

RELATING GENECOLOGICAL VARIATION IN WHITE SPRUCE TO  
ECOLOGICAL LAND CLASSIFICATION IN CENTRAL CANADA

by

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## ABSTRACT

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Keywords: Cauchy function, ecological land classification, ecodistricts, genecology, GIS, natural selection, provenance, regression, seed sources, white spruce.

Genetic diversity can be seen as a fundamental element in forest sustainability. Information about the genetics of trees can be obtained from provenance studies. Previous research has demonstrated that white spruce exhibits a high amount of genetic diversity. This study related genetic variation in white spruce to the ecodistrict level of the ecological land classification maps released by the Canada Committee on Ecological Land Classification in 1995. Seed sources were grouped according to ecodistricts using height data collected from white spruce provenance trials established in 2002. ANOVA results revealed significant differences between provenances, suggesting the presence of genetic variation. Results showed that provenances grouped in some of the ecodistricts were significantly different; these ecodistricts were subdivided into operational ecodistricts on the basis of post hoc LSD tests. Using mean provenance height, quadratic regressions were applied to the data to identify which climate variables most strongly predict provenance growth. Response functions were carried out for January, November and December maximum temperatures as well as for mean April precipitation using the Cauchy function. Despite the finding of genetic differences between provenances, their optima for the four selected climate variables were very similar. For the most part, maps of optimal areas did not correspond to ecodistrict boundaries, which means that although provenances have successfully adapted to local conditions, they would achieve optimum height growth elsewhere. The extreme similarity of the mapped optimum areas suggested that no genetic variation was present between the provenances while the statistical results showed the exact opposite. The finding of significant differences between provenances within ecodistricts suggested that, in some cases, ecodistricts were not reflective of genetic variation. There could be other factors influencing genetic variation which have been unaccounted for and the ecodistrict maps released in 1995 may need to be revised using more advanced ecological knowledge and more sophisticated mapping technology. Although the level of correspondence was not perfect, it was concluded that genetic variation in the height growth of white spruce generally follows ecological land classification boundaries.

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## INTRODUCTION

Genetic diversity provides species with the capacity to adapt and evolve to changing environmental conditions (Rajora *et al.* 2005). The stability and function of forest ecosystems are dependent, in part, upon the health and genetic diversity of forest tree species (Rajora *et al.* 2005). The conservation of genetic diversity, therefore, can be seen as the foundation of forest sustainability (Rajora *et al.* 2005). For gene management and conservation, it is important to determine the amount and distribution of genetic variability within the range of a species (Furnier *et al.* 1990). Patterns of genetic variation are useful for informing seed transfer guidelines and for delineating breeding zones (Li *et al.* 1997). Information on the population genetic structure of a species is usually obtained through common garden studies (Furnier *et al.* 1990). Provenance tests, or common garden studies, use study sites where many different seed sources (populations) from one species are grown together (Ying and Yanchuk 2006). Since they are growing in a common environment, any differences observed between the growth of seed sources can be attributed to genetic differences (Parker *et al.* 1996). This observed genetic variation usually coincides with changes along an environmental gradient or cline (Heslop-Harrison 1964).

The investigation of relationships between living organisms and their environment is the essence of land classification (Rowe 1996). The purpose of ecological land classification (ELC) is the division of the landscape into ecosystem units which become the basis for the development of resources and for environmental conservation (Bailey 1983). At a scale of about 1:2,000,000, the ecodistrict level of classification is considered to be a useful unit for environmental management (Marshall *et al.* 1996). Patterns of vegetation are considered to be indicators of climate so the

geographic distribution of plants is the primary criterion for the delineation of regional ELC boundaries (Bailey 1983). Ecological variation occurs over a transitional zone, however, so that the definition of boundaries will always be somewhat subjective (Bailey 1983). Although it may appear that the boundaries delineated in ELC maps are definitive, Rowe (1996) states that maps are hypotheses which need to be tested and improved. Yet despite minor updates, there have been few efforts to revise ELC maps since their release in 1995.

Distributed across North America, white spruce (*Picea glauca* (Moench) Voss) grows under a variety of climatic and soil conditions (Li *et al.* 1993). A large volume of genetic research has been carried out for white spruce because of its high economic value (Khalil 1984). In Canada and the Northeastern U.S.A., white spruce is used for lumber, pulp, wood products and reforestation (Li *et al.* 1993). The wide ecological amplitude of white spruce implies large amounts of genetic variation within the species (Li *et al.* 1997). In general, the patterns of variation in white spruce have been found to be clinal (Lesser and Parker 2004).

Using data collected from provenance tests, the objectives of this study are to develop response functions for white spruce populations; to develop response functions for ecodistricts; to map areas resulting in optimal performance as predicted from the response functions and to compare the maps of optimal growth with ecodistrict boundaries. This study will attempt to relate patterns of genetic variation of white spruce to ELC boundaries. If genetic variation is influenced by changes in the environment as delineated by ELC, then the patterns of variation observed in white spruce will correspond to ecodistrict boundaries in Ontario and western Quebec.

## LITERATURE REVIEW

This section will provide a review of the relevant literature regarding provenance research and will outline previous genecological studies carried out for white spruce. Then a brief look at natural selection will be followed by a review of landscape ecology, landscape genetics and ecological land classification since this study includes concepts from all of these fields of research. Studies involving an explicit spatial dimension are challenging, but are also necessary since spatial structure is now known to be an essential element in ecological theory (Turner *et al.* 2001). The study of the relationships between organisms and spatial heterogeneity is interdisciplinary, however, a synthesis of the many fields involved has not yet emerged (Turner *et al.* 2001).

### Provenance research

According to Heslop-Harrison (1964), it has been well established that plants display genetically based ecological differentiation. The study of ecologically based genetic variation is termed genecology, coined by Turesson in 1923 (Langlet 1971). The terms 'genecology' and 'ecological genetics' will be used interchangeably in this thesis because their definitions are sufficiently similar. Genetic variation is known to exist in most natural populations although the precise amount of genetic variation has yet to be discovered (Hartl 1980). The fundamental aim of genecology is to study genetic variation resulting from environmental selection pressures (Heslop-Harrison 1964). The challenge in genecology is to separate adaptive variation from random variation and, in turn, to separate adaptive variation into genetic and non-genetic components (Heslop-Harrison 1964).

It is more common for a species to be composed of separate breeding populations than it is for the species to form one single breeding population (Merrell 1981). For species with large ranges, individuals from different parts of the range are usually reproductively isolated by distance (Merrell 1981). Adaptive variation in a species can be demonstrated experimentally by investigating whether or not populations from different areas vary in their response to different environmental conditions (Heslop-Harrison 1964). This has most commonly been accomplished by the comparative cultivation of populations from throughout a species' range and is known as provenance testing or common garden studies (Heslop-Harrison 1964) (the terms 'provenance', 'seed source' and 'population' will be used interchangeably). There are various sources of confusion inherent in the design of provenance tests; the number of populations sampled, the form of material collected, the uniformity of the test sites, the selection of growth characters and the potential for genotype by environment interactions represent a few of the challenges in designing statistically sound and biologically meaningful experiments (Heslop-Harrison 1964).

It is important to sample populations in a manner which reduces the possibility of a single genotype being sampled repeatedly. This type of error can lead to an overall decrease in within-population variation which can confuse the significance of between-population differences. The emphasis should be placed on sampling as many different populations as possible rather than on overall sample size (Heslop-Harrison 1964).

The experimenter generally has two choices in the form of material that can be used in a provenance study. Mature living plants can be transplanted to the test site or seed can be collected from mature plants and sown at the test site. In using mature plants, a known population is sampled whereas, if seed is used, the population is not

necessarily known since it has not yet undergone ecological selection (Heslop-Harrison 1964).

The nature of the provenance test is such that the growing environment is uniform which eliminates direct environmental modification of the plant. This common practice can hide a plant's genetic capacity to react to unique environments. In addition, the test environment could suppress certain environmentally induced characteristics while evoking others never before observed in the natural habitat (Heslop-Harrison 1964).

Another challenge in provenance studies is in choosing which growth characters will be measured and analyzed (Heslop-Harrison 1964). It is quite common for morphological and phenological traits to be investigated; however, it is argued that physiological responses are more representative of the plant's reaction to the habitat which makes physiology a better indicator of adaptation (Heslop-Harrison 1964). Plant adaptation should be viewed as both an adjustment to current conditions as well as the ability to adjust to future conditions (Matyas 1996). Survival is often seen as the ultimate test of adaptation and other evidence is viewed as being circumstantial (Heslop-Harrison 1964). There has been much debate regarding the use of qualitative versus quantitative traits. Quantitative traits are usually preferred since their frequency distributions are approximately normal and since most geographic variation can be associated with quantitative differences (Merrell 1981).

Adaptation can be observed as a function of geographic, climatic or biotic variables (Jaramillo-Correa *et al.* 2001), each of which can influence traits differently so that the optimum environment for one trait will not necessarily be optimum for others (Raymond and Lindgren 1990). Therefore, experimenters must decide which traits will

be used as an index of growth and adaptation (Raymond and Lindgren 1990).

Adaptation can be assessed via three fitness components: the ability to cope with a variable environment, the ability to compete and the ability to reproduce (Ying and Yanchuk 2006). The trait most commonly used to assess fitness in trees is total height since it provides adaptive advantages in competition and reproduction (Ying and Yanchuk 2006).

It is assumed that height is a trait under the control of selection given that there is a selective advantage to being tall since a tall tree receives more sunlight and is better positioned for reproduction (Furnier *et al.* 1990). Trees that begin increasing their height too early in the spring may be damaged or killed by spring frost, however, if a tree allocates resources disproportionately to height, then other plant functions like reproduction may be compromised (Furnier *et al.* 1990). Selection for height while seedlings are young is likely to play a critical role in survival and reproduction since trees must grow quickly to compete successfully in the environment (Jaramillo-Correa *et al.* 2001). Since white spruce is an early post-disturbance invader, rapid early height growth is especially important (Jaramillo-Correa *et al.* 2001). It has been argued that survival and fecundity are better measures of fitness, but it can often take many years for mortality to occur so that a large sample would be required to ensure statistical precision (Wu and Ying 2004). In addition, it can be prohibitively expensive to monitor the fecundity of all trees at a test site (Wu and Ying 2004), thus another benefit to using height as an index for fitness is that height growth is easily measurable (Rweyongeza *et al.* 2004).

Correlations between environmental variables and plant responses are considered to be the best form of circumstantial evidence of adaptation (Heslop-Harrison 1964).

One of the main advantages of regression techniques is its simple application to data obtained from natural populations (Rausher 1992). The finding of a significant correlation between provenance response and an environmental variable suggests that natural selection has had a strong influence on a particular population (Ying and Yanchuk 2006). Nevertheless, the use of regression analysis to measure natural selection is sometimes criticized due to concerns surrounding multivariate collinearity (Wu and Ying 2004).

Multicollinearity occurs when the predictor variables are interdependent, as opposed to being strictly independent. In regression analysis, coefficients predict the change in the dependent variable as caused by changes in the independent variable with all other variables remaining constant. However, if the independent variables exhibit multicollinearity, then it would be highly unlikely for one variable to change on its own without influencing others. For example, temperature and precipitation are closely related so that a change in one is often accompanied by a change in the other. It has been recommended that Principle Components Analysis (PCA) can be used in situations with severe multicollinearity to reduce the number of predictor variables. One of the drawbacks to PCA is that principle components are arbitrary when considered in terms of fitness which can make biological interpretations difficult. Another suggestion for reducing the number of predictor variables is to manipulate the data by summing, averaging or eliminating highly correlated variables; however these procedures can confound tests of significance. Yet, despite the potentially problematic aspects of the method, regression analysis is still considered to be a valuable research tool (Mitchell-Olds and Shaw 1987).

Finally, the presence of a significant genotype by environment (GxE) interaction can confuse the results of a provenance study. If a provenance exhibits different growth patterns at different test sites, then it can be said that a GxE interaction exists. In such cases, a provenance which had the best performance at one site may have the worst performance at another site. The problem of GxE interactions can be intensified for species that exhibit clinal variation, like white spruce. Raymond and Lindgren (1990) suggest two approaches available to a researcher when a significant genotype by environment interaction has been found. The first approach is to classify and group environments so that the genotype by environment interactions are minimized. The second approach is to classify genotypes as being stable or unstable based on their relative performance across a range of tested environments so that the unstable ones can be removed from the analysis, thereby reducing overall GxE interactions. Genecological studies combining both classification of environments and of genotypes are useful in the delineation of breeding zones (Raymond and Lindgren 1990).

Populations of a species are commonly found in clumps or aggregates as opposed to being evenly distributed in space, which provides evidence for the influence of some non-random patterns on their distribution (Hartl 1980). Also, populations usually exhibit a hierarchical structure consisting of groups within groups (Hartl 1980). The method of grouping populations together for statistical analyses has been met with some criticism, the basis of which is that comparing regional means would obscure variational continuity (Heslop-Harrison 1964). However, many studies have been conducted where populations were placed into groups. Weidman (1939) grouped populations into regional races based on morphology while Wright and Baldwin (1957) grouped them into regional ecotypes. Parker *et al.* (1996) grouped jack pine and black



spruce seed sources according to plant association and soil type and found that these categories of the FEC classification system in northwestern Ontario corresponded to natural selection units. Jaramillo-Correa *et al.* (2001) pooled white spruce provenances into six regional populations based on ecological regions in Quebec.

Provenance studies can be expensive and time-consuming, especially for long-lived species like trees which take many years to reach maturity (Furnier *et al.* 1990). The expense of common garden studies can also be a problem for non-commercial tree species with little or no economic value (Furnier *et al.* 1990). Nevertheless, provenance research has proven itself invaluable in providing empirical evidence of genetic variation within species and may be one of the most important contributions of forestry to the biological sciences (Matyas 1996).

#### Genetic variation in white spruce

As one of the most widely distributed conifers in North America, white spruce is known to exhibit large amounts of genetic variation (Nienstaedt and Teich 1972). Significant differences between provenances for height growth have been documented by Genys (1965), Holst (1960), Holst (1962), Nienstaedt (1969), Teich *et al.* (1975), Nienstaedt and Riemenshneider (1985), Khalil (1986), Furnier (1990), Li *et al.* (1993), Li *et al.* (1997) and Lesser and Parker (2004). Clinal variation in white spruce has been demonstrated by Nienstaedt and Teich (1972), Khalil (1986), Furnier (1990), Morgenstern and Copis (1999), Li *et al.* (1997), Jaramillo-Correa *et al.* (2001), Lesser and Parker (2004) and Rweyongeza *et al.* (2007). The common trends found by many authors were general south to north and east to west gradients (Morgenstern and Copis 1999). These gradients are largely influenced by natural selection brought about by

environmental pressures, but the impact of the environment varies depending on the genetics of the species (Morgenstern 1996).

Khalil (1984) concluded that white spruce was sensitive to differences in soil nutrition at the test sites and that this sensitivity increased as the trees aged. Teich and Holst (1974) found evidence for the support of limestone ecotypes for white spruce although Lesser *et al.* (2004) were unable to corroborate those findings. There has been little evidence of white spruce ecotypes for narrow environmental conditions and it is more common to find the existence of broad climatic or geographic ecotypes (Morgenstern 1996).

Species are sometimes distributed continuously as opposed to being clumped into obvious populations (Schwartz and McKelvey 2009). Li *et al.* (1993) found that white spruce populations from southeastern Ontario were not well differentiated and may form a single homogeneous population. Li *et al.* (1997) argued that eastern populations of white spruce appeared to be only moderately differentiated because of the large amount of environmental homogeneity in eastern Canada. Another theory is that the recent glacial retreat has not allowed sufficient time for the processes of natural selection to result in microadaptation of white spruce in that area (Li *et al.* 1997). Previous studies have provided some evidence in support of dividing the entire population of white spruce into an eastern and a western population (Nienstaedt and Teich 1972). Although it may be an over-simplification, such a division is reinforced by the existence of refugia and migration routes from the recent glacial period (Nienstaedt and Teich 1972). It is theorized that white spruce populations which survived the Illinoisan and Wisconsin glaciers have resulted in genetically distinct eastern and

western populations, with the demarcation line between them located at approximately 95°W (Nienstaedt and Teich 1972).

Furnier *et al.* (1990) observed that northern and western populations of white spruce performed poorly at a test site in Minnesota. Cherry and Parker (2003) discovered that when planted in the north, southern white spruce provenances outperformed local sources and predicted that northern sources would perform better when transferred to warmer locations. Lesser and Parker (2004) found that height growth (among other traits) could be explained by longitude and various temperature variables related to the growing season. White spruce growth in Ontario appeared to be affected by patterns of precipitation as observed along a longitudinal gradient (Lesser and Parker 2004). This study also found that southern sources outperformed local provenances (Lesser and Parker 2004).

### Natural selection

Heredity is not the sole cause of variation in nature since environmental effects can also be responsible for observed differences (Erikson and Ekberg 2001). Natural selection is the process by which some individuals exhibit a higher frequency of reproductive success that is attributable to the individuals' fitness under the environmental conditions of the growing site (Erikson and Ekberg 2001). Natural selection is the primary process resulting in continuous clinal variation, especially for northern species where the environment is highly variable (Morgenstern 1996). But there has yet to be the development of ecological theories that can explain the non-linear dynamics of spatially heterogeneous systems (Wu and Hobbs 2002). Ultimately, the high level of complexity and the existence of non-linear relationships create a large amount of uncertainty surrounding landscape dynamics (Li and Wu 2007).

Heslop-Harrison (1964) contends that populations are best suited to the local conditions under which they are growing. If populations are adapted to their local environment as a result of natural selection, then it can be assumed that they would exhibit their adaptive behaviours when planted on a site outside of their native habitat (this is the basis for provenance testing) (Wu and Ying 2004). The concept of local optimality would likely be true if natural selection was the sole factor affecting adaptation and fitness (Ying and Yanchuk 2006). However in many instances, local optimality is not observed because other forces are constraining the effectiveness of natural selection, such as gene flow, adaptational lag, random genetic drift or historical events (Ying and Yanchuk 2006). Populations that are sub-optimally adapted to the local environment often exhibit a high amount of genetic diversity (Matyas 1996). The current genetic composition of a population should be viewed as one of many possible configurations and therefore it should be considered transient and not optimal (Erikson and Ekberg 2001).

Pattern recognition and process-seeking are at the core of natural science. The first steps are observation and establishment of the pattern of a natural phenomenon from which analysis, inference and testing of the causative process can then be used to quantify the pattern-process in a predictive model. A model is more robust if it is based on an understanding of the process rather than the pattern. The aim of provenance research is the identification of patterns and processes. Significant correlations between provenance response and climate variables implies a causative process of natural selection in the environment with the assumption that the stronger the correlation, the stronger the effects of natural selection. However, the verification of natural selection through experimental repeatability is not possible, thus it is inferred from statistics (Ying

and Yanchuk 2006). Regressions used to relate the growth of a seed source to climate are called response functions (Thomson and Parker 2008). The Cauchy function is a mathematical model used to estimate tree growth according to some optimum environmental variable (Lindgren and Ying 2000). The benefits of using the Cauchy function are that its parameters are biologically meaningful and they are easy to interpret (Lindgren and Ying 2000).

Climate is considered to be the driving force behind the spatial genetic differentiation of forest tree species (Rweyongeza *et al.* 2006; Ying and Yanchuk 2006). Patterns of variation in species with wide ranges tend to be dominated by regional climate-driven selection (Heslop-Harrison 1964). However, it is very challenging to determine the effects of climate-driven selection since populations can have different strategies to adapt to climate (Heslop-Harrison 1964). It is possible that one environmental variable could have a dominant selective influence so that the survival of a population would depend entirely on its ability to adapt to that one influence (Heslop-Harrison 1964). Realistically, environmental variables always interact in nature and in habitats where a number of environmental factors vary seasonally, adaptation could be more complex (Heslop-Harrison 1964).

#### Landscape ecology and landscape genetics

Landscape ecology studies the ecological response to spatial patterns (Turner *et al.* 2001). Historically, ecology often assumed spatial homogeneity either as a matter of convenience or simplicity and heterogeneity was usually seen as an unwelcome complication (Pickett and Cadenasso 1995). On the contrary, landscape ecologists view spatial heterogeneity as the main causal mechanism in ecosystems and spatial and

temporal dynamics are given equal consideration (Pickett and Cadenasso 1995). Spatial dynamics include the relationships between biotic interactions, abiotic constraints and disturbances (Turner *et al.* 2001), while temporal dynamics include population, community and evolutionary relations (Pickett and Cadenasso 1995).

Currently, researchers are proficient in quantifying landscape patterns but are lacking a sound understanding of the ecological importance of these quantified patterns. Indeed, studying the relationship between pattern and process is vital, even as it presents many challenges. The complexity of landscapes means that simple cause and effect relationships are not likely to be discovered. Despite a relatively small body of empirical evidence, there has been considerable progress in the study of spatial structure which is now understood to play an essential role in genetic processes at the individual, population and community levels (Turner *et al.* 2001).

It is worthwhile to explore some facets of population genetics before examining those of landscape genetics which can be seen as a cross between landscape ecology and population genetics (Manel *et al.* 2003). The metapopulation concept is often used in population genetics to describe species with large continuous populations that are divided into smaller spatial units depending on the movement range of individuals (Hanski 1999). Metapopulation studies are primarily interested in the migration, extinction and establishment of populations (Hanski 1999). In metapopulation analysis, it is assumed that an environment is divided into discrete patches of suitable habitat surrounded by areas of unsuitable habitat (Hanski 1999). Environments in nature, however, are complex so that the demarcation between suitable and unsuitable habitats may be more gradual than what is assumed in metapopulation studies (Hanski 1999). The effects of heterogeneous space on the dynamics of populations is acknowledged, but

not often studied in population genetics (Hanski 1999), which is why the field of landscape genetics is more appropriate to the current study. In addition, the field of population genetics focuses more on molecular approaches to studying genetic variation.

It is now known that spatial heterogeneity has influenced gene flow and population differentiation, but the underlying processes are still not well understood (Pickett and Cadenasso 1995). The field of landscape genetics studies the effects of landscape characteristics on the spatial distribution of genetic variation (Murphy *et al.* 2008). Unlike ecological genetics, landscape genetics incorporates a strong spatial element in the examination of genetic variation. Landscape genetics can be used to identify bioregions and to assess species' response to ecological variables and climate change (Storfer *et al.* 2007). Studies in this field are often complicated by the fact that genotypic measurements do not have a direct ecological interpretation, unlike ecological variables such as soil moisture or tree height (Murphy *et al.* 2008). Population genetic data obtained from known geographic locations facilitates the identification of spatial genetic patterns (Manel *et al.* 2003). Following data collection, statistics may be used to elucidate the spatial genetic pattern and to correlate it with landscape features; the spatial genetic pattern can then be visually represented using GIS (Manel *et al.* 2003). Accurate population subdivision may allow for the delineation of evolutionarily significant units, management units or conservation units (Manel *et al.* 2003).

According to Holdregger and Wagner (2008), as a relatively new field, there does not yet exist a conceptual framework within which to study landscape genetics. Likewise, there is no prescribed set of statistics or analytical tools, thus, landscape genetics combines approaches and methods from the fields of landscape ecology, population genetics and spatial statistics. Traditionally, the assessment of genetic

variation and population differentiation has been carried out through quantitative genetic methods in common-garden experiments which have been criticized as being notoriously labour and time intensive. In addition, it has been said that common-garden studies do not provide sufficient molecular genetic information. Genomic methods focused on the molecular level are sometimes considered superior, but admittedly, there are inherent difficulties in associating them with environmental variables in natural landscapes (Holdregger and Wagner 2008).

Population dynamics are primarily influenced by spatial heterogeneity, however this relationship has not been very well studied (Kareiva *et al.* 1990). A common approach to modeling complex environments is to subdivide the area into many smaller, spatially explicit patches (Kareiva *et al.* 1990). Some natural phenomena, such as ecosystems, can be divided or decomposed into discrete functional components within hierarchical systems whereby the component dynamics at one level influence those occurring at other levels in the hierarchy (Urban *et al.* 1987). Landscapes are generally arranged according to a sort of vertical structure where they are spatially nested and each level contains the level below it in the hierarchy, thus, complex landscapes can be broken down into simpler units to identify the results of patterns at different scales (Urban *et al.* 1987).

### Ecological Land Classification

Early land classification attempts in Canada were driven first by mineral exploration, then by agriculture and finally by the need for a renewable resource database (Oswald 1992). Ecological land classification (ELC) is used both for the development of resources and for conservation efforts (Bailey 1983). The units of ELC



have become the basis for estimations of ecosystem productivity and of ecosystem response to management practices (Bailey 1983).

