

**Juvenile development of 25 open-pollinated families
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with grey alder (*Alnus incana*)**

G.R. Larocque, J. Beaulieu, G. Daoust and C.-H. Ung

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TABLE OF CONTENTS

ABSTRACT	v
RÉSUMÉ.....	v
INTRODUCTION	1
MATERIALS AND METHODS	2
Study sites	2
Field measurements	3
Growth analyses.....	4
Data analysis	6
RESULTS	8
DISCUSSION.....	15
CONCLUSION	17
ACKNOWLEDGEMENTS	17
LITERATURE CITED	18

LIST OF TABLES

Table 1. List of eastern white pine provenances and family numbers planted on each experimental site	3
Table 2. Stem and branch traits measured on 25 eastern white pine families	4
Table 3. Summary of stem growth and crown development indices derived for the comparison of the productivity of 25 eastern white pine families	5
Table 4. Means and variance components for absolute and relative growth rates in height and dbh for 25 eastern white pine families.....	9
Table 5. Means and variance components for stem taper ratios, crown shape ratio, crown ratio and crown projection ratio in 25 eastern white pine families	10
Table 6. Means and variance components for the annual increment rate of the smallest branch measured on each of the first five whorls among 25 eastern white pine families	11
Table 7. Means and variance components for the annual increment rate of the longest branch measured on each of the first five whorls among 25 white pine families	13
Table 8. Observed significance of variances and covariances associated with the analysis of covariance for $\sqrt{\text{branch length per whorl}}$ using the branch basal diameter as covariate for 25 eastern white pine families	14
Table 9. Observed significance associated with the analysis of covariance for basal area increment at breast height in terms of absolute and relative growth rates using a competition index as covariate for 25 eastern white pine families	14

LIST OF FIGURES

Figure 1. Absolute and relative growth rates in height between 1993 and 1995 and between 1995 and 2000 for 25 eastern white pine families.....	9
Figure 2. Mean annual branch increment rate for the smallest branch on each whorl. The first number on incrvert*I& indicates the whorl number and the second number indicates the year (1 for 1995 and 5 for 1991)	11
Figure 3. Mean annual branch increment rate for the largest branch on each whorl. The first number on incrvert*I& indicates the whorl number and the second number indicates the year (1 for 1995 and 5 for 1991)	12

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ABSTRACT

There is renewed interest in the management of eastern white pine (*Pinus strobus* L.) for high-quality wood production. Several tree improvement programs have been implemented for the last few decades to better understand the genetic variability of eastern white pine. However, the genetic variation of eastern white pine has been evaluated mostly by comparing diameter or height growth of different families or provenances in common gardens with pure plantations. Growth comparison is insufficient because it does not evaluate the efficiency of different families to use site resources for productivity improvement. Crown attributes have received less consideration in genetic studies on eastern white pine. The objective of this study was to compare the performance of 25 eastern white pine families growing in mixed plantations with grey alder (*Alnus incana* [L.] Moench). Branch development traits and relative measures of crown development were used to compare the families. The results indicated that the variance components of the family effect were not significant for the dbh (diameter at breast height) and height growth variables and the different measures of crown development. The lack of significant variation among the 25 families was also observed for branch increment rate, the relationship between branch length and branch diameter and the relationships between diameter growth rate in terms of absolute and relative growth rates and a competition index. Thus, different families responded similarly to the effect of competition from grey alder. For all these relationships, the results also indicated that the variation in microsite conditions accentuated the differences in the family variance components.

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RÉSUMÉ

L'aménagement du pin blanc (*Pinus strobus* L.) pour la production de bois de grande qualité suscite un regain d'intérêt. Au cours des dernières décennies, plusieurs programmes d'amélioration génétique ont été implantés afin de mieux comprendre la variabilité génétique de cette espèce. Toutefois, les variations génétiques chez le pin blanc ont principalement été évaluées en comparant la croissance en diamètre ou en hauteur de différentes familles ou provenances établies en plantations pures dans des tests de provenance. La comparaison de la croissance est cependant insuffisante puisqu'elle n'évalue pas l'efficacité des différentes familles à utiliser les ressources du site pour améliorer leur productivité. Les études génétiques sur le pin blanc ont peu utilisé les caractères des cimes. L'objectif de la présente étude fut de comparer la performance de 25 familles de pin blanc croissant en plantations mélangées avec l'aulne rugueux (*Alnus incana* [L.] Moench). Les caractères de développement des branches et des mesures relatives de développement des cimes ont été utilisés pour comparer les familles. D'après les résultats obtenus, les composantes de la variance due à l'effet de la famille n'étaient pas significatives pour les variables de croissance en dhp (diamètre à hauteur de poitrine) et en hauteur et les diverses mesures de développement de la cime. L'absence de variation significative entre les 25 familles a aussi été observée en ce qui a trait aux taux d'accroissement des branches, à la relation entre la longueur et le diamètre des branches et aux relations entre les taux absolus et relatifs de croissance en diamètre et un indice de compétition. Par conséquent, les différentes familles ont réagi de façon similaire à la compétition exercée par l'aulne rugueux. Pour toutes ces relations, les résultats ont aussi indiqué que les variations dans les conditions du microsite ont accentué les différences dans les composantes de la variance familiale.

INTRODUCTION

The natural range of eastern white pine (*Pinus strobus* L.) extends over a large portion of northeastern North America. This relatively large distribution is likely due to the fact that eastern white pine can grow under different soil conditions, from well drained sandy soils to wet swamps (Farrar 1995), and climates (Wendel and Smith 1990). As its wood had excellent properties for end products such as ship masts, molding or furniture, eastern white pine was harvested intensively in the 19th and 20th centuries. Despite the demand, eastern white pine has not been managed intensively in recent decades because of extensive damage caused by white pine weevil (*Pissodes strobi* Peck) and white pine blister rust (*Cronartium ribicola* J.C. Fish.). Silvicultural practices were developed specifically to minimize the damage (e.g., Martineau 1984, Stiell and Berry 1985) and genetic improvement programs were implemented to breed for resistance (Kriebel 1983, Blada 2000, Fins et al. 2002, Kinloch and Dupper 2002). Thus, as the new silvicultural practices and breeding programs were somewhat successful in reducing damage from both pests, there has been a renewed interest in the reforestation of eastern white pine for high-quality wood production.

