TEN-YEAR GROWTH RESPONSE OF 45-YEAR OLD *PINUS BANKSIANA* LAMB. TO UREA FERTILIZATION AND LOW THINNING

by

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ABSTRACT

The objectives of this investigation were 1) to examine the duration and pattern of jack pine growth response to urea fertilization and low thinning, and 2) to examine methods commonly used in the measurement of fertilization and thinning trials in jack pine.

The study area was located near Chapleau, Ontario in a fire-originated jack pine stand. The stand was treated at age 45 with 336 kg urea-N/ha and a low thinning of 20 percent basal area in a 2 x 2 factorial design with four replicates.

At stand age 55, 80 trees were felled for stem analysis, representing 5 tree diameter classes within each stand treatment. Volume increment, height increment, measures of form, and local volume equations were determined from the stem analysis data. The local volume equations were applied to diameter frequency distributions at stand ages 45, 50, and 55 to calculate stand volumes at these ages. A growth model was developed to characterize the annual volume growth of individual trees. The model related the annual volume growth of an individual tree to its volume, and the stand volume. Aggregation of the annual volume increments of individual trees allowed annual stand volume increments to be estimated.

Individual trees responded to fertilization with greater 10-year volume increment and merchantable height increment. On a stand basis, fertilization resulted in about 20 m^3 ha^{-1} of additional gross volume growth during the ten-year response period. This volume growth response was greatest in the third and fourth years after fertilization. Fertilization appeared to have both a direct effect and an indirect effect. The direct effect was growth response to the improved nitrogen status, and this effect ceased 10 years after treatment. The indirect effect was greater growth due to larger average tree size, and this effect was still evident 10 years after treatment. Thinning had little effect beyond salvaging potential mortality.

An examination of methods commonly used to estimate growth responses to silvicultural treatments was made. The results suggest that it is necessary to use treatment-specific and age-specific local volume equations to accurately measure growth response to fertilization.

INTRODUCTION

Fertilization and thinning are silvicultural techniques which can increase the growth and merchantable yield of existing forest stands. To use these techniques effectively, forest managers must have quantitative information about the response of forest stands to fertilization and thinning. The task of providing such information is confounded by the fact that the actual response may be misrepresented by the mensurational methods used to detect it.

This thesis analyzes a fertilization and thinning study which was conducted near Chapleau, Ontario in a 45-year-old jack pine *(Pinus banksiana* Lamb.) stand. The analysis has two objectives:

1) to examine the duration and pattern of jack pine growth response to low thinning and urea fertilization.

2) to examine methods commonly used in measurement of fertilization and thinning trials in jack pine.

In this analysis local volume equations were developed from stem analysis data. Stand volumes at the time of treatment and at five and ten years after treatment were calculated by applying these volume equations to diameter frequency distributions. This permitted the calculation of the ten-year net volume and gross volume growth. To characterize annual volume growth, a growth model was developed relating individual tree volume growth to individual tree volume and stand volume.

The results of the analysis showed that the growth response to nitrogen fertilization lasted about ten years. The greatest responses occurred in the third and fourth years after treatment. There was little growth response to thinning. Serious error would have been incurred in estimates of volume increment if treatment-specific and stand age-specific local volume equations had not been used.

The discussion is divided into two parts. Part I is a discussion of the growth response of jack pine to fertilization and thinning. Part II is a discussion of mensurational methods. It includes an examination of the growth model, and also discusses how the results would have been affected had other mensurational methods been used.

LITERATURE REVIEW

Nitrogen relations

Nitrogen is essential for wood production in trees; it is a component of chlorophyll, amino acids, proteins, purines, alkaloids and vitamins (Lee 1968; Kozlowski 1971). The availability of nitrogen to trees on podzolic soils in the boreal forest is limited by the accumulation of organic nitrogen reserves, low mineralization rates, and strong biological competition for nitrogen. Because of these limits to nitrogen availability, northern coniferous forests generally show a growth response to nitrogen fertilization (Baule 1970; Weetman and Hill 1973; Armson et al. 1975).

The nitrogen cycle

Virtually all of the nitrogen that is taken up by trees is supplied by the soil, and most of the nitrogen in the soil originates from the atmosphere (Youngberg and Wollum 1968). Atmospheric nitrogen is added to soil by precipitation and biological fixation. The amount of nitrogen added to the earth's surface by precipitation varies, but generally ranges between 4 and 10 $kg.ha^{-1}.yr^{-1}$ (Wollum and Davey 1975). Nitrogen is fixed from the gaseous state by a number of organisms and biological processes. Free-living bacteria such as *Azotobacter* and *Clostridium*, along with blue green algae, probably fix about 1 to 5 $kg.^{-1}.yr^{-1}$ of nitrogen (Wollum and Davey 1975). It is possible that microbial fixation of nitrogen occurs on leaf surfaces (Wollum and Davey 1975), although little nitrogen fixation has been observed on jack pine leaves (Sucoff 1979). Nonleguminous symbiotic fixation occurs in species of the genera *Myrica*, *Comptonia*, *Alnus*, *Ceanothus*, *Elaeagnus*, *Shepherdia* and *Dryas* (Daly 1966). The rate of nitrogen fixation for these species varies greatly, but may be considerable. For instance, in Ontario, *Alnus rugosa* has been estimated to fix 150 kg $N.ha^{-1}.yr^{-1}$ (Daly 1966). Leguminous plants are rare in the boreal forest, and are therefore of minor importance as nitrogen fixers in this region.

The largest pool of nongaseous nitrogen in forest ecosystems is found in the soil. The amount of nitrogen contained in forest soils varies greatly. The coarse-to-medium sand soil of one jack pine ecosystem in northern Ontario contained about 4000 kg $N.ha^{-1}$, with 90 percent of the nitrogen in the mineral soil (Foster and Morrison 1976). The soil under a number of jack pine stands in New Brunswick contained an average of about 1500 kg $N.ha^{-1}$, with about 70 percent of the nitrogen in the mineral soil (MacLean and Wein 1977).

Ninety to ninety-five percent of soil nitrogen is in organic form such as amino acids and amino sugars (Wollum and Davey 1975). Nitrogen in organic form is not available to plants. The remainder of the soil nitrogen is in mineral form, including ammonium and nitrate, which can be taken up by plants, and nitrite, which cannot. Mineral nitrogen is present in soil solution and is held on soil colloids. In a 30-year-old jack pine stand in northern Ontario, over one half of the available nitrogen was in the organic zone (Foster and Morrison 1976). Mineralization of nitrogen, resulting from the breakdown of organic substrates by microbial activity, is promoted in well-aerated, warm, moist soils (Wollum and Davey 1975). Mineralization is inhibited in the cool, acid conditions common in the boreal forest region.

The second largest pool of nitrogen in a mature forest ecosystem is the vegetation. In a 30-year-old jack pine stand in northern Ontario, trees contained 165 kg $N.ha^{-1}$ and understorey vegetation contained about 6 kg $N.ha^{-1}$ (Foster and Morrison 1976). About 1/3 of the nitrogen in trees was contained in the foliage.

Nitrogen may return to the atmosphere from the soil by two pathways. First, ammonia may be lost from the soil by volatilization. This chemical process is favoured by high temperatures and high pH. Second, in poorly aerated soils of pH 5.5 or higher, nitrate may be reduced by anaerobic bacteria to gaseous nitrogen (N_2), and nitrous oxide (N_2O) (Armson 1977). This process is termed denitrification.

Biological competition exists between trees and other organisms for available soil nitrogen. Strong competitors include ericaceous plants (Weetman and Algar 1974) and soil microflora and microfauna (Weetman and Hill 1973).

Low mineralization rates and competition for nitrogen in the boreal forest may contribute to undersupply of nitrogen for jack pine growth. Morrison and Foster (1974) felt that available nitrogen supply exceeded demand by jack pine on a glacial till site, but supply may have been less than demand on a sandy site. Nevertheless, foliar analyses indicated that trees on both sites suffered from moderate nitrogen deficiency according to Swan's (1970) standards. Jack pine on silt loam in northern Ontario was also nitrogen deficient according to foliar analysis (Morrison and Foster 1977).

In general, the low total cation exchange capacity of shallow soils and coarse-textured soils contributes to nitrogen deficiency. The slow breakdown of soil organic matter in acid soils also contributes to nitrogen deficiency. Deficiency of nitrogen is a greater problem in mature forest stands than in younger stands, because large amounts of nitrogen are tied up in the forest stand and litter on the forest floor. Thus, mature jack pine stands growing on relatively coarse-textured, acid soils are generally nitrogen deficient.

Nitrogen fertilization

The most common sources of nitrogen in forest fertilization are ammonium nitrate and urea. Ammonium nitrate yields ammonium and nitrate in solution, and hydrolysis of urea produces ammonium.

Several factors influence the availability to plants of nitrogen added as fertilizer. There is some evidence that ammonium may be taken up by plants more readily than nitrate (Hauck 1968; Wollum and Davey 1976). Durzan and Stewart (1967) noted that jack pine seedlings supplied with ammonium grew better than those supplied with nitrate. Nitrogen source experiments with urea, urea formaldehyde, ammonium nitrate, and ammonium sulfate revealed no differences among these fertilizers with regard to jack pine volume growth (Morrison et al. 1976a). Both nitrate and ammonium are susceptible to loss from the soil. The nitrate ion released from nitrate fertilizers is subject to leaching, while ammonium is subject to volatilization to ammonia gas. About 30 percent of the nitrogen contained in urea may be lost through volatilization after fertilizer application to thin humus under jack pine (Morrison and Foster 1977). Nitrogen addded through fertilization rarely remains available for very long. For example, in acid forest soils, there is little chemical binding of NH_4^+ to humus; consequently this ion is subject to rapid immobilization (Knowles 1975).

Nitrogen added as fertilizer may serve as a 'primer' to stimulate mineralizaton of soil nitrogen (Wollum and Davey 1975). Foster and his coworkers (1980) found that, despite high carbon: nitrogen ratios in litter and humus under jack pine, a lack of available carbon limited microbial activity. Hydrolysis of added urea raised soil pH, favouring the solubilization of carbon from soil organic matter. Increased microbial activity was supported by the additional available carbon. In addition to the nitrogen added as fertilizer, nitrogen was made available by the increased decomposition of soil organic matter.

Much of the nitrogen fertilizer applied to the soil underneath jack pine stands is not taken up by trees. For example, in a 45-year-old jack pine stand, after losses to volatilization and immobilization in soil and competing vegetation, the equivalent of only about 23 percent of added urea-N was taken up by trees (Morrison and Foster 1977). Some of the added nitrogen immobilized in soil and vegetation may eventually have been released as organic matter decomposed.

Increases in needle length (Brix and Ebell 1969) and needle weight (Keay et al. 1968; Calvert and Armson 1975) of coniferous species follow the addition of nitrogen fertilizer to soil. The number of needles per shoot may also increase in species such as Douglas-fir *(Pseudotsuga menziesii* (Mirb.) Franco) (Brix and Ebell 1969; Gessel and Walker 1956). Needles become greener (Gessel and Walker 1956), and chlorophyll content and photosynthesis increase (Brix 1971; Keay et al. 1968). Nitrogen fertilization may increase the wood production efficiency of foliage as well as increasing the amount of foliage (Draper 1980).

The foliar concentration of nitrogen often increases following nitrogen fertilization (Roberge et al. 1968; Brix 1971; Calvert and Armson 1975; Kingston et al. 1978). Swan (1970) determined optimum foliar levels of nitrogen for the growth of jack pine seedlings. He found that good growth occurred in seedlings when foliar nitrogen ranged from 1.5 to 2.5 percent. Mature trees generally exhibit lower foliar nitrogen concentrations than seedlings. This difference may indicate nutrient deficiencies in older trees rather than differing nutrient requirements between seedlings and mature trees.

Fertilization may produce more foliage, thus diluting foliar nutrients. For instance, following fertilization with nitrogen, foliar concentration of nitrogen may not change, because increased foliage dry weight offsets the increase in nitrogen content (Swan 1970). Dilution may decrease the concentration of nutrients other than those applied through fertilization. Nitrogen fertilization decreased foliar potassium levels in young jack pine (Calvert and Armson 1975), and decreased foliar phosphorus, calcium, magnesium, manganese, zinc, and aluminum levels in young loblolly pine *(Pinus taeda* L.) (Wells 1970).

Fertilization affects the root growth of trees in various ways. According to Baule (1970) nitrogen-phosphorus-potassium fertilization generally increases root growth. He noted, however, that in some cases fertilization caused stand growth increases with little or no increase in root system size. Increasing the supply of nutrients may even lead to a decrease in the total length of roots. For example, Farrell and Leaf (1974) reported that the fertilization of red pine *(Pinus resinosa* Ait.) with potassium decreased the number of root tips while increasing the growth of the stem. This may indicate a shift in the allocation of growth from the roots to the stem.

Effects of fertilization on the growth of individual jack pine trees

Nitrogen fertilization may have differing effects on the growth of trees in different crown classes within a stand. In one study, dominant and codominant jack pine trees showed a greater growth response to fertilization than trees in lower crown classes (Kingston et al. 1978). A similar response has been observed in other species as well (Gessel and Walker 1956; Gessel and Shareef 1957; Knight 1963; Reukema 1968; Youngberg 1973; Gagnon et al. 1976; Van Nostrand 1979). Although the absolute growth response to fertilization is greatest in the largest trees of a stand, there may be little difference in the relative growth response between small trees and large trees (Miller and Cooper 1973).