In 1976, the Canada Committee on Ecological Land Classification (CCELC) was formed to develop a uniform, national ecological approach to the classification and mapping of terrestrial ecosystems. The ELC maps were to be used to ensure sustainable resource management and planning. However, researchers in the late 1980's produced various reports and studies which determined that although the CCELC's maps were conceptually sound, the spatial units required revision. It was also deemed necessary to include new technologies in the mapping process as well as to provide basic narrative descriptions of the levels of classification along with the maps (Marshall *et al.* 1996).

The Green Plan of 1990 emphasized the necessity for revisions of the 1976 ELC in an effort to shift the focus of environmental management from individuals to ecosystems (Marshall *et al.* 1996). To that end, the Green Plan established that on-going federal reporting of the state of Canada's environment would use ecosystems as the basic unit of assessment. It was thus that the Ecological Stratification Working Group was formed in 1991; it was a collaboration of Agriculture and Agri-Food Canada's Centre for Land and Biological Resources Research and Natural Resources Canada's Canadian Forest Service. Much like the initial classifications, the revisions included existing national maps such as Ecoclimatic Regions of Canada, Forest Regions of Canada and Physiographic Regions of Canada as well as the previous ELC 1976 maps. The process also included the use of LANDSAT imagery to ensure that boundaries were consistent across provinces and territories. In Ontario, the process included the works of Wickware and Rubec (1989) and Hills (1976).

The levels of land classification are arranged in a hierarchy from ecozone, ecoregion, ecodistrict, ecosection, ecosite to ecoelement (Marshall *et al.* 1996).

Ecozones, the broadest level, are characterized by macroclimate, major vegetation types and subcontinental physiographic formations (Marshall *et al.* 1996). Ecoregions are delineated according to regional physiography, surface geology, climate, vegetation, soil, water and fauna (Marshall *et al.* 1996). The subsequent levels are all contained within the next-highest level and are based on more and more regional environmental characteristics (Marshall *et al.* 1996). On a smaller scale of about 1:2,000,000, ecodistricts are considered to be useful units for environmental management (Marshall *et al.* 1996). Land classification boundaries are delineated according to changes in climate, vegetation, landform, drainage and soil (Rowe 1996). Although climate is the main driver in landscape variation, it is also affected by differences in landform which modify the climate over a given area (Rowe 1996). Thus, a logical basis for ecosystem delineation is observed climate as modified by landform (Bailey 1987).

According to Bailey and Zoltai (1985), there are two main approaches to ELC. The first approach assumes that one component, such as climate, exerts a dominant influence on an ecosystem; this is the traditional and preferred method. The second approach assumes that ecosystems are in a state of balance, so that a stable combination of factors should be considered in the classification (Bailey and Zoltai 1985). Quantitative and qualitative techniques can be applied to both approaches, however, there exists no clear consensus among researchers about which is best for the development of ELC (Hargrove and Hoffman 2005). It has been suggested that a quantitative approach allows the concept of ELC to be expanded into new realms; for example, a dynamic aspect can be added to ELC through quantitative methods that track

changes as a region shifts from one state to another over time (Hargrove and Hoffman 2005).

Whether approached from a quantitative or qualitative view, ecological variation occurs over a transitional zone so that the definition of boundaries will always be somewhat subjective (Bailey 1983). As stated in the introduction, there have not been any efforts to revise ELC map divisions for Canada since the re-release of the maps in 1995. In fact, the criteria most commonly used in ELC are assumed to be appropriate, but they have not been verified (Bailey and Zoltai 1985). Maps of ELC for Ontario were based on the works of Wickware and Rubec (1989) and Hills (1961), however, neither works included explicit descriptions of the methodologies or ecological theories used in the delineation of map units (Perera *et al.* 1996). McMahon *et al.* (2004) contend that there is no widely accepted and clearly articulated theoretical basis for ELC in North America which is problematic given that classification methods should be explicitly based on relevant ecological theory (Rowe and Sheard 1981).

## METHODS

White spruce seed was obtained from 127 different sources located in Ontario and western Quebec. The collected seed was from wild stands and each collection was composed of five or more open-pollinated families from within a 1 km<sup>2</sup> area. The seed was provided by cooperatives and was seeded in Jiffy pots between January and March 2002 in the Lakehead University greenhouse (Lesser and Parker 2004). A map of seed sources and test locations is shown in Figure 1.

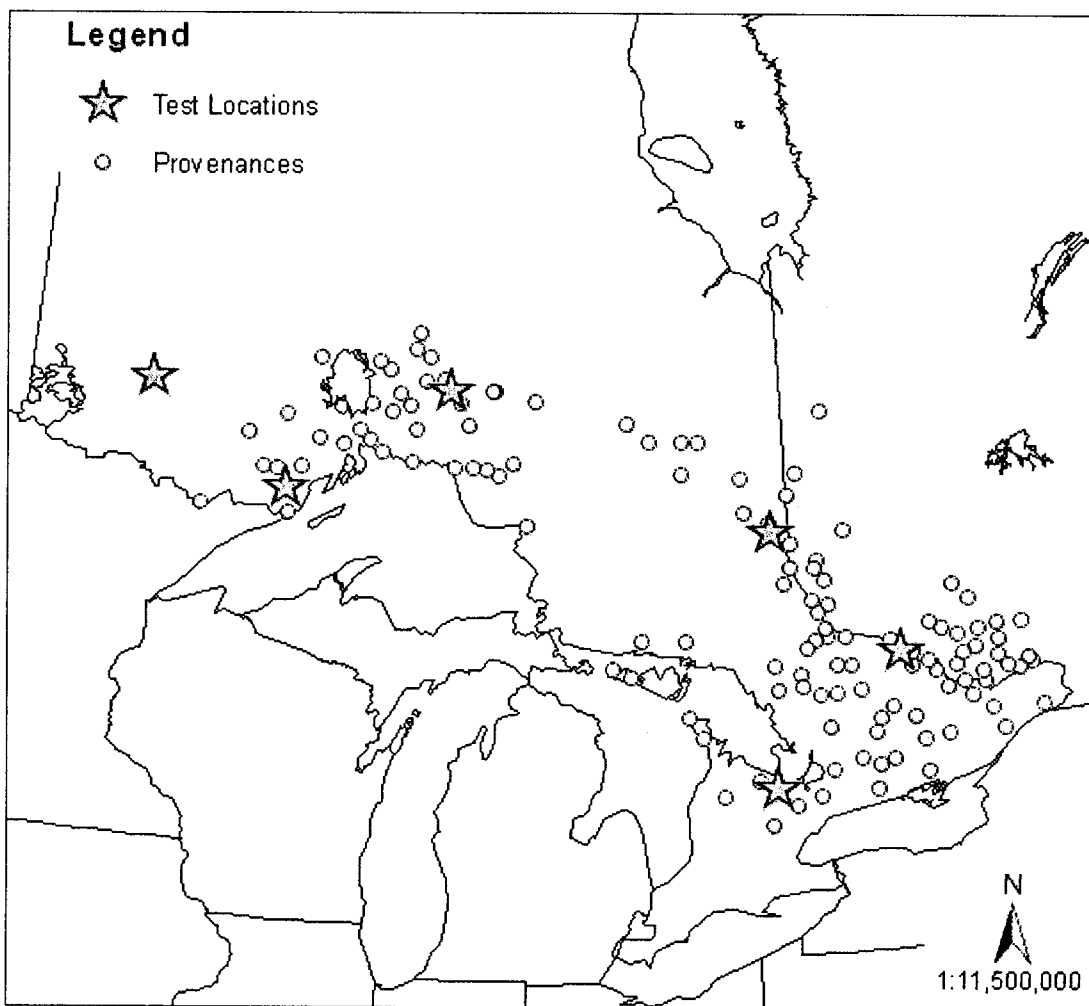


Figure 1. Location of white spruce seed sources and provenance test sites in Ontario.

From west to east, test sites were located at Dryden, Kakabeka Falls, Longlac, Angus, Englehart and Petawawa. Using 2m spacing, all tests were established in June

and July of 2002 except for the Angus test which had previously been a greenhouse trial and was later established in the field in 2003. The six test sites were set up as completely randomized designs with three blocks, each having 10 single tree plot repetitions of all 127 provenances. Geographic coordinates for each of the test sites and provenances are shown in Table 1 and 2, respectively.

Table 1. Geographic coordinates of provenance test sites.

Provenance Test	Longitude	Latitude	Elevation (m)
Dryden	-92.59	49.77	406
Kakabeka Falls	-89.70	48.41	373
Longlac	-86.35	49.81	338
Angus	-80.00	44.30	220
Englehart	-79.87	47.79	209
Petawawa	-77.47	46.05	135

Table 2. Geographic coordinates of white spruce provenances.

Prov. No.	Lat. (dd)	Long. (dd)	Elev. (m)	Location	Prov. No.	Lat. (dd)	Long. (dd)	Elev. (m)	Location
1	45.07	74.83	80	Cornwall	46	46.25	78.50	183	Canton Cameron
2	45.67	74.97	155	St-Andre Avellin	47	45.87	78.70	442	Oster
3	45.73	75.05	152	St-Andre Avellin	48	49.35	78.70	289	Lac Wawagosis
4	46.25	75.08	259	Camp 27	49	46.72	78.83	335	Lac Smith
5	45.62	75.23	100	Thurso	50	46.28	78.85	229	Rutherglen
6	45.65	75.45	15	Poupee	51	47.03	78.87	335	Baie Kelly
7	46.03	75.57	213	Lac Iroquois	52	46.38	78.90	305	Mattawan Tp
8	46.25	75.58	304	Ruisseau Murphy	53	44.47	78.90	280	Eldon
9	45.82	75.60	168	Val-Des-Bois	54	45.03	78.92	335	Hindon Tp
10	44.83	75.63	100	Augusta	55	47.33	78.93	305	Canton Gaboury
11	45.12	75.80	90	Marlborough Tp	56	46.60	79.00	306	Jocko Tp
12	45.47	75.92	107	Breckenridge	57	47.20	79.02	305	Lac Guay
13	45.62	75.93	244	Wakefield	58	45.47	79.03	370	Sinclair Tp
14	46.20	75.95	183	Bouchette	59	46.78	79.12	305	Canton Mercier
15	45.97	76.03	152	Aylwin	60	46.23	79.13	245	Bonfield Tp
16	46.63	76.07	244	Grand-Remous	61	44.12	79.18	290	Scott
17	45.32	76.18	121	Antrim	62	46.13	79.27	275	Chisholm
18	45.52	76.30	91	Wyman	63	48.53	79.30	224	Lac Hebecourt
19	46.15	76.33	274	Lac Cayamant	64	45.78	79.42	381	Strong
20	46.85	76.35	305	Lac Du Faucard	65	45.62	79.42	300	Armour Tp
21	45.75	76.40	213	Ladysmith	66	48.22	49.48	289	Lac Labyrinthe
22	46.25	76.63	274	Lac Osborne	67	47.58	79.50	213	N.Dame des Quinze
23	45.47	76.63	121	Renfrew	68	47.25	79.52	240	Lorrain Tp
24	44.82	76.68	180	Silver Lk	69	45.48	78.75	460	Peck Tp
25	45.68	76.80	137	Beachburg	70	47.03	79.68	306	Cobalt
26	45.90	76.27	244	Grove Creek	71	45.58	79.87	275	McKellar
27	46.35	76.87	274	Riviere-Coulogne	72	47.87	79.92	215	Englehart
28	45.83	76.95	122	Lac Cranson	73	45.92	79.93	245	East Mills
29	44.33	77.13	107	Tyendinaga	74	43.75	80.12	427	Erin
30	44.78	77.15	274	Barrie	75	44.35	80.33	503	Osprey
31	45.97	77.25	152	Sheenboro	76	48.03	80.37	304	Kirkland Lake
32	45.08	77.28	305	Denbigh	77	48.48	80.42	290	Bowman Tp
33	45.77	77.28	150	Alice	78	44.17	81.00	305	Bentinck
34	45.98	77.45	160	PNF	79	49.02	81.23	289	Clute 2
35	46.17	77.67	183	Rolphon	80	49.77	85.42	245	Pagwa
36	45.27	77.70	366	Carlow	81	49.03	81.58	215	Fraserdale
37	44.55	77.75	229	Marmora	82	48.58	81.62	290	Robb To
38	45.10	77.97	396	Bancroft	83	45.25	81.63	205	St. Edmunds
39	44.48	78.02	236	Dummer	84	46.32	81.65	243	Nairn Tp
40	44.92	78.07	365	Anstruther Tp	85	49.05	82.25	215	Gurney Tp
41	44.17	78.12	274	Haldimand	86	46.33	82.50	249	Proctor
42	45.53	78.27	396	Whitney	87	49.30	82.70	289	Cargill
43	44.60	78.38	300	Harvey	88	45.83	82.75	191	Elizabeth Bay
44	47.70	78.40	305	Canton Sebille	89	45.95	83.08	183	Meldrum Bay
45	45.87	78.45	442	Lister	90	49.62	84.58	275	Amott Tp

Table 2. Continued.

Prov. No.	Lat. (dd)	Long. (dd)	Elev. (m)	Location	Prov. No.	Lat. (dd)	Long. (dd)	Elev. (m)	Location
91	47.92	84.75	306	Wawa	110	49.47	87.57	460	Parks Lk
92	48.78	85.05	457	Bouchard	111	50.03	87.65	305	S Onaman R
93	48.62	85.32	305	White R	112	48.91	87.77	195	Mountain Bay
94	49.77	85.47	236	Highway 11	113	50.15	87.88	335	Auden
95	48.70	85.58	305	Moberg Tp	114	49.55	88.00	365	Beardmore
96	48.72	85.87	335	Strathearn	115	49.07	88.02	245	Limestone
97	49.28	85.97	305	Manitouwadge	116	49.20	88.22	229	Nipigon
98	49.60	86.15	305	Caramat	117	48.98	88.54	267	Stewart Lk
99	48.70	86.25	240	Pic R	118	49.05	89.05	275	Chief Bay
100	49.92	86.48	305	Kenogami	119	50.15	89.12	305	Waweig Lk
101	50.20	86.78	335	Nakina	120	48.65	89.41	457	LU Woodlot
102	49.87	86.87	365	False Crk	121	48.02	89.65	306	Pigeon R
103	50.53	87.02	335	O'Sullivan	122	49.37	89.75	425	Twist Lk
104	49.22	87.07	335	Long Lk	123	48.62	89.90	410	Shabaqua
105	50.32	87.09	328	Anaconda Rd	124	48.62	90.18	459	Shebandowan
106	44.98	81.37	191	Easnor	125	49.07	90.52	489	Upsala
107	48.78	87.12	200	Terrace Bay	126	48.07	91.42	428	Eva Lk
108	49.55	87.18	404	Grandpa Rd	130	44.00	79.67	240	King
109	49.70	87.42	365	Jellicoe					

Source: Adapted from Thomson (2008)

In August of 2007, the tests were re-measured for height, root collar diameter and elongation, however, this study only utilized the height data. Height data from each test site were analyzed for normality and heterogeneity using the CHART and UNIVARIATE procedures in SAS (SAS INSTITUTE 2000). The frequency distributions were observed for normal distribution patterns and values of skewness and kurtosis were obtained.

It is common in provenance testing to perform statistical analysis separately for all of the test sites and it is assumed that provenance performance will vary among sites. In order to test this assumption, a general Analysis of Variance (ANOVA) was carried out using tree height data from all of the tests using the GLM procedure in SAS (SAS INSTITUTE 2000) (equation 1); the Estimated Mean Squares (EMS) table and tests for significance are presented in Appendix I.

$$Y_{ijkl} = \mu + S_i + B_{(i)j} + P_k + SP_{ik} + PB_{(i)jk} + \epsilon_{(ijk)l} \quad [\text{Eq. 1}]$$

Where:

$$i = 1,6 \quad j = 1,3 \quad k = 1,127 \quad l = 1,10$$

$Y_{ijk}$  = the height of the trees measured in centimetres

$\mu$  = the overall mean

$S_i$  = the random effect of the  $i^{\text{th}}$  site

$B_{(i)j}$  = the random effect of the  $j^{\text{th}}$  block at the  $i^{\text{th}}$  site

$P_k$  = the random effect of the  $k^{\text{th}}$  provenance

$SP_{ik}$  = the interaction effect of the  $i^{\text{th}}$  site and  $k^{\text{th}}$  provenance

$PB_{(i)jk}$  = the interaction effect of the  $k^{\text{th}}$  provenance in the  $j^{\text{th}}$  block

$\epsilon_{(ijk)l}$  = the random effect of the  $l^{\text{th}}$  replicate of the  $k^{\text{th}}$  provenance of the  $i^{\text{th}}$  test site and the  $j^{\text{th}}$  block (assumed to be IID  $N(0, \sigma_\epsilon^2)$ )

Significant differences in tree height among provenances was tested using a random effects model (equation 2). Type I Sum of Squares were used to account for the unbalanced designs used in this study. Both site and provenance were considered to be random effects since the results will be generalized; the sites represent a sample of locations in Ontario and the provenances represent a random sample of all possible white spruce populations in Ontario and western Quebec. The EMS table and the tests for significance for equation 1 are displayed in Appendix I. Provenance differences at the individual test sites would be indicative of genetic variation and would enable further data analysis.



$$Y_{ijk} = \mu + P_i + B_j + PB_{ij} + \epsilon_{(ij)k} \quad [\text{Eq. 2}]$$

Where:

$$i = 1, 127 \quad j = 1, 3 \quad k = 1, 10$$

$Y_{ijk}$  = the height of the trees measured in centimetres

$\mu$  = the overall mean

$P_i$  = the random effect of the  $i^{\text{th}}$  provenance

$B_j$  = the random effect of the  $j^{\text{th}}$  block

$PB_{ij}$  = the interaction effect of the  $i^{\text{th}}$  provenance and the  $j^{\text{th}}$  block

$\epsilon_{(ij)k}$  = the random effect of the  $k^{\text{th}}$  replicate of the  $i^{\text{th}}$  provenance and the  $j^{\text{th}}$  block

(assumed to be IID  $N(0, \sigma_\delta^2)$ )

Coverages of the national ELC levels were downloaded from the Agriculture and Agri-Food Canada website ([http://sis.agr.gc.ca/cansis/nsdb/ecostrat/gis\\_data.html](http://sis.agr.gc.ca/cansis/nsdb/ecostrat/gis_data.html)). The ecodistrict ELC coverage was simplified to include only those ecodistricts relevant for this study (Figure 2A). Provenances were then grouped according to ecodistricts as shown in Figure 2B. It is hypothesized that the ecodistrict unit of classification is representative of the various environmental selection pressures exerted in these areas. By grouping the provenances into ecodistricts, we expect to see that provenances within an ecodistrict will have adapted similarly to the environmental conditions. Likewise, we expect that adaptive differences will be apparent between ecodistricts, given the different environmental conditions at each ecodistrict.

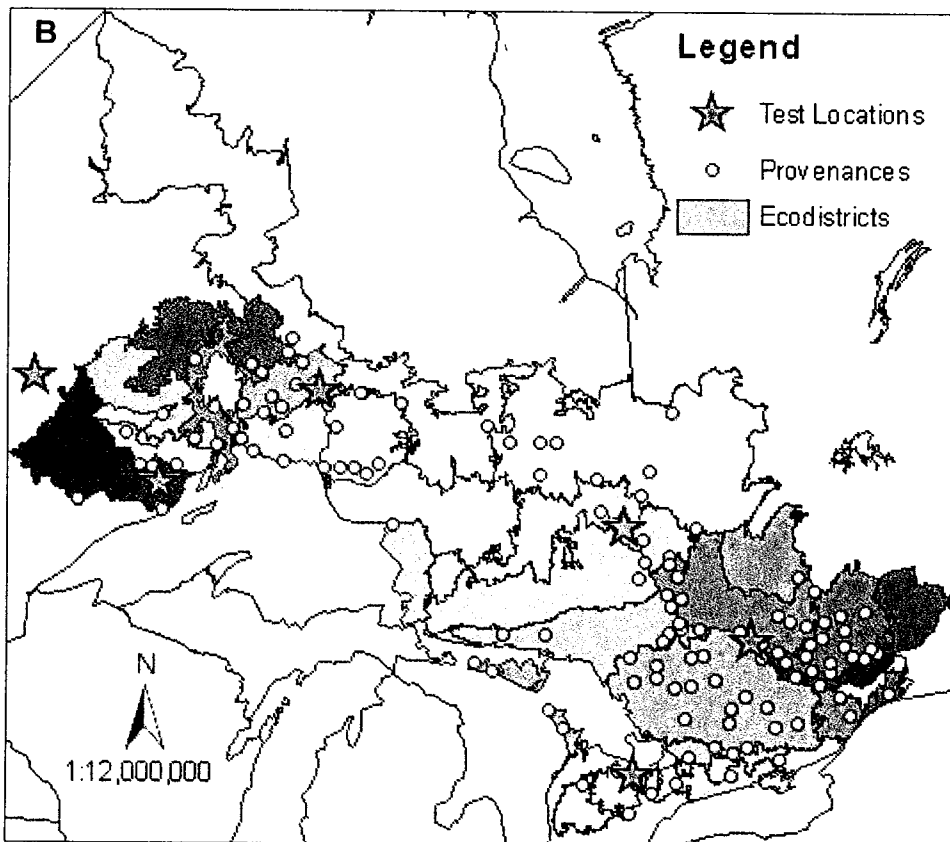
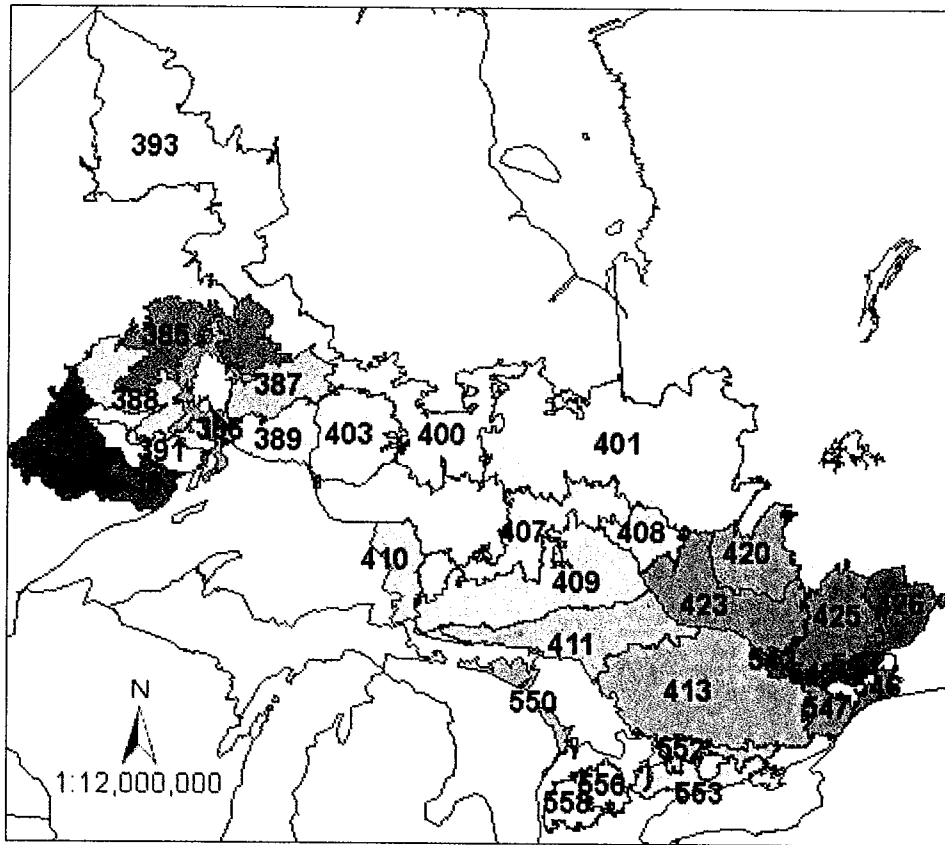


Figure 2. Map of ecodistricts (a) and location of provenances within ecodistricts (b).

Climatic data for the period 1971 to 2000 were obtained from Dr. Dan McKenney, Canadian Forest Service, Landscape Analysis and Application Section, Great Lakes Forestry Centre. Ontario-wide grids along with point data for the 6 test sites were provided for 65 climate variables. Maximum monthly temperature, minimum monthly temperature and mean monthly precipitation constituted 36 of the climate variables. The remaining 29 variables were derived using the BIOCLIM/ANUCLIM and SEEDGROW prediction systems (McKenney 2004). The derived variables consisted of growing degree days, temperature and precipitation amounts by quarter and growing period as well as growing season length, beginning and end. Elevation was also provided for each test site.