The establishment of eastern white pine plantations throughout northeastern North America generated several studies on the extent of genetic variation with respect to seed germination (e.g., English and Linehan 2001), flower induction (e.g., Ho and Schneckenger 1992, Daoust and Beaulieu 1999), survival (e.g., Anderson et al. 2002), tolerance to white pine weevil (e.g., Zsuffa 1985, Abubaker and Zsuffa 1991), resistance to cold hardiness (Lu et al. 2003) and growth traits (e.g., Abubaker and Zsuffa 1991, Beaulieu et al. 1996, Li et al. 1997, Joyce et al. 2002). In particular, studies on the genetic variation of growth traits provided essential information for the implementation of tree improvement programs for eastern white pine. However, the majority of these studies did not fully consider the potential interactions among different traits beyond traditional growth measures based on diameter at breast height (dbh) or height growth. Stem growth in terms of diameter and height depends to a large extent on morphological characteristics of crowns and complex interactions among ecophysiological processes that govern photosynthate allocation, which are influenced by both environmental and genetic factors (Zhang et al. 1996). For eastern white pine, variables related to crown attributes have not been considered much in genetic studies. Several studies conducted for other species concluded that crown attributes, such as shoot elongation or dimensions, may provide insight into the adaptation of different populations to a variety of abiotic and biotic growing conditions. Good examples are the studies by Bridgwater et al. (1985), Bridgwater (1990), Kaya and Isik (1997), Day et al. (2002) and Isik et al. (2002) for shoot growth and of King et al. (1992), St.Clair (1994a, 1994b), Dunlap et al. (1995), Larocque (2000) and Matziris (2000) for crown dimensions or relative measures of crown development. All these studies suggest that there is still little understanding of the complexity of the interactions among different traits that affect tree growth under different abiotic and biotic site conditions. For instance, significant differences in photosynthate partitioning were reported among different Douglas-fir families, whereas no significant differences existed in growth traits (St.Clair 1994a).

Most of the studies dealing with crown development in eastern white pine were conducted in natural stands and aimed at comparing the crown development of different species associated with white pine (e.g., Fajvan and Seymour 1993), modelling crown profile or the effect of competition on diameter growth (e.g., Schreuder and Swank 1974, Gillespie and Hocker 1986, Seymour and Smith 1987), better understanding the extent to which foliage acclimates to different light conditions (e.g., O'Connell and Kelty 1994, Messier et al. 1999), or describing twig and branch distributions (e.g., Owston 1969, Wilson 1998). There is a lack of

knowledge on the extent of genetic variation in crown and branch attributes of eastern white pine and on the degree to which this variation is correlated to that of stem growth. For instance, it can be hypothesized that the most efficient families for stemwood production are those with crowns that have the most efficient strategy for occupying their aerial growing space. Such questions must be examined because stem diameter growth is intimately associated with apical control in eastern white pine (Wilson 1998). There is much to be achieved in addressing these issues because they provide indications on which traits should be considered in breeding programs to maximize tree and stand productivity. Moreover, the performance of families may be affected by inter-specific competition (Harper 1977, Cannell 1978, Day et al. 2002). Therefore, it is necessary to examine how various tree morphological and physiological characteristics interact at the genetic level. This is even more important in mixed plantations. For eastern white pine, the majority of genetic studies were conducted in common gardens with pure plantations.

This study examined the crown, branch and stem development of 25 families of eastern white pine interplanted with grey alder (*Alnus incana*). The objectives were to (1) compare the performance in terms of productivity and growth efficiency and various crown characteristics (branch development and relative measures of crown development) of the different families, (2) examine the variation in the relationships among branch traits and (3) explore any possible effect of interspecific competition on the different families.

MATERIALS AND METHODS

Study sites

The experimental trial of different eastern white pine open-pollinated families and grey alder was established in 1989 on two sites in Quebec, Canada: (1) St-Gabriel-de-Valcartier (46° 56' N, 71° 30' W), north of Quebec City, and (2) St-Joseph-de-Lévis (46° 40' N, 71° 10' W), east of Quebec City. White pine seedlings originated from 25 families within each of five provenances (Table 1). Seeds were collected in 1977 for the Lac Emery provenance, 1982 for the Rivière-de-l'Aigle, Lac Kipawa and Lac Balsam provenances and 1980 for the Little River provenance. For all the Quebec provenances, half-sib family seeds were collected in natural stands from dominant trees distanced at least 50 m from each other. Half-sib family seeds from the Little River provenance were collected in five grafted clones that originated from locally selected white pines. These clones were growing in a seed orchard. Following a 3-week stratification treatment at 4°C, seeds were sown in a greenhouse in 1984 for 1 year before plantation in a nursery. The seedlings grew in the nursery from 1985 to 1989. When transferred to the experimental sites, the seedlings were about 80 cm high. Grey alder seeds, which were provided by the ministère des Ressources naturelles et de la Faune du Québec, were obtained from trees of unknown origin, but well adapted to the climatic conditions of the Great Lakes-St. Lawrence forest region. Seeds were sown in a greenhouse in 1987 and 1-year-old seedlings were transplanted to a nursery and grown there for 2 years. At the time of extraction, many seedlings were over 2 m high. All the bare-root seedlings were topped to 1.75 m.

Table 1. List of eastern white pine provenances and family numbers planted on each experimental site

Provenance location	Family numbers	Latitude N (°)	Longitude W (°)	Elevation (m)
Lac Emery, QC, Can.	183, 184, 185, 186, 187	46 53	73 14	274
Little River, VT, U.S.A.	422, 425, 426, 427, 428	44 29	73 06	110
Rivière-de-l'Aigle, QC, Can.	630, 633, 635, 638, 639	46 21	76 10	213
Lac Kipawa, QC, Can.	661, 662, 664, 743, 745	47 03	78 57	335
Lac Balsam, QC, Can.	731, 733, 736, 737, 739	46 15	76 54	244

The Valcartier site, which was farmed several decades ago, was colonized by several tree and shrub species before the establishment of the experimental trial, including balsam fir (*Abies balsamea* [L.] Mill.), black spruce (*Picea mariana* [Mill.] B.S.P.) and trembling aspen (*Populus tremuloides* Michx.). The soil texture was classified as a sandy loam on the first 15 cm and as a loamy sand below. Following clearcutting in the fall of 1988 and removal of the residual stumps in the spring of 1989, the site was ploughed and disc harrowed. The residual logs from non-commercial woody species and slashes were chipped and spread out over the site. Fertilizers (850 kg ha⁻¹ of 12-8-14+Mg) and lime (600 kg ha⁻¹) were then applied. White pine and grey alder seedlings were planted in June 1989. Simazine 80W (6 kg ha⁻¹) was sprayed in July 1989.

The Lévis site was established on the hilly part of a farm. The soil texture was classified as a gravelly loam. As the drainage conditions varied along the position on the hill, three blocks were laid out along the slope of the hill to obtain drainage conditions as homogeneous as possible within each block. The three blocks laid out from the top to the bottom of the hill were characterized as moderately well to imperfectly drained, moderately well to poorly drained, and imperfectly to poorly drained, respectively. Before plantation, glyphosate (5 L ha⁻¹) was sprayed and the site was ploughed and disc harrowed. White pine and grey alder seedlings were planted in June 1989. Simazine 80W (6 kg ha⁻¹) was sprayed in July 1989.

The white pine seedlings were planted in alternate rows and columns with grey alder at a spacing of 2 m x 1.5 m such that each white pine was surrounded by four grey alders. The mixed plantation system was established so that the companion species would provide shade to the eastern white pine seedlings. Shade was reported to be necessary for young eastern white pine to prevent white pine weevil attacks (Stiell and Berry 1985). Four seedlings of each white pine family tree were randomly located within each block. The seedlings were surveyed on both sites in July 1990 to detect problems (mortality, damage, etc.). Weeds and herbaceous plants were removed on both sites in 1990 and 1991 by brushing and manual removal.

