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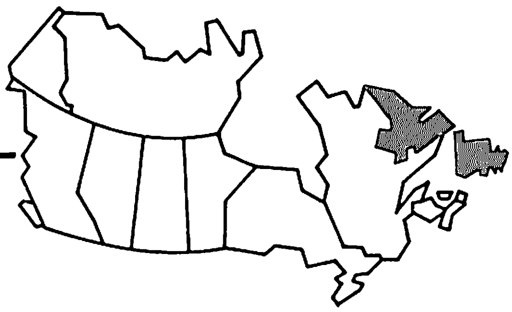
A Spacing Trial in a Precommercially Thinned Stand of Black Spruce at North Pond: Stemwood Production During the First Five Years After Thinning



M.B.Lavigne, J.G.Donnelly and R.S. vanNostrand

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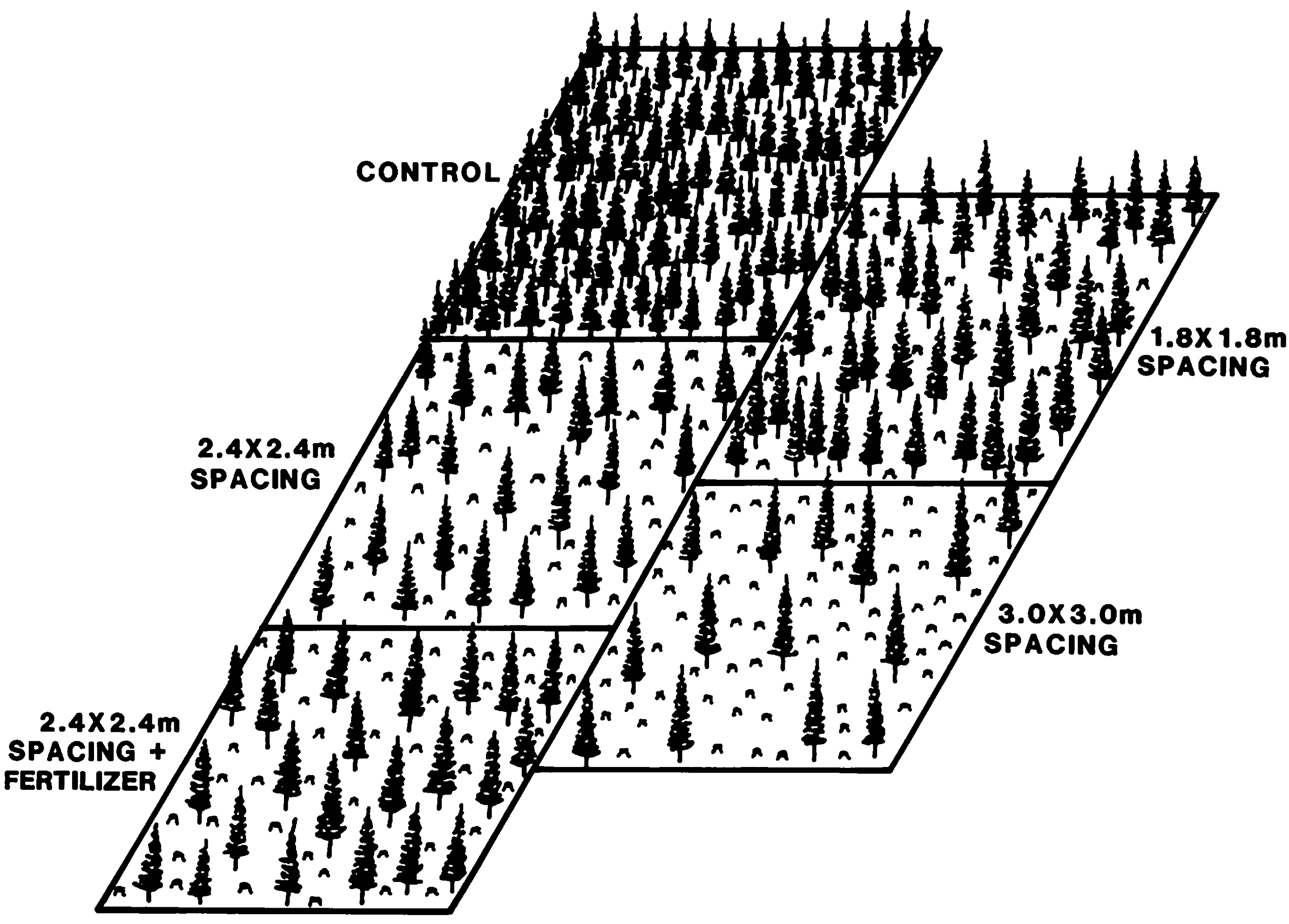

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by
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Abstract

Stemwood production rates per hectare and per tree for the five years immediately after thinning were compared among plots of various spacings in a young black spruce stand (*Picea mariana* (Mill.) B.S.P.) Some thinned plots were fertilized with 200 kg/ha of nitrogen. Production rates per hectare were inversely related to width of spacing. By contrast, production rate per tree increased with increased spacing. Fertilization increased periodic stemwood production rates when done in combination with thinning.

Rates of stemwood production per hectare were positively correlated to foliar weights per hectare, but rates of stemwood production per kilogram of foliage were negatively correlated to canopy foliar weights. Higher rates of stemwood production per kilogram of foliage were due in part to less stem surface area per unit of foliar weight and not solely to increased availability to trees of light, mineral nutrients and water. The rate at which stem surface area per unit of foliar weight increased was reduced by thinning and by fertilization. This effect of thinning will be the most enduring one and therefore will have the greatest effect on final yields.

Résumé

L'accroissement du bois de fût, à l'hectare et par arbre, pendant les cinq années qui ont immédiatement suivi la coupe d'éclaircie a été comparé entre des parcelles d'un jeune peuplement d'épinettes noires (*Picea mariana* (Mill.) B.S.P.), plantées à divers espacements. Certaines parcelles ont été amendées à l'azote à raison de 200 kg/ha. L'accroissement à l'hectare était en raison inverse de l'espacement. Par contre, l'accroissement par arbre a augmenté avec l'espacement. L'apport d'engrais a augmenté l'accroissement périodique du bois de fût lorsqu'il coincidait avec la coupe d'éclaircie.

L'accroissement du bois de fût à l'hectare a été corrélé positivement à la masse foliare à l'hectare, mais, par kilogramme de feuillage, il a été négativement corrélé à la masse foliare du couvert. Les accroissements supérieurs, par kilogramme de feuillage, ont été dus, en partie, à un quotient inférieur de la surface terrière par unité de masse du feuillage et non seulement au fait que les arbres profitaient d'un éclairage meilleur ainsi que d'un apport accru en éléments minéraux et en eau. L'accroissement du rapport de la surface terrière à la masse du feuillage a été rèduit par la coupe d'éclaircie et par l'amendement du sol. Cet effet de la coupe d'éclaircie se révélera le plus durable et, par conséquent, c'est lui qui déterminera le plus la production finale.