A nested ANOVA ( $p \leq 0.05$ ) was used to test for significant differences among the ecodistricts and to test for significant differences between provenances within ecodistricts. This was treated as a nested design since the provenances were grouped within the ecodistricts (equation 3). The EMS table and the tests for significance are shown in Appendix I. In situations where there were found to be significant differences between provenances within an ecodistrict, another random effects ANOVA ( $p \leq 0.05$ ) was carried out on only those provenances in the ecodistrict (equation 4). The EMS table and the tests for significance are shown in Appendix I. Least Significant Difference (LSD) tests with  $p \leq 0.05$  were then used to subdivide the ecodistricts. Using ArcMap (ESRI 2006), the ecodistrict polygons were divided so that the resulting subdivisions were as similar in area as possible. ANOVA was then repeated to test if provenances within a sub-ecodistrict were significantly different and if there were significant differences between ecodistricts. Since these subdivisions altered the original ecodistricts, they will hereafter be referred to as operational ecodistricts (OE).

$$Y_{ijk} = \mu + G_i + P_{(i)j} + E_{(i)jk} \quad \text{[Eq. 3]}$$

Where:

$$i = 1, 30 \quad j = 1, 127 \quad k = 1, 10$$

$Y_{ijk}$  = the height of the trees measured in centimetres

$\mu$  = the overall mean

$G_i$  = the fixed effect of the  $i^{\text{th}}$  ecodistrict

$P_{(i)j}$  = the fixed effect of the  $j^{\text{th}}$  provenance treatment in the  $i^{\text{th}}$  ecodistrict

$E_{(i)k}$  = the random effect of the  $k^{\text{th}}$  replicate of the  $j^{\text{th}}$  provenance in the  $i^{\text{th}}$  group

(assumed to be IID  $N(0, \sigma^2)$ )

$$Y_{ij} = \mu + P_i + E_{ij} \quad \text{[Eq. 4]}$$

$$i = 1, 127 \quad j = 1, 10$$

Where:

$Y_{ij}$  = the height of the trees measured in centimetres

$\mu$  = the overall mean

$P_i$  = the random effect of the  $i^{\text{th}}$  provenance

$E_{(ij)}$  = the random effect of the  $j^{\text{th}}$  replicate of the  $i^{\text{th}}$  provenance (assumed to be IID  $N(0, \sigma^2)$ )

Provenance means were calculated for each test site using the MEANS procedure

in SAS (SAS INSTITUTE 2000). As a screening procedure, mean height data were

related to 65 climate variables and 3 geographic variables (latitude, longitude and

elevation) using quadratic regression with the REG procedure in SAS (SAS INSTITUTE

2000) (equation 5). Variables were discarded if  $p$  was greater than 0.200 and/or  $R^2$  was

less than 0.4000. In a similar screening process, Rehfeldt *et al.* (2002) used a

significance level of  $p \leq 0.25$ , where regressions were discarded if  $p$  was greater than 0.25 or if  $R^2$  was less than 0.4000. The quadratic regression curves for the OE were displayed with a confidence interval of 80% since a  $p$  value of 0.200 was used for this step. The purpose of displaying the confidence interval was to assess whether the OE response curve was representative of the response of the provenances within the OE. If the observations fell within the confidence interval, then the OE response curve would be considered as representative of provenance response.

$$Y_{ij} = \mu + \beta_0 + \beta_1 X_j + \beta_2 X_j^2 + E_{ij} \quad [\text{Eq. 5}]$$

Where:

$$i = 1, 127 \quad j = 1, 10$$

$Y_{ij}$  = height of replication  $j$  for seed source  $i$

$\mu$  = the overall mean

$X_{ij}$  = the value of a climatic explanatory variable for replication  $j$  of seed source  $i$

$\beta_0, \beta_1, \beta_2$  = regression coefficients

$E_{ij}$  = the random effect of the  $j^{\text{th}}$  of the  $i^{\text{th}}$  provenance (assumed to be IID  $N(0, \sigma_e^2)$ )

Environmental variables with significance  $p \leq 0.200$  and  $R^2 > 0.4000$  were selected for use in the Cauchy functions. Provenance means were used to develop response functions for both individual provenances and for the OE groupings of provenances. The response functions were developed using the Cauchy function in SigmaPlot (Systat Software Inc. 2002), as shown below (equation 6). The response curve produced from the Cauchy function is presented in Figure 3.



$$y = \frac{a}{1 + \left(\frac{x - x_0}{b}\right)^2} \quad \text{[Eq. 6]}$$

Where:  
 x = the value of a variable used to describe the climate of a geographic location  
 y = the performance of a seed source for a specified value of x  
 a = the optimum performance of a seed source, represented by the peak of the response curve  
 x<sub>0</sub> = the value of the climate variable x that can be used to optimize performance of a seed source  
 b = the distance between the x values measured symmetrically around x<sub>0</sub>, within which the seed source achieves above 80% of its optimum performance (this value is related to the width of the response curve and can be used to describe genetic flexibility)

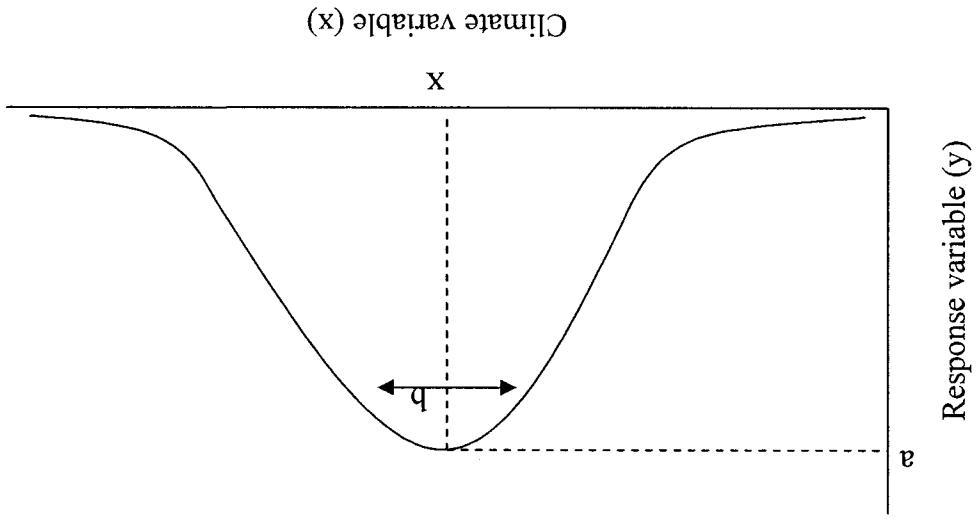


Figure 3. Example of the response curve produced by the Cauchy function.

Boxplots were added to each of the response curves in SigmaPlot (Systat Software Inc. 2002) to show the environmental conditions of the OE so that a comparison could be made between the conditions needed for optimal performance and current conditions. First, the ecodistrict coverage was converted to a grid format for each of the 55 OE; these OE grids were then used as geographic 'cookie cutters'. The range of the climatic variables used in the boxplots was obtained via the 'describe' function in grid using the Arc extension of the ArcInfo Workstation (ESRI 2006) for each of the four climate variables using the grid 'cookie cutters'. To simplify these graphs, the boxplots were displayed as a solid black bar along the x-axis.

Finally, using ArcMap (ESRI 2006), the values obtained from the Cauchy functions were used to create maps of geographic areas that could produce optimal provenance height. Contour lines were generated to demonstrate the exact locations where species would attain optimal height growth. An 'optimum range' was calculated based on the values from the Cauchy function to show the areas where provenances would achieve up to 80% of their optimum height growth. Maps of optimal provenance height performance were then compared with the 1995 ecodistrict maps.

## RESULTS

The height data for all test sites were approximately normally distributed.

Summary statistics for provenance height at each test site are shown in Table 3.

Frequency distributions are presented in Appendix II. The high mortality at the Longlac site resulted in a very small number of observations compared to the other test sites.

Mean provenance heights were tallest at the Kakabeka test and shortest at the Dryden

and Longlac tests. Values for mean and median were similar for all sites whereas the

values for mode were slightly different from the mean and median values. Measures of

skewness and kurtosis were less than 1 across all tests. Post hoc LSD tests revealed that

most of the test sites differed in terms of height growth, except for the Dryden and

Longlac sites which were found to be statistically similar.

Tree heights were significantly different among test sites, among provenances,

among blocks and also for the site by provenance interaction; the provenance by block

Table 3. Summary statistics for provenance height (cm) among test sites.

Test Site		*Results from LSD tests performed on the entire data set (equation 1).				
Statistic	Dryden	Kakabeka	Longlac	Angus	Englehart	Petawawa
N	3419	3564	257	2463	2275	2499
Min.	3.0	8.0	3.0	13.0	14.0	16.0
Max.	114.0	150.0	86.0	114.0	157.0	176.0
Mean	38.3	68.4	39.2	54.9	65.1	63.2
Median	36.0	68.0	38.0	55.0	63.0	62.0
Mode	31.0	63.0	33.0	50.0	70.0	61.0
St. Deviation	15.58	23.23	15.69	13.44	21.07	21.72
Variance	242.62	539.41	246.31	180.70	444.01	471.71
Skewness	0.6558	0.2207	0.4147	0.2074	0.5007	0.4150
Kurtosis	0.5613	-0.0910	-0.0864	0.2472	0.3113	0.2563
t Grouping*						
			A	E	D	B
						C



interaction was not significant (Table 4). The finding of a significant site by provenance interaction suggests the existence of a genotype by environment interaction. Post hoc LSD tests revealed that most of the sites were significantly different from each other while the Dryden and Longlac sites exhibited statistical similarities. The drastically different number of observations at the test sites as seen in Table 3 is reflective of mortality; the Kakabeka test exhibited the highest number of observations at 3564, while the Longlac site had the lowest number at only 257. LSD results for provenances across all test sites are displayed in Appendix III; provenance 1, from southeastern Ontario, was identified as the top performing provenance with a mean overall height of 67.033cm while provenance 100, from northcentral Ontario, was identified as the poorest performer with an overall height of 44.135cm.

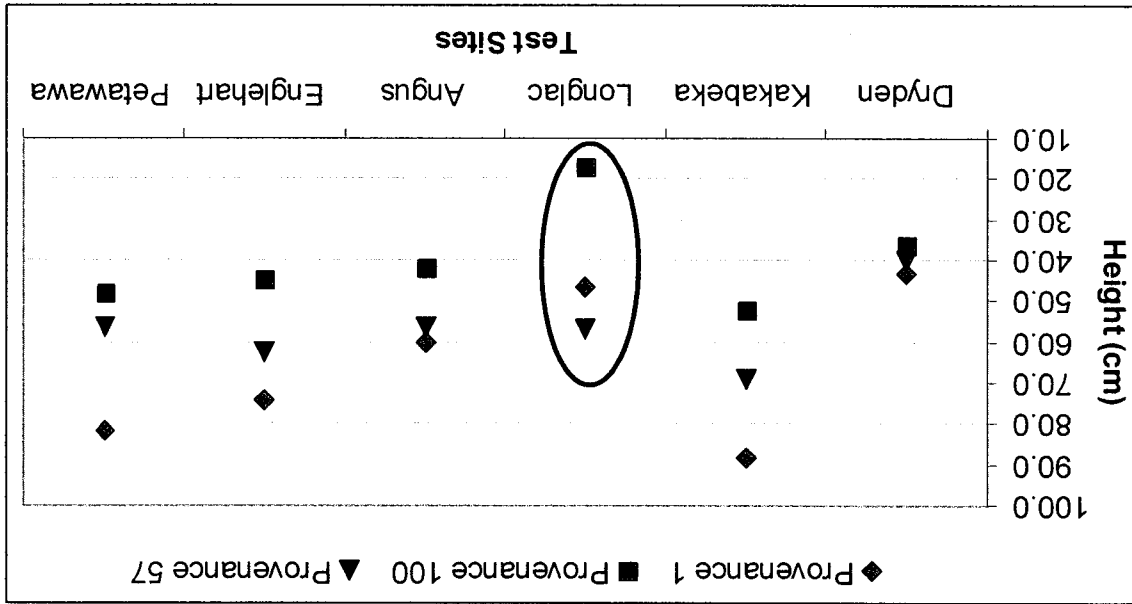
Source	D.F.	Type I SS	MS	F value	Pr > F
Site	5	1992696.533	398539.307	1173.84	< 0.0001
Prov	126	346868.667	2752.926	8.11	< 0.0002
Blk(site)	12	195349.168	16279.097	47.95	< 0.0003
Site*Prov	615	266933.539	434.038	1.28	> 0.0004
Prov*Blk(site)	1258	409876.331	324.313	0.96	0.8592

Table 4. Test for differences in height among sites, provenances and blocks.

Significant differences in height occurred among provenances and blocks (Table 5). Detailed ANOVA results are presented in Appendix IV. The finding of significant differences among provenances for height at the individual test sites supports the existence of genetic variation and enabled further study of the data. It is interesting that despite the existence of a strong block effect, the provenance by block interaction was not significant. Provenance means for each test site can be found in Appendix V. Figure 4 shows the relative performance of three provenances; the provenance by site

Thirty ecodistricts in Ontario and western Quebec were represented by provenances. Provenance distribution among the ecodistricts was uneven, with about half of the ecodistricts being represented by only one or two provenances. Figure 5 shows the number of provenances present in each ecodistrict. Significant differences were found between ecodistricts (Table 6), which supports the earlier assumption that

Figure 4. Mean height of three provenances at each test site; the oval indicates the provenance by site interaction.



Two of the blocks at the Longlac test exhibited complete mortality which altered the degrees of freedom and prevented the tests for the blk effect and for the prov\*blk effect. Two provenances at the Petawawa test exhibited complete mortality at block 1 which changed the degrees of freedom for the prov term (124) and for the prov\*blk term (248).

Statistics		Provenance Test					
Source	D.F.	Dryden	Kakabeka	Longlac <sup>x</sup>	Angus	Englehart	Petawawa <sup>t</sup>
Prov	126	< 0.0001	< 0.0001	0.1097	< 0.0001	< 0.0001	< 0.0001
Blk	2	< 0.0001	< 0.0001	-	< 0.0001	< 0.0001	< 0.0001
Prov*Blk	252	0.4719	0.6616	-	0.9624	0.676	0.5209

Table 5. Test for differences in height among provenances and blocks.

interaction is again revealed, which provides further evidence of a genotype by environment interaction.

adaptive differences would exist between ecodistricts. Detailed ANOVA results for equation 3 are presented in Appendix VI. Significant differences also occurred among the provenances within the 30 ecodistricts for all tests except Longlac (Table 6). These 30 ecodistricts, therefore, required subdivision which was accomplished using the results of LSD tests that were carried out for each test site. An example of the results from these LSD tests is presented in Table 7 for ecodistrict 547 at the Kakabeka Falls test; means with the same letter were not significantly different, therefore, this ecodistrict was subdivided so that provenances 17 and 10 were grouped together while provenance 11 was put into a separate group (associated p value was 0.0289).

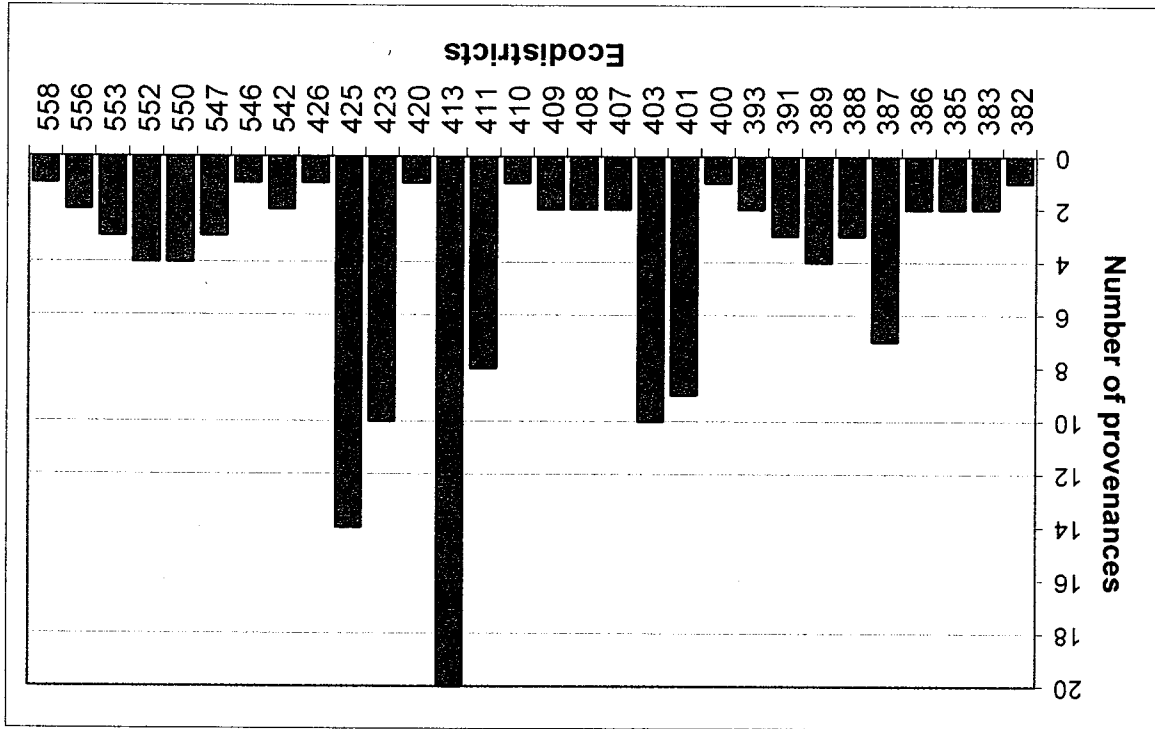


Figure 5. Number of provenances in each ecodistrict.

Table 6. ANOVA results for ecodistricts prior to subdivision and for operational ecodistricts following subdivision (equation 3).

Statistics		Provenance Test					
Source	D.F.	Dryden	Kakabeka	Longlac <sup>x</sup>	Angus	Englehart	Petawawa
Ecodistrict	29	< 0.0001	0.0003	0.0061	0.0017	< 0.0001	< 0.0001
Prov(Ecodistrict)	97	0.0079	< 0.0001	0.6488	0.0696	0.0212	0.0136
OE	54	< 0.0001	< 0.0001	0.0164	< 0.0001	< 0.0001	< 0.0001
Prov(OE)	72	0.0966	0.8216	0.5612	0.3708	0.2923	0.2428

\* Some of the provenances at the Longlac site experienced complete mortality which changed the different degrees of freedom for the Prov(Ecodistrict) term.

Table 7. LSD test results for ecodistrict 547 at the Kakabeka Falls test.

t Grouping	Mean	N	prov
A	74.379	29	17
A	72.241	29	10
B	57.680	25	11

Of the 30 ecodistricts, 18 required subdivision because significant differences

were found among provenances in these ecodistricts. Of the remaining 12 ecodistricts,

five did not require subdivision and seven ecodistricts were represented by only one

provenance. Table 8 shows a summary of these results; the test with the highest

significance (lowest p value) was used for the subdivision of the ecodistrict and was

considered to be representative of the within ecodistrict provenance variation across all

test sites; complete LSD results are presented in Appendix VII. The final list of

provenances in operational ecodistricts (OE) is displayed in Table 9. The subdivisions

increased the number of OE from 30 to 55. Following the subdivision a final ANOVA

( $p \leq 0.05$ ) revealed significant differences among the OE and no significant differences

among the provenances within OE (Table 6). A map of the final provenance groupings

in OE is displayed in Figure 6.

Table 8. List of provenances in ecodistricts.

Ecodistrict	Provenances	p value	Test used for subdivision
382	126	-	-
383	121, 123	-	-
385	111, 113	-	-
386	116, 119	-	-
387	100, 101, 102, 108, 109, 110, 114	$\leq 0.0001$	Kakabeka
388	117, 118, 122	0.0307	Petawawa
389	112, 115, 104, 107	0.0105	Kakabeka
391	120, 124, 125	0.0167	Petawawa
393	103, 105	0.0071	Angus
400	87	-	-
401	44, 48, 63, 66, 77, 79, 81, 82, 85	$\leq 0.0001$	Kakabeka
403	80, 90, 92, 93, 94, 95, 96, 97, 98, 99	0.0148	Angus
407	72, 76	-	-
408	55, 67	-	-
409	68, 70	0.0308	Dryden
410	91	-	-
411	46, 50, 52, 56, 60, 62, 84, 86	0.0003	Kakabeka
413	24, 30, 32, 33, 34, 35, 36, 38, 40, 42, 45, 47, 54, 64, 65, 69, 71, 73	0.0003	Kakabeka
420	20	-	-
423	16, 19, 22, 27, 28, 31, 49, 51, 57, 59	0.0026	Petawawa
425	3, 4, 5, 6, 7, 8, 9, 12, 13, 14, 15, 18, 21, 26	0.0019	Kakabeka
426	2	-	-
542	23, 25	0.0218	Kakabeka
546	1	-	-
547	10, 11, 17	0.0289	Kakabeka
550	83, 88, 89, 106	0.0159	Kakabeka
552	29, 37, 43, 53	0.0027	Englehart
556	74, 75	0.0033	Kakabeka
558	78	-	-

Table 9. Revised list of provenances in operational ecodistricts following subdivision.