The possible effects of fertilization on the stem form of jack pine have not been examined. In other species of pine, however, improvements in stem form have followed fertilization (Pegg 1966; Broerman 1968; Miller and Cooper 1973). On the other hand, there is some evidence that fertilization may worsen the stem form of Douglas-fir (Mitchell and Kellogg 1976; Flewelling and Yang 1976).

Effect of fertilization on the growth and yield of jack pine stands

The volume growth response of jack pine to urea fertilization has been examined in a number of studies (Table 1). In Scandinavia, it is felt that the pretreatment current annual increment is a factor of essential importance in predicting the size of growth response to fertilization (Hagner 1967). According to Hagner, growth response increases with increasing current annual increment. On the contrary, it is evident from Table 1 that the size of the growth response of jack pine to fertilization is unrelated to the current annual increment of controls.

The duration of growth response to fertilization has not been clearly established for jack pine. In Sweden, the growth response of Scots pine (*Pinus sylvestris* L.) to nitrogen peaks at 3 to 5 years after fertilization, and is completed after 8 years (Hagner et al. 1966). Black spruce (*Picea mariana* (Mill.) B.S.P.) in Quebec showed maximum growth response to nitrogen fertilization 7 to 8 years after treatment (Weetman 1975). The growth response to nitrogen fertilization often does not commence until the second growing season after fertilization (Mader 1973; Weetman et al. 1980).

The effect of fertilization on mortality of jack pine is unclear. After analyzing the results of a number of nitrogen fertilizer trials in jack pine, Weetman and his coworkers (1979)

Table 1. Volume growth response of jack pine stands to urea fertilization.

Source	Location	Stand age	Fertilizer type	Rate (kg/ha)	Response period	Control growth	Response[1]
						($m^3.ha^{-1}.yr^{-1}$)	
Weetman et al. (1976)	Quebec	40	urea-N	224	5	5.4	2.1
Weetman et al. (1976)	Ontario	56	urea-N	224	5	3.5	1.7
Weetman et al. (1976)	Ontario	48	urea-N	224	5	3.7	1.4
Weetman et al. (1976)	Ontario	45	urea-N	224	5	4.4	0.8
Weetman et al. (1976)	Manitoba	62	urea-N	224	5	4.7	1.1
Weetman et al. (1976)	Manitoba	70	urea-N	224	5	3.7	2.2
Weetman et al. (1976)	Manitoba	62	urea-N	224	5	2.5	1.3
Weetman et al. (1976)	Manitoba	62	urea-N	224	5	3.5	1.3
Weetman et al. (1978)	Quebec	46	urea-N	224	5	5.1	3.6
Weetman et al. (1978)	Quebec	44	urea-N	224	5	5.9	1.2
Weetman et al. (1978)	Quebec	54	urea-N	224	5	3.9	1.9
Weetman et al. (1978)	Quebec	48	urea-N	224	5	3.6	1.3
Weetman et al. (1978)	Quebec	46	urea-N	224	5	4.9	0.7
Weetman et al. (1978)	Ontario	40	urea-N	224	5	4.5	2.4
Weetman et al. (1978)	Ontario	31	urea-N	224	5	5.4	2.5
Weetman et al. (1978)	Ontario	28	urea-N	224	5	7.3	1.1
Weetman et al. (1978)	Ontario	21	urea-N	224	5	5.6	2.2
Weetman et al. (1978)	Ontario	21	urea-N	224	5	7.5	2.6
Weetman et al. (1979)	Quebec	38	urea-N	224	5	5.3	1.1
Weetman et al. (1979)	Quebec	42	urea-N	224	5	3.0	1.1
Weetman et al. (1979)	Quebec	54	urea-N	224	5	4.7	1.1
Weetman et al. (1979)	Ontario	49	urea-N	224	5	5.3	3.5
Weetman et al. (1979)	Ontario	49	urea-N	224	5	4.5	2.2
Weetman et al. (1979)	Ontario	56	urea-N	224	5	5.1	1.7
Weetman et al. (1979)	Ontario	56	urea-N	224	5	5.1	0.2
Weetman et al. (1979)	Ontario	33	urea-N	224	5	4.7	1.5
Weetman et al. (1979)	Ontario	36	urea-N	224	5	3.6	3.8
Weetman et al. (1979)	Saskatchewan	73	urea-N	224	5	3.2	0.6

[1] Response = fertilized growth - control growth

Table 1 (continued). Volume growth response of jack pine stands to urea fertilization.

Source	Location	Stand age	Fertilizer type	Rate (kg/ha)	Response period	Control growth	Response[1]
						($m^3 \cdot ha^{-1} \cdot yr^{-1}$)	
Hoyt (1973)	New Brunswick	55	urea-N	168	5	5.8	1.5
Hoyt (1973)	New Brunswick	39	urea-N	168	5	7.1	1.4
Kingston et al. (1978)	New Brunswick	45	urea-N	168	3	4.3	1.2
Morrison et al. (1976a)	Ontario	55	urea-N	224	4	5.0	1.7
Morrison et al. (1976a)	Ontario	55	urea-N	303	4	4.1	2.7
Morrison et al. (1976b)	Ontario	45	urea-N	224	5	6.1	1.1
Morrison et al. (1977b)	Ontario	45	urea-N	336	5	5.6	0.8
Morrison et al. (1977c)	Ontario	45	urea-N	336	5	5.7	1.2
Morrison et al. (1977d)	Ontario	55	urea-N	336	10	4.8	2.2
Wintson et al. (1977)	Ontario	45	urea-N	336	5	6.8	2.0

[1] Response = fertilized growth - control growth

could not discern any consistent effect of fertilization on mortality. Kingston et al. (1978) noted mortality was lower on fertilized plots than on control plots in jack pine. In other species, fertilization has been found to increase mortality (Gessel and Shareef 1957; Gessel and Walker 1956; Broerman and Koenig 1971; Lee 1974).

Thinning

Thinning is a means of controlling stand growth through control of stand density and structure. Whenever trees compete for light, water, or nutrients in a forest stand, thinning removes some of the competitors and allows growth resources to be divided among the remaining trees. This concentrates wood growth on fewer stems.

Three general theories have been stated regarding the relationship between stand growth and stand density:

1) According to Mar:Moller (1954), who studied European beech *(Fagus sylvatica* L.), stand increment in basal area or volume varies little over a wide range of density once full stocking has been achieved.

2) Assman (1970), working with Norway spruce *(Picea abies* (L.) Karst.), theorized that optimum basal areas exist for forest production, and that at densities greater or lesser than the optimum production declines.

3) Work by Baskerville (1965) in balsam fir (*Abies balsamea* (L.) Mill.), and Doucet and his coworkers (1976) in jack pine, suggests that stand growth increases with increasing stand density. It is possible, however, that this theory is a special case of either of the first two theories. It may be that densities high enough to show constant or declining production were not sampled.

Each of these theories may be valid for particular circumstances or for different species. Only according to Assman's theory can thinning actually increase the total wood production of a forest stand. Usually the benefits of thinning lie in salvaging mortality, concentrating wood growth on fewer stems, and shortening the rotation.

Intolerant species, such as jack pine, may be slow to respond to release once overtopped (Bella and De Franceschi 1974b). Consequently, thinning operations which favour the dominant and codominants in a jack pine stand will produce the greatest growth response. The competitive situation of dominants and codominants can be improved by several types of thinning: low thinning removes trees of small diameter or lower crown position; crown thinning removes some of the dominants and codominants and thus favours the remaining dominants and codominants; strip thinning favours the growth of residual trees in all crown classes, but especially those near the edge of the strip.

Effect of thinning on the growth of individual jack pine trees

In thinning trials in Manitoba and Saskatchewan, jack pine responded to thinning with greater diameter growth over a wide range of ages and sites (Bella and De Franceschi 1974b). In several jack pine thinning studies, the trees in the higher diameter classes of a stand (Bella and De Franceschi 1974b, Wilson 1952), or in the intermediate diameter classes (Bella and De Franceschi 1974a) show the greatest absolute increase in diameter growth following thinning. Nevertheless, trees in the smaller diameter classes may have the greatest relative increase in diameter growth (Bella and De Franceschi 1974b).

Since thinning stimulates jack pine diameter growth at breast height, it follows that volume growth will also be increased. Bella and De Franceschi (1974a) found that the greatest volume per tree occurred in the most heavily thinned portions of a jack pine stand thinned at age 40. Volume increment per tree was greatest at the widest spacing in jack pine stands thinned to various spacings at age 18 (Wilson 1952).

There are pitfalls in using diameter growth increase at breast height as a response variable for thinning studies. Morrison et al. (1976a) found that the average diameter increment of residual trees after low thinning of 55-year-old jack pine increased significantly. However, much of this increase may have resulted from the removal of the portion of the stand which was growing most slowly. Another problem is that the increase in diameter growth in both relative and absolute terms is affected by tree age, tree size, and site. This makes comparisons between studies difficult. An additional problem is that diameter growth response to thinning in the upper stem may be different from the response in the lower stem. Farrar (1961) noted that breast-high measurements will overestimate volume growth response to thinning if taper increases.

One effect often attributed to thinning is an increase in the taper of the remaining stems (Larson 1963; Kozlowski 1971). Thinning slows the upward recession of the crown and increases crown width and leaf growth. Total stem wood increment is increased and is redistributed to add more growth to the lower portions of the tree (Kozlowski 1971).

Increase in taper following thinning, although common, is not a universal occurrence (Larson 1963). Meyer (1931) studied the change in form quotient of ponderosa pine *(Pinus ponderosa* Law.) released by the removal of dominants and codominants. Trees of initially high form quotient decreased in form quotient, and trees of initially low form quotient increased in form quotient. Behre (1932) obtained similar results for red spruce *(Picea rubens* Sarg.) released by the cutting of dominants. Form quotient of ponderosa pine generally decreased after thinning (Myers 1963), but inspection of data presented in the study reveals that on one plot the form quotient of the largest trees increased after thinning. Again, the form quotient of all trees on a plot appeared to be approaching a common value. Form quotient of white spruce (*Picea glauca* (Moench) Voss) generally increased 10 years after thinning from below (Stiell 1970).

Little study has been made of form change in jack pine following thinning. Buckman (1964) thinned dense 5-year-old jack pine. He concluded that 22 years after thinning there was little difference in taper among control trees and trees at three different spacings.

In general, thinning does not appear to affect the height growth of jack pine (Buckman 1964; Bella and De Franceschi 1971, 1974a; Winston 1977). Wilson (1952) examined the height increment of trees 21 years after a jack pine stand was thinned to various spacings at age 18. The height increment of the smallest trees increased with wider spacing, but the height increment of the larger trees showed little difference among spacings.

In some species, differences in height growth between trees in thinned and unthinned stands may change with time. Height growth of Douglas-fir thinned at age 27 was less than controls 3 years after thinning (Crown et al. 1977), but greater 6 years after thinning (Hall et al. 1980).

Effect of thinning on the growth and yield of jack pine stands

Trends from 6 jack pine thinning experiments by Bella and De Franceschi (1974b) showed that the greatest basal area growth occurred when basal area was reduced 30 percent below that of fully stocked control plots. Results from jack pine thinning studies by Morrison and his coworkers (1976a, 1977b) suggested that stand growth was not reduced by 20 percent basal area removal, but was reduced by 40 percent basal area removal. Wilson (1952) found that 21 years after thinning 18 year old jack pine to various spacings, thinned plots had about the same volume increment as unthinned plots, although volume increment was slightly less at the widest spacing. Bella and De Franceschi (1974a) noted a greater stand basal area growth compared with controls during the 10-year period following both light and heavy thinnings of 40-year-old jack pine. In all of these studies, growth estimates were based on breast-high measurements. If form changes followed thinning, it is doubtful that these estimates accurately reflected actual stand volume growth.

Results of thinning studies in 40-year-old jack pine comparing low and crown thinning show that the length of the response period must be taken into consideration (Bella and De Franceschi 1974a, 1974b). Initially, better stand basal area response occurred with low thinning than with crown thinning. Ten years after thinning, however, the basal area growth of low thinned plots was surpassed by that of crown thinned plots.

The greatest amount of mortality in jack pine occurs in the lower crown classes and smaller diameter classes. These classes are removed by low thinning, so mortality decreases (Bella and De Franceschi 1974b). In addition, the more favourable com petitive status of residual trees following thinning may further reduce mortality. In general, less mortality occurs in thinned jack pine stands than in unthinned stands (Bella and De Franceschi 1974l, 1974b, Wilson 1952).

Strip thinning did not reduce mortality in a jack pine study by Bella (1974). Apparently the reduction of competition at the edges of the leave strips was not sufficient to reduce mortality within the strips.

Nitrogen fertilization and thinning

The combined effects of nitrogen fertilization and thinning on tree growth appear to be additive. This has been found for ponderosa pine (Agee and Biswell 1970), loblolly pine (Jones and Broerman 1977), black spruce (Weetman et al. 1980), and jack pine (Morrison et al. 1976a, 1977d).

