 2000). Any response variable that could not be significantly ($p \leq 0.05$) related to a climate variable was dropped from further analysis.

Remaining growth, phenology and cold hardiness variables from the two screening methods (ANOVA and simple linear regression) were then analysed with principal component analysis (PCA). The PCA was completed with SAS procedure PRINCOMP (SAS Institute 2000). The PCA summarized the main components of variation, and new summary variables were generated for each seed source which was standardized PCA scores for each component axis.

The PCA scores for each axis were then subjected to multiple linear regression analysis against the climate data to determine the best predictive model for each axis. Procedure REG with the maximum r^2 option was used (SAS Institute 2000). Only climate variables with tolerance values greater than 0.1 and significant ($p \leq 0.05$) *t*-values were used to avoid over-fit models (Parker and van Niejenhuis 1996).

Finally the regression models predicting each PCA axis were used along with the Ontario Climate Model (Mackay *et al.* 1996) to model the spatial pattern of adaptive variation across the study area. The GRID sub package of Arc/Info GIS (Environmental Systems Research Institute 1987) was used to generate the predicted PCA axes scores as spatial data. The GRID process used the regression model and multiplied the values from the pertinent OCM climate data grids in order to generate the modeled PCA axes values. The spatial grid was then transferred to ArcView (Environmental Systems Research Institute 1999) software for map production.

RESULTS

GROWTH AND PHENOLOGY

Survival

The DR test had the highest 1999 survival with 88.8 percent of the original trees remaining. By 2000 survival at DR declined by 2.6 percent; but by 2003, only 66.5 percent survived for the 26 provenances. C45 showed a similar trend with 1132 (85.8%) of the original trees surviving in 1999, and declining to 83.3 percent in 2000. Survival declined substantially to 57.4 percent by the fall of 2002 at C45 test. KRM test in 1999 had 76.7 percent survival.

Considerable mortality occurred during the 2000 growing season at each test site as indicated by the sample size in the leaf flushing (LS) and the leader elongation (LL) data in Table 4. At the C45 site eight trees did not survive to reach LS6 (leaves unfolded) while an additional 123 trees were damaged or died before the last day of elongation measurement. Similarly at both DR and KRM 5 trees and 72 trees respectively were lost during leaf flushing, and 28 (DR) and 16 (KRM) were damaged or died before the last elongation measure. The losses were due to unknown causes in some cases and to shoot shepard’s crook fungus in other cases.

Descriptive Statistics

C45 generally showed greater growth and earlier leaf flushing than did DR or KRM (Table 4). The mean values, as well as the range in values, for the variables increased through time at both forest sites, but larger values were shown by C45.

Leaves flushed at the most northern site, C45, before the other two sites. On average C45 took 17.5 days (from May 1st) to reach stage two compared with 23.2 days and 19.8 days for DR and KRM respectively (Table 4). However, the range of days to reach stage two was greater at C45 (35.5 days) than at either KRM (30.5 days) or DR (28.5 days). Even though DR and KRM on average reached the different leaf flush stages later than C45, the number of days on average to go from stage two through six was 18 days at C45 and 19.2 and 19.5 days at DR and KRM respectively. This trend at C45 of a wider range of days to reach each stage was demonstrated for each of the flushing stages. The range of days was 38 for trees to reach LS6 at C45, and only 30 days at DR and 25 days at KRM. KRM trees were at stage 6 after 52 days while C45 was six days behind for the last trees to reach LS6 despite earliest initiation of flushing (Table 4).

Mean height (HT) at C45 in 1999 was 92.1 cm which was 20.9 cm and 21.8 cm greater than KRM and DR respectively (Table 4). C45 also had a greater height range through time than DR. The range between the minimum and maximum height values at C45 increased from 161.5 cm to 300 cm over the period of 1999 to 2003, compared to DR height range from 126 cm to 226 cm for the same period.

Stem diameter (SD) mean values were also greater at C45 in both 1999 and 2000 (Table 4). KRM had the lowest mean diameter in 1999 of 9.4 mm even though the mean

Table 4: Descriptive statistics by site and for all sites combined for growth and phenological variables of 26 trembling aspen provenances in NW Ontario

Variable	CAMP 45					DOG RIVER					KREIKMANN					COMBINED SITES				
	N[a]	Mean	STD[b]	Min[c]	Max[d]	N[a]	Mean	STD[b]	Min[c]	Max[d]	N[a]	Mean	STD[b]	Min[c]	Max[d]	N[a]	Mean	STD[b]	Min[c]	Max[d]
HT99[e]	1132	92.1	24.5	20.0	181.5	1169	70.3	18.9	17.0	143	1008	71.2	15.8	25.5	129.0	3309	78.0	22.6	17.0	181.5
HT00	1089	109.8	30.6	10.8	211.5	1142	85.5	24.2	23.5	183	.	.	.	.	.	2231	97.3	30.1	10.8	211.5
HT02	750	141.5	40.3	54.0	332.0	881	111.5	31.6	31.0	258	.	.	.	.	.	1631	125.3	38.8	31.0	332.0
HT03	750	153.9	44.2	62.0	362.0	881	120.1	34.4	39.0	265	.	.	.	.	.	1631	135.6	42.7	39.0	362.0
SD99[f]	1131	12.0	2.7	4.3	22.4	1169	10.0	2.3	4.3	21.5	799	9.4	1.6	5.5	16.4	3099	10.6	2.5	4.3	22.4
SD00	1088	14.7	3.5	5.5	29.8	1142	11.9	2.9	5.6	28.2	.	.	.	.	.	2230	13.3	3.5	5.5	29.8
SD02	.	.	.	.	.	880	15.1	4.1	6.5	35.0	.	.	.	.	.	.	.	.	.	.
LS2[g]	509	17.5	5.1	10	45.5	1173	23.2	4.8	10	38.5	884	19.8	5.7	9	39.5	2566	20.9	5.6	9	45.5
LS3	1009	22.0	4.5	10	48.0	1177	30.2	3.7	10	41.0	942	26.5	4.5	7	42.0	3128	26.4	5.4	7	48.0
LS4	1100	25.2	5.0	12	50.5	1177	33.8	3.5	14	51.0	942	30.0	4.0	11	49.5	3219	29.8	5.6	11	51.0
LS5	1125	29.8	4.7	12	53.0	1177	37.5	3.1	26	53.5	943	33.9	3.8	19	52.0	3245	33.7	5.1	12	53.5
LS6	1124	35.5	4.8	20	58.0	1172	42.4	3.6	31	61.0	941	39.3	4.0	27	52.0	3237	39.1	5.1	20	61.0
LL28[h]	111	45.1	17.0	3	102	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
LL31	525	47.8	20.3	5	155	.	.	.	.	.	78	37.5	16.9	6	96	607	46.4	20.2	5	155
LL36	1026	55.1	24.7	5	195	58	31.2	12.7	5	63	470	36.5	16.7	3	109	1554	48.6	24.0	3	195
LL41	1083	62.9	28.2	5	214	894	30.8	14.9	2	95	861	42.7	21.3	3	143	2838	46.7	26.4	2	214
LL46	1087	79.7	35.5	6	270	1069	40.7	19.9	3	130	928	55.0	28.2	4	185	3084	58.7	33.1	3	270
LL51	1078	100.9	45.0	4	325	1140	54.6	27.5	2	170	925	68.5	34.9	4	224	3143	74.6	41.5	2	325
LL56	1001	130.4	58.8	5	402	1142	72.7	36.9	2	211	.	.	.	.	.	2144	99.8	56.8	2	431
LL61	.	.	.	.	.	1144	88.0	45.4	2	245	.	.	.	.	.	.	.	.	.	.

[a] N is the sample size

[b] STD is the standard deviation

[c] Min is the minimum

[d] Max is the maximum

[e] HT is height measured in cm in 1999(99), 2000(00), 2002(02) and 2003(03)

[f] SD is the stem diameter measured in mm in 1999(99), 2000(00) and 2002(02)

[g] LS is the leaf stage 2, 3, 4, 5 or 6 as the number of days from May 1, 2000

[h] LL is the leader length in mm measured on days 28, 31, 36, 41, 46, 51, 56, or 61 from May 1, 2000

height was slightly greater than DR. Between 1999 and 2003 diameter increased by 5.1 mm on average at the DR site.

Leader elongation measurements began when the leaf stage was scored at six (leaves unfolded). The first leader length measurements were recorded at C45 on day 28 for 111 trees (May 28, 2000). KRM followed with the first 78 trees measured on May 31st (day 31). DR had four trees with leaves unfolded (LS6) on day 31, but these are omitted from Table 5 due to the small number. Only 58 trees had leaves unfolded (LS6) on day 36 at DR. Leader length at KRM was measured 5 different days and over this period the mean length increased by 31 mm (Table 4). DR had a mean length increase of 31.2 mm and C45 of 34.6 mm for the first five measurements. C45 had the greater maximum value at the fifth measure (270 mm) compared to either DR (211 mm) or KRM (228 mm).

Provenance Variation

Three-Way ANOVA

Variation among provenances was significant for only a portion of the variables, as shown in Table 5. With all test sites combined the days to reach the leaf flushing stages showed significant variation among provenances for all stages and the percent variation explained ranged from 3.57 to 6.18 percent. Only three leader length measurements (day 41, 46 and 51) showed significant variation among provenances, but these expressed less than two percent of the variation. Height in 1999 was the only height or diameter variable to show significance among provenances, but was low with the percent of variation expressed less than one percent.

The block by provenance by test interaction was not significant ($p \leq 0.05$) for all but the days to reach LS2 (bud swelling); however, variation expressed only accounted for 1.1 percent of the total variation (Table 5). The block by provenance variation was also not significant ($p \leq 0.05$) in all but height in 2002 and days to leaf stage 6 with this effect accounting for 1.03 and 0.36 percent respectively of the total variation. Test by provenance interaction for height was significant in three of the four years measured (1999, 2002 and 2003), and the number of days to leaf flushing stages four (leaves clustered, expanding past bud scale), five (bud scales falling away, leaves separated but still curled) and six (leaves unfolded). However, the percent variation expressed by provenance interaction ranged from only 0.56 to 1.54 percent of the total variation. These significant tests by provenance interaction effects demonstrate a genotype by environment interaction in these variables, with accompanying rank changes among provenances.

Considering individual sources of variation, block effect was significant ($p \leq 0.05$) for only stem diameter measured in 1999 (Table 5). Test site effect however, explained the largest percent of variation ranging from 10.39 to 51.72 for all variables. Percent variation expressed was the highest in the latter days of leader measurement and in the leaf flushing stages LS3 through LS6. Leader length at the first measurement (day 31) expressed the lowest (10.39) percent variation. The block by provenance effect was significant ($p \leq 0.05$) for leaf stage six but only accounted for 0.36 percent of the variation.

Results from the three-way ANOVA indicate that the test by provenance interaction effects were important for height and days to leaf stage. Test effect showed the largest component of variation other than error variance but the days to leaf stage

Table 5: Percent variation and significance of growth and phenological variables for 26 trembling aspen provenances in NW Ontario

Variables		Height[a]				Stem Diameter[b]		Leader Length Day[c] (3) [e]						Days to Leaf Stage[d] (3) [e]				
Component		1999 (3)[e]	2000 (2)	2002 (2)	2003 (2)	1999 (3) [e]	2000 (2)	31	36	41	46	51	56	2	3	4	5	6
Test	%[f]	26.69	27.73	25.64	26.68	26.17	28.28	10.39	25.11	33.92	31.98	29.47	40.56	24.76	49.86	51.72	49.49	40.74
	sig.[g]	0.0011	0.0177	0.0064	0.0161	0.0003	0.0012	0.0538	0.0037	0.0003	0.0006	0.0006	0.0055	0.0002	<0.0001	<0.0001	<0.0001	<0.0001
Blk[h]	%	0.07	0	0	0	2.66	0.59	0	0	0	0	0	0	0.58	0	0.02	0.02	0.34
	sig.	0.4403	0.8922	0.9744	0.8538	0.0417	0.1790	0.6460	0.8734	0.6475	0.8139	0.9438	0.5323	0.780	0.4898	0.4031	0.3960	0.2277
Test * Blk	%	1.40	0.81	0.24	0.67	1.00	0.18	3.60	1.23	0.79	0.95	0.87	0.84	0.93	0.10	0.33	0.50	0.75
	sig.	<0.0001	0.0004	0.0064	0.0008	0.0012	0.1300	0.5965	0.0166	0.0007	<0.0001	<0.0001	0.0025	0.1592	0.1319	0.0105	0.0006	0.0001
Prov[i]	%	0.82	0.82	0.57	0.74	0.30	0.36	1.41	2.59	1.80	1.58	1.31	0.52	3.57	5.49	6.18	5.79	4.01
	sig.	0.0254	0.1409	0.4098	0.3006	0.2635	0.3203	0.4311	0.0727	0.0009	0.0010	0.0023	0.1990	0.0045	<0.0001	<0.0001	<0.0001	<0.0001
Test * Prov	%	0.56	0.65	1.39	1.14	0.41	0.23	0	0	0.28	0.48	0.38	0.46	0.41	0.45	0.94	1.54	1.52
	sig.	0.0487	0.1376	0.0076	0.0275	0.1895	0.1498	0.6920	0.8978	0.2954	0.1543	0.1690	0.1026	0.3065	0.0996	0.0018	<0.0001	<0.0001
Blk * Prov	%	0.08	0.75	1.03	0.50	0.02	0	0	0	0	0	0	0.36	0	0	0.14	0	0.36
	sig.	0.4277	0.1884	0.0195	0.1066	0.5920	0.2140	0.7084	0.8566	0.8163	0.9614	0.8548	0.1453	0.6638	0.7521	0.2486	0.3188	0.0459
Test * Blk * Prov	%	0	0.29	0	0	0	0	0	0	0	0	0	0	1.10	0.17	0	0	0
	sig.	0.7249	0.3756	0.8844	0.7646	0.8879	0.8822	0.3422	0.8673	0.6447	0.5573	0.6229	0.7278	0.0405	0.2361	0.7165	0.9700	0.9402
Error	%	70.38	68.96	71.13	70.27	69.43	70.35	84.60	71.08	63.22	65.02	67.98	57.36	68.65	43.93	40.67	42.65	52.29

[a] Height measured in cm in 1999, 2000, 2002 and 2003

[b] Stem diameter measured in mm in 1999 and 2000

[c] Leader length measured in mm on days 31, 36, 41, 46, 51, and 56 from May 1, 2000

[d] Days to leaf stages 2, 3, 4, 5, 6 measured as the number of days from May 1, 2000

[e] (2) or (3) under variable names indicate the number of tests the variable was measured

[f] % is the percent variation (intraclass correlation coefficient)

[g] sig. is the significance level

[h] Blk is test block

[i] Prov is provenance

was also notable. Therefore, the measurement and phenology data were separated by test for further analysis due to the large amounts of variation expressed among test sites.