Field measurements

Trees were measured in 1993, 1995 and 2000 (Table 2), respectively. While only height was measured in 1993, dbh and height were measured in 1995 and 2000 on all the trees. Branch traits were measured in 1995. The diameter at the branch base was measured on all the branches that were on the first five whorls from the tree top, i.e., corresponding to the last 5 years of growth on the plantation sites. For the present study, whorl 1 was at the top of the tree, i.e., the 1995 whorl. In addition, the length of each branch whorl on the smallest and largest branches and a randomly chosen branch on each of the five whorls was measured. These

measurements corresponded to the annual branch elongation rate from 1991 to 1995 on whorl 5, from 1992 to 1995 on whorl 4, from 1993 to 1995 on whorl 3, from 1994 to 1995 on whorl 2, and in 1995 on whorl 1.

Table 2. Stem and branch traits measured on 25 eastern white pine families

Trait category	Variable	Measurements year(s)
Stem	- Dbh (mm)	1995, 2000
	- Height (cm)	1993, 1995, 2000
	- Stump diameter (20 cm above the ground) (mm)	1995
	- Maximum crown width (m)	1995
	- Height to maximum crown width (m)	1995
	- Diameter at the base of whorls 1 and 5 (mm)	1995
Branch	- Diameter at branch base and length on all branches (mm)	1995
	- Annual branch elongation rate on the smallest and largest branches on the first five whorls (cm year ⁻¹)	1995

The intensity of competition of grey alder on white pine trees was expressed with a competition index using specific measurements in 1995. Stem height and the length of the longest branch facing a subject white pine were measured for each grey alder surrounding a white pine. Also, the distance between each grey alder and its subject white pine tree was measured. When these measurements were made in 1995, average height for grey alder was 4.57 m, varying from 0.40 to 7.20 m, and average height for all eastern white pine families was 2.76 m, varying from 1.25 to 4.70 m.

Growth analyses

Different stem growth and crown development indices were used to compare the productivity of the different families (Table 3). Absolute growth rate (AGR) is the rate of growth per unit time in both dbh and height. Relative growth rate (RGR), the rate of change in size per unit time per unit size, is considered as a measure of the productive capacity or growth efficiency of a plant (Causton and Venus 1981, Fitter and Hay 1987). According to Fitter and Hay (1987), RGR estimates the proportion of photosynthate partitioned for growth. It also provides a common base for comparison of the productivity of plants that differ in initial size, age or environmental conditions (Ledig 1974, Kramer and Kozlowski 1979, Radosevich and Osteryoung 1987). According to Brand (1991), RGR is a strong statistical indicator of the effect of treatments. Several studies indicated that RGR can be used to draw inferences on the occurrence of the onset of competition in young stands (e.g., Ford 1984, Cannell et al. 1984, Perry 1985, Larocque and Marshall 1993, Reed et al. 1995, Larocque 2000). Both AGR and RGR were computed for the periods between 1993 and 1995 and between 1995 and 2000 for stem height and for the period between 1995 and 2000 for dbh. Thus, the following variables were generated: AGRHEI93 and AGRHEI95 for the absolute height growth rate between 1993 and 1995 and between 1995 and 2000, respectively, RGRHEI93 and RGRHEI95 for relative height growth rate between 1993 and 1995 and between 1995 and 2000, respectively, and AGRDBH95 and RGRDBH95 for the absolute and relative dbh growth rates between 1995 and

2000, respectively. The stem diameter measurements at stump height and at the first and fifth whorl heights were used to derive the ratios of stem diameter on the first and fifth whorl to stump diameter (TaperW1 and TaperW5). These two ratios were used to compare stem form among the various families.

Table 3. Summary of stem growth and crown development indices derived for the comparison of the productivity of 25 eastern white pine families

Name	Abbreviation	Definition ¹
Stem growth indices		
Absolute growth rate	AGR	$\frac{W_2 - W_1}{T_2 - T_1}$
Relative growth rate	RGR	$\frac{\ln(W_2) - \ln(W_1)}{T_2 - T_1}$
Crown development indices		
Crown shape ratio	CSR	$\frac{\text{Crown width}}{\text{Crown length}}$
Crown ratio	CR	$\frac{\text{Crown length}}{\text{Stem length}}$
Crown projection ratio	CPR	$\frac{\text{Crown width}}{\text{dbh}}$

¹W_n is dbh or height at time T_n

Each crown development index provided a specific measure of crown efficiency or performance (Table 3). Crown shape ratio (CSR) provides a means to compare the efficiency of crowns to intercept solar radiation (Kaufmann and Watkins 1990, Kuuluvainen 1991, Pöykkö and Pulkkinen 1990, Wang and Jarvis 1990). Crown ratio (CR), a measure of vigour, is intimately related to the photosynthetic capacity of individual trees (Farrar 1984, Sprinz and Burkhardt 1987). The crown projection ratio (CPR) evaluates the ability of trees to use their horizontal growing space to produce stemwood. According to Smith (1963), CPR is related to the number of rings produced per unit length.

The intensity of competition between individual white pines and the four surrounding grey alders was modeled using a competition index developed by Richardson et al. (1999):

$$afh_{ij} = \frac{1}{H_{ij}} \sum_{c=1}^4 H_c \frac{2 \tan^{-1}\left(\frac{L_c}{D_c}\right)}{360} \quad (1)$$

where afh_{ij} is the competition index for the i^{th} subject tree within the j^{th} family representing the portion of the angle subtended by the crown of one of the competitors relative to a complete circle, the centre of which is the subject tree;

H_{ij} the height of the white pine tree (subject tree);

H_c the height of a competitor;

L_c the length of the longest grey alder branch facing the subject white pine; and

D_c the distance between the subject tree and the competitor.

According to the competition partitioning (Ung et al. 1997) into (1) the horizontal component represented by the subject tree's dbh and the neighbour trees' dbh, and (2) the vertical component represented by the height difference between the subject tree and neighbouring trees, most of the growth variation is explained by the horizontal component such that it would be difficult for surrounding trees to account for the small remaining growth variation. Thus, Richardson's index based on the vertical component is more appropriate for quantifying the effect of surrounding grey alders on white pine tree growth than the indices based on the horizontal component.

Data analysis

Four of the provenances used for this study originated from Quebec, Canada, and one was from Vermont, USA. As the provenances originated from a relatively restricted area of the eastern white pine's natural range, it was reasonable to treat the 25 families as part of the same population, considering the very low level of population differentiation in eastern white pine based on neutral biochemical markers (Beaulieu and Simon 1994) and similar climatic conditions.

Before merging the three blocks located at Lévis and the block located at Valcartier to form a randomized four complete blocks design, the family means per block of each growth variable were plotted against the overall family means in order to ensure that a family x block interaction was not created in doing so. Similar plots for every variable in both Valcartier and Lévis supported the decision to consider the four blocks as part of the same experimental design.

