THE EFFECTS OF SPACING AND GENETIC FACTORS ON GROWTH AND TREE FORM QUALITY TRAITS OF PLANTATION-GROWN JACK PINE

by

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ABSTRACT

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Key Words: spacing, group, family, tree form quality traits, jack pine, heritability, genetic correlation.

Overall tree form of jack pine (Pinus banksiana Lamb.) growing in natural stands varies from straight slender trees with compact crowns to broad, limby and even multi-stemed trees. Jack pine grown in plantations at conventional spacings of 2 m develops form traits undesirable for forestry utilization. The goal of this study was to investigate the effects and interaction of spacing and genetic factors on plantation-grown jack pine to determine the potential benefit of a selection program based on form traits. Ten wind-pollinated families were collected from each of six natural fire-origin stands from east and west of Lake Nipigon in northwestern Ontario that had been subjectively rated as good, average and poor in form. These sixty families making up six form-quality groups, together with an additional twenty plus tree families making up two more form-quality groups, were established at two planting sites with contrasting soil texture and fertility at spacings of 1, 2 and 3 m. Eight tree form quality traits--branch length, branch diameter, branch angle, branch number, relative branch diameter, relative crown width, number of crooks, and taper were measured and analyzed together with two growth traits--height and diameter at breast height (DBH) at age eight. General linear models were used to evaluate the effects of site, spacing, form-quality group, family and the relevant interactions on all traits except number of crooks which was not normally distributed. All jack pine growth and form traits except branch number were greatly affected by spacing. Most of the change in form traits occurred when spacing increased from 1 to 2 m with lesser change from 2 to 3 m. This effect was more pronounced at the more fertile test site. Form-quality groups were significantly different for only two of the form traits--branch length and branch angle with this effect again being more evident at the fertile test site. However, the family effect was significant for all seven tested form traits as well as the two growth traits suggesting that any of these traits would readily respond to family selection. A definite provenance effect was demonstrated for growth traits and stem taper; the western sources grew faster with more favourable taper. None of the form-quality group x spacing nor the family x spacing interactions were significant. Heritabilities and genetic correlations were determined for all traits separately for each spacing at each test site. Traits height, branch angle and taper had the highest heritabilities, with individual heritabilities of greater than 0.15, and the traits branch diameter, relative branch diameter and relative crown width had values less than 0.05. The two growth traits together with growth-related form traits tended to be strongly positively correlated with the exception of height and relative crown width. However, branch angle and branch number showed no strong correlations with any other tree form and growth traits. Both heritabilities and genetic correlations were more meaningful for the more fertile test site due to larger components of family variance.

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INTRODUCTION

Jack pine (*Pinus banksiana* Lamb.) is both the most widely distributed and economically important pine species in Canada (Janas and Brand 1988). Its wood is used extensively for general construction, pulp, railway ties, poles, pilings, and mine timbers (Hosie 1973). This species is also a principal reforestation species in several provinces in Canada.

In spite of its commercial importance, certain characteristics of jack pine are not favourable for saw log production. These characteristics include: 1) a relatively short life-span, 2) a tendency to grow slowly between the ages of 12 and 20 years in dense, fire-origin stands (Bella and DeFranceschi 1971, Day 1986, Wilson 1952), and 3) a high proportion of stem deformities and unacceptably high knot volumes in low density stands (Bella and DeFranceschi 1974, 1980).

Tree form quality of jack pine is affected by both environmental and genetic factors. Of the environmental factors influencing tree form, spacing effect plays a key role. As a general rule, close spacing produces better tree form than wider spacing. Based on this relationship, the rapid increase of reforestation by planting at wide spacings across Canada has raised concern by forest industry about the quality of wood produced in these plantations (Magnussen and Yeatman 1987a). Wider initial spacing is adopted as a means to reduce costs of reforestation and tending and to concentrate growth on fewer trees (Magnussen and Yeatman 1987a). Although initial spacing does not impact the total volume of wood produced in mature stands based on the law of constant final yield, it can influence the percentage of merchantable wood produced (Hamilton and Christie 1975, Jørgensen 1967). Wide initial spacing tends to increase stem taper and the size of branches, and adversely affects the yields and qualities of pulp and lumber (Balmer *et al.* 1975, Laidly and Barse 1979, Persson 1975a, 1975b, Reukema 1970). Thus, the financial returns from this type of management may be unacceptably low if poor quality, low value logs are produced (Ballard and Long 1988).

Genetic improvement can be an effective way of modifying branch and stem characters as: 1) it tends to be less costly than silvicultural manipulations (e.g. pruning, pre-commercial thinning), 2) usually the heritabilities of concerned traits in many commercial species are high (Morgenstern *et al.* 1975), and 3) the knowledge of genetic correlation between traits makes it practical to reach the goal of a balanced combination of improved characteristics (Velling 1988).

Phenotypically, jack pine is highly variable, making it a promising candidate for genetic improvement of stem quality (Polk 1972, Rudolph 1964, Rudolph and Yeatman 1982). A prerequisite for a genetic improvement program is quantification of major variables determining quality and their variability, and correlation under different silvicultural management practices. This type of information is needed during the juvenile stage when the first selections for growth rate and/or form quality are being made.

Although spacing and genetic factors play important roles in tree form quality, few studies to date have considered both aspects at the same time. Therefore, it is impossible to evaluate both effects at the same time, and the interaction between spacing and genetic factors largely remains unknown. This study was designed to a) quantify the influence of spacing and genetic factors on jack pine tree form quality, and b) determine if there are spacing x group and spacing x family interactions.

For the most part, the value of jack pine wood to forest industry is determined by branch size and branch size-related traits. To date, the breeding of jack pine has been based primarily on height and diameter growth in young field trials. As a result, little is known about the tree form quality traits and the genetic relationships between tree form quality traits and growth traits of jack pine. To describe the effects of spacing, group (stand), family, spacing x group, and spacing x family on tree form quality, this study focused on a number of tree form quality traits: absolute branch size (diameter and length), branch angle, number of dominant branches and relative branch diameter (branch diameter/stem diameter at the same whorl). In addition, two growth traits (stem height and diameter at breast height), relative crown width (the ratio of average crown diameter to height) and stem taper were also included in this study allowing for a comparison between form and growth traits.

The results from this study will help in clarifying the following hypotheses:

Hypothesis 1: Tree form quality of plantation-grown jack pine is affected greatly by an increase in initial spacing during the early growing stage.

Hypothesis 2: The group (stand quality) effect is significant. That is, progeny from good quality stands have better tree form quality than collections made from poorer quality stands.

Hypothesis 3: The family effect is significant for the tree form quality traits used in this study.

Hypothesis 4: Tree form quality traits have relatively high heritability.

Hypothesis 5: Genetic correlation between tree form traits and growth traits are relatively high.

LITERATURE REVIEW

A thorough review is carried out regarding the effects of spacing and genetic factors on tree form quality traits in coniferous tree species. First, the traits most closely related to tree form quality in coniferous species are illustrated. They are branch size and angle, stem taper and straightness, relative branch diameter and crown width. Then, studies on genetic factors, such as genetic variation in form quality traits, growth traits, heritability and genetic correlation of growth and quality traits are described. Third, spacing effect on growth and form quality traits was generalised based on relevant studies. Last, the interaction of spacing and genetic factors was reviewed.

JACK PINE LIFE HISTORY CHARACTERISTICS

Classification

Jack pine is classified into the subsection *Contortae* Little & Critchfield, of the section *Pinus,* of the subgenus *Pinus,* the hard pines. The subsection *Contortae* is characterized by two short (2-8 cm) leaves in a fascicle, two or more whorls of branches in one growing year and often serotinous cones (3-8 cm long) (Little and Critchfield 1969). This species is a small to medium-sized coniferous tree of the northern forests of the United States and Canada. This species is commonly regenerated from seed released by fire from persistent closed cones.

Species Range

The major portion of the jack pine range is in Canada, where its northern boundary extends eastward from the Mackenzie River in the Northwest Territories across the country to Cape Breton Island, Nova Scotia. The range then extends Southwest through Maine, New Hampshire, northern New York, central Quebec and northern Ontario, Michigan, extreme Northwest Indiana, Northeast Illinois. The range extends Northwest through Wisconsin, Minnesota, Manitoba, Saskatchewan, central Alberta, to the extreme Northeast of British Columbia (Burns and Honkala 1990).

Soil and Site Relationships

Jack pine is usually found on sandy soils to loamy soils, on thin soils over the granites, and metamorphosed rocks of the Canadian Shield, over limestone, on peats and on soil over permafrost. Jack pine can grow on very dry sandy or gravelly soils where other species can scarcely survive, but it grows best on well drained loamy sands where the midsummer water table is located from 1.2 to 1.8 m (4 to 6 ft) below the surface. It can not grow on alkaline soil, but it can grow on soils overlying limestone, and on calcareous soils (pH8.2), if a normal mycorrhizal association is present. Most commonly jack pine grows on level to gently rolling sand plains, usually of glacial outwash, fluvial, or lacustrine origin. Less commonly it occurs on esker, sand dunes, rock outcrops, and bald rock ridges. This species is found chiefly at elevations between 300 and 460 m

(1,000 and 1,500 ft), with a maximum of about 610 m (2,000 ft) above sea level (Rudolph and Laidly 1990).

Jack pine is a dominant or codominant species in the eight recognized Forest Ecosystem Classification Vegetation Types in Northwestern Ontario (Sims *et al.* 1989). In the overstory it associates with black spruce (*Picea mariana* (Mill.) B.S.P.), trembling aspen (*Populus tremuloides* Michx.), and white birch (*Betula papyrifera* Marsh.). Less frequently it associates with Balsam fir (*Abies balsamea* (L.) Mill.) and white spruce (*P. glauca (Moench)* A. Voss).

GROWTH TRAITS IN JACK PINE AND OTHER CONIFEROUS SPECIES

Genetic Variation

Genetic variation in height growth has been found to be significant in jack pine, facilitating genetic improvement in height growth (Adams and Morgenstern 1991, Magnussen and Yeatman 1989). Studies in other pine species also showed that genetic variation in growth was significant, such as in loblolly pine (*Pinus taeda* L.), lodgepole pine (*Pinus contorta* Doug. ex Loud.), radiata pine (*Pinus radiata* D.Don), Scots pine (*Pinus sylvestris* L.) and Caribbean pine (*Pinus caribaea* Morelet) (Eriksson *et al.* 1987, Jayawickrama and Balocchi 1993, Liu *et al.* 1997, Wright *et al.* 1990, Xie and Ying 1996).

Heritability

For jack pine, published individual heritability values range from 0.10 to 0.14 in diameter and 0.17 to 0.26 in height (Table 1). The average individual heritability was 0.11 for diameter and 0.20 for height. Adams and Morgenstern (1991) found that the individual and family heritabilities of jack pine for height were 0.17 and 0.74 respectively, which is consistent with Yeatman (1975).

Generally, for the species shown in Table 1, individual heritabilities for stem diameter, height, and volume range from 0.10 to 0.30 (Haapanen and Pöykkö 1993, Magnussen and Yeatman 1990, Morris *et al.* 1992). However, some studies, such as Kariuki (1998), indicated high family heritability estimates in jelecote pine (*Pinus patula* Schlechtend. & Cham.): 0.61, 0.69 and 0.70 for height, DBH (diameter at breast height) and volume production, respectively (Table 1).

Qin *et al.* (1997) showed that height, DBH and stem volume of Masson pine (*Pinus massoniana* Lamb.) at 5-10 years old were under moderate or high genetic control. At age 10 years, the heritabilities for the 3 growth traits were more stable with family genetic variation coefficients decreasing with age. Haapanen and Pöykkö (1993) revealed moderate individual heritability values for Scots pine, 0.2 to 0.5 for DBH and stem volume respectively. However, the heritability was 0.60 for height, which was probably overestimated due to the subjective sampling in which the six tallest trees on each plot were selected for measurement. In many other studies height has been rated as a

Table 1. Selected heritability estimates for growth traits from various studies.

Trait	Species	h^2	Reference
diameter	jack pine	0.24	Klein 1995
	jack pine	0.10	Magnussen and Yeatman 1990
	jack pine	0.10	Morris et al. 1992
	jack pine	0.14	Park et al. 1989
	jelecote pine	0.69^f	Kariuki 1998
	Scots pine	0.21	Haapanen and Pöykkö1993
height	jack pine	0.17	Adams and Morgenstern 1991
	jack pine	0.34	Klein 1995
	jack pine	0.18	Magnussen and Yeatman 1990
	jack pine	0.17	Morris et al. 1992
	jack pine	0.26	Park et al. 1989
	jelecote pine	0.61^f	Kariuki 1998
	Scots pine	0.60	Haapanen and Pöykkö 1993
volume	jelecote pine	0.70^f	Kariuki 1998
	Scots pine	0.22	Haapanen and Pöykkö 1993

Notes: h^2, ^{f} means family heritability, others are individual heritability values.

trait of relatively weak inheritance (Nilsson 1968, Palmberg 1970, Velling and Tigerstedt 1984).

Stand Density Relationships

With the rapid increase of reforestation by planting, it is necessary to understand the effect of initial spacing on growth and yield (Bella and De Francheschi 1974). Studies have shown that initial spacing affects stem form characteristics, and hence, the yields and qualities of pulp and lumber (Balmer *et al.* 1975, Laidly and Barse 1979, Persson 1975a, 1975b, Reukema 1970). Although initial spacing does not influence the total volume of wood produced in mature stands, net yield and financial returns usually increase with wider initial spacing (Hamilton and Christie 1975, Jørgensen 1967). In jack pine, studies have shown that the effect of spacing on diameter growth is significant: wider spacing generally resulted in a greater diameter (Adams 1928, Bella and Franceschi 1974, 1980, Godman and Cooley 1970, Ralston 1953, Rudolf 1951, Zavitkovski and Dawson 1978). This is in agreement with the results from other species (Evert 1971, Hamilton and Christie 1975, Hinners and Stratmann 1984, Jørgensen 1967, Reukema and Smith 1987, Xie *et al.* 1995). However, some studies in jack pine have reported that wider spacing may indirectly lower the DBH growth, at least during early growing stage, due to multiple stem formation and excessive stem taper (Bella and Francheschi 1974, 1980).

Height is relatively constant over a wide range of spacing. Dominant height is usually affected less by spacing (Evert 1971, Jørgensen 1967). Spacing had no consistent effect on height growth for jack pine, red pine and white spruce (Bella and Francheschi 1974). Some studies showed that close spacings had a negative effect on mean height (Evert 1971, Hamilton and Christie 1975, Jørgensen 1967, Magnussen and Yeatman 1987a), and wide spacings a detrimental effect upon stem straightness, which thus indirectly affected the mean height (Magnussen and Yeatman 1987a). Maximum average tree height is often found in an intermediate spacing (Bella and Francheschi 1974, 1980, Hamilton and Christie 1975, Magnussen and Yeatman 1987a, Ralston 1953). This is especially the case for jack pine. Increased planting density in shore pine (*Pinus contorta var.* contorta), on the other hand, stimulated height growth, and height growth responded to planting density earlier than diameter growth (Xie *et al.* 1995). For Scots pine, stand density had the smallest effect on height growth (Ryabokon 1978). For Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco.), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and western red cedar (*Thuja plicata* J. Donn ex D.Don.), top heights were initially a little taller at close spacings, but were similar at all spacings at age 25 as the initial advantage of close spacings disappeared over time. Lanner (1985) suggested the reason why trees can maintain a fairly uniform height growth under a wide range of densities. The smaller height increment of very dense stands may be partly explained by carbohydrate source-sink physiology. Under very dense conditions, the developing shoot is not provided with sufficient stored and actively synthesized food to optimize height growth (Janas and Brand 1988).

Bella (1986) found that spacing had a consistent effect on the height-DBH relationship in jack pine, where trees of equal DBH were about 1 m taller at narrow spacing than at wide spacing. No consistent trends emerged in height-DBH relationships for red pine and white spruce. These results suggest an optimum spacing of between 1.8 and 2.4 m for both jack pine and red pine in order to achieve rapid tree growth and high future timber yields. Unlike jack pine, red pine retains good tree form even at wide spacing (Bella 1986).

FORM TRAITS IN JACK PINE AND OTHER CONIFEROUS SPECIES

Past studies have shown that some traits, such as branch size, branch angle, stem straightness and taper are important characters indicating tree form quality. These traits are usually influenced by both genetic characteristics and environmental factors. Studies in genetic variation and heritability are summarized in this review. Genetic variation in tree form traits exist at provenance and/or family level, and the heritabilities of these traits are generally high. Spacing is an important environmental factor, which contributes a great deal in determining tree form quality. Conventionally, dense stands are used to improve stem quality, at the cost of a smaller log and longer rotations. And due to high cost of tending and thinning, wider initial spacing has become more popular in Canadian plantations, raising concerns regarding stem quality. As a result, the effect of spacing on both growth and tree form quality traits was reviewed in this paper.

Tree Form Quality Traits

In most cases, tree form quality is a complex of characters. It can be divided into components that have genetic variation and are thus usable as selection criteria and which can be evaluated in growing trees (Venäläinen *et al.* 1996). The number and size of branches are the most important log quality characteristics for many products (Barger and Ffolliott 1970, Grah 1961). All knots, regardless of size, reduce the strength of lumber (Grant *et al.* 1984). For example, the timber grade of Scots pine is dependent on the dimensions, total volume, location, form, and type of knots in the log (Petersson 1998). Knots greatly affect the properties of wood and this is reflected in wood quality when using existing grading systems (Anon. 1994) as a basis of evaluation. The strength and appearance of Scots pine sawn timber are especially susceptible to the occurrence of branches in saw log (Kellomäki and Väisänen 1989). The quality of sawn timber is determined as much as 70-80% by the occurrence of branches (Kärkkäinen 1980). Thus, branch size or knot size is used as a determinant for branchiness and knottiness, and for wood quality prediction (Briggs 1996, Colin 1992, Colin and Houllier 1991, Houllier *et al.* 1995). Depending on the market, both knot size and type (live or dead), affect lumber and veneer grades. In general, a tree with smaller, live knots would be worth more (Briggs 1996).

Desirable stem quality characteristics not only include decreased branchiness and reduced branch size, but also fewer stem deformities resulting from multiple leaders and improved branch angles in jack pine (Bella and DeFranceschi 1974, 1980). It is common in conifers that branch angles change from acute in the upper part of crown to more horizontal in the lower (Barber 1964, Cochrane and Ford 1978, Dietrich 1973, Ehrenberg 1963, Zimmermann and Brown 1971). Branch angles range from 55° to 70° for the 2- to 4-year-old branches in plantations spaced from 1 - 2 m in Scots pine (Ehrenberg 1963), Virginia pine (*Pinus virginia* Mill.) (Bailey *et al.* 1974), and jack pine (Schoenike *et al.*

1962). Generally, there is a 6 degree annual increase in branch angle of slash pine (Barber 1964) and lodgepole pine (Franklin and Callaham 1970). The age effect is caused by two opposing forces: gravity and radial stem growth (Zimmermann and Brown 1971), which were substantiated by the partial correlation of stem and branch diameter with branch angle. These correlations exist commonly in coniferous species (Bailey *et al.* 1974, Barber 1964, Dietrich 1973, Merrill and Mohn 1985). Because trees with narrow angles usually have larger knots than those with wide angles (Bailey *et al.* 1974, Dietrich 1973, Zimmermann and Brown 1971), the genetic improvement on branch angle has economic potential (Magnussen and Yeatman 1987a).

Stem taper is also important to both tree qualities, as well as to the resistance of tree stems to breakage by wind or snow. Tall, slender trees are more likely to be broken. Europeans suggest that the ratio of height to DBH (in cm) of the 100 largest trees per ha should be kept to less than about 80, and the average tree at 100 (van Tuyll and Kramer 1981). Stem taper causes diagonal grain in lumber, reducing its strength (Briggs 1996).

Relative branch diameter (the ratio of branch diameter to stem diameter at the same whorl)) and relative crown width (crown width adjusted for stem diameter below a sample whorl) were used, to show the trends of change in branch diameter compared with stem diameter, and crown width compared with stem height, respectively, in Virginia pine (Bailey *et al.*1974), Scots pine (Velling and Tigerstedt 1984), loblolly pine (Zobel and Talbert 1984), lodgepole pine (Yanchuk 1986), Douglas fir (St.Clair 1994) and jack pine (Adams and Morgenstern 1991).

Two main approaches to assess form quality in forestry have been used: the holistic approach and the multi-trait approach. The holistic approach attempts to judge directly the unity formed by the complex of characters: branch, crown and stem properties *etc.*. In this approach, only one visual score is obtained for the whole tree with respect to the quality requirements. This method is fast and easy compared with empirical measuring, but the accuracy is questionable due to subjectivity and inconsistency (Magnussen and Yeatman 1987a). The multi-trait approach has become more widely adopted in breeding programs (Cotterill and Zed 1980), although it is complex because it involves selecting several traits, and the accuracy of genetic parameter values (e.g. heritabilities and genetic correlations) derived for the advanced selection index methods still needs improvement (Zobel and Talbert 1984).

Genetic Variation

The magnitude of genetic variation varies depending upon the form traits being considered and the species. For jack pine, the form traits such as number of branches, number of leaders and crown density exhibited greater variation than did the growth traits such as height and diameter (Morris *et al.* 1992). The opportunity for genetic improvement of branch angle appeared to be feasible within the four jack pine seed lots considered by Magnussen and Yeatman (1987b). With a range of more than 30° in whole tree values of branch angle, it was confirmed that jack pine exhibits extreme phenotypic deviants ranging from upright to flat branches (Benzie 1977, Polk 1972, Rudolph and Yeatman 1982). Beaudoin (1996) also found that the difference among scots pine provenances was significant for branch angle. Further study is needed for genetic variation of tree form quality traits, such as branch size, relative branch size, etc. in jack pine.

For other coniferous species, at the provenance level, genetic variation in tree form quality traits was found to be significantly different for loblolly pine, Scots pine, Japanese Larch (*Larix kaempferi* (Lambert) Carr.) and Norway spruce (*Picea abies* (L.) Karst.) (Eriksson *et al.* 1987, Farnsworth *et al.* 1972, Krupski and Giertych 1996, Liu *et al.* 1997). In a provenance trial of Norway spruce, significant differences were obtained for characters of branch diameter, spike knots, stem straightness and branch angle among provenances (Krupski and Giertych 1996). For Douglas fir, considerable genetic variation was found for branch diameter and length adjusted for stem size and relative crown width (St. Clair 1994). For Scots pine, trees from the northern part of its distribution transferred a few degrees southwards were found to be straight and with thin branches and few spike knots (Stahl 1998). At the family level, differences were noted for approximately half of the quality characters among families of Scots pine (Eriksson *et al.* 1987). In the case of loblolly pine, although stem straightness was significantly different among provenances, the variations among families were not (Lu *et al.* 1997). Similarly for Scots pine, the differences between families for most quality characteristics were small (Makinen 1996).

Heritability

For many commercial species, the heritabilities of concerned traits are reasonably high (Morgenstern *et al.* 1975), the range of 0.1 to 0.4 (individual) has been established in conifers for branch angle, branchiness, self-pruning and wood density (Bailey *et al.*

1974, Barber 1964, Dietrich 1973, Ehrenberg 1961, Franklin and Callaham 1970, Nicholls *et al.* 1980). Selected individual heritability estimates for form quality traits from various studies are listed in Table 2. For branching characteristics, the individual heritabilities vary greatly, ranging from 0.01 to 0.73, with an average of 0.25 for all of the listed traits: branch diameter, relative branch diameter, number of branches and branch angle. To the extent that stem- and branch-form characteristics are strongly heritable, they are more easily manipulated via improvement programs than are height and volume growth rates (Wright 1976, Zobel and Talbert 1984).

Number of branches per whorl has a low to moderate heritability, its heritability values range from 0.01 to 0.19, and average 0.11 (Table 2). For jack pine, the heritability value was 0.10, and the values were 0.09, 0.09 and 0.01 for Scots pine, Douglas fir and Norway spruce, respectively.

Branch angle has the highest heritability for all of the traits listed, ranging from 0.09 to 0.73, and averaging 0.40. This trait was found to be the most strongly heritable trait, with individual and family heritabilities of 0.42 and 0.89, respectively, for jack pine, and the highest heritability in Virginia pine (Bailey *et al.* 1974).

The individual heritabilities for relative branch diameter range from 0.17 to 0.34 and average 0.28 (jack pine, 0.12) (Table 2). Compared with those of other traits, this value is low, and this is consistent with results from other species, such as Virginia pine (Bailey et al. 1974), loblolly pine (Zobel and Talbert 1984) and lodgepole pine (Yanchuk 1986).

Stem straightness has a relatively high heritability. Its values average 0.17 and range from 0.13 to 0.28. For jack pine, the individual heritability was 0.23. It ranges from 0.17 to 0.28 for radiata pine, and averages 0.13 for lodgepole pine.

Table 2. Individual heritability estimates for stem quality traits.