Problems in assessing growth response

A number of sources of error may confound the measurement of stand response to silvicultural treatment. Incorrect estimates of stand responses result when improper assumptions are made about the relationship between outside and inside bark diameters, when inappropriate volume equations are used, and when the effects of variation in initial stand density are ignored.

Overbark measurement of tree diameter with a diameter tape usually results in an overestimate of average diameter (Husch et al. 1972; Whyte and Mead 1976). Irregularities in the cross-sectional shape of the tree stem or in the thickness of the bark cause spaces between the tape and tree to be included in the average diameter. Also, the greater the departure of the shape of the stem cross-section from a circle, the greater the overestimate of average diameter will be. As a result of these sources of error, Reukema (1971) found that bark thickness measured on cut sections of Douglas-fir underestimated bark thickness based on tape measurement. In addition to previously mentioned causes, this underestimate may stem from bark loss during handling.

Fertilization has led to decreases in bark thickness of slash pine *(Pinus elliottii* Engelm.) (Broerman 1968), and Scots pine (Saikku 1973). As a result, inside bark volume based on outside bark diameter measurements may be underestimated.

In local volume equations, the relationship between volume and diameter changes with stand age (Evert 1976). This relationship may also be affected by fertilization and thinning (Whyte and Mead 1976; Evert 1977; Meng 1981). Consequently age-specific and treatment-specific volume equations should be used in the evaluation of volume growth response to silvicultural treatments.

Forest stands frequently display variation in density large enough to cause variation in growth responses generated by stand treatments (Wells et al. 1976). Pretreatment density variation can be taken into account by using initial basal area or volume as a covariate in assessing growth response to treatments

(Turnbull et al. 1970; Whyte and Mead 1976). According to Pritchett (1979), covariance analysis need not be used in the evaluation of fertilization trials, unless stand density varies more than 50 percent from plot to plot.

MATERIALS AND METHODS

Study area

Location and climate

The study area is located in northern Ontario, 25 km south south east of the town of Chapleau at latitude 47° 38' N, longitude 83° 15' W. It is within the Missinaibi-Cabonga Section (B.7) of the Boreal Forest Region (Rowe 1972), and the Height of Land Climatic Region (Chapman and Thomas 1968). Mean growing season length (based on 5.5°C) is 160 days, and the mean growing degree days above 5.5°C is 1220 (2200 based on °F). Mean annual precipitation is 787 mm, with 381 mm falling during the growing season. The mean annual water surplus is 330 mm (Chapman and Thomas 1968).

Soil Characteristics

Soil characteristics in the vicinity of the study area were examined by Morrison and Foster (1977) (Table 2). They reported that the soil is a Mini Humo-Ferric Podzol (Canada Soil Survey Committee 1974), developed in silt loam over loamy sand. The silt loam is of outwash origin with evidence of windworking, and the loamy sand commences approximately 3 dm below the mineral surface.

Table 2. Mean physical and chemical properties of soils in the vicinity[1] of a 45-year old jack pine stand.

		Texture				Available		Exchangeable			
Horizon	pH	S	Si	C	OM	N	P	K	Ca	Mg	CEC
		%					ppm	meq/100g			
L^2	4.6	-	-	-	89.2	1.02	49.5	5.03	12.98	4.50	65.2
F	4.4	-	-	-	69.1	1.04	44.2	2.51	12.97	3.45	71.7
H	4.4	-	-	-	35.5	0.60	25.8	1.32	9.00	1.75	56.6
Ae	4.6	36	57	7	2.0	0.06	1.6	0.26	0.94	0.21	9.8
Bf$_1$	5.5	35	63	2	1.4	0.06	1.7	0.16	0.34	0.08	9.0
IIBf$_2$	5.1	76	22	2	0.9	0.04	4.6	0.17	0.33	0.07	7.2

[1] After Morrison and Foster (1977)

[2] Includes mosses

Stand Characteristics

The study was conducted in a nearly pure stand of jack pine of fire origin. Prior to treatment, at stand age 45, stand density was 3430 stems/ha; basal area was 31.3 m^2/ha; and total standing volume was 199.4 m^3/ha. The diameter at breast height of the tree of mean basal area was 10.8 cm, and diameters ranged from 2.8 cm to 27.9 cm (Figure 1).

Mean height of dominant trees was 15.53 m, indicating a high site class II (Plonski 1974) and site index of 16.6 m at 50 years. The current annual volume increment was approximately 3.5 $m^3.ha^{-1}.yr^{-1}$. Intertree spacing factor, obtained by the ratio of the mean intertree distance to the height of the tree of mean basal area, was 13.3 percent. This indicates that the stand was closely spaced.

Experimental Design

The Canadian Forestry Service designed and installed the original fertilization and thinning experiment (Morrison et al. 1977c), and permitted its use for the present analysis. The trial was established in the spring of 1970. Two levels of urea fertilization (0 and 336 kg $N.ha^{-1}$) and two levels of thinning from below (0 and 20 percent of initial basal area removed) were applied to four replicates in a completely randomized 2 x 2 factorial design. Treatment plots were .04 ha in size. Diameters of all trees were tallied by Canadian Forestry Service personnel

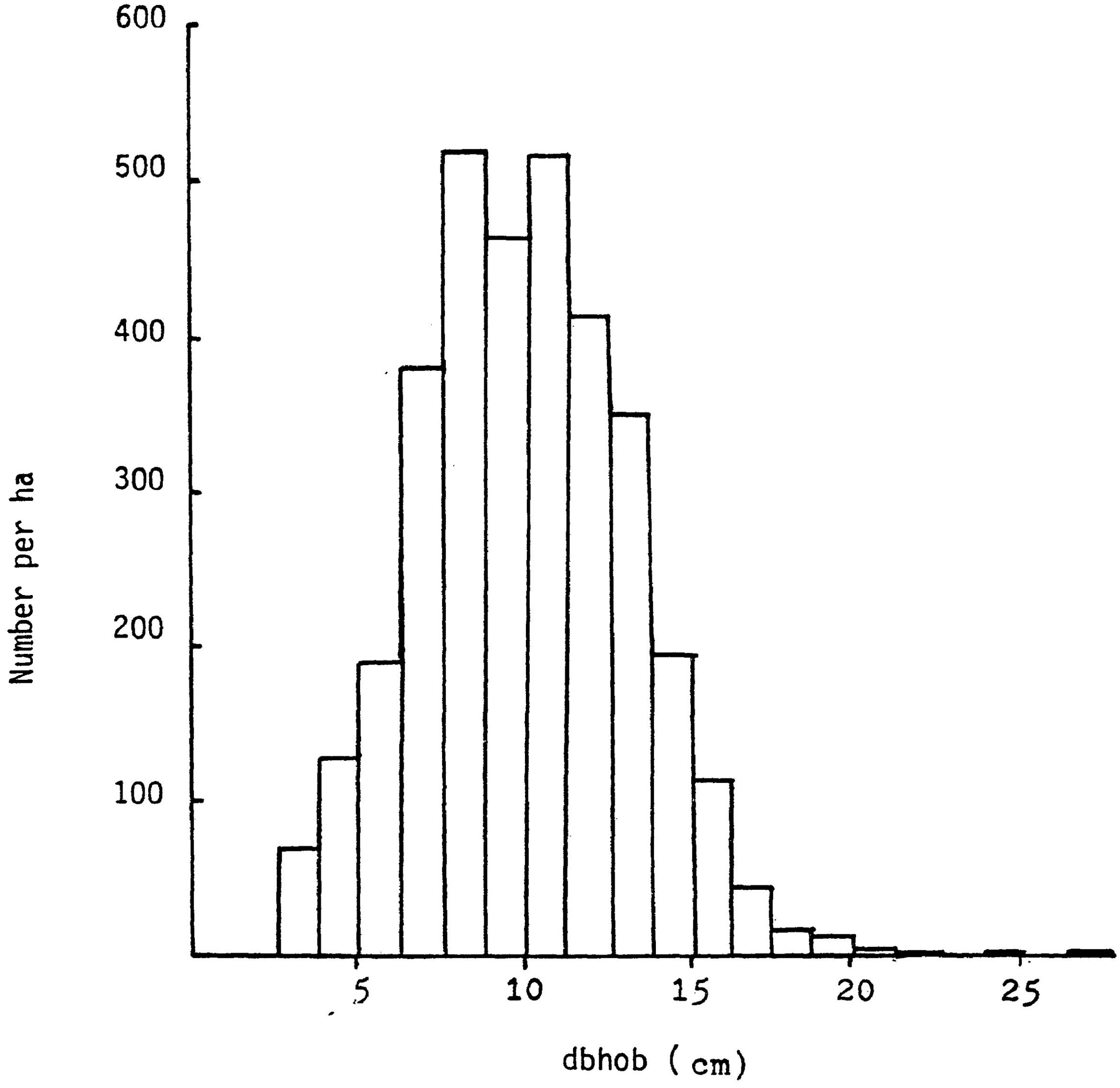

Figure 1. Diameter frequency distribution of a 45-year old jack pine stand.

at establishment, and at 5 and 10 growing seasons after establishment.

During the fall of 1979 and summer of 1980, one tree from each of 5 diameter classes was felled from each plot creating a 2 x 2 x 5 split plot design with 4 replicates. In all, 80 trees were felled and measured. Diameter classes were defined in English units with midpoints at 4, 5, 6, 7, and 8 inches (10.2, 12.7, 15.2, 17.8, 20.3 cm respectively). English units were dictated by the requirements of an independent Canadian Forestry Service study which shared the sample of felled trees.

Stem analysis

In each plot, one tree free from obvious defect was selected from each diameter class. Trees were felled and sectioned in October 1979 and August 1980. Discs were taken at 1 m intervals beginning at the base of the tree. The length from the uppermost disc to the tip of the leader was recorded.

The discs were transported to Thunder Bay and were stored until measurement. One group of discs was refrigerated, and the remainder were treated with fungicide and stored at room temperature. All discs were soaked in water prior to measurement to counteract shrinkage.

For each disc, the length of the average radius was calculated by measuring the largest inside bark diameter, and the perpendicular bisector to this diameter (Figure 2). The average

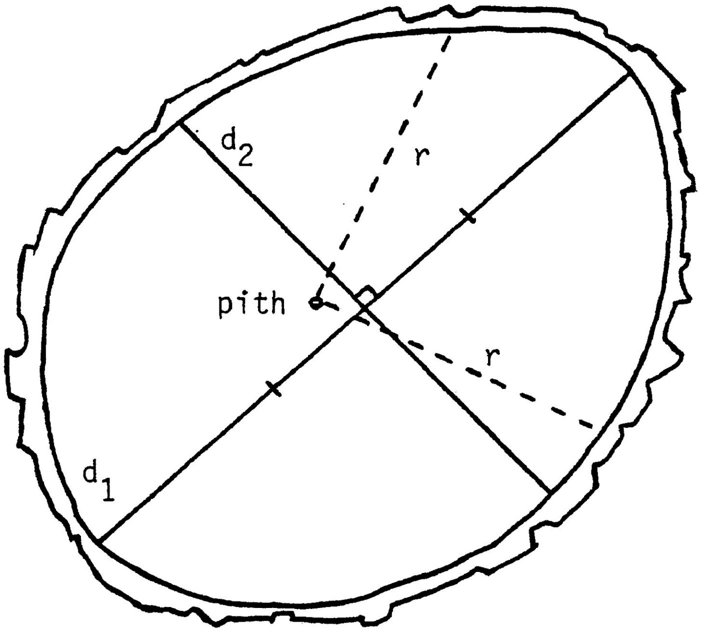

Figure 2. Location of average radius (r) on stem disc.
$r = .5\sqrt{d_1 d_2}$.

radius was calculated as one half of the geometric average of these two diameters ($r = .5\sqrt{D_1D_2}$). If the shape of the disc approximates an ellipse, this average radius will give the correct area of the disc when substituted into the equation for the area of a circle ($A = \pi r^2$) (Husch et al. 1972). Two average radii, from pith centre to disc edge, were located on each disc. The disc was smoothed with a knife, and pencil lines were drawn on, representing the average radii.

The rings on each disc were counted. Trees felled in 1980 had one more year of growth than trees felled in 1979, so one ring was deducted from the total count of the 1980 trees. The radius from the pith centre to the outside edge of the growth layer formed in 1964 was measured along each average radius line if the disc had more than 15 rings. This inner radius had a length equal to the length of the total radius minus the width of the last 15 rings formed. If 15 or fewer rings were present on a disc, the average radius of the pith was measured.

The bark thickness and the width of each of the last 15 rings were measured to the nearest .1 mm along both average radii on each disc. This represented the treatment period, and the 5-year period prior to treatment. A magnifying lens with attached scale was used for measurement of the 6, 7, and, 8 inch diameter trees, and the Holman Digimicrometer was used for measurement of the 4 and 5 inch trees.

For measurements made with the magnifying lens, the sum of the 15 ring widths added to the inner radius was compared to the total average radius. When differences larger than could be attributed to instrument error occurred, ring widths and radii were remeasured. Potential error in locating the average radius was 1 mm, and for each ring measured the potential error was .05 mm. Thus the allowable error was 1.75 mm, or less when fewer than 15 rings were measured.