The different growth and crown development indices were analyzed using a mixed ANOVA model:

$$y_{ijk} = \mu + \beta_i + f_j + s_{ij} + e_{ijk} \quad (2)$$

where y_{ijk} is the index estimated for the k^{th} tree ($k=1, \dots, 4$) from the j^{th} family ($j=1, \dots, 25$) in the i^{th} block ($i=1, \dots, 4$);

μ the overall mean effect;

β_i the effect of block i ;

f_j the random effect of the j^{th} family; it is assumed that f_j is an observation from a normal distribution with mean zero and variance σ_f^2 ;

s_{ij} the random plot effect; it is assumed that $s_{ij} \sim N(0, \sigma_s^2)$; and

e_{ijk} the random error term associated with the k^{th} tree of the j^{th} family in the i^{th} block; it is assumed that e_{ijk} is $\sim N(0, \sigma_e^2)$.

The analyses were undertaken using the SAS MIXED procedure (SAS Institute Inc. 2001). Denominator degrees of freedom of statistical tests in all analyses of variance performed were adjusted with the Satterthwaite method (Milliken and Johnson 1992). For each dependent variable, the family breeding values were predicted using the best linear unbiased prediction (BLUP) approach. Departure from the normal distribution and homogeneity of variance was tested for the residuals using statistics provided by the UNIVARIATE procedure (SAS Institute Inc. 2001). Both RGRDBH95 and CSR had to be transformed using the logarithmic transformation.

For each whorl, it was examined whether families differed significantly in the relationship between branch length and the diameter of the branch at its base by undertaking random coefficient model analyses using the MIXED procedure in SAS (SAS Institute Inc. 2001) with the following model:

$$y_{ijkl} = \mu + \gamma_i + f_j + u_{ij} + a_{ijk} + \beta d_{ijkl} + (b_j - \beta) d_{ijkl} + e_{ijkl} \quad (3)$$

where y_{ijkl} is the l^{th} branch ($l=1, \dots, 3$) length of a given whorl from the k^{th} tree ($k=1, \dots, 4$) of the j^{th} family ($j=1, \dots, 25$) in the i^{th} block ($i=1, \dots, 4$);

μ the overall mean effect;

γ_i the effect of block i ;

f_j the random effect of the j^{th} family, $f_j \sim N(0, \sigma_f^2)$,

u_{ij} the random plot effect, $u_{ij} \sim N(0, \sigma_u^2)$;

a_{ijk} the random effect associated with the k^{th} tree of the j^{th} family in the i^{th} block; it is assumed that $a_{ijk} \sim N(0, \sigma_a^2)$;

d_{ijkl} the basal diameter of the l^{th} branch of the k^{th} tree from the j^{th} family in the i^{th} block;

β the common slope for all the families in the relationship between branch length and branch diameter;

b_j the slope of the j^{th} family in the relationship between branch length and branch diameter; and

e_{ijkl} the random error term associated with the l^{th} branch of the k^{th} tree of the j^{th} family in the i^{th} block; e_{ijkl} is $\sim N(0, \sigma_e^2)$.

The model was reduced to its most parsimonious form by testing successively the significance of each variance component, starting with σ_a^2 and ending with σ_f^2 . If, based on a likelihood ratio statistic test, a given random effect was not significant at 0.30, it was excluded from the model.

An analysis of covariance was used to examine if the relationship between the basal area growth rate at breast height in terms of AGR and RGR and the competition index differed significantly among the families:

$$y_{ij} = \mu + \beta (afh_{ij} - \overline{afh}) + f_j + e_{ij} \quad (4)$$

where y_{ij} is the basal area growth rate at breast height in terms of absolute or relative growth rates for the i^{th} tree ($i=1,\dots,4$) from the j^{th} family ($j=1,\dots,25$);

μ the overall mean effect;

afh_{ij} the competition index for the i^{th} tree within the j^{th} family;

\overline{afh} the overall mean value of the competition index,

β the slope of the relationship between basal area growth rate at breast height and the competition index;

f_j the random effect of the j^{th} family; $f_j \sim N(0, \sigma_f^2)$ and,

e_{ij} the random error term associated with the i^{th} tree of the j^{th} family; $e_{ij} \sim N(0, \sigma_e^2)$.

Kendall's coefficient of rank correlation was used to determine the extent to which variation in traits was correlated among families. It was computed between TaperW1 and TaperW5 and between RGRDBH95 and CSR, CR and CPR. In particular, the computation of this coefficient for RGRDBH95 was important to examine if the most efficient families in terms of stemwood production were those that had the most efficient crowns.

RESULTS

On average, height AGR between 1993 and 1995 (AGRHEI93) was $40.4 \text{ cm year}^{-1}$, with the slowest family growing at a rate of $36.9 \text{ cm year}^{-1}$ and the fastest family growing at a rate of $44.0 \text{ cm year}^{-1}$ (Figure 1a). However, no significant family variation was found, but the plot and tree-to-tree components of variance were significant (Table 4). Average AGR for height between 1995 and 2000 (AGRHEI95) varied between 53.9 and $55.4 \text{ cm year}^{-1}$ among the families, with an overall average of $54.7 \text{ cm year}^{-1}$ (Figure 1a). No source of variation was significantly different from zero except for the tree-to-tree effect (Table 4). Average RGR for height between 1993 and 1995 (RGRHEI93) for the 25 families varied between 0.1514 and $0.1858 \text{ cm year}^{-1} \text{ cm}^{-1}$ (Figure 1b). Similarly to AGRHEI93, both plot and tree-to-tree variations were significantly different from zero (Table 4). Average RGR for height between 1995 and 2000 (RGRHEI95) was generally lower than RGRHEI93 and varied between 0.1349 and $0.1441 \text{ cm year}^{-1} \text{ cm}^{-1}$ (Figure 1b), with an overall average of $0.1397 \text{ cm year}^{-1} \text{ cm}^{-1}$. None of the effects was significant, except for the tree-to-tree one (Table 4). Average AGR for dbh (AGRDBH95) varied between 11.5 and $11.9 \text{ mm year}^{-1}$ among the families whereas average RGR for dbh (RGRDBH95) varied between 0.2228 and $0.2554 \text{ mm year}^{-1} \text{ mm}^{-1}$ among the families. While both the plot and tree-to-tree variations were significantly different from zero for RGRDBH95, only the tree-to-tree variation was significant for AGRDBH95 (Table 4). Overall, most of the observed variation was due to differences among trees within plots.