Two-Way ANOVA

Results from the analysis of variance conducted for each test site are shown in Table 6. Analysis of variance by site provided screening of each variable for significant provenance variation. The block by provenance effects were not significant at each of the 3 sites for all variables, except for height measured at DR in 2000. Height in 2000 at DR expressed 2.9% of the variation in the block by provenance effect; however, the variation was not significant among provenances for this variable. Overall, non-significant block by provenance interaction indicated uniform performance across the sites.

A significant difference ($p \leq 0.05$) among provenances was expressed in 36 of the 48 trait variables across all 3 sites (Table 6). Leaf flushing differences among provenances explained the highest percent of variation, other than error variation. Leaf flushing variation among provenances was significantly different for the days to reach each of the 6 stages at each site, except for C45 days to reach LS2 (buds swelled), possibly due to the sample size. The percent variation expressed among provenances for leaf flushing tended to increase and then decrease moving from leaf stage two through six at each test site. At C45, the differences among provenances expressed for leaf flushing stages increased almost ten percent from LS3 to LS4 then reached a maximum of 19.77 percent variation among provenances for LS5. LS6 then explained 14.01 percent variation among provenances. KRM demonstrated a marked increase of 10 percent in variation expressed between LS2 to LS3. LS4 through LS6 expressed 13.82

down to 8.31 percent variation among provenances. DR expressed 6.64 percent variation among provenances in LS2 then increased to roughly ten percent for both LS3 and LS4. LS6 expressed a significant difference among provenances but this effect only explained 2.42 percent of the variation.

Where leaf flushing showed strong among provenance variation, only two-thirds of the leader elongation measurements showed significant difference among provenances (Table 6). The first two measurement days at the forest sites and the first at KRM were not significant likely due to the small sample sizes encountered (i.e. many leaves still flushing). As more trees moved from leaf flushing to elongation the significance of the provenance effect tended to increase as shown by the increase in provenance variation at day 36 over day 28 and day 31 at C45. C45 significant provenance variation accounted for 3.07 and 3.06 percent of the variation for lengths day 36 and day 41 respectively, while variation expressed at day 46 accounted for 2.73 percent. While at DR the significant provenance effects expressed days 41 to 61 ranged from a maximum 2.97 percent variation explained at day 51 to a minimum of 1.53 percent of variation explained at day 41. KRM, the farm field site, demonstrated the highest range of leader length variation expressed among provenances ranging from 4.02 to 6.75 percent. KRM LL31 (day 31) provenance variation explained over 15 percent of the variation, but was not significant.

Stem diameter expressed significant provenance variation at the DR site only and explained from 1.79 to 2.98 percent of the variation. Each of the four height measures at C45 and the KRM 1999 measurement demonstrated significant variation among provenances accounting for approximately 2 percent of the variation. DR 2002 and

Table 6: Percent variation and significance of growth and phenological variables by test site for 26 trembling aspen provenances in NW Ontario

		Camp 45				Dog River				Kreikmann			
Variable		Blk[a]	Prov[b]	Blk * Prov	Error	Blk	Prov	Blk * Prov	Error	Blk	Prov	Blk * Prov	Error
HT99[e]	%[d]	0	2.14	0	97.86	2.55	0.81	1.84	94.80	6.28	2.31	0	91.42
	sig.[e]	0.4744	0.0085	0.659		0.0004	0.2182	0.0752		<0.0001	0.0009	0.9588	
HT00	%	0.41	2.36	0.46	96.77	2.04	1.49	2.90	93.58	.	.	.	.
	sig.	0.0857	0.0177	0.3728		0.0026	0.1100	0.0248		.	.	.	.
HT02	%	0.19	2.65	0	97.16	0.36	3.38	0.34	95.93	.	.	.	.
	sig.	0.152	0.0292	0.4224		0.1025	0.0081	0.509		.	.	.	.
HT03	%	1.25	2.03	0	96.73	0.30	3.61	0.33	95.76	.	.	.	.
	sig.	0.0109	0.0334	0.5709		0.122	0.0068	0.4689		.	.	.	.
SD99[f]	%	4.04	0	0	95.96	4.71	2.04	0.80	92.45	9.09	1.26	0	89.65
	sig.	<0.0001	0.3448	0.6968		<0.0001	0.035	0.2426		<0.0001	0.078	0.9836	
SD00	%	0.96	0.08	0	98.95	1.23	1.79	0.34	96.64	.	.	.	.
	sig.	0.0116	0.1887	0.9323		0.0093	0.0427	0.3613		.	.	.	.
SD02	%	.	.	.	.	0	2.98	0	97.02	.	.	.	.
	sig.	.	.	.	.	0.6127	0.0177	0.5924		.	.	.	.
LS2[g]	%	0	2.67	0	97.33	4.52	6.64	1.60	87.24	1.54	5.21	1.83	91.43
	sig.	0.8800	0.0924	0.5230		<0.0001	<0.0001	0.1147		0.0073	0.0026	0.1539	
LS3	%	0.92	8.67	0.45	89.96	0	10.27	0.23	89.50	0	15.25	0.08	84.67
	sig.	0.1800	<0.0001	0.4504		0.9185	<0.0001	0.409		0.9884	<0.0001	0.3828	
LS4	%	1.55	18.23	0.15	80.07	0.05	10.03	0.18	89.74	0	13.82	0	86.18
	sig.	0.002	<0.0001	0.4821		0.3769	<0.0001	0.4868		0.5382	<0.0001	0.6344	
LS5	%	1.84	19.77	0	78.40	0.52	8.43	0	91.05	0.09	10.35	0	89.55
	sig.	0.0001	<0.0001	0.856		0.0395	<0.0001	0.7646		0.2798	<0.0001	0.9084	
LS6	%	2.48	14.01	0	83.51	1.88	2.42	2.11	93.59	0.94	8.31	0	90.75
	sig.	<0.0001	<0.0001	0.837		0.0034	0.0286	0.0583		0.0084	<0.0001	0.8686	

Table 6 (continued) : Percent variation and significance of growth and phenological variables by test site for 26 trembling aspen provenances in NW Ontario

		Camp 45				Dog River				Kreikmann			
Variable		Blk[a]	Prov[b]	Blk * Prov	Error	Blk	Prov	Blk * Prov	Error	Blk	Prov	Blk * Prov	Error
LL28[h]	%	0	0.52	0	99.48	.	.	.	.	.	.	.	.
	sig.	0.9734	0.393	0.9156		.	.	.	.	.	.	.	.
LL31	%	3.79	0.07	0	96.14	.	.	.	.	4.71	15.33	6.93	73.03.
	sig.	0.0017	0.2976	0.6813		.	.	.	.	0.9023	0.2435	0.0981	
LL36	%	1.64	3.07	0	95.28	1.65	0	1.95	96.39	2.93	6.75	0.83	89.49
	sig.	0.0025	0.0107	0.4256		0.3276	0.85	0.4507		0.0995	0.0093	0.2788	
LL41	%	1.39	3.06	0	95.54	0	1.53	0	98.47	1.63	4.18	0.52	93.67
	sig.	0.0043	0.002	0.6956		0.2607	0.0506	0.7765		0.0228	0.0044	0.3866	
LL46	%	1.62	2.73	0	95.65	1	2.17	0	96.83	1.34	4.02	0	94.64
	sig.	0.0019	0.0031	0.7178		0.0035	0.0013	0.9453		0.0155	0.001	0.6733	
LL51	%	0.98	1.27	0	97.75	0.62	2.97	0	96.41	2.17	4.02	0	93.80
	sig.	0.0127	0.0504	0.7683		0.0277	0.0012	0.6890		0.0023	0.0012	0.6377	
LL56	%	1.94	1.02	0.23	96.81	0.47	2.69	0	96.84	.	.	.	.
	sig.	0.0033	0.1773	0.4756		0.0431	0.0027	0.6396		.	.	.	.
LL61	%	.	.	.	.	0.44	2.39	0.07	97.10	.	.	.	.
	sig.	.	.	.	.	0.0755	0.0089	0.04879		.	.	.	.

[a] Blk is test block

[b] Prov is provenance

[c] HT is height measured in cm in 1999 (99), 2000 (00), 2002 (02) and 2003 (03)

[d] % is the percent variation (intraclass correlation coefficient)

[e] sig. is the significance

[f] SD is stem diameter measured in mm in 1999 and 2000

[g] LS is the days to leaf stage 2, 3, 4, 5, 6 measured as the number of days from May 1, 2000

[h] LL is the leader length measured in mm on days 28, 31, 36, 41, 46, 51, 56 and 61 from May 1, 2000

2003 height variation among provenances accounted for 3.38 to 3.61 percent of the total. Error ranged from 78.4 to 99.48 percent.

Only the variables described above that demonstrated significant variation among provenances were included in further analysis.

Geographic Patterns

Variables that demonstrated a significant provenance variation were ranked by mean value to enable the general patterns of performance to be described across the study area (Table 7, 8, 9). Leaf flushing demonstrated the clearest geographic pattern, and the growth variables generally showed weaker trends (Table 7).

Leaf flushing expressed a clinal pattern from west to east. The earliest to flush were the most westerly sources 1, 2 and 3 (Table 7, Figure 1). Source 17, the most northern source, also flushed as early as the western sources at the three test sites. The northwest sources 8 through 11 varied in flushing rank as did the Thunder Bay area sources. The latest sources to flush were sources 13, just east of Thunder Bay and 24 and 25, the most eastern sources. Provenance ranks changed among the test sites for provenances 4, 18 and 22. Source 4 and 22 both flushed earlier at C45 than DR and KRM. Source 18 flushed earlier at KRM than the two forest sites.

Height growth did not have as clear a pattern as the phenology variables and clear rank changes between tests were demonstrated (Table 8, Figure 1). The best performance at C45 was shown by sources 1 and 8 in the west and northwest respectively, while 8 and 9 (both in the northwest) had the greatest height at DR. Source 1, among the best at C45 and also KRM ranked poorly at DR. Source 23, near Thunder Bay, performed well at DR but not as well at the other sites. Sources 16 and 22 (east of

C45) had less growth on average in the field tests but preformed better at KRM the southern test. Source 2, in the west, preformed poorly at both KRM and DR, the two sites nearest the source, but improved at C45, the most northerly site. Source 25 consistently ranked poorly in height at each test.

The northern (17-18) and northwest (8-11) sources demonstrated greater stem diameter growth in general over the most southwest (1-3) and eastern sources (24-25) (Table 8, Figure 1). Sources west and north of Thunder Bay varied in rank and did not demonstrate a clear pattern of growth.

Leader growth was variable across the study area (Table 9 , Figure 1). Source 17, the most northern source, and sources 19 and 20 near Thunder Bay, generally demonstrated greater length growth at each of the test sites. However, source 13, also grew poorly at each site. Source 18, which is north of C45, performed well at the forest sites but at the poorly at the field site KRM. The northwestern sources 8-11 ranked generally greater at the more local DR test site than the other two sites. The western sources (1-3) generally ranked higher than the sources local to Thunder Bay for leader length growth.