OE	Provenances	OE	Provenances
382	126	411C	52, 60
383	121, 123	413A	58, 73
385	111, 113	413B	32, 33, 34, 35, 36, 37, 42, 65
386	116, 119	413C	30, 38, 45, 64, 69
387A	101	413D	24, 40, 47, 54, 71
387B	102, 108, 109, 114	420	20
387C	100, 110	423A	27, 28
388A	117	423B	16, 19, 22, 49
388B	118, 122	423C	31, 51, 57, 59
389A	112, 115	425A	6, 7, 9, 13, 21, 26
389B	104, 107	425B	3, 4, 8, 14, 15, 18
391A	125	425C	5, 12
391B	120, 124	426	2
393A	105	542A	25
393B	103	542B	23
400	87	546	1
401A	44, 63, 66	547A	10, 17
401B	48, 77, 79, 81, 82, 85	547B	11
403A	94, 95, 99	550A	88, 89
403B	80, 90, 92, 93	550B	83, 106
403C	96, 97, 98	552A	39, 43, 53
407	72, 76	552B	29
408	55, 67	553A	41
409A	68	553B	61, 130
409B	70	556A	74
410	91	556B	75
411A	46, 50	558	78
411B	56, 62, 84, 86		

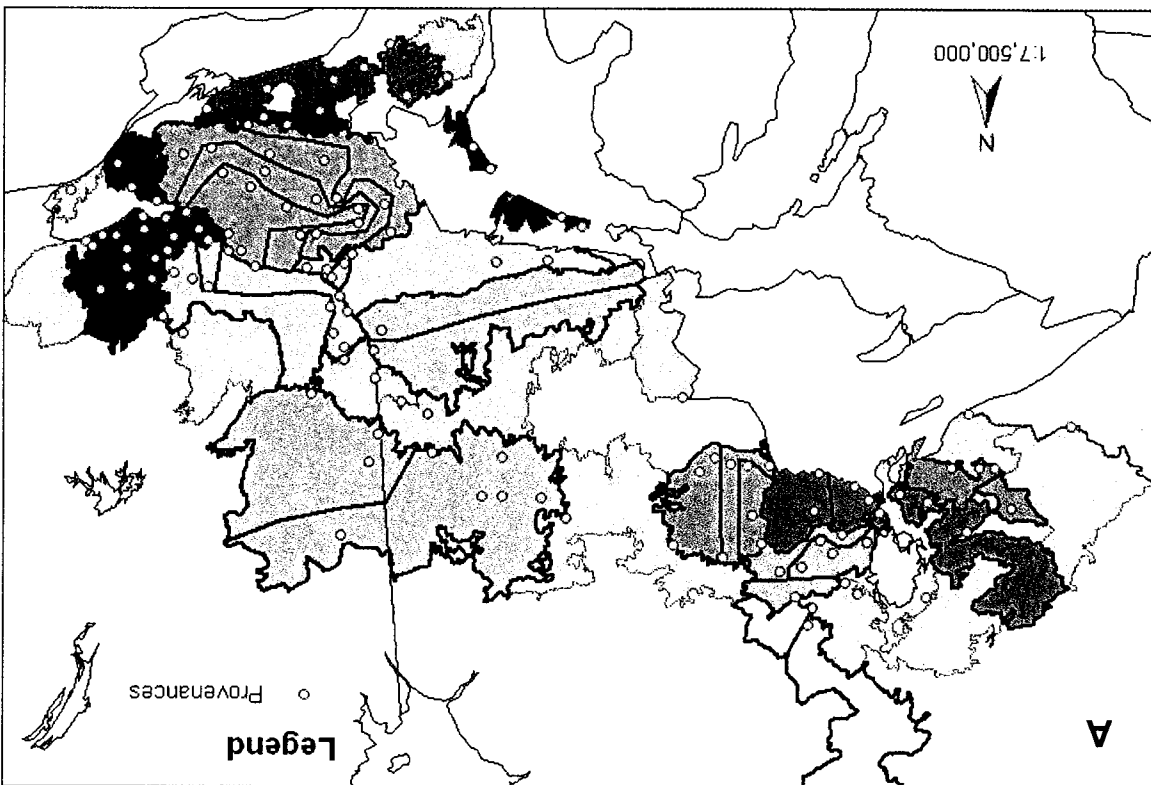
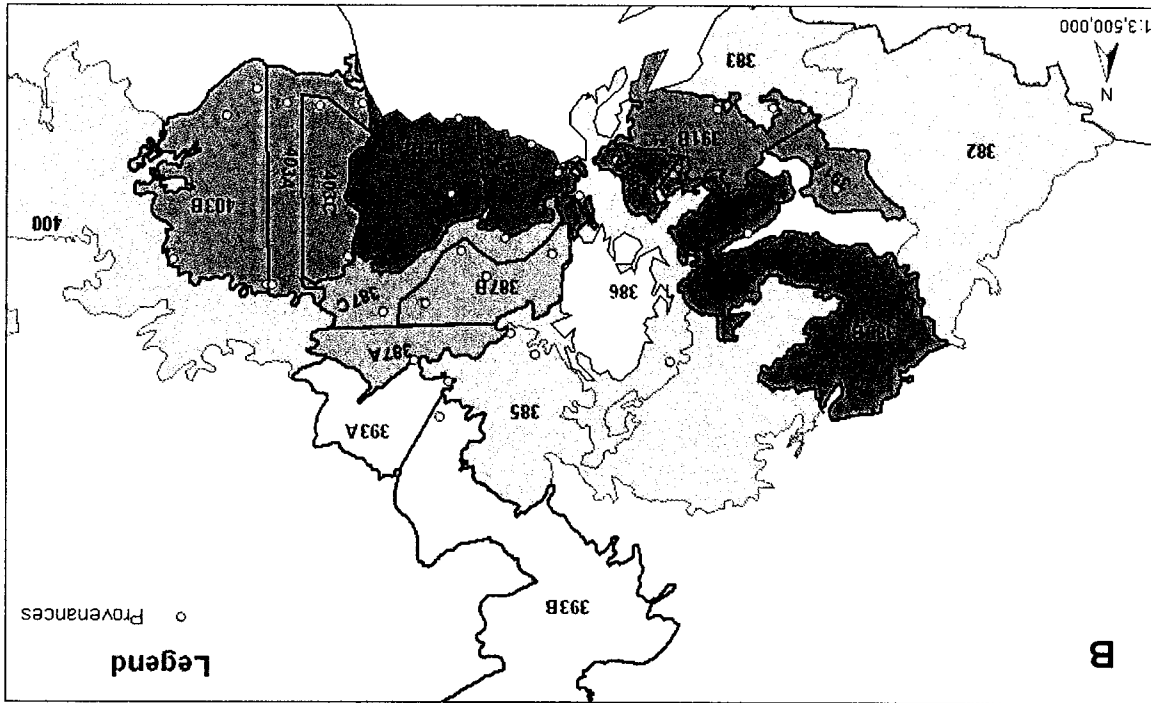
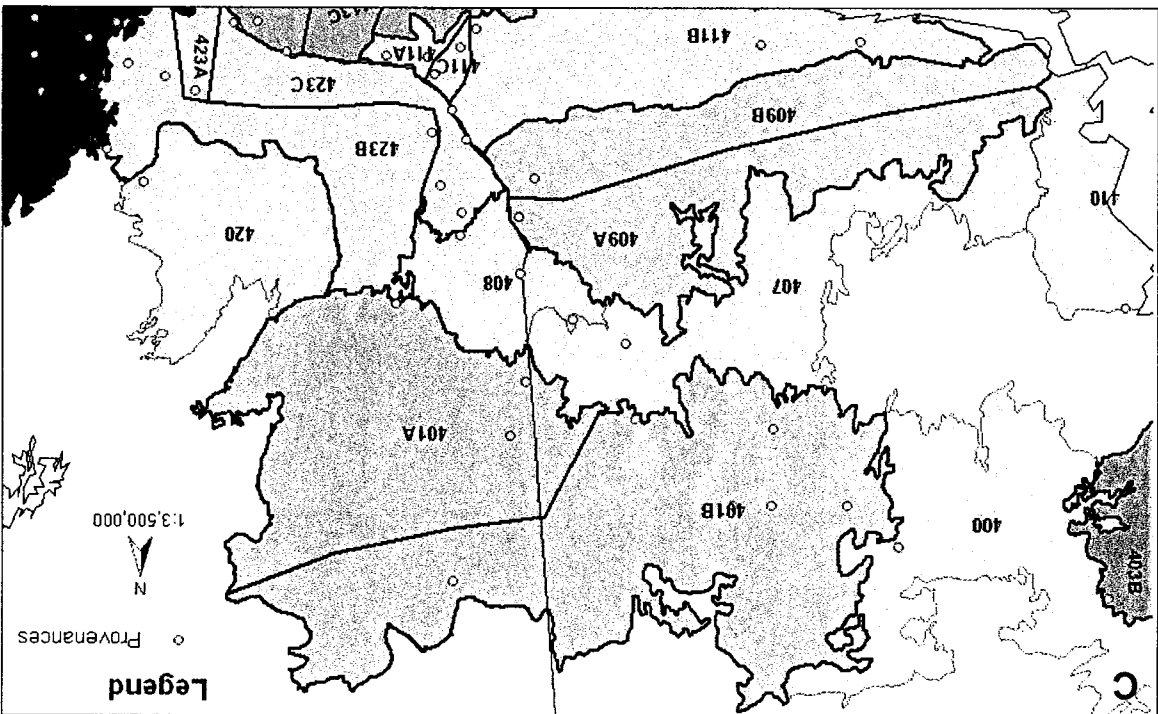
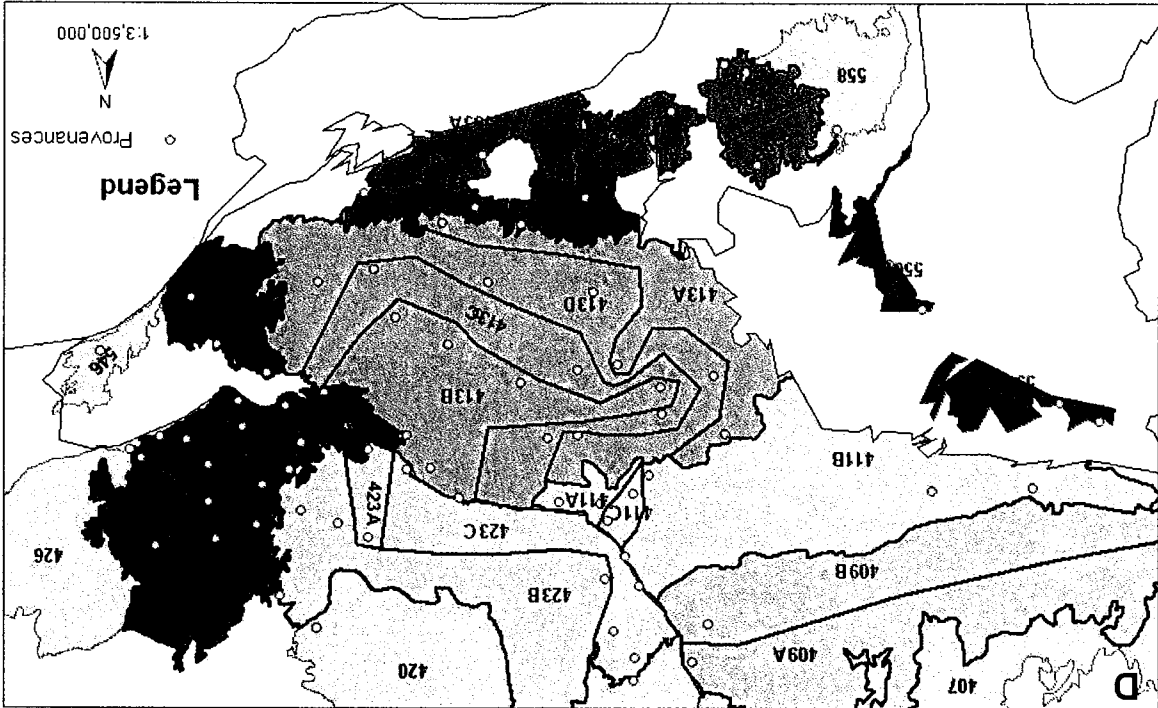


Figure 6. (A) Map of provenances in operational ecodistricts. The grey colour represents ecodistricts which were not subdivided; subsections of the original ecodistricts are displayed in the same colour. (B) Close up map of operational ecodistricts 382 to 403C. (C) Close up map of operational ecodistricts 400 to 425B. (D) Close up map of operational ecodistricts 407 to 558.





Using provenance means, quadratic regressions (response functions) were determined from the data. Due to the large number of OE, results will be provided for five OE that were considered to be representative of northwestern, northern, central and southern Ontario and western Quebec (Figure 7). Since the three selected temperature variables all produced very similar results, only those for December maximum temperature are presented. Table 10 shows quadratic regression results for December maximum temperature and mean April precipitation for the five representative OE and for the provenances within them. Quadratic regression results for OE and provenances are presented in Appendices III and IX, respectively.

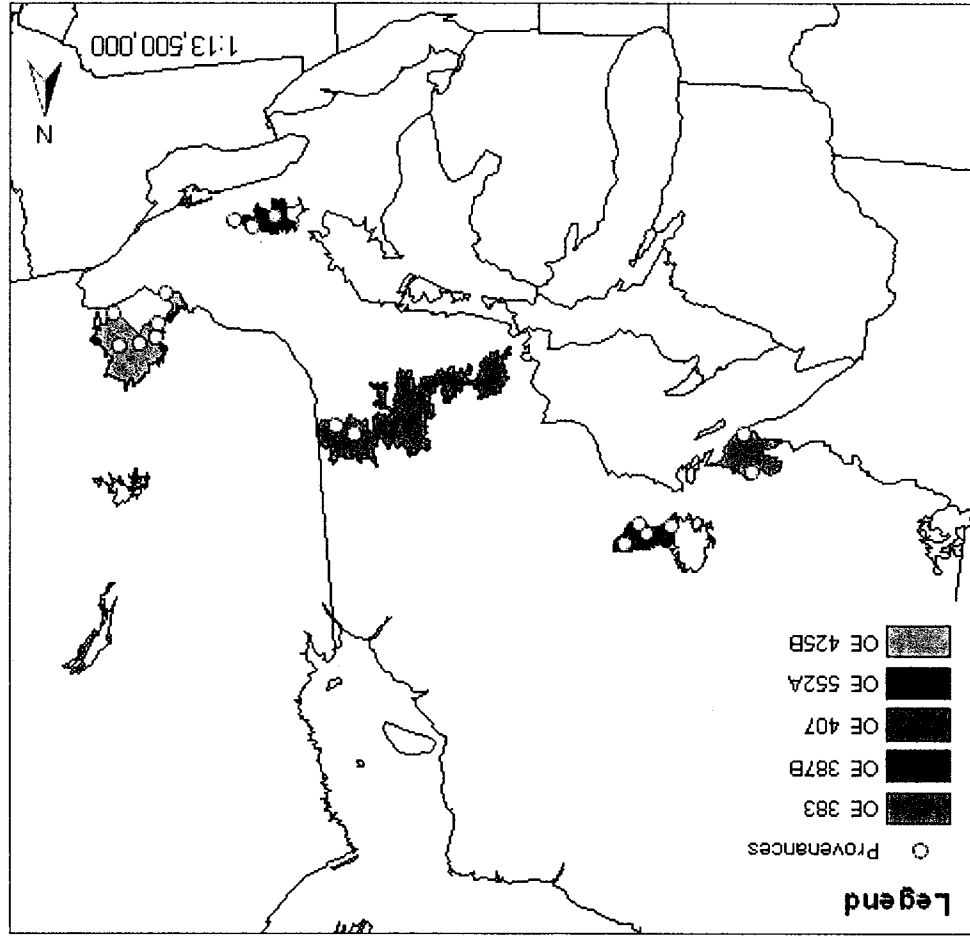


Figure 7. Map of the five representative operational ecodistricts.

Table 10. Significance and  $R^2$  values from quadratic regression results of tree height versus December maximum temperature and mean April precipitation.

OE or Provenance	December max. temperature		Mean April precipitation	
	p value	$R^2$	p value	$R^2$
OE 383	0.0001	0.9262	0.0093	0.7372
P121	0.0656	0.9344	0.3094	0.6906
P123	0.0437	0.9563	0.1776	0.8224
OE 387B	0.0001	0.7597	< 0.0001	0.7345
P102	0.1542	0.7125	0.2263	0.6286
P108	0.0445	0.8744	0.0994	0.7845
P109	0.0762	0.8202	0.0185	0.9300
P114	0.1869	0.8131	0.0947	0.9053
OE 407	0.0033	0.7607	0.0046	0.7402
P72	0.1882	0.6716	0.1471	0.7214
P76	0.2763	0.5758	0.0532	0.8585
OE 425B	0.0001	0.7646	< 0.0001	0.6808
P3	0.0530	0.9470	0.0532	0.9468
P4	0.0211	0.9236	0.1625	0.7022
P8	0.2119	0.6446	0.1264	0.7481
P14	0.0603	0.8463	0.2645	0.5880
P15	0.0090	0.9567	0.0507	0.8630
P18	0.1357	0.7359	0.1586	0.7070
OE 552A	0.0001	0.8465	0.2243	0.7757
P39	0.1106	0.7696	< 0.0001	0.7509
P43	0.0363	0.8904	0.1645	0.6997
P53	0.0097	0.9546	0.0185	0.9300

Quadratic regression curves for the five representative OE for December maximum temperature and mean April precipitation are shown in Figures 8 through 17. Provenance height (cm) is located along the y-axis with December maximum temperature ( $^{\circ}\text{C}$ ) and mean April precipitation (mm) along the x-axis. Quadratic regression curves for January and November maximum temperature are presented in Appendices X and XI, respectively. Since most of the provenance points fell within the confidence interval, the OE response was considered to be a good representation of

provenance response. The points that fell outside the confidence interval were from the Kakabeka test (Figures 8, 12 and 13), the Longlac test (Figures 11, 15 and 17) and the Petawawa test (Figure 9). In some cases, points from more than one test fell outside the confidence interval (Figures 10, 14 and 16). The response curves for the different OE were very similar for the variables presented, despite the fact that different provenance were used in generating them.

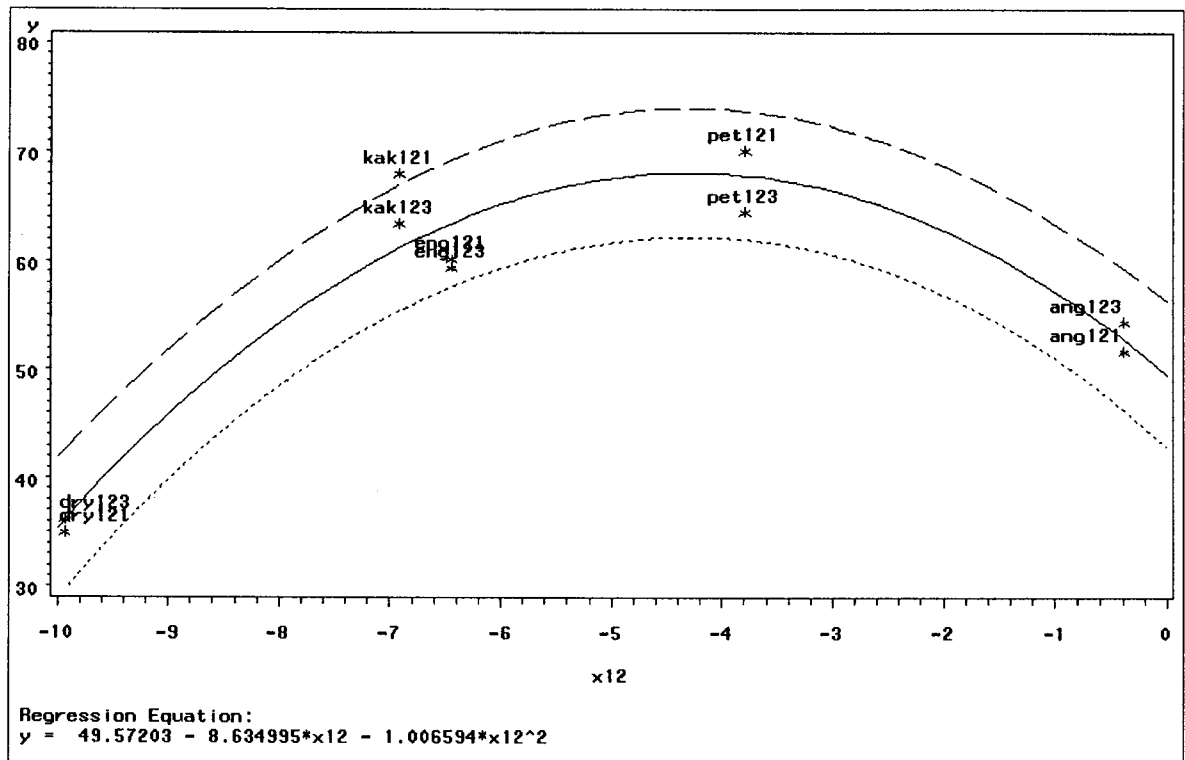


Figure 8. Quadratic regression curve of tree height (y-axis) versus December maximum temperature (x-axis) for OE 383.

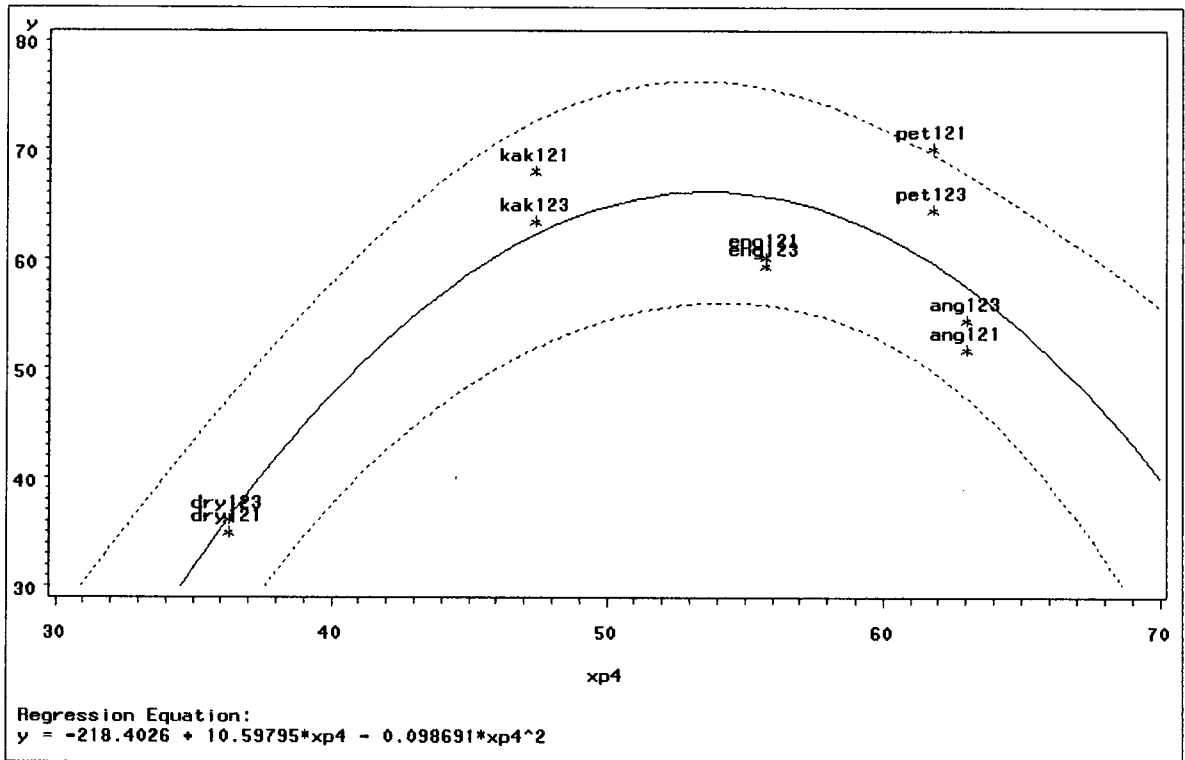


Figure 9. Quadratic regression curve of tree height (y-axis) versus mean April precipitation (x-axis) for OE 383.

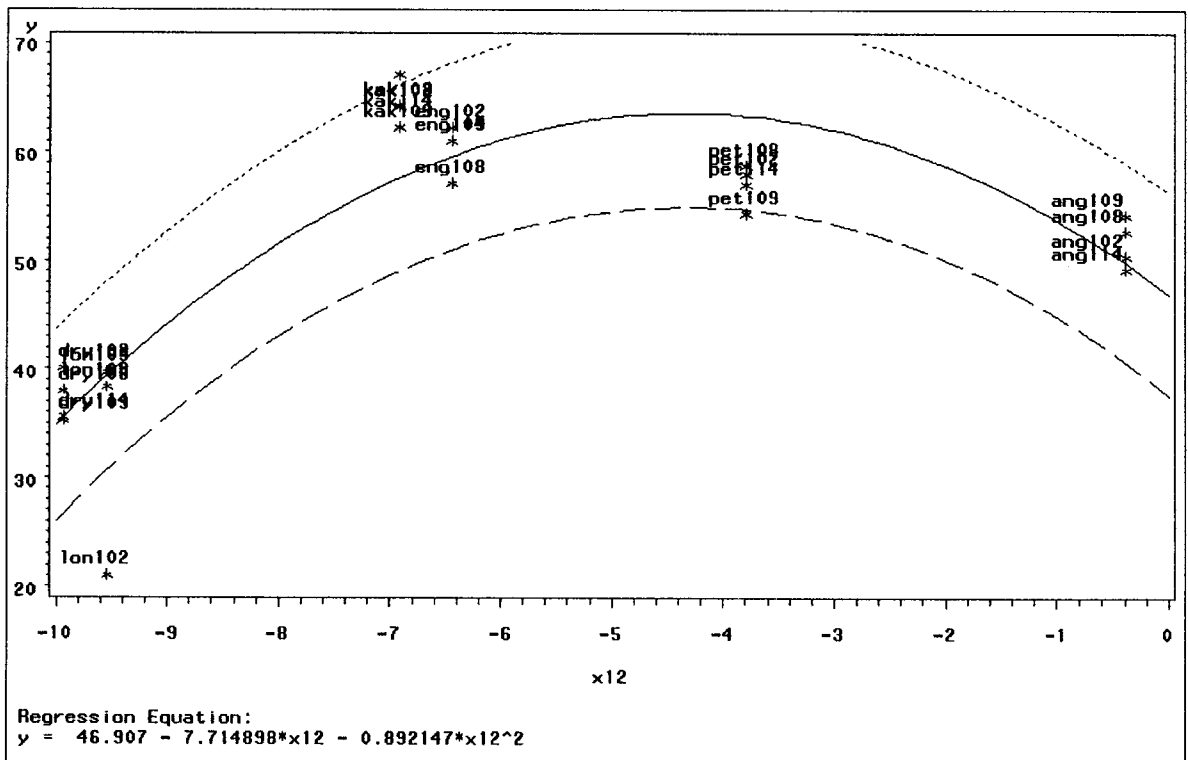


Figure 10. Quadratic regression curve of tree height (y-axis) versus December maximum temperature (x-axis) for OE 387B.