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A Spacing Trial in a Precommercially Thinned Stand of Black Spruce at North Pond: Stemwood Production during the First Five Years after Thinning

by

M.B. Lavigne, J.G. Donnelly and R.S. van Nostrand

Introduction

Precommercial thinning of overstocked stands of balsam fir (*Abies balsamea* (L.) Mill.) and black spruce (*Picea mariana* (Mill.) B.S.P.) is an essential component of the silviculture program in Newfoundland. Additional yields might be realized by refining treatments. The gains attributable to precommercial thinning can be calculated and refinements identified only when reliable predictions of yield are available.

Annual stemwood production rates depend on a number of factors that vary over time. These factors (i.e., foliar weight per hectare and stem surface area per hectare) change at unequal rates in plots thinned to different spacings. Therefore, comparisons of periodic stemwood production rates by plots of different spacing will yield different conclusions in different periods and thus cannot be used to reliably indicate optimal spacing. Optimal spacing can be chosen only on the basis of final yield and optimal rotation length.

A data base does not yet exist for predicting final yields of precommercially thinned stands in Newfoundland because thinning has been practiced only for a short time. In a cooperative study the Department of Forest Resources and Lands, Corner Brook Pulp and Paper Ltd., Abitibi Price Inc. and the Canadian Forestry Service have established spacing trials in precommercially thinned stands across Newfoundland (Donnelly *et al.* 1986) to provide the data necessary for making reliable yield predictions. In the meantime, data collected from these trials will be analyzed to provide more knowledge on site and stand factors controlling growth and yield in thinned and unthinned plots. These, combined with data from other sources, will enable provisional yield predictions to be made.

The first spacing trial of the cooperative study to be remeasured was in a black spruce stand at North Pond. Stem production rates during the first five years after thinning were calculated and used to examine the influences of some factors controlling rates of production. A more thorough analysis of the roles of other site factors will be possible when data from additional sites become available.

Conceptual Model for Analyzing Rates of Stemwood Production

The rate of stemwood production is the product of rate of acquisition of resources (carbon dioxide, light, water, mineral nutrients) and the rate of conversion of these resources into stemwood.

$$P = \text{Resource Acquisition} \times \text{Conversion Rate} \qquad [1]$$

where P = periodic annual production of stemwood

Environmental factors, and characteristic of trees affect these two components of stemwood production. Site determines the supply of resources available to the trees and hence the upper limit of resource acquisition. Site occupancy determines the degree to which the stand is accessing the available resources. Site occupancy is a function of the quantities of foliage and roots in a stand and their rates of activity. Conversion rate is the product of the various processes within trees that use acquired resources.

Principles of growth analysis can be used to combine factors that control production into an explanatory equation. This approach provides a basis for incorporating factors of the environment as determinants of yield into predictions by considering how they influence physiological processes (Evans 1972, Satoo and Madgwick 1982). The first step is to distinguish between periodic increment and production rate of stemwood by using the expression:

$$PAI = P - M \qquad [2]$$

where PAI = periodic annual increment of stemwood
P = periodic annual production of stemwood
M = periodic annual loss of stemwood through mortality.

Net assimilation rate is a growth analysis term that relates growth to foliar weight:

$$E = P/FW \qquad [3]$$

where E = rate of annual stemwood production per unit of foliar weight
FW = foliar weight per hectare.

Moreover, annual stemwood production can be described as the balance between photosynthesis and respiration as follows:

$$P = APS \times Ph - R \qquad [4]$$

where Ph = annual net photosynthetic production per hectare
R = annual stem respiration per hectare
APS = proportion of net photosynthetic production allocated to stems.

By substituting Equation 4 into Equation 3 and re-arranging terms, annual stem production per unit of foliar weight can be related to physiological processes and plant morphology.

$$E = (APS \times Ph - R) / FW \qquad [5]$$

$$= APS \times p - r \times SFR \qquad [6]$$

where p = rate of annual net photosynthesis per unit of foliar weight
r = rate of stem respiration per unit of stem surface area
SFR = stem surface area per unit of foliar weight.

By re-arranging Equation 3 annual stemwood production can be described as the product of stemwood production per unit of foliar weight and foliar weight per hectare.

$$P = E \times FW \qquad [7]$$

Then Equation 6 can be substituted into Equation 7 to show how annual stemwood production per hectare depends on physiological processes and plant morphology.

$$P = (APS \times p - r \times SFR) \times FW \qquad [8]$$

With these equations, current stemwood production rates can be examined as a function of the current state of the stand, rather than as a function of stand age and time elapsed since the silvicultural treatment.

Rate of photosynthesis and stand foliar weight determine the degree to which trees access available resources of the site. The role of mineral nutrients and water can be incorporated by expanding upon Equation 6 to consider their effects on rates of photosynthesis (p) and allocations to stems (APS). Stem surface area per unit of foliar weight (SFR) and rates of stem respiration per unit of stem surface (r) control the proportion of acquired resources used for respiration rather than converted into new stemwood.

Materials and Methods

Study Site

The spacing trial is located in the Canadian Forestry Service experimental area at North Pond in Central Newfoundland (48°41'N, 54°33'W) within Rowe's (1972) Forest Section B.28a (Rowe 1972). It is on a moderate, north-facing slope. Land capability for forestry is rated at four by the Canada Land Inventory and as medium by the provincial forest management inventory. The original stand contained more than 14 000 stems per hectare of predominantly black spruce which regenerated naturally after cutting during the winter of 1954 and wildfire in the spring of 1961.

Experimental Design

Four spacings are being compared: unthinned (approximately 1.15 m), 1.8 m, 2.4 m and 3.0 m. In addition, nitrogen fertilization at a rate of 200 kg/ha of N, applied as urea, in combination with spacing to 2.4 m is being tested. The experiment has been laid out as a thrice replicated randomized complete block. Each treatment plot is 0.25 ha. Permanent sample plots have been established within treatment plots and untreated plots for monitoring stand growth and development. Plot sizes vary with spacing so that there would be approximately 100 trees in each thinned permanent sample plot.

Treatment plots were spaced between mid-July and early September 1981. Fertilizer was applied on 10-11 May 1983. Heights and breast-height diameters of all trees in permanent sample plots were first measured between 11 August and 16 September 1981. Plots were remeasured between 29 September and 31 October 1986.

Total height (± 0.1 m), breast-height diameter (± 0.01 cm) and crown length (± 0.1 m) were recorded for all trees in a plot.

Sampling Foliage

Samples for foliar nutrient analysis were collected in October of 1985 and 1986. Samples were taken from the top one third of the crowns of codominant trees.

Sub-samples consisting of exactly 100 current-year and 100 one-year-old needles were chosen from the 1986 foliage for measurement of surface areas. Projected leaf areas were measured with an LI-3100 area metre. These sub-samples were weighed so that foliar surface area per unit of oven-dried foliar weight could be calculated.

Calculating Volume, Weights and Surface Areas

Volumes in all plots were calculated using the equation of Ker (1974).

$$V = 4.327 * D^2 / [3.092 + (77.15/H0)] \quad [9]$$

where V = volume, dm^3
D = breast-height diameter, cm
H = total height, m.