Relationship to Climate Variables

Variables demonstrating significant provenance variation in the ANOVA results were subjected to simple linear regression (Table 10). The leaf flushing data showed the strongest significant ($p \leq 0.05$) linear relationships to a climate variable with coefficient of determination (r^2) values ranging from 0.3235 to 0.5769 and significance values less than 0.0024. Height measures at C45 related to climate significantly for three of the four variables. The r^2 values for significant C45 height relationships ranged from 0.1537 to

Table 7: Leaf flush mean and rank data by provenance for 26 provenances of trembling aspen in NW Ontario.

	Dog River										Camp 45								Kriekmann									
prov[a]	LS2[b]	LS2 Rank	LS3[c]	LS3 Rank	LS4[d]	LS4 Rank	LS5[e]	LS5 Rank	LS6[f]	LS6 Rank	LS3	LS3 Rank	LS4	LS4 Rank	LS5	LS5 Rank	LS6	LS6 Rank	LS2	LS2 Rank	LS3	LS3 Rank	LS4	LS4 Rank	LS5	LS5 Rank	LS6	LS6 Rank
1	20.5	1	27.0	1	30.9	1	35.3	1	40.5	1	18.6	1	18.7	1	23.5	1	29.7	1	14.9	1	20.6	1	24.9	1	29.4	1	35.1	1
2	20.9	2	27.4	2	32.0	3	36.0	3	41.4	2	18.7	2	19.8	2	24.3	2	31.4	2	19.3	10	24.3	4	28.8	4	33.0	4	38.9	6
3	22.0	7	28.3	3	31.9	2	35.6	2	41.7	5	19.5	3	21.6	3	26.7	3	32.5	3	16.7	2	23.0	2	27.3	2	31.7	2	37.1	2
4	24.0	19	31.0	18	34.7	20	38.2	20	42.8	20	20.6	5	25.0	8	29.8	10	35.4	13	21.8	25	28.1	23	31.4	23	35.2	23	40.3	23
5	24.0	20	31.6	22	35.4	25	38.9	25	43.6	25	23.1	21	26.7	20	31.8	24	36.8	21	19.9	15	27.6	19	31.0	19	34.6	19	39.9	17
6	22.0	8	29.8	9	33.7	10	37.3	8	42.1	11	22.2	14	25.4	15	30.4	15	36.2	15	17.6	3	27.4	16	30.5	15	34.3	16	39.5	13
7	23.2	13	30.3	12	33.8	11	37.6	14	42.4	14	20.7	6	24.3	6	29.3	8	34.8	5	20.4	18	26.5	10	29.7	6	34.1	11	39.2	10
8	22.4	9	29.4	6	32.9	6	36.9	6	42.3	13	21.4	10	25.4	13	30.0	13	35.3	11	18.5	5	26.8	12	30.0	10	33.7	8	39.2	9
9	24.1	21	30.6	15	34.0	13	37.5	10	42.3	12	22.5	19	26.5	19	30.6	16	36.0	14	20.2	17	27.9	22	31.5	24	35.3	24	40.6	24
10	23.7	17	30.7	16	34.7	19	37.7	17	42.6	16	22.2	16	25.8	16	30.3	14	36.5	20	18.0	4	26.7	11	30.0	11	34.2	13	39.6	14
11	23.8	18	31.5	21	35.2	22	38.5	22	43.5	23	22.0	13	25.4	14	31.2	20	36.3	18	18.8	7	26.0	6	29.8	9	33.6	5	39.7	15
12	21.7	6	29.5	7	33.5	8	37.3	9	41.5	3	21.1	8	24.6	7	29.2	7	35.0	7	19.3	9	26.2	7	29.7	7	33.9	9	39.4	11
13	26.1	26	32.2	26	36.1	26	39.4	26	44.4	26	24.3	25	27.9	25	32.6	26	37.7	24	21.7	24	27.8	21	31.3	22	35.4	25	40.7	25
14	25.9	25	31.7	25	35.3	24	38.7	24	43.3	22	23.4	22	27.1	23	31.1	19	37.3	22	21.5	23	28.3	25	31.2	21	34.9	21	40.3	22
15	24.6	22	30.7	17	34.4	18	37.9	19	42.7	19	21.2	9	25.1	10	29.4	9	35.2	10	19.1	8	25.9	5	29.3	5	33.6	6	39.1	8
16	23.3	15	31.0	19	34.3	17	37.7	16	42.6	18	22.2	15	26.2	17	30.7	17	36.3	17	20.7	20	27.7	20	30.8	18	34.2	12	39.4	12
17	21.4	3	29.0	4	32.2	4	36.1	4	41.6	4	20.9	7	23.6	4	29.1	6	34.9	6	18.7	6	23.7	3	27.3	3	31.8	3	37.5	3
18	23.3	14	29.6	8	33.6	9	37.6	12	42.1	9	22.3	17	25.0	9	30.0	12	35.0	8	21.3	22	27.5	17	30.7	17	34.5	18	40.0	18
19	21.7	5	29.3	5	32.8	5	36.6	5	41.7	6	19.8	4	24.0	5	28.5	4	35.1	9	19.4	11	26.5	9	30.1	12	34.1	10	38.9	7
20	23.2	11	30.4	13	34.2	16	37.6	13	42.1	10	21.7	11	25.1	11	29.9	11	35.4	12	19.8	14	26.4	8	29.8	8	33.6	7	38.8	5
21	21.5	4	29.8	10	33.3	7	37.0	7	42.5	15	21.8	12	25.3	12	29.1	5	34.6	4	19.7	13	26.9	13	30.4	13	34.2	15	39.8	16
22	22.4	10	30.2	11	33.9	12	37.9	18	42.6	17	23.6	24	26.9	22	31.4	22	37.4	23	19.5	12	27.4	15	30.6	16	34.2	14	38.6	4
23	23.6	16	31.0	20	34.2	15	37.7	15	41.9	8	24.5	26	28.0	26	32.3	25	38.0	26	20.5	19	27.4	14	31.0	20	34.8	20	40.2	21
24	24.9	24	31.6	23	35.3	23	38.6	23	43.2	21	23.5	23	26.9	21	31.7	23	37.7	25	21.3	21	28.3	24	31.7	25	35.2	22	40.1	19
25	24.9	23	31.6	24	35.0	21	38.3	21	43.6	24	23.0	20	27.4	24	31.4	21	36.5	19	22.7	26	28.5	26	32.3	26	35.8	26	41.5	26
26	23.2	12	30.4	14	34.1	14	37.5	11	41.8	7	22.3	18	26.4	18	30.8	18	36.3	16	20.2	16	27.5	18	30.5	14	34.4	17	40.2	20

[a] Prov is the provenance identification

[b] LS2 is the variables days to reach leaf stage 2

[c] LS3 is the variable days to reach leaf stage 3

[d] LS4 is the variable days to reach leaf stage 4

[e] LS5 is the variable days to reach leaf stage 5

[f] LS6 is the variable days to reach leaf stage 6

Table 8: Height and stem diameter mean and rank values by provenance for 26 provenances of trembling aspen in NW Ontario.

	HEIGHT														Stem Diameter							
	Camp 45								Dog River				Kriekmann		Dog River						Kriekmann	
prov[a]	1999	1999 Rank	2000	2000 Rank	2002	2002 Rank	2003	2003 Rank	2002	2002 Rank	2003	2003 Rank	1999	1999 Rank	1999	1999 Rank	2000	2000 Rank	2002	2002 Rank	1999	1999 Rank
1	103.20	2	117.71	3	152.78	3	167.05	3	106.97	20	116.22	17	73.38	5	9.9	18	11.6	18	14.5	21	9.2	19
2	93.43	11	107.55	17	136.87	15	151.53	15	94.60	26	102.48	26	66.26	24	8.8	26	10.4	26	13.3	25	8.9	26
3	93.77	9	106.41	19	140.97	12	157.80	8	117.00	8	125.59	8	72.33	11	9.5	23	11.4	22	14.7	17	9.9	3
4	92.59	13	109.26	14	146.48	8	157.48	9	112.55	11	121.23	12	69.00	21	10.5	3	12.3	7	16.4	5	9.1	22
5	88.34	21	105.22	21	129.39	24	140.10	24	111.83	13	123.00	10	69.35	20	9.9	16	11.9	12	15.1	11	9.5	12
6	96.91	4	114.13	6	143.50	11	155.00	12	114.04	9	123.96	9	67.29	23	10.4	6	12.6	5	15.0	13	9.2	18
7	89.85	17	108.92	16	144.33	10	154.78	13	107.12	19	114.03	20	70.66	18	9.9	17	11.5	20	14.2	23	9.0	24
8	103.48	1	126.73	1	164.32	1	174.36	2	120.74	4	132.87	2	76.94	1	9.9	15	11.8	14	15.5	8	9.6	8
9	93.92	8	111.90	11	151.61	4	161.25	6	130.24	1	138.08	1	73.24	6	10.7	1	12.9	1	16.9	1	9.8	5
10	87.20	22	98.60	25	133.09	22	146.64	20	118.86	5	127.36	6	75.14	3	10.3	7	12.2	8	16.4	4	10.0	1
11	88.98	18	107.20	18	138.00	14	146.85	18	118.65	6	126.65	7	71.92	13	10.0	12	11.8	13	14.9	14	9.9	2
12	93.41	12	117.07	4	159.66	2	174.86	1	103.57	23	112.70	22	74.36	4	9.7	21	11.6	19	13.8	24	9.8	6
13	94.54	6	113.89	7	134.23	21	146.77	19	112.59	10	119.34	14	63.53	25	10.2	10	12.0	10	15.1	12	9.0	25
14	93.44	10	110.44	12	151.54	5	161.82	5	108.02	17	116.05	18	70.85	17	9.8	19	11.6	17	14.6	19	9.5	10
15	91.77	16	113.29	9	145.92	9	156.47	10	117.27	7	128.24	5	76.76	2	10.5	4	12.6	4	16.6	3	9.6	9
16	86.29	24	100.55	24	125.74	25	138.91	25	105.39	22	113.97	21	73.00	7	9.1	25	11.3	23	14.6	20	9.7	7
17	88.46	20	105.39	20	136.30	18	151.77	14	121.37	3	130.26	4	72.88	9	10.4	5	12.5	6	15.9	7	9.4	13
18	86.78	23	108.94	15	138.15	13	155.38	11	107.53	18	117.68	15	70.20	19	10.7	2	12.6	3	16.0	6	9.2	17
19	96.44	5	114.31	5	146.53	7	162.56	4	108.21	16	115.34	19	71.50	15	10.1	11	11.9	11	14.4	22	9.1	23
20	94.29	7	113.56	8	136.87	16	147.30	17	109.11	15	116.51	16	71.93	12	9.8	20	11.3	24	14.8	16	9.1	21
21	97.79	3	119.09	2	151.29	6	159.00	7	105.41	21	111.81	23	72.91	8	10.0	14	11.7	16	14.9	15	9.4	14
22	88.59	19	102.30	23	132.32	23	146.50	21	102.97	24	107.38	24	72.54	10	10.0	13	11.8	15	14.6	18	9.8	4
23	92.51	14	109.52	13	134.44	20	145.97	22	121.64	2	130.38	3	68.56	22	10.3	8	12.7	2	16.7	2	9.5	11
24	85.74	25	104.29	22	134.88	19	145.20	23	109.86	14	120.11	13	71.89	14	10.2	9	12.2	9	15.3	10	9.4	15
25	80.47	26	96.41	26	125.27	26	133.73	26	97.51	25	103.27	25	62.65	26	9.4	24	11.0	25	13.2	26	9.1	20
26	92.28	15	112.38	10	136.86	17	149.39	16	111.88	12	121.72	11	71.17	16	9.5	22	11.5	21	15.4	9	9.3	16

[a] Prov is the provenance identification

Table 9: Leader length measured from the number of days from May 1, 2000, mean and rank values by provenance for 26 provenances of trembling aspen from NW Ontario.