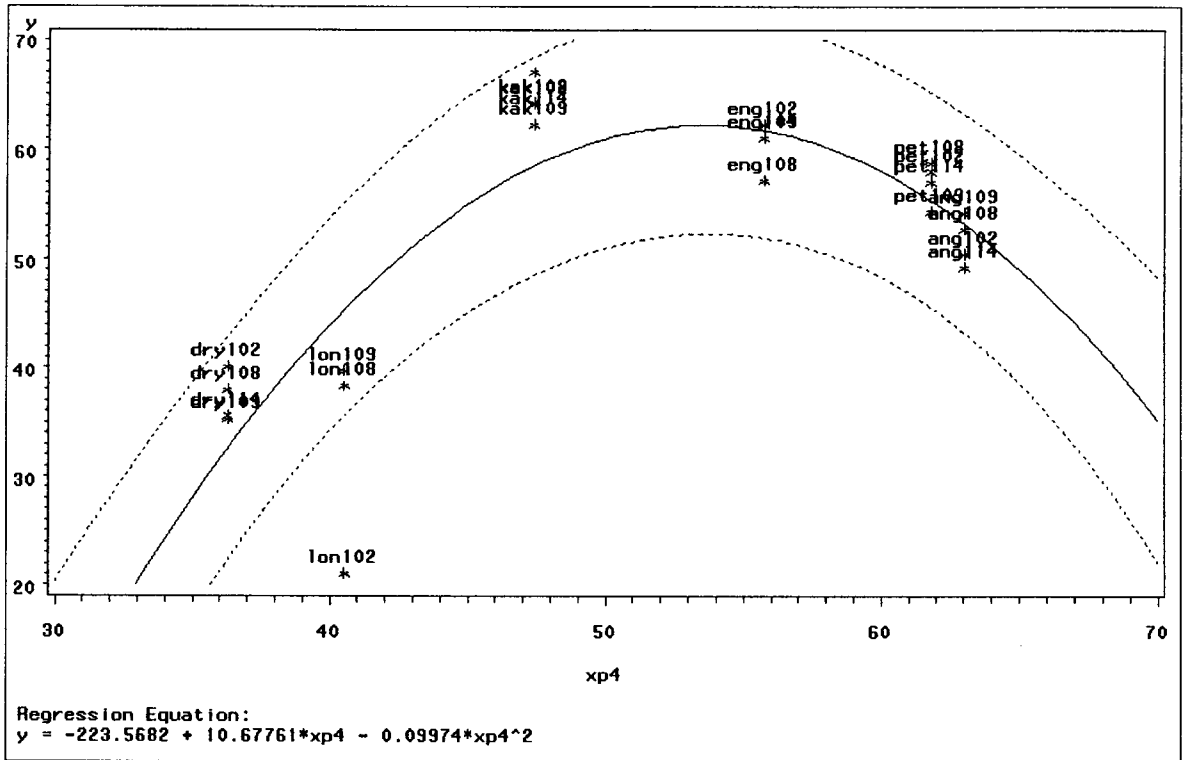


Figure 11. Quadratic regression curve of tree height (y-axis) versus mean April precipitation (x-axis) for OE 387B.

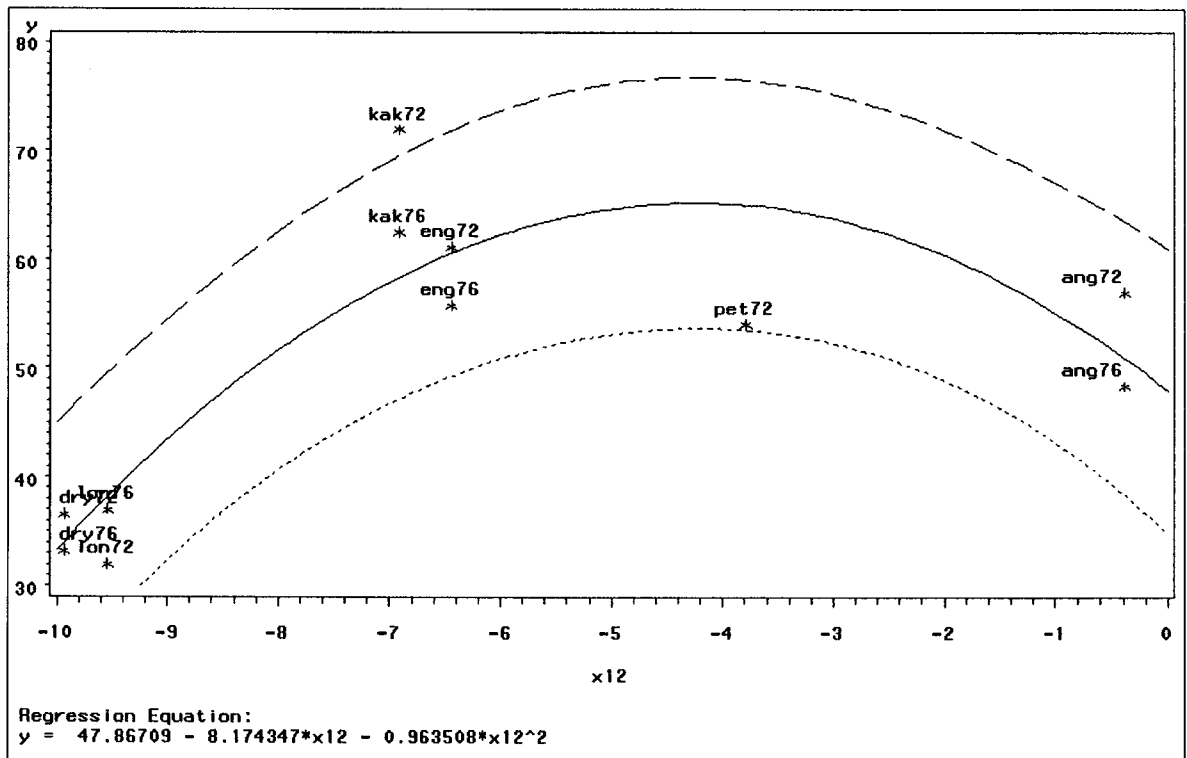


Figure 12. Quadratic regression curve of tree height (y-axis) versus December maximum temperature (x-axis) for OE 407.

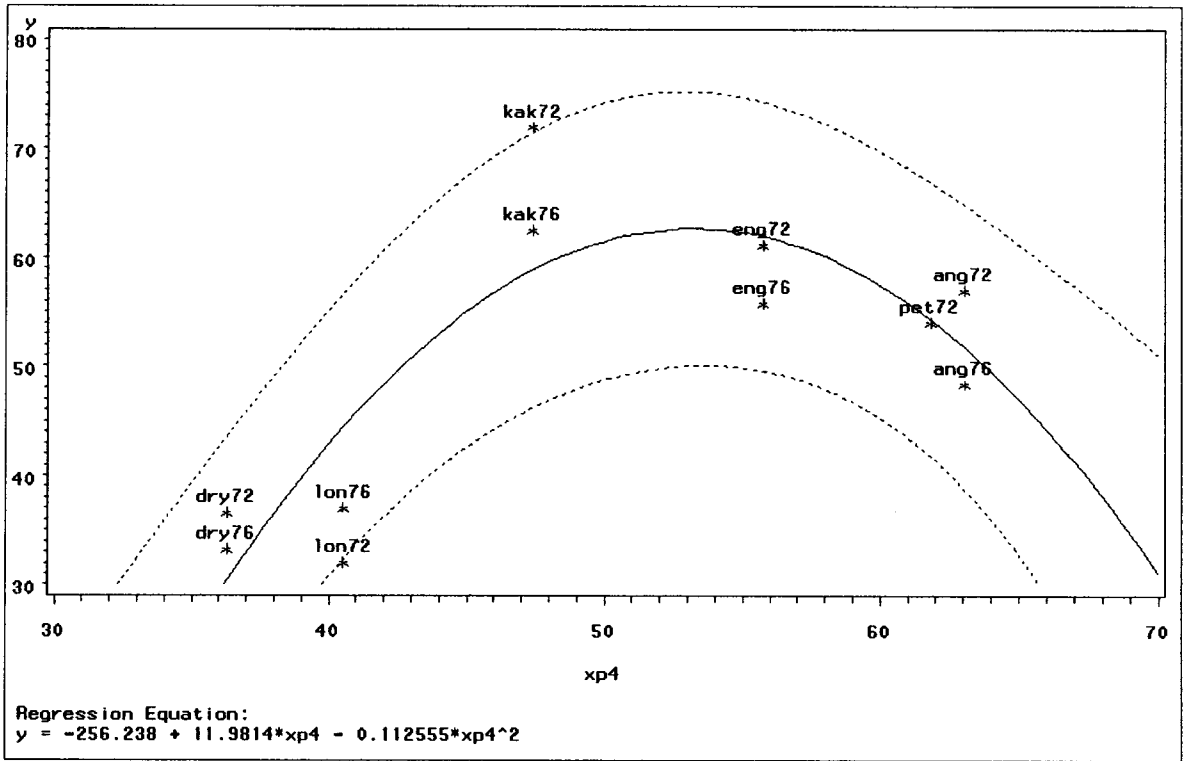


Figure 13. Quadratic regression curve of tree height (y-axis) versus mean April precipitation (x-axis) for 407.

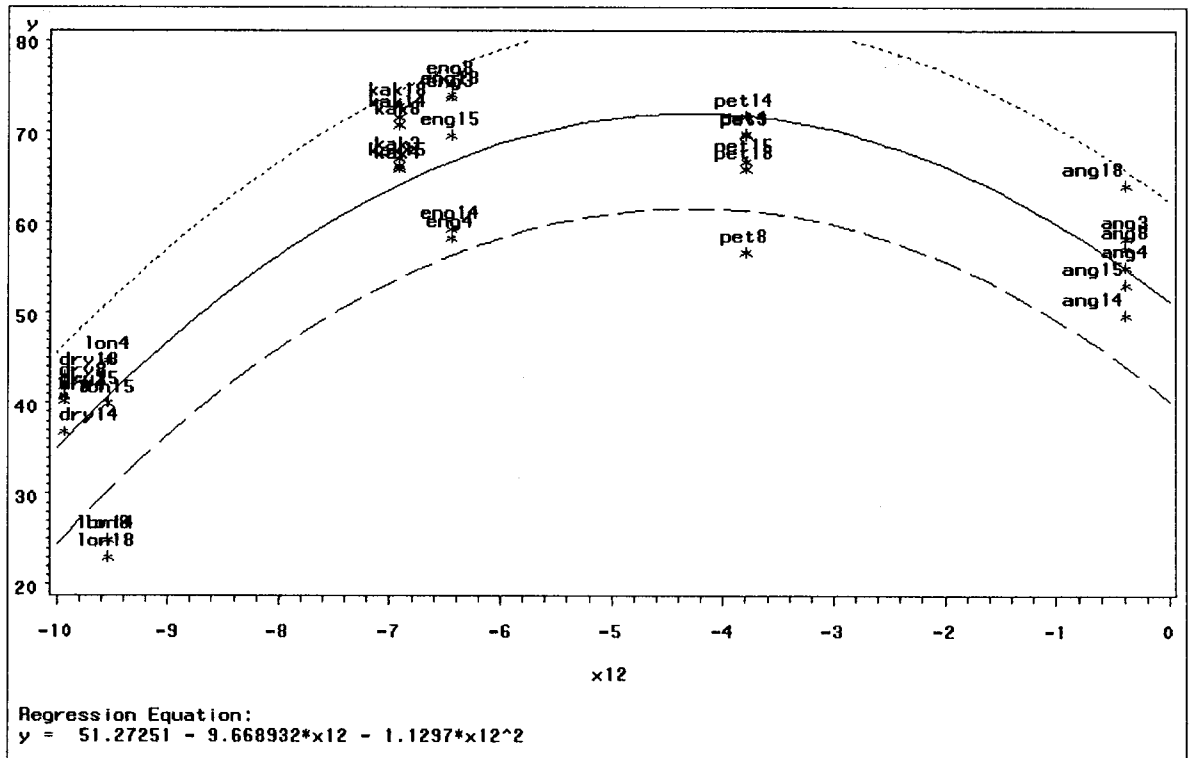


Figure 14. Quadratic regression curve of tree height (y-axis) versus December maximum temperature (x-axis) for OE 425B.

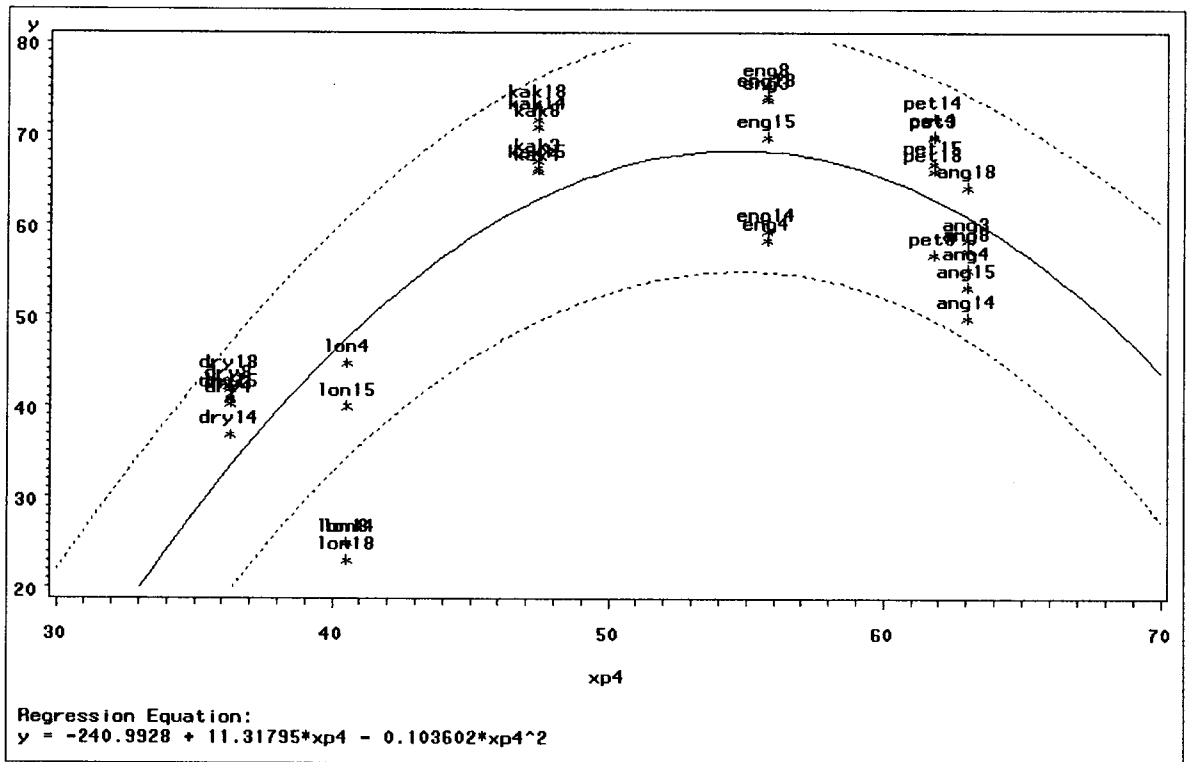


Figure 15. Quadratic regression curve of tree height (y-axis) versus mean April precipitation (x-axis) for 425B.

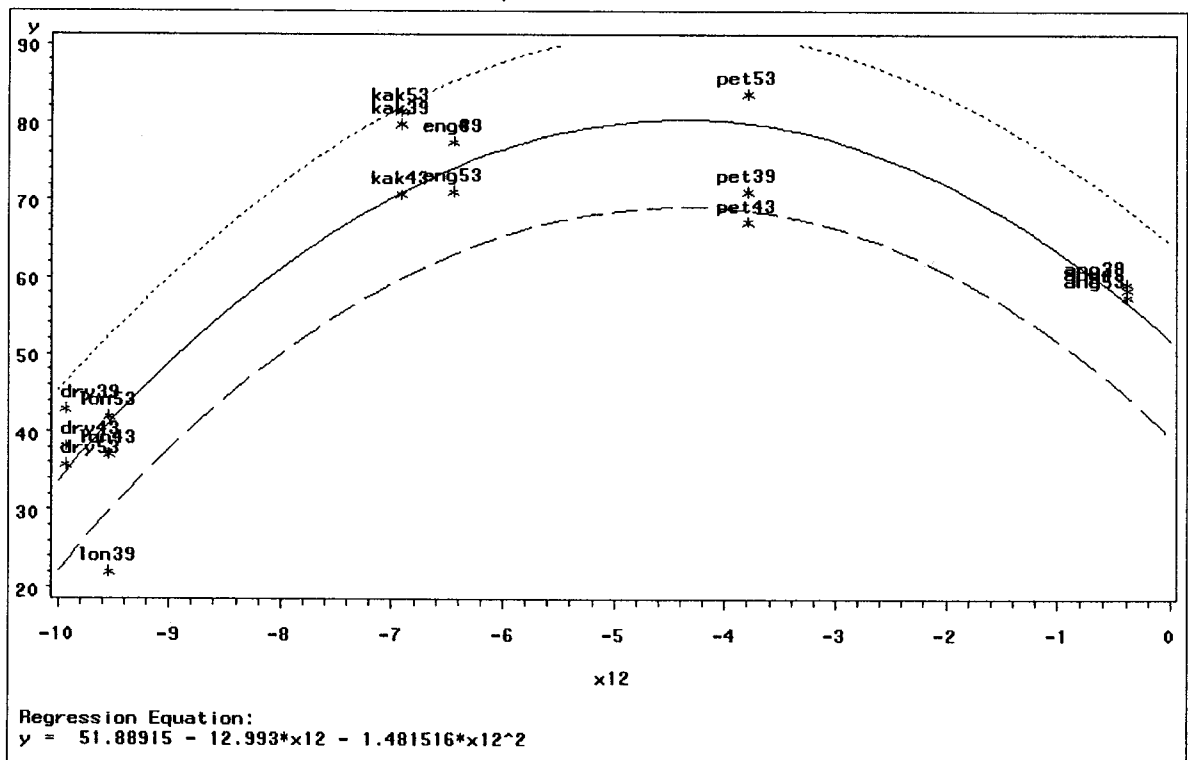


Figure 16. Quadratic regression curve of tree height (y-axis) versus December maximum temperature (x-axis) for OE 552A.

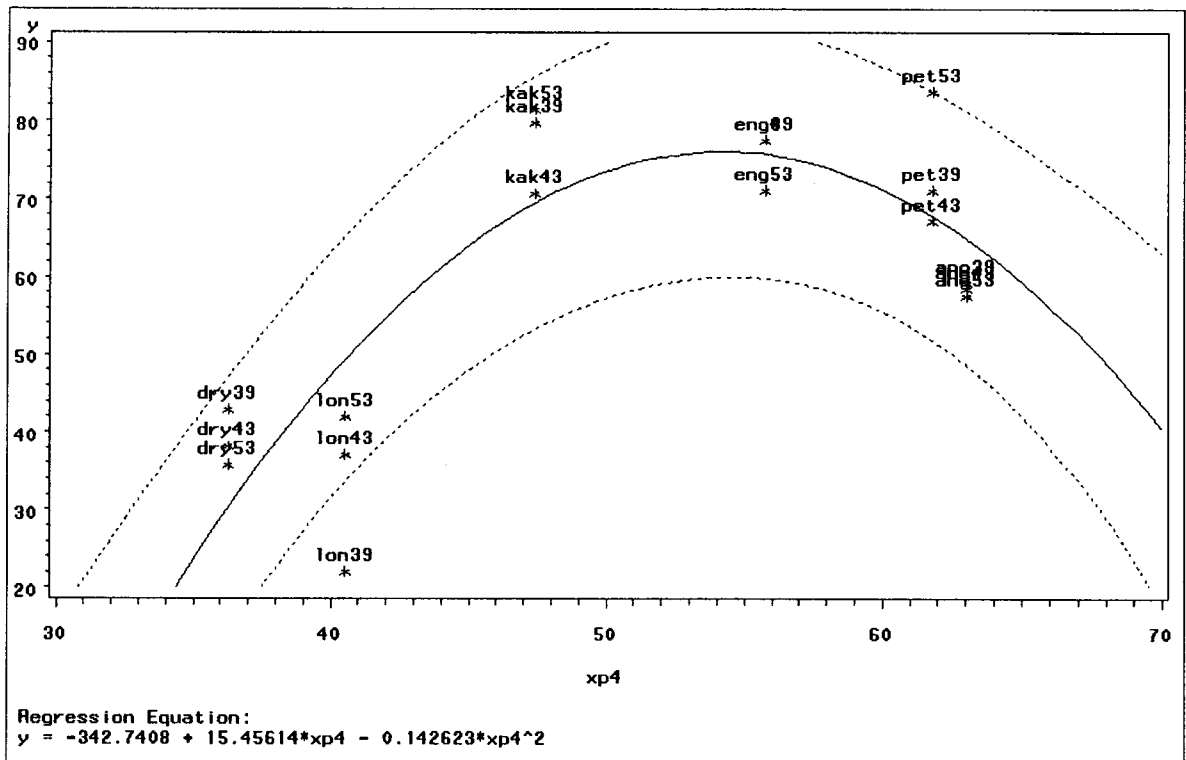


Figure 17. Quadratic regression curve of tree height (y-axis) versus mean April precipitation (x-axis) for OE 552A.

Climate variables were selected for further analysis if the results from the quadratic regressions showed both  $p \leq 0.2000$  and  $R^2 > 0.4000$ . The 11 most frequently selected climate variables for provenances and ecodistricts are displayed in Table 11. With the exception of September maximum temperature and annual precipitation, the selected variables were identical for provenances and operational ecodistrict groups (although their frequencies differed). The top 4 climate variables (December maximum temperature, January maximum temperature, April precipitation and November maximum temperature) were retained for further analysis since greater than 90% of ecodistrict results met the selection criteria for these variables; climatic values for these variables at the test sites are presented in Table 12.



Table 11. The eleven most frequently selected variables.

Climate Variable	Percentage of OE	Percentage of Provenances
December Max Temp	94	82
January Max Temp	92	82
April Precip	92	76
November Max Temp	91	81
Seasonality	89	80
Latitude	89	73
Annual Precip	79	-
Max Annual Temp	79	67
February Max Temp	77	59
October Max Temp	75	65
September Max Temp	-	59

Table 12. Climatic values for the selected variables at all test sites.

Test Site	January Maximum Temperature (°C)	November Maximum Temperature (°C)	December Maximum Temperature (°C)	Mean April Precipitation (mm)
Kakabeka	-9.43	0.43	-6.91	47.42
Englehart	-9.84	1.34	-6.44	55.75
Petawawa	-7.00	3.73	-3.79	61.81
Angus	-3.42	5.83	-0.39	63.03
Longlac	-12.62	-1.38	-9.54	40.52
Dryden	-12.61	-1.82	-9.93	36.30

The Cauchy response curves generated in SigmaPlot (Systat Software Inc. 2002) for the five representative OE are displayed in Figures 18 through 27; the solid bars along the horizontal axes are boxplots that represent the actual, full climate range of the ecodistrict. Cauchy response curves for January and November maximum temperature are presented in Appendices XII and XIII, respectively. In most cases, the OE response curve falls almost exactly between the curves generated for the individual provenances; this is easily seen in figures 18, 19 and 23. The boxplots in Figures 18 and 20 suggest that provenances in OE 383 and 387B are currently growing under conditions that are

slightly colder than their optimum. Figure 18 also clearly indicates a genotype by environment interaction (which has been observed for most of the provenances) since provenance 121 had superior performance at three of the tests while provenance 123 showed superior performance at the other two. The boxplots in Figure 22 and 26 show that provenances in OE 407 and 425B are growing near their optimum for December maximum temperature while Figure 24 shows that provenances in OE 552A are growing under warmer conditions than optimum. Figures 19 and 21 suggest provenances in OE 383 and 387B are growing under slightly drier climates than optimum, although Figure 19 does show quite a wide range for mean April precipitation, some of which is near optimum. Provenances in OE 425B are growing under optimum temperature conditions for December maximum temperature (Figure 26). Provenances within OE 407 are growing near optimum for April precipitation, however the complete range continues off-scale to about 69.12mm, which indicates that some provenances could be growing under conditions that are wetter than optimum (Figure 23). Similarly, the boxplot in Figure 27 is partially off-scale with a range of 62.776mm to 77.649mm. The boxplot in Figure 25 is completely off-scale with a range of mean April precipitation of 66.248mm to 72.295mm, which means that provenances in OE 552A are growing in wetter than optimum conditions.