Data analysis

Bark thickness

The average bark thickness of a disc was calculated as the average of the two measured bark thicknesses. Average bark thickness at breast height was obtained by calculating the average bark thickness of the 1 and 2 m discs, and interpolating.

Individual tree height

The annual height increment of each tree was determined for each year of the study period. The average annual height increment was estimated for each 1 m stem section as 1 m divided by the difference in ring numbers between the top and bottom of the section. The length of annual internodes containing discs was estimated to be the average of the annual height increments of the sections immediately above and below the disc. The annual height increment in the section between the uppermost disc and the tip of the leader was estimated to be the section length divided by one half less than the number of rings in the uppermost disc. This method is without error only when both ends of a section fall at the midpoint of an annual internode. On the average, however, this method should yield unbiased estimates of annual height increment. The effects of thinning, fertilization, and diameter on height increment for the period from stand age 45 to 55 were examined using analysis of variance.

Individual tree volume

Total tree volume was calculated for each year from stand age 45 to 55 using the stem analysis data, and estimated annual heights. The volume of each 1 m section was calculated for each year using Smalian's formula (Husch et al. 1972). To calculate the area for each end of the section, the widths of the appropriate number of rings were added to the inner radius for both average radii. Thus, two radii were calculated for each disc from stand age 41 to 55. Disc areas were estimated by multiplying these two radii by each other, and then this value was multiplied by π. For each year, the section volumes were added to give total tree volume. Annual volume increments for each year from stand age 41 to 55 were calculated by subtraction of appropriate total volumes. Analysis of variance was used to examine the effect of treatment on 10-year volume increment.

Measures of form

Both form factor and form quotient of each sample tree were calculated for each year from stand age 45 to 55. Form factor is determined by dividing total volume inside bark by basal area inside bark at breast height, and by total height. Form quotient is the diameter inside bark halfway between the tree tip and breast height, divided by the diameter inside bark at breast height. The midpoint diameter inside bark was estimated by interpolating between the diameter of the disc immediately above the midpoint, and the diameter of the disc immediately below the midpoint. Merchantable height was defined as the height to a 7 cm top inside bark. This height was estimated for each sample tree by interpolating between the height of the uppermost disc with an inside bark diameter greater than 7 cm and the height of the disc above. The effects of diameter, fertilization, and thinning on form factor, form quotient, and merchantable height were examined using analysis of variance.

Local volume equations

Local volume equations relating total volume inside bark to diameter at breast height inside bark were developed. Regression was used to estimate the coefficients of the allometric model, $V = aD^b$. Relationships were calculated for each treatment, for stand ages 45, 50, and 55. Regressions were tested for differences between treatments and ages.

Relation of dbhib to dbhob

It was necessary to make the volume equations based on inside bark diameter compatible with outside bark diameters. Linear regression was used to develop a relationship between diameter inside bark at breast height from stem analysis to diameter breast height outside bark from Canadian Forestry Service measurements. The relationship was calculated for stand ages 45, 50 and 55. Analysis of variance of bark thickness measured in the stem analysis was used to examine the possibility of treatment effect on bark thickness.

Diameter and basal area at breast height for each year were interpolated from the diameters of the 1 and 2 m discs. Little error was incurred by this interpolation, because the differences in the diameters of the 1 and 2 m discs were usually very small.

Diameter distributions and mortality

Lists of tree diameters were provided by the Canadian Forestry Service. Trees were measured overbark in English units to the nearest 0.1 inch (.254 cm) on three occasions: spring 1970, spring 1975, and fall 1979. These dates correspond to stand ages 45, 50 and 55 respectively. Diameter frequency distributions, by .5 inch (1.27 cm) diameter classes, were constructed from these diameter lists.

Trees which died from stand age 45 to 50, and from stand age 50 to 55, were noted by comparing the three diameter tallies. Mortality frequency distributions by .5 inch (1.27 cm) diameter classes were constructed from this information. The local volume functions were applied to the mortality distributions to calculate the volume at the beginning of the period of trees that died during each five year period.

Mortality volumes for each 5-year period were defined as the volume at the beginning of the period of trees which died during the period. A t-test was used to compare 10 year mortality volume between unthinned-unfertilized (C) plots, and unthinned-fertilized (F) plots. The ten-year mortality volume that would have occurred had unthinned stands been thinned from below with a 20 percent removal of basal area was estimated. These mortality volumes along with the 10-year mortality volumes of thinned plots were compred using analysis of variance.

Stand volume growth

Total plot volume inside bark was calculated by applying the local volume functions to the plot diameter distributions for stand ages 45, 50 and 55. Net volume increase was calculated by subtraction of total volume at age 45 immediately after thinning from total volume at age 55. The diameter lists did not differentiate between trees removed by thinning and trees removed by mortality. For the thinned plots, the thinned portion was assumed to be 20 percent of plot basal area comprised of the smallest trees which had died. Gross volume growth was calculated by adding the mortality volume and the cut volume for the period to the net volume increase. Analysis of variance was used to examine the effect of treatments on stand net volume increase and stand gross volume growth.

Growth model

A growth model was developed to allow the annual volume increment of individual trees to be compared holding individual tree volume and stand volume constant. Aggregation of the annual volume increment of individual trees allowed the annual stand volume increment to be estimated. The relationship between the annual volume increment of an individual tree (ΔV), its present volume (V), and the volume of its associated plot ($\Sigma V_i n_i$) was hypothesized to be:

$$\Delta V = a_0 + a_1 V - a_2 \Sigma V_i n_i \qquad \text{Eq (1)}$$

where V_i denotes the mean tree volume of diameter class i

and n_i denotes the number of trees in diameter class i

The model suggests that the volume increment of an individual tree is proportional to tree size and is diminished in proportion to the volume of competing trees. Biologically these relationships seem reasonable, at least over a limited range of the dependent variables.

The coefficients a_0, a_1, and a_2 were estimated in two stages. In the first stage, multiple regression analysis of the unfertilized plot data was used to obtain least squares estimates of all three coefficients. Plot volumes used in the regression were for stand ages 45, 50 and 54, with the plot volumes for age 54 being interpolated between plot volumes for age 50 and 55. Tree volumes used were also for stand ages 45, 50, and 54, and tree volume increment values used were for stand ages 46, 51, and 55.

In the second stage, the estimates of a_0 and a_2 were fixed at the values determined in stage one. Equation 1 was then rearranged to solve for a_1:

$$a_1 = (\Delta V - a_0 + a_2 \Sigma V_i n_i)/V \qquad \text{Eq (2)}$$

Annual values of a_1 were thus calculated for both fertilized and unfertilized plots. Since actual measurements of plot volume ($\Sigma V_i n_i$) were available at 5-year intervals interpolation was used to estimate plot volumes in intervening years.

Thus, for both fertilized and unfertilized trees, a vector of 10 annual a_1 values was calculated. These values include year-to-year growth variation caused by uncontrolled environmental factors, as well as any growth response caused by fertilization.

The stand growth for each plot was simulated using the 1970 plot diameter distributions, and applying the growth model. For each plot, the volume of individual trees in each diameter class i (V_i) were summed to obtain the plot volume ($\Sigma V_i n_i$). Individual tree volume growth was calculated for each diameter class from the mean class volume and the plot volume. Individual tree volume growth was added to individual tree volume to obtain the next year's volume for each diameter class. Stand volume for each year was calculated by summing the volumes in each diameter class.

From the diameter lists, trees which died during the period 1970-1975, and during the period 1975-1979 were identified. In the model, this observed mortality was deducted from the growing stock throughout the simulated response period. For each five-year period, the observed mortality was distributed by randomly assigning the mortality trees to years within the period.The volume of a tree at the time of mortality was defined as the volume of the tree at the beginning of the five-year period.

The ten-year net volume increase and the ten-year gross volume growth described by the model was compared to actual values by the chi-squared test (Freese 1960).

The growth model was used to simulate the volume increment of trees of equal initial volume treated with and without fertilizer. The growth of trees in both treatments was calculated each year for 10 years following treatment using interpolated plot volumes in the growth model. The volume growth of the fertilized trees was expressed as a percentage of the volume of the control trees.

RESULTS

Individual tree results

Bark thickness

Analysis of variance showed that average bark thickness at breast height was significantly affected by diameter (Table 3). Bark thickness increased with diameter (Table 4).

Relationship between dhbib and dbhob

Regression equations relating diameter at breast height inside bark (dbhib) as determined by stem analysis to diameter at breast height outside bark (dbhob) from CFS measurements were not significantly different in slope or intercept for stand ages 45, 50, and 55. Consequently, the following pooled regression for all three stand ages was calculated:

Eq. (2) $\text{dbhib} = -.46 + .95\ \text{dbhob}$

$(r^2 = .988;\ F_1/_{232} = 19{,}633;\ Sy.x = .32)$

Local volume equations

The volume equations relating Vib to dbhib were of the general form:

Eq (3) $\text{Vib} = a(\text{dbhib})^b$.

Pooled volume equations for ages 50 and 55 were significantly different in intercept from the pooled volume equation at age 45 ($F_1/_{157}$ = 27.4, 110.5 respectively) (Figure 3; Table 5). At age 50, the volume regressions for both the thinned and un-

Table 3. Effects of fertilization (F), thinning (T), and tree diameter (D) on individual tree response of 45-year old jack pine - ANOVA F-ratios.

	Source						
Response variables	F	T	D	FxT	FxD	TxD	FxTxD
Ten-year height increment	2.31	1.13	40.11*	0.72	0.47	1.65	0.95
Ten-year volume increment	33.09*	0.00	154.51*	0.09	2.99*	0.33	0.16
Bark thickness at breast height	0.68	0.07	20.16*	0.87	0.51	0.56	2.52
Ten-year merchantable height increment	7.19*	0.02	24.06*	0.27	1.61	2.33	1.35
Ten-year change in form factor	0.62	0.51	2.99*	0.00	0.25	1.15	0.50
Form factor at age 55	2.22	0.93	11.42*	0.00	0.30	1.50	0.14
Ten-year change in form quotient	0.03	0.10	0.40	0.93	0.20	0.98	0.53

*significant effect at the 5 percent level

Table 4. Effects of fertilization, thinning, and diameter on individual tree response of 45-year old jack pine

Treatment		Ten year height increment (m)	Ten year volume increment (m^3)	Bark thickness (cm)	Ten year change in merchantable height (m)	Ten year change in form factor	Form factor at age 55	Ten year change in form quotient
4"	C	1.38a	0.0123a	0.254a	1.72ab	-0.0054ab	0.590cde	0.0009a
	F	1.18ab	0.0129a	0.235a	1.68ab	0.0030ab	0.605de	0.0255a
	T	0.90a	0.0096a	0.228a	1.29a	0.0008ab	0.589cde	0.0085a
	FT	1.14ab	0.0140a	0.260a	1.22a	0.0063b	0.613e	-0.0120a
5"	C	1.92bcde	0.0129a	0.275a	1.71ab	-0.0122ab	0.570abcde	0.0033a
	F	1.50abc	0.0241a	0.309ab	1.71ab	-0.0060ab	0.584bcde	0.0011a
	T	1.18ab	0.0200a	0.254a	1.86abc	-0.0063ab	0.576abcde	-0.0102a
	FT	1.74bcd	0.0275a	0.255a	2.66cdefg	-0.0044ab	0.591cde	-0.0229a
6"	C	2.34def	0.0482b	0.318ab	2.35bcdef	-0.0173ab	0.561abcd	-0.0060a
	F	2.82f	0.0662bc	0.386abc	3.16fg	-0.0157ab	0.563abcd	-0.0112a
	T	2.81f	0.0508b	0.346abc	2.66cdefg	-0.0189ab	0.535a	0.0011a
	FT	3.24f	0.0670bc	0.374abc	3.29g	-0.0281a	0.549abc	0.0086a
7"	C	2.83f	0.0670bc	0348abc	2.32bcdefg	-0.0169ab	0.562abcd	-0.0075a
	F	3.04f	0.0952d	0.355abc	3.14fg	-0.0122ab	0.570abcde	0.0031a
	T	2.76f	0.0741c	0.413abc	2.45bcdefg	-0.0229ab	0.539ab	-0.0061a
	FT	2.82f	0.0966d	0.364abc	2.89efg	-0.0114ab	0.539ab	0.0045a
8"	C	2.71ef	0.0987d	0.486bc	2.76defg	-0.0166ab	0.541ab	-0.0044a
	F	3.05f	0.1228e	0.395abc	3.02efg	-0.0255ab	0.549abc	-0.0040a
	T	2.27cdef	0.0860cd	0.383abc	2.25bcde	-0.0073ab	0.552abc	0.0090a
	FT	2.62ef	0.1200e	0.508c	2.93efg	0.0046b	0.550abc	0.0045a

Corresponding letters in a vertical column indicate no significant difference, Duncan's new multiple range test (p=.05).

thinned fertilized trees were significantly different in intercept from the control trees ($F_{1/37}$ = 4.7, 4.7 respectively). At age 55, the volume regression for the fertilized-unthinned trees differed significantly in intercept from the volume regression for control trees ($F_{1/37}$ = 5.0) (Table 5). Because of these differences, separate volume equations were used for each treatment for ages 50 and 55.