	Leader Length																							
	Camp 45								Dog River								Kriekmann							
Prov[a]	Day 36	Day 36 Rank	Day 41	Day 41 Rank	Day 46	Day 46 Rank	Day 51	Day 51 Rank	Day 46	Day 46 Rank	Day 51	Day 51 Rank	Day 56	Day 56 Rank	Day 61	Day 61 Rank	Day 36	Day 36 Rank	Day 41	Day 41 Rank	Day 46	Day 46 Rank	Day 51	Day 51 Rank
1	61.0	6	69.9	4	80.7	12	101.0	15	39.4	16	53.2	14	71.8	14	81.7	19	43.0	5	53.8	1	64.9	5	78.7	5
2	61.4	5	68.0	6	85.2	8	104.3	9	40.3	13	49.2	21	65.3	22	77.0	22	41.0	6	41.3	13	52.4	14	58.2	22
3	58.4	7	67.9	7	85.4	7	100.5	16	44.8	6	59.1	6	78.3	5	92.3	7	38.8	7	50.6	4	66.5	3	84.2	1
4	56.9	11	67.6	8	86.4	5	108.0	5	38.5	17	51.5	17	65.9	21	77.8	21	33.1	17	37.8	21	49.5	21	62.5	19
5	48.8	22	58.5	18	75.2	20	96.1	20	32.4	26	45.3	26	62.3	24	78.3	20	34.3	14	39.0	19	51.6	16	69.4	10
6	50.6	18	57.4	20	70.1	22	87.1	24	45.3	4	59.8	5	75.5	8	89.4	8	36.2	11	36.7	23	48.7	23	58.0	23
7	55.8	13	63.7	13	82.9	9	104.1	10	39.7	14	52.7	15	70.0	17	86.8	15	32.4	19	43.2	11	54.4	12	70.0	9
8	51.6	16	60.4	16	80.5	14	107.2	6	37.4	22	48.0	22	66.6	20	84.0	18	43.0	4	48.6	5	65.9	4	82.7	4
9	53.8	14	65.1	11	82.9	10	102.8	12	43.8	8	62.4	4	84.9	3	103.6	3	34.8	13	40.6	16	49.9	20	64.8	17
10	47.8	23	55.9	23	68.1	24	86.5	25	40.3	12	55.6	11	72.8	12	88.3	13	30.9	21	36.6	24	47.9	24	57.0	24
11	47.6	24	56.5	21	77.7	18	96.9	19	43.0	9	54.7	12	75.9	7	88.2	14	24.5	26	37.0	22	48.8	22	61.7	20
12	63.9	2	69.8	5	85.9	6	105.5	7	47.0	2	65.8	2	96.6	1	108.1	2	51.3	1	52.5	3	66.9	2	82.9	3
13	45.4	26	51.5	25	64.5	26	85.8	26	36.8	23	47.0	24	59.5	26	74.7	26	28.6	25	32.4	26	42.2	25	52.3	26
14	51.4	17	61.6	14	79.0	16	104.9	8	37.6	19	50.1	20	70.5	15	88.7	11	32.8	18	39.6	17	54.9	11	71.8	8
15	57.9	8	65.3	10	82.7	11	103.9	11	37.5	21	51.3	18	71.8	13	88.6	12	37.9	8	45.3	8	56.7	8	69.1	11
16	49.2	21	56.5	22	69.5	23	89.9	22	38.3	18	51.2	19	69.4	18	85.2	17	33.6	15	38.8	20	51.5	17	65.7	16
17	63.4	3	72.7	2	91.9	2	115.6	2	49.9	1	68.6	1	90.8	2	108.4	1	45.4	2	52.7	2	69.4	1	83.9	2
18	57.8	9	64.3	12	80.3	15	102.6	13	43.0	10	58.8	8	78.2	6	94.8	6	29.5	24	33.8	25	41.9	26	53.0	25
19	62.4	4	71.1	3	86.6	4	109.2	4	44.9	5	58.9	7	75.3	9	89.1	9	32.3	20	44.6	9	58.3	7	72.6	7
20	57.4	10	66.8	9	88.8	3	109.4	3	45.4	3	62.6	3	83.2	4	100.1	4	36.7	10	45.3	7	61.6	6	76.1	6
21	51.8	15	60.8	15	78.2	17	99.9	17	44.3	7	57.2	10	70.3	16	85.6	16	37.6	9	46.2	6	55.3	10	66.3	15
22	49.5	19	53.6	24	70.3	21	91.1	21	37.6	20	51.9	16	66.7	19	76.4	24	30.8	22	40.7	15	50.5	18	66.4	14
23	46.9	25	49.5	26	65.1	25	87.1	23	39.6	15	54.3	13	74.8	10	88.8	10	35.4	12	42.7	12	54.3	13	68.3	13
24	56.4	12	59.3	17	80.7	13	102.4	14	33.4	25	45.5	25	60.5	25	75.0	25	30.1	23	40.9	14	51.7	15	64.2	18
25	49.2	20	58.5	19	76.3	19	98.9	18	36.6	24	47.5	23	64.2	23	76.9	23	43.1	3	39.3	18	50.5	19	61.6	21
26	64.9	1	73.1	1	93.9	1	117.4	1	40.5	11	57.5	9	74.7	11	95.7	5	33.1	16	43.5	10	55.6	9	68.8	12

[a] Prov is the provenance identification

0.2260. C45 leader length variables were significant with r^2 values from 0.1800 to 0.2143. KRM leader length variables had lower r^2 values than leader length at C45, and only LL41 was significant (p=0.0397) with an r^2 value of 0.1647. DR leader length variables, as well as the height and stem diameter variables, were all significantly related to climate variables and had slightly higher r^2 values than the other sites. The DR r^2 values ranged between 0.2208 and 0.2542 for leader length, were 0.2918 and 0.3279 for height 2002 and height 2003 respectively, and ranged from 0.1873 to 0.3108 for stem diameter.

Mean temperature during the growing season (mnt3) was the most common predictor of the variables with r^2 values between 0.1537 and 0.5769. Precipitation variables appeared as the best predictors (r^2 between 0.1691 and 0.2542) in 4 of the 31 significant relationships.

The climate variables explained less variation in the C45 height data than at KRM or DR. Height in 1999 at KRM and 2002 and 2003 at DR were best predicted by growing degree days in period 2 (the first six weeks of the growing season) with r^2 values ranging from 0.2665 to 0.3279. C45 height was best predicted by precipitation in the entire growing season (Period 3) for 1999 (r^2 0.1691), by June maximum temperature for 2002 (r^2 0.1537), and by the range of temperature during the entire growing season (Period 3) for 2003 (r^2 0.2260).

Stem diameter measured at DR demonstrated that as age increased the most predictive climate variable moved to earlier in the year. Stem diameter in 1999 was best predicted (r^2 0.1873) by precipitation in the latter part of the growing season (period 4). In 2000, the length of the entire growing season was the best predictor (r^2 0.3108);

finally in 2002 March mean temperature best related to height at DR and had an r^2 value of 0.2700.

August precipitation best predicted (r^2 0.2542) the last leader elongation measurement at DR (LL61). August maximum temperature predicted the elongation measure at C45 day 36 (r^2 0.1800) and day 41 (r^2 0.2143). For the remaining leader measurements the range of temperature in period three and the mean temperature in period three were the best predictor with r^2 values ranging from 0.1647 at KRM LL41 up to 0.2479 for LL46 at DR.

Leaf flushing (LS2-LS6) demonstrated the strongest relationships and greatest consistency to climate variables compared to the other variables studied. Different expressions of mean temperature during the growing season (Period 3) explained between 32 to 57 percent of the variation in leaf flushing. May and June mean temperature best predicted leaf stage at C45 with r^2 values ranging from 0.4714 to 0.5769. KRM and DR stage two was best predicted by June mean temperature (r^2 0.4704) and August maximum temperature (r^2 0.4517) respectively. The stages three through six at both KRM and DR were predicted by mean temperature in the growing season with r^2 values between 0.3235 and 0.5598.

The simple linear regressions resulted in four variables that demonstrated no significant relationship to a climate variable. Three of the 4 were leader length measurements at KRM (LL36, LL46, LL51) and last was height in 2000 at C45. These variables were eliminated from further analysis as no relationship was significantly demonstrated.

Table 10: Simple linear regression results of growth and phenological variables from 26 trembling aspen provenances in NW Ontario variables to climate data

	Camp 45			Dog River			Kreikmann		
Variables	Climate Variable[a]	r^2	Signif.[b]	Climate Variable[a]	r^2	Signif.	Climate Variable[a]	r^2	Signif.
HT99[c]	prec3	0.1691	0.0369	.[d]	.	.	gdd2	0.2665	0.0069
HT00	rngt3	0.0836	0.1519	.	.	.	.	.	.
HT02	junmaxt	0.1537	0.0476	gdd2	0.2918	0.0044	.	.	.
HT03	rngt3	0.2260	0.0141	gdd2	0.3279	0.0022	.	.	.
SD99[e]	.	.	.	prec4	0.1873	0.0272	.	.	.
SD00	.	.	.	grslng	0.3108	0.0031	.	.	.
SD02	.	.	.	marmnt	0.2700	0.0065	.	.	.
LS2[f]	.	.	.	augmaxt	0.4517	0.0002	junmnt	0.4704	0.0001
LS3	junmnt	0.5145	<0.0001	mnt3	0.4242	0.0003	mnt3	0.5456	0.0001
LS4	junmnt	0.5769	<0.0001	mnt3	0.3684	0.0010	mnt3	0.5598	<0.0001
LS5	maymnt	0.4714	<0.0001	mnt3	0.3613	0.0012	mnt3	0.5369	<0.0001
LS6	junmnt	0.5226	<0.0001	mnt3	0.3235	0.0024	mnt3	0.4610	0.0001
LL28[g]	.	.	.	.	.	.	.	.	.
LL31	.	.	.	.	.	.	.	.	.
LL36	augmaxt	0.1800	0.0307	.	.	.	augmaxt	0.1185	0.0851
LL41	augmaxt	0.2143	0.0172	.	.	.	mnt3	0.1647	0.0397
LL46	febprec	0.2107	0.0183	rngt3	0.2479	0.0096	mnt3	0.1457	0.0544
LL51	.	.	.	rngt3	0.2208	0.0154	mnt3	0.0878	0.1416
LL56	.	.	.	rngt3	0.2454	0.0101	.	.	.
LL61	.	.	.	augprec	0.2542	0.0086	.	.	.

[a] Climate data: prec3 is precipitation in period 3, rngt3 is the range of temperature in period 3, junmaxt is June maximum temperature, junmnt is June mean temperature, maymnt is May mean temperature, augmaxt is August maximum temperature, febprec is February precipitation, gdd2 is growing degree days in period 2, prec4 is precipitation in period 4, grslng is the growing season length, marmnt is March mean temperature, augprec is August precipitation, Period 2 is the first six weeks of the growing season, Period 3 is the entire growing season and Period 4 is the latter part of the growing season calculated as Period 3 minus Period 2.

[b] Signif. is the significance value

[c] HT is height measured in 1999 (99), 2000 (00), 2002 (02) and 2003 (03)

[d] Growth and phenology variables that showed no significant ($p \leq 0.05$) variation among provenances from the ANOVA results were not included in simple linear regression analysis

[e] SD is stem diameter measured in 1999 (99) and 2000 (00)

[f] LS are the days to leaf stages 2, 3, 4, 5, 6 measured

[g] LL is the leader length measured on days 28, 31, 36, 41, 46, 51, 56 and 61 from May 1, 2000

PATTERNS OF ADAPTIVE VARIATION

Principal Component Correlation Matrix

Generally, measures within tests were strongly and positively correlated for the growth and phenological variables as shown in the PCA analysis correlation results (Table 11). Height measures within tests were strong and positively correlated. C45 correlation between height measures was strong between the older year measurements (0.96), but weaker (0.76) between 1999 and 2002 and also 1999 and 2003. DR had a strong correlation of 0.98 between 2002 and 2003 height. Leaf flush and leader length correlations within sites between the different stages generally were greater than 0.80. The correlation value tended to be the higher between adjacent stages or days of measurement at both C45 and DR. Stem diameter at DR related best between the 1999 and 2002 data with a correlation of 0.93.

The test differences noted in the 3-way ANOVA (Table 5) are demonstrated by the general pattern of weak to moderate positive correlation among height and leader length variables at different sites. For instance, C45 height to DR height was weakly correlated with values ranging from 0.17 to 0.24. KRM height 1999 correlated with C45 height 2003 the strongest with a value of 0.51. Leader length between tests generally ranged from 0.40 to 0.55. Leaf flushing however was more strongly correlated between sites with correlations ranging from 0.58 to 0.91.

Within site correlations between leader length and leaf flushing at each site were negative and ranged from -0.22 to -0.74 in value (Table 11). As well, leader length to leaf flushing correlations between test sites were also negative and moderate correlations in general. Height to leader length correlations within the same site were positive and weak to moderately strong while between sites the relationship was weak and positive in all cases, but between C45 leaders lengths and DR height. Leader length to diameter correlations between different sites were weak and negative but leaf flushing to diameter was positive and weak.

Correlations of the cold hardiness variables with the growth and phenology values tended to be weak, and with the direction of the relationship varying (Table 11). Height at both forest tests was very weakly correlated the CF and CVS data but KRM height was positively related to the October CF -33°C at 0.55 and CF critical temperature at 0.59. KRM height to the VCF data was not as strong but remained positive.

Leader length correlations were consistently similar in magnitude (-0.05 to -0.43) with September CF data, but positive with both CF and CVS October variables (0.14 to 0.43). Leaf flushing correlations were moderately negative and consistent (-0.10 to -0.47) with all cold hardiness variables except September CF at -10°C where the relationship was positive at all three sites and values ranged from 0.20 to 0.31).