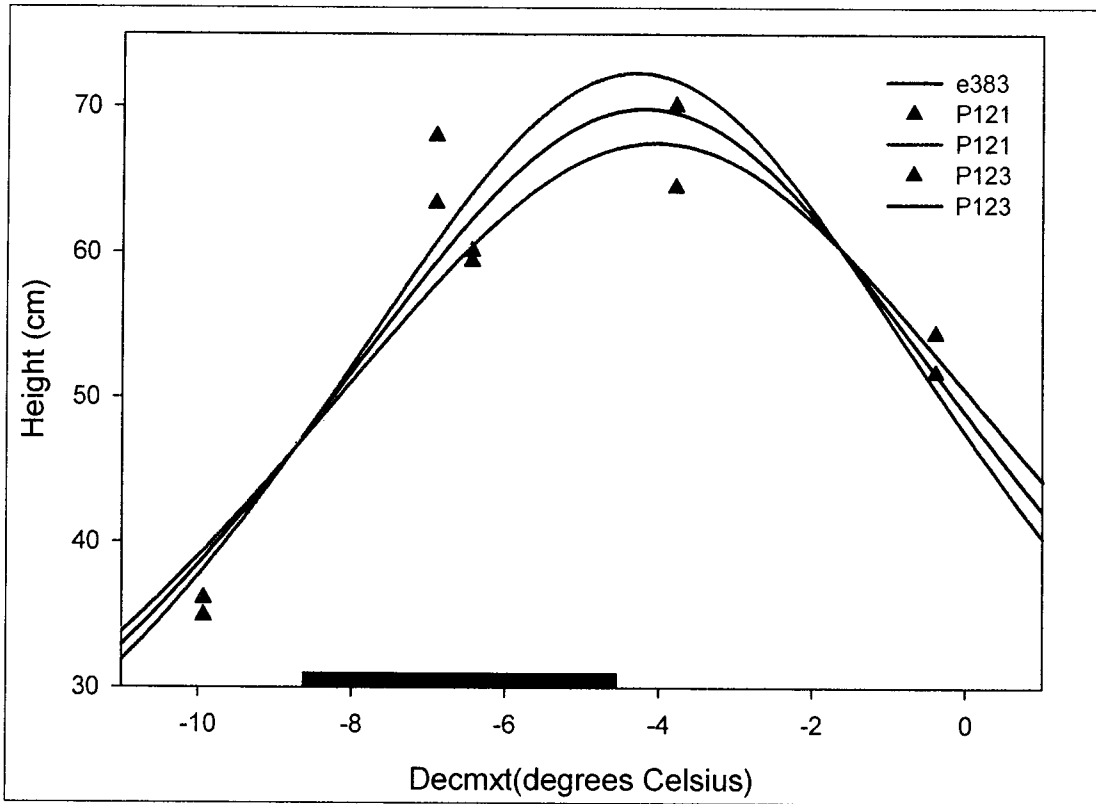


Figure 18. Response curve for OE 383 versus December maximum temperature.

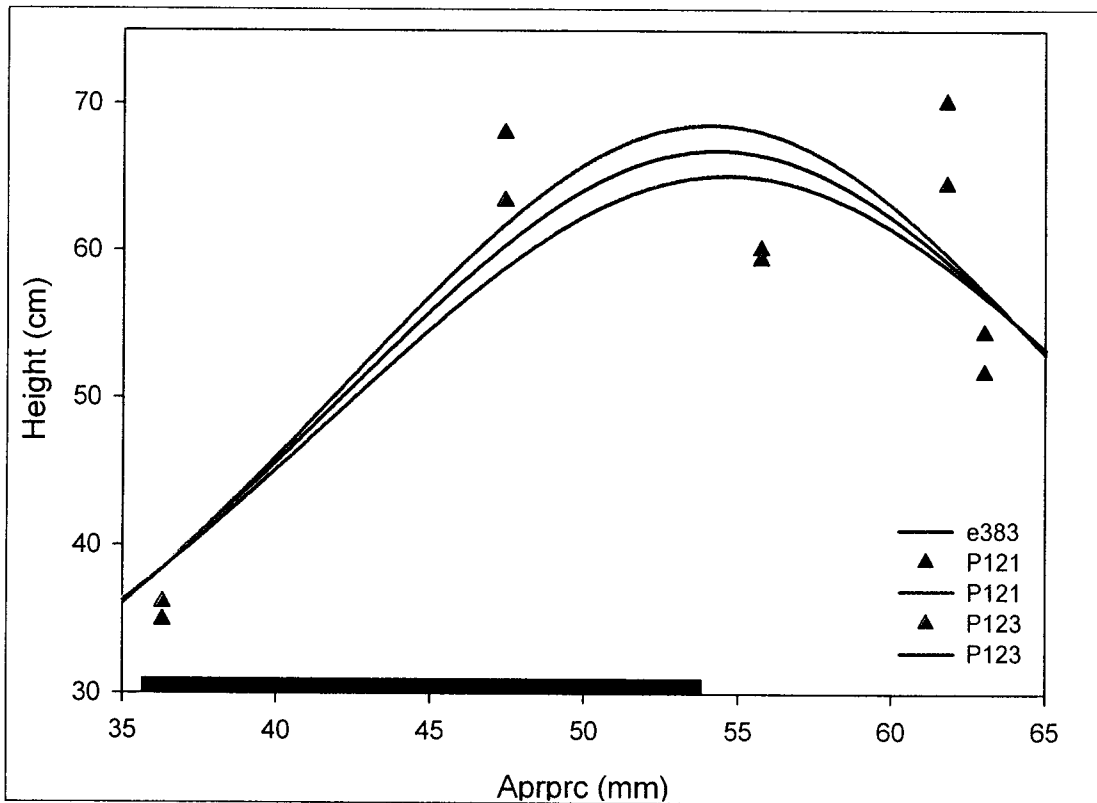


Figure 19. Response curve for OE 383 versus mean April precipitation.

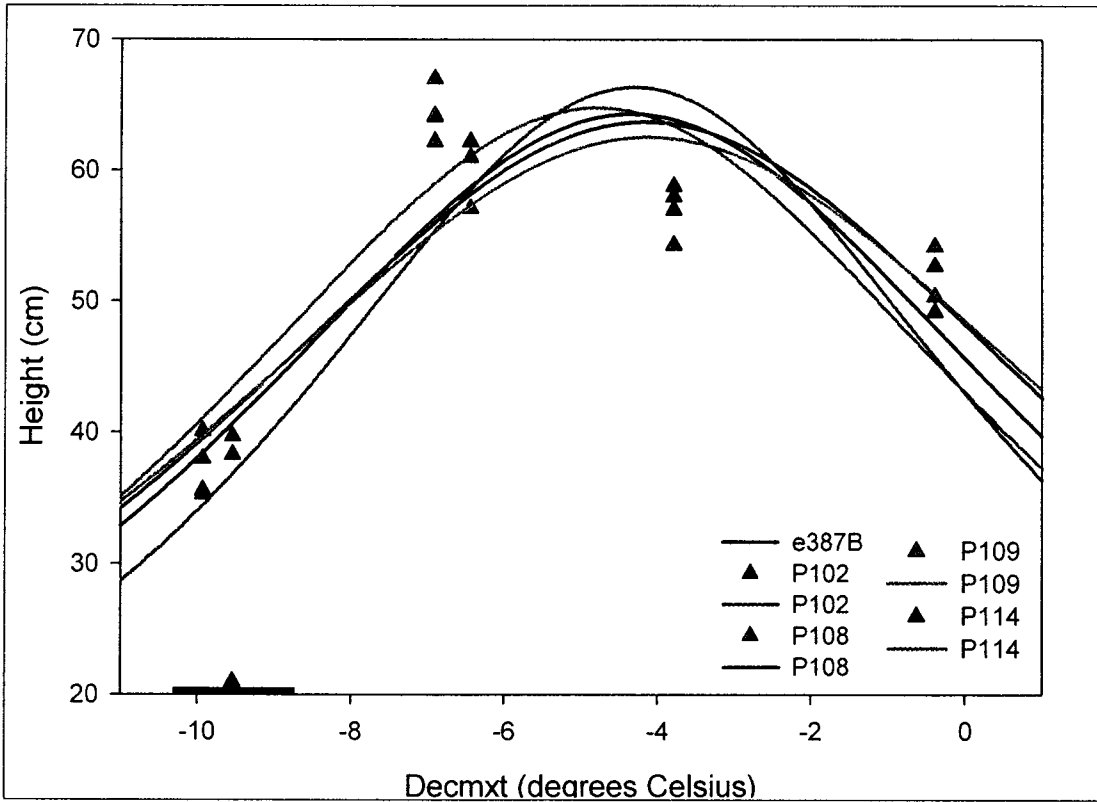


Figure 20. Response curve for OE 387B versus December maximum temperature.

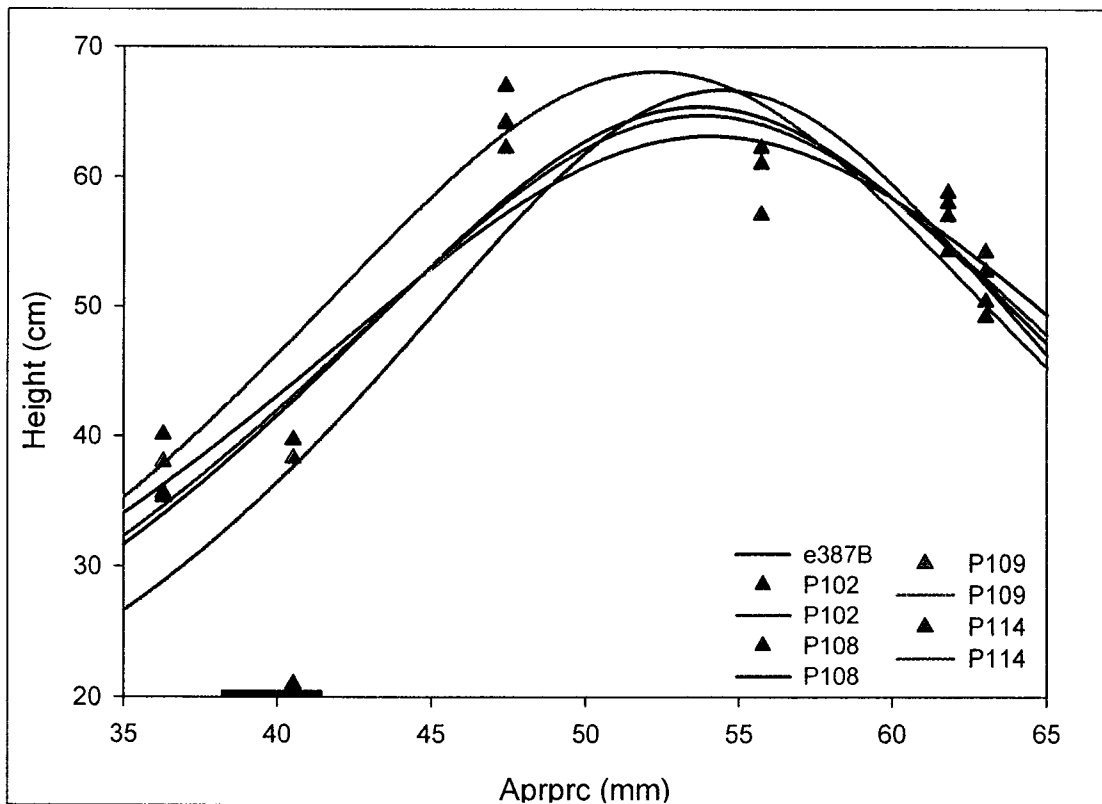


Figure 21. Response curve for OE 387B versus mean April precipitation.

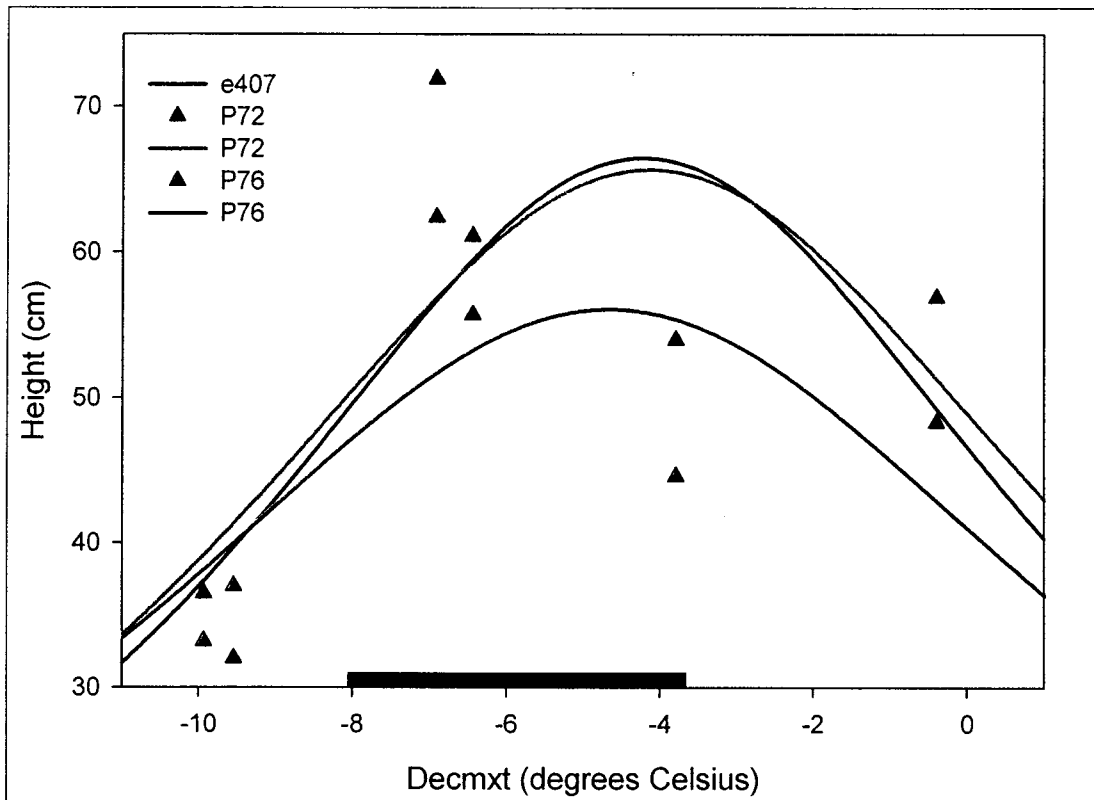


Figure 22. Response curve for OE 407 versus December maximum temperature.

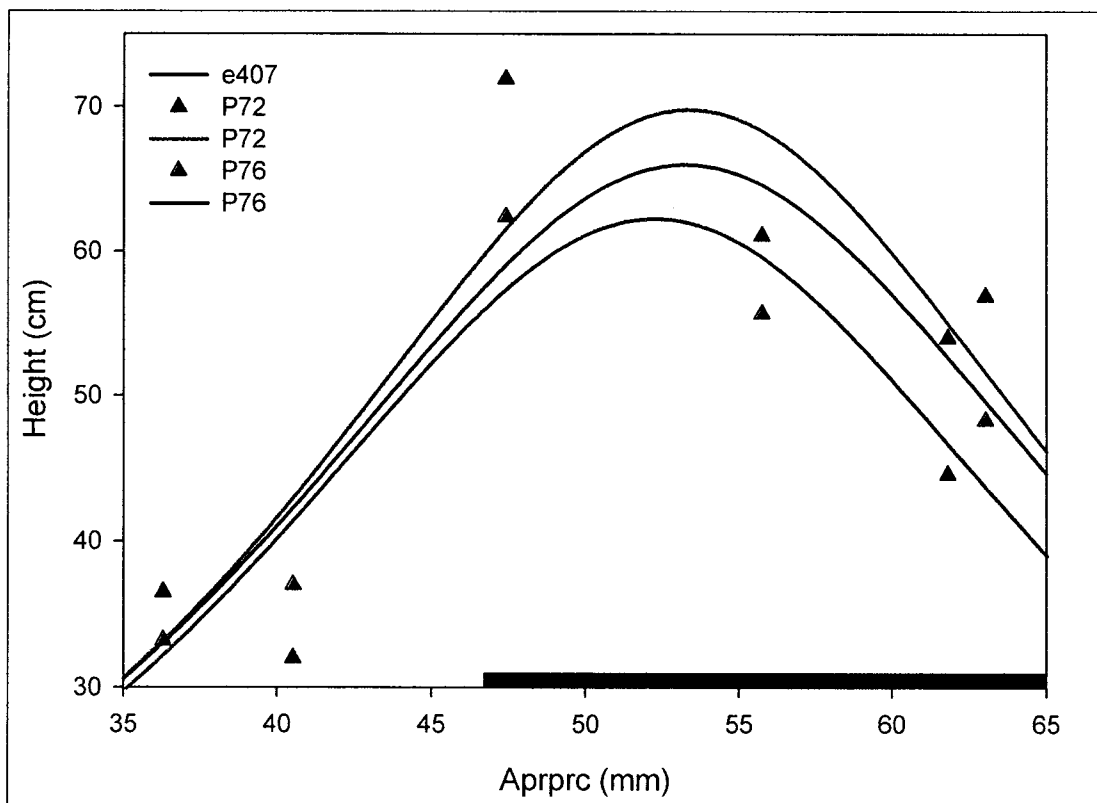


Figure 23. Response curve for OE 407 versus mean April precipitation (boxplot is partially off-scale).

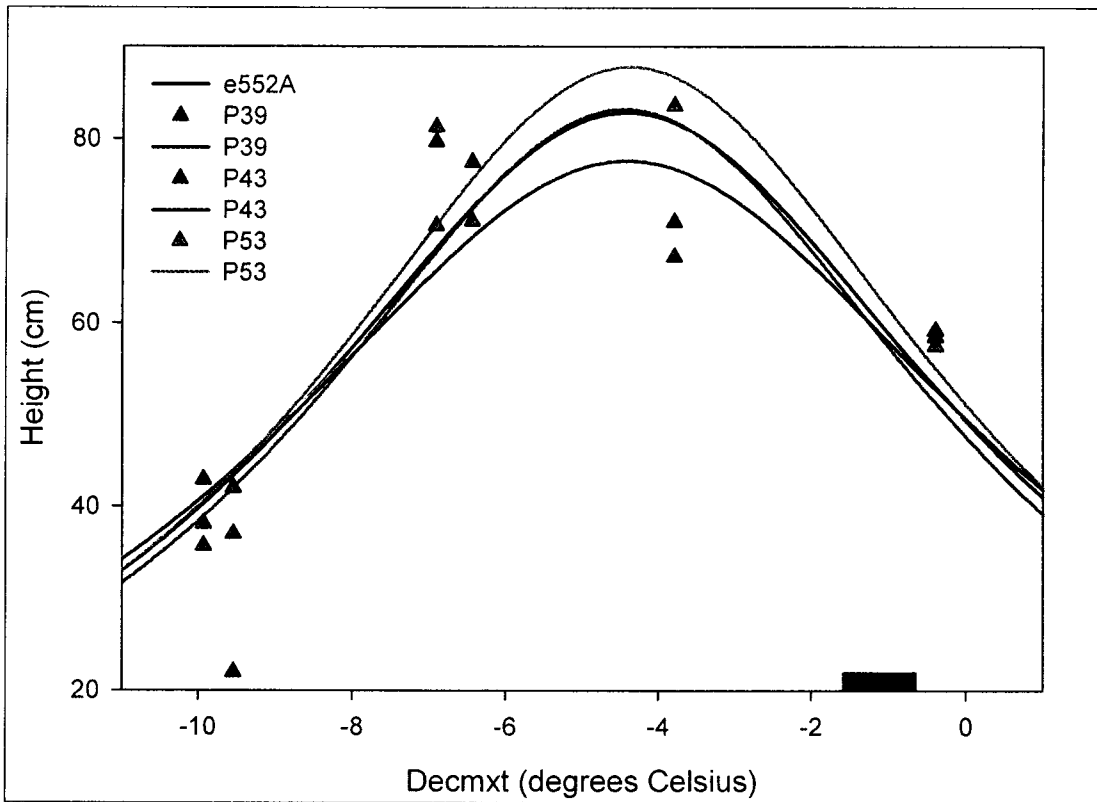


Figure 24. Response curve for OE 552A versus December maximum temperature.

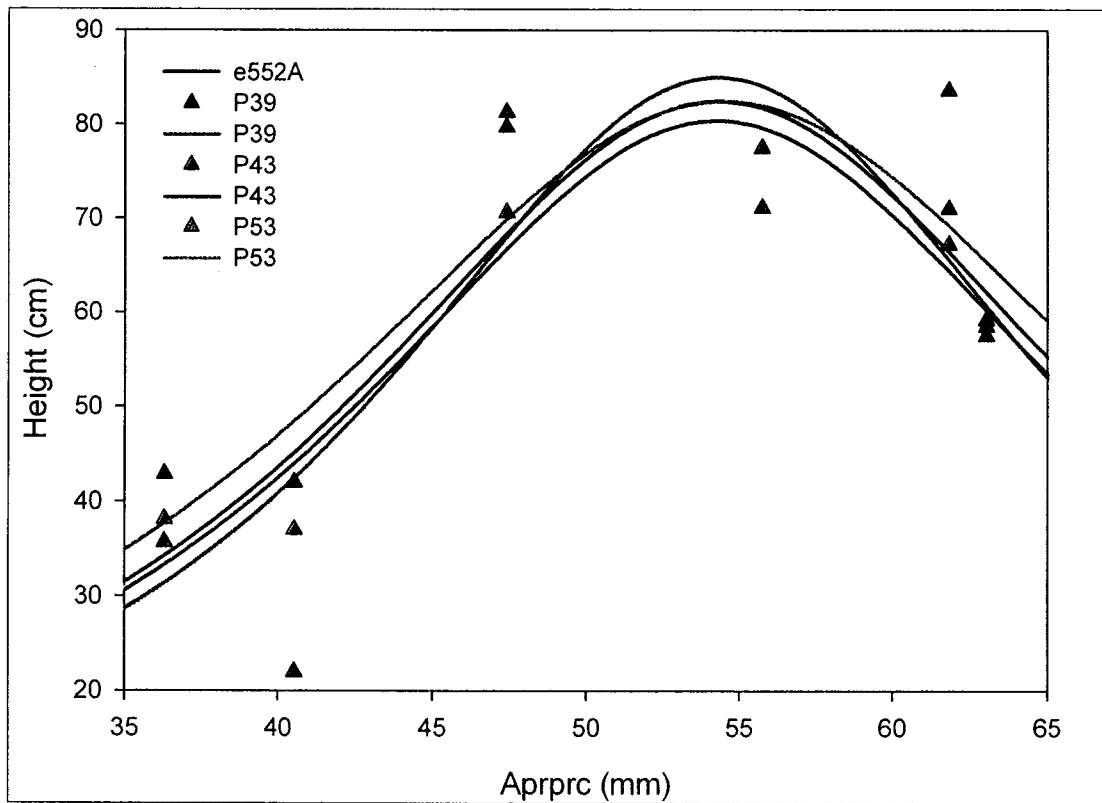


Figure 25. Response curve for OE 552A versus mean April precipitation (boxplot is completely off-scale).

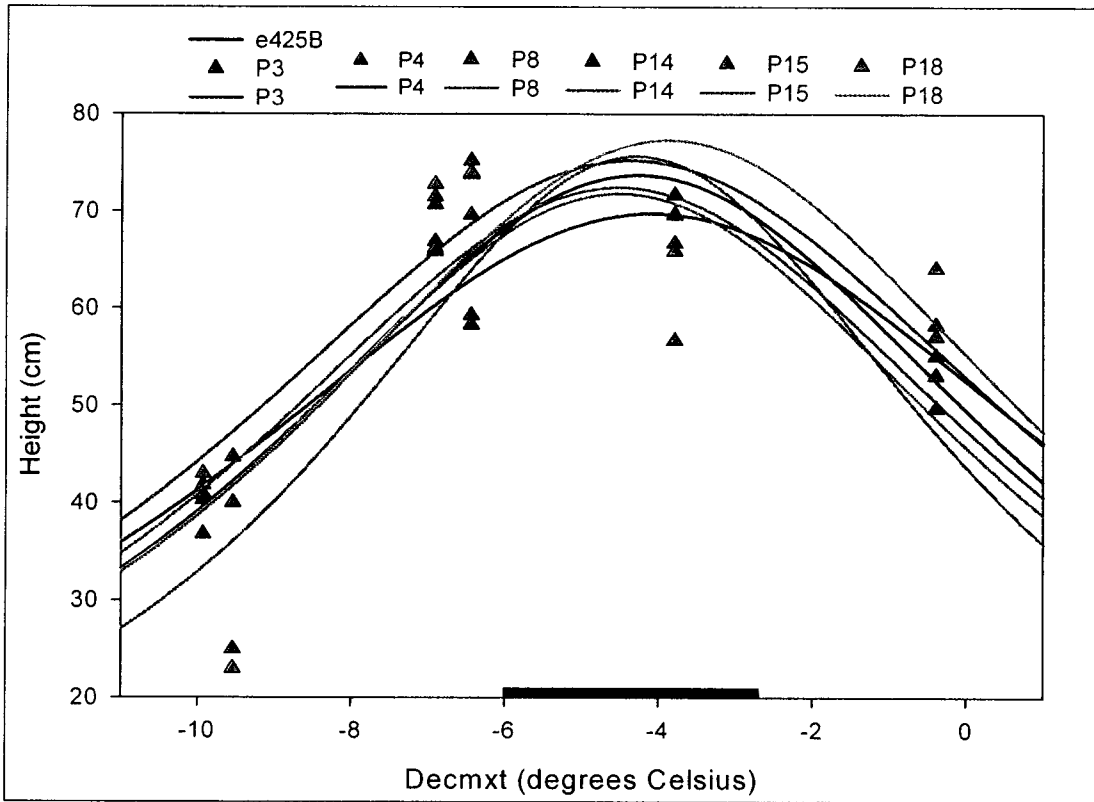


Figure 26. Response curve for OE 425B versus December maximum temperature.