Form

Analysis of variance showed that 10-year merchantable height increment was significantly affected by both diameter and fertilization (Table 3). Fertilized trees had a mean 10-year merchantable height increment of 2.55 m, compared to 2.16 m for unfertilized trees. Merchantable height increment generally increased with diameter (Table 4).

Analysis of variance showed that the 10-year change in form factor was significantly affected only by diameter (Table 3). Form factor generally decreased during the 10-year period and the decrease was greater with increasing diameter (Table 4).

Analysis of variance showed that form factor at age 55 was significantly affected only by diameter (Table 3). Form factor decreased with increasing diameter. Fertilized trees averaged slightly larger than unfertilized trees but the difference was statistically non-significant at the 5 percent level (Table 4).

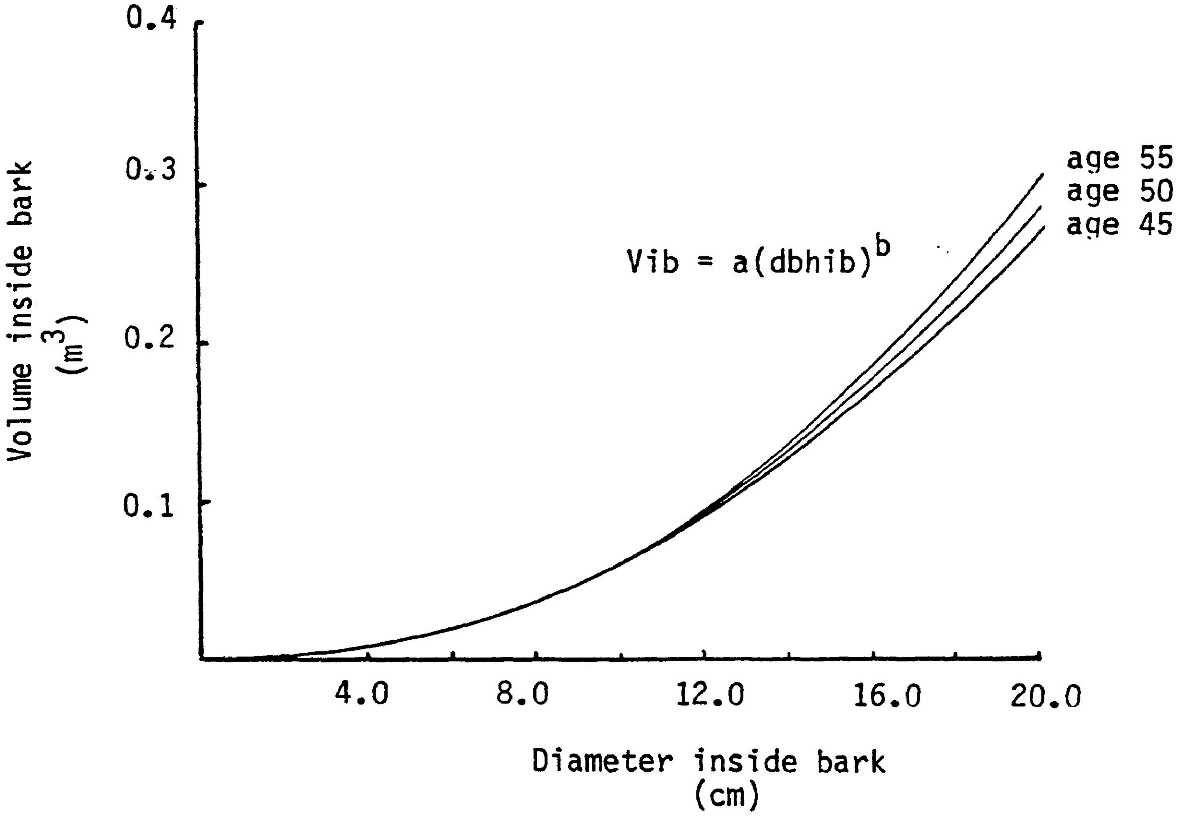

Figure 3. Pooled local volume equations for jack pine at 3 stand ages. The coefficients a and b are presented in table 5.

Table 5. Least squares estimates of the coefficients of a and b in the local volume equation Vib = a(dbhib)^{b}, for three stand ages and four stand treatments. Vib is in m^{3} and dbhib is in cm.

Stand age	Treatment	Coefficient		r^2	n	$S_{y \cdot x}$
		a	b			
45	pooled	3.7405×10^{-4}	2.2011	.985	80	.024
50	pooled	3.7891×10^{-4}	2.2143	.990	80	.022
50	C	3.3141×10^{-4}	2.2582	.989	20	.016
50	F	4.1121×10^{-4}	2.1872	.993	20	.026
50	T	3.2747×10^{-4}	2.2713	.991	20	.023
50	FT	4.0723×10^{-4}	2.1901	.992	20	.022
55	pooled	3.4792×10^{-4}	2.2663	.992	80	.022
55	C	3.2551×10^{-4}	2.2865	.992	20	.025
55	F	3.8987×10^{-4}	2.2296	.993	20	.009
55	T	3.0574×10^{-4}	2.3141	.994	20	.024
55	FT	3.7592×10^{-4}	2.2337	.993	20	.027

Height increment

Analysis of variance showed that 10-year height increment was significantly affected only by diameter (Table 3). Height increment was greatest in trees of largest diameter (Table 4). Fertilized trees had greater height increment than unfertilized trees, but this difference was not significant at the 5 percent level.

Individual tree volume increment

The mean annual total volume increment for individual trees was compared for each treatment and diameter class (Figure 4). Within each diameter class volume increment followed a similar trend for each treatment from stand age 51 to 45, the pretreatment period. There was little, if any, volume growth response to any treatment at stand age 46, the first growing season following treatment.

In the 8 inch diameter class, the volume increment of fertilized trees exceeded that of unfertilized trees from stand age 47 to stand age 53 (Figure 4a). In the 7 and 6 inch diameter classes, the volume increment of fertilized trees exceeded that of unfertilized trees from stand age 47 to stand age 55 (Figure 4b, c). Volume growth response to fertilization was smaller and of shorter duration in the 5 and 4 inch diameter classes (Figure 4d, e).

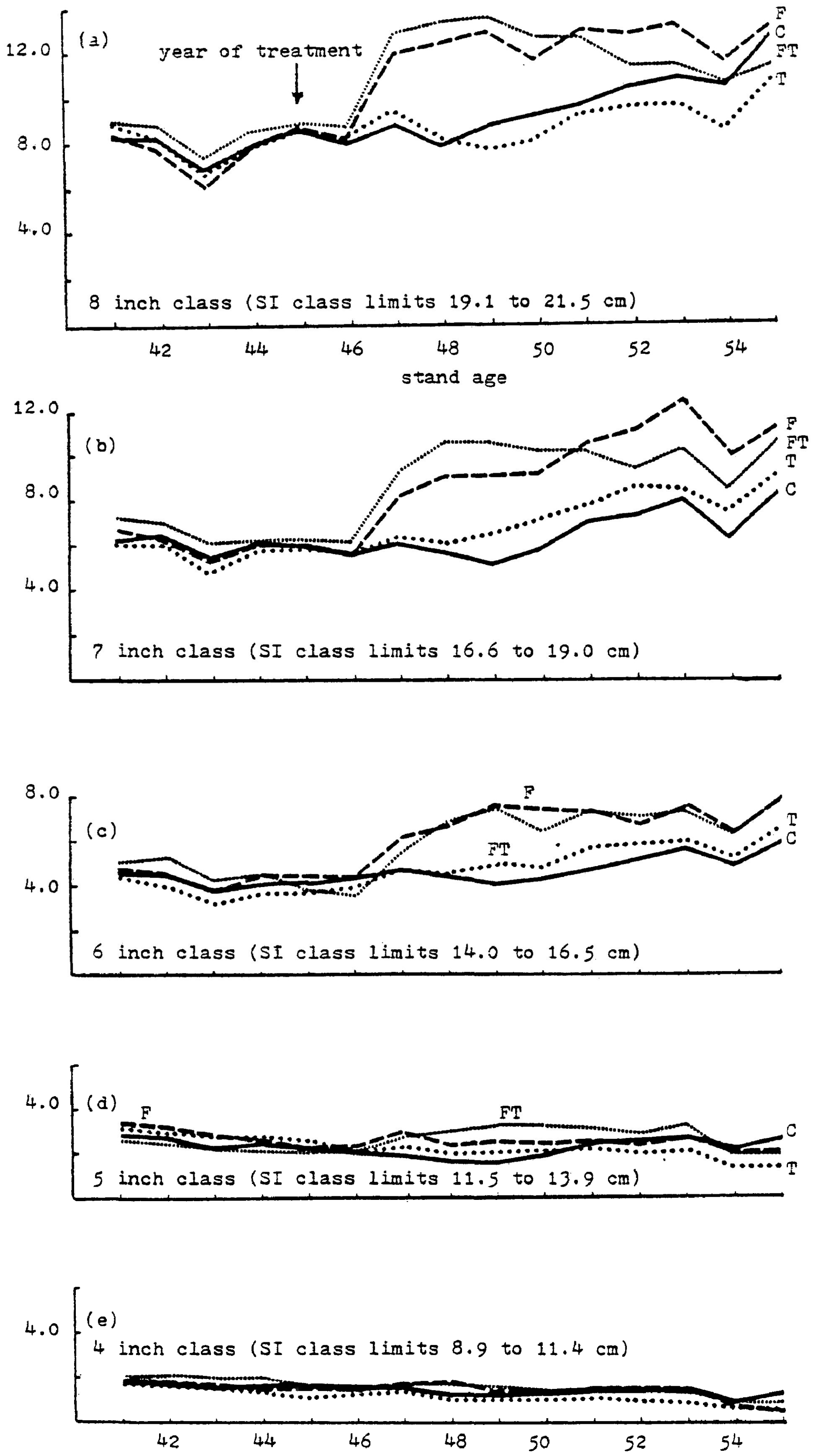

Figure 4a,b,c,d, and e. Mean annual volume increment of trees in 8, 7, 6, 5, and 4 inch diameter classes respectively. The choice of diameter classes in English units is explained on page 27.

Differences in the mean annual volume increment between thinned and unthinned trees were generally not great, and showed no consistent pattern. For example, thinned-unfertilized trees showed less volume increment than unthinned-unfertilized trees in the 8 inch class, while the opposite was true in the 7 inch class (Figure 4a, b).

Analysis of variance showed that total volume increment during the 10-year response period was significantly affected by both fertilization and diameter (Table 3). There was a significant fertilizer-diameter interaction. Fertilized trees had greater volume growth, as did trees of larger diameter. The fertilizer response was greatest in the largest diameter classes (Table 4).

Stand growth

Thinned treatments showed the greatest net increases in volume, and by stand age 55, the total volume of the thinned treatments was almost as great as the total volume of the unthinned treatments. Fertilized treatments had greater net volume increases than did unfertilized treatments (Table 6).

The 10-year gross volume growth of fertilized plots was significantly greater than that of unfertilized plots (Table 7). Gross volume growth of thinned plots was slightly less than that of unthinned plots.

Table 6. Ten-year net volume increase of jack pine thinned (T) and fertilized (F) at age 45.

Treatment	Volume - age 45 (m^3/ha)	Volume - age 55 (m^3/ha)	Net volume increase (m^3/ha)
Control	195.419	230.750	35.331 a
F	191.944	240.756	48.812 ab
T	172.650	224.831	52.181 ab
FT	169.125	228.594	59.469 b

Net increase values followed by the same letter are not significantly different, Duncan's new multiple range test.

Table 7. Ten-year gross volume growth of jack pine thinned (T) and fertilized (F) at age 45.

Treatment	Ten-year net volume increase (m^3/ha)	Ten-year mortality (m^3/ha)	Ten-year gross volume growth (m^3/ha)
Control	35.331	37.088	72.419 a
F	48.812	43.538	92.350 b
T	52.181	19.106	71.288 a
FT	59.469	27.731	87.200 b

Gross volume growth values followed by the same letter are not significantly different, Duncan's new multiple range test.

Regression analysis showed that gross growth was not significantly related to initial plot volume for unthinned plots ($r^2 = .07$; $F = .43$), or for thinned plots ($r^2 = .06$; $F = .37$).

Mortality

There was no significant difference in 10-year mortality volume between fertilized-unthinned plots, and unfertilized-unthinned plots ($t_6\text{df} = .64$), or between fertilized-thinned plots, and unfertilized-thinned plots ($t_6\text{df} = 1.40$).

Analysis of variance was carried out on the mortality volume in the largest trees comprising 80 percent of the plot basal area. Although mortality was higher for fertilized plots than for unfertilized plots, and higher for thinned plots than unthinned plots, none of the differences were statistically significant at the 5 percent level (Table 8).

Growth model

The stage one estimates of the coefficients in equation 1 were:

$$\Delta V = .0008704 + .0556V - 1.170 \times 10^{-5}\ \Sigma V_i n_i$$

($r^2 = .907$; V contributes .903, $\Sigma V_i n_i$ contributes .004).

ΔV is in $m^3\ yr^{-1}$,

V is in m^3,

and $\Sigma V_i n_i$ is in $m^3\ ha^{-1}$.

