COMPETITION TRIALS OF *PINUS BANKSIANA* AND *POPULUS TREMULOIDES* UNDER A RANGE OF PROPORTIONS AND DENSITIES

By

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ABSTRACT

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Key Words: Competition trials, Replacement series, *Pinus banksiana*, *Populus tremuloides*.

This study was the first study designed specifically to analyze the competitive effects of density and species mixture for both *Pinus banksiana* and *Populus tremuloides* seedlings during the initial stages of growth and development. To this end, replacement series experiments with jack pine and trembling aspen seedlings were used in both a greenhouse and field study. In a 12-week greenhouse pot study species ratios of 100/0, 75/25, 50/50, 25/75, and 0/100 were planted at densities of 729, 2,844, and 10,000 plants/m^2. In a field study, similar mixes were planted at densities of 17, 83, 204, 494, and 2,500 plants/m^2. This field test will be continued for a period of three to four growing seasons.

In the greenhouse study, jack pine assumed a dominant role at the highest density (10,000 plants/m^2). As the density was lowered, trembling aspen gained dominance over the pine in the mixtures. This relationship was reflected in relative crowding coefficients, as well as in replacement series diagrams for relative yield. Also, it was determined that an adjustment in allocation of biomass with respect to the dominant competitor occurred. Trembling aspen increased its percentage biomass allocated to leaf weight, when jack pine was the dominant competitor. However, the aspen seedlings allocated a greater percentage to stem weight in response to aspen assuming the dominant role. A final observation included the lowering of aspen survival as the percentage of aspen in mixture increased. Increased density further accentuated this relationship. Jack pine survival was consistently high across the range of treatments.

From the preliminary measurements carried out on the field trial, it was found that both aspen height growth and crown development were affected by species composition. In general, as the percentage of aspen decreased at a given density, both height and crown volume increased. Furthermore, both height growth and crown volume for jack pine decreased, as density decreased. The cause for this response to density was related to the influence of environmental factors.

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INTRODUCTION

In northwestern Ontario, the relationship between jack pine (*Pinus banksiana* Lamb.) and trembling aspen (*Populus tremuloides* Michx.) in early stand development is of special importance. Both species are common and they occupy an overlapping niche. Therefore, this mixture frequently occurs in both natural stands and plantations. Turkington, *et al* (1977) identified that strong competitive interactions occur between plants with similar site requirements, hindering or preventing their coexistence. Insight into the mode of competition between these two tree species will permit forest managers to prescribe timely, efficient silvicultural treatments to ensure the desired management objectives.

The essential qualities that determine the ecology of a species can only be detected by studying the reaction of individuals of that species to their neighbours (Harper 1964).

Since plants are immobile, they are forced to live in the same lateral relationship with their neighbours throughout their life. A plant may respond to this close proximity of neighbours by failure of seeds to germinate, death, or survival with a plastic development (Harper 1964b). Competitive pressures from neighbours are continuous, and where environmental conditions are relatively homogeneous, are the principal factors directing community change within a forest stand. The hardships imposed by neighbouring plants include shortage of such environmental resources as light, water, and nutrients (Donald 1963). When the neighbouring plants are of the same species, the problems of autotoxicity (Trenbath and Harper 1973), and greater susceptibility to epidemic disease (Gibson 1956) must also be considered.

Essentially similar effects are found in mixed plant communities. Reduced plant yield, as compared to yields from monocultures, may be caused by competition for environmental resources. However, it could also be due to an allelopathic effect (Massey 1925) or to the presence of neighbours promoting disease incidence (Chamblee 1958) or lodging (Probst 1957).

A common objective of forest management is to produce large quantities of quality timber in the shortest time possible. This practice, in part, includes being able to control and manipulate the effects of intra- and interspecific competition. Although many effects of competition can be identified, we do not fully understand its mechanism. Moreover, the complexity of interacting factors make it difficult to separate the components of competition effects. The major measurable effects of competition on forest trees include: (1) increase in mortality, (2) reduction of total biomass, and (3) modification of tree form.

In the boreal forest, jack pine is considered an important tree species by forest managers (Kabzems and Kirby 1956). Trembling aspen, however, is classed as a major competitor of jack pine in this forest region (Shirley 1941). Therefore, the inclusion of trembling aspen on managed jack pine sites poses a serious threat to an increased yield of desired jack pine products. Furthermore, the effects of competition may be most severe on juvenile plants, since it is during this early stage of rapid development that the greatest demands are being made upon the essential factors in the environment.

The purpose of the present study was to investigate the effects of competition on jack pine and trembling aspen seedlings during the initial stages of plant development. More specifically, this research attempted to illustrate changes in plant vigour as related to changes in density and species composition. Therefore, this study concentrated mainly on mortality and biomass changes. These measurable effects of competition are good indicators of plant vigour (Silvertown 1982). To this end, the present study used both a randomized complete block design (greenhouse trial) and a split-plot design (field trial) in order to examine the effects of both density and species compositon in a mixture of young trembling aspen and jack pine.

LITERATURE REVIEW

Attempts to study the phenomena of coexistence on a local scale have resulted in extensive theoretical and empirical studies relating to competition and niche (Werner 1979). This chapter examines the existing literature on plant competition. Most studies have concentrated on the following important attributes of agronomic plant development:

(1) production potential,
(2) emergence date (or timing of rapid growth),
(3) resource allocation,
(4) plastic growth response, and
(5) mortality.

Other contributions have come from the areas of computer-modelling, especially with regards to forest trees, and relationships in natural plant associations.

Experimental Design

Two contrasting experimental designs have been used to investigate the effects of neighbouring plants (Trenbath and Harper 1973). In one design an "indicator species" is sown at the same density, whether in monoculture or in mixture. Mixtures are produced experimentally by the addition of plants of other species to stands of the "indicator species". The major problem associated with this additive design is that the effects due to a change of the neighbours' genotype are confounded with effects due to a difference in density.

In the second design, monocultures and mixtures are sown at the same overall density. The mixtures are produced by substituting plants of a monoculture with plants of another genotype. Varying degrees of substitution produce a range of mixtures with varied proportions. Such an experiment is called "a replacement series" (deWit 1960). McGilchrist and Trenbath (1971), in their paper which reviewed techniques used to analyze competition experiments, supported the use of this type of experimental design. Harper (1977) claims that this is the most informative design on interspecific competition since the density effects which confound the interpretation of additive experiments are ruled out, leaving only the effects of species' proportions (Harper 1977).

Density Experiments with Single Species

Production Potential

Two major agronomic studies concentrated on this area of competition research. Hodgson and Blackman (1956) studied the competitive effects of varying density on the development of *Vicia faba* in a series of multifactorial experiments where the spacing both between and within rows was simultaneously altered.

The other study was carried out by Liddle, *et al*

(1982). The authors attempted to determine the effects of size and shape of available growing space, and the size and proximity of neighbouring plants, upon the growth of individual plants in populations of *Festuca rubra* over a ten month period.

The major results from the above two studies were:

(1) as density increases, the number of fruits per plant and the extent of branching falls progressively (Hodgson and Blackman 1956),

(2) production performance of individual plants becomes increasingly positively correlated with available growing space as growth proceeds (Liddle, *et al* 1982), and

(3) a significant positive correlation also emerges between the mean distance of a plant to its immediate neighbour and its performance (Liddle, *et al* 1982).

Taking a more progressive approach, Weiner (1982) built a simple model to estimate reproductive potential based upon the number, distance, and species of neighbours. The model, for two species, is:

$$Rt_1 = N_1 \times \frac{Rmax}{1 - C_1 \times (N_1 - 1) + C_2 \times N_2} \qquad [1]$$

where: Rt_1 - total seed production of species # 1,

Rmax - is the reproductive output in the absence of competition for species # 1,

N_1 - number of individuals of species # 1 per unit area,

N_2 - number of individuals of species # 2 per unit area,

C_1 - a constant expressing the effect of an individual of species # 1, and

C_2 - a constant expressing the effect of an individual of species # 2.

The effect of increasing competition, in the model, is to reduce seed production in a "hyperbolic fashion", and the contribution of each individual to this effect is in inverse proportion to the square of its distance from the test individual. This distance factor was incorporated in the constants within the above equation.

The model was tested on populations of two annual knotweeds. A least squares fit of the model accounted for over 80 % of the variance in seed production.

Emergence Date

In attempts to verify the existence of a "-3/2 power law of self-thinning", White and Harper (1970) concluded that the cause of the thinning phenomenon in plant populations is that differential growth rates occur among its members. This relationship leads to a development of a pattern of dominance and suppression. The smallest plants eventually die, thereby leaving additional space and nutrients for the larger, vigorously growing plants.

In a later study, Ross and Harper (1972) observed that during the emergence of a monospecific seedling population a dominance hierarchy was established. This hierarchy severely influenced the future development of each individual. This conclusion was determined from a series of experiments, with *Dactylis glomerata* at high densities.

In a more recent experiment, Fowler (1984) found that individuals which germinated early were on average larger than those that germinated late, and had more flowers.

Resource Allocation

In a study by Snell and Burch (1975), two major questions were addressed:

(1) does a plant's pattern of resource allocation respond to varying levels of intraspecific competition and nutrient availability, and

(2) how does increased intraspecific competition and decreased nutrient levels affect net reproductive effort?

The authors found that the pattern of resource allocation in *Chamaesyce hirta* was significantly affected by both density and nutrient availability. Furthermore, increased intraspecific competition and decreased nutrient levels produced decreases in the proportion of total plant energy allocated to reproductive tissues in all units tested. The following generalizations were made. As competition increased:

(1) reproductive biomass increased,

(2) leaf weight decreased,

(3) stem weight increased, and

(4) root weight increased.

Species Mixture Experiments

Another group of researchers has designed experiments that attempt to identify specific growth responses to changes in species composition of closely related herbaceous species.

Production Potential

A common result found in experiments dealing with the relationship between species mixture and production potential was that one species attained a dominant position in the stand, and therefore severely hampered the production of the suppressed species. However, different developmental strategies were discovered.

Lee (1960), using two barley varieties (Atlas 46 - a strong competitor; Vaughn - a weak competitor), determined that superior root development in Atlas 46 allowed this variety to efficiently gather nutrients from a fairly limited area of the soil mass. As a result, the Vaughn variety was placed under stress when both species were dependent upon the same soil area for water and nutrients.

In studies dealing with mixed rice populations, it was observed that light was a major factor for which competition occurs (Jennings and Aquinto 1968). Furthermore, the weaker competitors (vegetatively small, erect, sturdy rice varieties) consistently have higher yields than their highly competitive counterparts when in pure stands (Jennings and deJesus 1968). This relationship is due to the intense competition occurring between neighbouring plants of the strong competitor variety.

Scarisbrick and Ivrins (1970) found that light intensity was also the major limiting factor for British pasture grasses. From the results of greenhouse experiments, the authors theorized that increased daylength would have enhanced the competitive ability of ribgrass in mixture. Ribgrass was dramatically suppressed by intense competition exerted by ryegrass and clover.

In a slightly different approach, Rabinowitz, *et al* (1984) determined that sparse species of prairie grasses were generally strong competitors. Therefore, these grass species were rare due to another undetermined factor. Their study was a greenhouse deWit replacement series experiment spanning 5 - 15 months.

Resource Allocation

A significant study on this topic was carried out by Turkington (1983b). He attempted to illustrate how a plant allocates its available resources on a seasonal basis and how this pattern can be altered in the presence of different neighbouring species.

Over a range of different neighbours, *Trifolium repens* responded quite differently in terms of leaf and flower fluxes, stolon extension rates, final population sizes, and final dry weight. Turkington (1983b) stressed, however, that any particular response is neither "better" nor "worse" than any other. In all treatments, the clover was able to persist and displayed an array of responses to different environments.

Plastic Growth Response and Mortality

Cook (1965) grew populations of *Eschscholiza californica* (California poppy) on soils which they do and do not occur naturally. *E.californica* and *Avena fatua* were grown singly and together, in different proportions, on an artifical slope with a constant water table. When grown alone, poppies survived in greater numbers and flowered closer to the bottom of the slope than when grown competing with *A. fatua*. They responded more plasticly to intraspecific than to interspecific competition. However, mortality was higher in response to interspecific competition. Cook (1965) concluded that there also seemed to be a certain degree of "genetic specialization" in relation to edaphic conditions.

Plant Associations

Turkington and others examined some of the complexities of species relationships in communities where several legumes and several grasses are common. In their first report, (Turkington, *et al* 1977) demonstrated that different legumes formed consistent relationships with different grass species. Each legume was strongly associated with a particular combination of grass species. The authors suggested that each legume-grass combination is selected through the ability of the combination to utilize the soil environment more efficiently than random combinations of species.

The most striking result from the second study by Turkington (1979) was that the number of survivors (*T. repens* and *M. sativa*) and the dry weight (*T. repens*) was greatest when the species were transplanted back into swards of the grass species from which they had been sampled.

The above relationship was further strengthened by an indepth study by Turkington and Harper (1979). The most remarkable feature to emerge from this experiment was the strength of the interaction between site and clover "type" in the field, and between grass-associate and clover "type" in the sown plots. Each clover "type" performed best when grown in the site from which it had originally been sampled, or in association with the grass species that dominated that site. This feature is known as the "Principal Diagonal Effect". Turkington and Harper (1979) felt that this relationship points to a finer and more subtle specialization of organisms to the environment than had previously been recognized within plant communities.

In the final study of the series, Turkington (1983) attempted to influence the patterns of dry matter distribution for two genotypes of *T. repens* by altering their competitors.

Both genotypes responded to increasing percentages of unfamiliar neighbours by producing more inflorescences and by distributing proportionately more dry matter to inflorescence production.

Shrub Establishment

Serious attempts have been made to restore perennial grasses to rangelands, as well as shrubs to winter game ranges. The purpose of several studies have been, therefore, to gain an understanding of the basic factors controlling competition between the desired and undesired plant species.

Schultz, *et al* (1955) found that there was a direct correlation between the amount of herbaceous vegetation, especially grasses, and the number and vigour of brush seedlings when the two kinds of plants were growing together. Brush seedling mortality was correlated with grass density. It was felt that although competition for nutrients, light, and space occurs; the availability of soil moisture is the most striking factor influencing seedling survival.

Holmgren (1956) dealt with the influence of annual weeds on establishment, growth rate, and survival of artifically seeded bitterbrush (*Purshia tridentata*). A variety of "key" aspects of the competitive effect of annuals were revealed. These aspects were:

(1) In cheatgrass stands, few bitterbrush seedlings were able to survive the first summer. The competitive effect of cheatgrass generally becomes manifest early in the growing season, coinciding with its period of rapid growth.

(2) Bitterbrush seedlings are better able to compete with broad-leaved, summer-annual weeds than with cheatgrass. The competitive effect of broad-leaved annuals becomes manifest later in the first growing season, coinciding again with their period of rapid growth. Therefore, die-off of bitterbrush seedlings takes two to three years.

(3) Bitterbrush seedlings that grow their first season in freedom from competing weeds are vigorous. Subsequent invasion of weeds results in only neglible or no mortality, but it causes a slowing up in the growth rate of bitterbrush.

Litav, *et al* (1963) identified similar relationships, as above, in their work in the Mediterranean hill region of Greece. They were looking specifically at *Poterium spinosum*, the most common shrub in the Mediterranean region, and *Avena sterilis*, the leading annual.

It has been determined that annual grasses outcompete shrub seedlings by extending their roots more rapidly during the winter, thus gaining control of the site before the shrub seedlings become established. The early maturation of annuals depletes the stored moisture supply prior to the needs of shrubs (Harris 1967). The above relationship was largely determined from a study between *Bromus tectorum* (European cheatgrass) and *Agropyron spicatum*.

Experiments Combining Density and Species Mixture

A few researchers have noted that interactions between density and species mixture can have a pronounced effect on productivity. The important findings from this group of experiments are summarized in the following section.

Production Potential

Preliminary results in this area are as follows:

(1) a dominant species can be expected to suppress a weak competitor in all mixtures at all but the lowest densities (Black 1960 - working with *Trifolium pratense* and *Medicago sativa*), and

(2) mixtures tended to yield more than the mean yields of their two components and tended to have a greater consistency of performance (England 1968 - working with two cocksfoot and two ryegrass varieties).

Timing of Growth

Buttery and Lambert (1965) examined the growth and productivity of *Glyceria maxima* and *Phragmites communis* in a primary fen in which "A" was known to have succeeded "B".

Where *G. maxima* showed maximum growth, *P. communis* was completely suppressed. The success of *G. maxima* over *P. communis* under such conditions appeared to be due to its rapid production of an extremely dense sward in spring, before the *P. communis* shoots could develop.

Where some reduction in *G. maxima* growth occurred, *P. communis* shoots penetrated the sward and increasingly intercepted the available light. Therefore, *P.communis* was a serious competitor to *G. maxima* only after a marked reduction in *G. maxima* productivity.

Resource Allocation

Robson (1968) studied the life histories of all S.170 tall fescue tillers grown in large pots from April 1962 to July 1964. Competition for light and nutrients in May, caused many tillers to die. However, the surviving plants did not vary greatly in size. Robson theorized that a tiller in a favoured position, producing excess substrates, utilized these substrates to expand daughter tillers. Thus, while a single favourably placed tiller might not dominate a plant in the sense that it would grow much larger than all other tillers, it might dominate in the sense that its offspring would become more numerous than those of less favourably place tillers.

Plastic Growth Response and Mortality

Marshall and Jain (1969) found that density induced greater mortality and a striking plastic reduction in the size and reproductive potential of both *Avena fatua* and *Avena barbata*. Furthermore, the weaker competitor (*A.*

barbata) had relatively greater mortality and plastic growth responses. It was postulated that although co-existence between these two species could occur, the percentage of *A. barbata* expected at equilibrium varied from approximately 30% at the lowest density to less than 10% at the highest density. This significantly lower percent composition of the weaker competitor illustrates a strong interaction between increasing density and species mixture with the intensity of competition from the dominant species. In a different approach, Mack and Harper (1977) determined the effects of neighbours are not diffused through a population, but involve rather precise, quantifiable local interactions. They also noted that 69% of the variation in individual plant weight can be accounted for by the size and distance, as well as the pattern of distribution of neighbours.

Plant Associations

In a general survey paper, Turkington and Cavers (1979) showed that the presence of grasses slowed down the rate of clump formation in legumes and hindered the rate of development of associations.

In a more in-depth study, Turkington and Harper (1979b) found that *T. repens* avoids the interspecific interference of clumped species and has a low frequency of intraspecific contacts. Turkington and Harper (1979b) generalized that for any species where intraspecific competition is weaker than interspecific effects, survivorship would be greater in clumps. If intraspecific competition is greater, it would "pay" to wander and explore.

Competition Experiments Incorporating Environmental or Genetic Variables

Although these types of factors are not being considered in the present study, I felt it was important to realize that significant competition studies incorporating these factors have been carried out. The effects of the environment must be considered when interpreting results of any field study and allowances for genetic variability must take place to avoid confounding their effects with the measured factors.

Environmental Influences

An early experiment was designed by Snaydon (1962) which looked at the influence of competition between contrasting populations of *Trifolium repens* on contrasting soils. A greenhouse pot study was established where populations from each soil type were grown seperate or mixed, on each of the two soils (acid and calcareous).

It was determined that the ability of the "calcareous" populations to utilize iron, magnesium, and potassium at low concentrations gave them a slight competitive advantage over the "acid" populations.

A more recent study by Lee and Carvers (1981) examined the effects of shade on growth, development, and resource allocation patterns of three species of foxtails (*Setaria*). It was illustrated that the three species demonstrated morphological adaptations to the shading treatments imposed (71%, 41%, and 19% of full sunlight), as follows:

(1) stem elongation occurred with increased shade,

(2) leaf area became relatively greater with reduced light intensity because the biomass allocated to leaves was used to produce large, thin leaves; rather than smaller, heavier ones,

(3) reduction in reproductive effort occurred in response to reduced light, and

(4) an increased percentage of biomass was allocated to leaves - with a corresponding drop in stem biomass- as shade was increased.

Genetic Influences

An extensive study of the interactions between various genotypes in four varieties of barley, four varieties of wheat, and eight barley genotypes which had survived up to 18 generations of mutual selection in a heterogeneous population was carried out by Allard and Adams (1969). The authors concluded that natural selection appeared to preserve genotypes which interact synergistically.

Turkington (1983c) summed up his work with genotypes of *Trifolium repens* by stating that the measured characters (ie: leaf production, final dry weight, flower production) were subject to some degree of genetic control and modified to varying extents by the environment.

Competition Experiments Dealing with Forest Trees

Studies on the effects of density on forest trees have a long history. Evert's (1973) annotated bibliography lists 388 citations covering the period from about 1950 to 1971. The following section reviews 15 important studies which help to trace the historical development of forest competition experiments.

Resource Allocation

Most studies on resource allocation have dealt with mature forest stands. Borman (1965), working with suppressed white pine (*Pinus strobus*) trees, identified an important ecological phenomena. He found that, although food and growth regulators moving to the roots failed to stimulate the cambium to produce secondary xylem, they were sufficient to produce primary root growth and possibly secondary phloem. Therefore, in suppressed trees the investment of a higher and higher proportion of the decreasing energy supply is directed into tissues that require annual renewal. The net effect is to prolong the survival of the individual.

Baskerville (1965) studied resource allocation in 38 to 45 year-old balsam fir stands. He looked at the distribution of dry matter in the above-ground tree components: foliage, cones, stem wood, stem bark, branch wood, branch bark, and dead branches. As with Borman (1965), Baskerville identified an unique adaptation of suppressed trees to prolong their life through greater efficiency in energy production. In general, trees with small crowns produced more tissue per pound of foliage than trees with large crowns. Baskerville (1965) hypothesized three explanations for this phenomenon:

(1) small crowned trees have a low light saturation point of photosynthesis,

(2) small crowned trees have a high proportion of shade needles in suppressed crowns, and

(3) the favourable distribution of dry matter among tree components in small trees.