Trait	Species	h^2	Reference
branch diameter	Scots pine	0.21	(1)
Relative branch diameter	Douglas fir	0.34	(2)
	Jack pine	0.12	(6)
	Scots pine	0.17	(3)
	Scots pine	0.24	(1)
Number of branches	Douglas fir	0.09	(2)
	jack pine	0.10	(4)
	Norway spruce	0.01	(5)
	Scots pine	0.09	(3)
Branch angle	Douglas fir	0.06	(2)
	jack pine	0.42	(6)
	Norway spruce	0.44	(5)
	Scots pine	0.22	(3)
	Scots pine	0.24	(1)
stem straightness	jack pine	0.23	(6)
	lodgepole pine	0.13	(7)
	radiata pine	.17-.28	(8)
Number of crooks	jack pine	0.10	(4)
Number of leaders	jack pine	0	(4)
crown diameter	jack pine	0.08	(4)
Relative crown width (rcw)	Scots pine	0.31	(3)
	Scots pine	0.43	(1)
Relative crown height (rch)	Scots pine	0.19	(1)
crown density	jack pine	0	(4)

Note: Rcw is the ratio of crown diameter to stem height, and rch is the ratio of crown height to stem height. (1) Haapanen and Pöykkö 1993, (2) St. Clair 1994, (3) Velling and Tigerstedt 1984, (4) Morris *et al.* 1992, (5) Merrill and Mohn 1985, (6) Adams and Morgenstern 1991, (7) Yanchuk 1986, (8) Cotterill and Zed 1980.

Relative crown width is measured both as crown width per unit crown length and crown width adjusted for stem diameter below a sample whorl. In Douglas fir the individual heritabilities were 0.32 and 0.25, respectively (St.Clair). The crown width relative to stem height in a Scots pine had an estimated heritability of 0.31.

All of the studies above show that the parameter (heritability), attributed as "genetic" is actually a unique trial parameter that refers only to the population and conditions under which they have been obtained (Falconer 1981).

Stand Density Relationships

As noted above, the size of branches represents the most important log quality characteristic (Barger and Ffolliott 1970, Grah 1961). Wood grade decreases as the size of knots increases (Tustin and Wilcox 1974). Stand density is a factor of prime importance among the properties of stand structure controlling the formation, growth, death and natural pruning of branches (Fujimori 1975, Kellomäki and Tuimala 1981). As a result, density control of stands can increase timber quality in any conifer stand (Vuokila 1968).

A number of studies have been carried out to determine the influence of initial spacing on form quality of trees (Scots pine - Abetz 1970, Kellomäki *et al.* 1992, Kellomäki and Väisänen 1986, Persson 1977, Salminen and Varmola 1993, Spellman and Nagel 1992, Varmola 1980a; other *Pinus* sp.- Bramble *et al.* 1949, Stevenson and Bartoo 1939, Ware and Stahelin 1948; Norway spruce - Handler and Jakobsen 1986, Kramer *et al.* 1971, Merkel 1967). These studies have shown that branch size, stem taper and the size of the living crown are reduced by closer spacing.

Branch size on the first log in pines largely depend on initial stand density (Ballard and Long 1988). Wood produced in a widely-spaced plantations has larger knots and hence, inferior strength properties than wood produced from dense stands (Balmer *et al.* 1975, Laidly and Barse 1979, Persson 1975b). For Scots pine, Salminen & Varmola (1990) reported that the influence of spacing was very modest, whereas Persson (1977) and Varmola (1980a) found it stronger; the wider the spacing, the thicker the branches, even with the equal stem size. Varmola (1980a) went so far as to regard stand density as the most important factor affecting the quality of Scots pine. Jokinen and Kellomäki (1982) found that the number of live branches per tree and the diameter and length of the thickest branch in a whorl decreased with increasing stand density in Scots pine. For spruce, branch thickness at 1.3 m above ground level depended on stand density only, but at 2.5 m it depended on both density and rectangular design (Handler and Jakobsen 1986). For shore pine, increasing planting density reduced the proportion of stem defects and disease- and insect-damaged trees (Xie *et al.* 1995).

Poorer stem form in pines grown at wide spacings during the juvenile stage is a common observation (Evert 1971, Magnussen and Yeatman 1987a, Varmola 1980a). The evidence found in jack pine supports these findings (Bella and Franceschi 1971, 1980, Magnussen and Yeatman 1987a, Ralston 1953, Rudolf 1951, Rudolph 1964). Magnussen and Yeatman (1987a) reported a relatively high proportion of "runt" trees and trees with crooked stems in the 2 m spacing. Although form quality in dense stands is usually good, a high risk of serious snow damage may outweigh any quality gain in close spacings (Kramer 1979, Magnussen and Yeatman 1987a, Neary *et al.* 1974, Yeatman 1974).

Excessive stem taper is unacceptable in the manufacture of some specialty products, such as power poles (American National Standards Institute 1979). Taper also reduces the amounts of recoverable lumber in a log (Ballard and Long 1988). Reukema and Smith (1987) found that the *H/D* ratio (height / DBH) at age 25 is strongly influenced by spacing. The closer the spacing, the larger the ratio. The closest spacing 0.9 meters had a taper value of 138 for Douglas fir, and widest spacing 56 for cedar. The ratio declines with increasing age. According to the "pipe model" theory (Kellomäki *et al.* 1989), the cross-section of the stem equals the sum of the cross-sections of the branches above. This explains why stem taper ratio decreases with the increase of age due to branch dieback (Bramble *et al.* 1949, Niemistö 1995).

For tree form, jack pine has a tendency to develop irregular crowns in wide spacing. The crown becomes wide and bushy with multiple leaders and stems. The correlation between the crown irregularity and spacing was highly significant (Bella and De Francheschi 1974), and an optimum spacing of between 1.8 and 2.4 m was suggested for jack pine (Bella 1986).

For crown width, spacing has great effect on crown development (Bella 1986, Bella and Francheschi 1974). Crown width showed a gradual increase with spacing for jack pine, red pine and white spruce. For jack pine, the increase in crown width was more pronounced and quite dramatic for large trees (above 12 cm DBH) at the widest spacing. Thus wide crowns correspond to heavy branches and greater stem taper.

GENETIC CORRELATION BETWEEN GROWTH AND FORM TRAITS

Genetic correlation is used to quantify the impact of selection based on one or several traits on the other traits. It may be positive, zero, or negative. Table 3 lists selected genetic correlations for coniferous species. The table shows that the genetic relationships between branch angle and quality, tree size and productivity were zero. Branch angle in jack pine was not significantly correlated with adverse stem quality traits. This trait had weak negative genetic correlation with height, but did not correlate strongly with any other trait (Adams and Morgenstern 1991). Studies on other species such as Norway spruce (Lewark 1981) and slash pine (*Pinus elliottii* Engelm.) (Strickland and Goddard 1965) also found branch angle had little or no relationship to tree size. This indicates that branch angle is independently inherited. However, some other studies disagree with this hypothesis (Bailey *et al.* 1974, Barber 1964, Dietrich 1973, Haapanen and Pöykkö 1993, Merrill and Mohn 1985). Trees with narrow angles usually have larger knots than those with wide angles (Bailey *et al.* 1974, Dietrich 1973, Haapanen and Pöykkö 1993, Zimmermann and Brown 1971).

Table 3 also indicates that tree form quality traits and growth traits had negative genetic correlation, indicating that improvement in growth may decrease stem form quality (Liu *et al.* 1997, Morris *et al.* 1992, Paques 1996a, Sun and Liu 1997). Morris *et al.* (1992) found that stem height and diameter had very strong genetic correlation with number of crooks along stems of jack pine (Table 3). Giertych (1986) found that there were strong genetic correlations between branchiness, straightness and self-pruning of Scots pine. Scandinavian provenances had straight stems but low productivity, whereas inland continental provenances were highly productive but had poorer form. Paques (1996) also found that for Japanese larch at the provenance level, negative correlations between tree form and growth vigour existed. In Scots pine, the genetic correlation between form quality and growth traits appeared to be slightly unfavourable with respect to multi-trait breeding (Haapanen and Pöykkö 1993).). However, stem straightness had no evident genetic correlation with growth rate of loblolly pine (Table 3).

Branch diameter had positive genetic correlations with stem height and diameter, while relative branch diameter had negative correlations with the growth traits in Scots pine (Haapanen and Pöykkö 1993). This relationship means that selections for trees with superior stem height and diameter may also increase branch diameter, but may not increase relative branch diameter. Therefore, multi-trait selection may be favourable for in this species. A positive genetic correlation between height and taper in jack pine is believed to reflect a relatively longer crown in some families (Magnussen and Yeatman 1987a). Morris *et al.* (1992) found that crown diameter had stronger genetic correlation with stem height than with stem diameter, and both stem height and diameter had weak genetic correlation with number of branches. This indicates that stem height and diameter were not strongly correlated with crown shape and number of branches. The low genetic correlation between number of branches and the two growth traits probably suggested an independent inheritance of number of branches (Table 3).

Table 3. Genetic correlations between growth and form traits in coniferous species.

Trait	Species	Correlation	Reference
Branch angle - productivity	Scots pine	0	(1)
Branch angle - tree size	jack pine	0	(2)
Branch angle - stem quality	Scots pine	0	(1)
Growth rate - stem straightness	loblolly pine	0	(3)
Growth rate - tree form	loblolly pine	<0	(4)
Growth rate - tree form	loblolly pine	<0	(5)
Growth rate - tree form	Japanese larch	<0	(6)
Height - crown diameter	jack pine	0.44	(7)
Height - number of crooks	jack pine	0.93	(7)
Height - number of branch	jack pine	0	(7)
Height - taper	jack pine	>0	(2)
Height - branch diameter	Scots pine	0.26	(8)
Height - relative branch diameter	Scots pine	-0.18	(8)
DBH - crown diameter	jack pine	0.18	(7)
DBH - number of crooks	jack pine	0.82	(7)
DBH - number of branch	jack pine	0.17	(7)
DBH - relative branch diameter	Scots pine	-0.32	(8)
DBH - branch diameter	Scots pine	0.46	(8)
Adjusted branch diameter (a.b.d.) - Adjusted branch length (a.b.l)	Douglas fir	0.59	(9)

Notes: a.b.d. (or a.b.l.) is the ratio of branch diameter to stem diameter (or the ratio of branch length to stem height). Reference: (1) Giertych 1986, (2) Magnussen and Yeatman 1987b, (3) Lu et al. 1997, (4) Liu et al. 1997, (5) Sun and Liu 1997, (6) Paques 1996, (7) Morris et al. 1992, (8) Haapanen and Pöykkö1993, and (9) St.Clair (1994).

St.Clair (1994) showed that adjusted branch diameter and adjusted branch length had a moderate positive correlation for Douglas fir. Haapanen and Pöykkö (1993) also found that the genetic correlation between each pair of branching traits (branch diameter, relative branch diameter, branch angle) in two different whorls (4th and 7th from the top) for Scots pine were moderately correlated (0.63 to 0.66), and those between these traits and other traits were very similar and independent of the position of the whorl. Thus, the quality associated with branch characteristics of young pines can be assessed quite accurately using a single whorl and with better accuracy by using the upper part of the crown. St. Clair (1994) also found that tree size was genetically correlated with larger branch diameter (1.18), steeper branch angle (-1.07), and more branches per whorl (0.26). Large trees that were efficient producers of wood relative to growing space had full, tall, narrow crowns. This particular crown structure is in agreement with theoretical models of the effect of crown shape on light interception and stand productivity (Jahnke and Lawrence 1965, Kellomäki *et al.* 1985).

Adams and Morgenstern (1991) revealed that the strongest genetic correlation was between crown quality and branch diameter (0.88) in jack pine. This result could be anticipated because relative crown width was included in crown quality, and generally, longer branches are larger in diameter. Stem straightness showed a strong positive correlation with crown quality (0.78) and branch diameter (0.72). Evaluation of both traits is probably not necessary in the future.

INTERACTIONS OF SPACING AND GENETIC FACTORS

Magnussen and Yeatman (1987a) found that "genoptye" x spacing interaction was significant for stem and branch diameter . With only four genetically well-buffered seed lots tested, this finding applies only to mass selection. Although genotype x spacing interactions are important in practice, little information has been published on this subject regarding better defined "genotypes" such as half- or full-sib families (Campbell and Wilson 1973, Cannell 1982, Fries 1984, Magnussen and Yeatman 1987a). Further studies are clearly needed in this field.

MATERIALS AND METHODS

During the summer of 1989, natural jack pine stands were chosen from the eastern and western areas of the former North Central Region of Ontario. Three stands ranging from good to poor form extremes were selected in each of the two areas (Fig.1). From each of the six stands, ten trees were randomly selected with two constraints: (1) parent trees were separated by a minimum of 100 meters, and (2) a minimum of 20 closed cones per tree were available. Microsite, competitors and parent trees were measured to quantify stand conditions on an individual tree basis, such as depth to bedrock, distance and crown dimensions of competitors, stem straightness, taper, shape, height, DBH of parent trees, etc. (Morris and Parker 1992). An additional 20 families from a total of 400 were selected from Ontario's tree improvement program (from the Lake Nipigon western breeding zone), based on an early measurement (3 year-old) of one family-test (Morris *et al.* 1992). The families exhibiting the best growth (10) and highest form quality (10) were incorporated into the current study (Fig.1 and Appendix 2). The eight family groups were determined according to stand quality and location of families (Table 4).

Up to one hundred cones were collected from each parent tree in June 1989, and bagged separately. Seeds were extracted and stored. For each parent, 480 seedlings were established in a greenhouse in early winter, 1989. The seedlings (current crop, leech tube containers) were grown in the greenhouse throughout the winter, receiving water and nutrients, and transported to two planting sites in early June, 1990. Two planting sites were chosen with differing site quality, the fertile, moist, fine-soiled site referred to here as Camp 45,

Table 4. Quality and location of family groups (stands) in jack pine.

Group number	Symbol	Family number	Location	Quality of stand
1	E-G	1-10	east of Lake Nipigon	good
2	E-A	11-20	east of Lake Nipigon	average
3	E-P	21-30	east of Lake Nipigon	poor
4	W-G	31-40	west of Lake Nipigon	good
5	W-A	41-50	west of Lake Nipigon	average
6	W-P	51-60	west of Lake Nipigon	poor
7	G-G	61-70	LNWBZ	good in growth
8	G-F	71-80	LNWBZ	good in form

Note: LNWBZ = Lake Nipigon western breeding zone. For details regarding G-G and G-F, see Appendix 2.

and the nutrient-poor, sandy site referred to here as Camp 602. The seedlings were planted in 4 blocks in each of the two sites. Each block contained 5 different spacings: 0.25, 0.50, 1.00, 2.00, 3.00 m. Within each of the spacing regimes, 5 replicates of the 80 families were randomly located in sing-tree plots. Therefore, a total of 16,000 seedlings (400 seedlings/density x 5 densities x 4 blocks x 2 sites) were used. An additional 7000 seedlings were required to establish two buffer rows around all 40 density blocks (5 densities x 4 blocks x 2 sites). On both planting sites (Fig. 1 and Appendix 1), manual site preparation and /or weed control were executed during fall/winter 1989, to provide a uniform planting site on typical boreal cutovers. Manual weed control has been conducted periodically for the duration of the experiment (more details regarding the collection site, site quality and parent tree stands of this study can be found in Morris and Parker 1992).

During the first two years, dead trees were replaced with overwinter containerized stock from the same seedling lot and flagged as refills to maintain the integrity of the initial spacings. Every fall, health/damage assessments were done. Thus, it was possible to run analyses with all or non-damaged trees.

In 1998, data were collected from both test sites (Fig. 1) for the following measurements: number of crooks, total height, $\mathrm{dia}_{0.5}$ (stem diameter at 0.5 m height) and DBH (diameter at breast height). In addition, both northward and eastward branches were measured in whorl 95 (initiated in 1995) for traits branch length, branch diameter, branch angle and number of dominant branches. Of the five spacings, only three spacings were included for this study: the 1 m, 2 m and 3 m spacings.

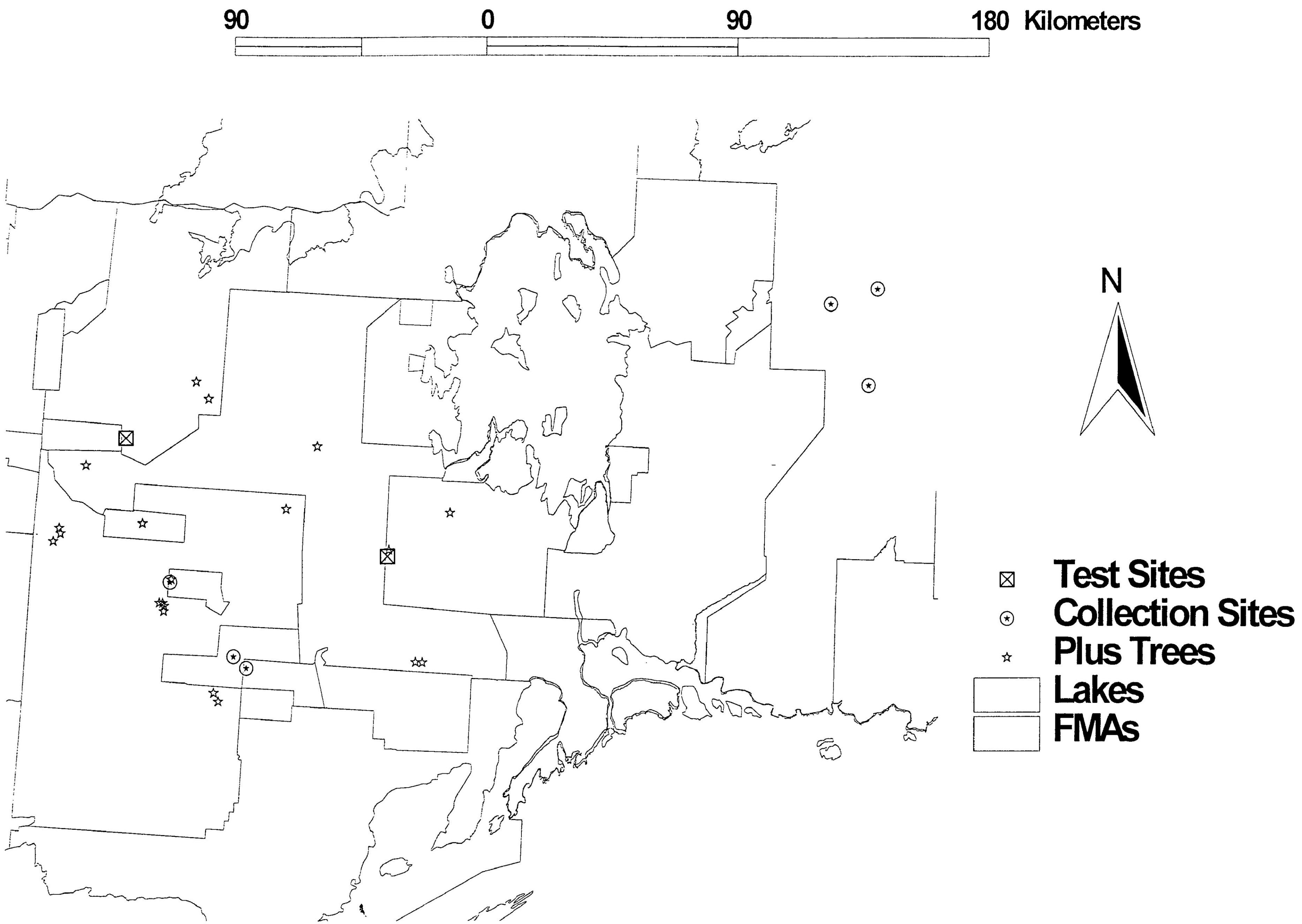

Fig. 1. Collection Sites, Test Sites and Plus Tree Locations

Noticeably damaged trees were not measured for branch traits. These included: the trees with no leading branches (mostly caused by weevil damage) and thus with irregular crown shape, and the trees with no normal or healthy branches in whorl 95 (in this case, the branches were mostly eaten by animals, such as moose). Average branch diameter, length and angle were determined using the average values of northward and eastward branches. Number of dominant branches was defined as those branches, which dominated in whorl 95, and number of crooks was measured by counting the crooks (bend) along a stem. Relative branch diameter was defined as the ratio of average branch diameter to stem diameter in whorl 95, and relative crown width represented the ratio of average crown diameter (double the average branch length) to height. Stem taper was calculated as follows (Forslund 1991):

$\text{Taper}=1.40 \times \text{height} / d_{0.3}$

where: $d_{0.3} = (1 - \text{height}_{0.3} / \text{height}) \times d_{0.5} / (1 - 0.5 / \text{height})$

$= (1 - 0.3) \times d_{0.5} / (1 - 0.5 / \text{height})$

$d_{0.5}$ is stem diameter at 0.5 meter height

height is the total height of stem

Statistical Analyses

The following ten variables were used for statistical analysis: number of dominant branches, average branch diameter, average branch length, average branch angle, height, DBH, relative branch diameter, relative crown width, taper and number of crooks. First, SAS procedures Chart and Univariate were used to check if these variables were normally distributed (SAS Institute Inc. 1996). The results showed that nine of the ten traits followed a normal distribution. Number of crooks, however, did not.

SAS procedure GLM was used to run ANOVAs for the nine normally distributed traits. Although this was an experiment of randomized complete block design, preliminary tests showed that block effect and block related interactions were zero or very close to zero. Thus, the model was simplified as Eq.1:

$$Y_{ijklm} = \mu + S_i + P_j + SP_{ij} + G_k + SG_{ik} + PG_{jk} + SPG_{ijk} +$$

$$F_{(k)l} + SF_{i(k)l} + PF_{j(k)l} + SPF_{ij(k)l} + \varepsilon_{(ijkl)m} \qquad \text{Eq.1}$$

$$i = 1, 2; \quad j = 1, 2, 3; \quad k = 1 \text{ to } 8; \quad l = 1 \text{ to } 10; \quad m = 1 \text{ to } n$$

where: Y_{ijklm} = the response variable of the mth replication of the ith family within the kth group of the jth spacing of the ith site, μ = the overall mean, S_i = the fixed effect of the ith site, P_j = the fixed effect of the jth spacing, SP_{ij} = the interaction effect of the ith site and the jth spacing, G_k = the random effect of the kth group, SG_{ik} = the interaction effect of the ith site and kth group, PG_{jk} = the interaction effect of the jth spacing and the kth group, SPG_{ijk} = the interaction effect of the ith site and the jth spacing and the kth group, $F_{(k)l}$ = the random effect of the lth family within the kth group, $SF_{i(lm)n}$ = the interaction effect of the ith site and the lth family within the kth group, $PF_{k(lm)n}$ = the interaction effect of the jth spacing and the lth family within the kth group, $SPF_{ij(k)l}$ = the interaction effect of the ith site and the jth spacing and the lth family within the kth group, and $\varepsilon_{(ijkl)m}$ = the random effect of the mth replication of the lth family within the kth group of the jth spacing of the ith site, assumed IID(0, $\sigma_{\omega t}{}^2$). Here the values for n ranged between 15 and 17 depending on the response variable in question and the number of missing values, n = (actual observations measured) / (s x p x g x f), where s, p, g, and f were number of sites, spacings, groups and families, respectively

After further preliminary test, the non-significant 3-way interactions were pooled into the experimental error and the simplified linear model was as Eq.2. According to Eq.2, the expected mean squares table was developed as in Table 5. SAS procedure SNK (Student-Newman-Keuls) was used for multiple comparison test (SAS Institute Inc. 1996).

$$Y_{ijklm} = \mu + S_i + P_j + SP_{ij} + G_k + SG_{ik} + PG_{jk} + F_{(k)l} + SF_{i(k)l} + PF_{j(k)l} + \varepsilon_{(ijkl)m} \qquad \text{Eq.2}$$

To calculate heritabilities, variance components for each of the nine traits were produced by SAS procedures VARCOMP (SAS Institute Inc. 1996). Heritabilities were calculated separately for each spacing at each site; the model was as Eq.3.

$$Y_{ijk} = \mu + B_i + G_j + BG_{ij} + F_{(j)k} + BF_{i(j)k} + \varepsilon_{(ijk)l} \qquad \text{Eq.3}$$

$$i = 1, 2, 3, 4; \quad j = 1 \text{ to } 8; \quad k = 1 \text{ to } 10; \quad l = 1 \text{ to } n$$

where: Y_{ijkl} = the response variable value of the lth replication of the kth family within the jth group of the ith block, μ = the overall mean, B_i = the fixed effect of the ith block, G_j = the random effect of the jth group, BG_{ij} = the interaction effect of the ith block and jth group, $F_{(j)k}$ = the random effect of the kth family within the jth group, $BF_{i(j)k}$ = the interaction effect of the ith block and the kth family within the jth group, and $\varepsilon_{(ijk)l}$ = the random effect of the lth replication of the kth family with the jth group of the ith block. In the model n = (actual observations) / (b x g x f), where b, g and f were number of blocks, groups and families, respectively.

Table 5. Expected mean squares (EMS) table associated with Eq.2.