Values of a_1, the coefficient of V, were calculated for each year to characterize the growth response of individual trees

Table 8. Ten-year mortality volume in the largest trees comprising 80 percent of plot basal area in jack pine thinned (T) and fertilized (F) at age 45.

Treatment	Ten-year mortality volume (m^3/ha)
Control	12.206
F	16.431
T	19.106
FT	27.731

There were no significant differences among mortality volumes at the 5 percent level.

to fertilization. Mean annual values of a_1 for unfertilized trees ranged between .0475 and .0587 during the 10 year period from stand age 45 to 55 (Figure 5). For fertilized trees, the value of a_1 was about the same as for unfertilized trees in the first growing season after fertilization. In the second and third growing seasons after fertilization, the a_1 values peaked at .074. During the remainder of the response period, the a_1 values gradually declined to the level of unfertilized trees. Relative to the unfertilized trees, the greatest response in the values of a_1 for fertilized trees occurred in the third and fourth growing seasons after treatment.

Simulated volume growth of individual trees

According to the growth model, trees of average initial basal area (dbhob = 10.8 cm) that had been fertilized showed 79 percent more volume growth 3 years after treatment than did unfertilized trees of the same initial diameter (Figure 6). For larger trees the relative increase in growth was not as large, but response continued 10 years after fertilization.

Simulated stand growth

Annual net volume increase described by the growth model (Figure 7) showed great variability between years within treatments. A comparison of the simulated 10-year net volume increase and actual net volume increase by the chi-squared test showed that the simulation predicted net volume increase to within +17.5 m^3

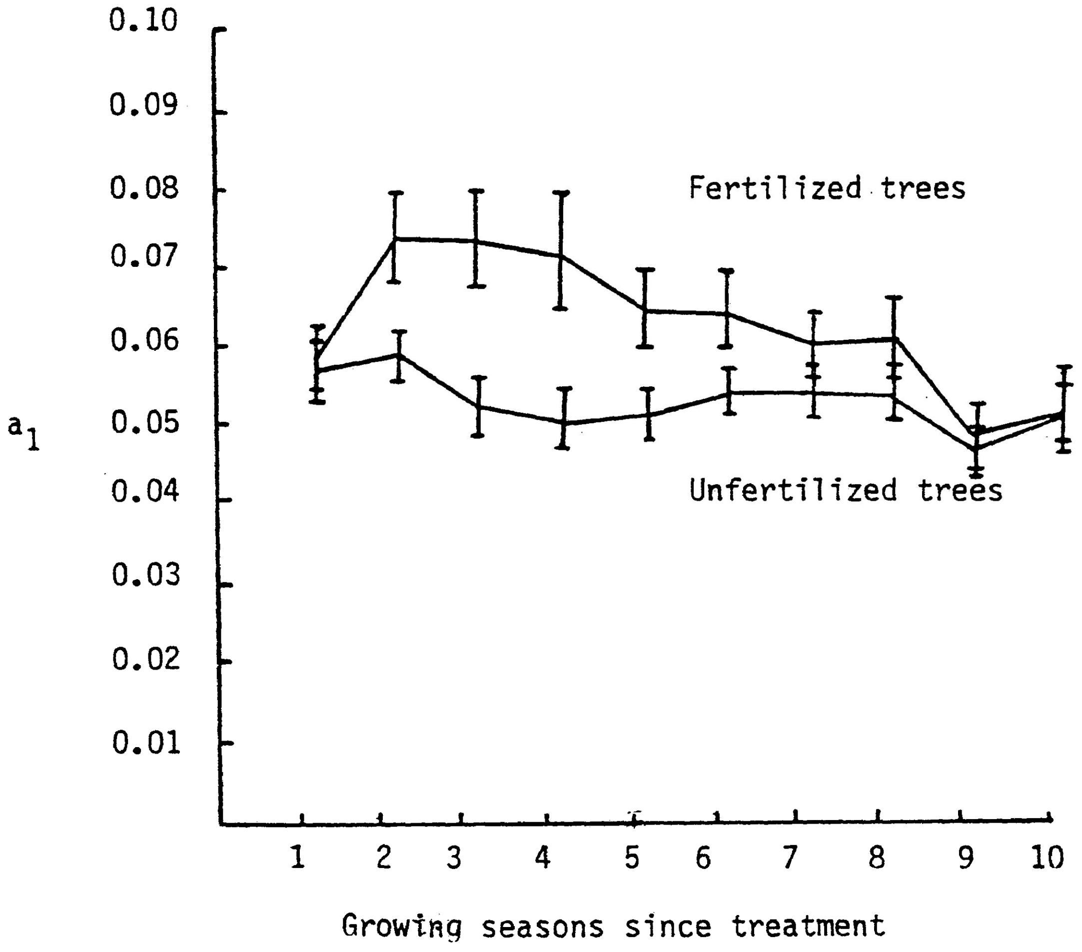

Figure 5. Annual values of a_1 coefficient (equation 1) for fertilized and unfertilized jack pine trees treated at age 45. Vertical bars represent 95 percent confidence limits.

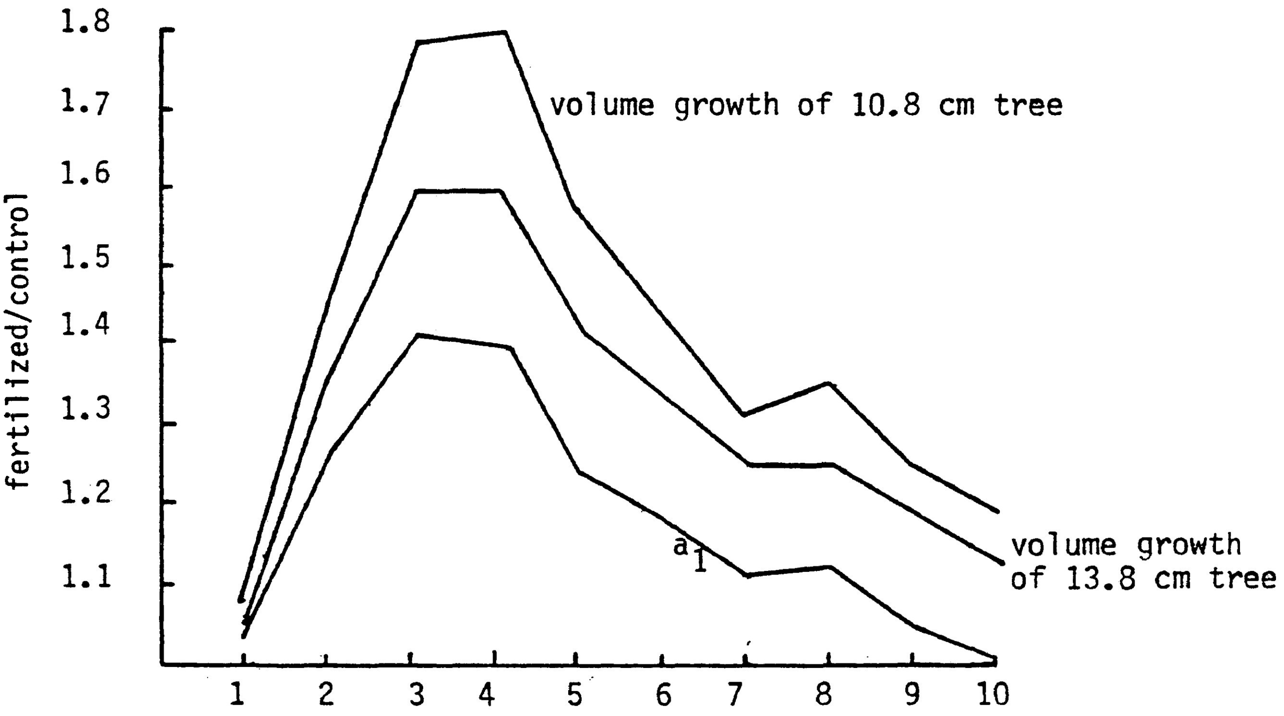

Figure 6. Simulated volume growth of fertilized trees relative to simulated volume growth of control trees, and value of a_1 for fertilized trees relative to value of a_1 for control trees. Control values = 1.0.

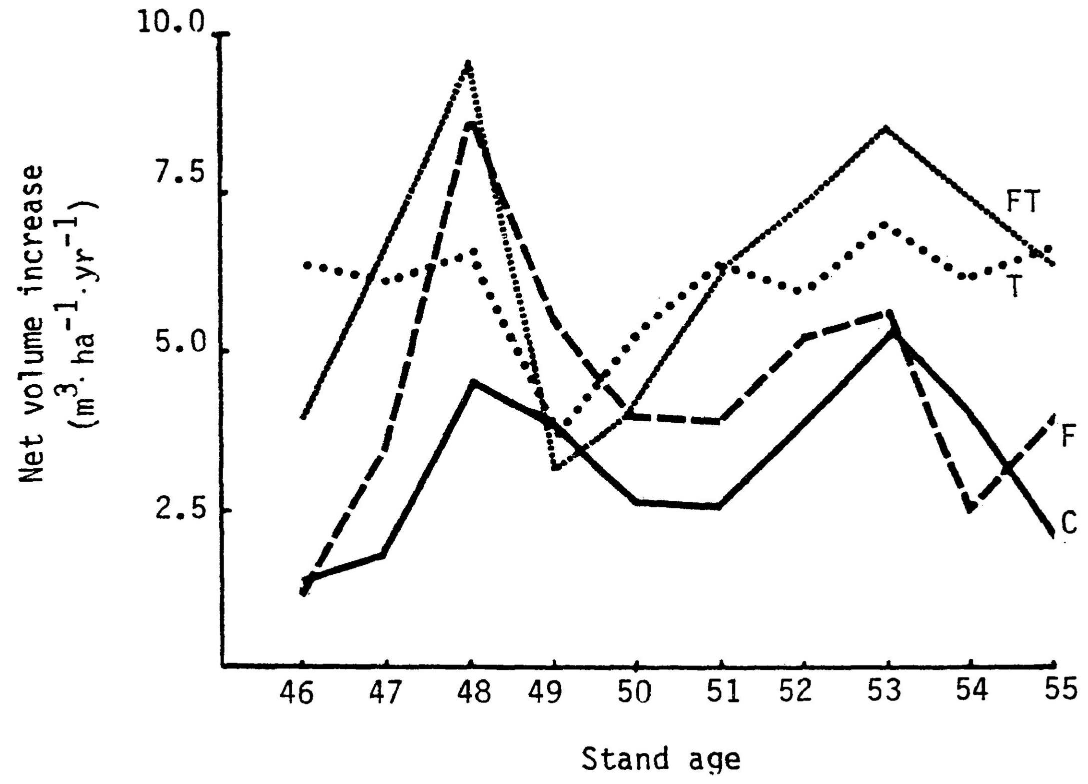

Figure 7. Simulated net volume increase of a jack pine stand thinned (T) and fertilized (F) at age 45.

ha^{-1} (the mean net volume increase was 49.000 m^3 ha^{-1}), for an average accuracy of ± 36 percent. For unthinned plots, simulated net volume increase showed a bias of -12.0 to -12.5 percent; for thinned plots, bias was 6.0 to 7.9 percent (Table 9).

Annual gross volume growth showed far less variability than net increase (Figure 8). A comparison of simulated and actual 10-year gross volume growth by the chi-squared test showed that the simulation was accurate to ± 16.0 m^3 ha^{-1}. This is an average accuracy of ± 20 percent (based on average gross growth of 80.825 m^3 ha^{-1}). For unthinned plots, simulated gross growth showed a bias of -3.1 to -3.3 percent; for thinned plots bias was 6.0 to 8.0 percent (Table 10).

Table 9. Actual and simulated ten-year net volume increase of a jack pine stand thinned (T) and fertilized (F) at age 45.

Treatment	Actual increase (m^3/ha)	Simulated increase (m^3/ha)	Bias
Control	35.331	30.900	-12.5%
F	48.813	42.969	-12.0
T	52.181	56.288	+ 7.9
FT	59.469	63.019	+ 6.0
mean	48.949	48.294	- 1.3

Table 10. Actual and simulated ten-year gross volume growth of a jack pine stand thinned (T) and fertilized (F) at age 45.