Morris (1983), dealing with juvenile seedlings, illustrated the competition effects of density and species mixture on a suppressed tree species. As overall density increased and species composition of the suppressed tree species decreased, the following effects occurred:

(1) reduced growth rates,

(2) increased mortality, and

(3) an adjustment to a lower leaf weight/total weight ratio.

The species used in this greenhouse experiment were *Populus tremuloides* (dominant species) and *Populus balsamifera* (suppressed species).

Stand Development

The trees in juvenile, natural stands are distributed more or less at random, as a result of the random dispersal of seeds. However, this relationship is species dependent. As the stand matures, there is a slight tendency toward a more uniform spacing as competition increases and unsuccessful competitors are removed from the stand (Cooper 1961).

Laessle (1965), working in natural stands of sand pine, subtantiated Cooper's (1961) findings. Laessle showed that stands under 23 years old were either clumped or essentially randomly distributed. Stands older than 23 years of age showed significant to highly significant movement toward regular spacing.

The above relationship was tested in plantations of *Picea sitchensis* by Ford (1975). Three major conclusions were determined from this study:

(1) the establishment of local hierarchies occurred during the seedling phase, when relative growth rate (RGR) was linearly related to plant weight,

(2) the development of a distinct upper canopy of large plants occurred which were evenly distributed in space and had similar maximal RGR's, and

(3) there was stability in the upper canopy, but mortality of small plants did occur.

The relationship of local hierarchies, discussed by Ford (1975), was studied in more detail by Moller, *et al* (1978). They found that soon after a stand of woody plants becomes established the size-frequency distribution is a negatively skewed, bell-shaped curve. This distribution subsequently becomes positively skewed and is maximum just before suppressed trees begin to die. Eventually the distribution approaches normality after substantial thinning occurs.

Effect of Thinning

Staebler (1956) studied the effect of a controlled release on the growth of individual Douglas-fir trees. He found that a thinning program which removed the chief competitor of a selected crop tree markedly increased the growth of that tree. Additional, but much smaller increases in growth, were obtained by the removal of two to three competitors.

Effect on Diameter by Competitors

Steneker (1963) carried out a study to assess competition in a white spruce-trembling aspen stand. The purpose of the investigation was to determine how the diameter increment of individual white spruce trees was influenced by the proximity of surrounding trees.

Basal area summation gave the best correlation with diameter increment, as 55% of the variance in diameter increment was accounted for by the basal area of surrounding trees within a ten foot radius. An additional 21% of the variation was accounted for by including trees within a 15 foot radius.

Genetic Relationships

An interesting relationship was illustrated by Sakai and Mukaide (1967) with their work in standing forests of *Cryptomeria japonica*. It was found, by partitioning the phenotypic variance or covariance into genetic, environmental, and competitional components, that in the clonal forests both the genetic and competitional variances were statistically zero (ie: trees in a clone are isogenic and they do not compete with each other). In seed-propagated forests, however, competitional variance proved to be considerably large.

This relationship was also identified by Tauer (1975), who investigated the intergenotypic competition in black cottonwood grown under greenhouse conditions. However, the author did warn that, unlike annual crops, trees may require several years of growth before their final competitive relationships are concretely established.

Competition Models

One area of competition research with forest trees which has had extensive development, is with the building of competition models. In general, these models attempt to predict the growth of a subject tree in response to competition from neighbouring trees.

Opie (1968) presented one of the first models to predict individual tree growth based upon the concept of "zones of influence". The zone of influence of a tree was defined as the total area over which the tree may at present obtain or compete for site factors. Therefore a maximal zone would be the area that could be occupied by a tree when unrestricted by competition.

The model is as follows:

$$S = (BAF/\ A_i) \quad \times \quad (A_i \times i) \qquad [2]$$

where: S - basal area density (square feet per acre),

BAF - basal area factor,

A_i - the area covered by parts of "i" circles.

This model places a weighting on competitors - the smallest competitor contributes less to the estimate than does the large competitor, regardless of the distance to the subject tree.

Bella (1971) advanced a new hypothesis regarding inter-tree competition, and the hypothesis was defined as a mathematical model. The model represented competitive interaction between individual trees. It consisted of two basic components:

(1) the influence zone of each tree (which is a function of its size), and

(2) the amount and nature of interaction (which depends on the distance between and relative size of the competing tree and its competitors and also on a power of relative tree sizes).

Bella (1971) felt that the model's sensitivity to parameter changes indicated that both components were equally important in describing the competition effect. Competition indicies, of this model, accounted for approximately 57% of the variance in diameter increment.

In 1976, Daniels presented a model modified from Hegyi's index (1974). The model was:

$$CI_i = (D_j / D_i) \,/\, DIST_{ij} \qquad [3]$$

where: CI_i - competition index of subject tree "i",
D_i - dbh of tree "i", and
$DIST_{ij}$ - distance between tree "i" an competitor "j".

Daniels (1976) defined "n" to include all trees within a 3.05m (10 ft) radius of the subject tree. However, "n" was changed so that competitors were choosen based on their size and distance from the subject tree - neighbours having influence circles intersecting the subject tree were included as competitors.

In a recent study, Weiner (1984) added an additional variable of neighbour size (Si). This new model measures interference on a subject tree, as follows:

$$W = k \times S_i / (d_i^2) \qquad [4]$$

where: W - interference,

k - the effect of a neighbour (as expressed as a constant),

S_i - size of the ith neighbour, and

d_i - distance to the ith neighbour.

The model was tested with data from a 20-year old, even-aged stand of *Pinus rigida*. The total size of the neighbours within two metres of a subject tree was shown to clearly be the most important factor in determining the differences in individual growth rates.

Jack Pine Ontogeny

Pinus banksiana (jack pine) is a short-lived, small-to-medium coniferous forest tree. In general, jack pine is found on burned areas where there is little severe plant competition and where soil is acid and has very good drainage and aeration (Kaufman 1945).

Natural stands of jack pine are confined largely to soils of the podzol region: melanized sands, podzolic sands, sandy podzols, and the gley-podzolic sands (Wilde, *et al* 1949). Jack pine grows most commonly on level to gently rolling sand plains, usually of glacial outwash, fluvial, or lacustrine origin (Eyre and LeBarron 1944). It also occurs on eskers, sand dunes, rock outcrops, and bald rock ridges (Raup 1946).

In the boreal forest region the most common associates of jack pine are *Populus tremuloides*, *Betula papyrifera*, *Picea mariana*, and sometimes *Picea glauca* and *Populus balsamifera* (Raup 1946). Jack pine is one of the most intolerant trees in the region (Graham 1954). In Ontario, 16 species have been arranged in descending order of tolerance from *Abies balsamea*, the most tolerant, to *Prunus pensylvanica*, the least tolerant. Jack pine is ranked 13 - less tolerant than *Pinus resinosa* but more tolerant than *Populus tremuloides* (Horton and Bedell 1960). Furthermore, it has been found that jack pine is more tolerant in the seedling stage (Bates and Roeser 1928). Young jack pine seedlings can exist in light as low as 2.4 percent of full sunlight. However, more light is required for establishment (Shirley 1945).

In general, jack pine is classed as a pioneer species on burns or other exposed sandy sites. However, in the absence of fire or other catastrophes, jack pine tends to give way to other more tolerant or faster-growing species, except on the poorest, driest sites where it may long persist and form an edaphic climax (Moss 1953; Kabzems and Kirby 1956).

Trembling Aspen Ontogeny

Populus tremuloides (trembling aspen) is a small-to-medium, fast-growing, and generally short-lived deciduous tree. Trembling aspen grows on a great variety of soils ranging from shallow rocky soils and loamy sands to heavy clays. However, better growth and development occur on soils that have developed from a gray glacial drift rich in lime (Stoeckler 1948). In addition to having an abundance of lime, the best aspen soils are usually porous, loamy, and humic (Zehngraff 1947).

Trembling aspen grows with a large number of trees and shrubs over its extensive range. In the boreal forest, trembling aspen is found most commonly with *Pinus banksiana*, *Picea mariana*, *Betula papyrifera*, and *Picea glauca*.

Ripe trembling aspen seed are not dormant, and natural germination occurs within a day or two after dispersal if a suitably moist seedbed is reached (Faust 1936). The primary root of seedlings has very slow growth for several days, and during this critical period the young germinate depends upon a brush of long delicate hairs to perform the absorptive functions (Moss 1938). These hairs are effective only if the surface soil is moist.

Trembling aspen more commonly reproduces by means of root suckers, much less commonly by root collar sprouts, and occasionally by stump sprouts (Sandberg and Schneider 1953). In general, the number of suckers produced is proportional to the degree of a cutting, with the greatest number arising after a complete clear cut (Zehngraff 1949).

Trembling aspen is rated as very intolerant, a characteristic it retains throughout its life (Baker 1949). It has been classed as an aggressive pioneer species and readily colonizes burns (Shirley 1941).

Present State of Knowledge

Practically all of the work on the competition effects of density on forest trees has dealt with the problems of plantation spacing and modeling growth under various levels of density. Furthermore, those studies which have looked at natural stands dealt mainly with mature stands. Therefore, most densities studied to date are much lower than those of juvenile seedling populations, and published results (reviewed by Evert 1971) have limited application to the design of a study such as the present one.

Formal studies of species mixes are even more rare than ecologically oriented seedling density studies in forest trees. Most of the information on species interactions has stemmed from observation in natural systems.

Jack pine and trembling aspen are both classed as intolerant, pioneer species which readily colonize similar disturbances (ie: burns, clear cuts). Due to this close association, it would be expected that these two species often compete with each other in nature. The present study is the first such work to look specifically at the competitive relationships between jack pine and trembling aspen. The experiment is an extension of work initiated by Morris (1983), as previously cited.

METHODS AND MATERIALS

Greenhouse Study

Experimental Design

A randomized complete block design was used for a greenhouse trial involving three density levels and five species mixtures in a "replacement series". A total of 15 treatment combinations were included in each of five blocks. These combinations are outlined in Table 1.

Table 1. Treatment combinations for the greenhouse study.

Treatment Comb.	Sp. At*	Comp. Pj*	Density (cm^2/plant)	Density (plant/m^2)	Border rows
1	100	0	1.00	10,000	3
2	75	25			
3	50	50			
4	25	75			
5	0	100			
6	100	0	3.52	2,844	2
7	75	25			
8	50	50			
9	25	75			
10	0	100			
11	100	0	13.71	729	
12	75	25			
13	50	50			
14	25	75			
15	0	100			

* - At and Pj are abbreviations for trembling aspen and jack pine, respectively.

The principal reason for the use of such high densities in the greenhouse study was to ensure that adequate competition between neighbouring plants in all treatments occurred during the 12 week growing period. This intense competition accentuated the effects on plant development of the significant factors.

The plants located within the border rows were not included in any analysis.

There are several possible ways that the plants could be arranged to produce the desired mixtures. A systematic layout, as illustrated in Figure 1 and 2, was selected in order to maintain a high level of interspecific competition within the various mixtures.

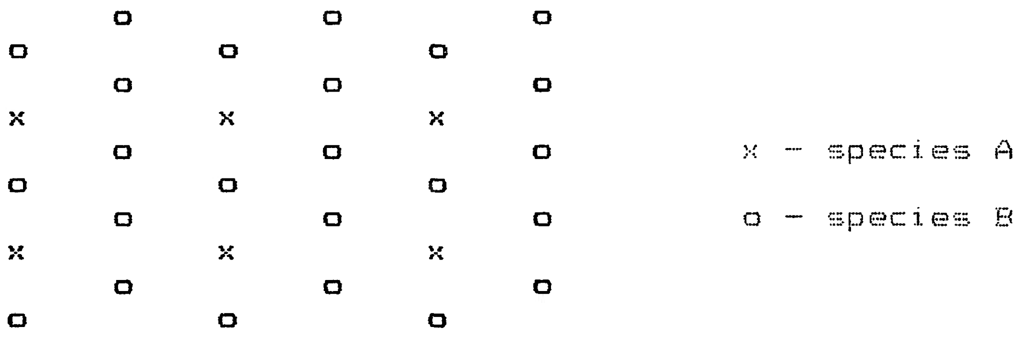

Figure 1. Planting design for the 75/25 (25/75) mixture.

o	x	o	x	o	x
x	o	x	o	x	o
o	x	o	x	o	x
x	o	x	o	x	o
o	x	o	x	o	x

x - species A

o - species B

Figure 2. Planting design for the 50/50 mixture.

The linear model and analysis of variance table for this experimental design are outlined in Appendix 1. The design allows for the testing of both main effects (density and species mixture) and their interaction.

Establishment of Experiment

In the spring of 1983, seeds from 10 trembling aspen trees were collected near Thunder Bay, Ontario. A local jack pine seed source (northern Ontario), which included numerous open-pollinated families, was obtained in the spring of 1984. All the seed of each species was mixed prior to sowing.

A total of 75 containers (50 - 20cm diameter plastic pots; 25 - 34cm diameter pots) were filled with a sphagnum peat moss - vermiculite soil mixture (60% peat / 40% vermiculite by weight) in early June, 1984. The larger pots were needed to adequately accomodate the lowest density level (729 plants/m^2).

On June 19, 1984, several seeds were sown, at each pre-determined location, in the prepared containers as dictated by treatments. These containers were then placed in mist chambers for six days. An additional period of three weeks was needed to thin seeded locations and transplant healthy plants into locations where all germinants had died. There was 100% occupancy at the initiation of periodic measurements on July 21, 1984. Containers were watered as required and given weekly fertilizer applications of 20N-20P-20K, at 100 parts per million.

A serious leaf and shoot blight (*Fusicladium* spp.) was detected on the trembling aspen in mid-July. Bi-weekly spraying of Benlate and Manzate, alternately, (at a concentration of 1.0 g/l) controlled the bacterial disease. This situation was further complicated by the presence of red-spider mites on the aspen. Weekly spray treatments of Kelthane (at a concentration of 2.5 ml/gal) controlled the effect of the mites. Although the majority of the plants survived the onslaught of the bacterial infection and the parasitic activity, reductions in growth rate were noted during weeks six through eight of the study.

Measurement of Experimental Results

Turkington (1983) illustrated that periodic growth measurements could provide additional information concerning the sequence of events in time. Various treatments may be the same size at harvest, but they may have achieved this by quite different means. Therefore, three plants per species per treatment combination per block were randomly selected for the following periodic growth measurements:

(a) total height (cm),

(b) two measurements of crown diameter (cm) - at the widest diameter and at a right angle to the first measurement, and

(c) crown height - from the uppermost tip of new growth to lowest living leaf (cm).

By combining the crown measurements, a value for crown volume (cm^3) was obtained using the following formulae:

$$V = \Pi r^2 h \quad , \qquad [5]$$

where: V - volume (cm),

r^2 - the square of crown radius (cm),

h - crown height (cm),

Π - constant (3.1415926).

It should be noted that variations from the cylindrical crown volume calculated may differ from actual crown forms for both species. Therefore, the values used in any analysis must be considered as relative values rather than absolute values.

Plants were allowed to grow for a period of 12 weeks and were harvested on Sept.10, 1984. At this time, six randomly selected plants per species were harvested from each container. Above-ground parts of the plants were placed, individually, in paper bags and dried at 100 degrees celcius for 24 hours. The survival percentage was determined for each pot at harvest. Dry weights for shoot and leaves of individual plants were determined in milligrams.

Plot means were then computed, by species, for the following:

(a) mean oven dry weight/plant (mg),
(b) leaf weight/total weight ratio (%),
(c) survival (%), and
(d) biomass production per unit area (g/m^2).

Analysis of Experimental Results

Relative yield (deWit 1960) components were computed from biomass per unit area and Relative Crowding Coefficients (deWit and van den Bergh 1965) from data on mean biomass per plant. Relative yield values were then presented in replacement series diagrams, as discussed by Harper (1977).

The analysis of variance was used to evaluate the effects of density and species mixture on jack pine and trembling aspen, independently. The following growth parameters were tested:

(a) survival (%),
(b) oven dry weight (mg),
(c) final height (cm),
(d) crown volume (cm^3), and
(e) leaf weight/total weight ratio (%).

Simple correlations between the growth parameters analyzed are presented in Appendix 2.

Tukey's procedure was used to determine whether statistical differences between treatment means occurred. Graphical comparisons were made to visually identify the significant variations in growth patterns effected by density and species mixture.

Field Study

Experimental Design

A split-plot design which included six replications of five density levels (main plots) and five species mixtures (sub-plots) was used in the field trial. The 25 treatment combinations are outlined in Table 2.

As in the greenhouse test, the species in the mixtures were systematically located within sub-plots. A layout for one replication (block) is illustrated in Appendix 3. All species mixes within each density level were located together. This design not only aids in planting and measuring; but also minimizes the border effects from the surrounding plots.

The linear model and analysis of variance table for this experimental design are outlined in Appendix 4. The design allows for testing of both main effects (density and species mixture) and their interaction.

Table 2. Treatment combinations for the field study.

Treat. Comb.	Sp. Mixture		# of plants per plot	Density (cm^2/ plant)	Density (plants/ m^2)	# of border rows
	At*	Pj*				
1	100	0	144	4.00	2,500	4
2	75	25				
3	50	50				
4	25	75				
5	0	100				
6	100	0	144	20.25	494	4
7	75	25				
8	50	50				
9	25	75				
10	0	100				
11	100	0	121	49.00	204	3
12	75	25				
13	50	50				
14	25	75				
15	0	100				
16	100	0	100	121.00	83	
17	75	25				
18	50	50				
19	25	75				
20	0	100				
21	100	0	100	576.00	17	2
22	75	25				
23	50	50				
24	25	75				
25	0	100				

* - At and Pj are abbreviations for trembling aspen and jack pine, respectively.

Establishment of the Experiment

The seed source for this portion of the project was the same as that for the greenhouse study. On April 16, 1984, 125 trays of the small Spencer-Lemaire containers ("Ferdinand") were seeded to jack pine and placed in mist chambers for five days. On April 25, 1984, another 125 trays were seeded to trembling aspen and placed in mist chambers for five days. The later seeding of aspen was necessary in order to ensure that the height of all seedlings was relatively similar at time of out-planting.

All trays were thinned to one plant per compartment during the first week of May, 1984. Trays were moved into a shade-house on June 4, 1984 (7 weeks after sowing). Two weeks later they were placed in full sunlight.

The selected test area (approximately 1000 m^2) is located in Thunder Bay, Ontario on Lakehead University property near the School of Forestry's nursery and adjacent to a larger test site prepared for provenance tests. A preliminary soil analysis was carried out in the fall of 1983, in order to determine the suitability of the site. The soil description is given in Appendix 5. There was no apparent moisture gradient, hard pan, or other features which might detract from the area as a test site.

The area was sprayed with Glyphosate (Roundup) on May 28, 1984 and subsequent dead vegetation was removed from the site. A private contractor plowed and disked the area in mid-June, as for an agricultural crop. The area was further worked with a roto-tiller and rake before planting commenced on June 22, 1984.

Planting of the six replications took a total of two and one-half weeks. Additional trees were used as replacements for those seedlings that were unsuccessfully transplanted. Complete weed control was accomplished, manually, during the entire growing season - a total of three sets of weedings were required.

The occurence of a leaf and shoot blight on the aspen (*Fusicladium* spp.) near the end of July made it necessary to spray benlate and manzate (at a concentration of 1.0 g/l), alternately, until the end of August. Weekly sanitation (removal of severely infected leaves) was carried out to reduce the spread rate of the bacterial infection.

Populations of woolly aphids on the aspen were erradicated by spraying malathion (at a concentration of 5 ml/gal) on July 30, 1984.

Kelthane (at a concentration of 2.5 ml/gal) was sprayed in mid-August to combat the presence of red-spider mites on the aspen.

The plots were watered when required (during a dry period in July and early August), using a Wajax fire pump and a sprinkler system. The seedlings were given an initial fertilizer treatment, after planting, at 200 parts per million of 20N-20P-20K. On July 30, 1984, the plots were fertilized with ammonium nitrate (at a rate of 200 kg/ha) and super phosphate (at a rate of 100 kg/ha).

Measurement of Experimental Results

Four plants per species per treatment combination per block were randomly selected, excluding border plants, for periodic growth measurements. The first measurement was taken five weeks after planting and continued for eight and one-half weeks (Sept. 19, 1984). Measurments recorded included:

(a) total height (cm),

(b) two measurements of crown diameter - at the widest diameter and at a right angle to the first measurement (cm), and

(c) crown height - from the uppermost tip of new growth to the lowest living leaf (cm).

Crown volume data were then calculated, as in the greenhouse study (see function [5]).

Analysis of Experimental Results

An analysis of variance was used to evaluate effects of density and species mixture on jack pine and trembling aspen, independently. The following first season growth parameters were tested:

(a) total height (cm), and

(b) crown volume (cm^3).

Since the field trial will be continued for three to four growing seasons before harvesting, no biomass data were available for analysis.

Tukey's procedure was used to determine whether statistical differences between treatment means occurred. Graphical comparisons were made to visually identify the significant variations in growth patterns effected by density and species mixture.

RESULTS

Greenhouse study

Height and crown volume data were taken periodically during the 12 week experiment. These data have been summarized in Appendices 6 and 7, respectively. The standard deviations of the means for each treatment have been tabulated and are presented in these appendices.

At the time of harvest, survival percentage was determined and is presented in Table 3.

Table 3. Arithmetic mean of survival percentage by density and species mixture for greenhouse study.