Source	df	EMS
Site	1	$\sigma^2 + 3n\sigma^2_{sf} + 30n\sigma^2_{sg} + 240n\,Ø(S)$
Spacing	2	$\sigma^2 + 2n\sigma^2_{pf} + 20n\sigma^2_{pg} + 160n\,Ø(P)$
Site x Spacing	2	$\sigma^2 + 80n\,Ø(SP)$
Group	7	$\sigma^2 + 6n\sigma^2_{f} + 60n\sigma^2_{g}$
Site x Group	7	$\sigma^2 + 3n\sigma^2_{sf} + 30n\sigma^2_{sg}$
Spacing x Group	14	$\sigma^2 + 2n\sigma^2_{pf} + 20n\sigma^2_{pg}$
Family	72	$\sigma^2 + 6n\sigma^2_{f}$
Site x Family	72	$\sigma^2 + 3n\sigma^2_{sf}$
Spacing x Family	144	$\sigma^2 + 2n\sigma^2_{pf}$
Pooled Error	480n-322	σ^2
Total	480n -1	

Note: The pooled error includes the 3-way interactions site x spacing x group and site x spacing x family.

The expected mean squares (EMS) associated with Eq.3 are presented in Table 6. Standard errors were estimated as described by Becker (1984) for variance components and heritability. Narrow-sense heritabilities on an individual-tree basis and family heritabilities were estimated as Eq.4a and Eq.4b from Becker (1984).

$$h_f^2 = \frac{\sigma_f^2}{\frac{\sigma_e^2}{nb} + \frac{\sigma_{fb}^2}{b} + \sigma_f^2} \qquad \text{Eq.4a}$$

$$h_i^2 = \frac{4\sigma_f^2}{\sigma_e^2 + \sigma_{fb}^2 + \sigma_f^2} \qquad \text{Eq.4b}$$

where: h_f^2 is the family heritability, h_i^2 is the individual heritability, σ_f^2 is the family variance component, σ_e^2 is the error variance component, σ_{fb}^2 is the interaction variance component of family and block.

Genetic correlations were calculated from variance components, which were obtained from SAS procedure VARCOMP REML (Stonecypher 1992). Variance components for each pair of traits for each spacing at each site were estimated and genetic correlation were calculated as Eq.5 (Falconer 1981):

$$r_g(xy) = \frac{\mathrm{cov}_f(xy)}{\sqrt{\sigma_f^2(x)}\sqrt{\sigma_f^2(y)}} \qquad \text{Eq.5}$$

where: $r_g(xy)$ is the genetic correlation between traits x and y, $\mathrm{cov}_f(xy)$ is the family covariance between traits x and y, $\sigma^2_f(x)$ is the family variance for trait x, $\sigma^2_f(y)$ is the family variance for trait y.

Table 6. Expected mean squares (EMS) associated with Eq.3.

Source	df	EMS
Block	b-1	$\sigma^2 + n\sigma_{fb}^2 + \mathrm{f}n\sigma_{gb}^2 + \mathrm{gf}n\Phi(B)$
Group	g-1	$\sigma^2 + \mathrm{b}n\sigma_f^2 + \mathrm{bf}n\sigma_g^2$
Block x Group	(b-1)(g-1)	$\sigma^2 + n\sigma_{fb}^2 + \mathrm{f}n\sigma_{gb}^2$
Family	g(f-1)	$\sigma^2 + \mathrm{b}n\sigma_f^2$
Block x family	(b-1)g(f-1)	$\sigma^2 + n\sigma_{fb}^2$
Error	bgf(n-1)	σ^2

RESULTS AND DISCUSSION

THE EFFECTS OF SPACING AND GENETIC FACTORS

This study focused on the effects of spacing and genetic factors (mainly form-quality groups) on two growth traits and eight tree form quality traits. The site effect for all traits and the site x family interactions for height, DBH and taper indicated by the ANOVAs were not discussed in detail as they were not the focus of this study.

Height

The effect of spacing

Height growth was notably affected by spacing in 8 year-old, plantation-grown jack pine (Table 7). Trees planted at the 1 m spacing grew, on average, 10 cm higher than those in the 3 m spacing and 5 cm higher than those in the 2 m spacing. All of these differences were significant ($p < 0.05$) (Table 8). The site x spacing interaction was very significant (Table 7). At the nutrient-poor site (Camp 602), the mean heights of each spacing were very close to the site mean of height for all three spacings; while at the fertile site (Camp 45), trees grown at the 1 m spacing exhibited the highest growth rate and the 3 m spacing the lowest (Fig. 2). This pattern most likely arose as the trees at the fertile site grew faster, and, as a result the crowns closed quicker in the tighter spacings. After crown closure and as a response to increased competition for light, trees tend to

Table 7. ANOVA results for the effects of spacing, group and family on height growth of jack pine.

Source	df	MS	F Value	Pr > F
Site	1	523.04	1319.62	<0.01
Spacing	2	6.38	56.69	<0.01
Site x spacing	2	24.23	122.60	<0.01
Group	7	5.13	7.35	<0.01
Site x group	7	0.39	1.42	0.21
Spacing x group	14	0.11	0.51	0.92
Family (group)	72	0.70	3.53	<0.01
Site x family (group)	72	0.28	1.42	<0.05
Spacing x family (group)	144	0.22	1.11	0.18
Pooled Error	7297	0.20		
Total	7618			

Note: Group identities are in Table 4.

Table 8. Results of multiple comparisons for the effect of group and spacing on height growth of jack pine.

Source		Mean (m)	SNK Grouping
	1 x 1 m	3.24	a
Spacing	2 x 2 m	3.19	b
	3 x 3 m	3.14	c
	G-G	3.29	a
	G-F	3.26	ab
	W-P	3.23	bc
Group	W-G	3.22	bc
	W-A	3.20	c
	E-A	3.13	d
	E-P	3.10	de
	E-G	3.08	e

Note : Means with the same letter are not significantly different ($\alpha = 0.05$) for each source.

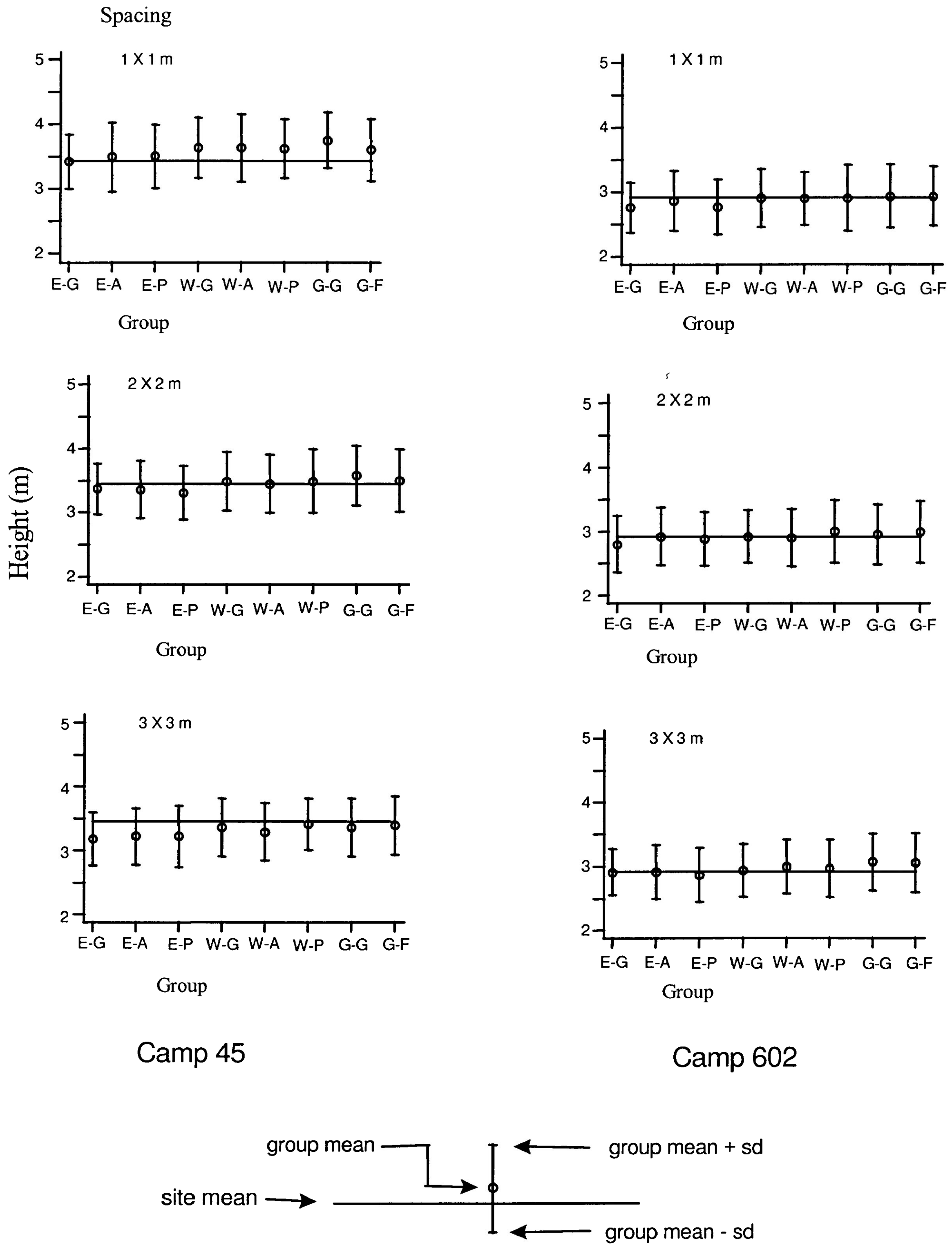

Fig. 2. Group and spacing effects on height in jack pine (Group identities are in Table 4, sd = standard deviation).

allocate a greater amount of resources to the apical meristem, resulting in increased height growth. At the poor site, crown closure had not yet occurred not only for 2 m and 3 m spacings, but also for most of the 1 m spacings. Janas and Brand (1988) found that height was relatively constant over a wide range of spacing in jack pine.

The effect of genetic factors

Genetic factors play a very important role in height growth, both at the group level (quality of stands) and family level (Table 7). The two plus tree groups (G-G and G-F) had the best height growth of all the eight groups. The trees sourced from west of Lake Nipigon grew much better than those from the east of the lake (Table 8). For both Camp 45 and Camp 602, the mean height of the groups from east of the lake (E-G (east good form), E-A (east average form) and E-P (east poor form)), had lower values of height than did the groups from west of the lake (W-G (west good), W-A (west average) and W-P (west poor)).

Although the site x group interaction did not reach significant level, the difference between groups was more notable for Camp 45 than for Camp 602 (Fig.2). This result is understandable because the two plus tree groups were also selected from west of Lake Nipigon, and the trees from west of the lake grew better in the two planting sites, both of them located west of Lake Nipigon.

The notable provenance effect (regional effect of genetic difference, such as that of east and west of Lake Nipigon) was in agreement with that of early studies (Yeatman

1974 and Rudolph and Yeatman 1982), they found that the provenance from east of Lake Nipigon was the slowest-growing ones at all ages to 19 years.

In addition to this group effect, family also had a significant effect on height growth of jack pine (Table 7). The 23 fastest growing families in the 80 families were all from the west of the lake, and the 9 slowest growing families in height growth were all from the east (Appendix 3.1). Among these best families, 7 were from G-G, 5 from W-G, 4 from W-P, 4 from G-F and 3 from W-A. Among those slowest growing families, 4 were from E-P, 4 from E-G and 1 from E-A. It is clear that families from the west of Lake Nipigon grew much better than those from the east of the lake. The significant site x family interaction was not presented in detail as height was not the most concerned trait in this study.

Genetic variation at the family level may be inconsistent, based on earlier studies. Early studies in jack pine support our finding that there is significant difference in growth traits among families (Magnussen and Yeatman 1989) in jack pine. The results in Masson pine were in agreement with those in jack pine (Qin *et al.* 1997). However, there were little or no difference among families of pitch pine (*Pinus rigida* P. Mill.) (Kuser and Ledig 1987), and jelecote pine (Kariuki 1998). It is noteworthy that families from different provenances were much more variable than those from within provenances. In this study both inter- and intra-provenance variation was involved in the analysis of variance in jack pine families.

Spacing x genetic interactions

The spacing x group and spacing x family interactions did not exist for height growth of jack pine, although genetic factors played an important role at both the group and the family level (Table 7).

Diameter at Breast Height (DBH)

The effect of spacing

In the mixed model analysis of variance, the spacing effect was very significant ($p < 0.01$) on diameter growth of jack pine (Table 9). The results of multiple comparisons of mean DBH showed that for all of the three pairs of spacing comparisons, the differences reached a significant level (Table 10). The mean DBH of 3 m and 2 m spaced trees were over 7 and 6 cm greater than that of 1 m, respectively. Although the 3 m and 2 m spacings only had 1 cm difference in mean DBH, this difference was also significant (Table 10). The site x spacing interaction was very significant (Table 9). For Camp 45, both the DBH means of 3 m and the 2 m spacings were about 3 mm over the site mean of DBH; only that of the 1 m spacing was more than 6 mm below the site mean (Fig. 3). For Camp 602, the magnitude of DBH mean differences among spacings was different. The mean of the 1 m spacing was about 4 mm below the site mean, while the mean of the 2 m spacing was 1 mm above the site mean and the 3 m spacing had a mean value of 3 mm above the site mean.

The analysis above revealed that at age 8, jack pine DBH was greatly reduced when spacing changed from 2 m to 1 m. When the spacing was decreased from 3 m to 2 m, DBH growth was not so greatly influenced. However, this result presumably depends on age. This result is consistent with findings from earlier studies that found a significant

Table 9. ANOVA results for the effects of spacing, group and family on diameter growth of jack pine.

Source	df	MS	F Value	Pr > F
Site	1	637903.52	2221.58	<0.01
Spacing	2	33799.51	627.43	<0.01
Site x spacing	2	2767.12	35.39	<0.01
Group	7	785.58	3.26	<0.01
Site x group	7	287.14	2.39	<0.05
Spacing x group	14	53.87	0.67	0.80
Family (group)	72	240.96	3.08	<0.01
Site x family (group)	72	120.10	1.54	<0.01
Spacing x family (group)	144	80.75	1.03	0.38
Pooled Error	7294	78.18		
Total	7615			

Note: Group identities are in Table 4.

Table 10. Multiple comparisons for the effect of spacing and group on diameter at breast height of jack pine.

Source		Mean (mm)	SNK Grouping
Spacing	3 x 3 m	42.10	a
	2 x 2 m	41.10	b
	1 x 1 m	35.05	c
Group	G-G	40.81	a
	G-F	40.26	ab
	W-G	39.98	ab
	W-P	39.72	bc
	W-A	39.41	bc
	E-P	38.80	cd
	E-A	38.27	d
	E-G	38.03	d

Note: Means with the same letter are not significantly different ($\alpha = 0.05$) for each source.

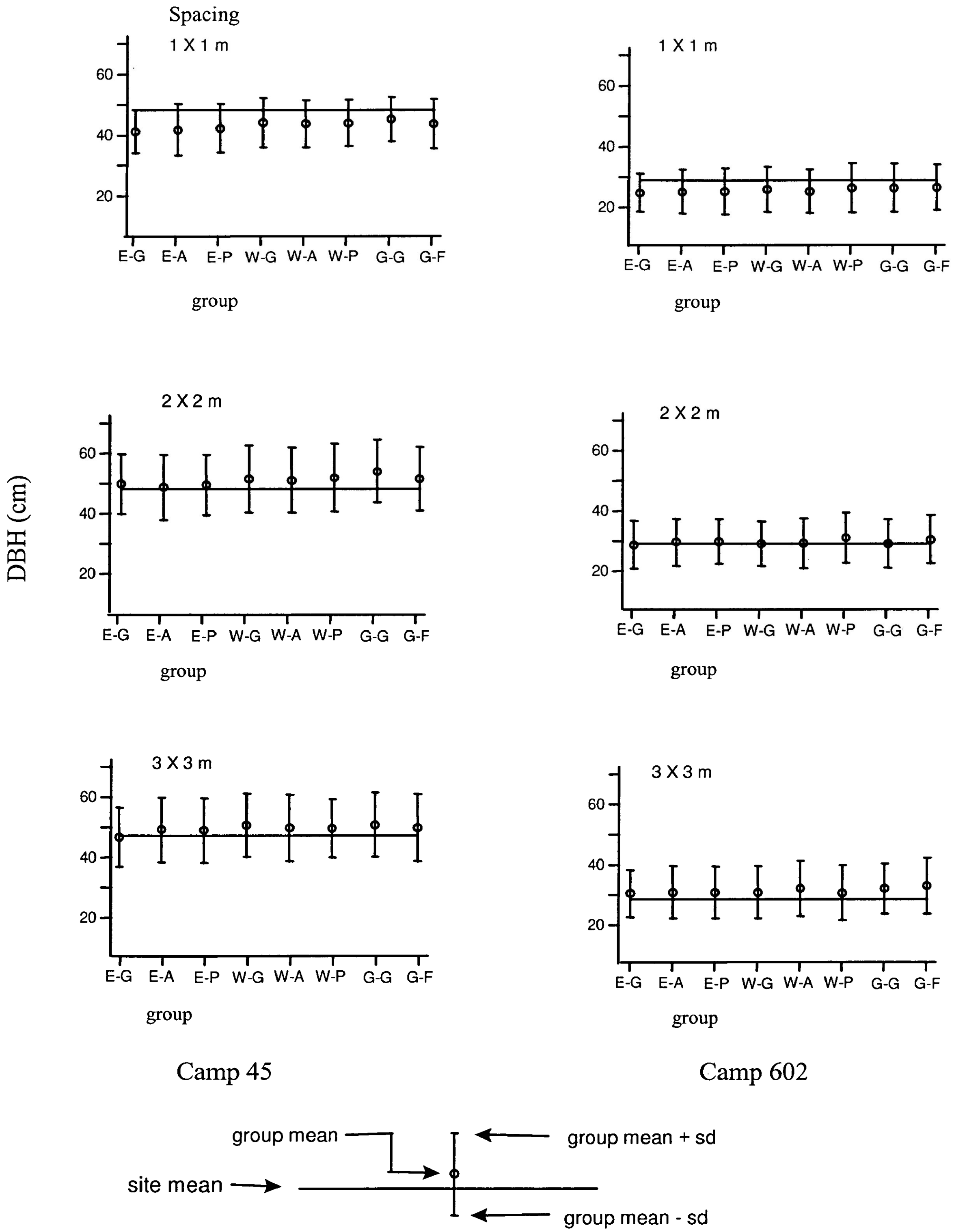

Fig. 3. Group and spacing effects on diameter at breast height in jack pine (Group identities are in Table 4, sd = standard deviation).

effect of spacing on diameter growth, and a wider spacing generally results in a greater diameter (Evert 1971, Hamilton and Christie 1975, Jørgensen 1967, Rudolf 1951). This result has been duplicated by many other jack pine spacing trials (Adams 1928, Bella and Franceschi 1974, 1980, Godman and Cooley 1970, Ralston 1953, Zavitkovski and Dawson 1978). However, some studies mentioned that wide spacing may lower the DBH growth during early growing stage, due to multiple stem formation and excessive stem taper (Bella and Francheschi 1974, 1980).

The effect of genetic factors

At the group level, the difference of DBH reached a level of 1% significance resulting primarily from provenance effect. The comparisons of mean DBH between groups indicated that the two plus tree groups had better diameter growth than all the others, and trees from the west of Lake Nipigon had significantly better diameter growth than those from east of the lake (Table 10). At the family level, the difference of DBH was also significant. The family means showed similar results as height: 19 of the 23 fastest grown families in DBH were from west of the lake (Appendix 3.2). Among those families, 5 were from G-G, 4 from G-F, 4 from W-G, 3 from W-A and 3 from W-P. Of the four families from east of the lake, 2 were from E-A and one from E-G and E-P. As was true for height, 8 of 9 of the slowest diameter growth families were from east of the lake.

The site x group interaction reached significant level. The difference of mean DBH among groups was more notable in fertile Camp 45 than in nutrient-poor Camp 602

(Fig. 3). In Camp 45, it was easily identified that the two plus tree groups G-G (good in growth) and G-F (good in form) had the highest value of mean DBH. In Camp 602, this trend among groups was not evident. The mean DBH growth of the groups in the 2 m spacing was almost identical for this site (Fig. 3). The significant site x family interaction was not presented in detail in this study as DBH was not the most concerned trait in this study.

The significance of genetic variation at both the group (with evident provenance effect) and family level has been supported by a variety of studies, these studies showed that genetic variation in diameter at breast height was large at the provenance level. Among provenances of loblolly pine, Norway spruce, radiata pine, Scots pine and Caribbean pine, there were significant differences in growth and yield (Eriksson *et al.* 1987, Gunia and Zybura 1984, Jayawickrama and Balocchi 1993, Liu *et al.* 1997, Wright *et al.* 1990). Xie and Ying (1996) reported that in lodgepole pine, genetic variation of diameter at breast height was large at both the provenance and the family levels. As was the case for height, the provenance effect on DBH was always greater than the family effect and this difference tended to increase as the test aged. Kariuki (1998) revealed that among provenances of *Pinus oocarpa* (Scheide), there were significant differences in DBH.

According to this study, family level genetic variation was significant for jack pine. This result was supported by Magnussen and Yeatman (1989) in jack pine and by Qin *et al.* (1997) in Masson pine. On the other hand, Kuser and Ledig (1987) found that there was little variation among families within provenances of pitch pine. The same as height growth, Kariuki (1998) reported that among families of jelecote pine the differences in DBH were all non-significant.

Spacing x genetic interactions

There were no significant spacing x group and spacing x family interactions (Table 9). This indicates that no family (group) was favoured at wider or closer spacings in this study, and this result did not follow the hypothesis presented above.

Number of Dominant Branches

Spacing, group, spacing x group and spacing x family interaction did not significantly affect number of dominant branches (Table 11). However, site x spacing interaction was significant (Fig. 4). At family level, number of dominant branches differed significantly (Table 11). Family numbers 77 (G-F), 22 (E-P), 5 (E-G), 39 (W-G) had the highest numbers of dominant branches, with values of 5.13, 5.01, 5.00 and 4.97, respectively. Family number 55 (W-P), 66 (G-G), 60 (W-P), 12 (E-A) and 67 (G-G) had the lowest numbers of dominant branches, with values of 4.23, 4.18, 4.11, 4.07 and 4.07, respectively (Appendix 3.3).

Table 11. ANOVA for the effects of spacing, group and family on number of dominant branches of jack pine.

Source	df	MS	F Value	Pr > F
Site	1	452.38	301.97	<0.01
Spacing	2	0.11	0.05	0.96
Site x spacing	2	9.45	4.97	<0.01
Group	7	4.51	1.03	0.42
Site x group	7	1.50	0.72	0.65
Spacing x group	14	2.42	1.21	0.27
Family (group)	72	4.36	2.29	<0.01
Site x family (group)	72	2.09	1.10	0.26
Spacing x family (group)	144	2.00	1.05	0.33
Pooled error	7300	1.90		
Total	7621			

Note: Group identities are in Table 4.

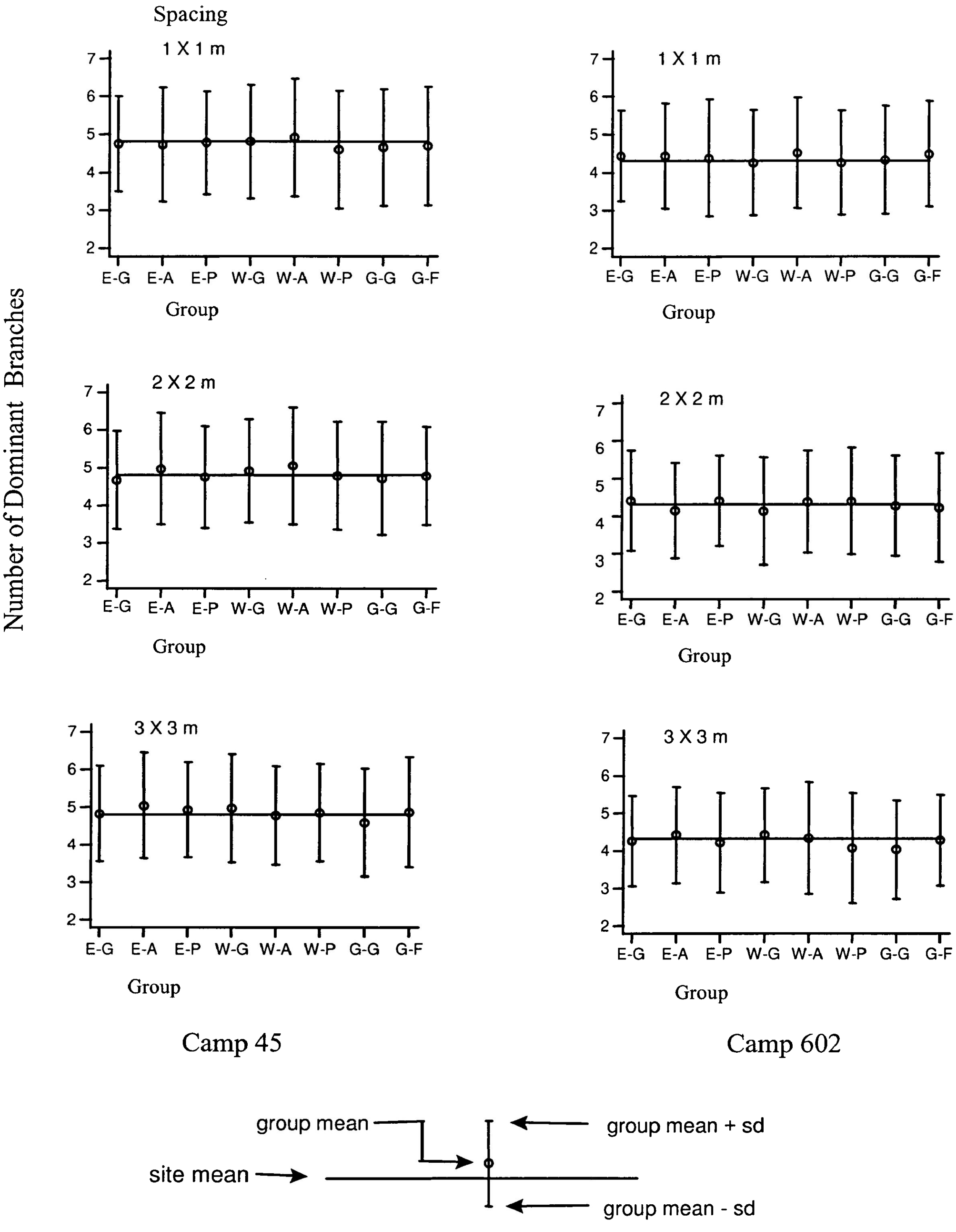

Fig. 4. Group and spacing effects on number of dominant branches in jack pine (Group identities are in Table 4, sd = standard deviation)

Number of dominant branches was quite different from height and DBH with respect to group and family effects. While no evident group effect was found, it should be possible to select trees with greater or fewer dominant branches.