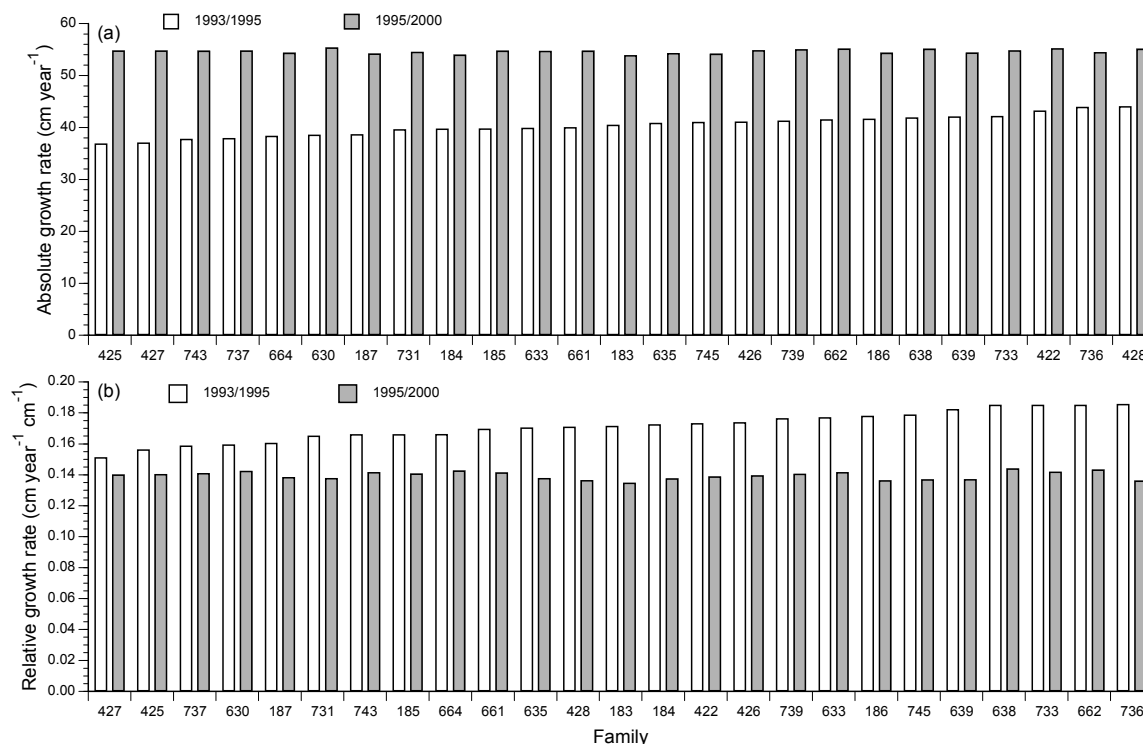


Figure 1. Absolute (a) and relative (b) growth rates in height between 1993 and 1995 and between 1995 and 2000 for 25 eastern white pine families.

Table 4. Means and variance components for absolute and relative growth rates in height and dbh for 25 eastern white pine families

Trait ^a	Mean	Components of variance as % of the total variance ^b		
		Family	Plot	Error
AGRHEI93	40.42	0 ^{NS}	16.5 ^{**}	83.5 ^{**}
AGRHEI95	54.69	0.01 ^{NS}	3.2 ^{NS}	96.8 ^{**}
RGRHEI93	0.1716	0 ^{NS}	18.7 ^{**}	81.3 ^{**}
RGRHEI95	0.1397	1.5 ^{NS}	10.5 ^{NS}	88.0 ^{**}
AGRDBH95	11.71	0.3 ^{NS}	3.6 ^{NS}	96.1 ^{**}
RGRDBH95	0.2380	0 ^{NS}	28.7 ^{**}	71.3 ^{**}

^aSee Table 3 for definitions

^bNS: not significant, and **: significant at 1% probability level

Mean TaperW1 varied from 0.125 to 0.140 among the families, with an overall average of 0.133. Variation due to differences among plots and among trees within plots was significantly different from zero at $\alpha = 0.05$ (Table 5). Mean TaperW5 was about five times greater than mean TaperW1 and varied from 0.6614 to 0.6814. The variation due to family effect was not significant and each source of variation explained about the same percentage of total variation as for TaperW1 (Table 5). Kendall's coefficient of rank correlation between TaperW1 and TaperW5 was 0.34 (significant at $\alpha = 0.05$).

Table 5. Means and variance components for stem taper ratios (TaperW1 and TaperW5), crown shape ratio (CSR), crown ratio (CR) and crown projection ratio (CPR) in 25 eastern white pine families

Trait	Mean	Components of variance as % of the total variance ^a		
		Family	Plot	Error
TaperW1 [*]	0.1326	0 ^{NS}	12.6 [*]	87.4 ^{**}
TaperW5 [†]	0.6731	0.5 ^{NS}	15.4 [*]	84.1 ^{**}
CSR	1.1955	1.5 ^{NS}	14.0 [*]	84.5 ^{**}
CR	0.6153	0 ^{NS}	21.4 ^{**}	78.6 ^{**}
CPR	13.47	0.3 ^{NS}	13.1 [*]	86.6 ^{**}

^a NS: not significant, *: significant at 5% probability level, and **: significant at 1% probability level

^{*}TaperW1 = diameter at whorl 1 height/stump diameter. Whorl 1 designs the whorl at the top of the tree

[†]TaperW5 = diameter at whorl 5 height/stump diameter

Mean CSR varied between 1.16 and 1.26 among the families, but the family effect was not significant (Table 5). As for the taper variables, variation among plots explained a small proportion of total variation in mean CSR compared with the remaining variation due to tree-to-tree differences. Kendall's coefficient between CSR and RGRDBH95 was 0.28 (not significant at $\alpha = 0.05$). CR did not vary significantly among families, but the percentage of total variation explained by plots was about 40% higher than for other ratios estimated in this study (Table 5). Kendall's coefficient between CR and RGRDBH95 was 0.54 (significant at $\alpha = 0.05$). Mean CPR varied between 12.6 and 14.5 among the families, with an overall average of 13.5. As for the other ratios, both plot and tree-to-tree variations were significantly different from zero and explained over 99% of total phenotypic variation (Table 5). CPR was not significantly correlated with RGRDBH95.

For the branch increment rate of the smallest branch per whorl in year 1, there was a general pattern of increase for all the families from whorl 1 to whorl 3, followed by a decrease from whorl 4 to whorl 5 (Figure 2). A similar pattern was obtained for years 2 and 3 for which the greatest increment rate was generally obtained on whorl 4, followed by a slight decline on the fifth whorl. Branch increment rate for year 4 was generally greater on the fifth whorl than on the fourth one. For whorls 2 and 3, branch increment rate generally decreased with year. The same pattern was obtained for whorls 4 and 5, but only until year 2. Few sources of variation were statistically significant (Table 6). The variation due to family was significant only for incvert414 ($\alpha = 0.05$). The variation due to differences among plots was significant for incvert111 and incvert312 only and also at $\alpha = 0.05$. Over 90% of the variation was due to differences among trees within plot.