Stem weights (SW) were estimated using the equation for black spruce in Central Newfoundland produced by Lavigne (1982).

$$SW = 0.44123 + 0.01796 * D^2H \text{ (kg)} \quad [10]$$

Stem surface areas (SA) were estimated by the following equation:

$$SA = 0.06244 * (D^2H)1.599 \text{ (m}^2\text{)} \quad [11]$$

The coefficients of Equation 11 were calculated using data for balsam fir from Western Newfoundland (Lavigne unpublished). These balsam fir trees were approximately the same size as those in this spacing trial, hence this equation is likely more accurate than others available.

Foliar weights (FW) in 1981 were calculated using an equation for black spruce in Central Newfoundland (Lavigne 1982).

$$FW = 1.5 + 0.0065 * D^2H \text{ (kg)} \quad [12]$$

This equation was modified separately for thinned and unthinned plots to estimate foliar weights in 1986. Foliar weights in unthinned plots were estimated using:

$$FW_u = 1.25 + 0.0065 * D^2H \text{ (kg)} \quad [13]$$

Foliar weights in thinned plots were estimated with this equation:

$$FW_t = 1.75 + 0.0065 * D^2H \text{ (kg)} \quad [14]$$

These changes to the equation reflected differences in crowns that developed since treatments were applied.

Periodic stemwood production was estimated by subtracting estimated stem size based on 1981 measurement of D and H from stem size estimated from 1986 measurements. In addition, rates of annual stemwood production per unit weight of foliage (E) were estimated as follows:

$$E = ((S86 - S81)/5) * ((\ln(FW86) - \ln(FW81)) / (FW86 - FW81)) \quad [15]$$

where S86, S81 = stem weights or stem volumes in 1981 and 1986
FW81, FW86 = foliar weights in 1981 and 1986

E is analagous to net assimilation rate, except that it applies only to stemwood production. Equation 15 was modified from Evans' (1972) equation for net assimilation rate.

Results

Effects of Treatments on Periodic Production

Periodic stemwood production and rates were significantly greater in unthinned plots than in thinned plots ($P \leq 0.01$) (Figure 1). Nitrogen fertilization significantly increased stem production rate in comparison to plots thinned to the same spacing ($P \leq 0.01$).

Because most trees in unthinned plots will not be of merchantable size when optimal rotation length is reached, per hectare stemwood production based on all trees overestimated production that eventually will be harvested in unthinned stands. To make the comparison more relevant stemwood production per hectare in thinned plots can be compared to production of crop trees in the unthinned plots (the largest 1000 trees per hectare based on 1981 breast-height diameters). One thousand was chosen as the number of crop trees per hectare in unthinned plots because we believed that high densities would prevent more trees from reaching merchantable size. Production rates per hectare in thinned plots were significantly greater ($P \leq 0.05$) than those of crop trees in unthinned plots except for the plots thinned to the widest spacing (Figure 1).

Mean tree diameter increments were significantly greater ($P \leq 0.01$) in thinned plots than in unthinned plots, and significantly greater ($P \leq 0.05$) in fertilized plots than in unfertilized plots (Figure 2a). Although the improvement in average diameter increment was less dramatic when treated plots were compared to crop trees in unthinned plots, treatment effects were statistically significant ($P \leq 0.05$) (Figure 2a). Average height growth in thinned plots was slightly greater than average height growth of all trees in the unthinned plots but was equal to that of crop trees in unthinned plots (Figure 2b). Mean tree stem weight and volume production rates were significantly greater ($P \leq 0.01$) in thinned plots than unthinned plots and significantly greater ($P \leq 0.05$) in fertilized plots than unfertilized plots (Figures 2c,d).

Factors Controlling Stemwood Production

Stand foliar weights were greatly reduced by thinning (Table 1), and were only 15-35% of those in unthinned plots five years after thinning. The reduction of foliar weights in thinned plots indicated that their site occupancies were less than those of unthinned plots, and therefore, that thinning has reduced the potential for annual stemwood production per hectare in treated plots during the five years after treatment.

Net increments in foliar weight per hectare were small in unthinned plots (Table 1) because foliar weights were near maximum for the site. Unthinned plots were at maximal site occupancy and presumably will continue to acquire resources at the site-limited rate for the remainder of the rotation. Net increases in foliar weight were greater in plots thinned to closer spacings than in plots thinned to wider spacings, and also was increased by fertilization. However, relative leaf growth rates were greater in plots thinned to wide spacings (Table 1), which means, for example, that plots thinned to wider spacing will double their canopy foliar weights in less time than plots thinned to closer spacings.

Table 1. Oven-dried weights of foliage and net increments of canopy foliar weight per unit of time and per unit of existing foliage.

TRT	Foliar Weights 1981	Foliar Weights 1986	Net Increment	RLGR*
	t/ha	t/ha	t/ha/5yr	t/yr/t
CONT	23.80	25.78	1.98	0.0160
1.8	5.42	9.14	3.72	0.1022
2.4	3.57	6.27	2.70	0.1098
3.0	2.12	3.78	1.66	0.1125
2.4+F	3.34	6.63	3.29	0.1320

* Relative leaf growth rate = net increment/5/average leaf weight/ha.

Periodic rates of stem production were highly correlated to stand foliar weights as shown by the following regression equations:

$$VPROD = 1.687 + 4.714 \times FW81 - 0.131 \times FW81^2$$
$$r^2 = 0.86,\ s^2 = 17.001 \qquad [16]$$

$$WPROD = 0.493 + 1.894 \times FW81 - 0.0534 \times FW81^2$$
$$r^2 = 0.85,\ s^2 = 2.780 \qquad [17]$$

where VPROD =5 year stem volume production per hectare
WPROD = 5 year stem weight production per hectare
n = 15.

The high r^2 in each of these regressions demonstrates that the reduction in site occupancy by thinning has played an important role in reducing periodic stem production per hectare in treated plots.

For plots with approximately equal foliar weight per hectare, stemwood production rates were usually less in those with more stem surface area per hectare (Figure 3). Because the ranges of values for stem surface areas in plots with approximately equal foliar weight were small, as evidenced by the high correlation between foliar weight and stem surface area (r = 0.99) (Figure 3), the effects of foliar weight and stem surface area were difficult to separate. When this data is combined with subsequent remeasurements and with data from other spacing trials in precommercially thinned black spruce stands the correlation between foliar weight and stem surface area will be less than it was for this data alone, and then it will be possible to use statistical methods to quantify their separate effects.

Thinning greatly reduced stem weight and stem surface area per hectare in the year of its application (Table 2). Reductions in stem surface areas were relatively less than reductions in foliar weights per hectare, so thinning significantly increased ratios of stem surface area to foliar weight in 1981 ($P \leq 0.05$). However, increases of stem surface per unit of foliar weight in the five years since thinning were less in treated plots than in unthinned plots in both absolute and relative terms.