It may be possible that the criteria for number of dominant branches is not very accurate because the values of this trait were determined by visual comparison, not by empirical measuring. The accuracy might be reduced due to subjectivity and inconsistency.

For genetic variation, Morris *et al.* (1992) found that genetic variation was greater in number of branches than in growth traits (height and diameter) in jack pine. However, St. Clair (1994) found little genetic variation for branch numbers per whorl in Douglas fir. Number of branches is one of the most important log quality characteristics (Barger and Ffolliott 1970, Grant *et al.* 1984, Grah 1961).

Average Branch Length (AVBL)

The effect of spacing

The effect of spacings on branch length was significant ($p < 0.01$) (Table 12). Trees grown at the 3 m spacing had 6.36 cm greater average branch length than those at the 2 m spacing, and trees grown at the 2 m spacing had 11.30 cm longer branches than those at the 1 m spacing. All of these differences were significant (Table 13).

Table 12. ANOVA for the effects of spacing, group and family on average branch length of jack pine.

Source	df	MS	F Value	Pr > F
Site	1	1130883.57	1393.44	<0.01
Spacing	2	194687.55	858.11	<0.01
Site x spacing	2	13634.07	36.99	<0.01
Group	7	1769.36	1.78	0.10
Site x group	7	811.58	2.55	0.02
Spacing x group	14	226.88	0.57	0.88
Family (group)	72	992.38	2.69	<0.01
Site x family (group)	72	317.81	0.86	0.79
Spacing x family (group)	144	400.07	1.09	0.23
Pooled error	7296	368.70		
Total	7617			

Note: Group identities are in Table 4.

Table 13. Multiple comparisons for the effect of spacing on average branch length of jack pine.

Spacing	Mean (cm)	SNK Grouping
3 x 3 m	89.78	a
2 x 2 m	83.42	b
1 x 1 m	72.12	c

Note: Means with the same letter are not significantly different ($\alpha = 0.05$).

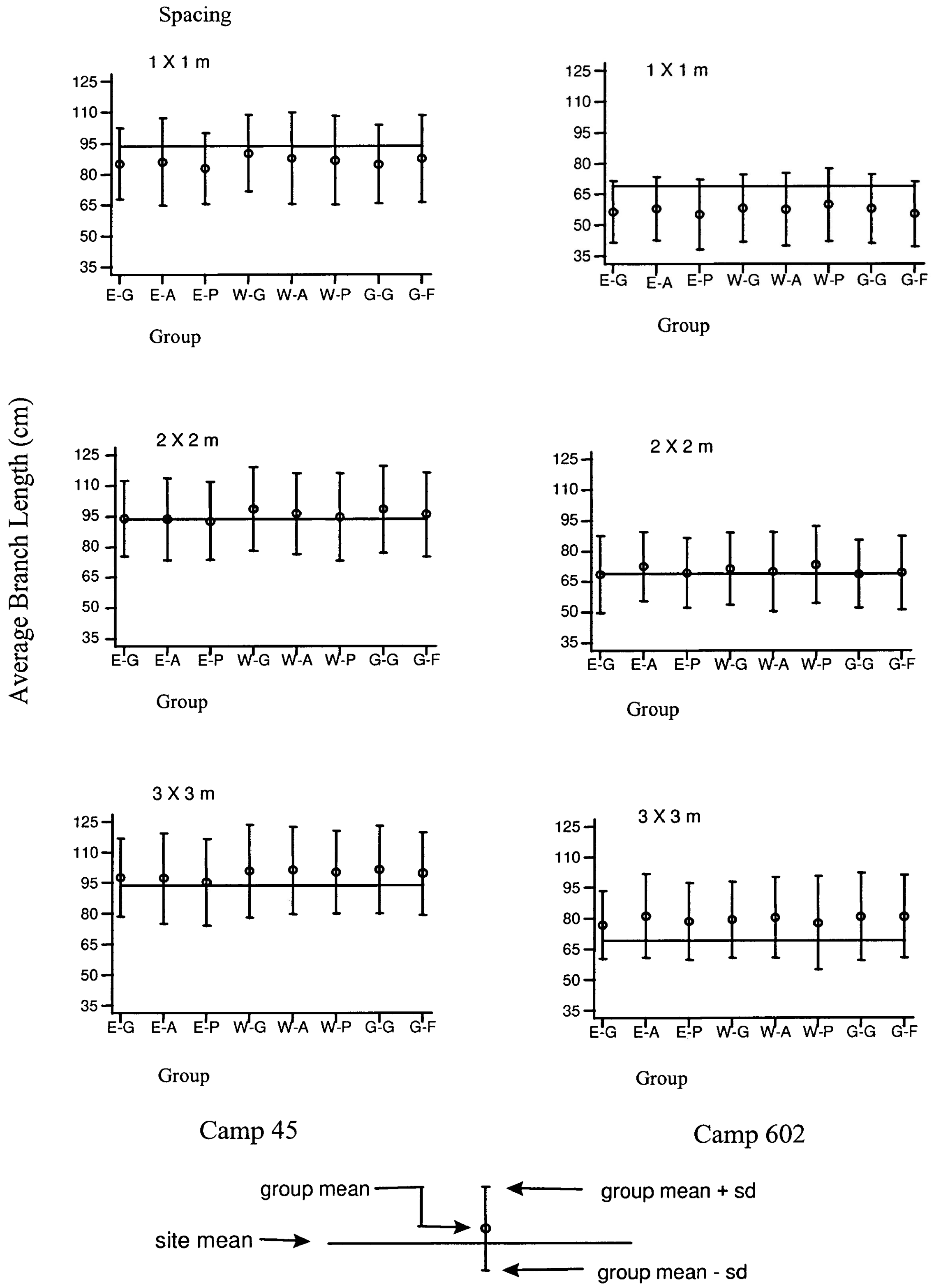

Fig. 5. Group and spacing effects on average branch length in jack pine (Group identities are in Table 4, sd = standard deviation).

The site x spacing interaction effect was very significant (Table 12). For the fertile Camp 45, the AVBL mean of the 3 m spacing was 4.4 cm longer than that of the 2 m spacing, and that of the 2 m spacing was 9 cm longer than that of the 1 m spacing (Fig. 5). For Camp 602, the difference of branch length among spacings was even greater. The AVBL for the 3 m spacing was 9 cm longer than that of the 2 m spacing, and the 2 m spacing was 12.2 cm longer than the closest 1 m spacing (Fig. 5). For both sites, the difference of AVBL between the 2 and 3 spacing was much smaller than that between the 1 and 2 m spacing. These differences were greater at Camp 602, where limited resources made the competition between trees more severe at the closer spacings.

The finding that spacing effect on branch length was significant for 8 year-old jack pine is consistent with those of a variety of studies (Scots pine - Abetz 1970, Kellomäki et al. 1992, Kellomäki & Väisänen 1986, Persson 1977, Salminen & Varmola 1993, Spellman & Nagel 1992, Varmola 1980a; other Pinus sp.- Bramble et al. 1949, Stevenson & Bartoo 1939, Ware & Stahelin 1948; Norway spruce - Handler & Jakobsen 1986, Kramer et al. 1971, Merkel 1967). These studies all found that branch length is reduced by closer spacing, and vice versa.

The effect of genetic factors

Group effect was not significant on average branch length of jack pine at age 8 (Table 12). However, the site x group interaction effect was significant. For Camp 602, differences between groups were very limited. For the fertile Camp 45, there were some notable differences between groups from west of Lake Nipigon and east of the lake; predictably, the groups from the west grew faster than those from the east.

The difference between families of jack pine was very significant (1%). Similar to the situation for height and DBH, a number of families from the west of Lake Nipigon had longer branch length than those from east of the lake (Appendix 3.4). Magnussen and Yeatman (1987b) found no significant difference of branch length between seed lots of jack pine.

Spacing x genetic interactions

No evident interactions between spacing and group, and between family and group were found (Table 12). These results followed the pattern of height and DBH, both of them also had no spacing x group and spacing x family interaction.

Average Branch Diameter (AVBD)

The effect of spacing

Spacing significantly affected branch diameter growth in 8 year-old jack pine (Table 14). The widest 3 m spacing had 1.64 mm greater AVBD than that of the 2 m spacing, and the 2 m spacing had 3.95 mm greater AVBD than that of the 1 m spacing. All of the differences reached significant level (Table 15). The site x spacing interaction was also very significant. For Camp 45, the group mean of the 3 m spacing was about 3 mm above

Table 14. ANOVA for the effects of spacing, group and family on average branch diameter of jack pine.

Source	df	MS	F Value	Pr > F
Site	1	34400.84	1883.12	<0.01
Spacing	2	20153.63	1716.42	<0.01
Site x spacing	2	264.75	25.27	<0.01
Group	7	19.37	0.75	0.63
Site x group	7	18.27	2.13	0.05
Spacing x group	14	11.74	1.12	0.35
Family (group)	72	25.68	2.45	<0.01
Site x family (group)	72	8.90	0.82	0.86
Spacing x family (group)	144	10.53	1.01	0.47
Pooled error	7255	10.48		
Total	7576			

Note: Group identities are in Table 5.

Table 15. The effect of spacing on average branch diameter of jack pine.

Spacing	Mean (mm)	SNK Grouping
3 x 3 m	15.42	a
2 x 2 m	13.78	b
1 x 1 m	9.83	c

Note: Means with the same letter are not significantly different ($\alpha = 0.05$).

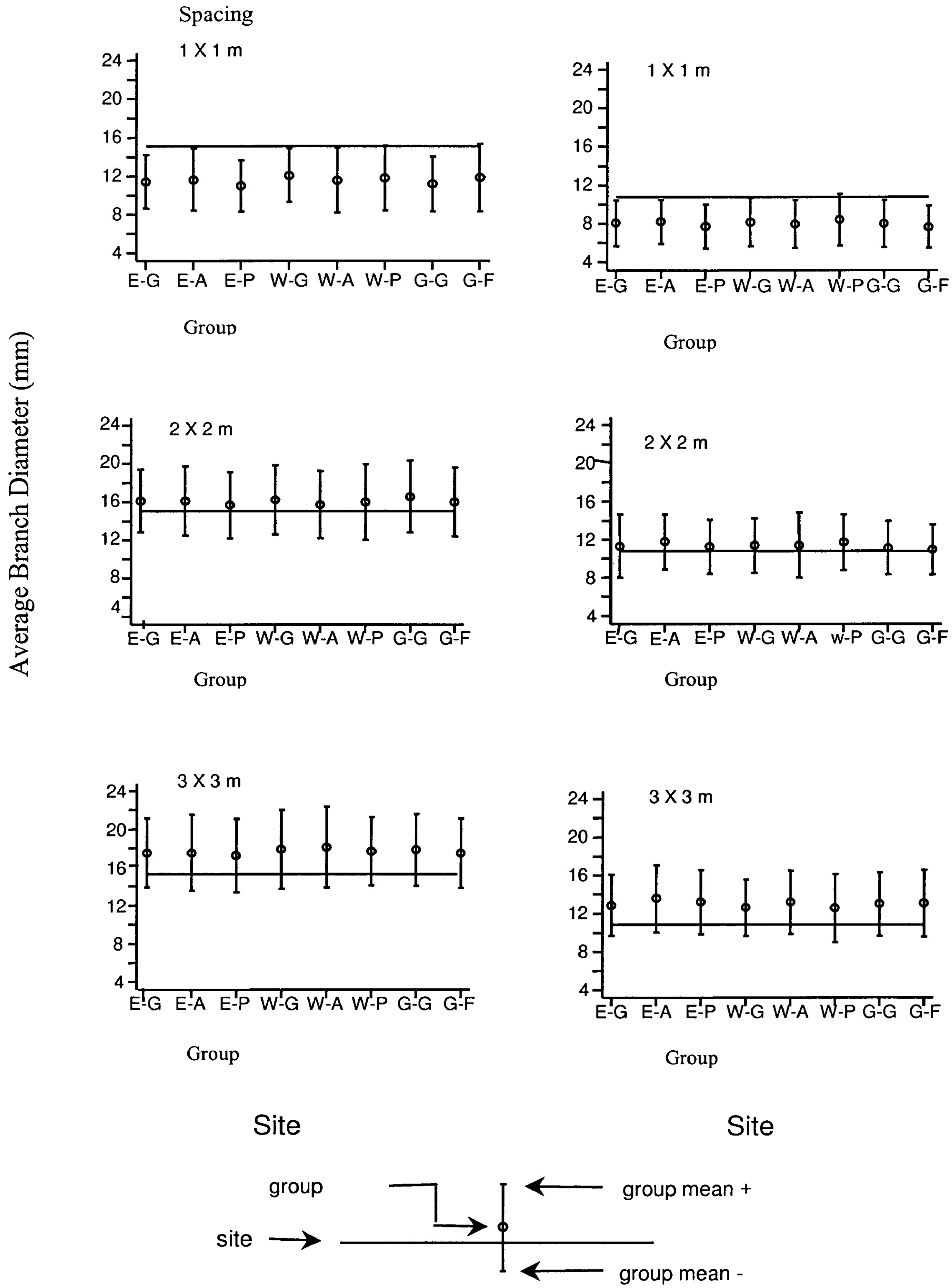

Fig. 6. Group and spacing effects on average branch diameter in jack pine (Group identities are in Table 4, sd = standard deviation).

the site mean; that of the 2 m spacing was 1mm above the site mean; and, the group mean of 1 m spacing was 4 mm below the site mean. For Camp 602, the group mean of the 3 m spacing was 2 mm above the site mean, that of the 2 m spacing was about 0.5 mm above the site mean, and that of the 1 m spacing was 2.5 mm below the site mean (Fig. 6).

From these results, it is evident that spacing strongly affects branch diameter growth of jack pine. Increasing spacing from 1 m to 2 m or 3 m will greatly increase branch diameter for 8 year-old jack pine, and the increase in spacing from 1 m to 2 m has much greater influence on branch diameter than from 2 m to 3 m. At the fertile site this effect is more pronounced than that at the poorer site.

This significant effect of spacing on branch diameter was consistent with a variety of studies in Scots pine (Abetz 1970, Kellomäki *et al.* 1992, Kellomäki & Väisänen 1986, Persson 1977, Salminen & Varmola 1993, Spellman & Nagel 1992, Varmola 1980a, b), other *Pinus* sp. (Bramble *et al.* 1949, Stevenson & Bartoo 1939, Ware & Stahelin 1948), and Norway spruce (Handler & Jakobsen 1986, Kramer *et al.* 1971, Merkel 1967). These studies all showed that branch diameter is reduced by closer spacing, and vice versa. For Scots pine, Salminen & Varmola (1990) reported that the influence of spacing was very modest, whereas Persson (1977) and Varmola (1980a) found it stronger. They found that the wider the spacing, the thicker the branches, and vice versa, even with the equal stem size. Varmola (1980a) found that stand density was the most important factor affecting the quality of Scots pine. He found that with increasing density, the stem form improved and branches became thinner.

The effect of genetic factors

There was no significant group effect on branch diameter growth (Table 14). The site x group interaction was close to significant. For both the fertile Camp 45 and the nutrient-poor Camp 602, the group means of branch diameter were very close to each other for each spacing. However, there were some differences between 3 m and the 1 m spacings for Camp 45 (Fig. 6). The difference among families in branch diameter growth was very significant (Table 14). Families from the west of Lake Nipigon usually had larger branch diameter than those from the east of the lake. However, some families from the west of the lake such as family number 66 and 72, were among those with the thinnest branch diameter (Appendix 3.5), even though the height and DBH growth of the two families were close to or over the family mean (Appendix 3.1 and 3.2). This result may indicate that branch diameter was independent from height and DBH, to some extent; and, it is possible to select families with high growth rate as well as very thin branch diameter. As branch diameter is among the traits that influence tree form quality the most, increased economic potential may be produced through multi-trait selection by improving tree form quality as well as maintaining the growth rate of plus trees at the same time.

For genetic variation, St. Clair (1994) found considerable variation for branch diameter adjusted for stem size in Douglas fir. As well, Krupski and Giertych (1996) found significant differences among provenances of Norway spruce for branch diameter and spike knots among provenances. However, Beaudoin (1996) found that the difference in branch diameter among provenances of jack pine was not significant. The same with radiata pine, Jayawickrama and Balocchi (1993) reported no significant differences in branch diameter, either at the population or subpopulation level.

Spacing x genetic interactions

There was no evident interaction effect on branch diameter between group and spacing, or between family and spacing.

Average Branch Angle (AVBA)

The effect of spacing

Spacing affected branch angle notably (Table 16). Trees grown at the 1 m spacing had the largest branch angle, with values 3.91 degrees greater than those grown at the 3 m spacing, and 3.03 degrees greater than those grown at the 2 m spacing. The 2 m spacing had values only 0.88 degrees greater than the 3 m spacing. All of the differences, including that between the two wider spacings, reached significance level (Table 17).

For both sites Camp 45 and 602, the 1 m spacing had the largest angle, with 6 out of 8 groups having about 3 degrees over the site mean (Fig. 7). In the 2 m spacing, approximately half of the groups had average site angle values, and the other half 1 to 2 degrees below the site means. For the 3 m spacing, 5 of the 8 groups in Camp 45 and all of the groups in Camp 602 had values 2 to 3 degrees below the site means of branch angle. These results indicate that an increase in spacing from 1 m to 2 m decreases branch angle significantly, and this reduction in branch angle was less when spacing increased from 2 to 3 m, at least during the juvenile stage. Branch angle is an important trait in determining the quality of the wood produced, and smaller branch angles tend to decrease wood quality (Bailey *et al.* 1974, Dietrich 1973, Zimmermann and Brown 1971). Thus, trees grown in 1 m spacing will produce trees with better wood quality. However, the

Table 16. ANOVA for the effects of spacing, group and family on average branch angle of jack pine.

Source	df	MS	F Value	Pr > F
Site	1	18401.12	67.73	<0.01
Spacing	2	9971.15	147.69	<0.01
Site x spacing	2	54.13	0.53	0.58
Group	7	535.63	1.12	0.38
Site x group	7	271.68	2.93	<0.01
Spacing x group	14	67.51	0.79	0.68
Family (group)	72	476.40	4.66	<0.01
Site x family (group)	72	92.85	0.91	0.69
Spacing x family (group)	144	85.23	0.83	0.93
Pooled error	7247	102.18		
Total	7568			

Note: Group identities are in Table 4.

Table 17. The effect of spacing on average branch angle of jack pine.

Spacing	Mean (degree)	SNK Grouping
1 x 1 m	64.06	a
2 x 2 m	61.03	b
3 x 3 m	60.15	c

Note: Means with the same letter are not significantly different (α = 0.05).

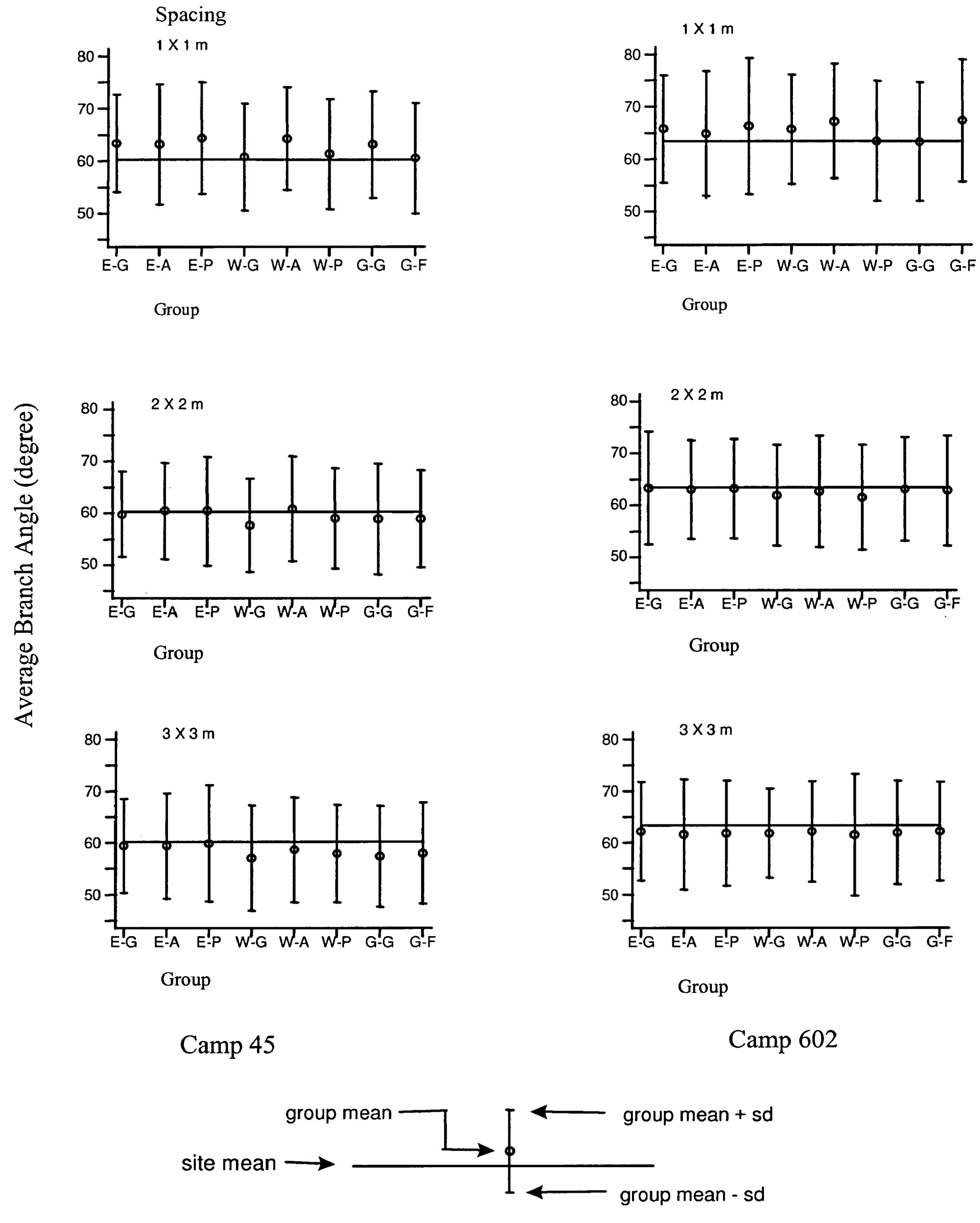

Fig. 7. Group and spacing effects on average branch angle in jack pine (Group identities are in Table 4, sd = standard deviation).

magnitude of this effect on wood quality needs further research. The site x spacing interaction was not significant (Table 16). Few studies had involved branch angle in spacing trials.

The effect of genetic factors

Group did not notably affect branch angle in jack pine (Table 16). However, the site x group interaction was significant (Table 16). For Camp 45, groups W-G, W-P and G-F had the lowest branch angle values at the 1 m spacing; while for Camp 602, E-A, W-P and G-G had the lowest values at the 1 m spacing. For Camp 602, the branch angle values of all groups were almost identical at the 3 m spacing, while the values for Camp 45 were much more variable (Fig. 7).