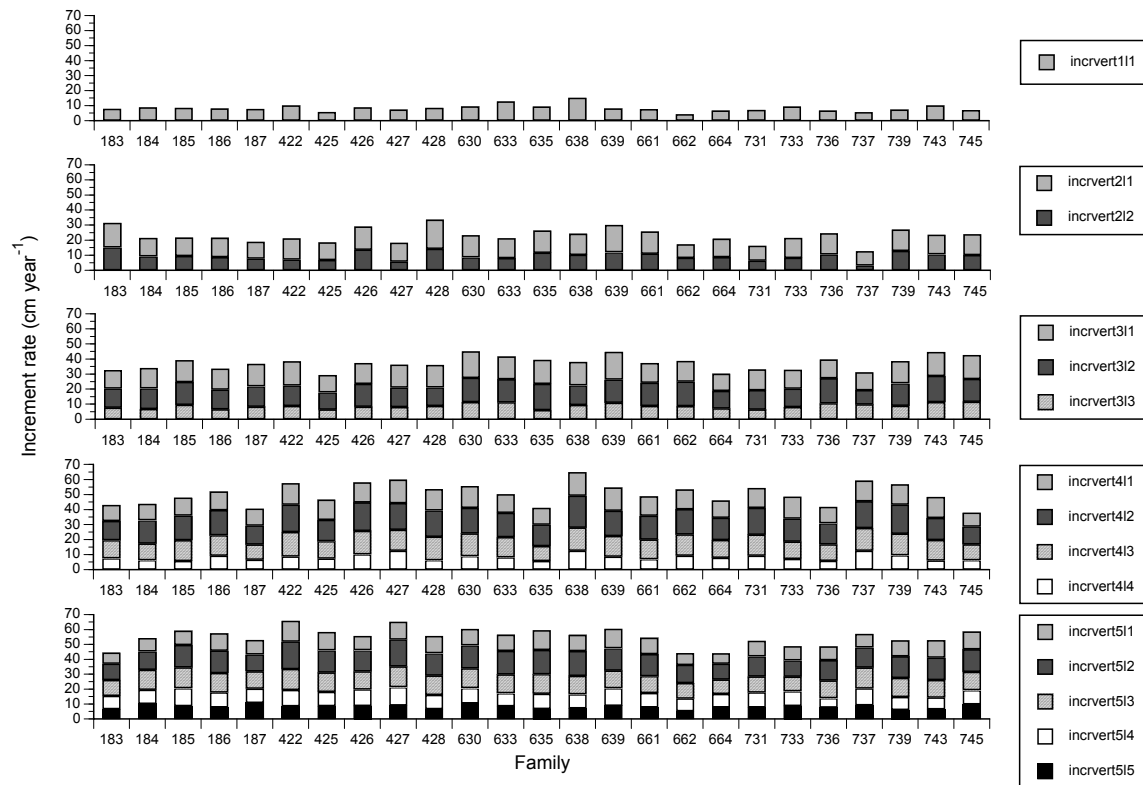


Figure 2. Mean annual branch increment rate for the smallest branch on each whorl. The first number on incrvert*|& indicates the whorl number and the second number indicates the year (1 for 1995 and 5 for 1991).

Table 6. Means and variance components for the annual increment rate of the smallest branch measured on each of the first five whorls among 25 eastern white pine families

Trait	Whorl number	Year	Mean	Components of variance as % of the total variance ^a		
				Family	Plot	Error
Incrvert111	1	1	8.24	0 ^{NS}	10.5 [*]	89.5 ^{**}
Incrvert211	2	1	13.49	2.5 ^{NS}	0 ^{NS}	97.5 ^{**}
Incrvert212	2	2	9.75	5.1 ^{NS}	0 ^{NS}	94.9 ^{**}
Incrvert311	3	1	14.42	0 ^{NS}	8.6 ^{NS}	91.4 ^{**}
Incrvert312	3	2	14.29	0 ^{NS}	9.6 [*]	90.4 ^{**}
Incrvert313	3	3	8.58	0 ^{NS}	2.9 ^{NS}	97.1 ^{**}
Incrvert411	4	1	13.00	2.4 ^{NS}	4.0 ^{NS}	93.6 ^{**}
Incrvert412	4	2	16.31	3.8 ^{NS}	0.7 ^{NS}	95.5 ^{**}
Incrvert413	4	3	13.35	2.0 ^{NS}	2.4 ^{NS}	95.6 ^{**}
Incrvert414	4	4	8.23	10.6 [*]	1.8 ^{NS}	88.2 ^{**}
Incrvert511	5	1	10.46	4.7 ^{NS}	0.4 ^{NS}	94.9 ^{**}
Incrvert512	5	2	14.38	1.6 ^{NS}	2.5 ^{NS}	95.9 ^{**}
Incrvert513	5	3	12.31	0 ^{NS}	4.8 ^{NS}	95.2 ^{**}
Incrvert514	5	4	9.76	1.4 ^{NS}	2.5 ^{NS}	96.1 ^{**}
Incrvert515	5	5	8.03	3.0 ^{NS}	2.5 ^{NS}	94.5 ^{**}

^a NS: not significant, *: significant at 5% probability level, and **: significant at 1% probability level

For the longest branch on each of the first five whorls, branch increment rate in year 1 was about the same for the first three whorls and decreased from whorl 3 to whorl 5 (Figure 3). For year 2, branch increment rate was very close in whorls 2 and 3, but decreased slightly from whorls 3 to 5. For years 3 and 4, branch increment rate generally decreased from whorls 3 to 5 and from whorls 4 to 5, respectively. Branch increment rate on whorl 5 in year 5 was the shortest for all the families, except for families 184, 733 and 737. Branch increment rate generally decreased from year 2 to year 1 on the second whorl. For whorl 3, branch increment rate generally increased from year 3 to year 2, but decreased from year 2 to year 1. A similar pattern was obtained for whorls 4 and 5. Branch increment rate increased from the oldest branch whorls (years 4 and 5 on whorls 4 and 5, respectively) up to year 2. While the variation among families was not significant for any of the whorls and years, plot variation was significantly different from zero for most of the traits (Table 7). Differences among trees explained most of the total variation, but to a lesser extent than for the smallest branch per whorl.