Density (plants per m^2)	Species Composition 100/0 Aspen	100/0 Jack Pine	75/25 Aspen	75/25 Jack Pine	50/50 Aspen	50/50 Jack Pine	25/75 Aspen	25/75 Jack Pine	0/100 Aspen	0/100 Jack Pine
	....	....	....	....	%	....	....	....	....	....
10,000	72		81	93	89	100	89	98		98
2,844	73		85	100	90	98	100	98		100
729	96	–	97	100	98	100	100	100	–	100

It can be seen that jack pine survival was only minimally affected by increased density (Table 4). Only at the highest density and in the lowest jack pine percent (75At/25Pj) was there any drop in survival.

The survival of trembling aspen, however, was found to be greatly affected by density and species mixture (Table 4). The lowest survival occurred in the 100At/0Pj mixture. The survival percentage increased as the aspen percentage decreased, peaking at the 25At/75Pj mixture. Furthermore, a pronounced increase in survival occurred at the lowest density (729 plants/m^2). Figure 3 gives additional information on the interacting effect density and species mixture had on trembling aspen survival.

Table 4. Analysis of variance for survival percent after an arc sine transformation.

trembling aspen:

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F
Block	4	449.34		
δ	0			
Density	2	9237.10	4618.55	26.91**
Block-Density	8	1372.79	171.60	
Sp.Comp.	3	4271.32	1423.77	17.72**
Block-Sp.Comp.	12	964.13	80.34	
Density-Sp.Comp.	6	2883.13	480.52	2.95*
Block-Density-Sp.Comp.	24	3904.15	162.67	
Exp. Error	0			
TOTAL	59	23081.96		

jack pine:

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F
Block	4	640.68		
δ	0			
Density	2	706.73	353.37	4.53*
Block-Density	8	624.38	78.05	
Sp.Comp.	3	99.77	33.26	1.43
Block-Sp.Comp.	12	277.97	23.16	
Density-Sp.Comp.	6	546.80	91.13	1.77
Block-Density-Sp.Comp.	24	1235.87	51.49	
Exp. Error	0			
TOTAL	59	4132.20		

Table 5. Results of a comparison of density treatments for average survival percent using Tukey's procedure.

Species	Density (plants per m^2)	Average Survival Percent	*Means contrasted at: p = .05	*Means contrasted at: p = .01
		.... %		
Aspen	10,000	81.69	a	a
	2,844	90.96	a	a
	729	99.58	b	b
Jack pine	10,000	98.97	a	a
	2,844	99.89	a	a
	729	100.00	b	a

* - Means spanned by the same letter (a,b) are not significantly different at the specified confidence level.

Table 6. Results of a comparison of species mixture treatments for average survival percent using Tukey's procedure.

Species	Species Composition	Average Survival Percent	*Means contrasted at: p = .05	*Means contrasted at: p = .01
	.... %	....		
Aspen	100	82.33	a	a
	75	92.08	b	a , b
	50	95.31	b , c	b
	25	97.93	c	b

* - Means spanned by the same letter (a,b,c) are not significantly different at the specified confidence level.

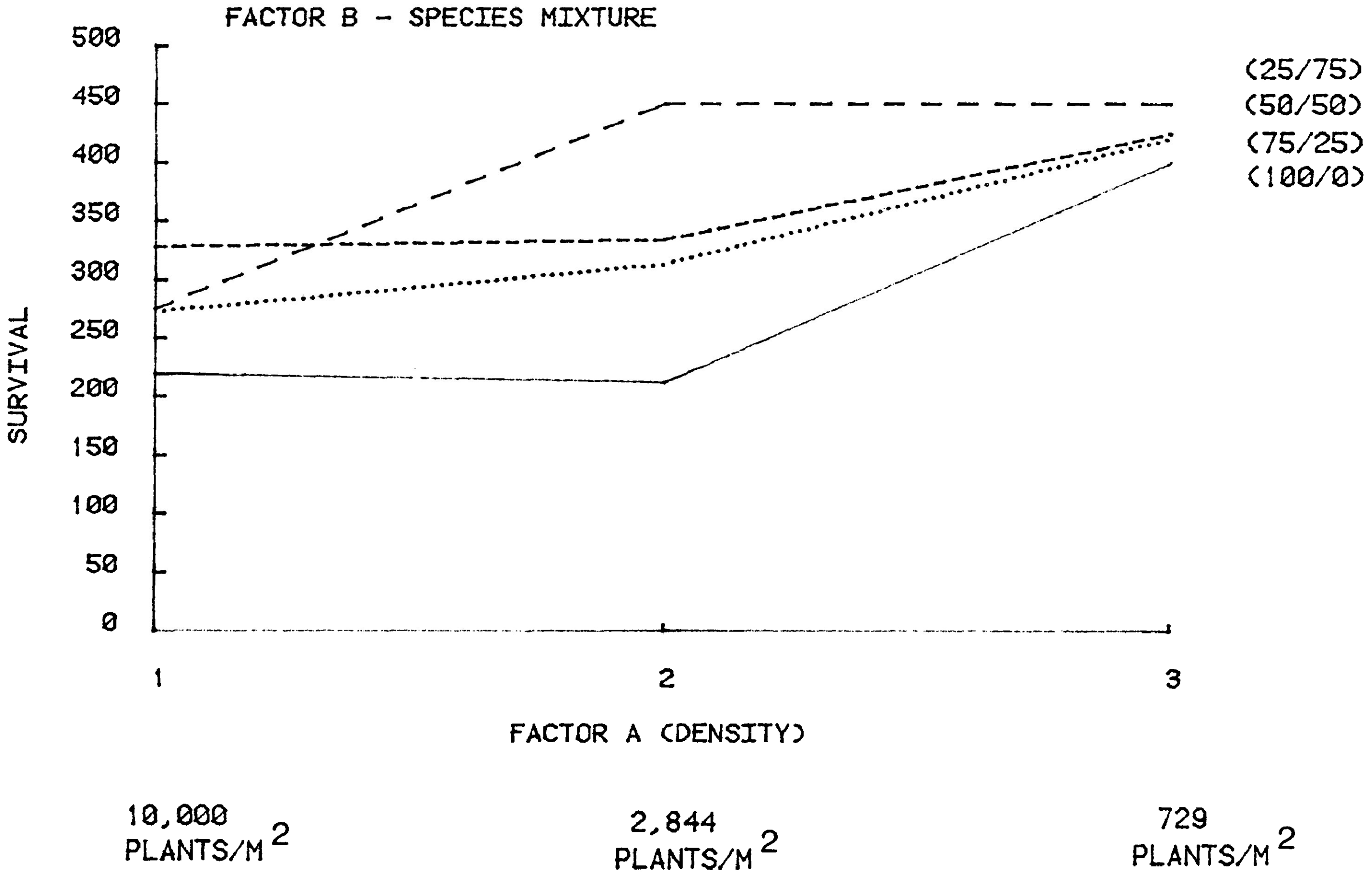

Figure 3. A graphical representation of the interaction between density and species mixture on trembling aspen survival in greenhouse study.

Figure 4 includes three graphs which illustrate variation in height growth due to density changes and species mixtures. The data used for the construction of these graphs are found in Appendix 6.

The most apparent effect illustrated in Figure 4 is the height suppression caused by increasing density. This effect occurred in both trembling aspen and jack pine, and was found to be highly significant (Table 7).

Figure 5 includes three graphs which illustrate variation in crown volume accumulation, as related to changes in density and species mixtures. The data used for the construction of these graphs are found in Appendix 7.

As with final height, final crown volume was also highly significantly affected by density changes (Table 9, 10). Figure 6 provides an additional look at the interacting effect of density and species mixture on final crown volume.

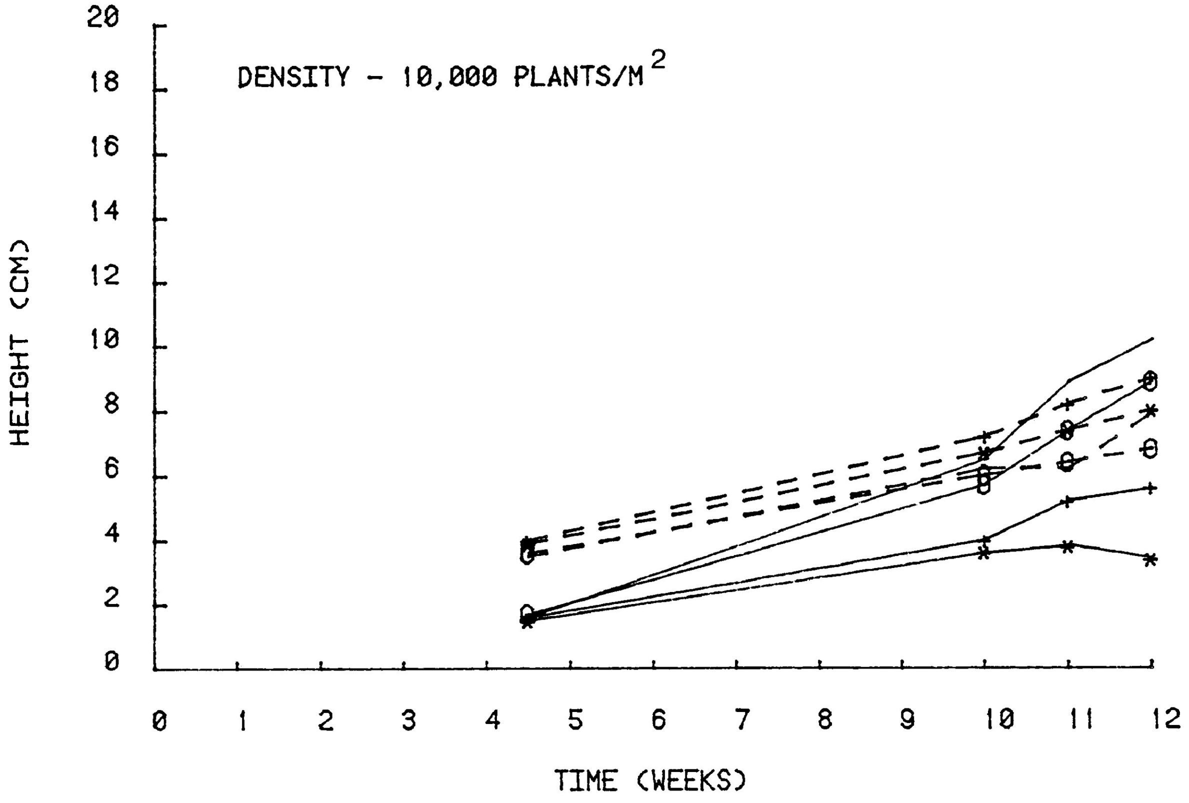

Figure 4a. Height growth comparisons over time at a density of 10,000 plants/m^2 for greenhouse study.

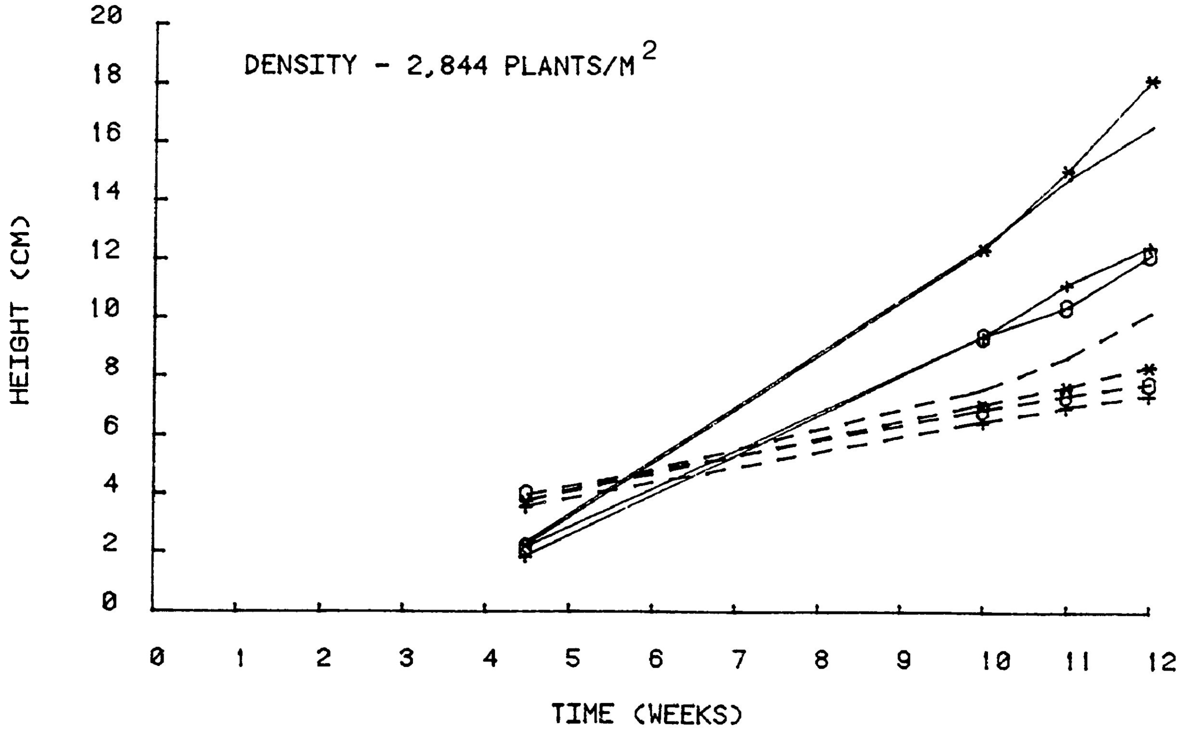

Figure 4b. Height growth comparisons over time at a density of 2,844 plants/m^2 for greenhouse study.

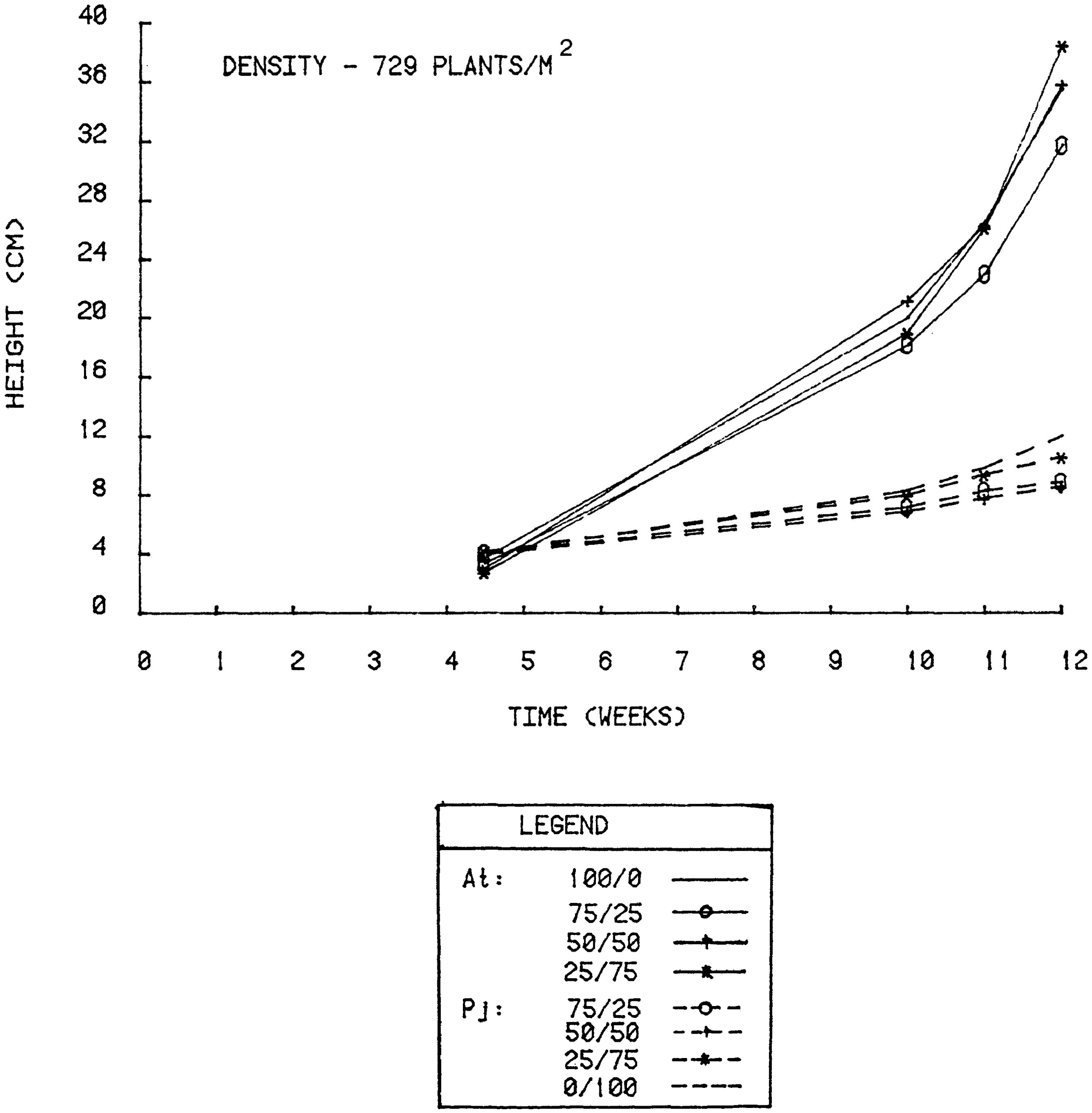

Figure 4c. Height growth comparisons over time at a density of 729 plants/m^2 for greenhouse study.

Table 7. Analysis of variance for total height at harvest in greenhouse study.

Trembling aspen:

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F
Block	4	539.72		
δ	0			
Density	2	8657.24	4328.62	40.94**
Block-Density	8	845.89	105.74	
Sp.Comp.	3	115.18	38.39	<1
Block-Sp.Comp.	12	760.45	63.37	
Density-Sp.Comp.	6	288.31	48.05	<1
Block-Density-Sp.Comp.	24	1435.35	59.81	
Exp. Error	0			
TOTAL	59	12642.14		

jack pine:

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F
Block	4	0.95		
δ	0			
Density	2	23.40	11.70	11.82**
Block-Density	8	7.89	0.99	
Sp.Comp.	3	4.88	1.63	<1
Block-Sp.Comp.	12	25.58	2.13	
Density-Sp.Comp.	6	15.70	2.62	1.87
Block-Density-Sp.Comp.	24	33.64	1.40	
Exp. Error	0			
TOTAL	59	112.04		

Table 8 summarizes Tukey's procedure, which was used to determine whether the mean heights were statistically effected by the density treatments.

Table 8. Results of a comparison of density treatments for average final height using Tukey's procedure.

Species	Density (plants per m^2)	Average Final Height	*Means Contrasted at:	
			p = .05	p = .01
		... cm ...		
Aspen	10,000	6.84	a	a
	2,844	14.84	a	a
	729	35.36	b	b
Jack Pine	10,000	7.81	a	a
	2,844	7.90	a	a
	729	9.18	b	b

* - Means spanned by the same letter (a,b) are not significantly different at the specified confidence level.

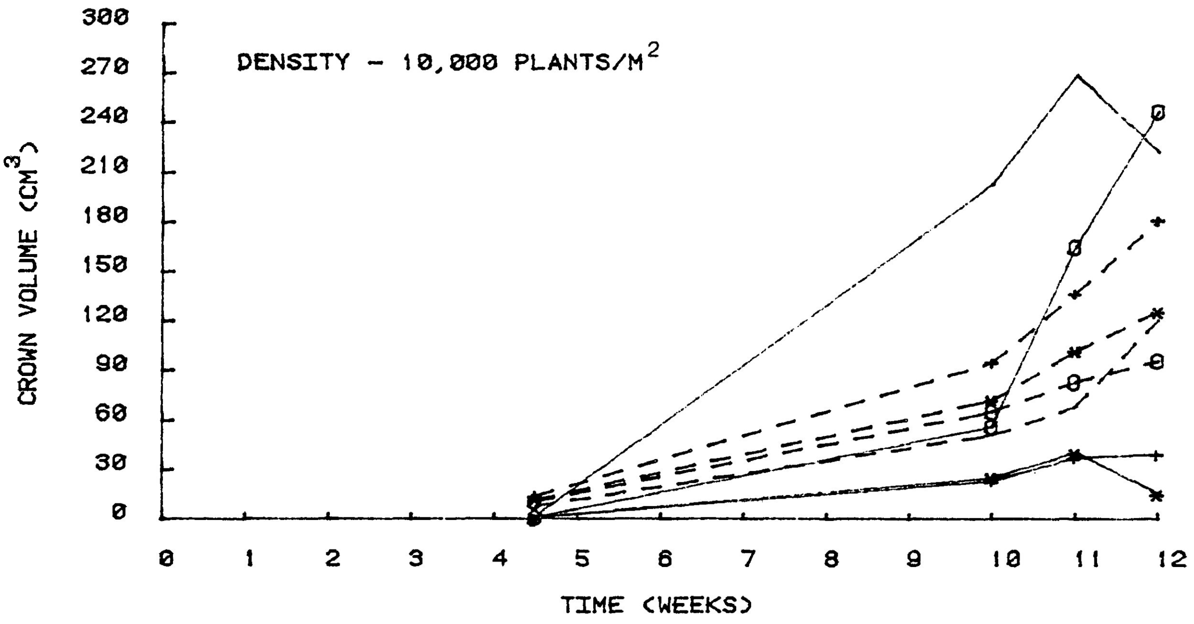

Figure 5a. Crown volume accumulation over time at a density of 10,000 plants/m^3 for greenhouse study.