Family greatly affected branch angle in jack pine (Table 16). Some families with a fast growth rate also had very narrow branch angles, such as family number 33 (W-G), 37 (W-G), 62 (G-G), 67 (G-G) (Appendix 3.6). However, other families such as 63 (G-G) with superior height (Appendix 3.1) and DBH growth (Appendix 3.2), also had a wide branch angle (Appendix 3.6). This pattern indicates that branch angle is an independent trait (more details are in Genetic Correlation presented later), and it should be possible to select families with good tree growth rate in growth traits and wide branch angle at the same time.

Several studies, such as Krupski and Giertych (1996) in Norway spruce and Beaudoin (1996) in jack pine, reported significant provenance effect for branch angle. Magnussen and Yeatman (1987b) found that the opportunity for genetic improvement of branch angle was possible for four jack pine seed lots. With a range of more than 30 degrees in whole tree values of branch angle, jack pine exhibited extreme phenotypic deviants ranging from upright to flat branches (Benzie 1977, Polk 1972, Rudolph and Yeatman 1982). These findings are in contrast to Douglas fir, of which St. Clair (1994) found no genetic variation of branch angle. The significant difference of branch angles among families in jack pine indicates that genetic improvement on branch angle is possible, and has economic importance (Magnussen and Yeatman 1987a, b).

Spacing x genetic interactions

No spacing x group and spacing x family interactions were found on branch angle of 8 year-old jack pine (Table 16).

Relative Branch Diameter (RBD)

The effect of spacing

Spacing affected relative branch diameter (branch diameter/stem diameter at the same whorl) significantly (Table 18). The wider 3 m and 2 m spacings had significantly greater values than those of the closest 1 m spacing (0.07 and 0.06 respectively). The difference between the two wider spacings was also significant, even though this difference was relatively small (0.01) compared with the above two values (Table 19).

The site x spacing interaction was also very significant. For the 1 m spacing, four of the eight groups had values very close to the site mean of Camp 45, while for Camp 602 no one group had so close a value to the site mean. For the 2 m spacing, the mean value of RBD was almost identical to the site mean in Camp 45, while for Camp 602 the mean value was 0.03 over the site mean. For the 3 m spacing, the mean values of six of

Table 18. ANOVA for the effects of spacing, group and family on relative branch diameter of jack pine.

Source	df	MS	F Value	Pr > F
Site	1	8.49	514.96	<0.01
Spacing	2	3.62	184.83	<0.01
Site x spacing	2	0.26	13.42	<0.01
Group	7	0.04	1.05	0.42
Site x group	7	0.02	0.87	0.53
Spacing x group	14	0.02	1.06	0.39
Family (group)	72	0.04	2.00	<0.01
Site x family (group)	72	0.02	0.94	0.62
Spacing x family (group)	144	0.02	0.92	0.75
Pooled error	6986	0.02		
Total	7307			

Note: Group identities are in Table 4.

Table 19. The effect of spacing on relative branch diameter of jack pine.

Spacing	Mean	SNK Grouping
3 x 3 m	0.59	a
2 x 2 m	0.58	b
1 x 1 m	0.52	c

Note: Means with the same letter are not significantly different (α = 0.05).

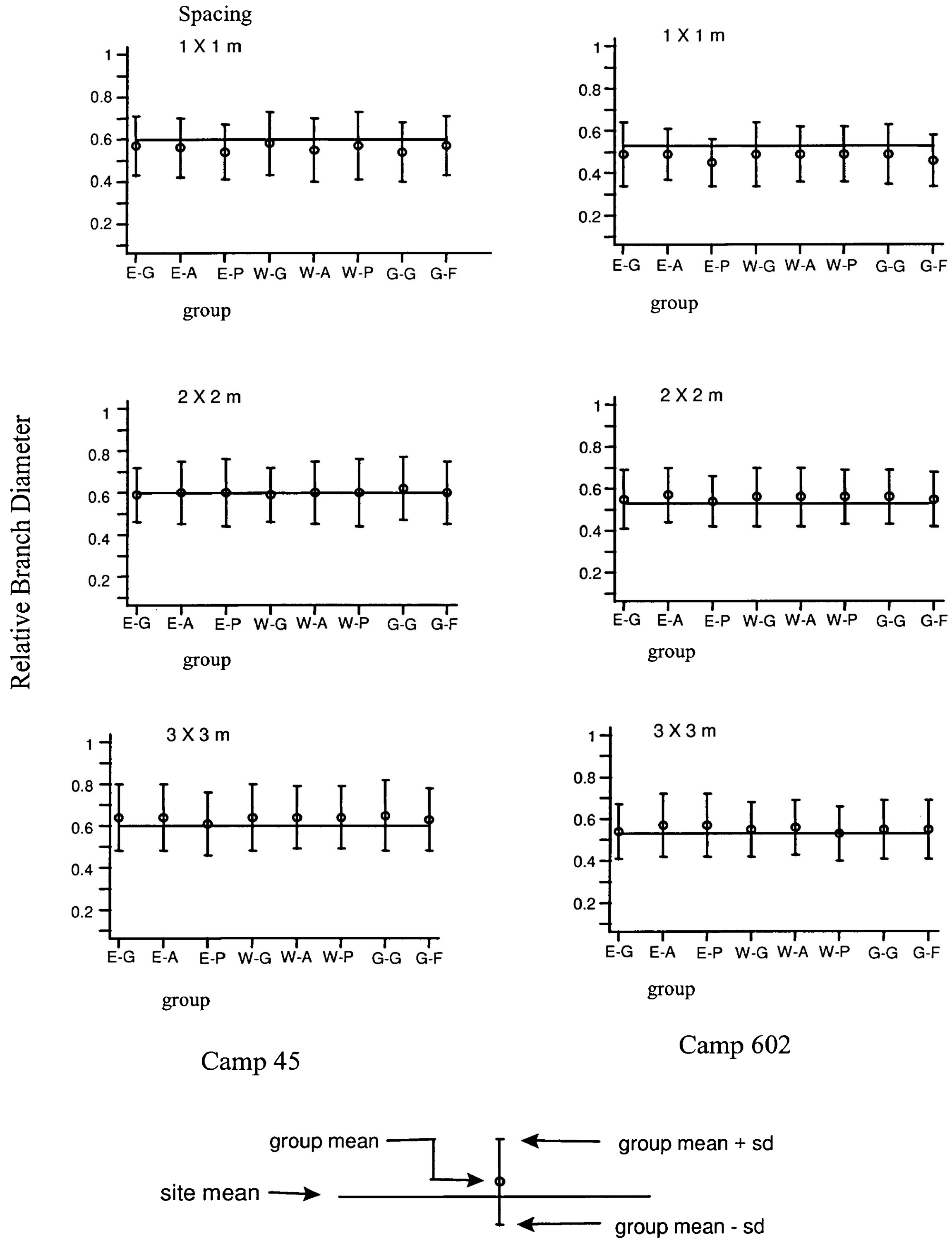

Fig. 8. Group and spacing effects on relative branch diameter in jack pine. (Group identities are in Table 4, sd = standard deviation).

the eight groups were 0.03 greater than the site mean in Camp 45, while only 3 of the eight groups had values close to 0.03 in Camp 602 (Fig. 8). At the fertile site this significant spacing effect was even greater.

These results indicate that at the closer spacing, the branches are relatively thinner, and vice versa. This is understandable considering that at the 1 m spacing the crown has been closed for some period of time, making the competition for light between branches very severe. In wide 2 m and the 3 m spacing, the crowns have not yet reached the state of closure at the time of measurement. The branches are still free to accept light, and thus have a good chance to grow thicker. Trees with low RBD values are more valuable, as branch diameter is the most important trait influencing wood quality of trees. By the view, increasing spacing will reduce the wood quality of trees, at least at the early growing stage. Few relevant studies have involved this trait with respect to spacing effect.

The effect of genetic factors

There was no significant difference among groups for relative branch diameter in jack pine (Table 18). As well, no group x site, and no family x site interactions existed either. However, the difference among families was very significant (Table 18). High growth rate and large branch diameter, did not necessarily correpond to its relative branch diameter. For example, family number 32, with the 21st fastest growth in height (Appendix 3.1), the 6th in DBH (Appendix 3.2), and the 11th thickest in branch diameter

(Appendix 3.5), ranked 77th out of the 80 families in relative branch diameter (Appendix 3.7). Plus trees with thick branches but very low relative branch diameter probably should be considered superior in tree form quality. Thus, it is possible to select trees with relatively thinner branches from families with superior growth rate. One of the prime goals of tree improvement of jack pine probably is selecting trees with relatively thinner branches and thicker stem diameter. Few studies have involved this trait.

Spacing x genetic interactions

No spacing x group and spacing x family interactions were found for relative branch diameter of 8 year-old jack pine (Table 18). These results are consistent with those of other traits. All of the traits demonstrate no spacing x group and spacing x family interactions in this study.

Relative Crown Width (RCW)

Relative crown width is the ratio of crown diameter to tree height (two times branch length/stem height), it is a measure of crown shape. The lower the value, the more narrower the crown will be.

The effect of spacing

Spacing significantly influenced the relative crown width of 8 year-old jack pine (Table 20). The differences between all three pairs of comparisons were very significant (Table 21). Trees in the widest 3 m spacing had a value of RCW 0.13 greater than those in the 1 m spacing, while in the 2 m spacing trees had a value of 0.08 greater than those in the closest 1 m spacing. The difference between the 2 m and 3 m spacing was only 0.05. Nonetheless, the smaller difference between the two wider spacings was significant. However, the site x spacing interaction was not significant (Table 20).

It is apparent that wider spacing causes a broader crown, and closer spacing a more narrower crown. This is because wider spacing provides more space for both above ground and beneath ground growth of jack pine with more sunlight, water and minerals in the soil. Conversely, closer spacing provides limited resources and energy for each tree, and competition is much more severe than for wider spacing.

The results of this study were supported by Bella (1986) and Bella and Francheschi (1974). These studies found that spacing had a great effect on crown development, and that crown width showed a gradual increase with spacing for jack pine, red pine and white spruce. In jack pine, the increase in crown width was more pronounced and quite dramatic for large trees (above 12 cm DBH) at the widest spacing. This is because jack pine has a tendency to develop irregular crowns in wide spacing. The crown becomes wide and bushy with multiple leaders and stems (trees with multiple leaders were encountered but excluded from this study as most of them were caused by weevil damage).

Table 20. ANOVA for the effects of spacing, group and family on relative crown width of jack pine.

Source	df	MS	F Value	Pr > F
Site	1	10.41	732.14	<0.01
Spacing	2	10.26	1050.65	<0.01
Site x spacing	2	0.03	2.31	0.10
Group	7	0.04	1.21	0.25
Site x group	7	0.01	1.11	0.36
Spacing x group	14	0.01	0.74	0.73
Family (group)	72	0.03	1.88	<0.01
Site x family (group)	72	0.01	0.93	0.64
Spacing x family (group)	144	0.01	0.95	0.64
Pooled error	7251	0.01		
Total	7572			

Note: Group identities are in Table 5.

Table 21. The effect of spacing on relative crown width of jack pine.

Spacing	Mean	SNK Grouping
3 x 3 m	0.57	a
2 x 2 m	0.52	b
1 x 1 m	0.44	c

Note: Means with the same letter are not significantly different ($\alpha = 0.05$).

The results from the 8 year-old jack pine plantation may suggest that the closest 1 m spacing is the optimum one out of all three spacings, while their results at age 20 suggested an optimum spacing of between 1.8 and 2.4 m for both jack pine and red pine in order to achieve rapid tree growth and high future timber yields (Bella 1986). It seems that the optimum spacing increases over time.

The effect of genetic factors

Group did not affect relative crown width notably (Table 20). Unlike group effect, family effect was very significant (Table 20). Although family number 63 was the number one in height (Appendix 3.1) and DBH growth (Appendix 3.2), its relative crown width was the number 79th of the 80 families (Appendix 3.8), indicating great potential for this family in not only growth rate but also slender crown shape. Considering also the very thin branch diameter discussed above, this family probably is one of the best in both growth rate and tree form quality. Families 72, 75 and 66 also had among the lowest values of relative crown width of the 80 families (Appendix 3.8), and the growth rate of these families was also very well above family mean (Appendix 3.1 and 3.2). Relative crown width probably has additional significance related to tree form quality as trees with slender crown shapes compete with each other less severely in the same spacing and produce more quality wood. As the difference of relative crown width among families was large, it is possible to select families with slender crown shapes. St. Clair (1994) also found considerable genetic variation existed for relative crown width in Douglas fir.

Spacing x genetic interactions

The interaction between spacing and group or between spacing and family was not significant for crown shape (Table 20). This indicates that no family or group demonstrated relative differences in relative crown width at the different spacings.

Stem Taper

The effect of spacing

In its simplest sense, taper is the ratio of height to diameter. In this study it is calculated as: taper = 1.40 x height/diameter of 30%, where diameter of 30% = (1-0.3) x diameter at 0.5 m/(1-0.5/height) (Forslund 1991). The greater this taper value, the more slender the stem form shape would be. Spacing had a significant effect on stem taper of jack pine (Table 22). The taper value of trees decreased 27.88 with the increase of spacing from 1 to 2 m, and was reduced only 10.87 as spacing increased further from 2 to 3 m (Table 23).

The site x spacing interaction was very significant. Although for both planting sites, taper values of trees in the 1 m spacing were well above the means of collective sites, and those in the 3 m spacing were clearly below the site means, the values were much closer to the site mean for Camp 602 than for Camp 45. It is especially the case for the 2 m spacing, four of the eight groups in Camp 602 had the same or close values to the site mean, while for Camp 45, values of all the groups were below the site mean (Fig. 9).

It is clear that increasing spacing will reduce taper values; the wider the spacing, the lower the stem taper; and vice versa. Some studies used a simple ratio of height to DBH as taper. Reukema and Smith (1987) found that the H-to-D ratio at age 25 for Douglas fir was strongly influenced by spacing. The closer the spacing, the bigger the ratio. This ratio declined with increasing age.

Stem taper values that are either too low or too high are not acceptable for tree quality or resistance of tree stems to breakage by wind or snow. Suitable stem tapers are essential for the manufacture of some specialty products, such as power poles (American National Standards Institute 1979). Excessive taper also reduces the amount of recoverable lumber in a log (Ballard and Long 1988). Trees that are too slender are more likely to be broken. Europeans suggest that the H-to-D ratio of the 100 largest trees per ha should be kept about 80 to 100 (van Tuyll and Kramer 1981).

The effect of genetic factors

Both group and family affected the stem taper of jack pine significantly (Table 22). Results of multiple comparisons showed those groups G-G (good in growth), G-F (good in form) and those from the west of Lake Nipigon had higher taper values than those from the east of the lake (Table 23). As the two plus tree groups were also from west of the lake, it is evident that the provenance effect exists for stem taper. Trees from the west of the lake have higher taper values than trees from the east of the lake in the two

Table 22. ANOVA for the effects of spacing, group and family on taper of jack pine

Source	df	MS	F Value	Pr > F
Site	1	629924.23	1570.46	<0.01
Spacing	2	974247.01	3923.92	<0.01
Site x spacing	2	11057.33	49.83	<0.01
Group	7	3267.07	4.26	<0.01
Site x group	7	401.11	1.37	0.23
Spacing x group	14	248.28	1.09	0.37
Family (group)	72	767.70	3.46	<0.01
Site x family (group)	72	294.01	1.33	0.05
Spacing x family (group)	144	227.96	1.03	0.39
Pooled error	7278	221.90		
Total	7599			

Note: Group identities are in Table 4.

Table 23. The effect of spacing and group on taper of jack pine.

Source		Mean	SNK Grouping
Spacing	1 x 1 m	127.72	a
	2 x 2 m	99.84	b
	3 x 3 m	89.03	c
Group	G-G	107.93	a
	W-A	107.23	ab
	G-F	106.42	abc
	W-P	106.29	abc
	W-G	105.49	bc
	E-A	104.75	cd
	E-P	103.67	d
	E-G	102.24	e

Note: Means with the same letter are not significantly different ($\alpha = 0.05$) for each source.

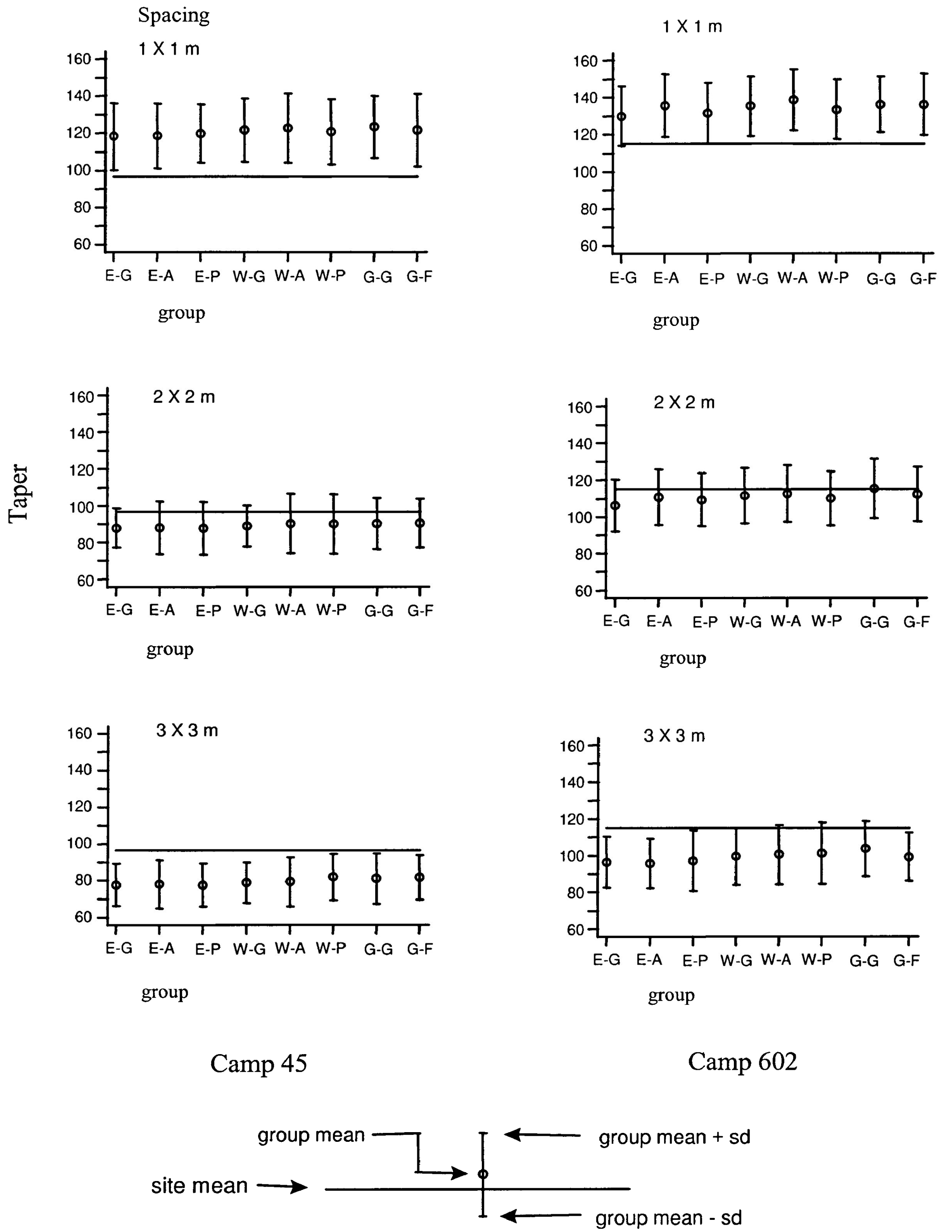

Fig. 9. Group and spacing effects on taper in jack pine (Group identities in Table 4, sd = standard deviation).

planting sites, both of which are located the west of Lake Nipigon. No evidence showed that trees from good quality stands (W-G and E-G) had larger (or better) taper values. As site x group interaction was not significant, this provenance effect was not affected by the quality of site. However, at the family level, the result was different. Both family and the site x family interaction was significant (Table 22). Family number 67 was the number one in taper value (Appendix 3.9), while its height was the number 7th (Appendix 3.1) and the DBH the 27th (Appendix 3.2) in the 80 families. The family number 63, which had the number one height and DBH growth, was the 28th in taper value (Appendix 3.9). This indicated that some families had higher stem tapers than others, and it is possible to select families with suitable stem taper as well as good growth rate. The significant site x family interaction was not presented in detail in this study as this trait was not the focus of this study. Few studies have involved this trait.

Spacing x genetic interactions

The interactions between spacing and group and between spacing and family were not significant (Table 22). This result was consistent with those of other traits used in this study. Generally, no trait has shown any spacing x group and spacing x family interaction, and this is against our hypothesis that these interactions exist. Few studies have involved these interactions.

Number of Crooks

Number of crooks was not normally distributed probably because the majority of the trees did not have any crooks along their stems. Spacing seemed to affect the number of crooks in the stem mainly at Camp 45 where the 3 m spacing produced noticeably more crooks (Fig.10). However, Magnussen and Yeatman (1987a) found that the proportion of trees with crooked stems in the 2 m spacing was relatively high. Several other studies have also found that at wide spacing, jack pine had a high frequency of stem deformities during juvenile stage (Bella and De Franceschi 1980, Janas and Brand 1988). Generally, stem form in pines is poor at wide spacings during the juvenile stage (Evert 1971, Magnussen and Yeatman 1987a, Varmola 1980a). It is possible that number of crooks was not the best trait to represent tree form straightness, a different trait such as the degree of stem straightness or sweep probably would make a difference.

Genetic factors played an important role in number of crooks in 8 year-old jack pine (Fig.10). For both sites and for all of the spacings, it was clear that group G-F (good in form) had the least number of crooks, and E-A (east average) had the most. Generally, for the groups from east of Lake Nipigon, the values of number of crooks showed low, high and low for groups E-G, E-A and E-P, respectively; while for the groups from west of the lake, W-G (west good) had fewer crooks than the other two groups. There seemed to be no evident difference in number of crooks between groups from east and west of the lake. In other words, there was no provenance effect observed for number of crooks.

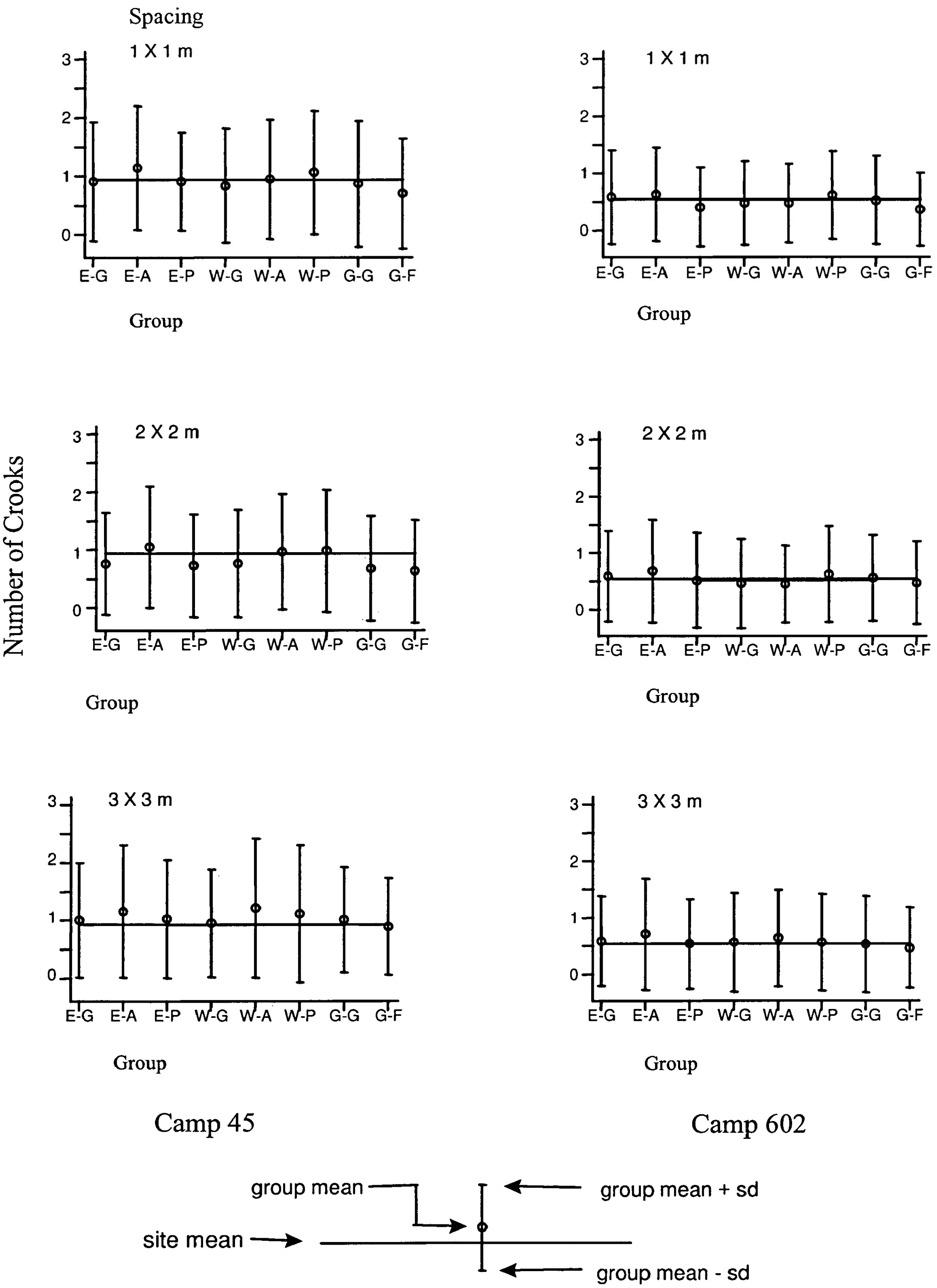

Fig.10. Group and spacing effects on number of crooks in jack pine (Group identities are in Table 4, sd = standard deviation).