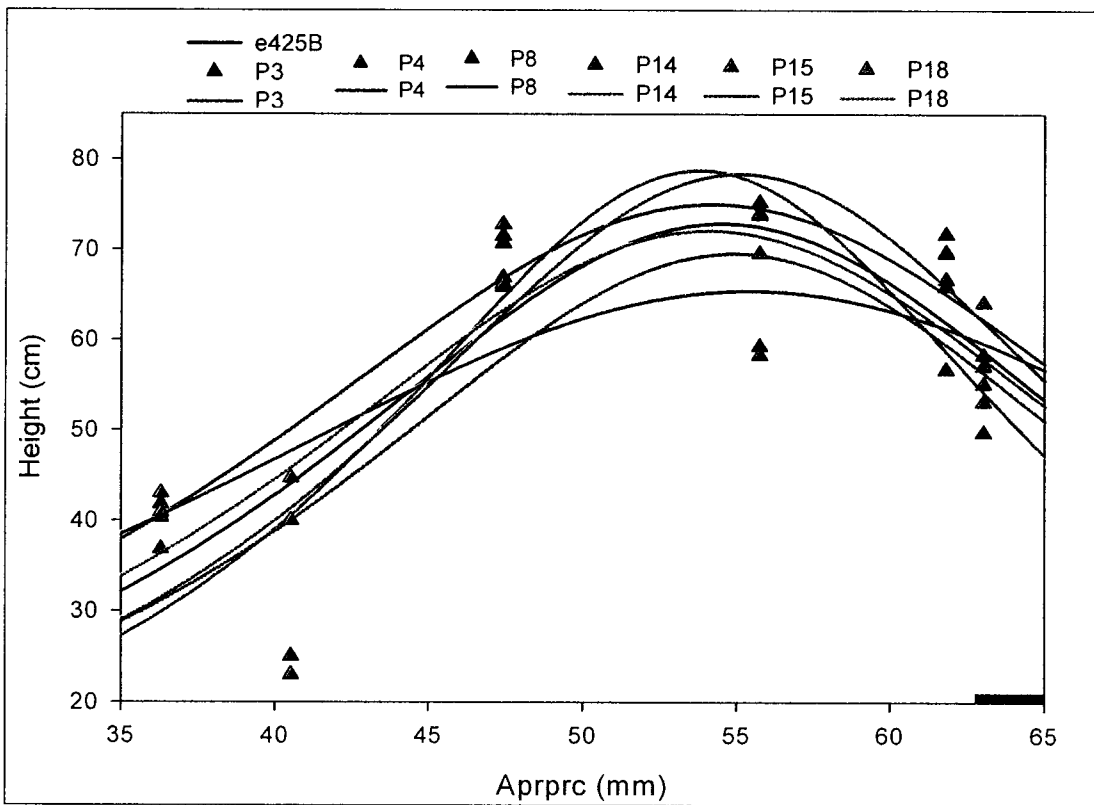


Figure 27. Response curve for OE 425B versus mean April precipitation (boxplot is partially off-scale).

Results from Cauchy response functions in Table 13 indicate that provenance 121 would attain optimal height growth at a location where December maximum temperature is equal to  $-4.3063^{\circ}\text{C}$ , while provenance 123 would attain optimal height where December maximum temperature is equal to  $-4.0600^{\circ}\text{C}$ . The response function for OE 383 falls in between those for the provenances, with an optimal maximum temperature of  $-4.1984^{\circ}\text{C}$  for the month of December. Complete Cauchy function results for all four climate variables are presented in Appendices XIV, XV, XVI and XVII, respectively.

Although provenances and ecodistricts displayed significant differences in performance, their optimum site conditions for height growth are very similar. This trend proved to be true for all four selected climate variables. Maps of optimal areas for December maximum temperature and mean April precipitation are displayed in Figures 28 through 37. To facilitate viewing overlap between optimum ranges and OE boundaries, the ecodistricts are displayed with up to 50% transparency so that the underlying temperature or precipitation grid is visible. As an example, the values for mapping the geographic areas that could produce optimal provenance performance for the five representative OE and their provenances are displayed in Table 14, along with the current climatic values of the OE. A range of optimum maximum temperature was obtained by adding and subtracting  $\frac{1}{2}$  of the  $b$  value to and from the value of  $x_0$ . Contour lines on the maps represent the precise values of  $x_0$  at which a provenance could achieve optimum growth. The wider ranges on the maps represent areas where the seed sources could achieve up to 80% of their optimum performance.



Table 13. SigmaPlot output for the five representative OE for December maximum temperature.

OE or Provenance	Cauchy Function Statistic			Regression Statistic		
	a	b	$x_0$	P	$R^2$	SE
OE 383	69.8633	6.4208	-4.1984	0.0006	0.8801	4.8193
P121	72.3358	5.9508	-4.3063	0.1031	0.8969	6.4962
P123	67.5481	6.9699	-4.0600	0.1015	0.8985	5.2163
OE 387B	64.3173	6.7996	-4.3495	$\leq 0.0001$	0.6972	6.9864
P102	66.3426	5.8450	-4.3143	0.1959	0.6627	12.3097
P108	63.7318	7.3652	-4.1825	0.0776	0.8181	6.0504
P109	62.5116	7.6903	-4.1334	0.1372	0.7340	7.4181
P114	64.7799	6.7569	-4.8067	0.2524	0.7476	8.6179
OE 407	66.4667	6.4712	-4.2174	0.0100	0.6841	8.4612
P72	65.6759	7.0538	-4.1352	0.2784	0.5737	12.7673
P76	56.1111	7.6956	-4.6709	0.3453	0.5078	10.0088
OE 425B	73.7296	6.0998	-4.2675	$\leq 0.0001$	0.7170	8.4432
P3	75.2219	6.7363	-4.3768	0.1088	0.8912	6.1012
P4	69.8180	7.1316	-4.1017	0.0238	0.9173	4.2817
P8	71.7864	5.9761	-4.5191	0.2829	0.5691	15.7817
P14	75.6740	5.0165	-4.2989	0.0752	0.8218	10.3005
P15	72.4896	6.2396	-4.5298	0.0204	0.9252	4.7256
P18	77.3398	6.1326	-3.8908	0.2078	0.6492	15.3693
OE 552A	82.8318	5.3677	-4.4176	$\leq 0.0001$	0.7843	9.3575
P39	83.2056	5.1451	-4.4573	0.1659	0.6981	15.9968
P43	77.6609	5.8627	-4.4256	0.0807	0.8132	9.5375
P53	87.7858	5.1551	-4.3757	0.0256	0.9132	7.6729

a = optimum height (cm); b = range around  $x_0$  where the seed source attains up to 80% of its optimum height;  $x_0$  = optimum climate value ( $^{\circ}\text{C}$ )

In Figures 28 and 29, the optimal zones for the two climate variables partially overlap with OE 383, but the contour lines are not located near the OE (Figures 28 and 29). The maps for OE 387B in Figures 30 and 31 show that the optimal zones and the contour lines do not overlap at all with the OE boundaries. In Figures 32 and 33 the optimal zones partially overlap with OE 407, with opposite portions of the OE showing overlap for temperature versus precipitation. The contour line in Figure 33 runs across

the top of the OE. The optimal zones for OE 552A do not overlap at all (Figures 34 and 35). Figure 36 shows that the optimal temperature zone for OE 425B completely overlaps and the contour line runs through the lower portion of the OE. On the contrary, Figure 37 shows no overlap between the optimal zone of mean April precipitation and OE 425B, this was the first OE to show complete overlap and was also the first to show overlap for one variable but not for the other. Optimal maps for January and November maximum temperature are presented in Appendices XVIII and XIX, respectively.

Table 14. Example of values from the Cauchy function that were used for mapping the optimum range of December maximum temperature.

OE or Provenance	b	b/2	$x_0$ (°C)	$x_0$ min. (°C)	$x_0$ max. (°C)	OE Decmxt Min. (°C)	OE Decmxt Max. (°C)	OE Decmxt Mean (°C)
OE 383	6.421	3.210	-4.198	-7.409	-0.988			
P121	5.951	2.975	-4.306	-7.282	-1.331	-8.63	-4.54	-6.82
P123	6.970	3.485	-4.060	-7.545	-0.575			
OE 387B	6.800	3.400	-4.350	-7.749	-0.950			
P102	5.845	2.923	-4.314	-7.237	-1.392			
P108	7.365	3.683	-4.183	-7.865	-0.500	-10.30	-8.73	-9.60
P109	7.690	3.845	-4.133	-7.979	-0.288			
P114	6.757	3.378	-4.807	-8.185	-1.428			
OE 407	6.471	3.236	-4.217	-7.453	-0.982			
P72	7.054	3.527	-4.135	-7.662	-0.608	-8.05	-3.66	-6.84
P76	7.696	3.848	-4.671	-8.519	-0.823			
OE 425B	6.100	3.050	-4.268	-7.317	-1.218			
P3	6.736	3.368	-4.377	-7.745	-1.009			
P4	7.132	3.566	-4.102	-7.668	-0.536			
P8	5.976	2.988	-4.519	-7.507	-1.531	-6.01	-2.69	-4.67
P14	5.017	2.508	-4.299	-6.807	-1.791			
P15	6.240	3.120	-4.530	-7.650	-1.410			
P18	6.133	3.066	-3.891	-6.957	-0.825			
OE 552A	5.368	2.684	-4.418	-7.101	-1.734			
P39	5.145	2.573	-4.457	-7.030	-1.885	-1.59	-0.64	-1.17
P43	5.863	2.931	-4.426	-7.357	-1.494			
P53	5.155	2.578	-4.376	-6.953	-1.798			

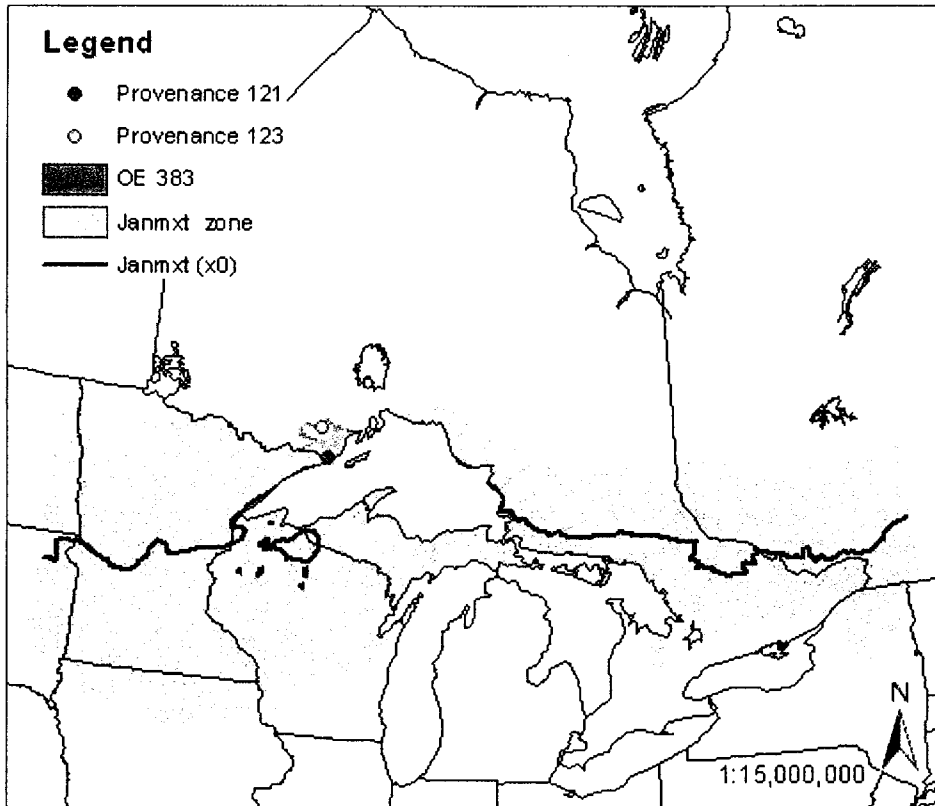


Figure 28. Optimal zone of December maximum temperature for OE 383.

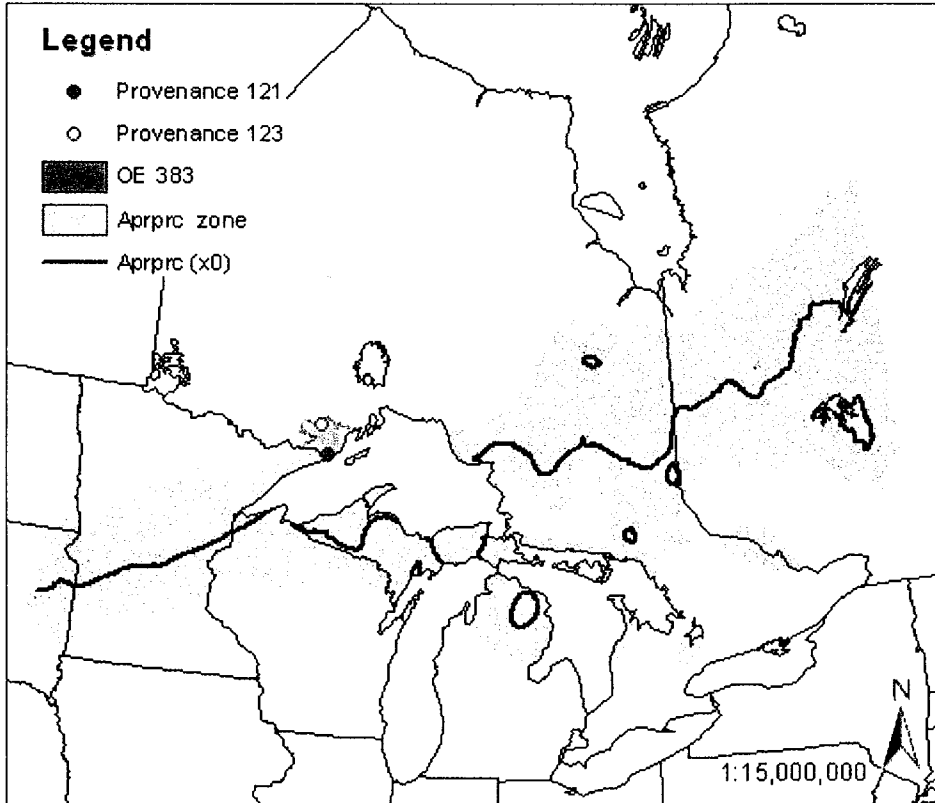


Figure 29. Optimal zone of mean April precipitation for OE 383.

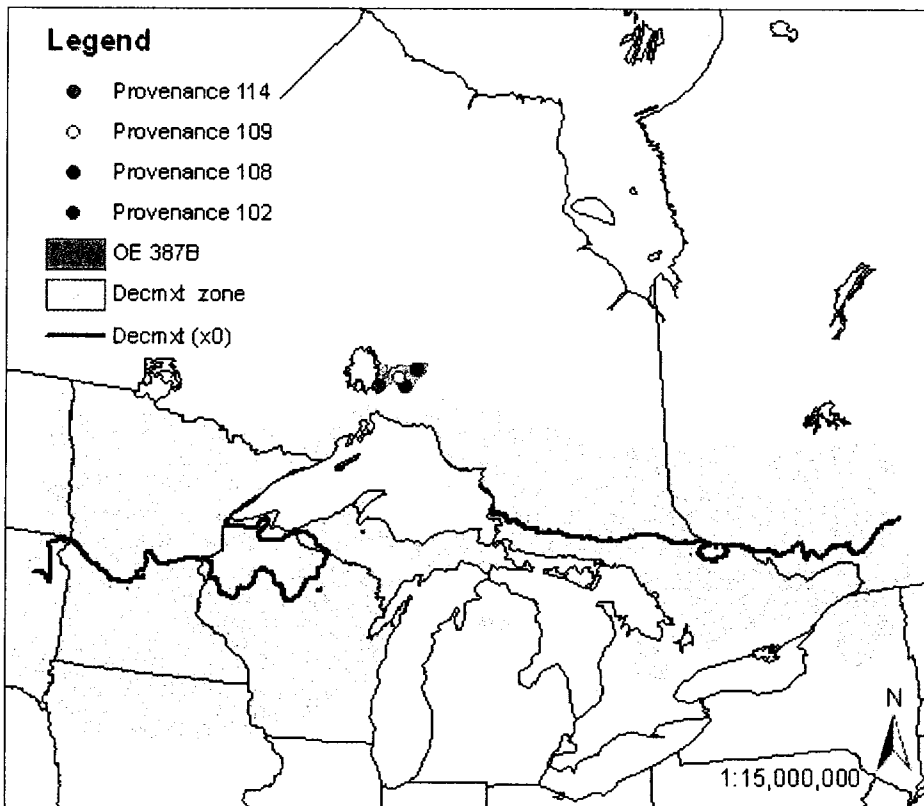


Figure 30. Optimal zone of December maximum temperature for OE 387B.

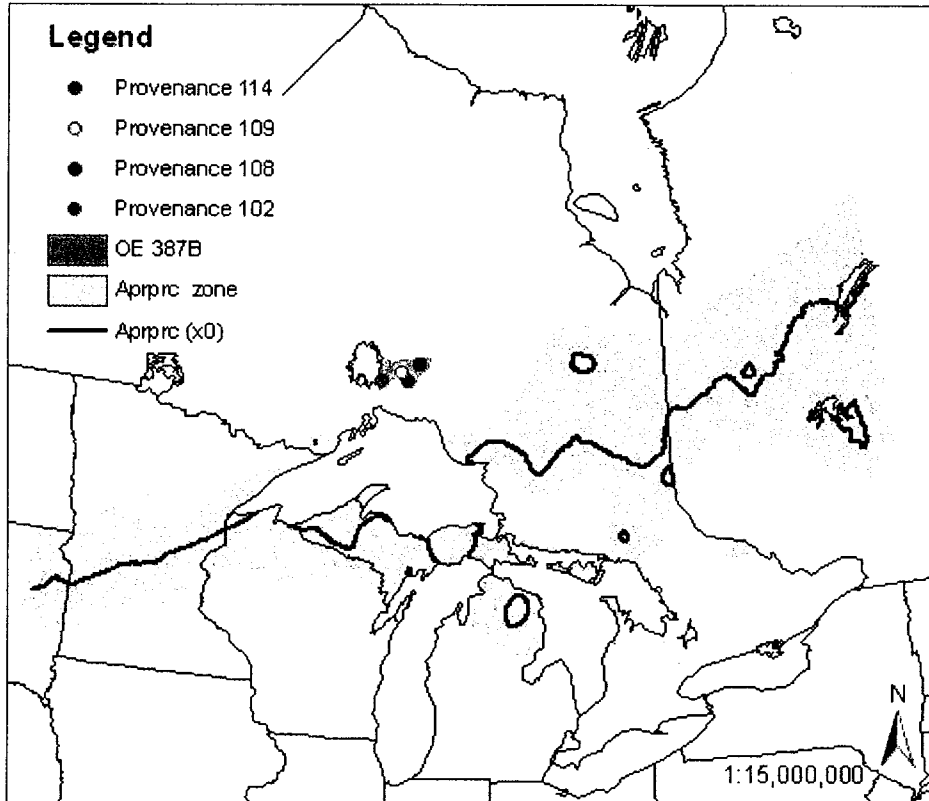


Figure 31. Optimal zone of mean April precipitation for OE 387B.

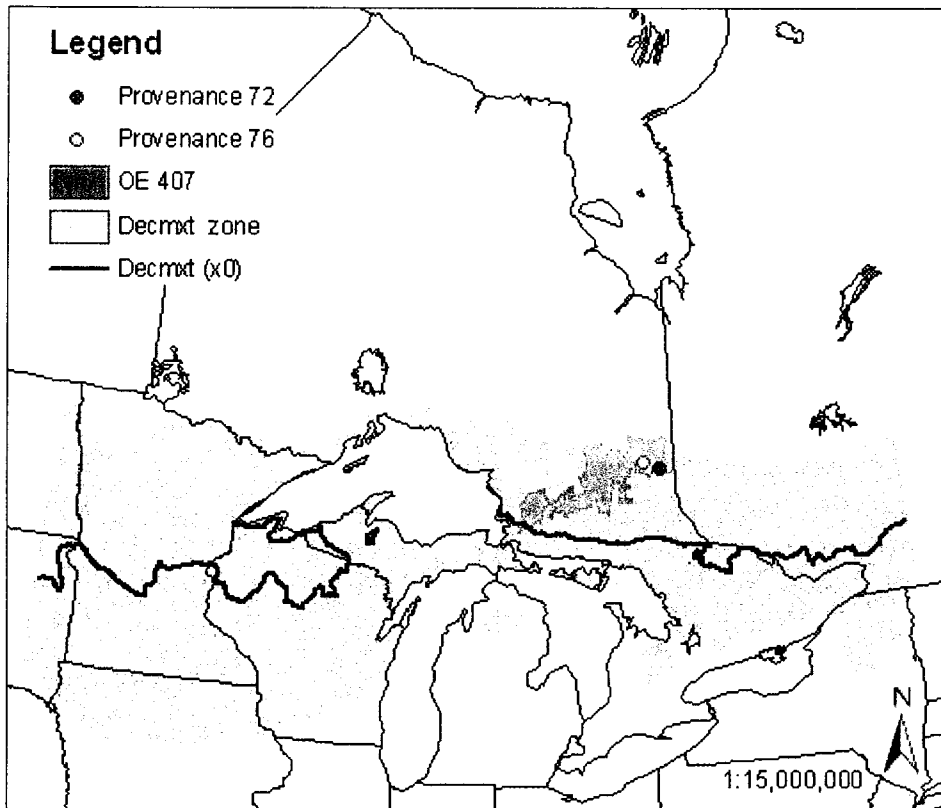


Figure 32. Optimal zone of December maximum temperature for OE 407.

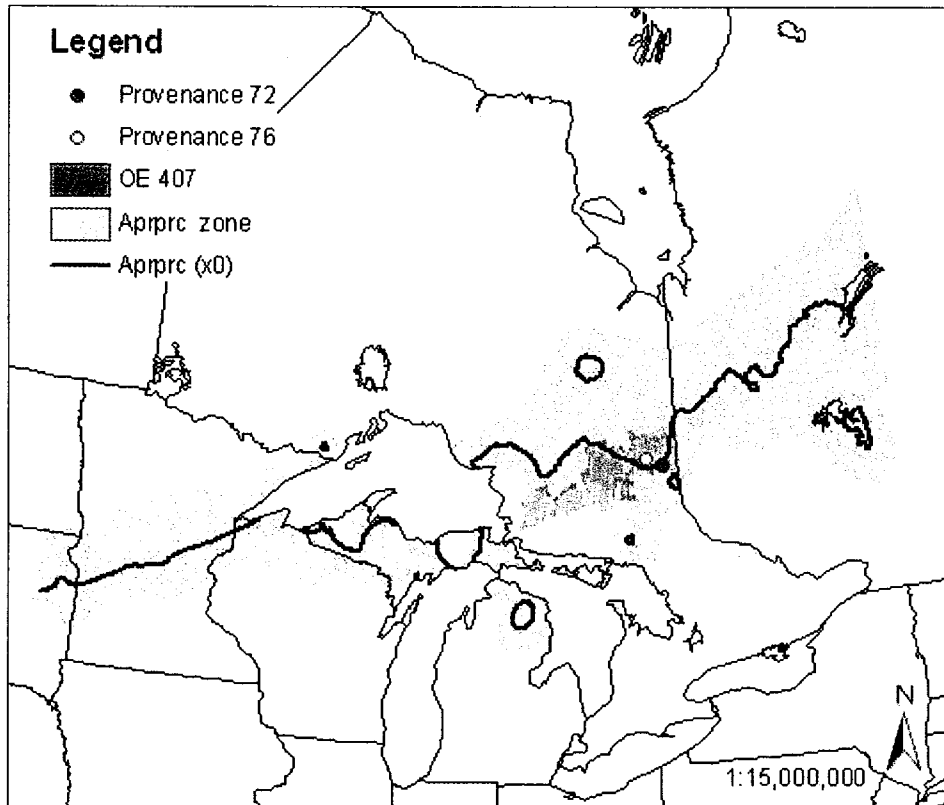


Figure 33. Optimal zone of mean April precipitation for OE 407.