Principal Component Analysis

A total of 39 trait variables, that demonstrated significant variation among provenances, as well as a significant relationship to climate data, were retained in the PCA analysis. The 39 variables included 17 of the original 33 growth variables, 14 of the 15 phenological variables, and eight of the 10 cold hardiness variables from Weng (2002). Cold hardiness data included the mean percent reduction in the Fv/Fm ratio for chlorophyll florescence and percent cambial damage assessed by visual scoring

Table 11: Principal component analysis correlation matrix of growth, phenological and cold hardiness (chlorophyll florescence and cambium visual scoring) for trembling aspen provenances in NW Ontario

	CHT99	CHT02	CHT03	CLS3	CLS4	CLS5	CLS6	CLL36	CLL41	CLL46	DHT02	DHT03	DSD99	DSD00	DSD02	DLS2	DLS3	DLS4	DLS5	DLS6
C[a]HT[b]99	1																			
CHT02	0.76	1.00																		
CHT03	0.76	0.96	1.00																	
CLS[c]3	-0.42	-0.39	-0.49	1.00																
CLS4	-0.43	-0.30	-0.42	0.93	1.00															
CLS5	-0.46	-0.35	-0.46	0.92	0.98	1.00														
CLS6	-0.46	-0.35	-0.45	0.91	0.97	0.98	1.00													
CLL[d]36	0.22	0.34	0.47	-0.68	-0.61	-0.61	-0.59	1.00												
CLL41	0.26	0.40	0.49	-0.74	-0.63	-0.63	-0.63	0.94	1.00											
CLL46	0.15	0.35	0.39	-0.60	-0.46	-0.45	-0.46	0.88	0.93	1.00										
D[e]HT02	0.19	0.21	0.17	0.19	0.23	0.28	0.25	-0.17	-0.09	-0.03	1.00									
DHT03	0.22	0.24	0.21	0.15	0.19	0.25	0.21	-0.11	-0.04	0.01	0.98	1.00								
DSD[f]99	0.04	0.21	0.19	0.30	0.31	0.35	0.33	-0.13	-0.12	-0.11	0.63	0.61	1.00							
DSD00	0.01	0.13	0.12	0.37	0.38	0.41	0.40	-0.17	-0.19	-0.21	0.73	0.73	0.93	1.00						
DSD02	0.04	0.07	0.05	0.31	0.33	0.35	0.33	-0.15	-0.13	-0.10	0.82	0.82	0.77	0.86	1.00					
DLS2	-0.45	-0.30	-0.42	0.72	0.75	0.74	0.72	-0.53	-0.48	-0.35	0.19	0.17	0.26	0.24	0.29	1.00				
DLS3	-0.51	-0.38	-0.52	0.83	0.91	0.91	0.89	-0.63	-0.59	-0.42	0.18	0.15	0.26	0.28	0.26	0.90	1.00			
DLS4	-0.51	-0.39	-0.53	0.80	0.85	0.86	0.84	-0.61	-0.59	-0.43	0.08	0.06	0.22	0.21	0.20	0.90	0.97	1.00		
DLS5	-0.48	-0.34	-0.47	0.80	0.84	0.85	0.83	-0.61	-0.60	-0.44	0.03	0.01	0.24	0.21	0.18	0.88	0.95	0.99	1.00	
DLS6	-0.46	-0.37	-0.51	0.68	0.72	0.75	0.70	-0.69	-0.62	-0.46	0.02	-0.01	0.14	0.08	0.05	0.84	0.88	0.90	0.90	1.00
DLL46	0.23	0.29	0.38	-0.40	-0.35	-0.32	-0.32	0.46	0.48	0.42	0.19	0.14	0.13	0.12	0.01	-0.57	-0.48	-0.52	-0.57	-0.57
DLL51	0.15	0.26	0.35	-0.28	-0.23	-0.20	-0.21	0.49	0.51	0.44	0.29	0.25	0.24	0.26	0.17	-0.48	-0.38	-0.44	-0.49	-0.58
DLL56	0.11	0.29	0.37	-0.25	-0.21	-0.18	-0.19	0.47	0.50	0.45	0.37	0.35	0.22	0.27	0.20	-0.40	-0.34	-0.40	-0.45	-0.57
DLL61	0.09	0.32	0.38	-0.15	-0.09	-0.06	-0.09	0.47	0.50	0.48	0.40	0.40	0.22	0.28	0.25	-0.27	-0.22	-0.29	-0.34	-0.47
K[g]HT99	0.29	0.49	0.51	-0.26	-0.18	-0.18	-0.16	0.26	0.28	0.28	0.39	0.43	0.19	0.24	0.35	-0.29	-0.25	-0.31	-0.31	-0.37
KLS2	-0.55	-0.34	-0.42	0.59	0.69	0.65	0.64	-0.26	-0.27	-0.11	-0.22	-0.24	0.05	0.02	0.03	0.69	0.72	0.70	0.72	0.64
KLS3	-0.42	-0.23	-0.35	0.76	0.89	0.85	0.85	-0.49	-0.49	-0.33	0.00	-0.02	0.20	0.23	0.19	0.69	0.82	0.81	0.82	0.69
KLS4	-0.44	-0.27	-0.39	0.74	0.86	0.81	0.82	-0.51	-0.51	-0.35	-0.04	-0.07	0.15	0.18	0.14	0.68	0.81	0.81	0.81	0.70
KLS5	-0.44	-0.24	-0.36	0.73	0.85	0.80	0.81	-0.47	-0.48	-0.33	-0.01	-0.04	0.20	0.21	0.17	0.71	0.81	0.81	0.81	0.70
KLS6	-0.45	-0.24	-0.37	0.69	0.81	0.76	0.75	-0.46	-0.44	-0.28	0.02	0.00	0.15	0.17	0.16	0.71	0.79	0.80	0.78	0.69
KLL41	0.45	0.50	0.55	-0.57	-0.56	-0.57	-0.57	0.61	0.60	0.55	0.04	0.07	-0.19	-0.18	-0.17	-0.64	-0.64	-0.73	-0.72	-0.69
SCF-10 [h]	-0.12	0.00	0.02	0.20	0.21	0.21	0.22	-0.27	-0.25	-0.30	-0.05	-0.01	-0.03	0.06	-0.01	0.22	0.22	0.23	0.29	0.27
SCF-15	0.27	0.26	0.33	-0.39	-0.47	-0.44	-0.46	-0.04	0.02	-0.12	0.03	0.06	0.04	0.01	-0.08	-0.27	-0.42	-0.36	-0.29	-0.20
SCF-20	0.06	0.08	0.15	-0.26	-0.27	-0.27	-0.28	-0.10	-0.03	-0.14	-0.16	-0.15	-0.16	-0.20	-0.15	-0.17	-0.28	-0.24	-0.17	-0.12
SCFCT [i]	0.00	-0.02	0.04	-0.27	-0.26	-0.24	-0.27	-0.15	-0.03	-0.15	-0.15	-0.13	-0.24	-0.24	-0.18	-0.11	-0.21	-0.16	-0.11	-0.05
OCF-33 [j]	0.14	0.30	0.31	-0.36	-0.31	-0.39	-0.36	0.35	0.37	0.31	-0.09	-0.05	-0.13	-0.08	-0.02	-0.33	-0.37	-0.38	-0.42	-0.39
OCFCT [k]	0.00	0.18	0.18	-0.32	-0.27	-0.33	-0.32	0.30	0.33	0.34	-0.17	-0.15	-0.24	-0.25	-0.11	-0.21	-0.27	-0.29	-0.32	-0.23
OVS-33 [l]	0.07	0.09	0.15	-0.44	-0.45	-0.42	-0.42	0.32	0.34	0.35	0.03	0.07	0.09	0.01	0.12	-0.35	-0.46	-0.43	-0.42	-0.33
OVSCT [m]	-0.06	0.05	0.09	-0.45	-0.44	-0.43	-0.43	0.29	0.32	0.34	-0.02	0.03	0.01	-0.07	0.06	-0.29	-0.42	-0.39	-0.38	-0.28

Table 11(continued): Principal component analysis correlation matrix of growth, phenological and cold hardiness (chlorophyll florescence and cambium visual scoring) for trembling aspen provenances in NW Ontario

	DLL46	DLL51	DLL56	DLL61	KHT99	KLS2	KLS3	KLS4	KLS5	KLS6	KLL41	SCF-10	SCF-15	SCF-20	SCFCT
DLL46	1.00														
DLL51	0.94	1.00													
DLL56	0.87	0.96	1.00												
DLL61	0.80	0.91	0.96	1.00											
KHT99	0.21	0.31	0.40	0.42	1.00										
KLS2	-0.37	-0.33	-0.33	-0.21	-0.49	1.00									
KLS3	-0.38	-0.31	-0.33	-0.19	-0.28	0.82	1.00								
KLS4	-0.40	-0.35	-0.37	-0.25	-0.38	0.84	0.98	1.00							
KLS5	-0.36	-0.31	-0.34	-0.21	-0.39	0.85	0.97	0.99	1.00						
KLS6	-0.32	-0.29	-0.29	-0.15	-0.42	0.84	0.92	0.95	0.96	1.00					
KLL41	0.40	0.43	0.47	0.43	0.52	-0.58	-0.69	-0.71	-0.70	-0.70	1.00				
SCF-10	-0.43	-0.39	-0.34	-0.28	-0.20	0.27	0.30	0.31	0.30	0.24	-0.18	1.00			
SCF-15	-0.06	-0.14	-0.08	-0.15	-0.01	-0.31	-0.32	-0.27	-0.28	-0.28	-0.05	0.38	1.00		
SCF-20	-0.31	-0.32	-0.29	-0.33	0.03	-0.14	-0.10	-0.10	-0.12	-0.18	-0.12	0.44	0.69	1.00	
SCFCT	-0.28	-0.31	-0.26	-0.30	-0.03	-0.12	-0.07	-0.06	-0.10	-0.14	-0.23	0.44	0.71	0.95	1.00
OCF-33	0.38	0.36	0.40	0.41	0.55	-0.29	-0.29	-0.33	-0.34	-0.28	0.43	-0.38	-0.17	-0.28	-0.27
OCFCT	0.21	0.19	0.25	0.27	0.59	-0.19	-0.28	-0.32	-0.33	-0.29	0.43	-0.43	-0.21	-0.19	-0.19
OVS-33	0.33	0.26	0.28	0.26	0.26	-0.23	-0.37	-0.39	-0.36	-0.32	0.20	-0.27	0.23	0.04	0.02
OVSCT	0.17	0.14	0.19	0.18	0.40	-0.25	-0.37	-0.39	-0.37	-0.34	0.25	-0.24	0.24	0.14	0.11

[a] C is Camp 45 test

[b] HT is height in 1999(99), 2000(00) and 2003(03) and is by test site

[c] LS is the leaf flushing stages 2 though 6

[d] LL is leader length measured days 36, 41, 46, 51, 56 or 61 from May 1, 2000

[e] D is the Dog River test

[f] SD is stem diameter measured in 1999(99), 2000(00) and 2003(03)

[g] K is the Kreikmann test

[h] SCF at -10, -15 and -20 degrees Celsius is September chlorophyll florescence damage

[i] SCFCT is the September chlorophyll florescence critical temperature

[j] OCF at -33 degrees Celsius is October chlorophyll florescence damage

[k] OCFCT is the October chlorophyll florescence critical temperature

[l] OVSat -33 degrees Celsius is the October cambium visual scoring damage

[m] OVSCT is the October cambium visual scoring critical temperature

The PCA reduced the number of dimensions by summarizing variation from 39 variables into uncorrelated principal component (PC) axes. The first four PC axes were important in expressing a total of 73.8 percent of the total variation (Table 12). The remaining 34 axes expressed 26.2 percent of the variation and were not considered for interpretation. PC Axis 1 summarized the greatest amount of variation at 41.5 percent. PC axes 2 through 4 explained 15.8, 10.0 and 6.3 percent of the total variation respectively.

Leaf flushing data from each of the three tests sites contributed the strongest positive eigenvector values to PC axis 1 with values ranging from 0.1878 (KLS2) to 0.2325 (DLS4) (Table 12). The highest negative values for PC axis 1 were displayed by C45 and DR leader elongation, C45 height and October cold hardiness variables; these negative values ranged from -0.1038 to -0.1813. The strong leaf flushing loading values indicated that PC axis 1 represented the leaf flush phenology and leader length. The sign changes indicated that late flushing sources would tend to express less leader length growth but have a higher frost injury (be less hardy) in October. Provenances 1, 2, 3, (in the southwest) and 17 (the most northern source) had the largest negative scores contributing to PC axis 1 (Table 13) and were the earliest to flush. The greatest positive scores were associated with provenances 13, 23, 24, 25 (Table 13) (east of Thunder Bay) which were the latest to flush but expressed lower frost injury in October.

Generally, PC axis 2 showed positive but variable eigenvectors values for the growth and phenological variables (Table 12). High loading values were expressed for DR height, stem diameter and leader length variables. C45 leaf flushing expressed greater positive values than C45 height, C45 leader elongation and KRM leader elongation. The height and diameter relationship to leader length is positive, as one increases in value the other does as well. The greatest negative values were demonstrated by the September cold hardiness data. The variable interaction summarized by PC axis 2 represents the DR growth potential of the seed sources in relation to September frost hardiness. Greater growth potential is expressed by sources which have greater elongation, height and diameter growth and express less frost damage in September. Provenances 1 and 2 (southwest) and 25 (east) contributed the most negative scores to axis 2, and provenances 9 (northwest), 15 and 17 (central and north) had the strongest positive scores.