HERITABILITY

Heritabilities of Different Spacings and Site Quality

The individual and family heritability values of nine traits were calculated for each spacing at each site in this study (Table 24 and Fig.11). The traits were height, taper, average branch angle (avba), diameter at breast height (DBH), average branch length (avbl), number of dominant branches (dom), relative branch diameter (rbd), average branch diameter (avbd), and relative crown width (rcw).

For height at Camp 45, the widest 3 m spacing had the highest values of 0.22 and 0.46 for individual and family heritabilities (Fig.11a). The closer spacings 2 m and 1 m had values of 0.14 - 0.15 for individual, and 0.38 for family heritabilities (Fig. 11b and c). At Camp 602, the widest and closest spacings had higher values of 0.15 for individual and 0.36-0.37 for family heritabilities (Fig.11d f). The intermediate 2 m spacing had lower values of 0.06 for individual and 0.18 for family heritabilities (Fig.11e).

For diameter at breast height at Camp 45, the widest spacing had much lower heritabilities than those of closer spacings. The 3 m spacing had estimates of 0.04 and 0.14 for individual and family heritabilities (Fig.11a), while the 2 m and the 1 m spacings had values of 0.20-0.22 for individual and 0.43-0.48 for family heritabilities (Fig.11b and c). At Camp 602, the closer spacings also had higher values. The 3 m spacing had values of 0.01 and 0.05; the 2 m spacing 0.06 and 0.19; and, the 1 m spacing 0.09 and 0.26 for individual and family estimates, respectively (Fig.11d, e and f).

For number of dominant branches at Camp 45, the widest 3 m spacing had the lowest values of 0 for both individual and family heritabilities (Fig.11a), the closer 2 m and 1 m spacings had values of 0.11 for individual and 0.29-0.30 for family heritabilities (Fig.11b and c). At Camp 602, the 2 m spacing had zero for individual and family heritabilities (Fig.11e), and the widest 3 m and closest 1 m spacings had values of 0.05-0.08 for individual and 0.15-0.25 for family heritabilities (Fig.11d and f).

For average branch length at Camp 45, the 1 m and 3 m spacings had lower values of 0.06-0.08 for individual and 0.18-0.24 for families (Fig.11a and c). The 2 m spacing had higher values of 0.15 and 0.40 for individual and family heritabilities (Fig.11b). At Camp 602, the closest 1 m spacing had the highest values of 0.06 and 0.19 for individual and family heritabilities, respectively (Fig.11f). The wider spacings 3 m and 2 m had very low values of 0.01 for individual and 0.03 for family heritabilities (Fig.11d and e).

For average branch diameter at Camp 45, the intermediate 2 m spacing had the highest values of 0.09 and 0.28 for individual and family heritabilities, respectively (Fig.11a). The widest and closest 3 m and 1 m spacings had values of 0.04-0.05 for individual and 0.13-0.17 for family heritabilities (Fig.11a and c). At Camp 602, only the widest 3 m spacing had low values of 0.03 for individual and 0.11 for family heritabilities (Fig.11d); the values for the other two spacings were all 0 (Fig.11e and f).

Table 24. Individual and family heritabilities (h_i^2 and h_f^2) for nine traits in three spacing and two sites of jack pine.

		Camp 45			Camp 602				
Var	h^2	3 m	2 m	1 m	3 m	2 m	1 m	Mean	SD
Height	h_i^2	0.22	0.14	0.15	0.15	0.06	0.15	0.15	0.05
	h_f^2	0.46	0.38	0.38	0.36	0.18	0.37	0.36	0.09
DBH	h_i^2	0.04	0.22	0.20	0.01	0.06	0.09	0.10	0.09
	h_f^2	0.14	0.48	0.43	0.05	0.19	0.26	0.26	0.17
DOM	h_i^2	0.00	0.11	0.11	0.05	0.00	0.08	0.06	0.05
	h_f^2	0.00	0.29	0.30	0.15	0.00	0.25	0.17	0.14
AVBL	h_i^2	0.08	0.15	0.06	0.01	0.01	0.06	0.06	0.05
	h_f^2	0.24	0.40	0.18	0.03	0.03	0.19	0.18	0.14
AVBD	h_i^2	0.04	0.09	0.05	0.03	0.00	0.00	0.04	0.03
	h_f^2	0.13	0.28	0.17	0.11	0.00	0.00	0.12	0.11
AVBA	h_i^2	0.16	0.25	0.15	0.05	0.15	0.08	0.14	0.07
	h_f^2	0.40	0.53	0.38	0.15	0.37	0.24	0.35	0.13
RBD	h_i^2	0.06	0.06	0.00	0.07	0.04	0.02	0.04	0.03
	h_f^2	0.17	0.21	0.00	0.21	0.13	0.08	0.13	0.08
RCW	h_i^2	0.04	0.09	0.00	0.00	0.00	0.01	0.02	0.04
	h_f^2	0.11	0.28	0.00	0.00	0.00	0.03	0.07	0.11
Taper	h_i^2	0.18	0.21	0.08	0.19	0.12	0.10	0.15	0.05
	h_f^2	0.43	0.48	0.25	0.41	0.32	0.27	0.36	0.09

Note: SD, standard deviation. DBH = diameter at breast height, DOM = number of dominant branches, AVBL = average branch length, AVBD = average branch diameter, AVBA = average branch angle, RBD = relative branch diameter, RCW = relative crown width.

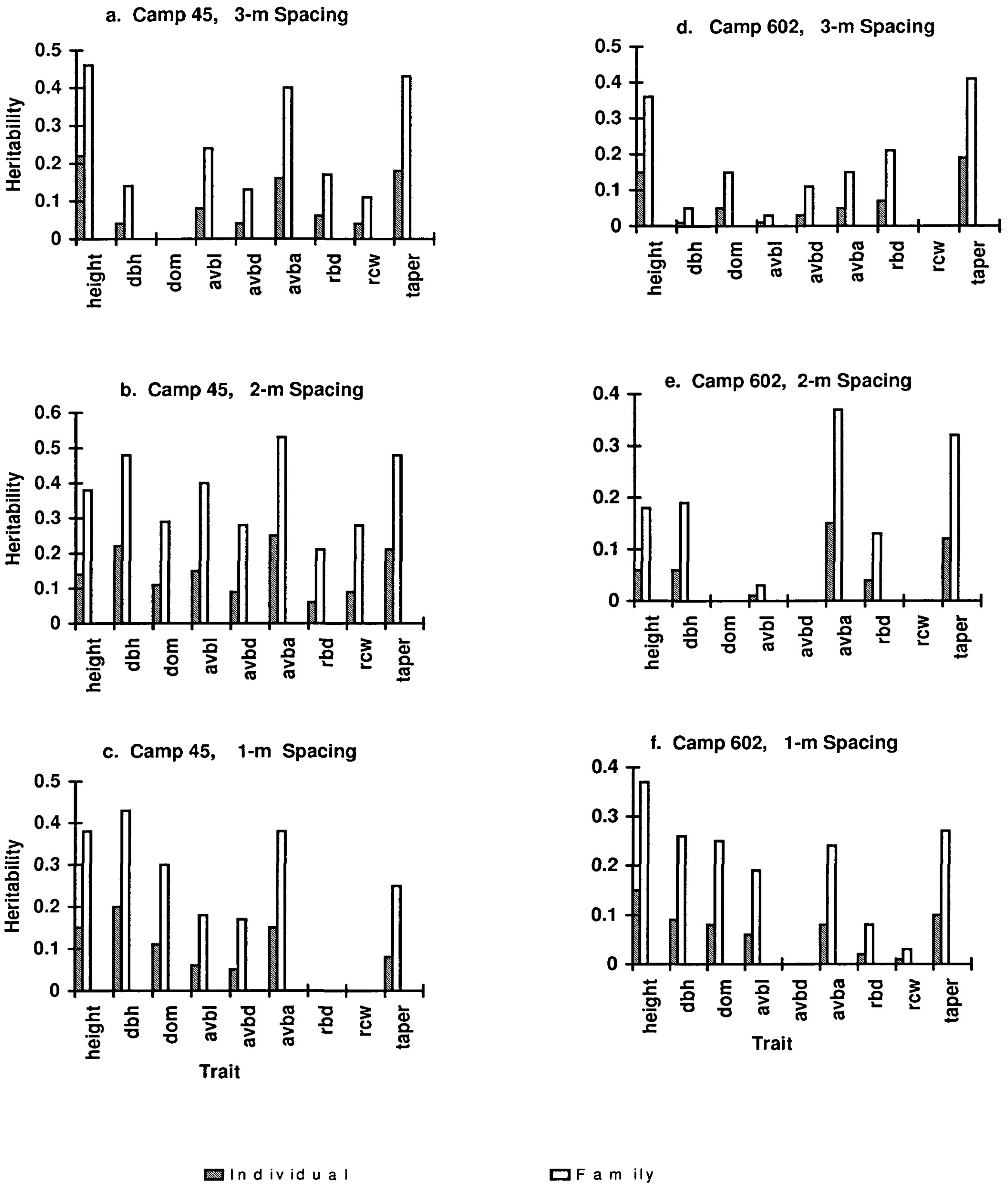

Fig. 11 Individual and family heritabilities for nine traits (terms are identified in Table 24), three spacings and two planting sites of jack pine.

For average branch angle at Camp 45, the closest 1 m and widest 3 m spacings had the lowest values of 0.15-0.16 for individual and 0.38-0.40 for family heritabilities (Fig.11a and c). The intermediate 2 m spacing had the highest value of 0.25 for individual and 0.53 for family heritabilities (Fig.11b). The pattern was similar at Camp 602, with the 1 m and the 3 m spacings having the lowest values of 0.05 and 0.08 for individual, and 0.15 and 0.24 for family heritabilities (Fig.11d and f). The 2 m spacing exhibited the highest heritabilies with values of 0.15 for individual and 0.37 for family heritabilities (Fig.11e).

For relative branch diameter at Camp 45, the closest 1 m spacing had the lowest values of 0 (Fig.11c). The other spacings had the same values of 0.06 for individual and 0.17-0.21 for family heritabilities (Fig.11a and b). At Camp 602, the closer spacing had lower heritabilities. The 3 m spacing had values of 0.07 and 0.21 (Fig.11d); the 2 m had 0.04 and 0.13 (Fig.11e); and the 1 m had 0.02 and 0.08 for individual and family heritabilities, respectively (Fig.11f).

For relative crown width at Camp 45, the individual and family heritability values were 0.04 and 0.11 for the 3 m spacing (Fig.11a), 0.09 and 0.28 for the 2 m spacing (Fig.11b), and 0 for the 1 m spacing, respectively (Fig.11c). At Camp 602, only the 1 m spacing had measurable values of 0.01 and 0.03 for individual and family heritabilities, respectively (Fig.11f); the other two spacings had values of 0 for individual and family heritabilities (Fig.11d and e).

For taper at Camp 45, the wider 3 m and 2 m spacings had values of 0.18 and 0.21 for individual heritabilities, and 0.43 and 0.48 for family heritabilities, respectively (Fig.11a and b). The closest 1 m spacing had the lowest values of 0.08 and 0.25 for individual and family heritabilities, respectively (Fig.11c). At Camp 602, the wider the spacing, the higher the heritabilities of stem taper, and vice versa. For the 3 m, 2 m and 1 m spacings, the individual heritabilities were 0.19, 0.12 and 0.10 respectively, and the family estimates were 0.41, 0.32 and 0.27, respectively (Fig.11d, e and f).

The Effect of Site on Heritabilities

Heritabilities were estimated for each site by averaging the 3 spacing values (Table 25). Considering all the nine traits used in this analysis, Camp 45, the moist and fertile site had higher heritability values than Camp 602, the drier, coarse-textured site (Table 25). This difference between sites reflects the results of previously observed ANOVAs.

For taper, rcw (relative crown width), dom (number of dominant branches), height and avbd (average branch diameter), the increases in heritability values from the poor to rich sites were moderate. They were 0.13 to 0.16 for taper, 0 to 0.04 for rcw, 0.04 to 0.07 for dom, 0.12 to 0.17 for height, and 0.01 to 0.06 for avbd, for the individual heritability values (Table 25). However, DBH, and avbl (average branch length) exhibited larger increases, such as 0.02 to 0.10 for avbl, and 0.05 to 0.15 for DBH. The only exception found among the nine traits was rbd (relative branch diameter), which decreased slightly from 0.05 to 0.04, from poor Camp 602 to fertile Camp 45 (Table 25).

Trees grown in the fertile site had many more resources (water and nutrition) to utilize in expressing the genetic information, this is probably the reason why they had higher heritablity values. On the other hand, trees grown in the poor site could only obtain limited water and nutrition, which restrained the expression of genetic inheritance.

The Overall Heritabilities

The overall individual and family heritabilities were presented as means in Table 24 and Fig.12. In this study, the individual heritability for height was 0.15 and family heritability was 0.36. This was the highest value of heritability of all the nine traits used in this study. This value of individual heritability was very close to the values found in relevant studies of jack pine, such as Morris (1992) of 0.17, Adams and Morgenstern (1991) of 0.17, and Magnussen and Yeatman (1990) of 0.18. However, Park *et al.* (1989) found a value of 0.26 for height of jack pine progenies, and Haapanen and Pöykkö (1993) estimated a value of 0.60 for the stem height of Scots pine (also the highest in that study). The family heritability of height found in this result was lower than that of 0.74 in Adams and Morgenstern (1991) for jack pine, and 0.61 in Kariuki (1998) for jelecote pine. Many factors such as species, provenances, size of populations and the site quality of planting trials might contribute to these differences.

The individual and family heritabilities for stem taper were 0.15 and 0.36 respectively (Table 24 and Fig12). These values were the same as the values for height, and were also the highest of all nine traits used in this study. Few studies have included this trait in evaluating heritability values up to date. Nevertheless, it is apparent that improving stem taper in jack pine is feasible through selection due to its relatively high heritability.

Table 25. The site means of individual and family heritabilities (h_i^2 and h_f^2, respectively) in jack pine.

Trait	Camp 45		Camp 602	
	h_i^2	h_f^2	h_i^2	h_f^2
Height	0.17	0.41	0.12	0.31
DHB	0.15	0.35	0.05	0.17
DOM	0.07	0.20	0.04	0.13
AVBL	0.10	0.27	0.02	0.08
AVBD	0.06	0.19	0.01	0.04
AVBA	0.19	0.44	0.09	0.26
RBD	0.04	0.13	0.05	0.14
RCW	0.04	0.13	0.00	0.01
Taper	0.16	0.39	0.13	0.33

Note: Traits are identified in Table 24.

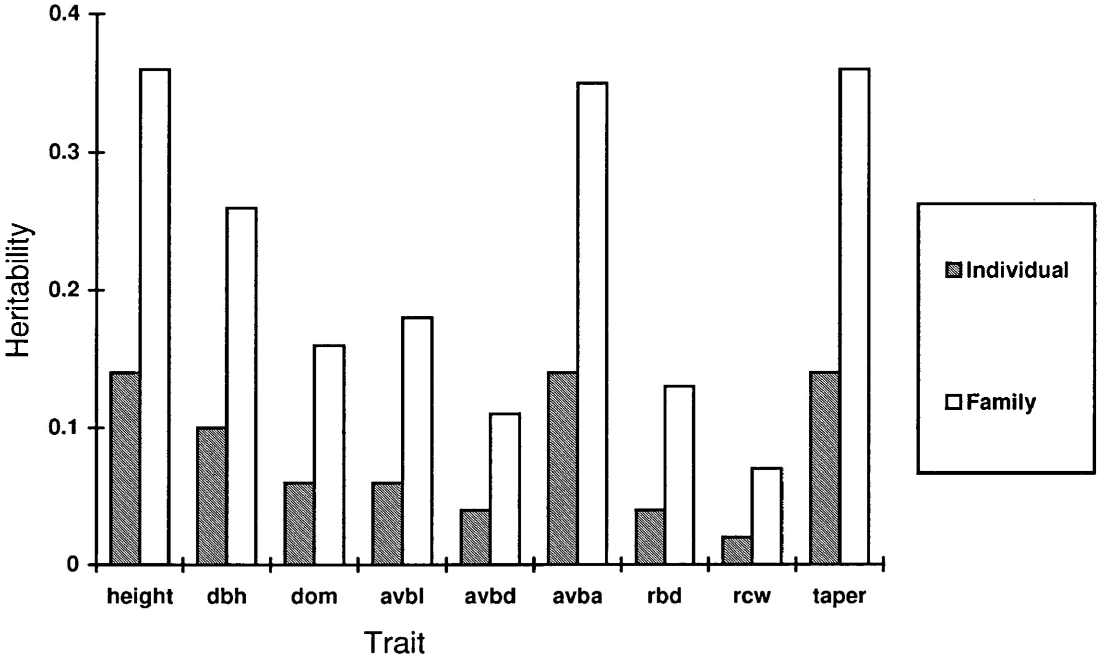

Fig. 12 The overall individual and family heritabilities of nine traits (terms are identified in Table 24.) in jack pine.

In this study, the overall individual and family heritability values for average branch angle were also relatively high, and very close to the values for height and taper (Table 24 and Fig12). Values of 0.14 for individual and 0.35 for family heritabilities were found. Earlier studies also found that branch angle is a strongly heritable trait (Adams and Morgenstern 1991, Bailey *et al.* 1974, Yanchuk 1986). Although the value of heritability in this study was lower than many other studies, this study is supported by findings in other studies that branch angle is a highly heritable trait. A number of studies examing this trait have shown that its value ranged from 0.06 to 0.73, with an average of 0.40 for individual heritability (Table 26). Branch angle was found to be the most strongly heritable trait, with individual and family heritability values of 0.42 and 0.89 respectively for jack pine (Adams and Morgenstern 1991). In addition, an estimate of 0.24 found by Haapanen and Pöykkö (1993) was not as high a value as compared to other traits used in that study.

The heritability values for diameter at breast height were somewhat lower with values of 0.10 for individual and 0.26 for family heritabilities (Table 24 and Fig. 12). For the nine variables used in this study, these values were moderately high. These values were also consistent with earlier studies. Both Magnussen and Yeatman (1990) and Morris (1992) estimated values of 0.10 for the individual heritability of jack pine, while Park *et al.* (1989) found a higher value of 0.14 for this trait. Although Haapanen and Pöykkö (1993) had a much higher value of 0.21, this value of 0.21 was very low compared to other traits determined in that study.

Table 26. Individual heritability estimates for branch angle from various studies.

Species	h^2	Reference
Douglas fir	0.49	Birot and Christophe 1983
Douglas fir	0.73	King et al. 1992
Douglas fir	0.06	St. Clair 1994
jack pine	0.42	Adams and Morgenstern 1991
Norway spruce	0.44	Merrill and Mohn 1985
Scots pine	0.22	Velling and Tigerstedt 1984
Scots pine	0.24	Haapanen and Pöykkö 1993

Values of heritability for average branch length were lower than those variables mentioned above. Values of 0.06 for individual and 0.18 for family heritabilities were found (Table 24 and Fig. 12). This result was low compared to the other traits in this study. This trait together with avbd (average branch diameter) was used in analyzing branch size, which is a very important trait in determining tree form quality. Nevertheless, few studies used average branch length as a variable for heritability analysis.

The individual and family heritabilities for number of dominant branches were 0.06 and 0.17, respectively (Table 24 and Fig. 12). These values were low to moderate compared to other traits used in this study. These values were equal to the values of average branch length, and slightly higher than the values of average branch diameter. However, the heritability estimates for these three branch traits were roughly equal, and they were all low, compared to the values of height (0.15, individual, the same hereafter), taper (0.15), branch angle (0.14) and diameter at breast height (0.10). A variety of studies have included this trait, and the results have showed that number of branches has a low to moderate heritability, ranging from 0.01 to 0.19, and averaging 0.10 (Table 27). Our study is in agreement with these findings. This indicates that number of dominant branches may be regarded as a possible trait for multi-trait selection, and it might be possible to select trees with more or fewer dominant branches.

For average branch diameter, the values for the individual and family heritabilities were 0.04 and 0.12, respectively (Table 24 and Fig. 12). These values were even lower than those of branch length. The values for this trait were very low compared to other traits in this study, actually the second lowest value in the nine traits. In Scots pine, branch diameter had an individual heritability of 0.21 (Haapanen and Pöykkö 1993). Compared to the heritability values in this study, the value of 0.21 in Haapanen and Pöykkö (1993) was very high. However, this value was the second lowest value among the 16 traits used in that study. Thus, it seems that both studies agree that branch diameter had a low heritability, compared to the high heritability values in taper, height, branch angle, etc. This indicates that multi-trait selection may not be an effective way in improving branch size because of the low heritability for this trait.

For relative branch diameter, values of 0.04 and 0.13 for individual and family heritabilities were estimated. These values, the same as those of branch diameter, also were very low estimates for heritability in the nine traits. This result was in agreement with that in Scots pine (Haapanen and Pöykkö 1993). Although the value of individual

Table 27. Individual heritability estimates for number of branches.

Species	h^2	Reference
Douglas fir	0.19	King et al. 1992
Douglas fir	0.09	St. Clair 1994
jack pine	0.10	Park et al. 1989
jack pine	0.10	Morris et al. 1992
Norway spruce	0.01	Merrill and Mohn 1985
Scots pine	0.09	Velling and Tigerstedt 1984

heritability was 0.24 for Scots pine, the value was very low compared to other 15 traits used in that study (Haapanen and Pöykkö 1993). Some other earlier studies found relatively high individual heritability for relative branch diameter as well, such as 0.34 in St. Clair (1994) for Douglas fir, 0.26 in King *et al.* (1992) for Douglas fir, and 0.17 in Velling and Tigerstedt (1984) for Scots pine. This study were not consistent with the results from those studies.

For relative crown width, the individual and family heritabilities were 0.02 and 0.07 respectively, the lowest of all nine traits. This result was not consistent with earlier studies. Velling and Tigerstedt (1984) estimated a value of 0.31 for crown width relative to stem height in Scots pine. Also for Scots pine, Haapanen and Pöykkö (1993) reported a value of 0.43 for the individual heritability of relative crown width. For Douglas fir, the individual heritabilities of relative crown width, measured both as crown width per unit crown length and crown width adjusted for stem diameter below a sample whorl, were 0.32 and 0.25, respectively (St.Clair 1994).

In this study, the crown diameter was drawn from average branch length. As a result, this may not be able to reflect the actual crown diameter due to the high variability in branch length of jack pine. As well, the branch length of the 5th growth year (95 whorl) were used for crown diameter calculation, possibly underestimating the actual value of crown diameters, because branches in whorl 94 and 93 were much longer than that of whorl 95.

For many commercial species, the heritabilities of important traits are reasonably high (Morgenstern *et al.* 1975). Adams and Morgenstern (1991) found that for crown quality and relative branch diameter in jack pine, the individual heritabilities were 0.11 and 0.12 respectively, and the family heritability values were 0.65 and 0.68 respectively. Compared with the heritabilities of other traits, these values are low in jack pine. This is consistent with results from other species, such as Virginia pine (Bailey *et al.* 1974), lodgepole pine (Yanchuk 1986), and loblolly pine (Zobel and Talbert 1984). In many species, stem- and branch-form characteristics are strongly heritable and more easily manipulated via improvement programs than are height and volume growth rates (Wright 1976, Zobel and Talbert 1984).

Site quality had a very pronounced effect on heritabilities: the poorer the site quality, the lower the heritability values. This may explain to some extent why different studies have varied values of heritability, even with the same species, and same provenances.

GENETIC CORRELATION

The Effects of Site and Spacing

The genetic correlation values between traits for each spacing at each site for 8-year-old jack pine are shown in Table 28. Due to the zero variance components for some variables, many genetic correlation values could not be calculated; this was especially the case for Camp 602, where a lot of values were missing for both 1 m and the 2 m spacings. Camp 45 had only a few missing values at the closest 1 m spacing (Table 28). This result may indicate that site affects genetic correlation between traits. The nutrient-poor Camp 602 provided fewer resources for the growth of jack pine trees, and this shortfall may have restricted the full expression of genetic variance between families.

Genetic correlation values for different spacings did not show consistent results regarding spacing effect (Table 28). For Camp 45, the closer spacing had larger values than did the wider spacing; while for Camp 602, wider spacings had larger values than did the closer spacing. There might be no spacing effect on genetic correlation values. Due to close to zero variance components for some traits, the genetic correlation values of these traits might be greatly exagerated such as DOM-RBD.