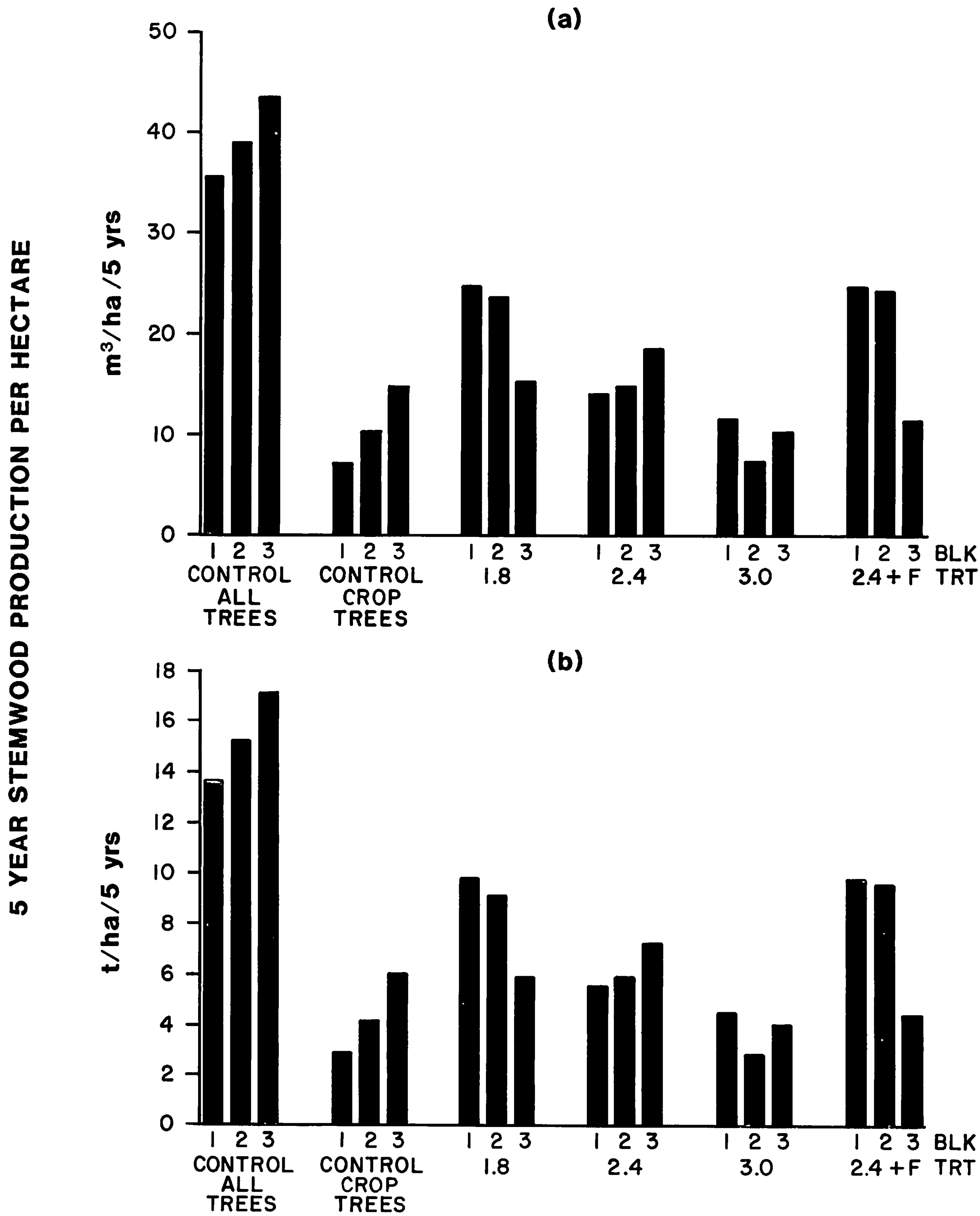


Figure 1. Stemwood production during the five years from 1982 to 1986 in thinned, fertilized and unthinned plots by all trees on plots and by crop trees (1000 trees/ha) in unthinned plots. (a) Production in terms of volume, (b) production in terms of stem weight.

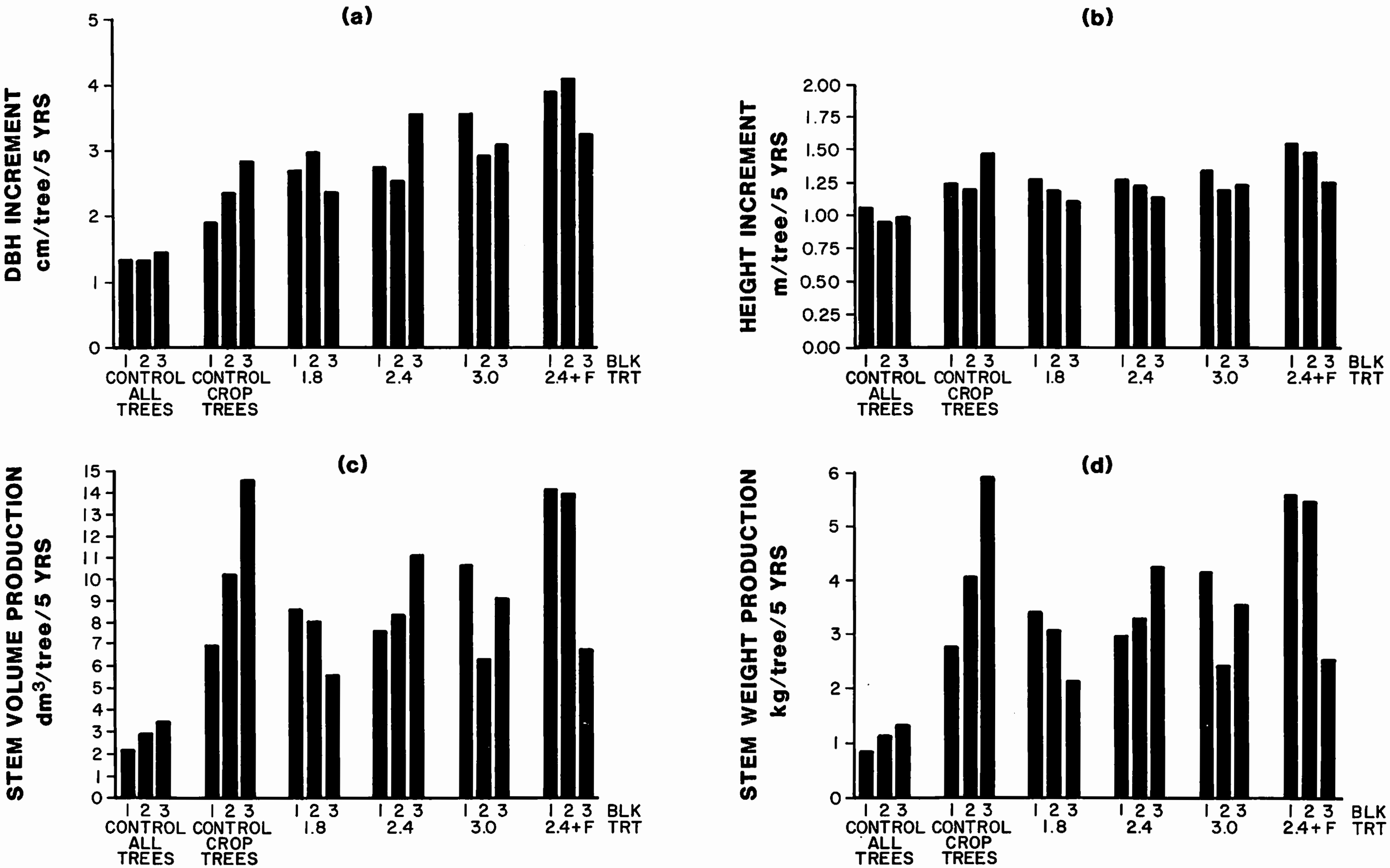


Figure 2. Average rates of production per tree for all trees on plots in thinned, fertilized and unthinned plots and for crop trees (1000 trees/ha) in unthinned plots for the five years from 1982 to 1986. (a) Average breast-height diameter increment, (b) average increments of total tree height, (c) average stem volume production, (d) average stem weight production.