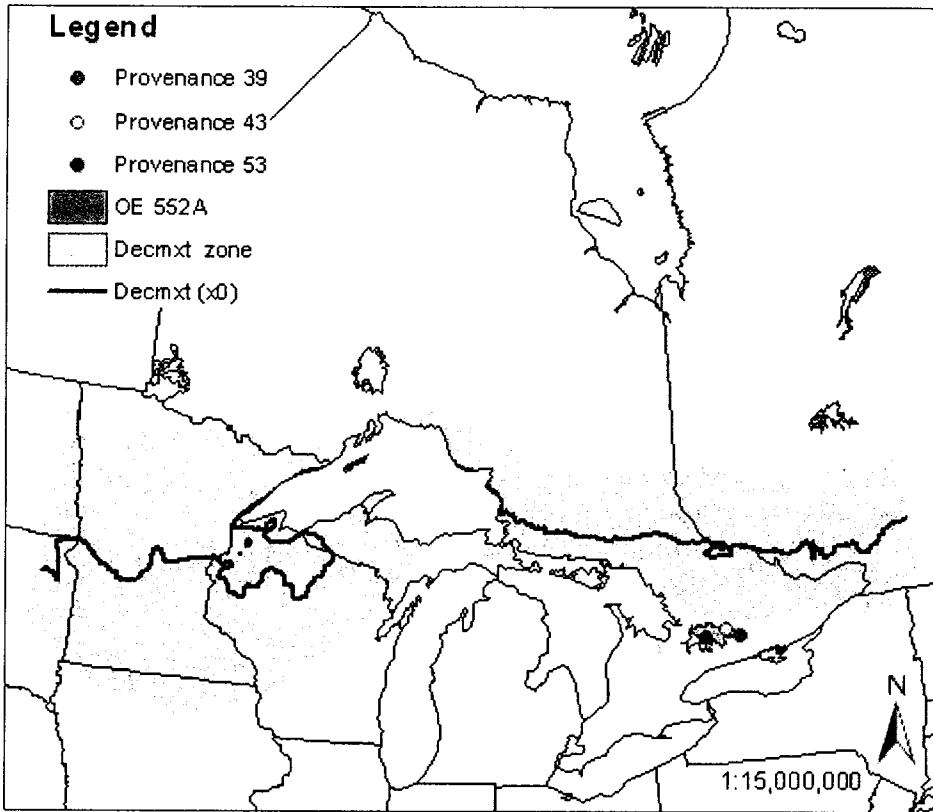


Figure 34. Optimal zone of December maximum temperature for OE 552A.

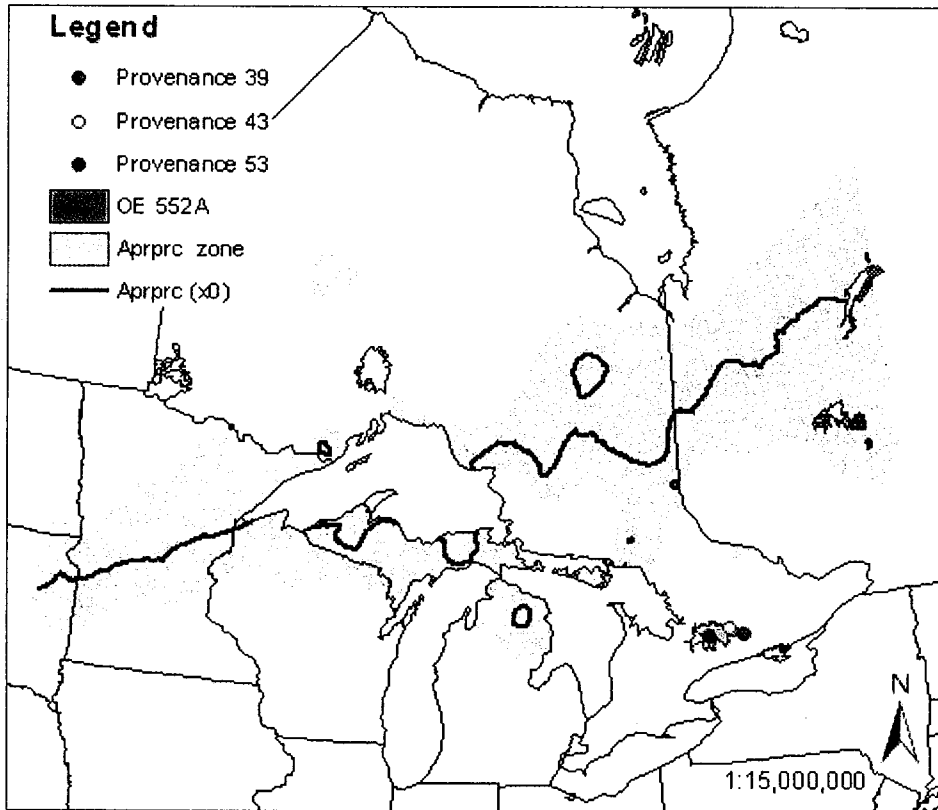


Figure 35. Optimal zone of mean April precipitation for OE 552A.

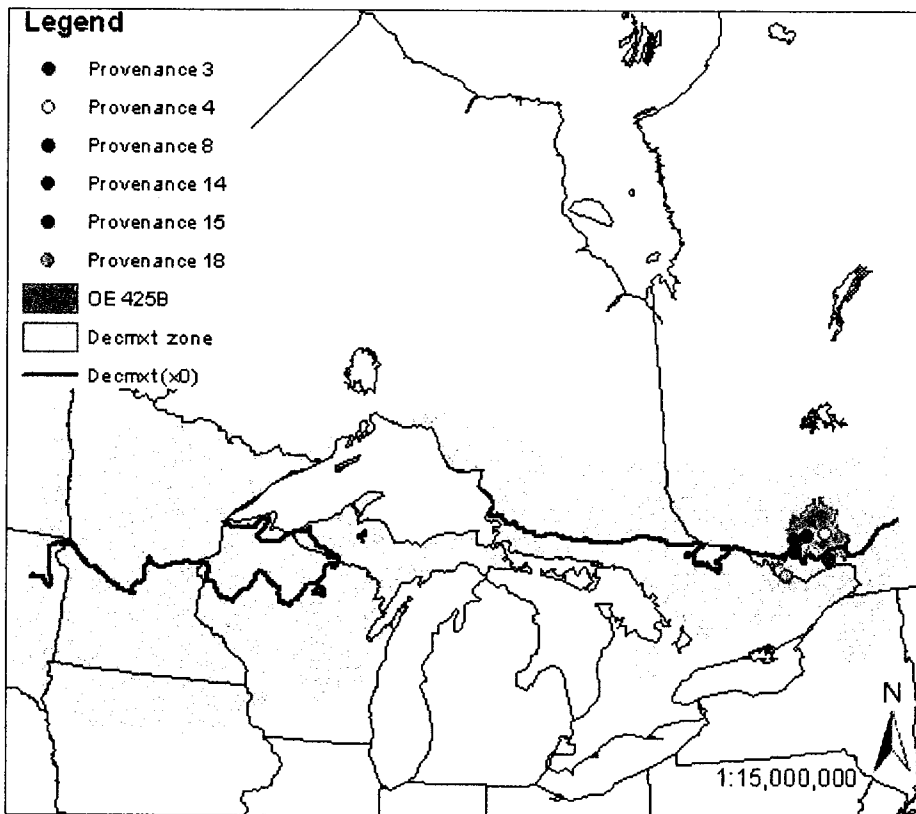


Figure 36. Optimal zone of December maximum temperature for OE 425B.

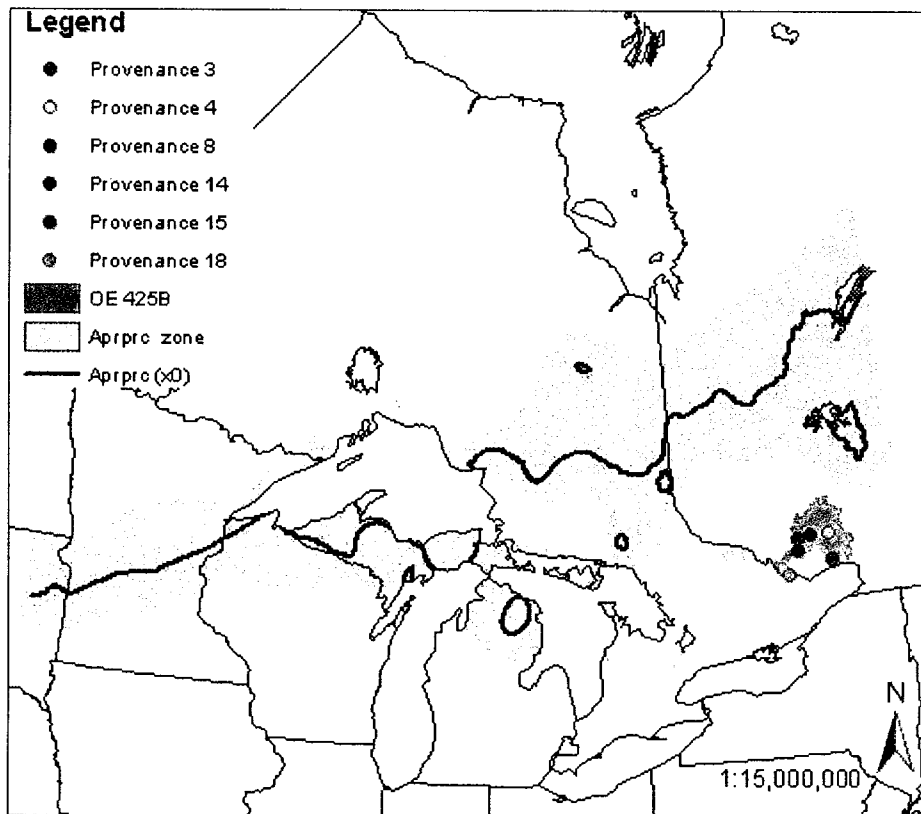


Figure 37. Optimal zone of mean April precipitation for OE 425B.



## DISCUSSION

The white spruce seed sources investigated in this study showed genetic variation, as evidenced by the finding of significant differences for height growth at the test sites. One of the most important findings of this study was that despite genetic differences, the response functions based on the climate variables indicated that provenance optima were very similar. The response functions and the maps for different seed sources all showed almost the same optima in terms of height growth for the selected climate variables. Other climate variables or other response variables could have yielded different results.

It was interesting that most of the selected climate variables were maximum temperatures for the fall and winter months and only two variables were related to precipitation. But this finding makes sense since the most important climatic elements affecting northern ecosystem productivity are cold temperatures, short growing seasons and limited precipitation (Oswald 1992). In retrospect, it would have been beneficial to perform response functions for the temperature seasonality variable as well since it was selected for 89% of operational ecodistricts (OE) and for 80% of provenances. It is possible that response functions for this variable would have produced different results.

Using earlier data collected from the same provenance trials as those used in the current study, Lesser and Parker (2004) found high positive correlations for monthly temperature variables with lower values for precipitation related variables and negative values for variables associated with the growing season. This supports the results of the current study since high positive correlations for maximum monthly winter temperatures were found, with April precipitation being the only positively correlated variable related to the growing season. Lesser and Parker (2004) found high positive correlations with

longitude, which is considered to be a surrogate for precipitation. The results from this study showed that of the three geographic variables, only latitude was highly positively correlated. Latitude is considered a surrogate for temperature which reinforces the findings that maximum monthly temperatures are strongly related to growth.

It is not surprising that this study would produce slightly different results from those reported by Lesser and Parker (2004) since the trees were only two years old at the time of measurement. At five years old, the trees may exhibit different growth characteristics because they have had more time to grow under their respective site conditions. Although early height growth is considered to be a good indicator of overall provenance performance (Li *et al.* 1993; Murray and Skeates 1984), it is possible that some of the variation becomes diminished over time.

Thomson (2008) also used data collected from the provenance trials featured in the current study and determined that temperature was a better predictor of white spruce performance than precipitation, which supports the results. Contrary to the current study, however, Thomson (2008) found that May, June and August temperatures produced the strongest regressions, suggesting that temperatures during the growing season played a critical role in white spruce growth. There were two important differences in the methodologies of these two studies. The current study used climate normals calculated from 1971 - 2000, whereas, Thomson (2008) used normals from the period of 1961 - 1990. In addition, the study conducted by Thomson (2008) included height, diameter, survival and increment variables while the current study utilized only height growth.

### Sources of experimental error

A common source of error in provenance research is inadequate experimental and sampling designs (Morgenstern 1996). Generally in provenance research for Ontario, sampling of provenances has concentrated in southern Ontario and Quebec, leaving provenances in the west and north being rarely sampled (Nienstaedt and Teich 1972). This is also true for the current study whereby provenances located east of Lake Superior and from northern and western Ontario were not well sampled. Nienstaedt and Teich (1972) recommend the use of 150 provenances sampled from the entire range of the species. The range of white spruce is very broad, however, and there are many problems in effective sampling across such large regions (Wu and Hobbs 2002). The current study used 127 provenances which is considerably more than some provenance experiments and it also had six separate test sites along with complete replication of all provenances at each test which makes the data quite robust.

This study only utilized height data, but it would be useful to perform the same analyses with the other growth variables that were measured (root collar diameter, elongation and survival). It would also be interesting to perform cluster analysis for all growth variables to see if the provenance groupings would be similar to the ecodistrict groupings. The idea to perform cluster analysis presented itself too late in the study which is why it was not carried out. In addition, it would be beneficial to include other species in this type of study to see if the trends hold true across tree species. This is an especially important point since ELC was carried out for ecosystems and not for individual species.

Unusual climatic events or unexpected damage can be a source of error in provenance research (Morgenstern 1996). Unfortunately, the Longlac test site exhibited

extreme mortality due to unexpected damage from an untimely herbicide application; this event could have biased the results obtained from the site. Although the trees at the Dryden site exhibited fairly good survival, most of them exhibited poor growth which has been attributed to poor site conditions owing to sandy soil which was badly affected by frost heaving. The unfortunate circumstances at the Longlac test were a result of human error while those at the Dryden site resulted from variations in environmental conditions. It could be argued that the data obtained from these tests should have been excluded from analyses, but it could also be argued that despite their unfortunate circumstances, these tests were still a useful source of information. In nature, plants are sometimes subjected to extreme conditions and they must either adapt or die. In provenance testing, it can be useful to include data from tests with extreme site conditions as it helps to provide a more thorough view of provenance response across a broad range of environments.

Some of the models used for statistical analysis in this study involved unbalanced designs. A different number of observations were available for the provenances which reflects the fact that some of the seedlings of a provenance did not survive. It is possible that comparisons were made between provenances which had a large number of observations and provenances which had a small number of observations. It is unavoidable that some mortality would occur; this is the nature of provenance research and the best solution to cope with this issue was to report the Type I Sum of Squares which is said to take into account the different number of observations in unbalanced designs [Dr. Shahi(pers. comm., May 2009)]. Also, there were a different number of provenances in the ecodistricts and in the operational ecodistrict (OE)

groupings; this was due to the geographic location of the ecodistricts, the uneven sampling of provenances and seedling mortality.

Although six test sites were used in this study, the results were generalized across Ontario and into western Quebec, where no field trials were located. Therefore, it is important to note the limitations of such an extension of the findings. Optimum ranges were predicted for provenances in Ontario and western Quebec that were grown at only six locations. It is possible that these test sites may not be a representative sample of environmental conditions across the study area. Increasing the number of test sites and ensuring that they are representative of conditions across the entire study area would reduce this concern.

As previously mentioned, provenances were not distributed evenly among the ecodistricts and OE. This study was never intended to be used in an ELC context, so it is understandable that provenance representation of the levels of classification would be uneven. It should also be noted that some of the provenances were located along ecodistrict boundaries. Marginally located provenances may not be representative of the provenances near the center of the ecodistrict. Since ecodistrict boundaries are somewhat subjective, it is possible that a provenance located on an ecodistrict boundary may be more representative of an adjacent ecodistrict rather than the one in which it was found. Another interesting issue is that the subdivision of the ecodistricts into OE sometimes involved grouping provenances that were not in close proximity to each other.

The natural variability of geography and ecology has often been categorized on the assumption that individual regions represent conditions that are homogenous and different from those within other regions (McMahon *et al.* 2004). In this study, it was

assumed that conditions within ecodistricts were homogeneous; yet the statistics suggested that variation was present within some ecodistricts. This variation could be responsible for the observed patterns of provenance performance. It is, therefore, logical to assume that there is some degree of environmental heterogeneity within ecodistricts. The existence of variation within ecodistricts is supported by ELC hierarchy where ecosection is the next lower level. This variation is beneficial to the species which live there because homogenous environments are considered to be unstable since they have an impaired ability to respond to change or disturbance (McMahon *et al.* 2004). Environments with spatial and temporal heterogeneity are those that produce the plasticity required for long-term ecosystem stability (McMahon *et al.* 2004).

ELC boundaries are not temporally static; they are in flux just as long-term climate fluctuates continually (Bailey 2005). Genetic information is usually a result of a combination of both past and current processes while landscape data are usually a reflection of current conditions only (Balkenhol *et al.* 2009). Therefore, there is the potential for a mismatch of temporal scales which can result in serious research errors (Balkenhol *et al.* 2009). It is possible that white spruce genetics have been strongly influenced by past events or conditions that no longer exist, which would make it difficult to interpret such phenomena using current environmental conditions. The climate variables obtained for data analysis were normals calculated from 1971 to 2000, but the trees used in this study were planted in 2002. While the climate normals used may not be representative of the growing conditions for the studied provenances, they are probably representative of the growing conditions of the seed parents.

Since most classification has ignored the human influence on ecosystems, the delineation of boundaries is often based on the potential niche of species, rather than on

the realized niche (Bailey 2005). The current study is no exception since the maps that were created do not account for areas of human development or resource exploitation. Studies that do not consider the effects of humans on the landscape can produce confounding results (Pickett and Cadenasso 1995). Humans have had various impacts on ecological landscapes through changing disturbance types and patterns, pollution and the introduction of alien species (Pickett and Cadenasso 1995). Sound knowledge of ecological niche theory is crucial for understanding the relationship between environmental change and species patterns (Hargrove and Hoffman 2005).

Although soils were used in ELC, this study did not include any specific soil components. To be relevant in classification systems, soil should be viewed as the integral aspect of the environment which has a reciprocal relationship with plants (Hills 1952). But it can be difficult to include soil components in large scale classification systems since many soil and vegetation variables exhibit considerable spatial variation on a small scale, even within a few meters (Iverson 2007). It is possible that small scale variations in soil could account for some of the patterns revealed in this study, for example, the possibility exists for white spruce ecotypes for limestone soils (Teich and Holst 1974).

#### Do ecodistrict boundaries reflect genetic variation?

The results from ANOVA generally support the existing ecodistrict boundaries, but it was necessary to create additional units to account for provenance differences within groups. The need for the creation of the operational ecodistrict units indicated that genetic variation for height growth did not always correspond to ecodistrict boundaries. If genetic variation corresponded perfectly to ecodistrict boundaries, there

would not have been significant differences between the provenances within some ecodistricts. This finding suggests that perhaps more ecodistricts are needed or that perhaps this study should have focused on the next lower hierarchical level: the ecosection. It would be useful to compare the operational ecodistricts OE with a map of the ecosection level, but it is currently not possible to obtain a GIS coverage of ecosections (the ecodistrict level is the lowest one that is available) and locating even a hard copy of the maps proved to be problematic. In retrospect, the results from ANOVA could have been used to not only subdivide them, but also to combine some of the existing ecodistricts. The fact that some of the ecodistricts needed to be subdivided and that some of them could have been combined could suggest that this study may have been justified in focusing on the ecodistrict level of classification.

Contrary to the ANOVA results, the maps generated from the results of the response functions provide very little support for genetic differences between provenances. The maps were a visual representation of the response functions which showed almost the same optimal conditions for December maximum temperature and mean April precipitation for all provenances. The maps also showed that ecodistrict boundaries often did not coincide with optimum ranges for the provenances which could mean that although provenances have successfully adapted to local conditions, they would achieve optimum height growth elsewhere.

A possible explanation for why ecodistrict boundaries were not always reflective of genetic variation in white spruce is that the ecodistrict map may need to be revised. It has been over a decade since the maps were re-released and our understanding of ecological processes has progressed in that time. Also, advances in mapping and remote sensing technologies have occurred which could greatly improve the quality of the maps.



If ELC maps were to be revised using both a more complete understanding of ecology and better mapping technology, it is possible that the levels of classification would be more reflective of ecological processes. Although the intended purpose of ELC was to improve ecosystem management, its role is still somewhat unclear and it has been a long time since the map boundaries were revisited.

To make a study of this nature more robust and more applicable to ELC, a few suggestions should be considered. Firstly, it should be stated that designing a more robust study than the one discussed previously would be very time consuming and costly, as is the nature of provenance and genetic research. The following suggestions are made assuming that one would have the necessary resources to fully implement the design. It would be very useful to sample provenances evenly across ecodistricts (or a given level of classification) to gain a more accurate view of performance both within and between ecodistricts. In addition to more representative provenance sampling, detailed soil information should be obtained from each ecodistrict and each test location. If funds permitted, molecular genetic approaches could be applied to the provenances to test for differences in genetic markers that could be related to the spatial components being studied. Provenances should be measured at regular intervals for many morphological and phenological traits and all traits should be used in the statistical analyses. In addition, the study should include as many climate variables as possible. The influence of past events and conditions on the genetics of the studied species should be evaluated. The most accurate climatic information should be obtained and the maps should reflect current land use patterns to account for restrictions on the potential niche. And finally, this design should be applied to multiple species. It would be relatively easy to use species such as jack pine and black spruce, for which a wealth of information

exists from a variety of common garden experiments. But other species, including shrubs and herbs should also be studied despite a relatively small amount of previous research.

## CONCLUSION

It was hypothesized that if genetic variation was influenced by changes in the environment as delineated by ELC, then the patterns of variation observed in white spruce would correspond to ecodistrict boundaries in Ontario and western Quebec. Based on the results of this study, it can be concluded that ecodistrict boundaries in central Canada are generally reflective of genetic variation in the height growth of white spruce. Thus although the hypothesis was not rejected, it is not considered to be fully explanatory since it was necessary to subdivide some of the ecodistricts into smaller units. This study seems to indicate that genetic variation of white spruce may be influenced by other factors that could have been unaccounted for in this study. Another possible explanation is that the ecodistrict boundaries themselves may require revision. The maps have remained largely unchanged since 1995 and it may be beneficial to revise them using more advanced knowledge and technology.

This may be one of the first studies that has attempted to relate genetic variation in forest tree species to ELC and is in keeping with the suggestion of McMahon *et al.* (2004) to try to use different types of data to reveal ecosystem patterns. However, these results should be viewed critically, as there were many potential sources of experimental error. Nonetheless, this study has produced interesting results which can provide direction for future studies of this nature.

In Ontario, forest management is closely linked to the concept of 'site regions' as developed by Hills (1961). The site region is defined as "an area of land within which the response of vegetation to the features of landform follows a consistent pattern" (Hills 1961). Early seed zones in Ontario were based on site regions and on administrative boundaries (Lesser and Parker 2004). It has been argued that although management

based on site regions allowed for the maintenance of survival and hardiness, it was not designed for the genetic management of seed (Teich *et al.* 1975). In 1952, Hills acknowledged that basic biological factors in classification should include the consideration of genetic units, but there is little or no mention of this in his later publications.

Plant populations are at risk because of continued human population growth, increased energy demand, resource exploitation and changing land use patterns (Morgenstern 1996). And despite an immense volume of research devoted to spatial ecology, ecological concepts are not fully integrated into land use planning, primarily because "...sustainability has not been properly defined in a spatially explicit context" (Vos *et al.* 2007). Sustainable development requires that decision making about a landscape be balanced between ecological, cultural and economic functions, both in the short and long-term (Herring 2005). The definition of sustainable development includes the implication that ecosystem functions are maintained by the spatial organization of the landscape (Vos *et al.* 2007). However, if current forest management regimes are based on a system that does not acknowledge genetic diversity as a key ecosystem component, then it could be said that these regimes are unsustainable. If genetic diversity is the foundation of forest sustainability (Rajora *et al.* 2005), then new management regimes should be designed with a focus on the genetic management and conservation of forest tree species.

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