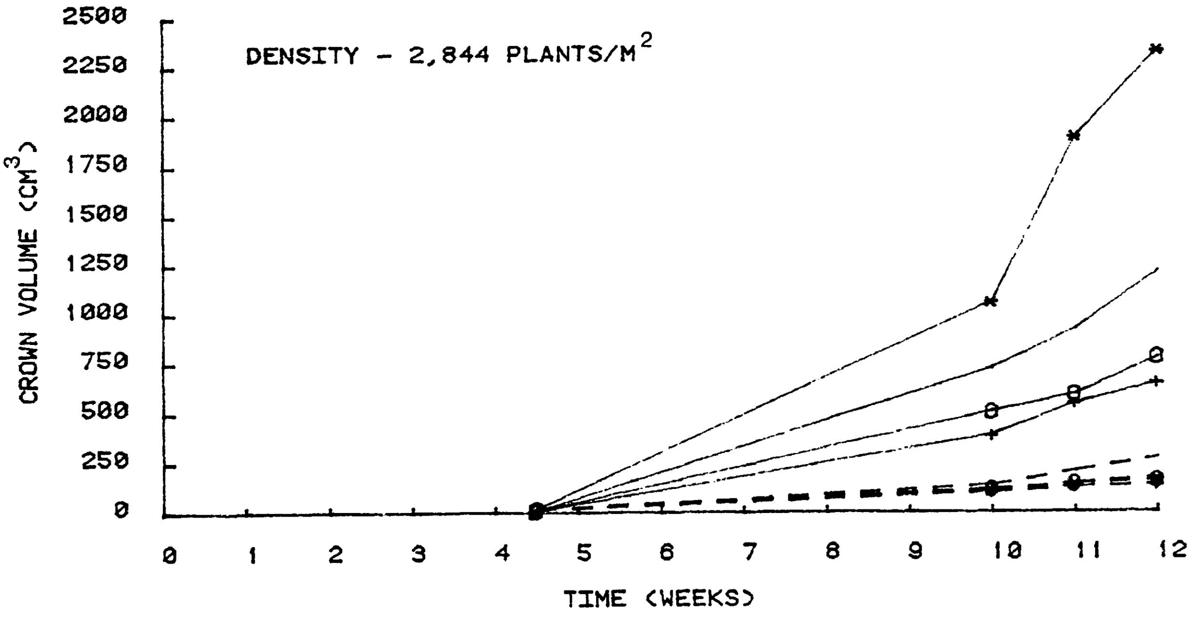

Figure 5b. Crown volume accumulation over time at a density of 2,844 plants/m^3 for greenhouse study.

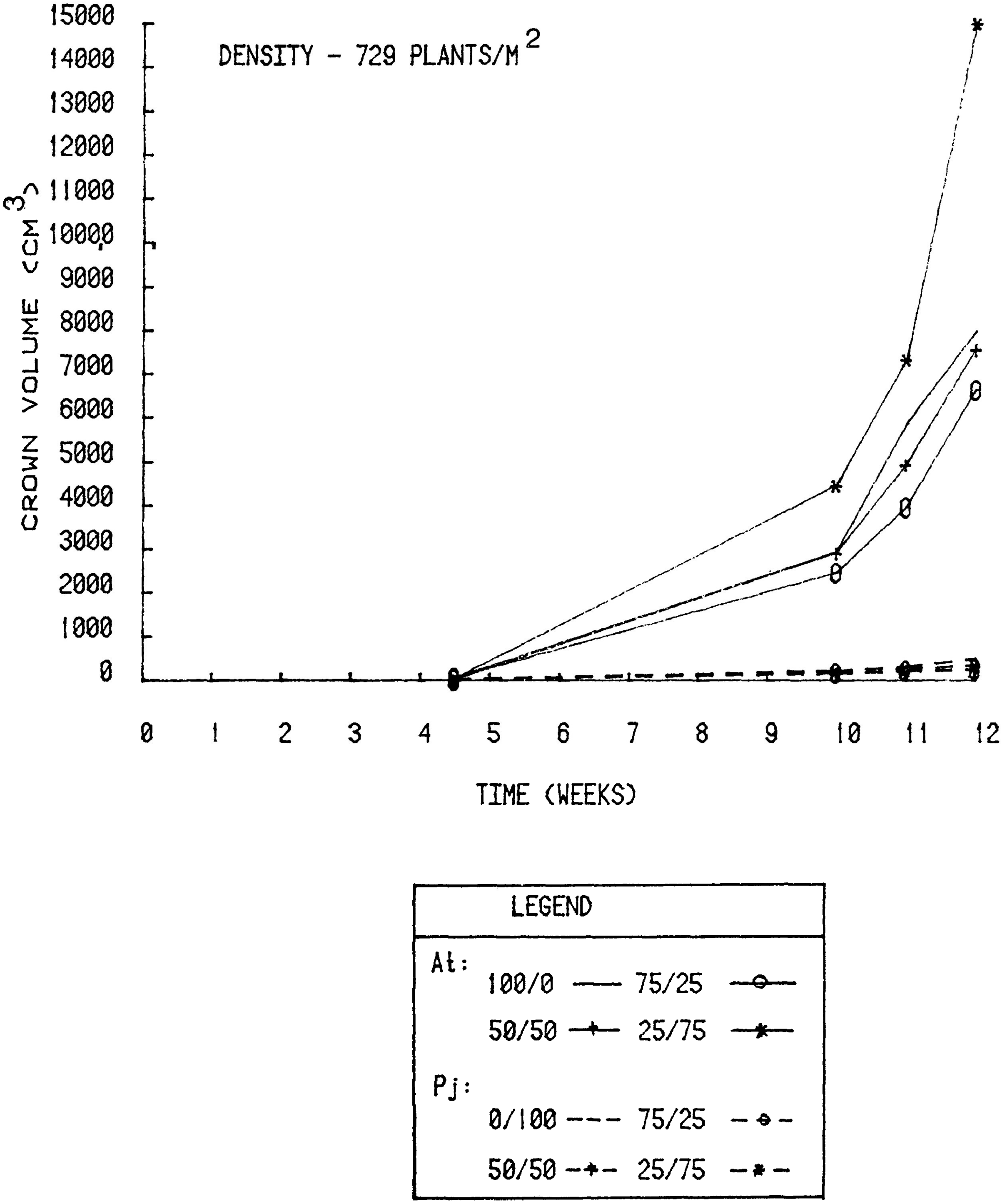

Figure 5c. Crown volume accumulation over time at a density of 729 plants/m^3 for greenhouse study.

Table 9. Analysis of variance for final crown volume in greenhouse study.

trembling aspen:

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F
Block	4	107000000		
δ	0			
Density	2	1010000000	507000000	18.35**
Block-Density	8	221000000	27600000	
Sp.Comp.	3	107000000	35500000	1.91
Block-Sp.Comp.	12	223000000	18700000	
Density-Sp.Comp.	6	136000000	22700000	1.02
Block-Density-Sp.Comp.	24	535000000	22300000	
Exp. Error	0			
TOTAL	59	2339000000		

jack pine:

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F
Block	4	55200		
δ	0			
Density	2	454000	227000	12.25**
Block-Density	8	148000	18500	
Sp.Comp.	3	150000	49900	3.43
Block-Sp.Comp.	12	175000	14600	
Density-Sp.Comp.	6	142000	23700	6.53**
Block-Density-Sp.Comp.	24	87300	3640	
Exp. Error	0			
TOTAL	59	1211500		

Table 10. Results of a comparison of density treatments for average final crown volume using Tukey's procedure.

Species	Density (plants per m^2)	Average Final Crown Volume	*Means contrasted at: p = .05	*Means contrasted at: p = .01
		.... cm^3		
Aspen	10,000	130.73	a	a
	2,844	1243.84	a	a
	729	9351.18	b	b
Jack pine	10,000	130.84	a	a
	2,844	185.19	a	a
	729	366.49	b	b

* - Means spanned by the same letter (a,b) are not significantly different at the specified confidence level.

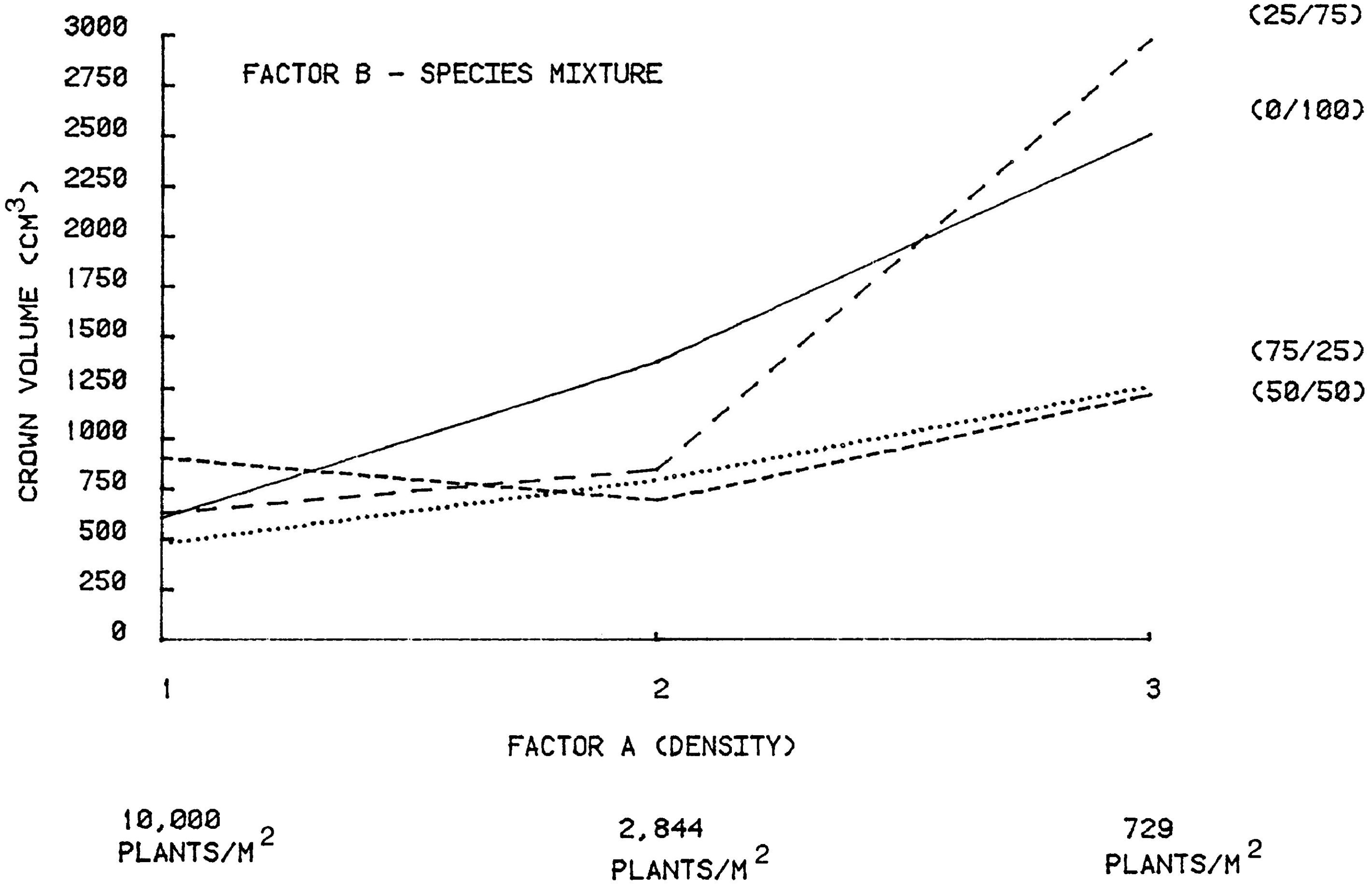

Figure 6. A graphical representation of the interaction between density and species mixture on jack pine final crown volume in greenhouse study.

Average plant weights for the corresponding treatments have been summarized in Table 11. These values were obtained from destructively sampling six plants for each species for all treatment combinations and all replications.

Table 12 presents the analysis of variance for individual plant biomass and Table 13 summarizes Tukey's procedure which was used to contrast the effects of the various treatments. Figure 7 gives an illustrated look at the interacting effect of density and species mixture on jack pine biomass.

Table 11. Arithmetic mean and coefficients of variation for total biomass by species mixture and density for greenhouse study.

Density (plants per m^2)	Species Composition									
	100/0		75/25		50/50		25/75		0/100	
	Aspen	Jack Pine	Aspen	Jack Pine	Aspen	Jack Pine	Aspen	Jack Pine	Aspen	Jack Pine
	mg									
10,000	47		45	50	15	40	16	39		37
	(136)*		(151)	(36)	(120)	(53)	(119)	(67)		(60)
2,844	301		203	67	265	61	271	61		91
	(145)		(127)	(36)	(146)	(48)	(75)	(43)		(56)
729	726		927	86	1188	92	1450	130		225
	(91)	–	(95)	(29)	(82)	(39)	(115)	(35)	–	(32)

* – values in parantheses are coefficients of variation expressed as percentages.

Table 12. Analysis of variance for individual plant biomass at harvest.

trembling aspen:

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Squares	F
Block	4	450000		
δ	0			
Density	2	11400000	5710000	88.00**
Block-Density	8	519000	64900	
Sp.Comp.	3	517000	172000	1.61
Block-Sp.Comp.	12	1290000	107000	
Density-Sp.Comp.	6	1160000	194000	2.26
Block-Density-Sp.Comp.	24	2060000	857000	
Exp. Error	0			
TOTAL	59	17396000		

jack pine:

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F
Block	4	690		
δ	0			
Density	2	89500	44700	73.66**
Block-Density	8	4860	607	
Sp.Comp.	3	27300	9090	20.98**
Block-Sp.Comp.	12	5200	433	
Density-Sp.Comp.	6	38100	6340	17.08**
Block-Density-Sp.Comp.	24	8910	371	
Exp. Error	0			
TOTAL	59	174560		

Table 13. Results of a comparison of density treatments for average plant biomass using Tukey's procedure.

Species	Density (plants per m^2)	Average Plant Biomass	*Means contrasted at:	
			p = .05	p = .01
		.... mg		
Aspen	10,000	30.83	a	a
	2,844	259.78	a	a
	729	1049.30	b	b
Jack pine	10,000	40.23	a	a
	2,844	69.86	b	a
	729	132.84	c	b

* - Means spanned by the same letter (a,b,c) are not significantly different at the specified confidence level.

Table 14. Results of a comparison of species composition treatments for average plant biomass using Tukey's procedure.

Species	Species Composition	Average Plant Biomass	*Means contrasted at:	
			p = .05	p = .01
	.... %	.... mg		
Jack pine	50	64.21	a	a
	25	67.33	a	a
	75	75.11	a	a
	100	117.25	b	b

* - Means spanned by the same letter (a,b) are not significantly different at the specified confidence level.

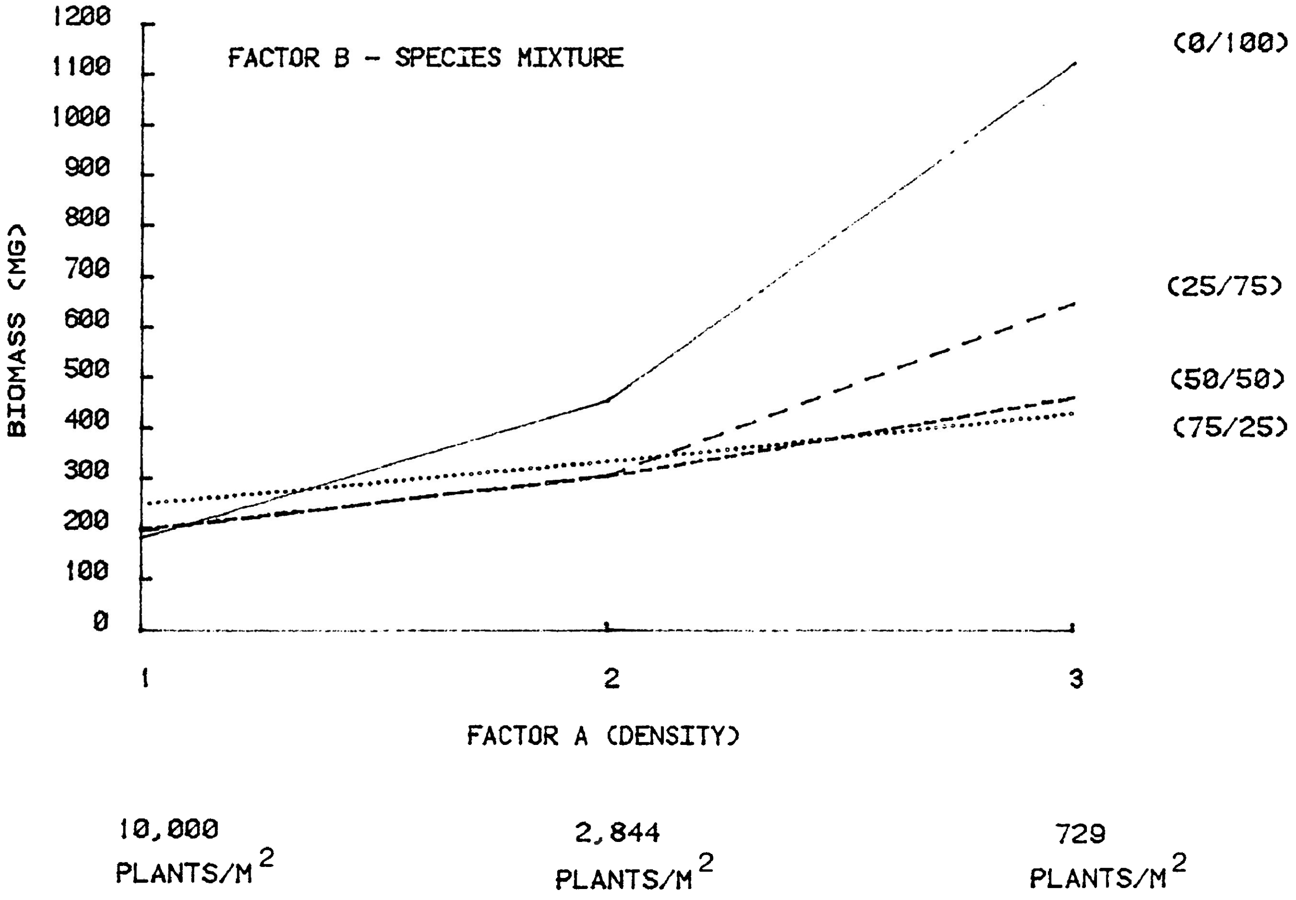

Figure 7. A graphical representation of the interaction between density and species mixture on jack pine biomass for greenhouse study.

Table 15 summarizes the calculated leaf weight/total weight ratios, as percentages.

Table 15. Arithmetic mean and coefficients of variation for leaf weight/total weight ratios by density and species mixture for greenhouse study.

Density (plants per m^2)	Species Composition 100/0 Aspen	Jack Pine	75/25 Aspen	Jack Pine	50/50 Aspen	Jack Pine	25/75 Aspen	Jack Pine	0/100 Aspen	Jack Pine
	....	....	....	....	.... %	....	....	....	....	....
10,000	75		73	78	74	78	70	78		79
	(12)*		(8)	(6)	(9)	(4)	(9)	(5)		(5)
2,844	70		72	78	70	77	71	78		78
	(10)		(13)	(4)	(11)	(4)	(9)	(5)		(4)
729	69		69	82	68	82	71	82		81
	(6)	–	(8)	(4)	(7)	(5)	(7)	(4)	–	(4)

* – values in parantheses are coefficients of variation expressed as percentages.

Table 16. Analysis of variance for leaf weight/total weight ratios after an arc sine transformation.

trembling aspen:

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F
Block	4	163.03		
δ	0			
Density	2	94.20	47.10	4.50*
Block-Density	8	83.79	10.47	
Sp.Comp.	3	1.59	0.53	<1
Block-Sp.Comp.	12	67.46	5.62	
Density-Sp.Comp.	6	79.74	13.29	1.55
Block-Density-Sp.Comp.	24	206.30	8.60	
Exp. Error	0			
TOTAL	59	696.11		

jack pine:

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F
Block	4	25.14		
δ	0			
Density	2	184.03	92.02	17.53**
Block-Density	8	42.02	5.25	
Sp.Comp.	3	5.19	1.73	<1
Block-Sp.Comp.	12	32.49	2.71	
Density-Sp.Comp.	6	10.78	1.80	<1
Block-Density-Sp.Comp.	24	108.92	4.54	
Exp. Error	0			
TOTAL	59	408.57		

Table 17. Results of a comparison of density treatments for average leaf weight/total weight ratios using Tukey's procedure.

Species	Density (plants per m^2)	Average Leaf wt./Total wt. Ratio	*Means contrasted at:	
			p = .05	p = .01
		.... %		
Aspen	10,000	73.09	a	a
	2,844	70.62	a , b	a
	729	69.40	b	a
Jack pine	10,000	77.80	a	a
	2,844	78.11	a	a
	729	81.85	b	b

* - Means spanned by the same letter (a,b) are not significantly different at the specified confidence level.

The values from Table 3 and Table 11 were incorporated in the following equation to calculate mean biomass yield for each treatment combination:

$$Y = W_t \times D_i \times S_u \times C , \qquad [6]$$

where: Y - yield (g/m),

W_t - average individual plant weight for a particular treatment (g),

D_i - initial density (plants/m^2),

S_u - survival (%),

C - composition percentage in mixture.

These data have been summarized in Table 18. Using the values in Table 18, relative yield components (Table 19) were determined, as follows:

$$Y_r \qquad \frac{Y_m}{Y_t}, \qquad [7]$$

where: Y_r – relative yield

Y_m – yield in mixture (g/m^2) of one species

Y_t – yield in pure stand (g/m^2) of same species

Table 18. Arithmetic mean biomass yield and total yield (in parantheses) for greenhouse study.

Density (plants per m^2)	Species Composition									
	100/0		75/25		50/50		25/75		0/100	
	Aspen	Jack Pine	Aspen	Jack Pine	Aspen	Jack Pine	Aspen	Jack Pine	Aspen	Jack Pine
	.... g/m^2									
10,000	337	–	274	117	67	199	36	287	–	364
	(337)*		(391)		(266)		(323)		(364)	
2,844	628	–	368	48	339	85	193	128	–	259
	(628)		(416)		(424)		(321)		(259)	
729	508	–	494	16	425	34	264	71	–	164
	(508)		(510)		(459)		(335)		(164)	

* – total yield obtained by combining both species.