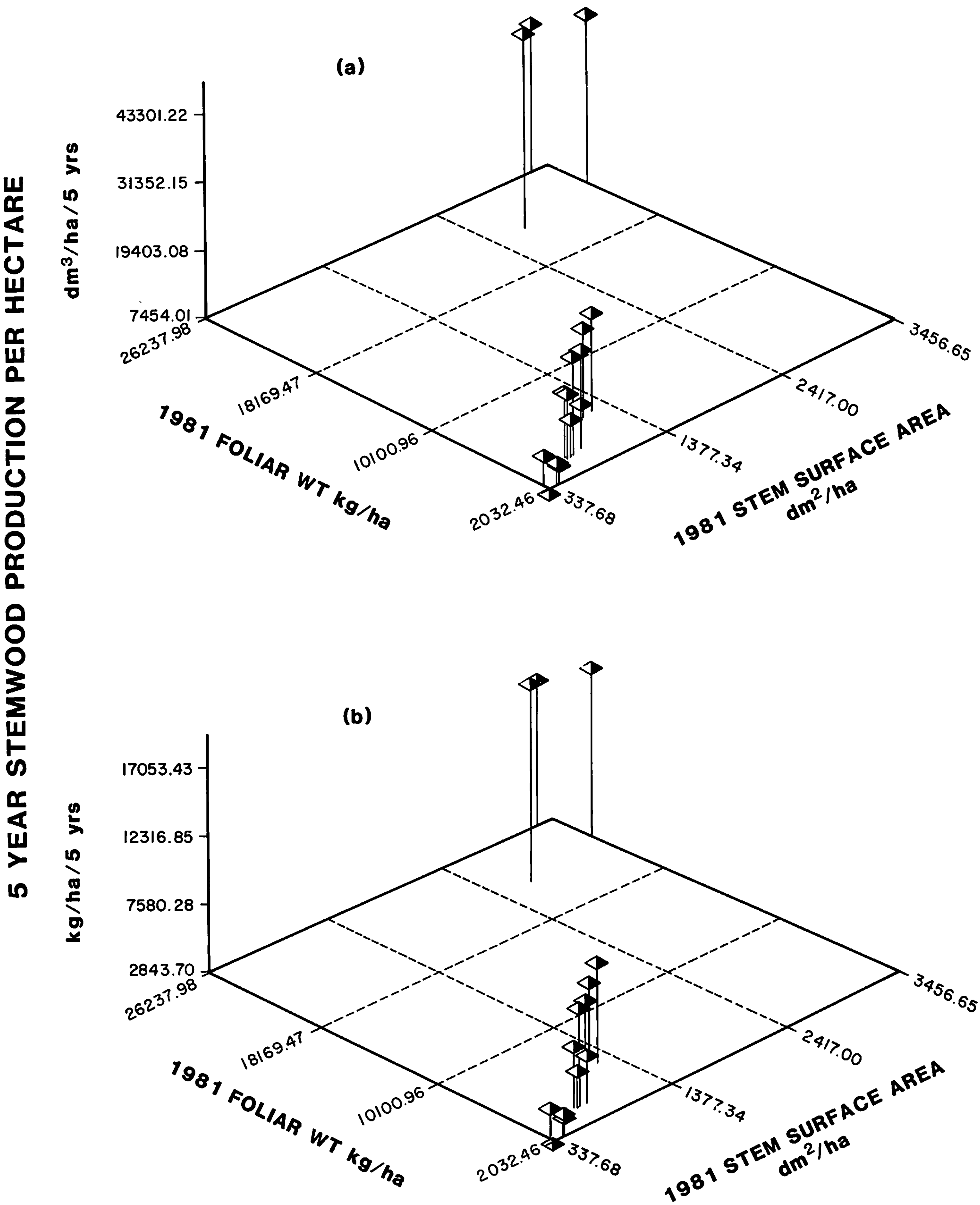


Figure 3. Three dimensional graphs showing correlations of stemwood production to foliar weight and stem surface area. (a) Stemwood production in terms of volume, (b) stemwood production in terms of weight.

Table 2. Stem surface areas and relationships between stem surface area and foliar weight in thinned and unthinned plots.

	Stem Surface Area		Stem Surface/Foliar Weight (SFR)			
					Periodic	Relative
	1981	1986	1981	1986	Change	Change*
TRT	m^2/ha		m^2/t		m^2/t/5 yrs	m^2/t/y/(m^2/t)
CONT	31.59	56.91	1.328	2.205	0.877	0.0997
1.8	10.68	20.64	1.960	2.255	0.295	0.0283
2.4	7.70	14.59	2.152	2.327	0.174	0.0157
3.0	4.11	8.64	1.935	2.284	0.349	0.0340
2.4+F	6.71	15.03	1.979	2.258	0.279	0.0295

* Relative Change = Periodic Change/5/average SFR.

Rates of annual stemwood production per kilogram of foliage were significantly greater ($P \leq 0.01$) in thinned plots than in unthinned plots (Figure 4), and in fertilized plots compared with unfertilized plots ($P \leq 0.05$) having equal foliar weight per hectare, and were negatively correlated to stand foliar weights (r = -0.80 for volume and r = -0.78 for weight).

Rates of stem production per unit of stem surface area were significantly greater ($P \leq 0.01$) in thinned plots than in unthinned plots, and also were significantly greater ($P \leq 0.05$) in fertilized plots than in unfertilized plots at the same spacing (Figure 5).

Fertilization significantly increased ($P \leq 0.05$) weights and surface areas per 200 needles, but not ratios of projected foliar area to foliar weight in comparison to all other plots (Figure 6). Foliar samples were collected near the top of canopies and hence represented sun foliage of each stand, rather than representing average needle morphologies of canopies with different foliar weights per hectare and spacings between trees. For this reason, it is not surprising that these measures of needle morphology did not differ significantly between thinned and unthinned plots.

Nitrogen fertilization did not significantly increase the N content of foliage collected in 1985 (Figure 7). However, uptake of nitrogen per hectare was greater by fertilized plots in comparison to unfertilized plots of the same spacing, because they produced larger increases in foliar weight per hectare and in stemwood growth. Fertilization significantly reduced ($P \leq 0.05$) ratios of phosphorous to nitrogen (Figure 8a) from which it can be inferred that phosphorous uptake per hectare was not increased by the addition of nitrogen. Ratios of potassium to nitrogen were equal in foliage of fertilized and unfertilized plots (Figure 8b), hence potassium uptake per hectare apparently increased at the same rate as nitrogen uptake.