PC axis 3 described the height and diameter growth at DR and C45 (but not at the other site) in relation to chlorophyll florescence (CF) damage in September and October. The height and diameter relationship to leader length is negative for axis 3. September chlorophyll florescence expressed the largest positive loading value range from 0.2177 to 0.2879 of any variable group. The October chlorophyll florescence loadings were of the same magnitude as the September CF loadings but opposite in sign. C45 and DR height were similar in magnitude to September cold hardiness and the height values that ranged from 0.1512 to 0.2669.

PC axis 3 summarized the portion of variation that demonstrated increased height and diameter growth with less leader elongation, greater September frost resistance and lower October frost resistance described by chlorophyll florescence. Sources in the east (20, 21, 25, 26) that contributed the greatest negative scores were slowest growing at DR and had less damage in September but more damage in October CF. Sources 8 and 9 in the northwest and 1 and 5 in the southwest had the highest positive axis scores and demonstrated better growth at DR and had more damage for CF values in September than October.

Table 12: Principal component analysis results for growth, phenology and cold hardiness (chlorophyll fluorescence and cambium visual scoring) data for 26 NW Ontario provenances of trembling aspen.

Eigenvalues of the Correlation Matrix

Axis	Eigenvalue	Difference	Proportion	Cumulative
1	16.185	9.989	0.415	0.415
2	6.196	2.263	0.158	0.573
3	3.932	1.460	0.100	0.674
4	2.472	0.310	0.063	0.738

Eigenvectors

Variable	PCA Axis 1	PCA Axis 2	PCA Axis 3	PCA Axis 4
C[a]HT[b]99[c]	-0.12922	0.03318	0.20401	-0.18501
CHT02[c]	-0.11690	0.11092	0.15122	-0.17149
CHT03[c]	-0.14705	0.09918	0.15811	-0.18567
CLS[d]3	0.21790	0.09959	-0.00886	0.00744
CLS4	0.22388	0.13143	-0.04280	-0.02274
CLS5	0.22253	0.14102	-0.02196	-0.01738
CLS6	0.22006	0.13596	-0.03151	-0.01826
CLL[e]36	-0.17919	0.04383	-0.16536	-0.15012
CLL41	-0.18138	0.05056	-0.13938	-0.13308
CLL46	-0.14515	0.07780	-0.19225	-0.10365
D[a]HT02	0.01266	0.30151	0.25868	0.06084
DHT03	0.00398	0.29406	0.26692	0.08029
DSD[f]99	0.04936	0.27661	0.21534	0.05720
DSD00[c]	0.05663	0.30197	0.23075	0.05756
DSD02	0.04808	0.29015	0.21738	0.16867
DLS2	0.20939	0.04846	-0.00846	0.08979
DLS3	0.23246	0.08072	-0.04981	0.02885
DLS4	0.23256	0.04253	-0.05186	0.03776
DLS5	0.23205	0.02231	-0.02610	0.03227
DLS6	0.21619	-0.03371	-0.01608	0.10843
DLL46	-0.14472	0.20096	-0.11701	-0.15874
DLL51	-0.12915	0.25825	-0.10791	-0.15971
DLL56	-0.12802	0.27033	-0.08645	-0.10672
DLL61	-0.10387	0.29338	-0.10701	-0.10126
K[a]HT99	-0.11075	0.18215	0.07542	0.22414
KLS2	0.18780	-0.01308	-0.17567	-0.05511
KLS3	0.21683	0.05297	-0.06417	-0.05483
KLS4	0.21955	0.02446	-0.06940	-0.06904
KLS5	0.21688	0.04305	-0.06892	-0.07861
KLS6	0.20858	0.04962	-0.09504	-0.06592
KLL41	-0.19355	0.06090	-0.05582	-0.08497
SCF-10[g]	0.08316	-0.11696	0.21777	-0.11282
SCF-15	-0.07163	-0.14275	0.34270	0.04923
SCF-20	-0.02877	-0.22118	0.28790	0.05227
SCFCRT[g]	-0.01820	-0.22599	0.26498	0.05930
OCF-33[i]	-0.12659	0.09918	-0.20829	0.28840
OCFCRT[j]	-0.10784	0.04312	-0.24188	0.36346
OVS-33[k]	-0.12314	0.04673	-0.04822	0.39697
OVSCRT[l]	-0.11864	0.01076	-0.05756	0.48573

[a] Variable names starting with C are from Camp 45 test

[b] HT is height

[c] 99 is the year 1999, 00 is the year 2000, 02 is the year 2002 and 03 is the year 2003

[d] LS is the leaf stage scores 2, 3, 4, 5 or 6

[e] LL is the leader length measurements on day 36, 41, 46, 51, 56, and 61 from May 1, 2000

[f] SD is the stem diameter

[g] SCF-10, -15 and -20 (degrees Celsius) are the percent reduction of the Fv/Fm ratio to the control

[h] SCFCRT is the September critical temperature for chlorophyll fluorescence damage

[i] OCF -33 are the percent reduction of the Fv/Fm ratio to the control at -33 degrees Celsius

[j] OCFCRT is the October critical temperature for chlorophyll fluorescence damage

[k] OVS-33 are percent cambial visual score damage -33 degrees Celsius

[l] OVSCRT is the October critical temperature for cambial visual scoring damage

October cold hardiness damage in relation to growth is summarized by the fourth PC axis. High positive loading values ranging from 0.2884 to 0.4857 were shown by the October CF and CVS variables. KRM height also showed a high loading value (0.2241) while C45 height, C45 leader length and DR leader length had the strongest negative loading values. This axis summarizes variation expressed among provenances where greater leader length is related to less October frost injury and where greater height at KRM is related to greater frost injury in October. Provenances 12 and 19 (central) and 26 (east) had the lowest negative scores for axis 4 while 10, 15 and 18 (northwest and north) had the highest positive scores.

Simple and Multiple Linear Regression Analysis

PC axes scores were regressed against climate data to demonstrate the pattern of adaptive variation. PC axes scores for each provenance are listed in Table 13. Scores for each provenance vary in magnitude and sign among the different axes.

Simple and multiple linear regression models significantly ($p \leq 0.05$) related climate variables to each PC axis (Table 14). PC axes 1 and 3 were best predicted by single variables; mean temperature in period 3 (the entire growing season) explained 55.86 percent of the variation in PC axis 1, and July precipitation explained 45.03 percent of the variation in axis 3.

January maximum temperature, December precipitation and the number of days until the start of the growing season combined to explain 47.5 percent of the variation in PC axis 2 (Table 14). Three temperature variables (February maximum temperature, December maximum temperature and June mean temperature) together explained 41.4 percent of the variation in PC axis 4.

Table 13: Principal component analysis scores for 26 provenances of trembling aspen in NW Ontario.

Provenance	PCA 1	PCA 2	PCA 3	PCA 4
1	-2.48336	-1.26771	1.47335	-0.23436
2	-1.35725	-2.55954	-0.67234	0.44030
3	-1.51615	-0.33634	0.40822	-0.25129
4	0.57566	-0.12258	0.84050	-1.03669
5	1.15496	-0.97127	1.18923	0.34345
6	0.11783	0.48382	0.78792	-0.96221
7	-0.11388	-0.80144	0.27114	-0.11692
8	-0.49161	0.06620	1.73789	0.69131
9	0.16967	1.78389	1.31385	-0.51835
10	0.32282	0.47164	0.74385	1.90552
11	0.48281	0.41017	0.02298	0.23089
12	-0.88959	0.67273	-0.98993	-2.12663
13	1.83963	-0.39817	0.54239	-0.81030
14	0.80721	-0.09211	-0.21288	-0.24103
15	-0.24252	1.17779	-0.40174	2.28822
16	0.53722	-0.96146	-0.57609	0.88227
17	-1.41946	1.79915	-0.77367	0.56399
18	-0.02615	0.40178	0.17251	1.07580
19	-0.71591	-0.06080	-0.05763	-1.30303
20	-0.47073	0.77101	-1.86623	0.60925
21	-0.35103	0.35772	-1.15633	0.22922
22	0.58996	-0.88231	0.21493	0.13882
23	1.00492	0.94670	0.92156	-0.79641
24	1.10650	0.04332	-0.61172	0.57034
25	1.32689	-1.50284	-1.80942	-0.05749
26	0.04156	0.57066	-1.51235	-1.51467

Geographic Patterns of Adaptive Variation

Adaptive variation was demonstrated by the significant relationship between the climate data and the growth, phenology and cold hardiness data that had demonstrated variation among provenances. The PC axes summarized the variation in the measured data and the regression model results related to climate were used to predict the PC axes scores using the Ontario Climate Model in ArcInfo GIS.

Mean temperature in the entire growing season was used to model PC axis 1 according to the parameter estimates presented in Table 14. The predicted pattern for PC axis 1 demonstrated a clinal pattern of adaptive variation from west to east expressed predominately by leaf flushing phenology (Figure 2). Western sources (1, 2, and 11) flushed earlier than the eastern sources due to greater mean temperature during the growing season (period3) in the west. Sources that flushed earlier demonstrated less adaptation to October cold hardiness. Height and leader length growth in the west were predicted by mean temperature in the growing season would be greatest in the west and suffer more damage from frost in October.

Table 14: Regression results of principal component axes representing growth, phenology, chlorophyll fluorescence and cambium visual scoring data with climate data for 26 provenances of trembling aspen in NW Ontario

PCA Axis	Parameters	Parameter Estimates	Significance	R-square
1	intercept	48.03853	<0.0001	0.5586
	mean temperature whole growing season	-3.71616		
2	intercept	-49.05665	0.0023	0.4750
	January maximum temperature	0.86097		
	December precipitation	-0.14985		
	start of growing season	0.53240		
3	intercept	-11.38009	0.0002	0.4503
	July precipitation	0.12213		
4	intercept	-28.10073	0.0074	0.4140
	February maximum temperature	-21.7713		
	December maximum temperature	1.48742		
	June mean temperature	1.7576		

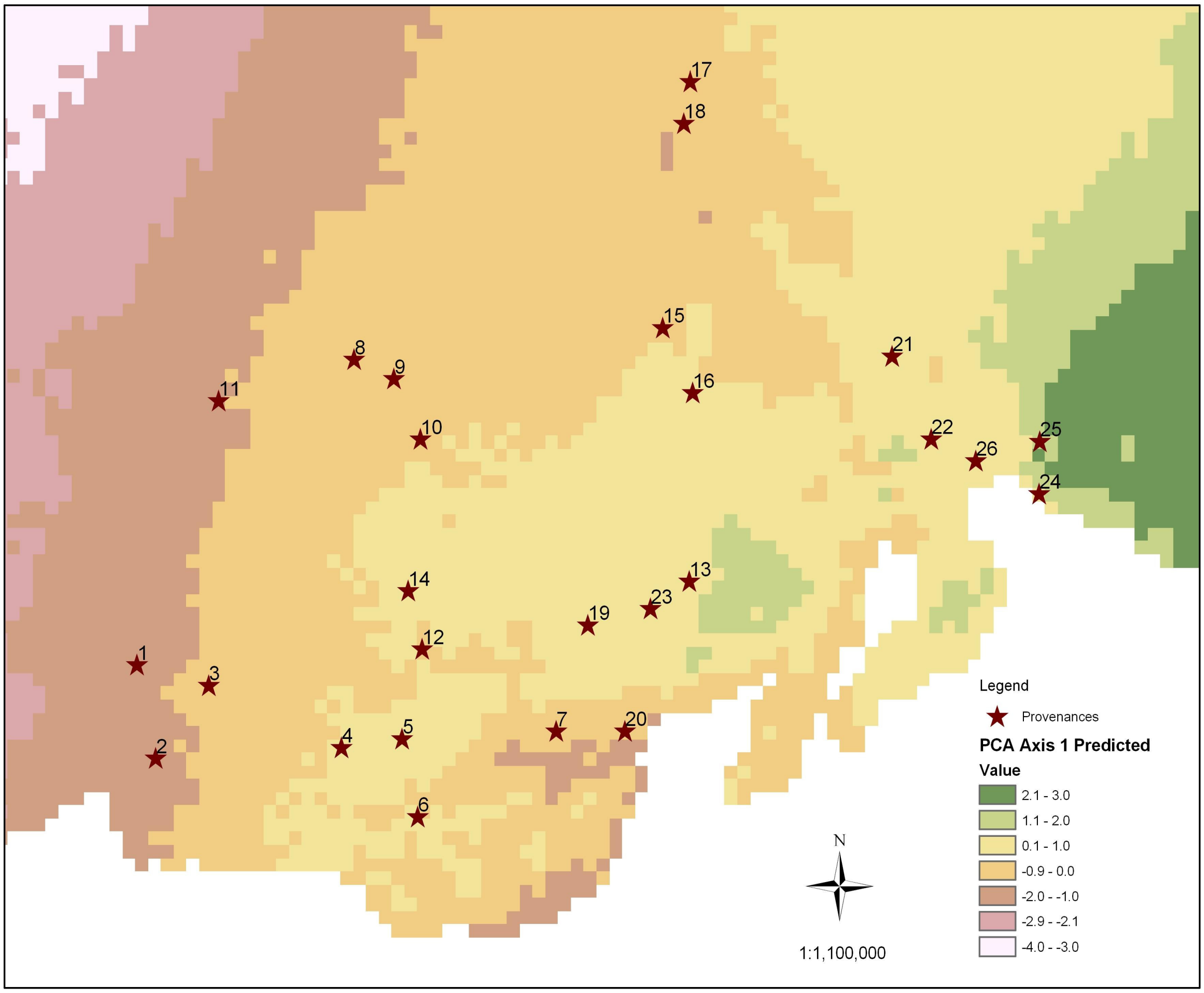

Figure 2: PCA axis 1 predicted by mean temperature in Period 3 (the entire growing season) for 26 trembling aspen provenances in NW Ontario.