Table 19. Relative yield for greenhouse study.

Density (plants per m^2)	Species Composition									
	100/0		75/25		50/50		25/75		0/100	
	Aspen	Jack Pine	Aspen	Jack Pine	Aspen	Jack Pine	Aspen	Jack Pine	Aspen	Jack Pine
10,000	1.00		0.81	0.32	0.20	0.55	0.11	0.79		1.00
2,844	1.00		0.59	0.19	0.54	0.33	0.31	0.49		1.00
729	1.00	-	0.97	0.10	0.84	0.21	0.52	0.43	-	1.00

Figure 8 is a series of three replacement series diagrams which express relative yield. The significance of relative yield components in a competition experiment have already been discussed. Data for the construction of the relative yield diagrams were obtained from Table 19.

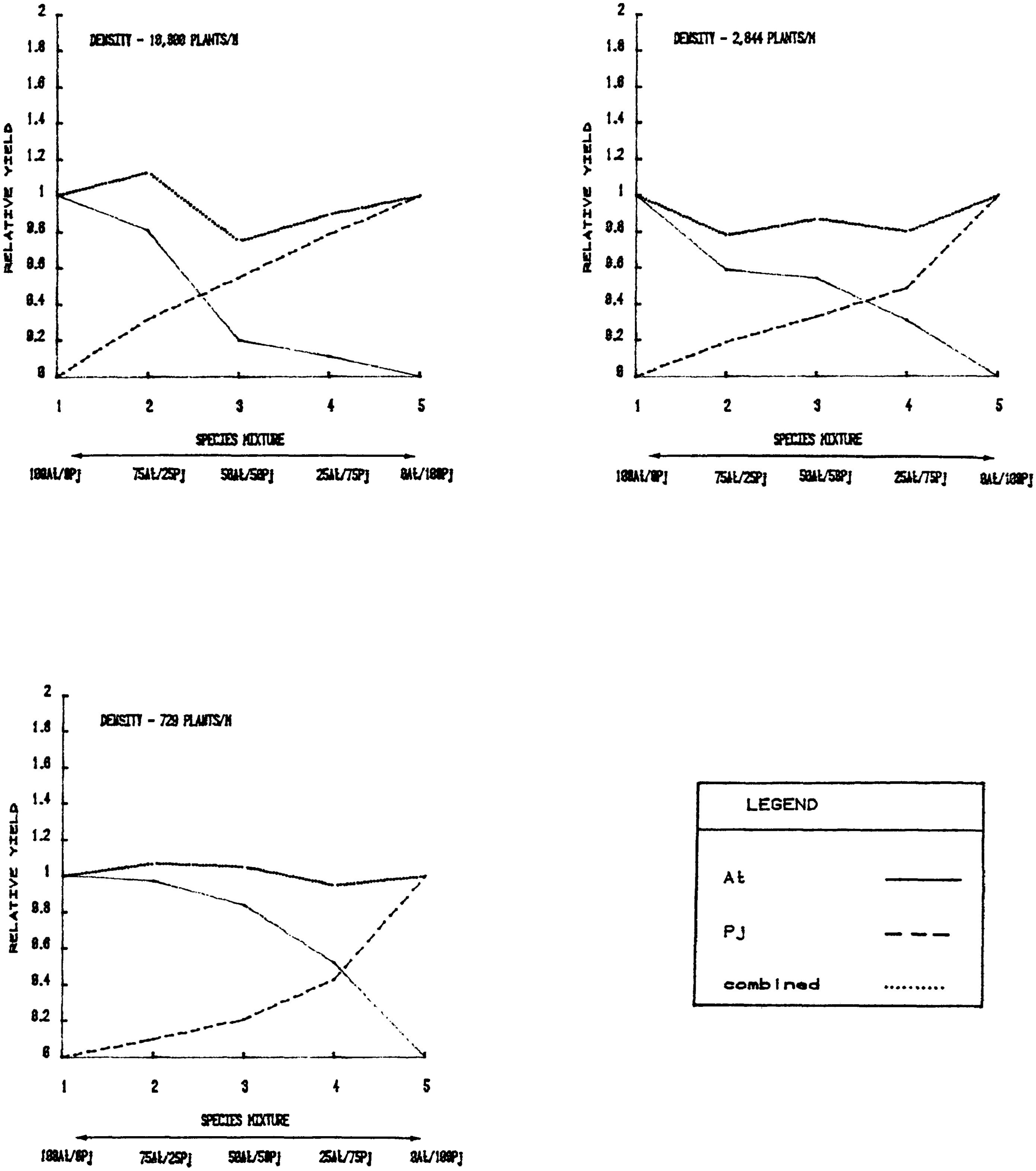

Figure 8. Replacement series diagrams expressing relative yield for three densities in greenhouse study.

A species that is productive in a pure stand may be an ineffective competitor. A formal measure of the aggressiveness of one species towards another, the "Relative Crowding Coefficient", can be derived from the results of a replacement series experiment (deWit and van den Bergh 1965):

$$RCC = \frac{YM_i / YM_j}{YP_i / YP_j}, \qquad [8]$$

where: RCC - relative crowding coefficient of trembling aspen with jack pine

YM_i - mean yield per plant of trembling aspen in mixture

YM_j - mean yield per plant of jack pine in mixture

YP_i - mean yield per plant of trembling aspen in pure stand

YP_j - mean yield per plant of jack pine in pure stand

Relative Crowding Coefficients of trembling aspen with jack pine can be found in Table 20.

Table 20. Relative Crowding Coefficients of trembling aspen with jack pine for greenhouse study.

Density (plants per m^2)	Species Composition 75 Aspen / 25 Jack Pine	 50 Aspen / 50 Jack Pine	 25 Aspen / 75 Jack Pine
10,000	0.71	0.30	0.32
2,844	0.92	1.31	1.34
729	3.34	4.00	3.46

Field Study

Height and crown volume data were taken three weeks after all blocks had been planted and continued until all shoot elongation had ceased (approximately nine additional weeks). These data have been summarized in Appendices 8 and 9, respectively. The standard deviations of the means for each treatment have been tabulated and are also presented in these appendices.

Figure 9 includes five graphs which illustrate variation in height growth due to density changes and species mixtures. The data used for the construction of these graphs are found in Appendix 8.

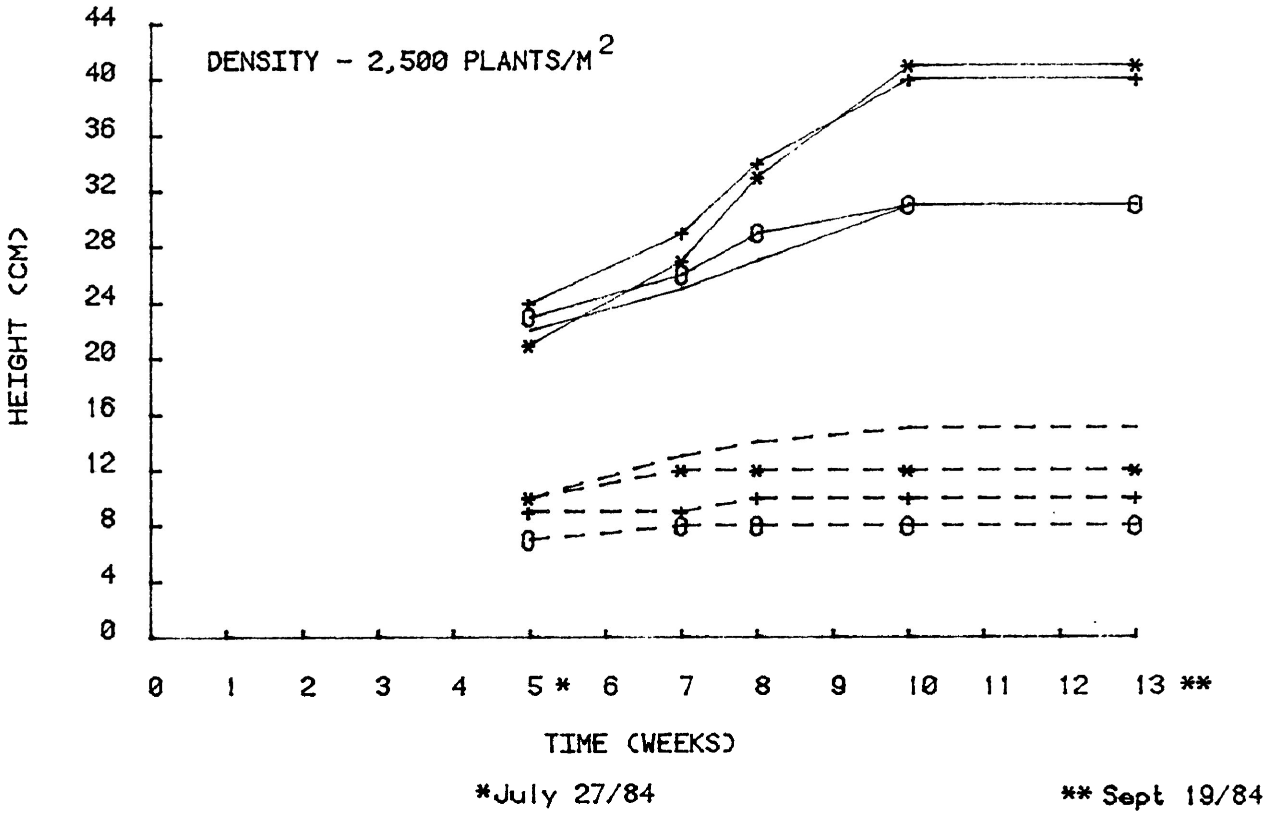

Figure 9a. Height growth comparisons over time at a density of 2,500 plants/m^2 for field study.

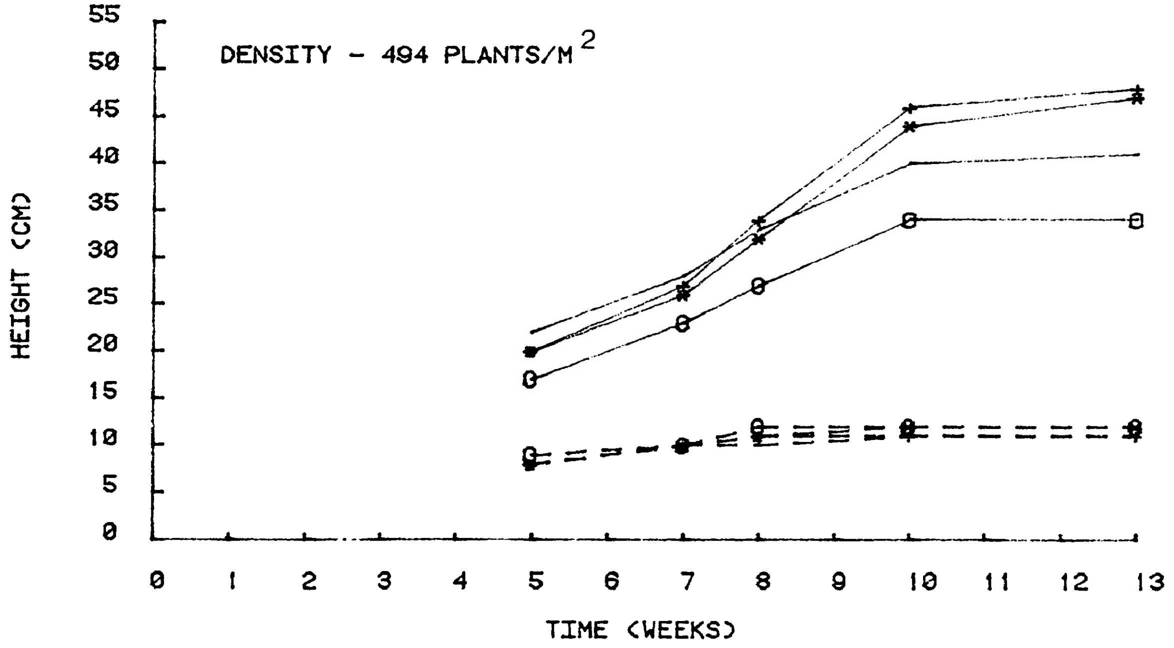

Figure 9b. Height growth comparisons over time at a density of 494 plants/m^2 for field study.

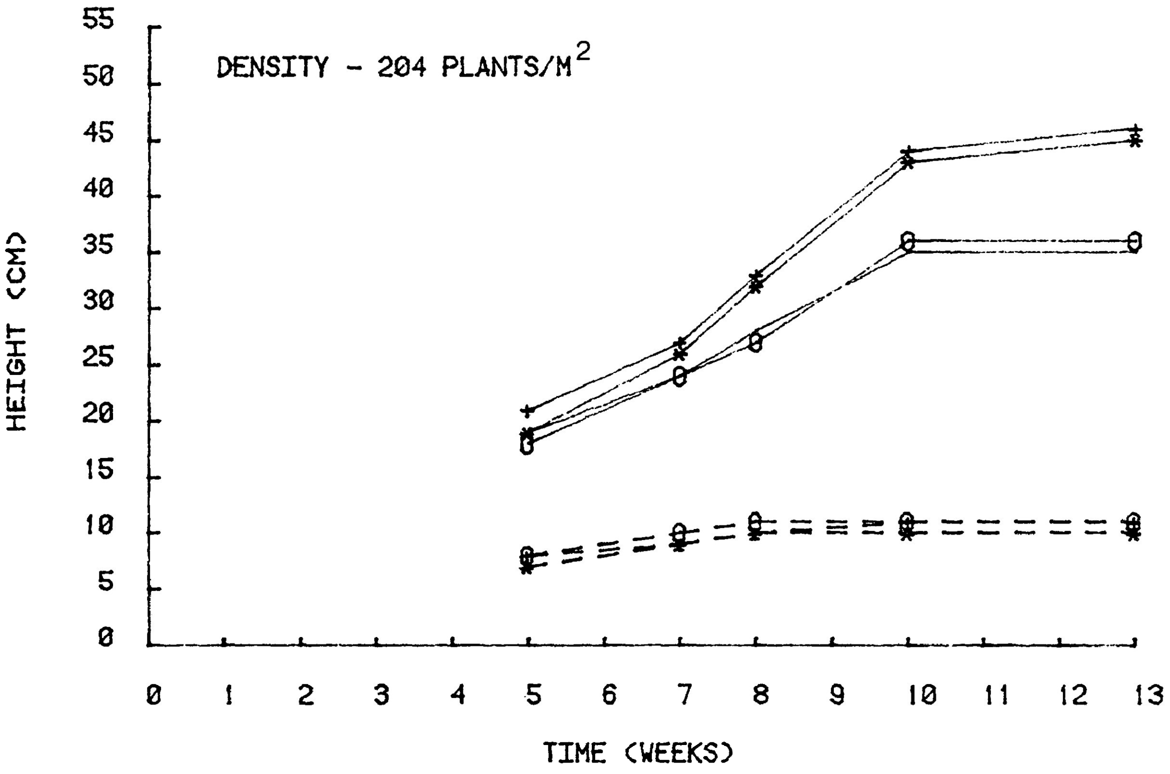

Figure 9c. Height growth comparisons over time at a density of 204 plants/m^2 for field study.

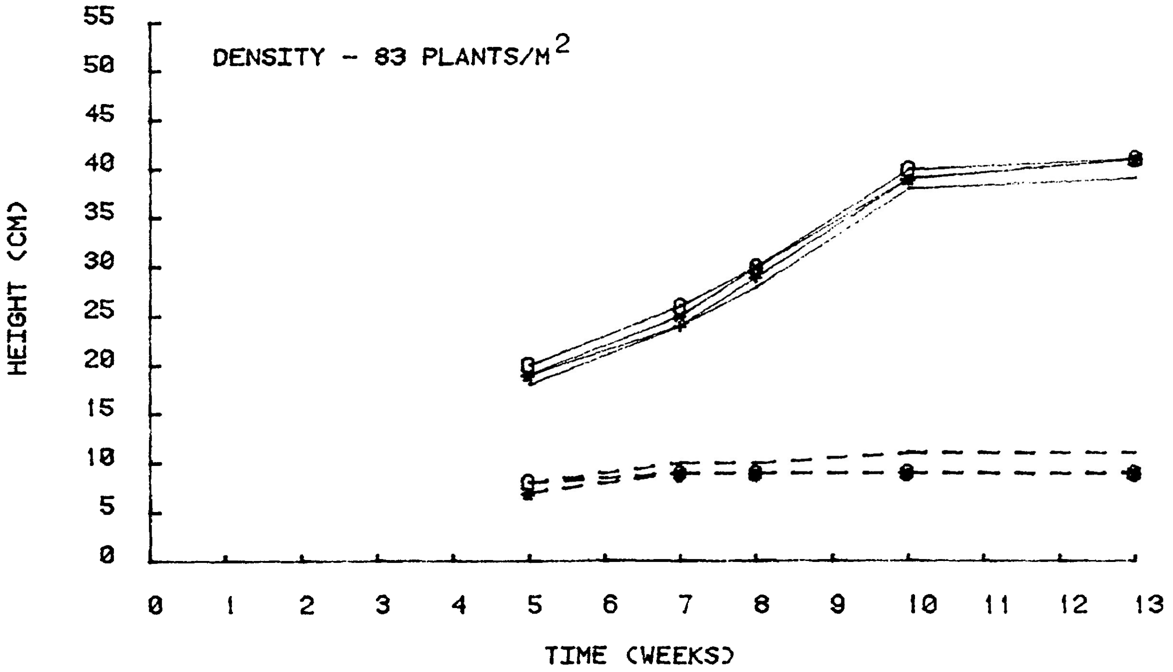

Figure 9d. Height growth comparisons over time at a density of 83 plants/m^2 for field study.

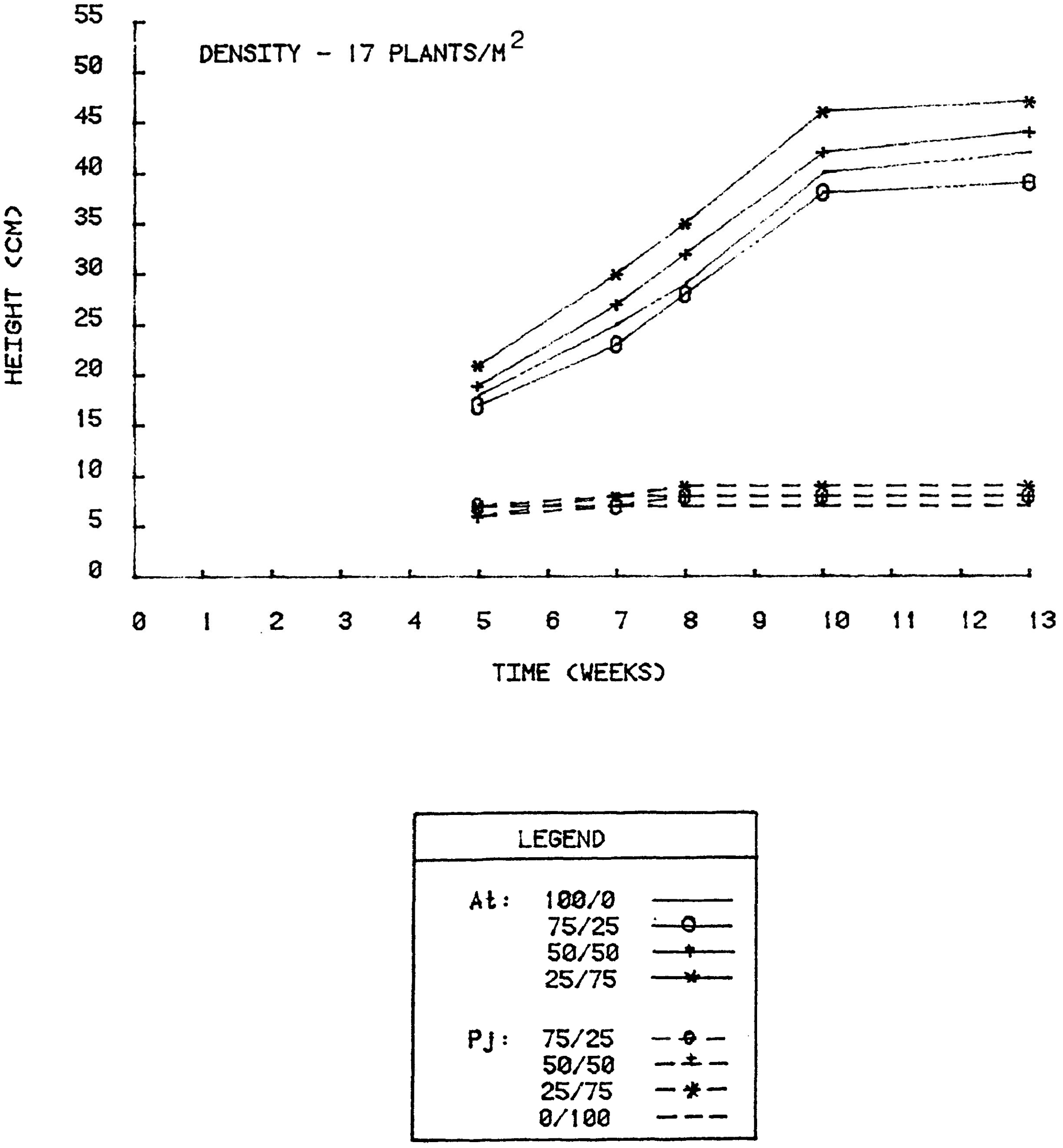

Figure 9e. Height growth comparisons over time at a density of 17 plants/m^2 for field study.