Discussion

Comparing Spacings

Responses to thinning can be evaluated by comparing growth per tree and by comparing growth per hectare for plots of different spacing. Plots thinned to the widest spacing had greatest responses to thinning and plots thinned to the narrowest spacing had the least response when comparing growth per tree. When growth per hectare is used to compare plots then unthinned plots outperformed thinned plots and plots with closer spacings outgrew plots with wider spacings. Therefore, no one spacing was clearly shown to be better than the other spacings by the stemwood produced during the first five years after thinning.

Managers can choose optimal spacing only when final yields and rotation lengths are known. It is not a straightforward matter to use the measurements of periodic growth rates reported here to project growth of these plots to their rotation ages, so that the optimal spacing can be identified. For instance it cannot be assumed that differences in growth rates in subsequent periods will be similar to those of the recently measured period. To estimate optimal spacing by using measurements of stem growth rates only it will be necessary to wait until the plots of this trial reach maturity. However, these plots can also be used to learn more about tree growth and stand development by relating differences in growth rates to differences in stand and site attributes. This knowledge can be the basis for predictions of future yields to compare spacings.

Site Occupancy and Production per Hectare

An instantaneous reduction in site occupancy is an inevitable consequence of thinning. Higher rates of stemwood production per hectare in unthinned plots (Figure 1) were achieved because of their higher rates of resource acquisition in comparison to thinned plots. But thinned plots recover their capacities to acquire resources as stand foliar weights and surface areas of absorbing roots return to the prespacing levels. Eventually treated plots will return to the same site-limited maximal annual rates of resource acquisition per hectare that are currently achieved only by unthinned plots, but the time taken will be a function of spacing.

While site occupancy was reduced after thinning, the remaining foliage and roots acquired resources at higher rates thereby resulting in higher rates of stemwood production per kilogram of foliage in thinned and fertilized

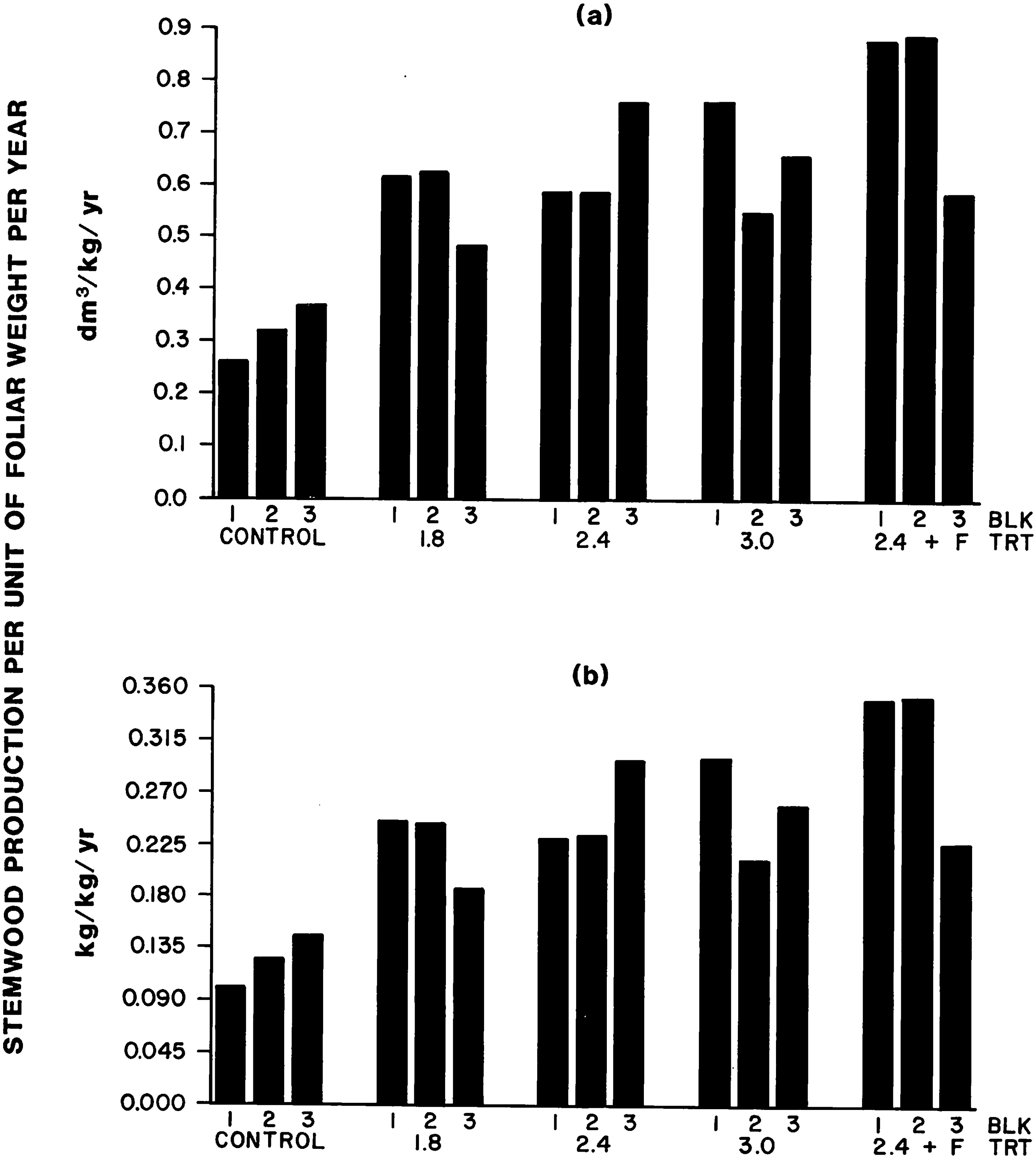


Figure 4. Stemwood production per unit of foliar weight in thinned, fertilized and unthinned plots averaged for the five years of production between 1982 and 1986. (a) Stemwood production in terms of volume, (b) stemwood production in terms of weight.