Treatment	Actual growth (m^3/ha)	Simulated growth (m^3/ha)	Bias
Control	72.419	70.200	-3.1%
F	92.350	89.344	-3.3
T	71.288	76.994	+8.0
FT	87.200	92.444	+6.0
mean	80.814	82.246	+1.8

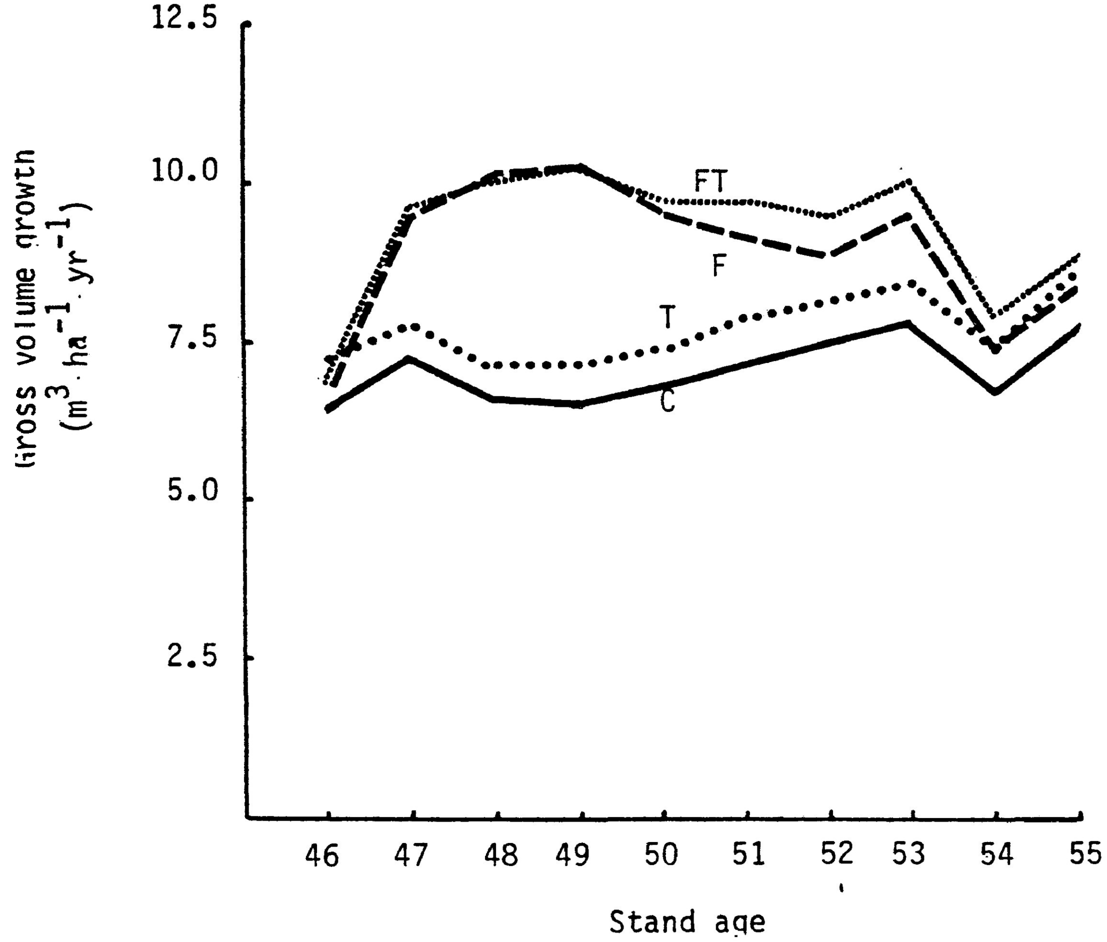

Figure 8. Simulated gross volume growth of a jack pine stand thinned (T) and fertilized (F) at age 45.

DISCUSSION

PART I: Growth response

Individual tree response to fertilization

Volume increment

The ten-year volume increment of fertilized trees was consistently greater than that of unfertilized trees (Table 4). Growth response generally commenced at age 47, the second growing season after treatment. Although a growth response to fertilization is clearly indicated, volume increments of trees in different treatments and in the same diameter class are not directly comparable. Trees were chosen from diameter classes at stand age 55, the end of the measurement period. Because growth responses occurred, trees in the same diameter class at age 55 may have been in different diameter classes at age 45. The growth model discussed in Part II was developed to allow direct comparison between the volume increments of trees in different treatments.

Form

The hypothesis that fertilization did not influence form factor can be examined using the results of analysis of variance of form factor and its increment. Form factor decreased with increasing diameter (Table 4). If fertilization had no effect on form factor, fertilized trees should have decreased in form factor more rapidly than unfertilized trees during the response period, because they showed more volume growth, and thus more diameter growth. Analysis of variance of form factor increment during the response period did not show this result (Table 4), supporting the alternative hypothesis: fertilization did affect form factor.

Trees were selected from diameter classes at the end of the response period. If form factor was not affected by fertilizations, form factor of fertilized trees should be the same as unfertilized trees of the same size class at the end of the response period. However, results of the ANOVA of form factor at age 55 suggest that form factor of fertilized trees was greater at age 55. This supports the hypothesis that form factor was influenced by fertilization.

Fertilized trees achieved greater merchantable height increment than did unfertilized trees. This suggests that proportionately more of the additional volume increment after fertilization accrued to the upper stem than to the lower stem. Cambial growth is largely regulated by the crown (Larson 1963; Kozlowski 1971). Fertilization increases the activity of the crown, and this increased activity is reflected in greater cambial growth in the portion of the stem within the crown than the portion of the stem below the crown.

Stand growth response to fertilization

The volume growth response to nitrogen fertilization was not surprising. Both the magnitude and pattern of growth response of jack pine to nitrogen fertilization are consistent with results of fertilizer trials in jack pine in Canada, and Scots pine in Scandinavia. The soil in the study area was medium-textured and acid, which does not favour nitrogen availability. Also much of the nitrogen on the site was immobilized in the standing biomass. Similar responses to nitrogen fertilization may be expected on medium-to-coarse textured, acid soils at the same stage of jack pine stand development.

Magnitude of growth response

The ten-year gross volume growth response to fertilization was about 2.0 $m^3.ha^{-1}.yr^{-1}$. This response is in the middle to upper range of observed responses of jack pine to urea fertilization at comparable rates (Table 1). When comparing fertilizer responses on an average annual basis the response period must be considered. In long response periods, declining responses at near the end of the period will reduce the average annual response. In this study the five year gross growth response was about 2.5 $m^3.ha^{-1}.yr^{-1}$. Differences between mensurational techniques must also be taken into account when comparing the results of different studies. For instance, form change due to fertilization was not considered in any of the studies listed in Table 1.

Pattern of growth response

The annual pattern of response revealed by the a_1 values (Figure 5) is similar to the basal area growth response pattern described by Hagner et al. (1966) for Scots pine. Greatest growth response occurred in the third and fourth year after fertilization, and response ended 10 years after fertilization.

The temporary nature of the growth response to nitrogen fertilizer is well documented. Added nitrogen is probably only available for the first year after fertilization (Morrison and Foster 1977). Trees retain much of the nitrogen taken up in the first year by translocating nitrogen from foliage before it is dropped (Mead and Pritchett 1975). Despite this translocation, the extra nitrogen taken up by trees is gradually lost through litterfall, and loss of branches. Recycling of the added nitrogen probably also played a role in extending the response period to ten years. Added nitrogen that had been immobilized in litter, minor vegetation, and soil organic matter may have been released through decomposition of these materials. This increased cycling diminished with time as the added nitrogen was more or less permanently immobilized in additional standing biomass and litter.

Mortality

There was large variation in the volume of mortality among plots, but on the average fertilized plots showed greater mortality than unfertilized plots. In all of the diameter classes sampled, the 10-year volume growth of individual trees was greater for fertilized trees than unfertilized trees, and in absolute terms, the growth response was greater in the large diameter classes than in the small diameter classes (Table 4). Thus after fertilization, growth of all trees increased, but the greater growth of larger trees may have contributed to the increased suppression and eventual mortality of smaller trees. The apparently shorter response period of 4- and 5-inch trees (Figure 4) also indicates that suppression of the growth of small trees may have occurred following fertilization. An increase in mortality following fertilization is a disadvantage, but not a serious one in this case, because most of the mortality occurred in the smallest stems.

Growth response to thinning

Response to thinning was small or non-existent for most of the response variables examined; the portion of the stand removed probably provided little competition. Individual tree volume growth and form were unaffected by thinning (Table 3).

Thinned plots showed larger net volume increases on a stand basis than unthinned plots. This occurred mainly because thinning removed many of the trees that otherwise might have died in the ensuing 10 years. Gross volume growth of thinned treatments was slightly less than that of unthinned treatments. Because growth of individual trees was not increased following thinning, the reduced amount of growing stock resulted in a slight depression of gross volume growth. The reduction in gross growth was slight because the portion of the stand removed by thinning was the portion contributing the least growth.

The main benefit of the thinning was the harvest of trees that otherwise might have been lost to mortality. Low thinning before or at the time of fertilization might have captured growth that was lost to increased mortality caused by fertilization. A heavier thinning may have resulted in a greater growth response.

PART II: Growth model and mensurational methods

Growth model

An individual tree growth model (equation 1) was developed for two reasons:

i) Sample trees were chosen from dbh classes at the end of the response period. It was possible to compare growth of trees of equal size at the end of the response period, but it was not possible to compare growth of trees that were of equal size at the beginning of the response period. If any growth response had occurred, trees in the dbh class at the end of the response period would have been in different dbh classes at the beginning of the period, and therefore not directly comparable. If the trees had been selected from dbh classes at the initiation of treatment it would have been possible to compare the growth of trees that started at the same size. However, after several years of response it would not be possible to know whether the greater growth of a treated tree was due to continuing response to treatment, or due only to greater size.

ii) Using the diameter distributions it was possible only to determine the total plot volumes for stand ages 45, 50, and 55. It was not possible to calculate net volume increase or gross volume growth on an annual basis. Thus the pattern and duration of stand growth response could not be elucidated.

The model used to estimate volume growth of individual trees was adequate for the range of tree and stand volumes encountered in the stand studied. The term relating tree volume growth to stand volume is biologically reasonable: as stand volume, or competition, increases, growth of individual trees decreases. The increase in the variation of ΔV explained when the stand volume term was added to the regression was very small, although significant. Stand volumes values were based on .04 ha plots, and variation in density within these plots probably existed. If the stand volume used in the regression had accurately reflected the density in the immediate vicinity of the sample tree, more variation in ΔV might have been explained.

The a_1 coefficient (equation 1) provides a useful parameter for comparing the growth of fertilized and unfertilized trees. Stem volume growth is biologically related to the cambial surface area of the stem. Cambial surface area in turn bears a geometrical relationship to stem volume. Thus, the coefficient a_1 may be thought of as a specific growth parameter; that is a parameter that relates the amount of growth to the amount of that which is active in growth (Duff and Nolan 1957). Specific growth parameters were considered by Armson (1974) to be useful for evaluating and predicting growth response to fertilization. The a_1 coefficient has been used in assessing growth response of Douglas-fir to fertilization (Bower 1973).

Equation 1 is valid only within the range of the dependent variables observed in this study. Extrapolation outside this range is risky for two reasons.

First, to extrapolate the term relating tree volume gorwth to tree volume to larger tree sizes incorrectly implies that the annual volume increment of a tree increases without limit as tree volume increases.

Second, at stand volumes above 75 m^3 ha^{-1}, the growth of the smallest trees will be calculated as negative. In this study, when negative values were encountered growth was assumed to be zero. This problem was not serious because only the smallest trees, which in reality show little or no volume growth, were affected.

Simulated mortality volumes for the second five-year period were different from those observed (Table 11). The apparent cause of this discrepancy is that trees which died during the five-year period grew more slowly in the first five-year period than did the healthy trees on which the model was based. There were no discrepancies in mortality volumes in the first five-year period because mortality volume was defined as the

Table 11. Actual and simulated ten-year mortality volume of a jack pine stand thinned and fertilized at age 45.

Treatment	Actual mortality volume (m^3/ha)	Simulated mortality volume (m^3/ha)
Control		
age 45-50	19.425	19.425
age 50-55	17.663	19.850
age 45-55	37.088	39.275
Fertilized		
age 45-50	23.563	23.563
age 50-55	19.975	22.806
age 45-55	43.538	46.369
Thinned		
age 45-50	8.038	8.038
age 50-55	11.068	12.650
age 45-55	19.106	20.688
Fertilized/Thinned		
age 45-50	19.119	19.119
age 50-55	8.162	10.294
age 45-55	27.731	29.413

volume at the beginning of the period of trees which died during the period. On the average, 10-year mortality was overestimated by the model by 2.087 m^3 ha^{-1}, or 6.5 percent.

For the unthinned treatments the model underestimated 10-year gross volume growth by 3 percent. For thinned treatments gross volume growth predicted by the model overestimated actual gross volume growth by 6 to 8 percent. This bias occurred because the trees in the thinned plots did not respond immediately, if at all, to thinning. In the model, however, a weak, but significant, negative correlation existed between individual tree growth and stand volume. Thus, when thinning was incorporated into the model, trees responded immediately with greater growth. This false effect in the simulation perpetuated itself because the model assigned greater growth to larger trees than to smaller trees.

Great year-to-year variability was apparent in the simulated annual net volume increase. This variability results from the great variability in year-to-year mortality created by random assignment of mortality. This variability could have been reduced by averaging the results of a number of simulations. If the stand had actually been measured each year, however, variability similar to that described in the simulation would have been encountered.

The pattern of a_1 values reveals the direct effect of fertilization, which was a growth response resulting from improved nitrogen status. Fertilization may also result in an indirect, or tree size effect, as revealed by the pattern of gross growth of initial stand volume (Figure 8). Ten growing seasons after fertilization, the simulated gross volume growth of the fertilized trees was 8 percent above the simulated gross growth of the control treatment. Trees in the fertilized treatment were larger on the average than trees in the control treatment. This size difference caused the persisting greater gross growth of the fertilized treatment. The indirect effect of fertilization is also evident in Figure 6. Ten years after fertilization the value of a_1 for both fertilized and unfertilized trees was the same. At this point in time, however, the simulated volume growth of individual fertilizied trees was still greater than that of unfertilized trees.