Table 21. Analysis of variance of final height at the end of the first growing season for field study.

trembling aspen:

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F
Block	5	790.53		
δ	0			
Density	4	775.16	193.79	1.90
Block-Density	20	2038.19	101.91	
ψ	0			
Sp.Comp	3	1459.76	485.59	7.57**
Block-Sp.Comp.	15	961.74	64.12	
Density-Sp.Comp.	12	571.56	47.63	<1
Block-Density-Sp.Comp.	60	4314.21	71.90	
Exp. Error	0			
TOTAL	119	10911.15		

jack pine:

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F
Block	5	215.01		
δ	0			
Density	4	214.82	53.71	10.23**
Block-Density	20	105.03	5.25	
ψ	0			
Sp.Comp.	3	38.76	12.92	2.11
Block-Sp.Comp.	15	91.77	6.12	
Density-Sp.Comp.	12	173.09	14.42	7.14**
Block-Density-Sp.Comp.	60	121.41	2.02	
Exp. Error	0			
TOTAL	119	959.89		

Table 21 presents the analysis of variance associated with the height growth for both species. It can be seen that density has little effect on the height growth of trembling aspen. However, jack pine height growth was highly significantly affected by density. Figure 10 illustrates the interacting effect density and species mixture had on jack pine height.

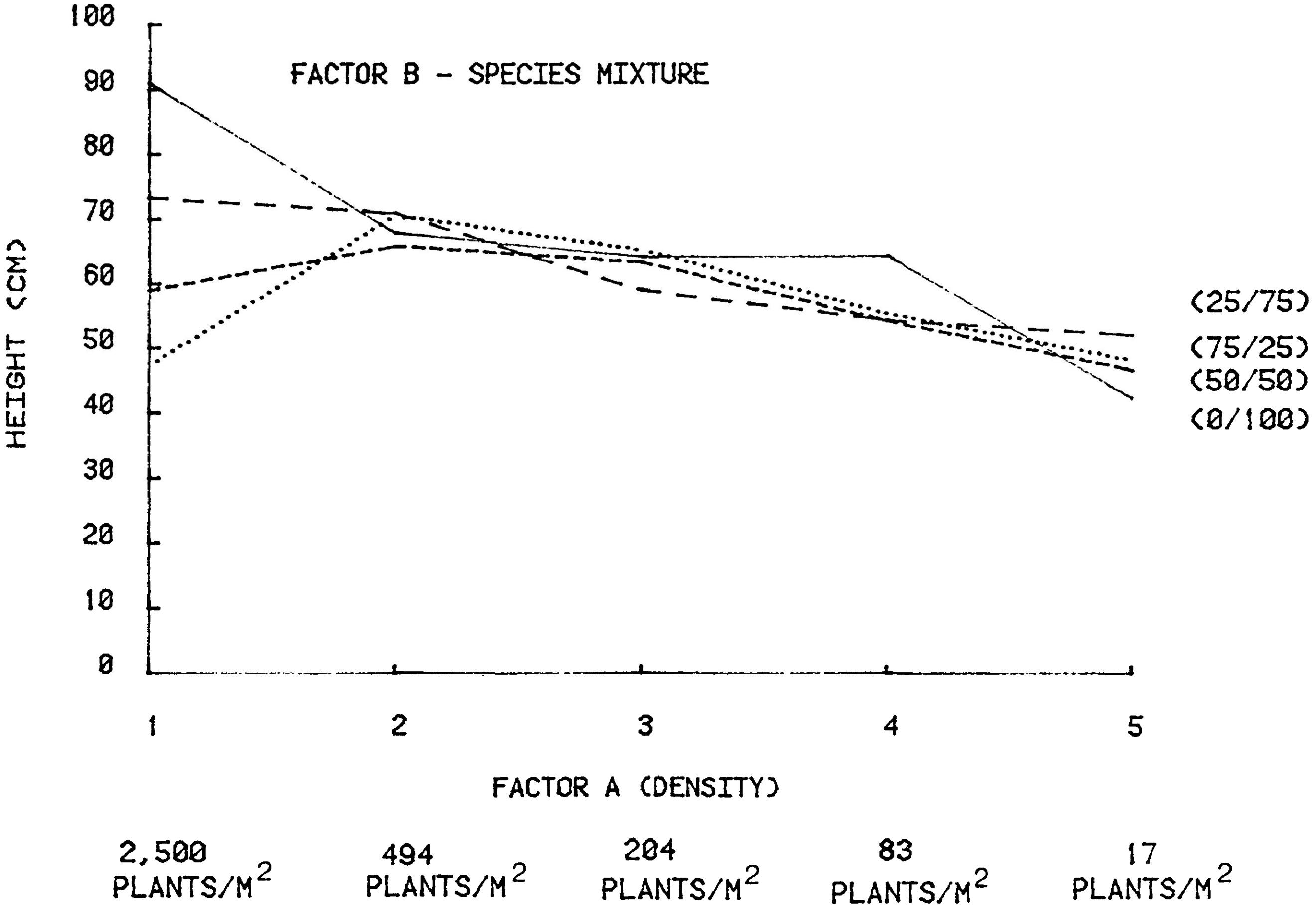

Figure 10. A graphical representation of the interaction between density and species mixture on jack pine height for field study.

Table 22. Results of a comparison of density treatments for average final height using Tukey's procedure.

Species	Density (plants per m^2)	Average Final Height	*Means contrasted at: p = .05	*Means contrasted at: p = .01
		.... cm		
Jack Pine	17	7.87	a	a
	83	9.28	a , b	a , b
	203	10.47	b , c	b
	2,500	11.26	b , c	b
	494	11.50	c	b

* – Means spanned by the same letter (a,b,c) are not significantly different at the specified confidence level.

Table 23. Results of a comparison of species mixture treatments for average final height using Tukey's procedure.

Species	Species Composition	Average Final Height	*Means contrasted at: p = .05	*Means contrasted at: p = .01
	..... %	.... cm		
Aspen	75	36.43	a	a
	100	37.59	a	a , b
	50	43.62	b	a , b
	25	44.23	b	b

* – Means spanned by the same letter (a,b) are not significantly different at the specified confidence level.

Figure 11 includes five graphs which illustrate variation in crown volume accumulation due to density changes and species mixtures. The data used for the construction of these graphs are found in Appendix 8.

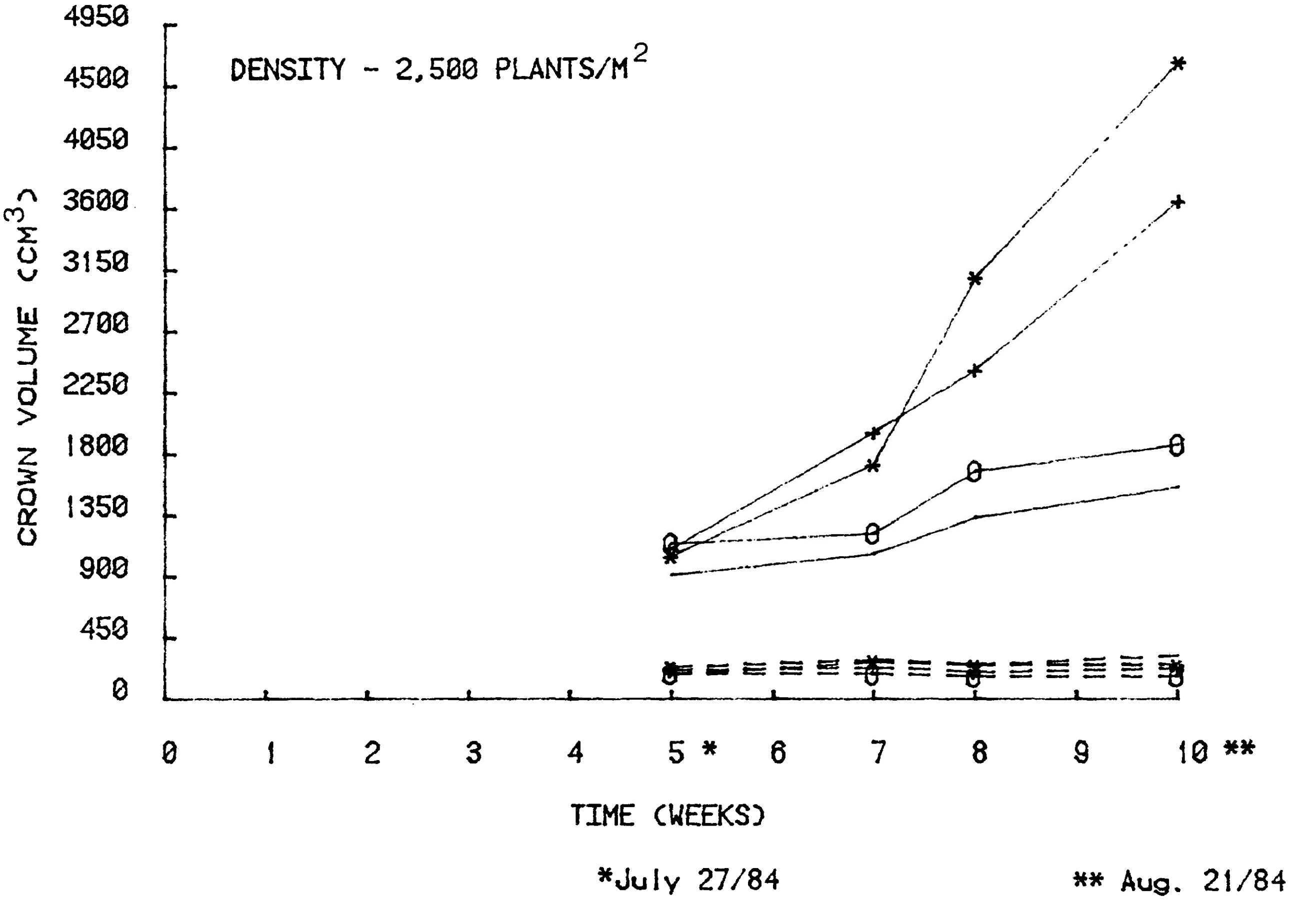

Figure 11a. Crown volume accumulation over time at a density of 2,500 plants/m^3 for field study.

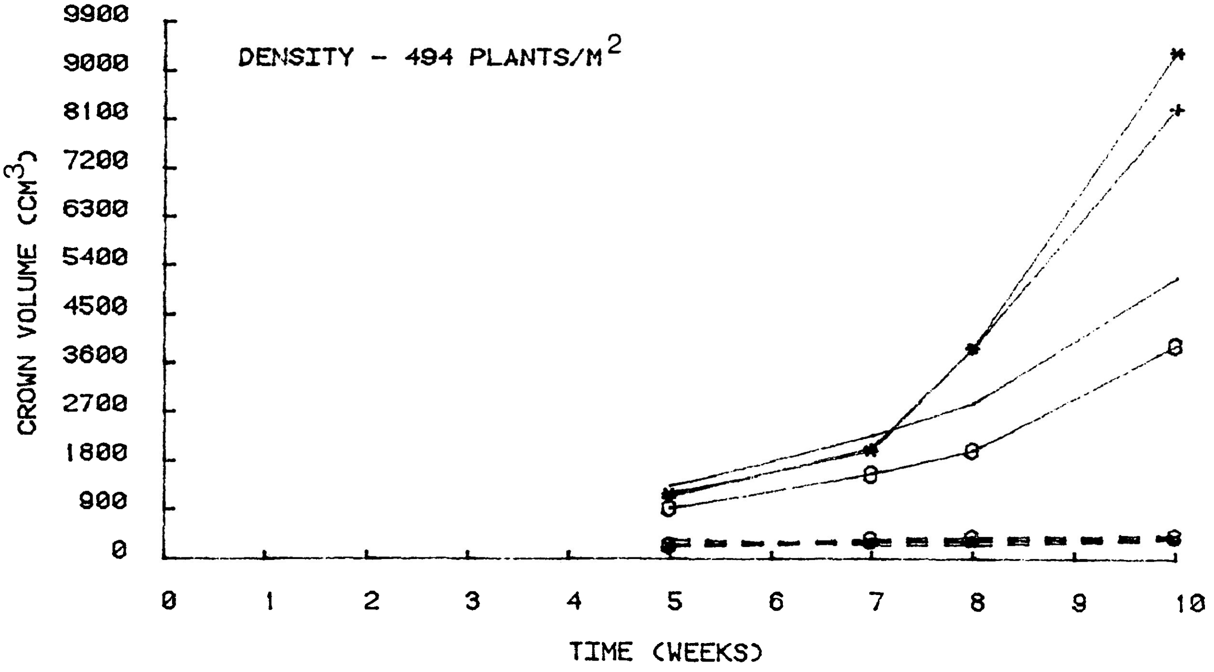

Figure 11b. Crown volume accumulation over time at a density of 494 plants/m^3 for field study.

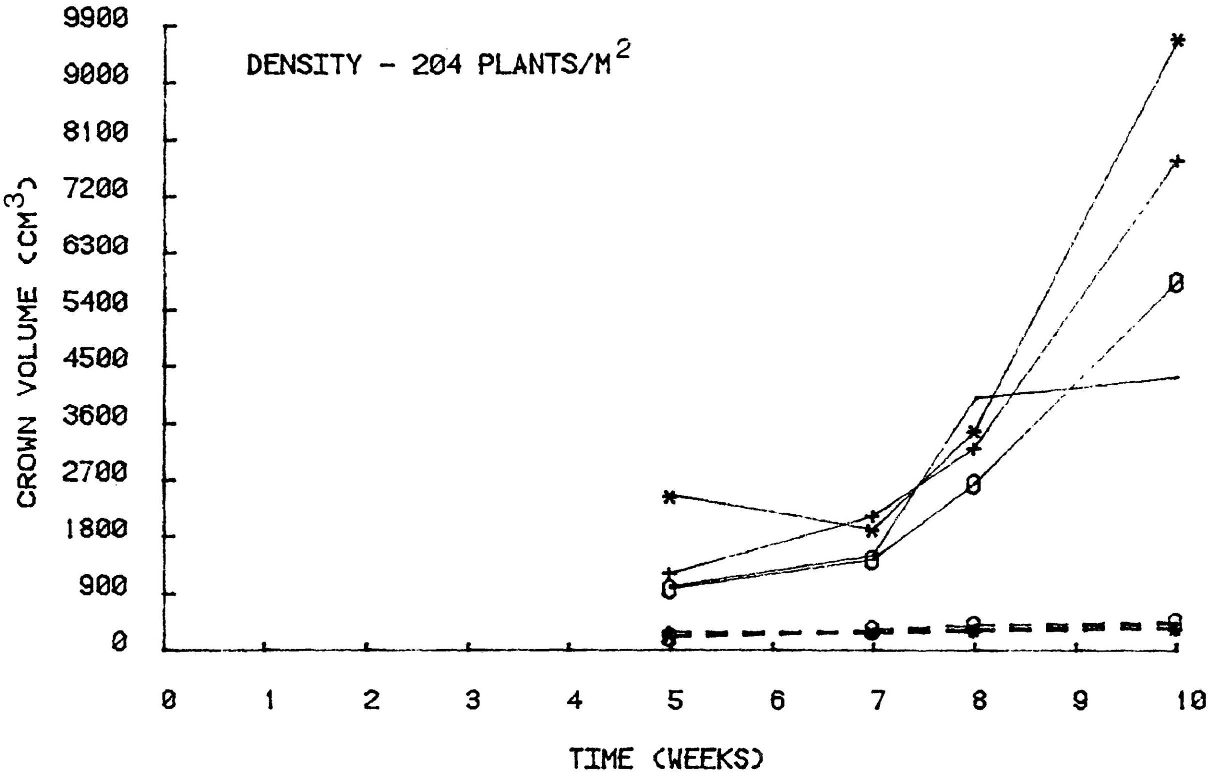

Figure 11c. Crown volume accumulation over time at a density of 204 plants/m^3 for field study.

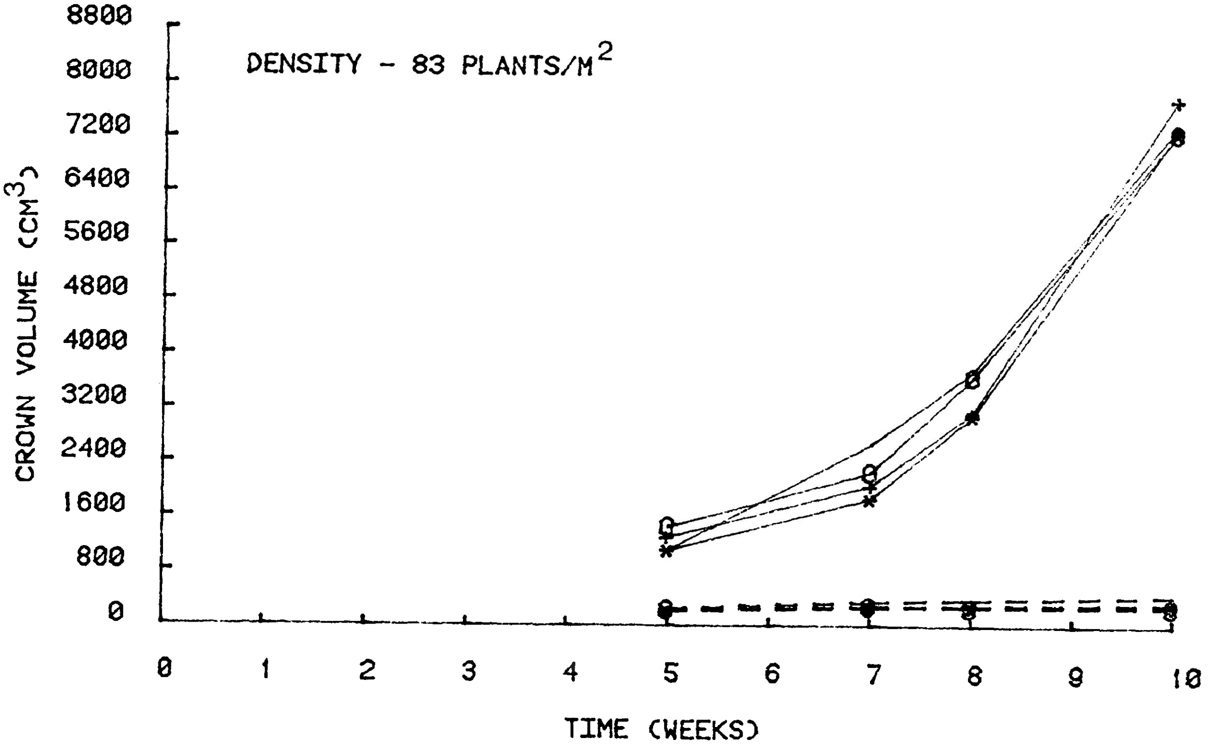

Figure 11d. Crown volume accumulation over time at a density of 83 plants/m^3 for field study.

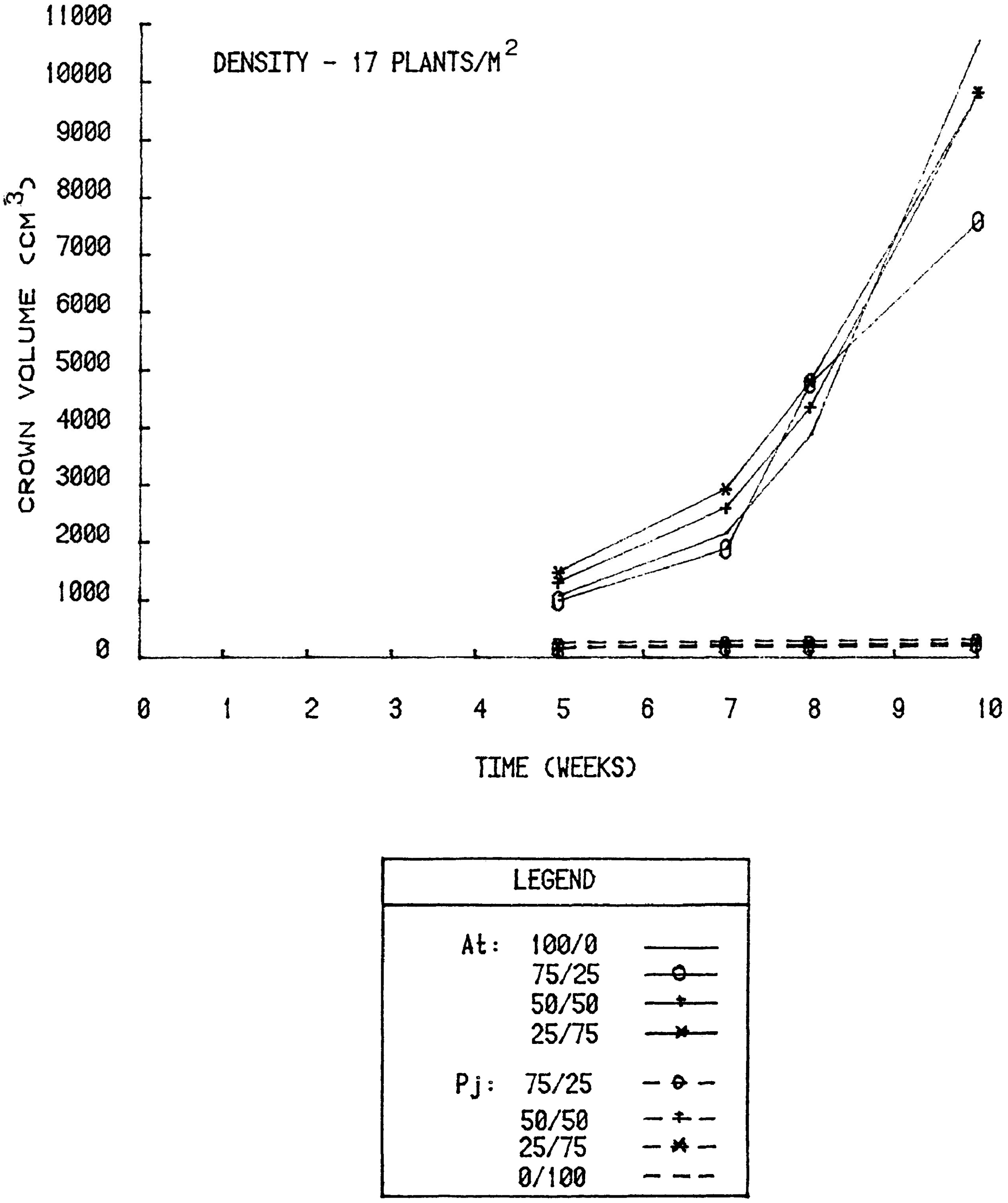

Figure 11e. Crown volume accumulation over time at a density of 17 plants/m^3 for field study.