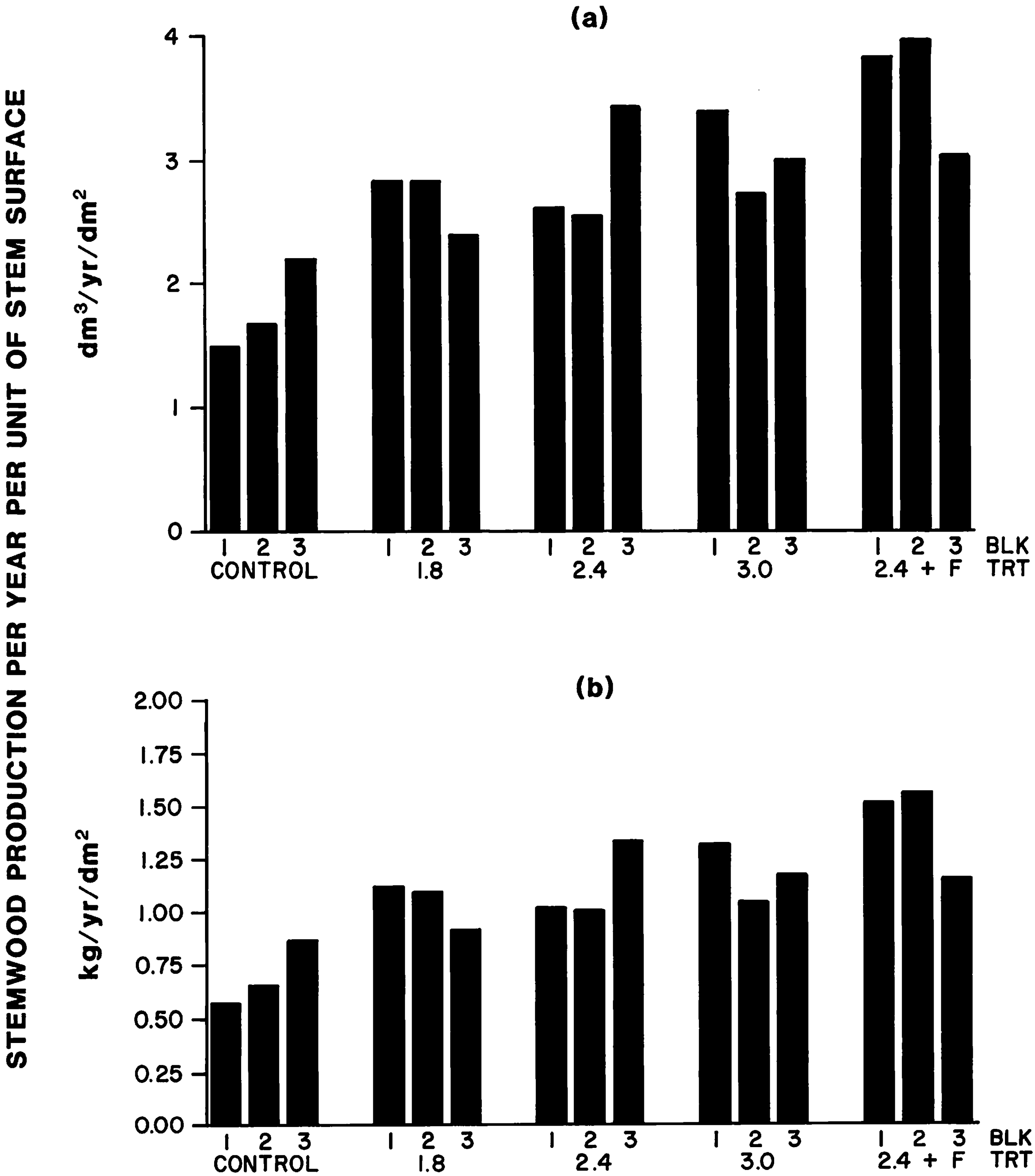


Figure 5. Stemwood production per unit of stem surface area in thinned, fertilized and unthinned plots averaged for the five years of production between 1982 and 1986. (a) Stemwood production in terms of volume, (b) stemwood production in terms of weight.

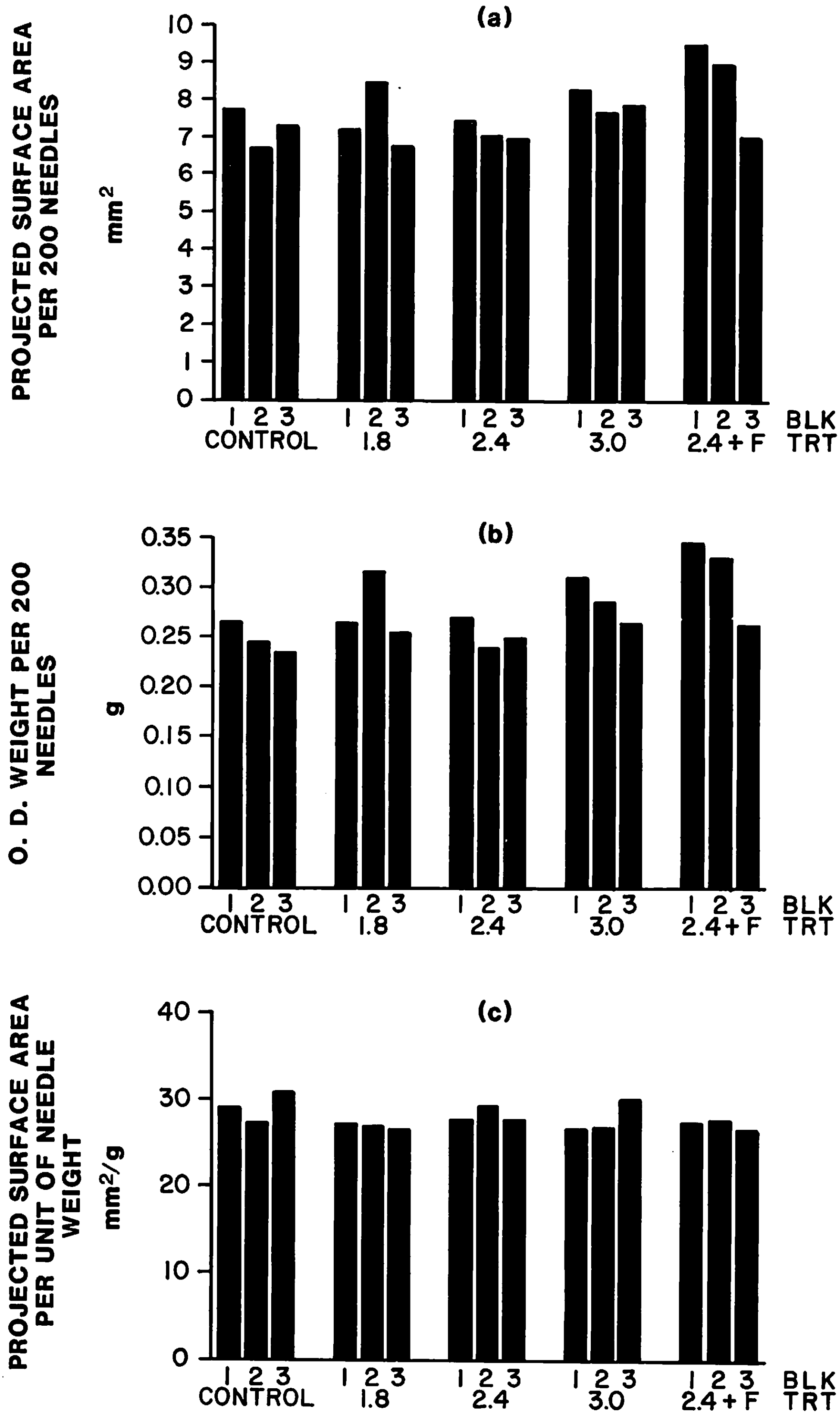


Figure 6. Morphological characteristics of foliage from the upper canopies of thinned, fertilized and unthinned plots collected in October 1986. (a) Projected needle areas per 200 needles, (b) oven-dried weights per 200 needles, (c) ratios of needles surface area to foliar weight.