Table 28. Genetic correlation between growth and tree form traits for each spacing at each site for jack pine.

Genetic	Camp 45			Camp 602		
Correlation	1 m	2 m	3 m	1 m	2 m	3 m
Height-DBH	0.86	0.70	1.01	0.87	0.80	1.12
Height-DOM	-0.21	-0.05	0.06	0.37		-0.46
Height-AVBL	0.83	0.61	0.40		1.05	1.67
Height-AVBD	0.81	0.49	0.14			0.19
Height-AVBA	-0.21	-0.45	0.02	0.42	-0.24	-0.30
Height-RBD		0.43	-0.11	-0.29	0.26	0.13
Height-RCW	-0.46	-0.32		-0.16		
Height-taper	0.50	0.59	0.71	0.71	0.42	0.92
DBH-DOM	0.00	-0.18	0.51	0.21		-0.65
DBH-AVBL	0.70	0.40	0.24		0.90	1.34
DBH-AVBD	0.78	0.53	0.19			-0.09
DBH-AVBA	-0.46	-0.39	0.28	0.62	-0.39	0.00
DBH-RBD		0.31	-0.34	-0.69	-0.11	-0.07
DBH-RCW	-0.43	-0.26	0.12	-0.41		
DBH-taper	-0.01	-0.10	0.66	0.29	-0.19	1.08

To be continued.

Table 28 (Cont'd): Genetic correlation between growth and tree form traits for each spacing at each site for jack pine.

Genetic	Camp 45			Camp 602		
Correlation	1 m	2 m	3 m	1 m	2 m	3 m
DOM-AVBL	-0.16	-0.33	-0.22	-0.08	-	0.39
DOM-AVBD	-0.32	-0.35	0.06			0.74
DOM-AVBA	0.18	0.19	0.19	0.08		0.39
DOM-RBD		-0.43	-0.78	0.22		1.13
DOM-RCW	0.06	-0.32	-0.24	-0.68		
DOM-taper	-0.28	-0.02	-0.52	0.57		-0.47
AVBL-AVBD	0.87	0.80	0.78			0.05
AVBL-AVBA	-0.79	-0.51	-0.16		-0.44	-0.79
AVBL-RCW	0.23	0.49	0.44			
AVBL-RBD		0.54	0.53		0.03	
AVBL-taper	0.49	0.36	0.35		0.81	
AVBD-AVBA	-0.60	-0.33	-0.16			1.03
AVBD-RBD		0.90	0.67			0.69
AVBD-RCW	-0.19	0.37	0.60			
AVBD-taper	0.31	0.05	-0.06			0.44
AVBA-RBD		-0.33	-0.36	-0.30	0.28	0.77
AVBA-RCW	-0.87	-0.10	-0.02	-0.38		
AVBA-taper	0.35	-0.11	0.18	-0.11	0.16	-0.48
RBD-RCW		0.33	0.12			0.46
RCW-taper	-0.03	-0.36	-0.43	-	-	-
Absolute mean	0.43	0.37	0.34	0.39	0.43	0.61

Note: Traits are identified in Table 24.

The Overall Genetic Correlations

The overall genetic correlations between traits of jack pine were generated as the mean of up to six values listed in Table 28 (Table 29). In this study genetic correlation was the focus; Pearson correlation coefficients were also calculated for comparison (correlation means genetic correlation hereafter).

Height had strong correlation with average branch length (0.91), DBH (0.89) and relatively high correlation with taper (0.64); moderate with average branch diameter (0.41) and relative crown width (-0.31); weakly negative with average branch angle (-0.13); little correlation with number of dominant branches (-0.06) and relative branch diameter (0.08) (Table 29). This indicated that an increase in height growth will increase branch length (0.91) and probably increase branch diameter (0.41), but will not increase relative branch diameter (0.08) and relative crown width (-0.31). Haapanen and Pöykkö (1993) supported this finding in Scots pine; they found that stem height had a weak Correlation with branch diameter (0.26), negative correlation with relative branch diameter (-0.18), and negative correlation with relative crown width (-0.38) for the 4th

Table 29. Genetic (above) and Pearson correlation (below) between traits of jack pine.

	Height	DBH	DOM	AVBL	AVBD	AVBA	RBD	RCW	Taper
Height	-	0.89	-0.06	0.91	0.41	-0.13	0.08	-0.31	0.64
DBH	0.77		-0.21	0.72	0.35	-0.06	-0.18	-0.37	0.29
DOM	0.18	0.21		-0.08	0.03	0.21	0.04	-0.30	-0.14
AVBL	0.38	0.48	0.09		0.63	-0.54	0.37	0.39	0.50
AVBD	0.30	0.37	0.02	0.85		-0.02	0.75	0.26	0.19
AVBA	-0.13	-0.17	0.20	-0.32	-0.40		0.01	-0.34	0.00
RBD	-0.04	0.07	-0.03	0.53	0.65	-0.30		0.45	0.02
RCW	-0.23	0.03	-0.02	0.79	0.67	-0.25	0.56		-0.36
Taper	0.30	-0.20	-0.02	-0.18	-0.24	0.07	-0.27		

Note: Traits are identified in Table 24.

whorl from the top. This finding was also consistent with the results in Adams and Morgenstern (1991), who reported that stem height was negatively correlated with crown quality (relative crown width was largely included) (-0.44) and relative branch diameter (-0.53) in jack pine. The difference between the two studies was understandable because of the difference in quantifying the traits, scored by visual assessment in Adams and Morgenstern (1991) and empirical measurements in the current study for the traits involved. It seems slightly unfavourable that height was positively correlated with branch diameter (0.41), but the fact that height had little or negative correlation (0.08 to -0.18) with relative branch diameter and moderately negative with relative crown diameter (-

0.38 to -0.31) was very favourable for multi-trait selection. Enhancement of height growth will not increase relative branch size and relative crown size, even though there is some increase in absolute branch size. Another result is that the increase in height growth will probably also increase stem taper (0.64).

Diameter at breast height had strong correlation with average branch length (0.72); moderate with average branch diameter (0.35) and taper (0.29); moderately negative with relative crown width (-0.37), weakly negative with number of dominant branches (-0.21) and relative branch diameter (-0.18), and essentially no correlation with average branch angle (-0.06) (Table 29). This finding was supported by Haapanen and Pöykkö (1993), who found that stem diameter was moderately correlated with branch diameter (0.46), negatively correlated with relative branch diameter (-0.32), and had no correlation with relative crown width (0.01) for the 4th whorl from the top in Scots pine. In other words, the increase in total tree height will enhance stem diameter, as well as branch length, branch diameter and stem taper, but will not increase relative crown width, dominant branch number per whorl, relative branch diameter, or branch angle. This is consistent with the correlations between height and other traits mentioned above, and these results are favourable for multi-trait selection.

Number of dominant branches had little correlation with average branch length (-0.08), average branch diameter (0.03), height (0.06) and relative branch diameter (0.04). It had weak correlation with average branch angle (0.21) and weakly negative with DBH (-0.21), and taper (-0.14) (Table 29). As mentioned above, number of dominant branches had no correlation with height (-0.06) and weakly negative correlation with DBH (-0.21). It is clear that number of dominant branches has no strong correlation with any other branch diameter would strongly affect relative branch diameter (0.75), but not relative crown width (0.26) and stem taper (0.19). Branch diameter has no genetic relationship with branch angle (-0.02) nor number of dominant branches (0.03).

Average branch angle had little correlation with relative branch diameter (0.01) and taper (0.00) and weakly negative correlation with relative crown width (-0.34) (Table 29). As mentioned above, it also had no correlation with average branch diameter (-0.02) and DBH (-0.06), weakly negative with height (-0.13), weakly with number of dominant branches (0.21) and moderately negative with average branch length (-0.54). As this trait had a high value of heritability (0.14, individual), the fact that branch angles have no strong genetic correlation with any other traits strongly supports the hypothesis that branch angles are independently inherited.

This result was consistent with Magnussen and Yeatman (1987b), they reported that branch angle had no genetic correlation with branch diameter (0.04) and stem diameter (0.01) in jack pine. And this was also supported by Adams and Morgenstern (1991), who reported that branch angle had weak correlations with crown quality (or relative crown width) (0.28) and relative branch diameter (0.28) in jack pine. As mentioned above, the difference between the two studies probably resulted from the different methods used by the two studies. Results from other species such as Norway spruce (Lewark 1981) and slash pine (Strickland and Goddard 1965) also supported that branch angles had little or no genetic relationship to tree size.

However, some other studies showed that branch angle had genetic correlations with stem and branch diameter in coniferous species (Bailey *et al.* 1974, Barber 1964, Dietrich 1973, Merrill and Mohn 1985). As well, Haapanen and Pöykkö (1993) found that branch traits used in this study. Few earlier studies involved this trait in genetic correlation analysis.

Average branch length was relatively strongly correlated with average branch diameter (0.63); moderately with taper (0.50), relative branch diameter (0.37) and relative crown width (0.39); moderately negatively with average branch angle (-0.54) (Table 29). As mentioned above, branch length will increase with the improvement of growth rate (with height 0.91, DBH 0.72). With this increase in branch length, branch diameter (0.63) will also increase. With the increase in branch size, stem taper (0.50) may be improved, and there is a chance that relative branch size (0.37) and relative crown size (0.39) will be enhanced as well. This seems contradictory that branch size was moderately positive correlated with relative branch and crown size. As mentioned above, the improvement of growth rate will increase branch and crown size, but not relative branch and crown size. The low heritabilities of traits involved (0.02-0.06, individual) in the calculation of genetic correlation may magnify errors in correlation values. Nevertheless, it will not cover the fact that height and DBH have no or negative correlation with relative branch and crown size.

Average branch diameter had no correlation with average branch angle (-0.02); strong correlation with relative branch diameter (0.75); weak with relative crown width (0.26) and taper (0.19). As mentioned above, it had no correlation with number of dominant branches (0.03), moderate with height (0.41) and DBH (0.35), and relatively strongly correlated with average branch length (0.63) (Table 29). The positive genetic correlation between branch diameter and growth traits (height and diameter) were supported by Haapanen and Pöykkö (1993). This result also showed that the increase in angle negatively correlated with the absolute and relative branch diameter (-0.67 to -0.28) in two whorls (4th and 7th from the top). Branch angle positively correlated with growth traits stem diameter and height in the upper whorl (0.22 to 0.30) but negatively in the lower one (-0.38 to -0.05). It is probably because that branch angle changes over time. The older the branch, the wider the branch angle (Barber 1964, Cochrane and Ford 1978, Dietrich 1973, Ehrenberg 1963, Zimmermann and Brown 1971).

Relative branch diameter had moderate correlation with relative crown width (0.45) and no correlation with stem taper. It had no correlation with number of dominant branches (0.04) and average branch angle (0.01) and height (0.08), weakly negative correlation with DBH (-0.18), moderate correlation with average branch length (0.37) and strong correlation with average branch diameter (0.75) (Table 29). Because relative branch diameter had no evident correlation with growth traits (diameter and height), the improvement in growth rate will not increase relative branch diameter. This was supported by Haapanen and Pöykkö (1993), who reported that relative branch diameter had weakly negative genetic correlation with height (-0.18) and DBH (-0.32) in Scots pine.

Relative crown width had moderate correlation with average branch length (0.39) and relative branch diameter (0.45), moderately negative with average branch angle (-0.34), height (-0.31) and DBH (-0.37), weak with average branch diameter (0.26), and weakly negative with number of dominant branches (-0.3), taper (-0.27) (Table 29). Because the increase in stem height and diameter will not increase relative crown width, it is favourable for multi-trait breeding because we do want to increase growth rate and decrease relative crown width at the same time. This trait does not strongly correlated with any other traits, almost all of the existing relationships with the traits used were moderate, favourable or unfavourable. This finding was consistent with Haapanen and Pöykkö (1993), who found that relative crown width had weakly negative correlation with diameter (-0.06) and height (-0.13) in Scots pine.

Taper had weakly negative correlation with relative crown width (-0.27). It had relatively strong correlation with stem height (0.64), moderate with average branch length (0.50), weak with average branch diameter (0.19) and DBH (0.29); weakly negative with number of dominant branches (-0.14) and no with avba (0.00) (Table 29). In other words, stem taper may be improved with the increase of stem height, and with this progress in taper, branch length will probably increase, but not relative crown width.

CONCLUSIONS

During the early growing stage, the tree form quality of plantation-grown jack pine is affected greatly by initial spacing. Most of the quality traits used in this study reacted negatively to a great extent with the change of spacing from 1 m to 2 m. When spacing increased further from 2 m to 3 m, quality traits changed less, although this change also reached significant level. Usually, spacing had a greater effect at the fertile test site than at the poorer site. While these results are not extensive enough to determine an optimum spacing for the best form and growth, it is evident that at age eight this optimum is not greater than 2 m.

There were no significant group (stand) effects for the tree form quality traits branch diameter, branch length, branch angle, number of dominant branches, relative branch diameter and relative crown width. Progeny of trees from good quality stands did not have significantly better form than those originating from poorer quality stands. These results suggest that there is no advantage in confining selections to wild stands with superior form. Progeny of trees from the two plus tree groups were not significantly better than those from non-plus tree groups for most of the quality traits. However, family effect was significant for all of the tree form quality traits. A definite provenance effect was noted for growth and some form traits. The two groups of related families of plus trees consistently demonstrated superior performance in growth (height and DBH). Generally, families from west of Lake Nipigon had higher growth potential in height, DBH, and associated branch length, branch diameter, and taper. However, this did not apply to branch angles, number of dominant branches, relative branch size and relative crown size. The difference among groups in branch size and angles, if any, were more clearly expressed at the fertile site than at the poor site.

Neither group (wild stand quality) x spacing interaction nor family x spacing interaction was shown to exist in this study.

Branch angle and stem taper had the highest heritability of all the tree form quality traits (h_i^2 = 0.14-0.15), and branch length and number of dominant branches had low values (both h_i^2 = 0.06). The very important traits branch diameter and relative branch diameter had very low values (h_i^2 = 0.04). Relative crown width had the lowest heritability value (h_i^2 = 0.02). The growth traits height and diameter had moderate to high heritability values (h_i^2 = 0.15 for height and 0.10 for DBH). Trees grown at the fertile site had higher heritability values than those at the poor site.

Branch angle and number of dominant branches had no strong genetic correlation with any other traits used in this study. Branch length had strong genetic correlations with height (0.91) and DBH (0.72). Branch diameter, however, had much lower values with the traits (0.41 for height and 0.35 for DBH). Furthermore, relative branch diameter had no genetic correlations with the growth traits (0.08 for height and –0.18 for DBH). Taper had a relatively strong genetic correlation with height (0.64) and moderate with DBH (0.29). The genetic correlation between branch diameter and branch length was quite strong (0.63), and the genetic correlation for branch size and relative branch size was high (0.75). These results confirm that simultaneous selection for growth and form traits should be possible for jack pine.

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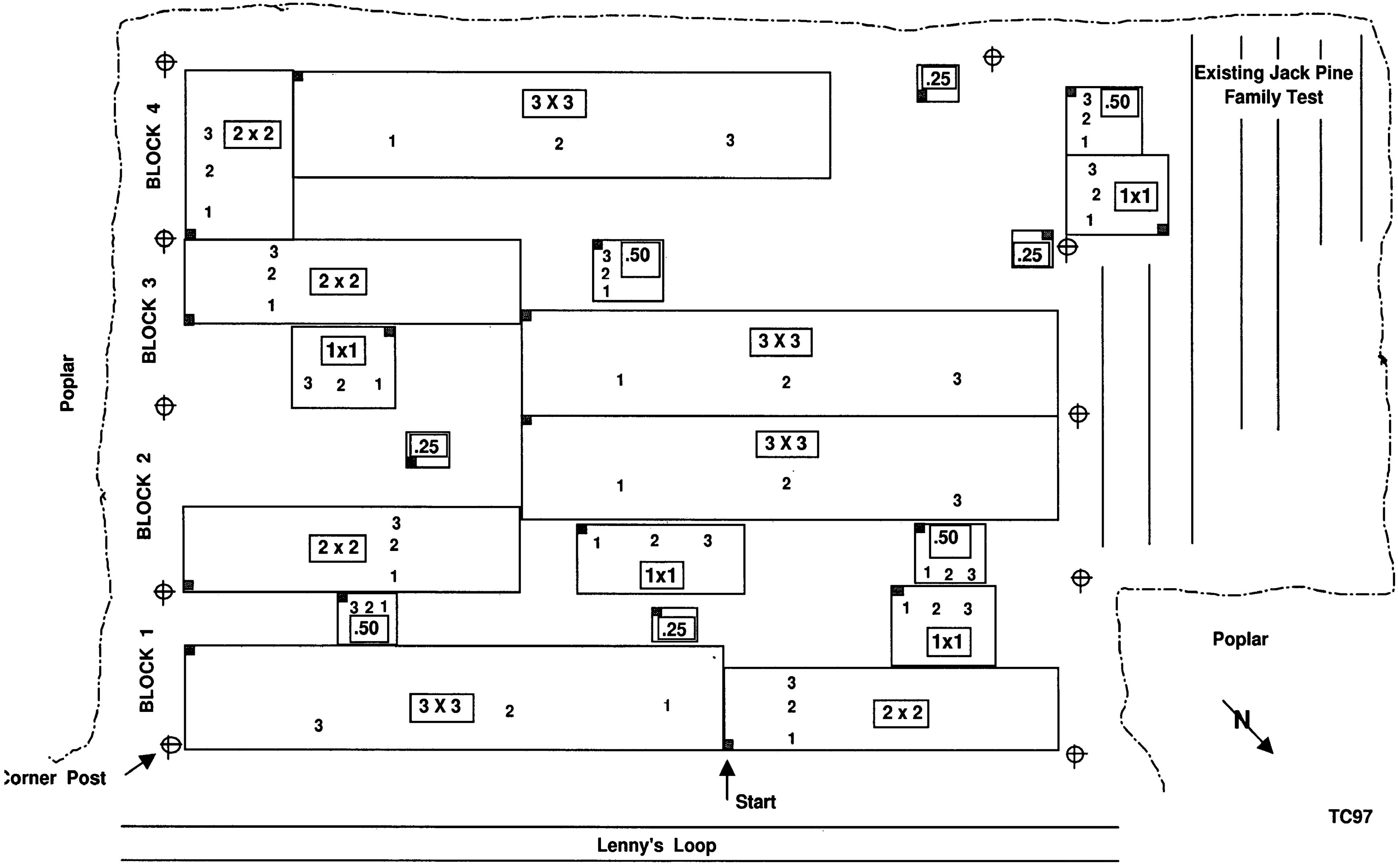
APPENDIX

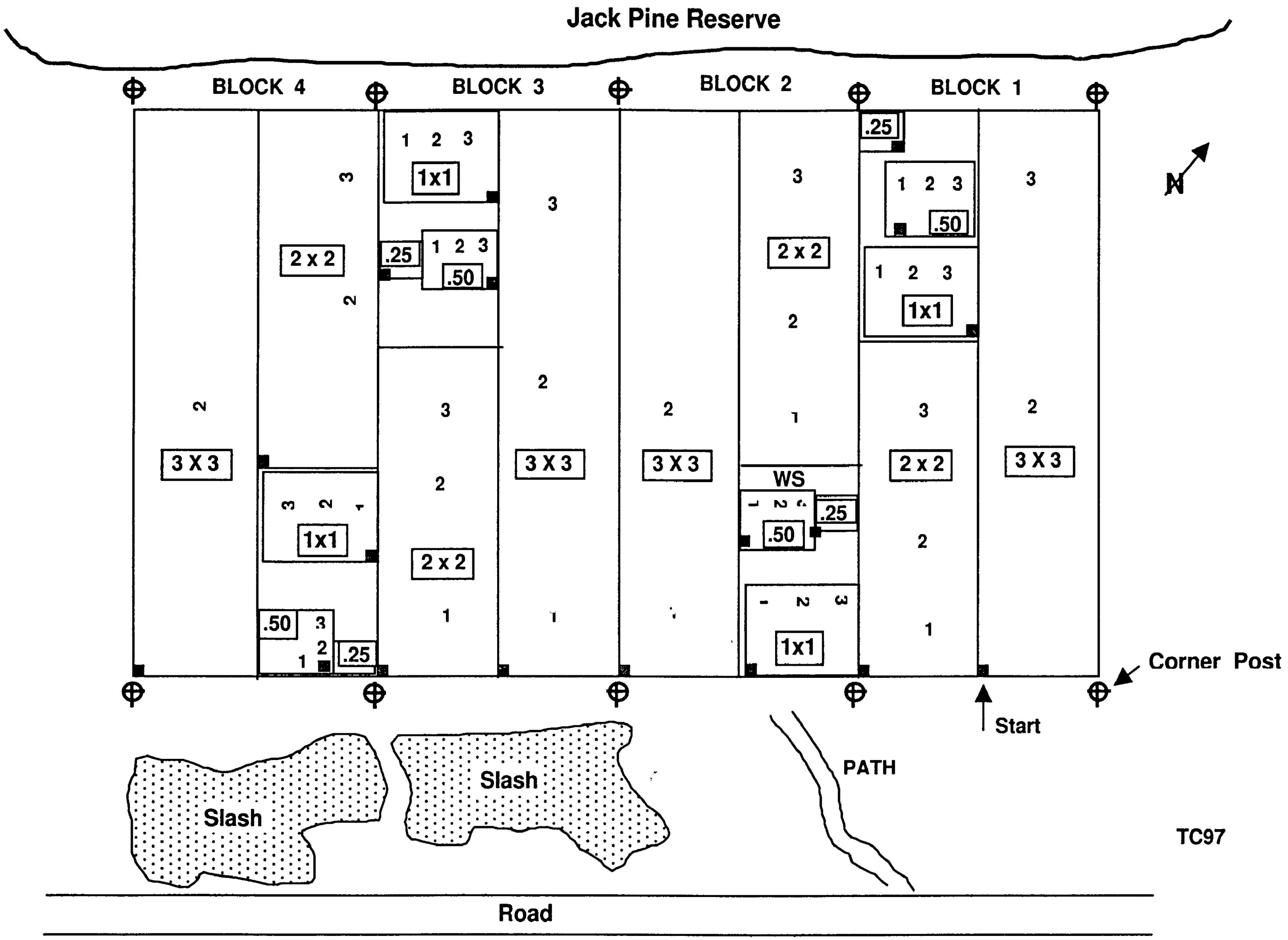
Appendix 1. Jack pine planting sites layout (the following two pages).

JACK PINE FAMILY/SPACING TEST CAMP 45
est. 1990



TC97

JACK PINE FAMILY/SPACING TEST CAMP 602
est. 1990



Appendix 2. Plus tree information.

Plus tree group	Test family number	Plus tree family number	Longitude (West)	Latitude (North)
Good in growth (G-G)	61	226	90.02	48.83
	62	400	90.35	49.12
	63	252	90.78	49.53
	64	074	90.08	48.82
	65	383	90.32	49.08
	66	184	90.33	49.08
	67	224	80.92	49.25
	68	268	90.48	49.37
	69	157	89.27	49.33
	70	373	90.27	49.82
Good in form (G-F)	71	071	90.35	49.10
	72	351	89.65	49.60
	73	350	90.85	49.33
	74	165	89.03	48.95
	75	101	90.28	49.20
	76	388	90.20	49.77
	77	321	89.07	48.95
	78	193	89.78	49.40
	79	270	90.88	49.32
	80	070	88.93	49.412

Note: More plus tree information was presented in Table 4.

Appendix 3. The family means of nine traits for jack pine.

_Appendix 3.1 The family means of stem height for jack pine.