Table 24. Analysis of variance of final crown volume at the end of the first growing season for field study.

trembling aspen:

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F
Block	5	167000000		
δ	0			
Density	4	538000000	135000000	7.76**
Block-Density	20	347000000	17400000	
ψ	0			
Sp.Comp.	3	165000000	54900000	5.07*
Block-Sp.Comp.	15	162000000	10800000	
Density-Sp.Comp.	12	124000000	10300000	<1
Block-Density-Sp.Comp.	60	630000000	10500000	
Exp. Error	0			
TOTAL	119	2133000000		

jack pine:

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F
Block	5	794000		
δ	0			
Density	4	520000	130000	4.32*
Block-Density	20	602000	30100	
ψ	0			
Sp.Comp.	3	50200	16700	1.51
Block-Sp.Comp.	15	166000	11100	
Density-Sp.Comp.	12	300000	25000	2.29
Block-Density-Sp.Comp.	60	654000	10900	
Exp. Error	0			
TOTAL	119	3086200		

Table 25. Results of a comparison of density treatments for average final crown volume using Tukey's procedure.

Species	Density (plants per m^2)	Average Final Crown Volume	*Means contrasted at: p = .05	p = .01
		.... cm^3		
Aspen	2,500	2939	a	a
	494	6698	b	a , b
	203	6919	b	a , b
	83	7432	b	a , b
	17	9475	b	b
Jack pine	2,500	236	a	a
	17	252	a , b	a
	83	338	a , b	a
	494	384	a , b	a
	203	395	b	a

* - Means spanned by the same letter (a,b) are not significantly different at the specified confidence level.

Table 26. Results of a comparison of species mixture treatments for average final crown volume using Tukey's procedure.

Species	Species Composition	Average Final Crown Volume	*Means contrasted at: p = .05	p = .01
	..... %	.... cm^3		
Aspen	75	5294	a	a
	100	5832	a , b	a
	50	7473	a , b	a
	25	8171	b	a

* - Means spanned by the same letter (a,b) are not significantly different at the specified confidence level.

DISCUSSION

To date, only a limited number of studies have addressed the competitive nature of jack pine or trembling aspen. The majority of studies on jack pine competition deal with plantation spacings and the effects of various thinning regimes (Schantz-Hansen 1931, Eyre and LeBarron 1944, Guilkey and Westing 1956, and Horton and Bedell 1960). The bulk of work done on trembling aspen has come from the Lake States. These studies, again, have concentrated on silvicultural techniques used to increase production of natural stands (Kittredge and Gervorkiantz 1929, Shirley 1941, Zehngraff 1947, and Gervorkiantz 1956). Therefore, it is significant to note at this time that the present study is the first such study to look specifically at the competitive nature of both jack pine and trembling aspen seedlings during the initial stages of growth and development.

The greenhouse portion of the present study serves as the major basis for this discussion. The reason for this is that it has been completed. The use of biomass data is essential in identifying "key" competitive effects and relationships. Furthermore, the relative growth rates of the seedlings in the greenhouse study were substantially higher than those of the field study, thereby amplifying the effects of competition in a relatively short period of time.

The slower growth rates coupled with much lower densities, in the field study, resulted in minimal significant effects after the first year of growth. Destructive sampling will not be done until the third or fourth growing season. Although concrete conclusions concerning competitive effects between trembling aspen and jack pine, in the field, cannot be made at this time, various trends will be discussed.

It has been noted (Appendix 2) that relatively high correlations between the following measured growth parameters in the greenhouse study existed:

(1) total height versus crown volume (trembling aspen),

(2) total height versus crown volume (jack pine), and

(3) oven dry weight versus leaf wt./total wt. ratio (jack pine).

The assumption of independence between these variables in the univariate approach to the analysis used in this study can be argued as incorrect. Therefore, some readers may wish to analyze the data using multivariate techniques.

Greenhouse Study

Hierarchy of Resource Exploitation

White and Harper (1970) stated that within any community a "hierarchy of resource exploitation" is established, which results in differential growth rates among its members. Plants at the bottom of this hierarchy are referred to as "suppressed", and those at the top are classed as "dominant".

In mixtures of species, resources are usually unequally divided between species so that one of them is over-represented among the dominants (Bazzaz and Harper 1976).

In the present study, the existance of such a hierarchy was established between trembling aspen and jack pine. However the species which took on the dominant role was dependent on density. At the highest density level (10,000 plants/m^2), jack pine assumed the dominant role. Once the density was lowered, trembling aspen gained dominance over the pine seedlings in the mixtures.

Table 10 illustrates this changing role of dominance. With density at the highest level, the jack pine seedlings were able to produce slightly larger crowns than those for trembling aspen (approximately 130 cm^3/plant). Once the density was lowered, aspen crowns increased exponentially; whereas only minimal increases occurred for the jack pine crowns, mainly in the pure stands of jack pine. In the lower densities, the aspen competed mainly with other aspen seedlings for growing space. Therefore only aspen in the 25At/75Pj mixture were able to aquire a large crown volume at this density level (729 plants/m^2).

Although the effect of species mixture did not show up as significant in the analysis of variance (Table 7), some important trends can be identified from Figure 4. In the highest density, the jack pine actually took a dominant role in mixture and probably caused the reduced aspen height growth in all the mixes. However, at the lowest density, the availability of initial growing space allowed the aspen to overtop the jack pine. This aspen dominance reduced the growth of the pine, relative to the height of the pine seedlings in a pure stand of equal density.

The effect of developing dominance in growth was cumulative, since once an advantage was gained it progressively increased. This progressive increase was illustrated in Figure 4 and 5, which show increased separation between the two species as time progressed.

It must be noted that density had a pronounced effect on individual plant biomass, for both species. At the highest density, individual jack pine seedlings had greater dry weights than did the trembling aspen (Table 13). Once the density was lowered, the aspen seedlings were able to suppress the jack pine and produced increasingly greater individual biomass. Only in pure stands did the jack pine seedlings attain appreciable biomass (Table 14). Furthermore, individual aspen seedlings produced less biomass as the percentage of aspen decreased at the highest density (Table 11). The reverse was true at the lowest density. At this density, aspen seedlings produced greater biomass as the percentage of aspen decreased (Table 11). This relationship demonstrates a shift in the main competitor. At the highest density, aspen is mainly competing with jack pine seedlings. However, at the lower density aspen is primarily competing with other aspen seedlings.

Additional evidence in this shift in dominance is shown in Table 19 (Relative Yield). At the highest density, aspen's relative yield dropped off significantly from 1.00 at 100%At/0%Pj to 0.11 at 25%At/75%Pj as the jack pine percentage increased. Jack pine yield dropped off more slowly, ranging from 1.00 at 0%At/100%Pj to 0.32 at 75%At/25%Pj, as its percentage declined toward zero. Once the density was lowered, the aspen took on a more dominant role. This feature is apparent as relative yield curves for aspen become convex (Figure 8). The reason for this change in relative yield trend is that a shift in dominance occurred. At the highest density, jack pine was the dominant species; at the lower densities aspen assumed this dominant role.

Explanation for Shifting Dominance Pattern

The above mentioned shift in aggressiveness of the two species can be better illustrated using relative crowding coefficients.

Table 20 illustrates the dramatic change in relative crowding coefficients for aspen as density was changed. The value below 1.00 demonstrates that jack pine was dominant at 10,000 plants/m ; whereas at 729 plants/m^2 the value was greater than 3.00, demonstrating a reversal of dominance. A value of 1.00 is considered to be a neutral position. Harper (1961) also determined that there was a shift of competitive ability with changing density.

In general, trembling aspen has the ability to accumulate biomass at a far superior rate than jack pine. Therefore, the following question must be raised: Why does jack pine remain dominant at the highest density?

The above question can be answered by looking at the germination phase of the experiment. Under greenhouse conditions, trembling aspen germinates one to two days after dissemination (Faust 1936). Jack pine, given the same greenhouse conditions, takes up to two weeks to germinate (Fraser 1959). However the young germinants quickly stand erect and are approximately 30mm tall. Initial growth of the aspen germinants is relatively slow, and they are only 5 - 10mm tall after the jack pine have germinated. In the highest density, the jack pine formed a closed canopy immediately after germination. This crown closure severely hampered the development of the overtopped aspen seedlings. However, it must be noted that sufficient densities to form this closed canopy almost never occur in nature.

At the lower densities, complete canopy closure by the jack pine did not occur, allowing the aspen to develop at a much faster rate. The aspen quickly overtopped the slower developing pine seedlings and became the dominant species.

Allocation of Resources

The way an organism allocates the quantity of limited amounts of resources to growth, maintenance, and reproduction, as well as the timing of these allocations will affect its fitness (Snell and Burch 1975). Harper (1977) points out that a density-stressed individual is not simply a miniature version of its vigorous low-density counterpart. During the growth of plants under density stress the allocation of assimilates between different structures becomes proportionately altered. Ogden (1970) described suppressed plants as long, slender and etiolated with a relatively increased proportion of non-photosynthetic to photosynthetic tissue (ie: stem to leaf). Harper (1977) explained that many of the weaker individuals in a population extend their foliage to the top of the canopy but do this by means of long, spindly stems and a proportiontely greater respiratory burden. Their net assimilation rate may therefore be expected to be lower than that of the dominant plants in the canopy (White and Harper 1970).

The above-mentioned relationships have come from studies dealing with pure stands of a given species. In mixed stands, the growth patterns of the species in question may vary greatly from each other. This variation in growth may cause a shift in the dominant competitor and thereby alter the expected allocation of resources for a given species. This feature was illustrated in the present study as trembling aspen seedlings adjusted their biomass allocation with respect to the dominant competitor. At the highest density (10,000 plants/m^2), jack pine seedlings dominated the various treatments. As a result, trembling aspen seedlings expanded their crowns laterally rather than vertically. This growth pattern resulted in an increase in their percentage biomass allocated to leaf weight. At the lowest density (729 plants/m^2), aspen was mainly competing with other aspen seedlings. Therefore, in order to overtop neighbouring aspen, individual aspen seedlings allocated a larger percentage of biomass into stem weight (ie: lower LW/TW ratio). This adjustment in resource allocation is illustrated in Table 15 and Table 17.

A reverse response occurred in jack pine. As the dominant competitor in the highest density, the jack pine seedlings were forced to compete with other pines. This intraspecific competition resulted in a shift to a greater percentage of biomass being allocated to stem weight. At the lowest density, jack pine took on the role of an understory species. Therefore, the pine seedlings increased the percentage of leaf weight in order to capture as much light as possible (Table 15 and Table 17).

Mortality

Individuals can suffer greater competition from conspecifics than from plants of the other species. In such a situation the total competitive effects suffered by a population is relatively small when a species is the minority component in a mixture. However, the overall competitive effects increase directly with a corresponding increase in frequency of the species in the mixture. This phenomenon is known as "frequency-dependent interference" (Harper and

McNaughton 1962).

The best example of this phenomenon, from the present study, is found in Table 3 (trembling aspen survival). It can be seen that the survival of aspen is not only reduced by higher density, but also by species composition (Table 4). As the percentage of aspen in the mixture increased, the survival decreased significantly. The lowest survival occurred in the 100At/0Pj mixture. Increased density accentuated this relationship. A contributor to this mortality of aspen, other than direct competition, was the presence of a leaf and shoot blight (*Fusicladium* spp.). This bacterial disease rapidly spreads as contact with other aspen seedlings increases. Therefore, at the highest density (10,000 plants/m^2) and highest aspen composition (100At/0Pj) the blight was most severe. Although the blight may not have directly caused the death of the aspen seedlings, reduced vigour led to increased competitive effects and eventually mortality of several infected seedlings.

The jack pine seedlings were not affected by any pathogens. In general, jack pine survival was relatively stable (Table 5). Only at the highest density (10,000 plants/m^2) and in the lowest jack pine percent composition (75At/25Pj) was there any drop in survival.

Yield Components

Whittington and O'Brien (1968) noted that in mixtures the intraspecific competition of the better competitor was lessened and it grew more rapidly than in pure stands. Therefore, the mixture should out-yield the highest yielding of the comparative pure plots.

In the present study, although an increase in individual plant weight of the main competitor can be noted (Table 11), an increase in total production within the mixtures does not occur. The replacement series diagrams of relative yield (Figure 8) clearly illustrate that the total relative yield curve has a concave appearance. The shape demonstrates an antagonistic relationship between the two species. As the density is lowered, this relationship became less pronounced - the curve took on a more linear shape.

It should be noted that this study dealt with forest tree species, which have long life spans. It is therefore possible that a change in shape of the relative yield curves could occur during different phases of these species' ontogeny.

Field Study

In general, aspen height growth was not significantly affected by density. It is felt that the higher densities as well as the wider range of densities used in the greenhouse study (10,000 plants/m^2 to 729 plants/m^2) as compared to the field study (2,500 plants/m^2 to 17 plants/m^2) caused immediate crown closure. Therefore immediate, intense competition among neighbouring plants accentuated the effect of density on height growth. In the field study, plants were "free-to-grow" for a greater proportion of the growing season. Once crown closure is achieved and the competition among neighbouring plants intensifies, density should become a significant factor influencing height growth.

It should be noted, however, that species mixture did have a pronounced affect on height growth (Figure 9 and Tables 21 & 23). As the percentage of aspen decreased, height growth tended to increase. A similar relationship was evidenced in crown development for the aspen transplants (Figure 11 and Tables 24 & 26). Therefore, larger crowns were a result as the percentage of aspen decreased in the mixtures. Furthermore, density affected the accumulation of crown volume (Tables 24 & 25). At the highest density (2,500 plants/m^2), crown closure occurred at time of planting; thereby drastically reducing the ability of the aspen to expand their crowns. Crown expansion increased exponentially as the density was lowered to 17 plants/m^2 and the aspen fully occuppied the site.

A reverse response, to what was anticipated, occurred in the growth of jack pine. As density decreased, jack pine height growth and crown volume accumulation also decreased (height - Figure 9 and Tables 21 & 22; crown volume - Figure 11 and Tables 24 & 25). The reason for this reversed response may have been related to the influence of the environment. The pine transplants had relatively weak stems with lush needle development. At the highest densities, a form of "mutualism" occurred as stems were supported by the tightly-packed seedlings. This relationship reduced the determental effects of wind. At the lower densities, the pine transplants were greatly affected by the wind and accompanying higher transpiration rates, causing early bud set and reduced overall growth.

It is felt that once the pine transplants become established and competition at the higher density levels increases, the reversed growth response to density will be nullified. Similar responses to those found in the greenhouse study should occur at the highest density and move through to the lowest density in a systematic fashion.

Milthorpe (1961) considered that any deficiency of soil water or nutrients would cause the accelerated suppression of the subordinate. Similarly, Trenbath and Harper (1973) suggested that the development of a slight deficiency of soil factors where competition for light was already occurring caused an approximately 4-fold increase in the depression shown by a series of subordinates. At present, the data from the field study does not support the above influence of the environment. However, the environment may begin to play a more important role in increasing the competitive effects between the two species during the next few growing seasons.

Ecological Significance

Variation Within Measured Parameters

Before the ecological significance of the results can be addressed, the problem of wide variations between individuals within a treatment must be considered. This problem of wide variation within treatments tends to be a common problem with competition experiments. Mead (1968), in his attempts to develop a competition model which effectively estimates the magnitude of competition effects between neighbours, stated that "although the results obtained are of considerable interest, the variation within treatment means is extremely high." A series of Tables (Appendix 6, 7, 8, & 9) have included the standard deviations associated with height growth and crown volume accumulation for both the greenhouse and field studies. Tables 11 & 15 have included the coefficients of variation for total biomass and leaf wt./total wt. ratios, respectively. Important concerns over the magnitude of the variances are noted below.

(1) Variation in the greenhouse study was greater than that found for the field study (compare Appendices 6 & 7 with Appendices 8 & 9).

(2) Variation in plant biomass was greater in the pure stands than in the mixtures for greenhouse study (Table 11).

(3) Greater variation occurred in trembling aspen growth than occurred in jack pine (Greenhouse study - Appendices 6 & 7, Table 11 & 15; Field study - Appendices 8 & 9).

(4) Variation in crown volume was greater than any other measured parameter, especially in the greenhouse study.

(5) Block variation was low and not considered as a serious problem in the analyses.

Experiments have demonstrated that divergence of relative growth rates do occur between early and late emerging individuals. Early emergers continually increase their ability to capture resources at the expense of the later emergers, and in doing so increase their physical zone of influence. This appears to be the mechanism by which the distribution of plant weights within a population becomes skewed as the population grows, before self-thinning (Ross and Harper 1972). Since, in the present study relative growth rates for the greenhouse study far exceed those of the field study, the variation within the treatments would also be expected to be much larger.

Allard (1961) presented evidence that the biomass of individual plants in mixtures vary less than those in pure stands. Allard and Bradshaw (1964) have called this effect "population buffering" and compared its effects to those of buffering of the individual genotype due to heterozygosity. In the present study, this "population buffering" is well illustrated in Table 11. A summary of this relationship can be found in Table 27.

Table 27. Summary of coefficients of variation for individual plant biomass from greenhouse study data.

Density (plants/ m^2)	Species Composition Aspen pure	Aspen mixture	Jack Pine pure	Jack Pine mixture
	....	%	....	
10,000	136	130*	60	52
2,844	145	116	56	42
729	91	97	32	35

* - mixture values are the mean for the three associated mixes

Sakai (1961) has pointed out that the growth of plants can be influenced by their neighbours in three distinct ways:

(1) the effect of density - limiting space and nutrition for a plant,

(2) intragenotypic competition - some plants, within one genotype may outgrow their neighbours because of advantages gained through chance environmental factors, and

(3) intergenotypic competition - differential growth of unlike genotypes due to the inherent differences between them.

In contrast to crop plants, intergenotypic competition in forest trees has been studied only to a minor degree (Adams 1980). Results of these investigations concur with the general conclusions reached in crop plants and indicate that intergenotypic competition can have quite significant effects on the growth of trees at the seedling stage (eg: Tauer 1975). Tauer (1975) found wide variations in growth of black cottonwood seedlings. Therefore, it would seem reasonable to expect that this characteristic would be present in trembling aspen.

The excessively large variations associated with the crown volume parameter can probably be attributed to the serious infection of *fusicladium* spp. (aspen leaf and shoot blight).

Competitive Exclusion Principle

Where two species in a stable environment share the same niche, with an identical factor(s) limiting population growth, the two species will compete severely. This competition will virtually always lead to the exclusion of one species. This conclusion is known as the "competitive exclusion principle" or Gause's principle (Gause 1934). In the boreal forest, pure stands of jack pine are almost exclusively of fire origin. Dense sapling stands with 10,000 to 40,000 or more trees per acre can develop (Guilkey and Westing 1956). It is at this stage that the jack pine may exclude the invasion of the site by trembling aspen or other pioneer species. This feature was illustrated in the greenhouse study which showed that jack pine can be a dominant competitor at extremely high densities. Unfortunately, the density level where jack pine dominated (10,00 plants/m) almost never occur in nature. The reason for this is a combination of a lack of a homogeneous germination bed and lower germination percent due to poorer environmental conditions. Therefore, one would have to expect invasion of aspen pockets even in an area with excellent natural regeneration of jack pine.

Cook (1965) felt that intraspecific competition was mainly characterized by plastic response or depauperation, while interspecific competition mainly resulted in mortality. Therefore a young stand of jack pine would have reduced growth, but show only minimal self-thinning. However, if an extremely hot slash fire reduced the number of jack pine germinants, aspen would almost assuredly invade the site. Quickly and effectively, the aspen would overtop the pine seedlings and eventually reduce the pine percentage in the stand by way of direct mortality.

An Inference Concerning Genetic Variability

It is felt, among ecologists, that explanations of the behaviour of plants and animals must come ultimately from consideration of the evolutionary forces that have determined fitness (Turkington and Harper 1979).

Lee (1960) felt that the role of intraspecific competition in natural selection is in the moulding of the gene pool in the direction of conditioning greater adaptability. McNaughton and Wolf (1970) asserted that increased intraspecific competition by the more abundant species of a pair will produce in it greater genetic differentiation, while the less abundant species will tend toward genetic uniformity due to more interspecific competition.

Although it is highly speculative, the high genetic variability of trembling aspen - as suggested by high variance in the measured growth parameters of this project - may be directly related to its intense competitive nature. Jack pine, which is generally a weaker competitor than aspen, tends to illustrate a pattern of genetic uniformity.

Limited Portion of Ontogeny Studied

Critical work on competitive mechanisms deal either with the situation in short-lived crops established under largely artifical conditions, or else with the processes at work in short-term experimental cultures of the competing plants. Experimental studies with individual populations or simple combinations of species are effective for elucidating elementary processes within the community. However, the problems of extrapolating from these to the whole community are formidable, if not insurmountable (MacIntosh 1970).

Ford (1975) warned that investigations restricted to a few years can study only a limited section of the complete cycle of the forest crop. Relationships established at one point in time may not remain stable throughout the life history of the population. Therefore, the relationships identified in this study may not remain the same through the life history of these two species. It is hoped that by extending the field study over three to four growing seasons, any shift in the major relationships dealing with the competitive nature of these two tree species will be identified.