Mensurational methods

Inappropriate mensurational methods may result in poor estimates of the actual growth response to silvicultural treatment. In this section, volumes that would be obtained using a localized Honer's volume equation are compared with volumes calculated from the local volume equations developed in this study. In addition the relative merits of gross volume growth and net volume increase as measures of stand growth are discussed.

Volume equations

Local individual tree volume equations based on diameter breast height inside bark, developed from stem analysis provided highly accurate ($r^2 > .98$) estimates of volume inside bark, provided the volume equations were stratified by stand age and treatment. In many studies, however, standard volume equations, such as Honer's (1967), are used to estimate the volume of trees. These standard volume equations are localized by preparing a height/diameter relationship from a measure subsample of trees. Serious error may result in estimates of the volume of trees if stand age and treatment effects in the height/diameter relationship are ignored. In the present study, regressions relating individual tree height to dbhib were significantly different among the three stand ages examined. For a given diameter, tree height increased with stand age (Fig. 9; Table 12).

The error incurred by using age-inappropriate height/diameter relationships in localizing standard volume equations can be illustrated by using the data from this study. When the height/diameter relationship used to localize Honer's volume equation is appropriate to the stand age, errors in estimating the volume of control trees are not large (Table 13). If the age 45 height/diameter relationship had been used in Honer's equation to estimate individual tree volume at age 55, underestimates as large as 11 percent would have resulted.

The error resulting from using a localized Honer's volume equation can be examined on a stand basis as well. If the appropriate height/diameter relationship had been used, total stand volume for control plots would have been underestimated by 2.1

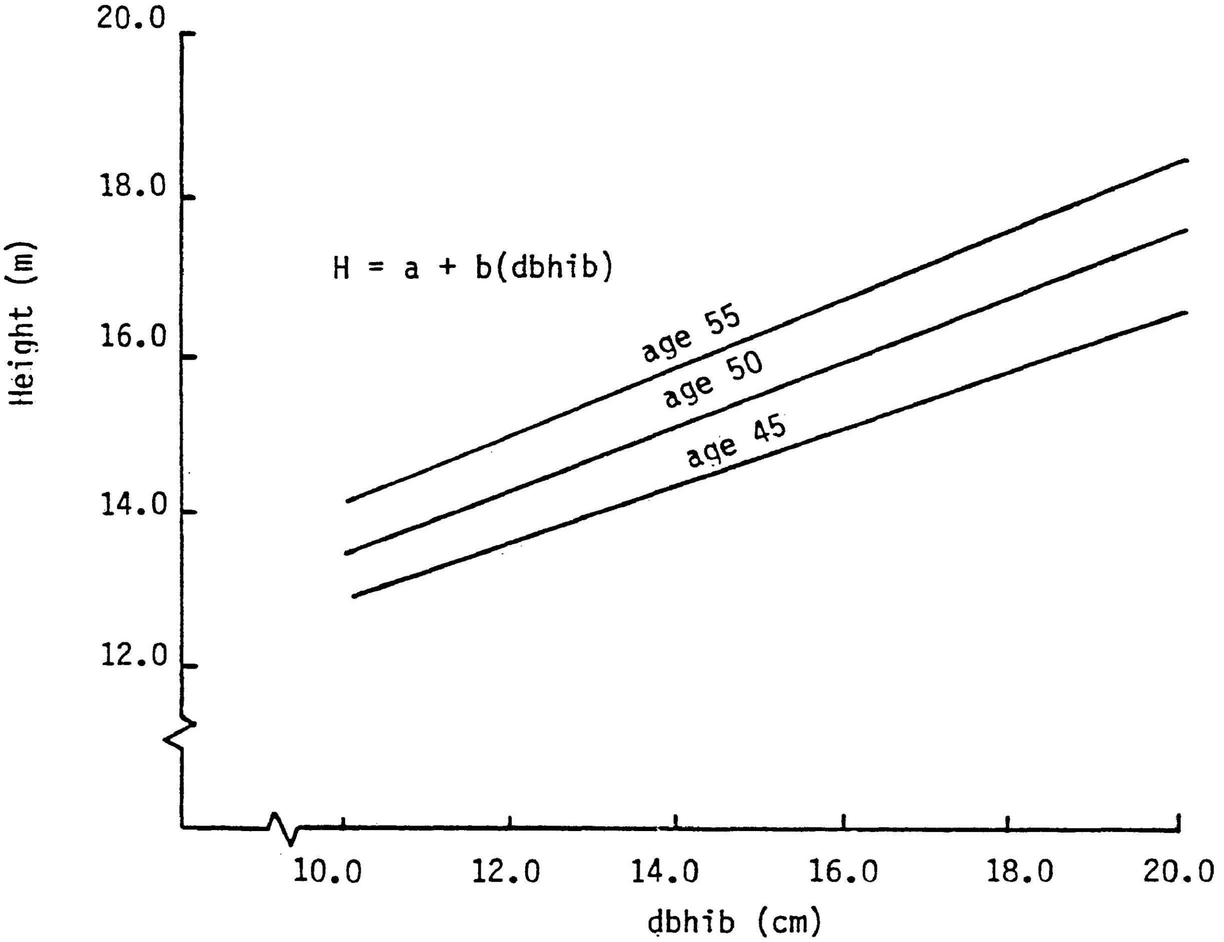

Figure 9. Pooled height/diameter relationships for 3 stand ages. The coefficients of a and b are presented in table 12.

Table 12. Height/diameter relationships for 3 stand ages and 4 stand treatments.

		r^2	n	$S_{y \cdot x}$
age 45				
pooled	$H = 9.33 + .359D$	.684	80	.61
age 50				
pooled	$H = 9.45 + .404D$	.770	80	.65
C	$H = 9.00 + .419D$	.773	20	.68
F	$H = 9.74 + .382D$	.763	20	.65
T	$H = 9.16 + .442D$	.761	20	.76
FT	$H = 9.85 + .379D$	.862	20	.48
age 55				
pooled	$H = 9.80 + .430D$	.752	80	.84
C	$H = 9.56 + .433D$	.782	20	.78
F	$H = 10.09 + .404D$	.762	20	.82
T	$H = 9.30 + .478D$	.735	20	1.00
FT	$H = 10.21 + .408D$	.773	20	.81

H = height (m)
D = dbhib (cm)

Table 13. Individual tree volume for selected tree diameters at 3 stand ages based on 2 volume equations. For each age, the local volume equation is based on untreated tree data. Honer's volume equation is based on the untreated height/diameter relationship for each age.

		Volume equation		
	dbhob	local	Honer's	Honer's[1] error
age 45	10 cm	.04760 m^3	.04693 m^3	-1.4 %
	12	.07244	.07044	-2.8
	14	.10305	.10009	-2.9
	16	.13962	.13754	-1.5
	18	.18233	.18127	-0.6
	20	.23132	.23258	+0.5

	dbhob	local	Honer's	Honer's[1] error	Honer's$_{45}$[2] error
age 50	10 cm	.04785	.04764	-0.4	-2.0 %
	12	.07362	.07244	-1.6	-4.5
	14	.10569	.10375	-1.9	-5.6
	16	.14435	.14216	-1.5	-5.0
	18	.18982	.18824	-0.8	-4.7
	20	.24232	.24254	+0.1	-4.2

	dbhob	local	Honer's	Honer's[1] error	Honer's$_{45}$[2] error
age 55	10 cm	.04996	.04996	0.0	-6.5
	12	.07732	.07586	-1.9	-9.8
	14	.11150	.10852	-2.7	-11.4
	16	.15287	.14855	-2.9	-11.1
	18	.20171	.19651	-2.6	-11.3
	20	.25828	.25297	-2.1	-11.0

[1] Error incurred using Honer's volume equation localized with age-appropriate height/diameter relationship.

[2] Error incurred using Honer's volume equationlocalized with age 45 height/diameter relationship.

m^3 ha^{-1} at age 50, and by 4.4 m^3 ha^{-1} at age 55 (Table 14). The ten-year net volume increase would have been underestimated by 2.3 m^3 ha^{-1}. If the age 45 height/diameter relationship had been used in the calculation of stand volume at age 55, an underestimate of 20.5 m^3 ha^{-1} would have resulted. The 10-year net volume increase would have been 16.9 m^3 ha^{-1}, or 47.9 percent of the actual value. Thus, large errors in estimates of volume increase would have resulted in the same height/diameter relationship had been used in the calculation of volume at both stand age 45 and 55.

Serious error in the estimation of volume and volume increment may also result by ignoring changes in form caused by silvicultural treatment. In this study, the volume equations for both thinned and unthinned fertilized trees were significantly different from the volume equations for control trees at age 50, and the volume equation for fertilized-unthinned trees differed significantly from that of the control trees at age 55. These differences are shown for selected diameters in Tables 15 and 16. The error, on a stand basis, incurred by ignoring form change can be examined by comparing the actual stand volumes for the unthinned-fertilized plots with volumes calculated using the control tree local volume equation (Table 17). Use of the control volume equation would have resulted in an underestimate of 7.3 m^3 ha^{-1} in the total volume at age 55 of the unthinned-fertilized plots. These plots had an acutal ten-year net volume increase 13.5 m^3 ha^{-1} greater than the control plots. If the control tree

Table 14. Stand volume at 3 ages, and 10-year net volume increase of control treatment estimated using local and Honer's volume equations.

Volume equation	Volume age 45 (m^3/ha)	Volume age 50 (m^3/ha)	Volume age 55 (m^3/ha)	Net volume increase (m^3/ha)
Local	195.419	209.45	230.750	35.331
Honer's, localized with age-appropriate height/diameter relationship	193.333	207.643	226.388	33.055
Honer's localized with age-45 height/diameter relationship	193.333	202.186	210.251	16.918

Table 15. Individual tree volumes at 3 diameters of C, F, and FT treatments at age 50.

dbhob (cm)	C_{50}	F_{50} (volume in m^3)	FT_{50}
10	.04785	.05074	.05058
15	.12418	.12778	.12754
20	.24232	.24413	.24387

Table 16. Individual tree volumes at 3 diameters of C and F treatments at age 55.

dbhob (cm)	C_{55} (volume in m^3)	F_{55}
10	.04998	.05281
15	.13127	.13541
20	.25828	.26196

Table 17. Net increase in volume of fertilized treatment using local volume equation for control and fertilized trees.

Volume equation	Volume-age 45 (m^3/ha)	Volume-age 55 (m^3/ha)	Ten year net increase	Net increase over control
Local - fertilized	191.944	240.756	48.812	13.481
Local - control	191.944	233.463	41.519	6.188

volume equation had been used, this response would have been calculated as 6.188 m^3 ha^{-1}, 45.9 percent of the actual value.

Measures of stand growth

When plot mortality is highly variable from plot to plot, as it was in this study, gross volume growth is a better measure of volume growth than net volume increase. Variable mortality contributes to variable net volume increase values, and statistical identification of treatment effects is more difficult. Use of 10-year gross volume growth as a response parameter allowed identification of the effect of fertilization, while use of 10-year net volume increase did not. Gross volume growth also provides a better basis for comparison of thinned and unthinned treatments. The greater net volume increase of thinned treatments in this study was not caused by increased tree growth, but by decreased mortality.

Direct comparison between mortality of thinned and unthinned treatments was not possible because low thinning removes much potential mortality. In this study, comparison of mortality in thinned plots with mortality of the largest trees comprising 80 percent basal area of the unthinned plots provided an adequate means of comparing mortality.

In this study the range of initial plot volumes was from 178.85 to 216.05 m^3 ha^{-1}. Mean pretreatment plot volumes for C, F, T, and FT treatments were 195.42, 191.94, 206.01, and 204.325 m3 ha-1 respectively. Variation in the initial volume of unthinned plots did not contribute signficantly to the variation in subsequent gross growth of these plots. Variation in the initial volume of thinned plots immediately after thinning also did not contribute significantly to subsequent gross growth. Because density variations were not large enough to cause significant variation in growth, covariance analysis was not used in this study.

CONCLUSIONS

Nitrogen fertilization of a 45-year old jack pine stand with 336 kg urea-N/ha resulted in a gross volume growth response of about 2.0 $m^3.ha^{-1}.yr^{-1}$ over a 10 year period. Little or no response to fertilization occurred in the first year after treatment, and maximum responses occurred in the third and fourth years. Ten years after fertilization, the gross volume growth of the fertilized plots had returned to a level close to that of the unfertilized plots.

The removal of 20 percent of basal area by low thinning had little effect on growth. Presumably the main effect of low thinning was to salvage trees that otherwise would have been lost to mortality.

The growth model used in this study provided a good method for identifying the annual pattern of response to fertilization in unthinned stands. It was less useful for identifying the annual pattern of response to thinning.

Assessment of growth response to fertilization requires more accurate techniques than are commonly used. When estimating height for use in Honer's standard volume equation, it is necessary to use age-appropriate height/diameter relationships. Honer's standard volume equation should not be used to estimate the volume growth response following fertilization, because form changes caused by fertilization may cause serious error. It is concluded that it is necessary to develop separate local volume equations for each treatment and stand age to include the effects of age and form changes on estimates of volume growth.

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