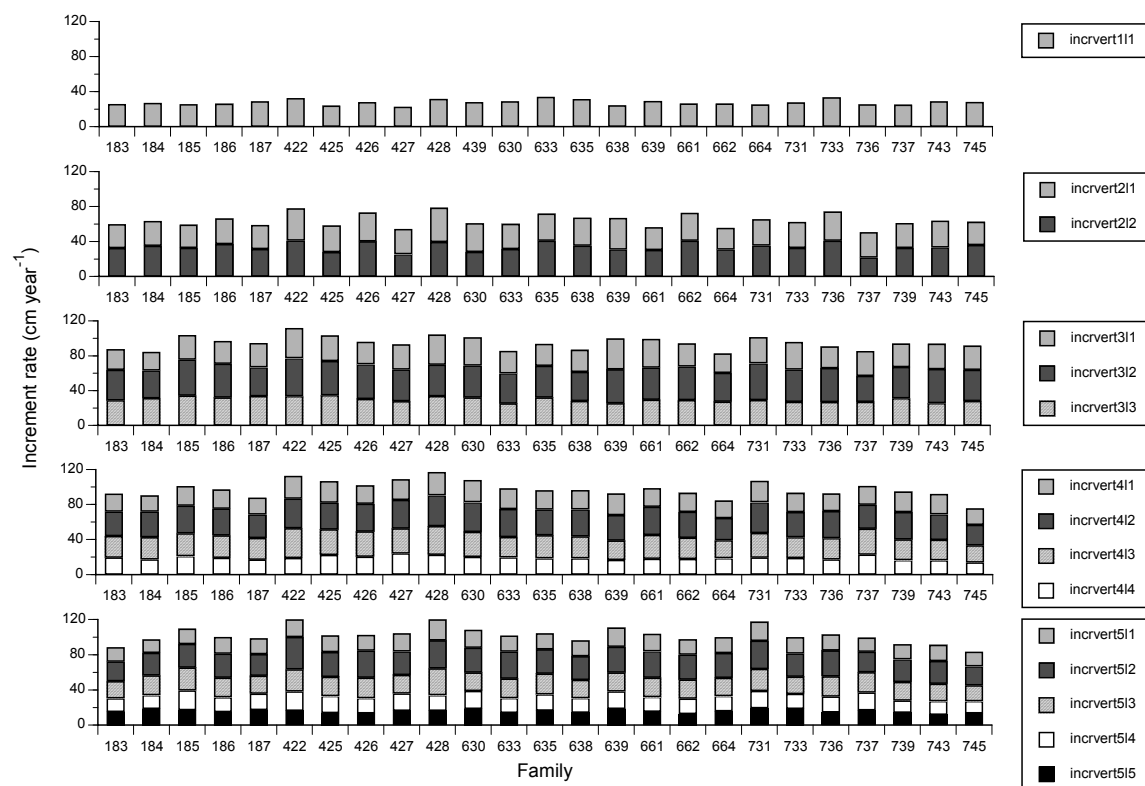


Figure 3. Mean annual branch increment rate for the largest branch on each whorl. The first number on incrvert*1& indicates the whorl number and the second number indicates the year (1 for 1995 and 5 for 1991).

Table 7. Means and variance components for the annual increment rate of the longest branch measured on each of the first five whorls among 25 white pine families

Trait	Whorl number	Year	Mean	Components of variance as % of the total variance ^a		
				Family	Plot	Error
Incrvert1I1	1	1	27.76	0 ^{NS}	9.1 ^{NS}	90.1 ^{**}
Incrvert2I1	2	1	30.27	0 ^{NS}	18.4 ^{**}	81.6 ^{**}
Incrvert2I2	2	2	33.86	4.1 ^{NS}	17.6 ^{**}	88.0 ^{**}
Incrvert3I1	3	1	27.99	5.3 ^{NS}	9.1 ^{NS}	85.6 ^{**}
Incrvert3I2	3	2	36.85	0 ^{NS}	8.9 ^{NS}	91.1 ^{**}
Incrvert3I3	3	3	29.46	0 ^{NS}	5.0 ^{NS}	95.0 ^{**}
Incrvert4I1	4	1	21.29	0 ^{NS}	13.2 [*]	86.8 ^{**}
Incrvert4I2	4	2	30.21	2.0 ^{NS}	8.7 ^{NS}	90.3 ^{**}
Incrvert4I3	4	3	25.82	6.8 ^{NS}	16.1 ^{**}	77.1 ^{**}
Incrvert4I4	4	4	19.01	0 ^{NS}	14.8 ^{**}	85.3 ^{**}
Incrvert5I1	5	1	18.63	2.1 ^{NS}	13.4 [*]	84.5 ^{**}
Incrvert5I2	5	2	27.53	4.0 ^{NS}	11.8 [*]	84.2 ^{**}
Incrvert5I3	5	3	22.06	7.0 ^{NS}	9.9 [*]	83.1 ^{**}
Incrvert5I4	5	4	17.80	1.3 ^{NS}	23.1 ^{**}	75.6 ^{**}
Incrvert5I5	5	5	15.62	0 ^{NS}	23.0 ^{**}	77.0 ^{**}

^a NS: not significant, *: significant at 5% probability level, and **: significant at 1% probability level

The common slope of the regression of branch length as a function of branch diameter for the 25 families was significantly different from zero for every whorl (Table 8). For the family level, neither the variance of the slopes nor the covariance between the slope and the intercept was significant for any of the whorls. At the plot level, except for whorl 1, there were significant variations for the intercept, the slope and the covariance intercept-slope. Variation from tree to tree was highly significant in whorls 1, 2, 4 and 5 for the intercept, the slope and the covariance intercept-slope as well. There was also highly significant variation at the plot level for the three parameters.

Table 8. Observed significance of variances and covariances associated with the analysis of covariance for $\sqrt{\text{branch length}}$ per whorl using the branch basal diameter as covariate for 25 eastern white pine families

Source of variation	Whorl 1	Whorl 2	Whorl 3	Whorl 4	Whorl 5
<i>Fixed effects</i>					
Basal branch diameter	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Block	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
<i>Random effects</i>					
Family – intercept		–	–	–	0.0822
Family – cov (int.*slope)	0.2411	–	–	–	–
Family – slope					
Plot – intercept	0.0235	0.0186	< 0.0001	0.0014	0.0013
Plot – cov (int.*slope)	0.2131	0.0500	< 0.0001	0.0019	0.0015
Plot – slope	0.1718	0.0119	< 0.0001	0.0002	0.0003
Tree – intercept	< 0.0001	< 0.0001	–	< 0.0001	< 0.0001
Tree – cov (int.*slope)	< 0.0001	< 0.0001	–	< 0.0001	< 0.0001
Tree – slope	< 0.0001	< 0.0001	–	< 0.0001	< 0.0001

The relationships between absolute and relative growth rates and the competition index afh were highly significant (Table 9). The coefficients of determination were 0.72 and 0.65 for absolute and relative growth rates, respectively. However, there was no significant variation for both growth rates adjusted for the competition index at the family level. Significant variation was observed only at the tree level.

Table 9. Observed significance associated with the analysis of covariance for basal area increment at breast height in terms of absolute and relative growth rates using a competition index (afh) as covariate for 25 eastern white pine families

	$\sqrt{\text{Absolute growth rate}}$			Relative growth rate		
	df [†]		P > F	df		P > F
	dfn	dfd		dfn	dfd	
<i>Fixed effects</i>						
Blocks	3	307	< 0.0001	3	311	< 0.0001
Afh	1	319	< 0.0001	1	311	< 0.0001
<i>Random effects</i>						
			P > Z			P > Z
Family			0.0732			0.4182
Error			< 0.0001			< 0.0001

[†] df, degrees of freedom; dfn, degrees of freedom of the numerator; dfd, degrees of freedom of the denominator

DISCUSSION

The differences in AGR for both dbh and height obtained in this study were less important than originally anticipated, in contrast to several studies that reported significant differences in cumulative dbh and height for different provenances or families of eastern white pine (e.g., Wright et al. 1970, Van Haverbeke 1988, Genys 1990, Abubaker and Zsuffa 1991, Beaulieu et al. 1996, Li et al. 1997, Joyce et al. 2002). Despite the fact that the variance components were not significant for both height AGR and RGR, the results obtained nevertheless indicated that the amplitude of differences among the families tended to diminish from the 1993-1995 period to the 1995-2000 period. This trend probably resulted from the significant plot effect in 1993 (Table 5). Two reasons may explain this pattern. First, it is possible that changes in gene expressions due to phenotype effect occurred during this period. According to Woo et al. (1994), Kaya and Isik (1997) and Day et al. (2002), the genes that affect the development of meristems, which ultimately influence height growth, change as trees become older, modifying the pattern of genetic variation. Second, it is also possible that this pattern resulted primarily from the effect of competition. Height growth between 1993 and 1995 took place when the white pines were smaller than the surrounding grey alders. In 1995, white pines were about 2.5 m tall, while grey alders were about 4.5 m tall. Thus, it is likely that white pines had been growing under relatively low light conditions until 1995. Then, as white pine grew taller under more favourable light conditions, competitive conditions changed, modifying the amplitude of the expression of phenotypic variation among the families (see Franklin 1979, Tuskan and van Buijtenen 1986, St.Clair and Adams 1991, St.Clair 1994a). The highly significant tree-to-tree variation for all growth indices suggests that eastern white pine growth is highly influenced by microsite conditions and has the capability to quickly respond to changes in light conditions (Wendel and Smith 1990).