It must also be noted that the relationships determined in this study using trembling aspen seedlings would differ greatly when using aspen regeneration of sucker origin. Aspen suckers rely on a pre-existing, mature root system for resources during the early stages of development. Therefore, height growth would be far more rapid and the effect from competition of neighbours much less for an aspen sucker than those of an aspen seedling in a similar situation.

A final point that must be noted is that the results from the field study may differ on another soil type. Each species may react differently when located on other sites, thereby altering the competitive nature of the species in question.

CONCLUSIONS

The present study was the first study designed specifically to analyze the competitive effects of both trembling aspen and jack pine seedlings. The effects of both density and species mixture were examined using replacement series experiments in a greenhouse as well as a field study. The significant responses to the various treatments are summarized below.

Greenhouse Study

(1) A "hierarchy of resource exploitation" was established. However the species which took on the dominant role was dependent on density. At the highest density level (10,000 plants/m^2), jack pine assumed the dominant role. Once the density was lowered, trembling aspen gained dominance. The relative crowding coefficients clearly demonstrated this shift in dominance with changing density.

(2) Trembling aspen seedlings adjusted their biomass allocation with respect to the dominant competitor, as follows:

- (a) when jack pine was the main competitor, aspen increased the percentage biomass allocated to leaf weight, and
- (b) when aspen was the main competitor, aspen increased the percentage biomass allocated to stem weight.

The reverse response occurred in the jack pine seedlings.

(3) The phenomenon known as "frequency-dependent interference" was illustrated best by the survival data for trembling aspen. In general, as the percentage of aspen in mixture increased at a given density, survival decreased. Increased density further accentuated this relationship.

Field Study

(1) In general, aspen height growth was not significantly affected by density. However as the percentage of aspen decreased at a given density, height growth tended to increase.

A similar relationship was evidenced in crown development for the aspen transplants. Furthermore, high density tended to drastically reduce the ability of the aspen to expand their crowns.

(2) Both height growth and crown volume accumulation for jack pine decreased, as density decreased. The cause for this reversed response to density was related to the influence of environmental factors (ie: wind).

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APPENDICES

APPENDIX 1

Experimental Design for Greenhouse Study

Linear Model:

$$Y_{ijklm} = M + B_i + \delta_{(i)j} + D_k + BD_{ik} + S_l + BS_{il} + DS_{kl} + BDS_{ikl} + E_{(ijkl)m}$$

$i = 1,2,\ldots,5 \quad j = 1 \quad k = 1,2,3 \quad l = 1,2,\ldots,4 \quad m = 1$

where: Y – measured parameter

M – overall mean

B_i – the effect of the i^{th} block

$\delta_{(i)j}$ – restriction of all treatments in i^{th} block

D_k – the effect of the k^{th} density

BD_{ik} – the effect of the 2-way interaction between the i^{th} block and the k^{th} density

S_l – the effect of the l^{th} species mixture

BS_{il} – the effect of the 2-way interaction between the i^{th} block and the l^{th} species mixture

DS_{kl} – the effect of the 2-way interaction between the k^{th} density and the l^{th} species mixture

BDS_{ikl} – the effect of the 3-way interaction between the i^{th} block, the k^{th} density, and the l^{th} species mixture

E – experimental error

ANOVA table for the linear model:

Source of Variation	Degrees of Freedom	Expected Mean Squares	Experimental F-ratio	Critical F-ratio .05	Critical F-ratio .01
Block	4	$\sigma^2 + 12\sigma_\delta^2 + 12\sigma_B^2$	no test		
δ	0	$\sigma^2 + 12\sigma_\delta^2$			
Density	2	$\sigma^2 + 4\sigma_{B\cdot D}^2 + 20\phi_D^2$	MS(D) / MS(BD)	4.46	8.65
Block-Density	8	$\sigma^2 + 4\sigma_{B\cdot D}^2$	no test		
Sp.Comp.	3	$\sigma^2 + 3\sigma_{B\cdot S}^2 + 15\phi_S^2$	MS(S) / MS(BS)	3.49	5.95
Block-Sp.Comp.	12	$\sigma^2 + 3\sigma_{B\cdot S}^2$	no test		
Density-Sp.Comp.	6	$\sigma^2 + \sigma_{B\cdot D\cdot S}^2 + 5\phi_{D\cdot S}^2$	MS(DS) / MS(BDS)	2.51	3.67
Block-Density-Sp.Comp.	24	$\sigma^2 + \sigma_{B\cdot D\cdot S}^2$	no test		
Exp.Error	0	σ^2			
TOTAL	59				

APPENDIX 2

Simple Correlations Between Growth Parameters for Greenhouse Study

Species	Growth Parameters		r^2
At	Total Height versus Crown Volume	0.832	0.692
Pj	Total Height versus Crown Volume	0.874	0.764
At	Oven Dry Weight versus Leaf Wt/Total Wt Ratio*	0.620	0.384
Pj	Oven Dry Weight versus Leaf Wt/Total Wt Ratio*	0.837	0.701

* - these measurements were taken from a second set of randomly selected seedlings

Note: Correlations between growth parameters for the field study were not applicable as final measurements used in the analysis of variance were not taken during similar weeks.

APPENDIX 3

Layout for a single block in field study

2,500 plants/m^2		494 plants/m^2		202 plants/m^2		83 plants/m^2		17 plants/m^2	
100/0		75/25		50/50		25/75		0/100	
25/75	50/50	0/100	25/75	75/25	0/100	100/0	75/25	100/0	25/75
75/25	0/100	50/50	100/0	100/0	25/75	0/100	50/50	75/25	50/50

Note: The individual plot sizes will increase from the highest density to the lowest densities.

APPENDIX 4

Experimental design for field study

Linear Model:

$$Y_{ijklmn} = M + B_i + \delta_{(i)j} + D_k + BD_{ik} + \psi_{(ijk)l} + S_m + BS_{im} + DS_{km} + BDS_{ikm} + E_{(ijklm)n}$$

$$i = 1,2,\ldots,6 \quad j = 1 \quad k = 1,2,\ldots,5 \quad l = 1 \quad m = 1,2,3,4 \quad n = 1$$

where: Y - measured parameter

M - overall mean

B_i - the effect of the ith block

$\delta_{(i)j}$ - restriction of all treatments in the ith block

D_k - the effect of the kth density

BD_{ik} - the effect of the 2-way interaction between the ith block and the kth density

$\psi_{(ijk)l}$ - design restriction (all treatments of kth density together)

S_m - the effect of the mth species mixture

BS_{im} - the effect of the 2-way interaction between the ith block and the mth species mixture

DS_{km} - the effect of the 2-way interaction between the kth density and the mth species mixture

BDS_{ikm} - the effect of the 3-way interaction between the ith block, kth density, and mth species mixture

E - experimental error

ANOVA table for the linear model:

Source of Variation	Degrees of Freedom	Expected Mean Squares	Experimental F-ratio	Critical F-ratio .05	Critical F-ratio .01
Block	5	$\sigma^2 + 4\sigma_\psi^2 + 20\sigma_\delta^2 + 20\sigma_B^2$	no test		
δ	0	$\sigma^2 + 4\sigma_\psi^2 + 20\sigma_\delta^2$			
Density	4	$o^2 + 4o_\psi^2 + 4o_{B\text{-}D}^2 + 24\phi_D$	MS(D) / MS(BD)	2.87	4.43
Block-Density	20	$o^2 + 4o_\psi^2 + 4o_{B\text{-}D}^2$	no test		
ψ	0	$o^2 + 4o_\psi^2$			
Sp.Comp.	3	$o^2 + 5o_{B\text{-}S}^2 + 30\phi_S^2$	MS(S) / MS(BS)	3.29	5.42
Block-Sp.Comp.	15	$o^2 + 5o_{B\text{-}S}^2$	no test		
Density-Sp.Comp.	12	$o^2 + o_{B\text{-}D\text{-}S}^2 + 6\phi_{D\text{-}S}^2$	MS(DS) / MS(BDS)	1.92	2.50
Block-Density-Sp.Comp.	60	$\sigma^2 + o_{B\text{-}D\text{-}S}^2$	no test		
Exp.Error	0	σ^2			
TOTAL	149				

APPENDIX 5

Soil description for field study area

Sample No.	Horizon	pH	% Sand	% Silt	% Clay	Textural class
1	A	6.0	44.4	35.2	20.4	loam
	B	5.2	40.8	39.2	20.0	loam
	C	6.4	35.6	49.4	15.0	loam
2	A	6.3	19.6	59.2	21.2	silt loam
	B	6.2	11.6	69.2	19.2	silt loam
	C	6.7	2.8	80.2	17.0	silt loam
3	A	6.1	27.2	50.0	22.8	silt loam
	B	6.6	27.2	52.0	20.8	silt loam
	C	6.5	0.0	83.0	17.0	silt loam

APPENDIX 6

Weekly height growth data for greenhouse study

Density (plants per m^2)	Sp. Comp.	TIME (weeks)							
		4.5		10		11		12	
		Aspen	Jack Pine	Aspen	Jack Pine	Aspen	Jack Pine	Aspen	Jack Pine
10,000	100/0	1.6		6.5		8.9	-	10.2	-
		(0.4)*		(3.7)		(5.7)		(6.6)	
	75/25	1.7	3.6	5.7	6.0	7.4	6.4	8.9	6.8
		(0.3)	(0.4)	(2.7)	(1.5)	(3.3)	(1.5)	(4.7)	(1.5)
	50/50	1.6	4.0	4.0	7.2	5.2	8.2	5.6	9.0
		(0.3)	(0.3)	(1.7)	(1.0)	(2.1)	(1.0)	(2.5)	(1.0)
	25/75	1.5	3.9	3.6	6.7	3.8	7.4	3.4	8.0
		(0.3)	(0.6)	(2.2)	(1.8)	(2.7)	(2.2)	(2.0)	(2.4)
	0/100	-	3.5	-	6.2	-	6.2	-	7.9
			(0.4)		(1.5)		(1.4)		(2.2)
2,844	100/0	2.4		12.5		14.8		16.6	
		(0.7)		(7.0)		(7.4)		(9.0)	
	75/25	2.2	4.0	9.4	6.9	10.4	7.4	12.2	7.8
		(0.4)	(0.4)	(6.3)	(0.6)	(8.1)	(0.9)	(9.3)	(1.1)
	50/50	1.9	3.6	9.4	6.5	11.2	7.0	12.5	7.4
		(0.5)	(0.6)	(4.9)	(1.3)	(6.3)	(1.6)	(7.1)	(1.6)
	25/75	2.3	3.8	12.4	7.1	15.1	7.7	18.2	8.4
		(0.5)	(0.5)	(5.6)	(1.2)	(7.6)	(1.6)	(10.7)	(2.0)
	0/100	-	3.8	-	7.6	-	8.7	-	10.2
			(0.5)		(1.2)		(1.5)		(2.0)
729	100/0	3.8		20.0		26.6		35.5	
		(1.1)		(5.1)		(7.5)		(11.4)	
	75/25	3.4	4.1	18.2	7.2	23.0	8.3	31.7	8.9
		(0.7)	(0.4)	(5.5)	(1.2)	(6.9)	(1.3)	(11.3)	(1.3)
	50/50	3.0	4.0	21.2	6.9	26.3	7.8	35.8	8.6
		(0.8)	(0.4)	(6.7)	(0.9)	(7.7)	(1.0)	(14.9)	(1.1)
	25/75	2.8	4.2	19.0	8.0	26.1	9.4	38.4	10.6
		(0.9)	(0.5)	(8.5)	(0.9)	(10.9)	(1.3)	(15.0)	(1.4)
	0/100	-	4.1	-	8.3	-	9.9	-	12.0
			(0.3)		(1.3)		(1.3)		(1.8)

* - numbers in parantheses are standard deviations.

APPENDIX 7

Weekly crown volume data for greenhouse study

Density (plants per m^2)	Sp. Comp.	TIME (weeks) 4.5 Aspen	4.5 Jack Pine	10 Aspen	10 Jack Pine	11 Aspen	11 Jack Pine	12 Aspen	12 Jack Pine
10,000	100/0	2	-	203		269	-	222	-
		(1)*		(272)		(365)		(230)	
	75/25	1	11	56	65	165	83	247	96
		(1)	(6)	(54)	(40)	(186)	(61)	(328)	(65)
	50/50	1	14	23	95	37	137	39	181
		(1)	(5)	(27)	(41)	(45)	(56)	(46)	(68)
	25/75	1	12	25	72	40	102	15	126
		(1)	(6)	(37)	(49)	(23)	(73)	(20)	(84)
	0/100	-	8	-	51	-	68	-	121
			(4)		(46)		(56)		(122)
2,844	100/0	11		738		923		1215	
		(7)		(782)		(951)		(1255)	
	75/25	8	19	506	118	595	143	779	159
		(5)	(10)	(774)	(35)	(943)	(57)	(1233)	(63)
	50/50	11	15	389	102	548	128	651	138
		(10)	(8)	(399)	(64)	(603)	(78)	(689)	(80)
	25/75	18	18	1061	109	1897	145	2331	169
		(12)	(7)	(1101)	(47)	(2037)	(71)	(2563)	(87)
	0/100	-	15	-	136	-	208	-	275
			(8)		(61)		(118)		(147)
729	100/0	77		2944		5872		7971	
		(56)		(1148)		(3095)		(5360)	
	75/25	66	22	2462	165	3969	232	6644	251
		(36)	(5)	(1783)	(59)	(2761)	(90)	(5346)	(109)
	50/50	37	22	2934	168	469	207	7569	243
		(32)	(12)	(2731)	(42)	(4626)	(45)	(8544)	(56)
	25/75	52	27	4473	212	7346	278	15220	351
		(29)	(8)	(4339)	(67)	(7129)	(71)	(15049)	(97)
	0/100	-	26	-	225	-	320	-	501
			(9)		(77)		(92)		(149)

* - numbers in parentheses are standard deviations

APPENDIX 8

Weekly height growth data for field study

Density (plants per m^2)	Sp. Comp.	TIME(weeks) 5*		7		8		10		13	
		Aspen	Jack Pine	Aspen	Jack Pine	Aspen	Jack Pine	Aspen	Jack Pine	Aspen	Jack Pine
2,500	100/0	22 (5)**	--	25 (7)		27 (9)		31 (13)	-	31 (13)	-
	75/25	23 (7)	7 (1)	26 (10)	8 (2)	29 (12)	8 (2)	31 (15)	8 (2)	31 (15)	8 (2)
	50/50	24 (4)	9 (1)	29 (6)	9 (3)	34 (8)	10 (3)	40 (13)	10 (2)	40 (13)	10 (2)
	25/75	21 (3)	10 (2)	27 (5)	12 (2)	33 (7)	12 (2)	41 (11)	12 (3)	41 (12)	12 (3)
	0/100	-	10 (1)	-	13 (1)	-	14 (2)	-	15 (2)	-	15 (2)
494	100/0	22 (4)		28 (5)		33 (7)		40 (13)		41 (13)	
	75/25	17 (4)	9 (1)	23 (6)	10 (2)	27 (8)	12 (2)	34 (13)	12 (2)	34 (13)	12 (2)
	50/50	20 (4)	8 (1)	27 (5)	10 (2)	34 (6)	11 (2)	46 (11)	11 (2)	48 (12)	11 (2)
	25/75	20 (3)	8 (1)	26 (5)	10 (1)	32 (6)	11 (2)	44 (10)	12 (2)	47 (12)	12 (2)
	0/100	-	8 (1)	-	10 (1)	-	10 (1)	-	11 (2)	-	11 (2)
204	100/0	19 (4)		24 (7)		28 (9)		35 (11)		35 (11)	
	75/25	18 (3)	8 (1)	24 (4)	10 (2)	27 (6)	11 (2)	36 (12)	11 (2)	36 (13)	11 (2)
	50/50	21 (3)	8 (1)	27 (4)	9 (2)	33 (5)	10 (2)	44 (7)	11 (3)	46 (8)	11 (3)
	25/75	19 (3)	7 (1)	26 (4)	9 (1)	32 (4)	10 (1)	43 (7)	10 (1)	45 (8)	10 (1)
	0/100	-	7 (1)	-	9 (2)	-	10 (2)	-	11 (2)	-	11 (2)

* - first measurement was taken on July 17th, 5 weeks after planting commenced.

** - numbers in parentheses are standard deviations.

.. Cont'd

APPENDIX 8 (cont'd):

Density (plants per m^2)	Sp. Comp.	TIME (weeks) 5		7		8		10		13	
		Aspen	Jack Pine	Aspen	Jack Pine	Aspen	Jack Pine	Aspen	Jack Pine	Aspen	Jack Pine
83	100/0	18	–	24		28		38	–	39	–
		(3)		(7)		(8)		(12)		(13)	
	75/25	20	8	26	9	30	9	40	9	41	9
		(3)	(1)	(5)	(1)	(6)	(2)	(9)	(2)	(10)	(2)
	50/50	19	7	24	9	29	9	39	9	41	9
		(2)	(1)	(3)	(1)	(4)	(1)	(9)	(1)	(10)	(1)
	25/75	19	7	25	9	30	9	39	9	41	9
		(4)	(1)	(7)	(2)	(7)	(2)	(9)	(2)	(10)	(2)
	0/100	–	8	–	10	–	10	–	11	–	11
			(1)		(1)		(2)		(2)		(2)
17	100/0	18		25		29		40		42	
		(5)		(6)		(7)		(11)		(12)	
	75/25	17	7	23	7	28	8	38	8	39	8
		(3)	(1)	(5)	(1)	(7)	(1)	(10)	(1)	(12)	(1)
	50/50	19	6	27	8	32	7	42	8	44	8
		(4)	(1)	(7)	(1)	(8)	(1)	(12)	(1)	(13)	(1)
	25/75	21	7	30	8	35	9	46	9	47	9
		(5)	(1)	(7)	(1)	(9)	(1)	(12)	(2)	(13)	(2)
	0/100	–	6	–	7	–	7	–	7	–	7
			(1)		(1)		(1)		(1)		(1)

APPENDIX 9

Weekly crown volume growth for field study

Density (plants per m^2)	Sp. Comp.	TIME(weeks)							
		5		7		8		10	
		Aspen	Jack Pine	Aspen	Jack Pine	Aspen	Jack Pine	Aspen	Jack Pine
2,500	100/0	916		1069	–	1336		1554	–
		(347)*		(698)		(940)		(1516)	
	75/25	1141	183	1219	181	1674	161	1865	160
		(584)	(59)	(780)	(61)	(1266)	(60)	(1647)	(61)
	50/50	1107	208	1961	229	2421	194	3661	222
		(367)	(43)	(826)	(82)	(1310)	(73)	(2505)	(84)
	25/75	1050	234	1722	285	3097	246	4676	245
		(444)	(62)	(835)	(96)	(1465)	(91)	(2819)	(88)
	0/100	–	181	–	268	–	246	–	316
			(50)		(80)		(74)		(108)
494	100/0	1340		2254		2857		5175	
		(518)		(865)		(1344)		(3591)	
	75/25	925	245	1552	341	1989	383	3937	423
		(497)	(46)	(900)	(97)	(1598)	(123)	(3260)	(164)
	50/50	1137	224	2040	293	3881	333	8322	368
		(428)	(59)	(952)	(79)	(1805)	(111)	(4245)	(153)
	25/75	1208	231	1987	298	3884	320	9360	389
		(436)	(61)	(966)	(64)	(1928)	(88)	(4418)	(132)
	0/100	–	337	–	235	–	248	–	356
			(60)		(61)		(64)		(137)
204	100/0	1023		1512		4011		4339	
		(538)		(727)		(1292)		(2443)	
	75/25	985	226	1455	331	2648	398	5856	448
		(349)	(75)	(664)	(105)	(1543)	(161)	(4005)	(219)
	50/50	1238	300	2146	279	3219	312	7784	345
		(483)	(62)	(724)	(61)	(726)	(97)	(2389)	(163)
	25/75	2458	248	1925	305	3490	329	9697	359
		(330)	(63)	(516)	(78)	(1229)	(104)	(3237)	(113)
	0/100	–	212	–	306	–	334	–	426
			(72)		(99)		(126)		(189)

* – numbers in parentheses are standard deviations

...Cont'd

APPENDIX 9 (cont'd):

Density (plants per m^2)	Sp. Comp.	TIME(weeks)							
		5		7		8		10	
		Aspen	Jack Pine	Aspen	Jack Pine	Aspen	Jack Pine	Aspen	Jack Pine
83	100/0	1120 (463)	-	2675 (1906)		3758 (2432)		7394 (4619)	-
	75/25	1461 (476)	235 (83)	2259 (916)	291 (98)	3672 (1846)	274 (97)	7283 (2745)	278 (102)
	50/50	1302 (581)	211 (53)	2062 (630)	267 (65)	3146 (1145)	285 (77)	7785 (3545)	297 (97)
	25/75	1119 (482)	224 (61)	1874 (1030)	281 (82)	3106 (1813)	296 (94)	7310 (3595)	332 (147)
	0/100	-	256 (55)	-	343 (101)	-	380 (141)	-	446 (215)
17	100/0	1086 (529)		2171 (1134)	-	3886 (1998)		10699 (6041)	
	75/25	1002 (417)	173 (48)	1890 (1053)	203 (47)	4782 (1241)	218 (58)	7575 (3232)	248 (109)
	50/50	1322 (612)	176 (43)	2611 (1470)	220 (84)	4374 (2442)	212 (77)	9813 (6167)	239 (106)
	25/75	1504 (586)	256 (80)	2948 (1289)	282 (65)	4820 (2430)	286 (89)	9812 (5719)	319 (142)
	0/100	-	180 (47)	-	194 (48)	-	184 (54)	-	203 (87)