PC axis 2 was modeled by the parameters shown in Table 14 related to January maximum temperature, December precipitation and the number of days until the start of the growing season. The pattern of adaptive variation demonstrated for axis 2 showed a center of higher score values for the northern sources with a decrease in score values with movement southeast, south and southwest (Figure 3). Growth potential, represented by the growth variables, for the DR test, was greatest in the north and central areas and these areas also had less frost damage in September. Growth potential was shown to have a positive relationship between height, diameter and leader length. The higher predicted scores were related to a colder January maximum temperature, less December precipitation and an earlier start (number of days) to the growing season.

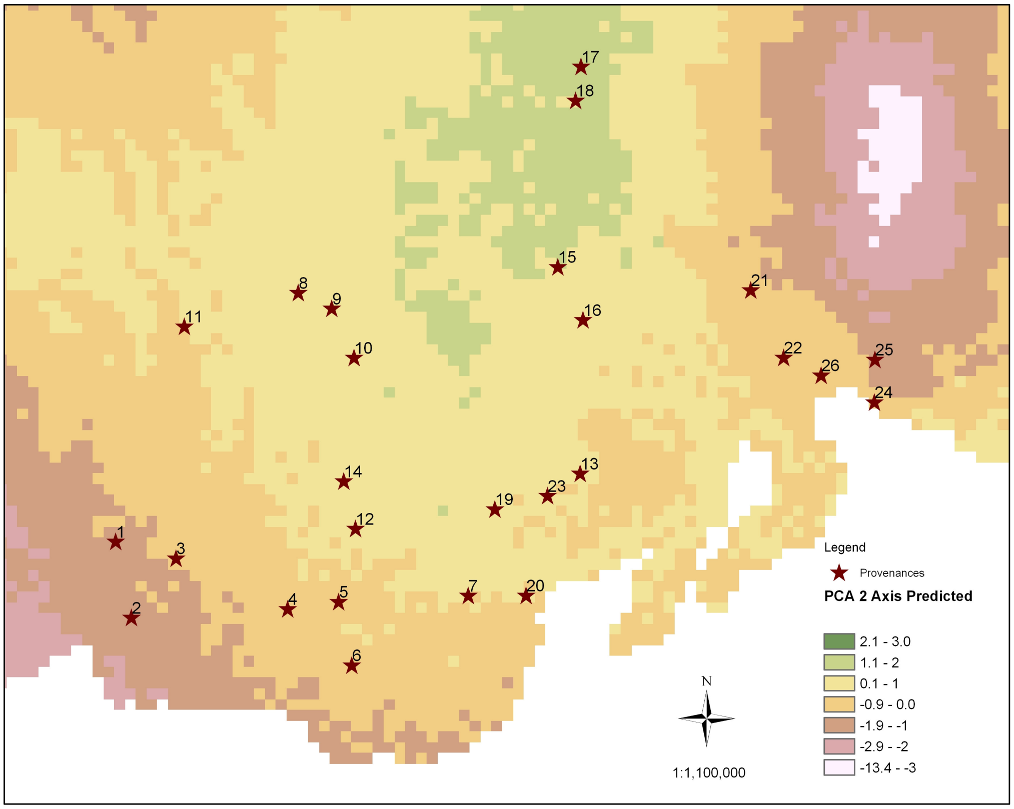

Figure 3: PCA axis 2 scores modeled by January maximum temperature, December precipitation and the number of days until the start of the growing season for 26 trembling aspen provenances in NW Ontario.

July precipitation predicted PC axis 3 according to the parameters in Table 14. The pattern of adaptive variation described growth potential, where height and diameter were negatively correlated, and where September and October CF damage was also negatively correlated. Growth potential related to cold hardiness moved from west to east as July precipitation increased. Greater height and diameter growth with less leader growth related to greater July precipitation occurred in the west were the frost damage measured by CF is greatest and October damage is less.

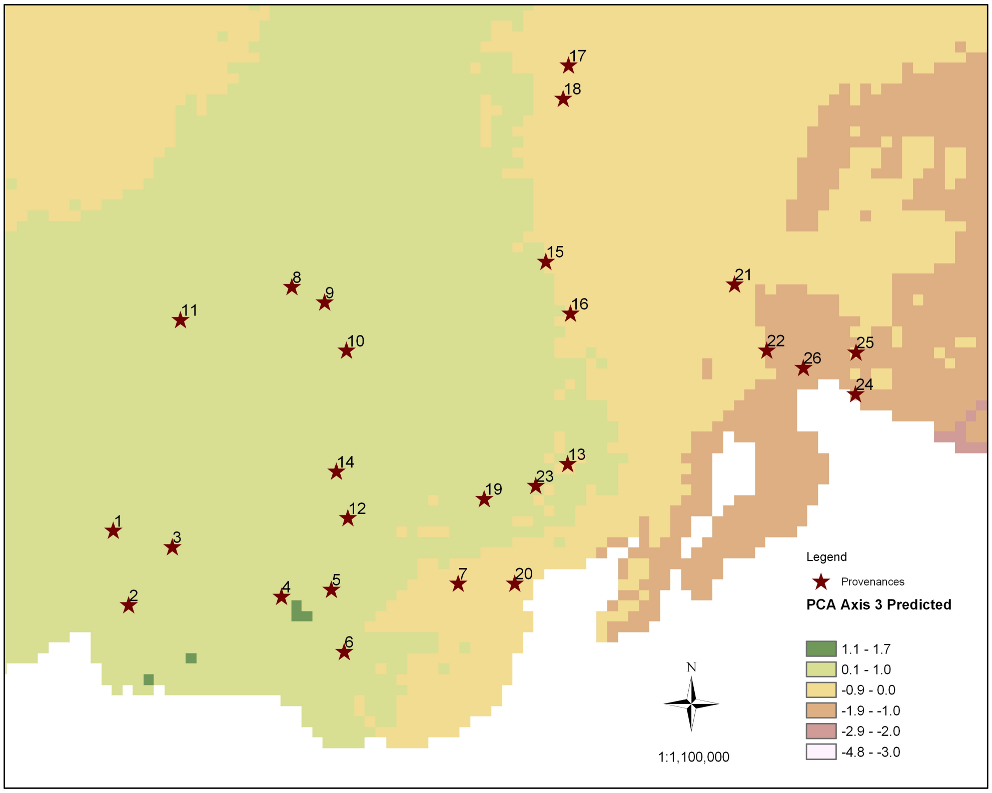

Figure 4: PCA axis 3 scores predicted by July precipitation for 26 trembling aspen provenances in NW Ontario.

PC axis 4 was modeled using parameter estimates for: February maximum temperature, December maximum temperature, and June mean temperature (Table 14). October cold hardiness demonstrated a clinal pattern of adaptive variation from the north to the southeast. Cold hardiness in October was related to a cooler June mean temperature, and warmer December and February mean temperatures. Sources that were taller at KRM, were at risk for more frost damage in October, where as longer leader lengths were associated with less damage from October frosts.

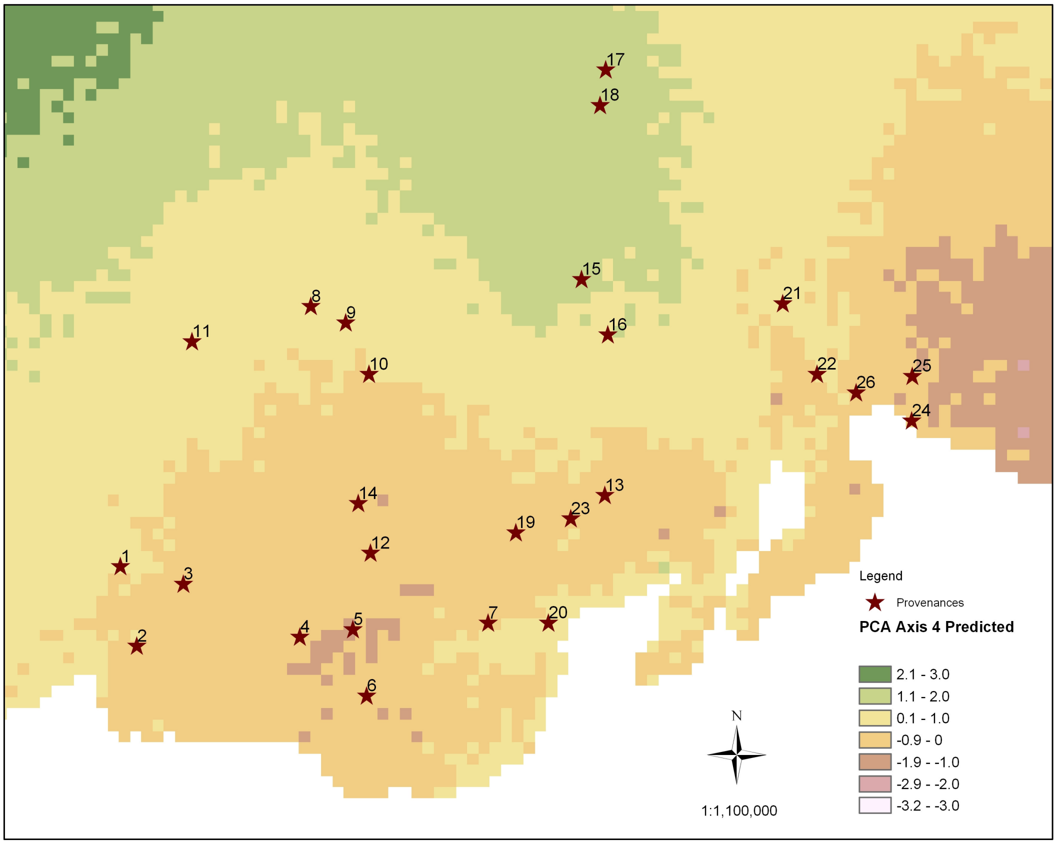

Figure 5: PCA axis 4 scores predicted by February maximum temperature, December maximum temperature and June mean temperature for 26 trembling aspen provenances in NW Ontario.

DISCUSSION

PROVENANCE EFFECTS

Leaf flushing data expressed the strongest among provenance variation at each trial site (between 2% to 19%) compared to growth measurements. This observation is not surprising as the timing of budburst in trembling aspen has been demonstrated to be an important indicator of adaptation (Lechowicz 1984; Leinonen and Hanninen 2002; Li et al. 2010; Morgenstern 1996). Similarly, budburst has previously shown strong patterns of genetic variation for a variety of northern tree species including trembling aspen (Morgenstern 1996; Li et al. 2010; Schreiber et al. 2013).

The analysis of variance for the leaf flushing data indicated a significant provenance by site (GxE) interaction for the later leaf flushing stages (4 through 6). This interaction seems to be attributed to scale effects with no performance rank changes among provenances at different sites (White et al. 2007). This result is supported by 1) the PCA results that showed strong positive values for each of the flush scores, and 2) the contribution each site and score having the same magnitude as the others. Also, the DR test site consistently had a smaller range of days to each flushing stage, while C45 consistently had the largest range, and KRM in between. Therefore, the scale effects did not hinder determination of the pattern of adaptive variation; rather, the effects indicate the need for trembling aspen provenances to be tested on a greater number of sites for study of provenance effects (White et al. 2007). Results of the present study further indicate that site quality to provenance adaptation needs additional study.

Tree height, while expressing significant provenance effects at each site, explained less than 3.6% of the total variation. Nonetheless, a significant site by provenance interaction (GxE) was indentified in the analysis of variance for height in 1999, 2002 and 2003 as shown in Table 5. Provenance rank data (Table 8) indicate that rank changes among provenances, rather than scale effects, as was shown for leaf flushing data, are the cause of the GxE in the height data as indicated in (White et al. 2008). While trembling aspen is not planted in northwestern Ontario to-date, the demonstrated GxE indicates that seed transfer potential, within a relatively small geographic region, is limited by provenance effects that can hinder growth performance.

Leader length measurements exhibited provenance variation, but the effect seemed to be confounded with the variation in overlapping flushing time. Early measurements showed little provenance effect on the first length measurement day (day 28) and the second measurement day 31, as not all trees had progressed through the leaf flushing stages at each site. Significant provenance effects materialized at later measurement days when all provenances had transitioned through the leaf flush stages and were then actively elongating. While this effect points to provenance differences, the expression and extent of the provenance effect was unfortunately further hindered by the presence of 1) shepard's crook fungus at the C45 and DR, and 2) forest tent caterpillar at KRM. Influence of the shepherd's crook fungus also impacted height measurement and the expression of provenance variation, especially where consecutive year's damage occurred, and probably contributed to the low percent variation expressed among provenances by the height data.