The influence of microsite seems to be so important that it might be difficult to show significant differences among families, unless a very large sample of families is tested. Also, it is likely that the provenance origins in terms of differences in environmental conditions play a key role. In particular, the climatic conditions of the regions from which provenances originate have a strong incidence on the performance at different locations (Genys 1990, Joyce et al. 2002). The fact that the provenances examined in this study originated from close regions characterized by relatively homogeneous climatic conditions is one factor that may explain the absence of significant differences in growth among the families, in contrast to Wright et al. (1970), Van Haverbeke (1988), Genys (1990), Abubaker and Zsuffa (1991), Beaulieu et al. (1996), Li et al. (1997) and Joyce et al. (2002).

Tree-to-tree effect was also significant for both TaperW1 and TaperW5, which is an additional indication that white pine growth is highly influenced by the environmental conditions in which the individual trees grow. The amplitude of variation among trees in both taper variables was about the same, which suggests that variation in individual response to the environment in terms of radial growth is of similar amplitude in all parts of the stem. Similarly to stem taper, only plot and tree-to-tree effects were significant for both CSR and CR. Hence, no significant variation among families was shown for crown form and crown recession rate (Table 5). This suggests that, even in the presence of surrounding grey alders, differences among families in the efficiency of their crown to intercept solar radiation and in the capability of their needles in the lower parts of the crowns to photosynthesize under reduced light conditions could be demonstrated. CSR has been used in other studies to assess the extent to which crowns acclimate to changes in light conditions when they interfere with the crowns of surrounding trees. Several studies for various conifer species indicated that long cylindrical crowns intercept solar radiation more efficiently in the presence of the crowns of surrounding competitors

(Jahnke and Lawrence 1965, Oker-Blom and Kellomäki 1982, Ford 1985, Karki and Tigerstedt 1985, Kellomäki et al. 1985, Kuuluvainen and Pukkala 1987, 1989, Kuuluvainen 1988, 1992, St.Clair 1994b). For this study, it was anticipated that the most efficient families to produce stemwood (greatest RGRs) would be those with crowns characterized by the greatest efficiency to intercept solar radiation. Our results did not support this hypothesis. Weak correlations were obtained between RGRDBH95 and CSR and CR. As mentioned previously, CPR is a measure of growth efficiency, similar in concept to RGR. The lower the CPR, the more efficiently a tree uses its horizontal aerial growing space to produce stemwood (see Ouellet and Zarnovican 1989). The absence of significant family rank correlation between RGRDBH95 and CPR indicated that, for the different eastern white pine families examined, there is no causal relationship between efficiency in terms of stemwood production and ability of their crowns to use their aerial growing space efficiently. These results are consistent with the conclusions by O'Connell and Kelty (1994), Wetzel and Burgess (1994) and Messier et al. (1999) who indicated that the crown of white pine does not have strong physiological or morphological plasticity. In particular, O'Connell and Kelty (1994) compared CSR and CR of eastern white pine saplings growing in open-grown and understory conditions. Both groups of saplings had similar heights. CSR and CR did not change much under different light conditions that differentiated open-grown and understory conditions.

Despite the low amplitude of variation obtained for CSR and CR, the results of this study do not dismiss entirely the existence of phenotypic variation in shoot plasticity among the different families of eastern white pine. First, there was a relatively large amplitude of variation in branch increment rate among the families, particularly for the longest branch (Figures 2 and 3). Second, the high percentages of the variance components for the tree-to-tree effect, all significant at the 1% probability level, suggested that trees responded in a significant way to changes in environmental conditions. But this could not be detected at the family level, which could be due to the relatively small numbers of families and trees per family tested in the present study or to the fact that only a small portion of total family variation of the species was assayed. The fact that the family-intercept and family-slope effects were not significant (Table 8) does not dismiss the existence of phenotypic variation in shoot plasticity. For instance, St.Clair (1994b) determined that several crown traits, including CSR and CR, differed significantly among different families of Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* [Mirb.] Franco). However, he also found that branch diameter and branch length were weakly correlated to genetic and phenotypic traits.

The significant relationships between the competition index (afh) and growth rate in terms of AGR and RGR indicated that both growth rate and efficiency to produce stemwood were affected by competition from grey alder. However, the results do not indicate that the families reacted differently to the effect of competition from grey alder. For AGR, the relationships derived in this study for several families compared favourably well with those derived by Elliott and Vose (1995) in which they used a competition index to model the intensity of competition from surrounding vegetation in young white pines. The r^2 for their relationship was 0.73. However, it is likely that this high coefficient of determination resulted from the use of cumulative growth, instead of AGR or RGR, as in the present study. For RGR, the relationships derived in this study were lower than for AGR. The relationships can be compared with those derived by Peterson and Squiers (1995) for white pine in which they used RGR as the dependent variable. Peterson and Squiers' (1995) competition index was based on size and distance of competitors and the greatest proportion of variation explained by their relationships was 20%. The good performance of the relationships between growth rate expressed in terms of AGR and RGR and the competition index without initial size of the subject tree indicated that the competition index adequately represented the effect of competition from grey alder. Several

studies on models predicting individual-tree growth using a competition index resulted in significant relationships only because the initial size of the subject tree was included in the relationships and accounted for a large part of the variation. It was mentioned in the literature that it is important to include initial tree size in this type of model to integrate the effect of past growing conditions and differences in genetic inheritance of individual trees (Barclay and Layton 1990, Cole and Lorimer 1994, Wimberly and Bare 1996). On the other hand, other authors indicated that the inclusion of initial size of the subject tree was not a good feature. Brand and Magnussen (1988) argued that the significance of initial size of the subject tree in this type of relationship was due to the fact that growth rate insightfully depends on tree size. According to Lorimer (1983), initial tree size is a significant predictor of future tree growth only when growing conditions such as stand density are not modified substantially.

CONCLUSION

The performance of different white pine families growing with grey alder was compared. The stem, crown and branch traits did not differ significantly among the families. Crown structure traits did not appear promising for selecting potential ideotype traits in white pine. Thus, the results of this study do not suggest that it is possible to achieve simultaneous genetic gain in terms of stem size and crown development for the population studied. This also means that crown traits cannot be used to select families that would optimize fibre production per unit area. However, a relatively small number of families were used in the present study. Future studies should include more families originating from an extended area to test whether the results of the present study are representative of the species. Moreover, a similar study should also be initiated using pure white pine progeny tests in order to determine the real effect of grey alder on the white pine families' growth habits and crown development.

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