Family No.	Group	Mean	Std.Dev	Family No.	Group	Mean	Std.Dev
63	G-G	3.43	0.58	79	G-F	3.20	0.48
53	W-P	3.39	0.51	2	E-G	3.19	0.52
51	W-P	3.38	0.56	11	E-A	3.19	0.53
78	G-F	3.38	0.52	40	W-G	3.19	0.51
60	W-P	3.35	0.58	80	G-F	3.18	0.49
76	G-F	3.35	0.54	15	E-A	3.17	0.50
67	G-G	3.34	0.57	23	E-P	3.17	0.51
77	G-F	3.33	0.54	8	E-G	3.16	0.44
39	W-G	3.32	0.54	10	E-G	3.16	0.55
73	G-F	3.32	0.58	12	E-A	3.16	0.51
64	G-G	3.31	0.60	22	E-P	3.16	0.56
44	W-A	3.30	0.55	56	W-P	3.16	0.55
34	W-G	3.29	0.54	19	E-A	3.15	0.51
36	W-G	3.29	0.50	47	W-A	3.15	0.61
48	W-A	3.29	0.48	50	W-A	3.15	0.55
54	W-P	3.29	0.50	7	E-G	3.14	0.43
68	G-G	3.29	0.57	20	E-A	3.13	0.54
33	W-G	3.28	0.56	57	W-P	3.13	0.53
61	G-G	3.28	0.56	59	W-P	3.13	0.54
69	G-G	3.28	0.53	5	E-G	3.12	0.43
32	W-G	3.27	0.54	27	E-P	3.12	0.49
41	W-A	3.27	0.49	17	E-A	3.11	0.52
62	G-G	3.26	0.50	18	E-A	3.11	0.57
13	E-A	3.25	0.50	3	E-G	3.10	0.48
29	E-P	3.25	0.56	58	W-P	3.10	0.54
38	W-G	3.25	0.55	74	G-F	3.10	0.55
65	G-G	3.25	0.51	37	W-G	3.09	0.48
71	G-F	3.25	0.59	49	W-A	3.09	0.52
31	W-G	3.24	0.49	43	W-A	3.08	0.53
70	G-G	3.24	0.61	14	E-A	3.07	0.51
75	G-F	3.24	0.51	35	W-G	3.06	0.58
24	E-P	3.23	0.45	6	E-G	3.03	0.50
45	W-A	3.23	0.54	25	E-P	3.02	0.51
46	W-A	3.23	0.47	4	E-G	3.01	0.49
55	W-P	3.23	0.51	9	E-G	3.00	0.48
66	G-G	3.23	0.56	16	E-A	3.00	0.49
30	E-P	3.22	0.56	28	E-P	2.99	0.46
42	W-A	3.22	0.57	26	E-P	2.98	0.49
72	G-F	3.21	0.55	1	E-G	2.94	0.44
52	W-P	3.20	0.62	21	E-P	2.89	0.47

Note: Group identities were determined in Table 4. Std.dev = standard deviation.

Appendix 3.2 The family means of diameter at breast height for jack pine.

Family No.	Group	Mean	Std.Dev	Family No.	Group	Mean	Std.Dev
63	G-G	43.45	14.16	27	E-P	39.49	12.14
41	W-A	42.66	14.22	40	W-G	39.44	13.04
33	W-G	42.65	15.00	70	G-G	39.40	14.25
64	G-G	42.33	15.86	56	W-P	39.37	14.61
30	E-P	42.31	14.45	8	E-G	39.30	12.25
32	W-G	42.05	14.65	25	E-P	39.28	13.03
78	G-F	42.01	13.73	17	E-A	39.24	13.85
50	W-A	41.80	14.55	48	W-A	39.22	13.31
77	G-F	41.69	14.00	72	G-F	39.18	13.25
60	W-P	41.68	14.21	5	E-G	39.13	11.30
76	G-F	41.41	13.57	80	G-F	39.06	13.43
71	G-F	41.26	13.17	29	E-P	39.03	12.89
44	W-A	41.22	15.24	42	W-A	39.03	14.05
51	W-P	41.20	12.66	46	W-A	38.99	11.73
69	G-G	41.18	13.75	23	E-P	38.93	11.96
2	E-G	41.06	13.64	7	E-G	38.80	11.82
53	W-P	41.00	12.95	37	W-G	38.69	13.27
39	W-G	40.87	14.26	10	E-G	38.61	14.43
15	E-A	40.65	14.46	12	E-A	38.52	13.09
36	W-G	40.65	12.75	26	E-P	38.47	13.16
61	G-G	40.64	14.51	20	E-A	38.07	12.54
65	G-G	40.60	13.61	45	W-A	37.96	12.03
19	E-A	40.55	14.08	47	W-A	37.89	12.69
75	G-F	40.55	12.74	49	W-A	37.88	13.27
54	W-P	40.49	11.46	57	W-P	37.62	13.16
79	G-F	40.46	10.87	43	W-A	37.57	13.84
67	G-G	40.44	13.08	11	E-A	37.45	10.70
22	E-P	40.34	15.59	74	G-F	37.26	13.87
13	E-A	40.26	12.26	4	E-G	37.09	12.17
68	G-G	40.26	13.15	3	E-G	37.06	11.72
31	W-G	40.15	12.60	58	W-P	36.74	12.76
34	W-G	40.07	14.36	9	E-G	36.59	12.59
66	G-G	40.06	13.43	16	E-A	36.59	12.09
73	G-F	39.96	12.79	6	E-G	36.57	11.90
52	W-P	39.94	14.09	1	E-G	36.16	11.84
24	E-P	39.92	11.04	35	W-G	35.99	12.70
55	W-P	39.81	13.20	18	E-A	35.61	12.90
59	W-P	39.73	14.16	14	E-A	35.46	12.00
38	W-G	39.72	13.74	28	E-P	35.23	11.64
62	G-G	39.71	13.05	21	E-P	34.55	10.91

Note: Group identities were determined in Table 4. Std.dev = standard deviation.

Appendix 3.3 The family means of number of dominant branches for jack pine.

Family No.	Group	Mean	Std.Dev	Family No.	Group	Mean	Std.Dev
77	G-F	5.13	1.66	74	G-F	4.57	1.60
22	E-P	5.01	1.45	78	G-F	4.57	1.39
5	E-G	5.00	1.33	80	G-F	4.57	1.35
39	W-G	4.97	1.59	64	G-G	4.56	1.60
15	E-A	4.96	1.43	19	E-A	4.55	1.36
48	W-A	4.94	1.40	42	W-A	4.55	1.49
10	E-G	4.88	1.41	2	E-G	4.54	1.11
44	W-A	4.85	1.45	35	W-G	4.54	1.31
46	W-A	4.85	1.53	76	G-F	4.54	1.15
56	W-P	4.81	1.43	50	W-A	4.53	1.15
54	W-P	4.80	1.61	45	W-A	4.52	1.49
47	W-A	4.78	1.70	3	E-G	4.51	1.27
18	E-A	4.77	1.53	20	E-A	4.50	1.52
8	E-G	4.76	1.34	68	G-G	4.50	1.44
41	W-A	4.76	1.65	29	E-P	4.49	1.52
16	E-A	4.74	1.52	30	E-P	4.49	1.16
28	E-P	4.72	1.35	43	W-A	4.49	1.30
17	E-A	4.70	1.20	52	W-P	4.49	1.33
40	W-G	4.70	1.38	34	W-G	4.48	1.23
63	G-G	4.70	1.50	49	W-A	4.45	1.48
11	E-A	4.69	1.35	9	E-G	4.44	1.33
37	W-G	4.69	1.65	23	E-P	4.42	1.34
59	W-P	4.69	1.48	31	W-G	4.42	1.35
70	G-G	4.67	1.33	36	W-G	4.39	1.30
7	E-G	4.65	1.20	72	G-F	4.39	1.44
32	W-G	4.65	1.55	73	G-F	4.37	1.21
33	W-G	4.65	1.51	58	W-P	4.35	1.51
51	W-P	4.65	1.31	61	G-G	4.35	1.33
79	G-F	4.65	1.59	4	E-G	4.33	1.22
13	E-A	4.64	1.38	6	E-G	4.33	1.19
24	E-P	4.63	1.32	62	G-G	4.29	1.47
71	G-F	4.63	1.50	27	E-P	4.28	1.41
21	E-P	4.61	1.37	53	W-P	4.27	1.47
26	E-P	4.61	1.26	75	G-F	4.27	1.08
57	W-P	4.60	1.45	1	E-G	4.25	1.12
14	E-A	4.59	1.52	55	W-P	4.23	1.38
65	G-G	4.59	1.38	66	G-G	4.18	1.45
69	G-G	4.59	1.52	60	W-P	4.11	1.31
25	E-P	4.57	1.37	12	E-A	4.07	1.31
38	W-G	4.57	1.44	67	G-G	4.07	1.31

Note: Group identities were determined in Table 4. Std.dev = standard deviation.

Appendix 3.4 The family means of average branch length for jack pine.

Family No.	Group	Mean	Std.Dev	Family No.	Group	Mean	Std.Dev
67	G-G	89.30	29.01	55	W-P	81.96	24.56
31	W-G	88.80	28.18	22	E-P	81.88	23.24
53	W-P	87.96	26.97	3	E-G	81.85	24.53
15	E-A	87.89	26.01	59	W-P	81.84	23.41
44	W-A	87.85	27.75	30	E-P	81.70	23.08
76	G-F	87.24	26.59	19	E-A	81.65	25.58
78	G-F	87.17	24.14	63	G-G	81.49	22.26
71	G-F	87.16	29.39	47	W-A	81.27	23.31
68	G-G	87.14	24.91	2	E-G	81.21	22.54
36	W-G	86.23	27.16	23	E-P	80.93	20.89
32	W-G	85.54	24.13	5	E-G	80.83	21.13
17	E-A	85.22	23.61	43	W-A	80.82	26.31
50	W-A	85.06	26.32	61	G-G	80.82	22.45
39	W-G	84.98	23.09	79	G-F	80.74	23.00
60	W-P	84.49	24.77	42	W-A	80.72	26.29
40	W-G	84.43	27.89	49	W-A	80.70	23.82
70	G-G	84.33	26.05	12	E-A	80.13	23.74
13	E-A	84.18	22.89	10	E-G	79.72	24.73
33	W-G	84.09	26.03	35	W-G	79.32	20.78
37	W-G	83.68	20.90	34	W-G	79.16	23.42
46	W-A	83.57	23.01	25	E-P	79.15	22.45
52	W-P	83.52	25.43	48	W-A	79.00	24.58
41	W-A	83.40	23.83	27	E-P	78.99	25.57
6	E-G	83.35	26.57	64	G-G	78.84	24.83
24	E-P	83.32	21.74	14	E-A	78.70	19.37
54	W-P	83.29	25.71	26	E-P	78.53	25.33
7	E-G	83.26	22.52	4	E-G	77.93	17.56
69	G-G	83.13	24.24	75	G-F	77.57	21.31
51	W-P	82.92	21.53	58	W-P	77.15	25.32
20	E-A	82.88	22.40	56	W-P	77.02	21.52
80	G-F	82.88	24.42	66	G-G	76.73	22.59
11	E-A	82.79	24.43	1	E-G	76.70	21.45
77	G-F	82.49	22.18	28	E-P	76.65	23.14
38	W-G	82.41	22.60	72	G-F	76.49	25.02
8	E-G	82.37	22.11	18	E-A	76.24	24.43
45	W-A	82.18	25.49	29	E-P	76.03	24.58
57	W-P	82.17	24.41	74	G-F	75.70	22.62
62	G-G	82.05	25.88	9	E-G	75.64	21.57
73	G-F	82.03	25.34	21	E-P	75.34	20.37
65	G-G	82.01	23.39	16	E-A	73.35	19.23

Note: Group identities were determined in Table 4. Std.dev = standard deviation.

Appendix 3.5 The family means of average branch diameter for jack pine.

Family No.	Group	Mean	Std.Dev	Family No.	Group	Mean	Std.Dev
31	W-G	14.40	4.88	23	E-P	13.04	3.95
50	W-A	14.21	5.43	10	E-G	13.03	4.40
17	E-A	14.13	4.37	57	W-P	13.03	4.44
67	G-G	14.10	5.60	11	E-A	13.02	4.57
33	W-G	14.03	5.20	5	E-G	12.93	4.38
15	E-A	13.87	5.04	26	E-P	12.93	4.88
53	W-P	13.80	4.73	38	W-G	12.93	4.06
36	W-G	13.73	4.46	75	G-F	12.91	4.34
8	E-G	13.69	4.58	27	E-P	12.87	4.89
71	G-F	13.62	5.09	45	W-A	12.85	4.48
19	E-A	13.61	5.23	49	W-A	12.83	4.78
78	G-F	13.53	4.71	42	W-A	12.81	5.03
65	G-G	13.48	4.44	12	E-A	12.80	4.34
41	W-A	13.47	4.55	61	G-G	12.78	4.24
52	W-P	13.47	4.66	64	G-G	12.77	5.03
60	W-P	13.42	4.19	73	G-F	12.77	4.71
24	E-P	13.40	4.36	4	E-G	12.73	3.79
3	E-G	13.39	4.71	32	W-G	12.72	4.38
76	G-F	13.39	4.86	54	W-P	12.67	4.63
13	E-A	13.37	4.32	14	E-A	12.66	4.13
25	E-P	13.34	4.50	47	W-A	12.66	4.27
40	W-G	13.30	5.20	79	G-F	12.66	4.25
46	W-A	13.27	4.73	30	E-P	12.62	4.20
63	G-G	13.24	4.18	1	E-G	12.61	4.46
6	E-G	13.19	5.19	62	G-G	12.59	4.28
59	W-P	13.18	4.73	35	W-G	12.50	4.30
69	G-G	13.18	4.94	48	W-A	12.46	4.60
44	W-A	13.15	5.12	43	W-A	12.45	4.39
77	G-F	13.15	4.19	58	W-P	12.43	4.73
20	E-A	13.12	4.13	21	E-P	12.39	4.22
2	E-G	13.11	4.32	34	W-G	12.32	4.14
68	G-G	13.11	4.62	56	W-P	12.32	4.20
80	G-F	13.11	4.67	18	E-A	12.24	4.30
22	E-P	13.10	4.55	9	E-G	12.23	4.15
55	W-P	13.10	4.78	74	G-F	12.20	4.28
7	E-G	13.09	4.34	66	G-G	12.16	4.52
70	G-G	13.08	4.39	72	G-F	12.14	4.60
37	W-G	13.07	4.12	16	E-A	12.09	3.89
39	W-G	13.07	4.55	29	E-P	12.04	4.57
51	W-P	13.06	4.19	28	E-P	11.80	4.14

Note: Group identities were determined in Table 4. Std.dev = standard deviation.

Appendix 3.6 The family means of average branch angle for jack pine.

Family No.	Group	Mean	Std.Dev	Family No.	Group	Mean	Std.Dev
25	E-P	66.61	11.12	57	W-P	62.15	9.46
18	E-A	66.29	10.36	2	E-G	62.14	9.47
49	W-A	66.13	11.74	50	W-A	62.12	11.00
63	G-G	65.54	9.65	10	E-G	61.99	9.74
38	W-G	65.19	9.44	7	E-G	61.98	10.07
47	W-A	64.87	10.41	30	E-P	61.90	11.27
29	E-P	64.80	12.29	28	E-P	61.79	12.00
56	W-P	64.71	9.94	26	E-P	61.37	10.31
11	E-A	64.54	10.57	78	G-F	61.33	10.80
70	G-G	64.52	10.10	35	W-G	61.11	9.52
42	W-A	63.95	9.24	79	G-F	60.94	11.24
72	G-F	63.88	11.41	52	W-P	60.90	10.79
13	E-A	63.85	9.69	75	G-F	60.78	10.65
48	W-A	63.76	10.23	55	W-P	60.76	11.79
64	G-G	63.69	10.40	27	E-P	60.69	11.79
73	G-F	63.62	10.19	71	G-F	60.56	10.84
22	E-P	63.47	11.42	5	E-G	60.54	9.81
34	W-G	63.44	9.48	20	E-A	60.42	10.74
21	E-P	63.35	9.79	32	W-G	60.40	10.34
14	E-A	63.29	10.52	76	G-F	60.35	10.43
24	E-P	63.21	10.42	68	G-G	60.16	8.54
65	G-G	63.17	10.32	60	W-P	59.71	9.92
6	E-G	63.01	10.97	23	E-P	59.64	9.28
41	W-A	62.96	9.78	19	E-A	59.59	10.97
1	E-G	62.92	10.67	16	E-A	59.55	9.21
3	E-G	62.90	8.65	66	G-G	59.45	10.26
45	W-A	62.90	10.03	31	W-G	59.35	10.13
51	W-P	62.83	10.43	46	W-A	59.32	8.59
39	W-G	62.77	9.55	61	G-G	59.25	9.85
9	E-G	62.55	9.27	15	E-A	59.19	10.98
40	W-G	62.51	10.03	36	W-G	59.12	9.69
44	W-A	62.51	11.28	80	G-F	59.09	10.12
69	G-G	62.47	11.17	54	W-P	58.80	9.85
74	G-F	62.45	11.51	53	W-P	57.91	11.06
4	E-G	62.39	9.58	58	W-P	57.91	9.92
12	E-A	62.38	11.90	43	W-A	57.68	10.88
17	E-A	62.34	9.55	67	G-G	57.54	12.01
59	W-P	62.32	11.13	62	G-G	57.44	9.92
77	G-F	62.32	8.98	37	W-G	56.80	9.90
8	E-G	62.16	9.35	33	W-G	56.26	10.03

Note: Group identities were determined in Table 4. Std.dev = standard deviation.

Appendix 3.7 The family means of relative branch diameter for jack pine.

Family No.	Group	Mean	Std.Dev	Family No.	Group	Mean	Std.Dev
67	G-G	0.64	0.17	7	E-G	0.56	0.15
17	E-A	0.61	0.15	12	E-A	0.56	0.15
31	W-G	0.61	0.14	13	E-A	0.56	0.16
35	W-G	0.61	0.16	16	E-A	0.56	0.15
8	E-G	0.59	0.16	19	E-A	0.56	0.15
22	E-P	0.59	0.15	25	E-P	0.56	0.14
33	W-G	0.59	0.17	36	W-G	0.56	0.15
52	W-P	0.59	0.16	37	W-G	0.56	0.14
59	W-P	0.59	0.17	44	W-A	0.56	0.16
6	E-G	0.58	0.15	45	W-A	0.56	0.14
11	E-A	0.58	0.14	57	W-P	0.56	0.16
15	E-A	0.58	0.15	75	G-F	0.56	0.14
24	E-P	0.58	0.14	76	G-F	0.56	0.14
40	W-G	0.58	0.16	80	G-F	0.56	0.15
41	W-A	0.58	0.15	1	E-G	0.55	0.15
47	W-A	0.58	0.15	4	E-G	0.55	0.14
50	W-A	0.58	0.16	26	E-P	0.55	0.15
53	W-P	0.58	0.14	34	W-G	0.55	0.13
58	W-P	0.58	0.17	39	W-G	0.55	0.15
60	W-P	0.58	0.15	49	W-A	0.55	0.14
65	G-G	0.58	0.15	54	W-P	0.55	0.14
69	G-G	0.58	0.16	55	W-P	0.55	0.14
70	G-G	0.58	0.15	62	G-G	0.55	0.15
2	E-G	0.57	0.13	74	G-F	0.55	0.15
10	E-G	0.57	0.16	79	G-F	0.55	0.15
14	E-A	0.57	0.14	9	E-G	0.54	0.15
20	E-A	0.57	0.15	18	E-A	0.54	0.14
23	E-P	0.57	0.14	21	E-P	0.54	0.14
38	W-G	0.57	0.15	27	E-P	0.54	0.17
42	W-A	0.57	0.16	48	W-A	0.54	0.15
43	W-A	0.57	0.15	51	W-P	0.54	0.14
46	W-A	0.57	0.14	56	W-P	0.54	0.15
61	G-G	0.57	0.15	63	G-G	0.54	0.14
68	G-G	0.57	0.15	64	G-G	0.54	0.16
71	G-F	0.57	0.17	72	G-F	0.54	0.15
73	G-F	0.57	0.15	29	E-P	0.53	0.16
77	G-F	0.57	0.14	32	W-G	0.53	0.13
78	G-F	0.57	0.15	28	E-P	0.52	0.15
3	E-G	0.56	0.13	30	E-P	0.52	0.13
5	E-G	0.56	0.15	66	G-G	0.52	0.13

Note: Group identities were determined in Table 4. Std.dev = standard deviation.

Appendix 3.8 The family means of relative crown width for jack pine.

Family No.	Group	Mean	Std.Dev	Family No.	Group	Mean	Std.Dev
15	E-A	0.55	0.14	10	E-G	0.51	0.14
6	E-G	0.54	0.15	12	E-A	0.51	0.13
17	E-A	0.54	0.13	22	E-P	0.51	0.12
31	W-G	0.54	0.14	23	E-P	0.51	0.11
37	W-G	0.54	0.12	27	E-P	0.51	0.17
50	W-A	0.54	0.16	28	E-P	0.51	0.14
3	E-G	0.53	0.13	33	W-G	0.51	0.14
20	E-A	0.53	0.13	38	W-G	0.51	0.13
40	W-G	0.53	0.17	39	W-G	0.51	0.12
44	W-A	0.53	0.14	43	W-A	0.51	0.13
57	W-P	0.53	0.15	45	W-A	0.51	0.13
59	W-P	0.53	0.14	65	G-G	0.51	0.13
67	G-G	0.53	0.15	69	G-G	0.51	0.13
68	G-G	0.53	0.13	76	G-F	0.51	0.14
71	G-F	0.53	0.17	79	G-F	0.51	0.14
1	E-G	0.52	0.14	2	E-G	0.50	0.12
4	E-G	0.52	0.10	9	E-G	0.50	0.13
5	E-G	0.52	0.13	30	E-P	0.50	0.11
7	E-G	0.52	0.12	42	W-A	0.50	0.14
8	E-G	0.52	0.13	54	W-P	0.50	0.14
11	E-A	0.52	0.14	55	W-P	0.50	0.12
13	E-A	0.52	0.14	58	W-P	0.50	0.15
14	E-A	0.52	0.13	60	W-P	0.50	0.12
19	E-A	0.52	0.15	62	G-G	0.50	0.14
21	E-P	0.52	0.14	74	G-F	0.50	0.13
24	E-P	0.52	0.13	77	G-F	0.50	0.13
25	E-P	0.52	0.13	16	E-A	0.49	0.12
26	E-P	0.52	0.14	18	E-A	0.49	0.14
32	W-G	0.52	0.12	51	W-P	0.49	0.11
35	W-G	0.52	0.11	56	W-P	0.49	0.12
36	W-G	0.52	0.14	61	G-G	0.49	0.12
41	W-A	0.52	0.15	73	G-F	0.49	0.13
46	W-A	0.52	0.13	34	W-G	0.48	0.11
47	W-A	0.52	0.15	48	W-A	0.48	0.14
49	W-A	0.52	0.14	64	G-G	0.48	0.15
52	W-P	0.52	0.14	66	G-G	0.48	0.12
53	W-P	0.52	0.14	75	G-F	0.48	0.12
70	G-G	0.52	0.13	63	G-G	0.47	0.12
78	G-F	0.52	0.13	72	G-F	0.47	0.13
80	G-F	0.52	0.13	29	E-P	0.46	0.13

Note: Group identities were determined in Table 4. Std.dev = standard deviation.

Appendix 3.9 The family means of stem taper for jack pine.

Family No.	Group	Mean	Std.Dev	Family No.	Group	Mean	Std.Dev
67	G-G	113.48	24.67	57	W-P	105.63	25.18
48	W-A	112.88	26.62	39	W-G	105.61	25.18
29	E-P	112.77	23.02	31	W-G	105.49	25.09
11	E-A	111.10	25.16	56	W-P	105.36	23.37
45	W-A	111.08	21.82	55	W-P	104.94	24.98
44	W-A	110.94	26.65	43	W-A	104.65	26.51
68	G-G	110.66	24.73	52	W-P	104.65	23.24
73	G-F	110.24	21.84	15	E-A	104.61	25.72
42	W-A	109.75	25.80	36	W-G	104.48	23.94
18	E-A	109.31	24.44	12	E-A	104.20	24.55
78	G-F	109.16	25.64	71	G-F	104.16	25.26
34	W-G	109.11	23.55	80	G-F	104.11	24.27
61	G-G	108.99	23.40	3	E-G	103.97	22.78
47	W-A	108.82	24.09	10	E-G	103.92	24.12
38	W-G	108.40	26.16	6	E-G	103.68	23.85
60	W-P	108.40	21.80	23	E-P	103.66	21.61
53	W-P	108.28	22.54	32	W-G	103.62	22.14
14	E-A	108.19	25.12	13	E-A	103.57	24.60
24	E-P	108.13	23.06	7	E-G	103.53	21.91
58	W-P	107.99	23.81	59	W-P	103.33	24.85
28	E-P	107.90	24.00	79	G-F	103.05	24.80
51	W-P	107.89	23.43	30	E-P	102.72	22.82
72	G-F	107.65	23.05	8	E-G	102.70	21.65
62	G-G	107.15	25.02	33	W-G	102.66	23.24
35	W-G	107.09	22.57	41	W-A	102.61	27.73
70	G-G	106.88	21.76	19	E-A	102.44	24.66
46	W-A	106.65	24.51	21	E-P	102.32	25.46
63	G-G	106.65	24.43	17	E-A	101.87	23.75
40	W-G	106.64	25.16	20	E-A	101.80	22.25
65	G-G	106.63	24.29	9	E-G	101.66	22.71
74	G-F	106.55	23.00	37	W-G	101.60	24.33
22	E-P	106.49	25.49	2	E-G	101.48	23.49
76	G-F	106.49	25.07	4	E-G	101.21	22.18
66	G-G	106.34	23.66	1	E-G	100.53	22.81
54	W-P	106.16	21.56	16	E-A	100.46	23.98
69	G-G	106.16	24.69	5	E-G	99.91	21.89
75	G-F	105.95	24.26	27	E-P	99.43	24.50
77	G-F	105.95	21.98	50	W-A	99.24	25.62
64	G-G	105.92	25.30	26	E-P	98.61	21.78
49	W-A	105.76	24.22	25	E-P	96.57	21.89

Note: Group identities were determined in Table 4. Std.dev = standard deviation.