ADAPTIVE VARIATION

Variables that demonstrated a significant provenance effect were investigated for relationship to climate data to describe patterns of adaptive variation. The provenance effect demonstrated for leaf flushing was related strongly to temperature during the growing season and demonstrated the clearest pattern of adaptive variation, both by simple linear regression analysis and through principal component analysis. These results are consistent with the understanding that temperature heat sums are considered the key environmental factor influencing budburst (Hunter and Lechowicz 1992; Li et al. 2010). However, the best predictor variable in this study was growing season temperature rather than any of the specific heat sum (degree-day) variables.

The PCA axis regressions (Table 14) did not improve on the predictive capacity of climate over simple linear regressions shown in Table 10. The simple linear regressions of climate data to each of the leaf flushing scores by test site showed significant relationships to climate with r^2 values ranging from 0.46 to 0.57. The predominant climate variables were temperature means in the growing season (either mean temperature in the growing season, or May or June mean temperature). The PCA axis 1 regressions produced similar results showing a significant relation to the mean temperature in the growing season with an r^2 value of 0.55. This result supports the possibility that the phonological variables, leaf flushing, rather is better studied than growth variables for understanding adaptive variation and the effects of climate change on local trembling aspen populations (Li et al. 2010).

A clinal longitudinal pattern of adaptive variation in leaf flushing, predicted by temperature in the growing season, was demonstrated with flushing earliest in the west and latest in the east as shown in Figure 2. This longitudinal pattern appears somewhat different from a larger study by Li et al. (2010) where trembling aspen sources from British Columbia to central Alberta demonstrated a latitudinal clinal pattern of variation for budburst, related to heat sums. Li's study follows the expected pattern of variation for leaf flushing; i.e. that northern sources would flush earliest and southern sources latest (Li et al. 2010; Lechowicz 1984; Leinonen and Hanninen 2002). The range of sources studied in this research covered roughly 1.75^{o} latitude and 2.5^{o} longitude, where as the sources of Li et al. (2010) covered a much more extensive range. The small study area has provided only a fragment of the pattern of adaptive variation in leaf flushing in this region. Also, the climate in the study area is strongly influenced by Lake Superior (Weng and Parker 2008). Lake effects, therefore, are influencing the patterns of adaptive variation expressed in the relatively small study area (Weng and Parker 2008).

The west to east pattern for leaf flushing is similar to the adaptive variation pattern demonstrated for cold hardiness, as measured by the electrical conductivity method, for these same provenances. Weng (2002) demonstrated a southwest to east pattern of adaptive variation related to growing degree days and August precipitation for October and November cold injury. In this cold hardiness study, frost injury decreased moving from southwest to east, however the pattern was generally weak (Weng 2002). The parallel similarities in geographic pattern between leaf flushing and cold hardiness may suggest that provenances flushing earlier are less hardy in October and November then eastern sources, and that the earliest to flush may be extending the growth season later than the eastern sources that were included. Unfortunately, leader length measurements were halted due to fungal issues and bud set was not scored in this study. Bud set data would help clarify this pattern of adaptive variation.

The genotype by environment interaction shown in the growth data was reflected in the PCA results with PC axis 2 being strongly influenced by growth data at the DR test site. Sources north of the test site generally performed better in height and leader length than sources in the southwest and southeast. Hence, the pattern of adaptive variation expressed among provenances demonstrated a weak latitudinal trend, related to winter temperature and precipitation and the start of the growing season. This geographic pattern is not what would be expected as southern trembling aspen sources were superior in height over local sources in a study by Schreiber et al. (2013). This anomaly may also be simply a reflection of the small provenance range and proximity to Lake Superior to the south.

The remaining two patterns of adaptive variation demonstrated by PCA included cold hardiness data, as measured by chlorophyll florescence and visual scoring, and growth data. The differences in the two patterns, expressed in PC axis 3 and 4, related generally more to differences in hardiness expressed by provenances in September verses October, than to different combinations of growth variables. A longitudinal pattern of adaptive variation was shown in PC axis 3 through the relation of July precipitation to height, stem diameter and leader length variables. As well, a correlation of both growth variables to September and October chlorophyll florescence variables was observed (Table 13). A latitudinal trend was shown for PC axis 4 where adaptive variation was expressed through a combination of winter temperatures and June mean temperature that predicted leader length and height potential together with October frost hardiness as measured by both chlorophyll florescence and visual scoring.

Weng (2002) noted no geographic pattern was shown for chlorophyll florescence or visual scoring hardiness data, and reported no differences between September and

October results. It was noted that hardiness progressed in two phases, the first from early to mid-September and the second from late September through October. The results of this study suggest that the analysis of growth data in conjunction with chlorophyll florescence or visual scoring hardiness data can help clarify the geographic patterns of adaptive variation. Also, the difference in pattern between the 3rd and 4th PC axes may reflect the two phases noted by Weng (2002) based on the differences in September verses October electrical conductivity data.

CONCLUSION

Patterns of adaptive variation expressed among 26 provenances of trembling aspen in northwestern Ontario have been demonstrated through both phenology and growth data, indicating significant genetic variation among trembling aspen provenances in this relatively small region. The results of this study indicate the need to further expand the range of provenances tested and numbers of trial locations established to better understand the patterns of adaptive variation. Such investigation over a much broader area is increasing important in the light of on-going and expected climate change.

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APPENDIX I

Appendix I: Climatic data summary for 26 trembling aspen provenances in NW Ontario as generated by the Ontario Climate Model (Mackey *et al.* 1996).

Variable	Mean	Standard Deviation	Minimum	Maximum
Maximum Temperature[a]				
January	-11.6	0.96	-13.1	-9.4
February	-7.4	0.67	-8.7	-6.2
March	-0.9	0.52	-1.7	0
April	7.9	0.68	7.0	9.3
May	16.0	0.70	15.1	17.3
June	20.2	0.66	19.1	21.3
July	23.9	0.47	22.8	24.5
August	22.2	0.38	21.5	22.8
September	15.8	0.47	15.3	16.8
October	9.0	0.49	8.3	10.1
November	-0.05	0.65	-1.0	1.6
December	-8.1	0.76	-9.3	-6.2
Minimum Temperature				
January	-26.1	1.40	-28.5	-22.4
February	-22.5	1.47	-25.8	-19.7
March	-15.5	1.38	-18.3	-12.4
April	-5.7	0.88	-7.3	-3.6
May	1.7	0.42	1.3	2.6
June	7.0	0.41	6.4	7.9
July	10.6	0.43	9.8	11.5
August	9.6	0.47	8.9	10.8
September	4.5	0.57	3.7	5.8
October	-0.7	0.48	-1.3	0.2
November	-9.6	1.00	-10.8	-7.6
December	-20.5	1.20	-22.3	-17.6
Mean Temperature				
January	-18.8	1.15	-20.8	-15.9
February	-15.0	1.06	-17.3	-12.9
March	-8.2	0.91	-10.0	-6.3
April	1.1	0.72	-0.2	2.3
May	8.9	0.50	8.3	10.0
June	13.6	0.46	12.8	14.5
July	17.21	0.37	16.6	17.9
August	15.9	0.32	15.4	16.6
September	10.1	0.47	9.6	11.3
October	4.1	0.46	3.5	5.2
November	-4.8	0.82	-5.8	-3.0
December	-14.3	0.97	-15.7	-11.9
Precipitation[b]				
January	45.0	3.83	33.3	50.1
February	33.5	2.46	26.7	36.5
March	46.0	3.46	36.8	51.4
April	40.0	3.16	34.0	45.2
May	71.5	4.08	63.9	76.3
June	90.9	5.42	82.6	101.1
July	93.2	5.49	80.3	99.8
August	87.9	2.08	83.3	91.8
September	88.9	3.18	82.0	93.3
October	75.3	4.94	67.5	85.4
November	56.1	6.46	45.0	68.9
December	50.1	8.03	34.9	66.8

Appendix 1 (continued): Climatic data summary for 26 trembling aspen provenances in NW Ontario as generated by the Ontario Climate Model (Mackey *et al.* 1996).

Variable	Mean	Standard Deviation	Minimum	Maximum
Precipitation				
Period 1[c]	122.7	9.12	102	136
Period 2	110.3	4.24	103	117
Period 3	449.3	18.57	420	490
Period 4	339.1	17.48	312	377
Growing Degree Days over 5°C				
Period 1	1.9	0.71	1	3
Period 2	238.3	10.28	217	257
Period 3	1262.5	58.47	1170	1390
Period 4	1024.8	58.08	943	1144
Growing Season[d]				
Days to the start	124.9	2.30	120	127
Days to the end	282.9	2.66	279	287
Length	159.2	4.42	153	167
Average Annual Temperature				
mean	0.8	0.54	-0.1	2.1
minimum	-5.6	0.71	-6.8	-3.7
maximum	7.2	0.45	6.6	8
Period 3 Temperature				
mean	12.9	0.20	12.5	13.3
range	24.6	0.46	23.5	25.2

[a] Temperature is in degrees Celsius

[b] Precipitation is in mm

[c] Period 1 refers to the 3 months prior to the growing season, Period 2 is the first 6 weeks of the growing season, Period 3 is the entire growing season and Period 4 is the difference between period 3 and period 2.

[d] Growing season variables are number of days

APPENDIX II

Appendix II: Mean percent reduction in the Fv/Fm ratio relative to the control at specific temperatures, the critical temperatures, and the percent cambium visual damage for 26 trembling aspen provenances in NW Ontario (from Weng 2002)

	Chlorophyll Fluorescence							Cambium Visual Scoring		
	September 15, 2000				October 1, 2000			October 1, 2000		
Pr/T[a]	-10	-15	-20	Crit_T1[b]	-22	-33	Crit_T2[c]	-22	-33	Crit_T3[d]
1	14.7	48.1	64.8	-16.52	27.0	36.2	-45.46	8.8	23.6	-30.72
2	22.4	49.7	62.2	-16.31	20.0	38.3	-45.96	19.6	44.8	-20.94
3	23.6	40.1	57.1	-17.90	23.0	35.9	-44.36	12.4	24.0	-29.29
4	31.3	35.2	60.2	-17.15	18.1	24.9	-58.60	8.4	20.0	-35.64
5	39.9	46.2	62.0	-15.28	18.2	24.3	-58.10	8.8	22.4	-30.93
6	21.3	38.0	47.4	-20.52	24.3	34.3	-61.75	14.0	26.4	-35.31
7	23.3	43.0	66.8	-16.29	16.1	28.1	-53.66	8.4	31.2	-26.65
8	25.0	43.4	69.0	-15.95	22.3	36.6	-43.57	12.8	36.0	-24.02
9	20.1	46.5	57.5	-17.44	15.5	33.2	-52.24	5.8	22.8	-32.42
10	18.8	37.8	61.7	-17.46	23.4	37.4	-42.36	19.6	31.6	-23.76
11	11.6	37.4	44.5	-20.72	18.5	30.7	-49.11	7.8	20.0	-33.90
12	27.9	34.7	45.4	-23.00	17.2	39.8	-44.69	12.0	17.2	-35.40
13	22.7	35.5	44.3	-22.32	16.0	20.1	-61.26	5.6	15.2	-41.39
14	29.5	36.4	53.6	-19.21	19.3	39.4	-42.78	9.2	20.0	-34.42
15	17.0	29.5	39.5	-24.49	30.2	51.4	-33.20	23.2	40.0	-20.35
16	25.9	35.1	57.8	-14.89	28.2	41.2	-39.81	12.4	20.0	-32.28
17	18.0	31.4	38.8	-24.9	22.6	40.2	-42.67	15.8	46.0	-21.36
18	20.5	46.3	62.7	-16.61	23.3	38.0	-44.24	16.8	42.0	-21.53
19	18.6	41.4	55.1	-18.64	25.4	33.4	-49.36	5.6	22.4	-33.64
20	7.1	26.4	37.7	-23.58	18.0	40.1	-38.74	12.4	40.4	-22.29
21	15.1	29.9	35.7	-26.21	26.2	48.0	-34.37	3.2	28.0	-29.72
22	22.4	32.8	67.7	-16.99	23.3	28.8	-49.98	10.8	19.6	-33.34
23	26.8	33.5	43.5	-24.22	13.5	26.9	-60.63	5.6	16.4	-39.49
24	19.6	31.7	39.1	-25.18	20.4	31.0	-47.03	17.2	20.0	-30.40
25	20.9	28.8	54.1	-19.63	20.0	33.0	-46.83	14.8	18.4	-32.60
26	12.1	18.8	43.6	-22.98	26.5	32.7	-50.15	12.0	14.8	-38.93

a Pr is the provenance and T is the temperature in degrees Celcius

b Crit_T1 is the critical temperature in September 2000 for chlorophyll fluorescence data

c Crit_T2 is the critical temperature in October 2000 for chlorophyll fluorescence data

d Crit_T3 is the critical temperature in October 2000 for cambium visual scoring data