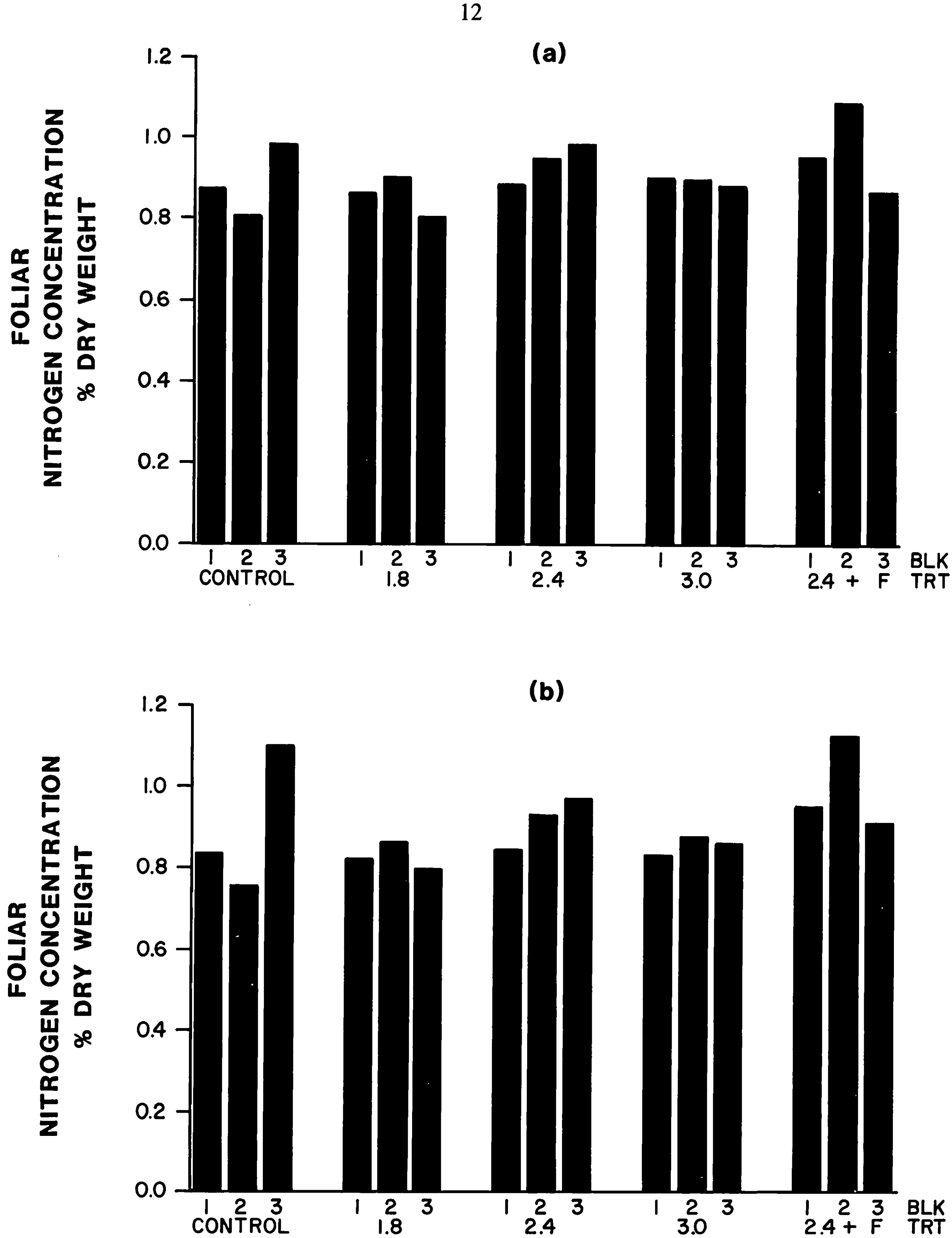
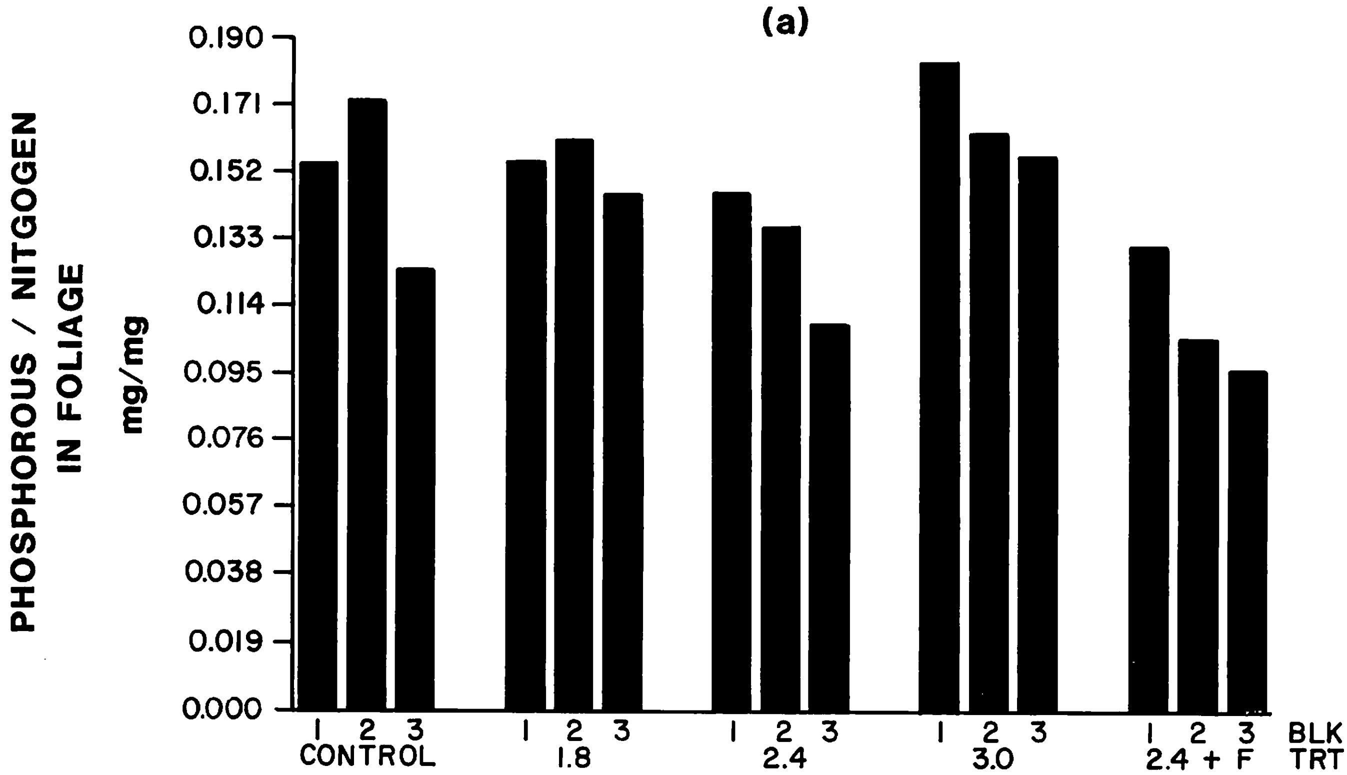


Figure 7. Foliar nitrogen concentrations on a dry weight basis for foliage collected in October 1985 from thinned, fertilized and unthinned plots. (a) Foliage produced in 1985, (b) foliage produced in 1984.



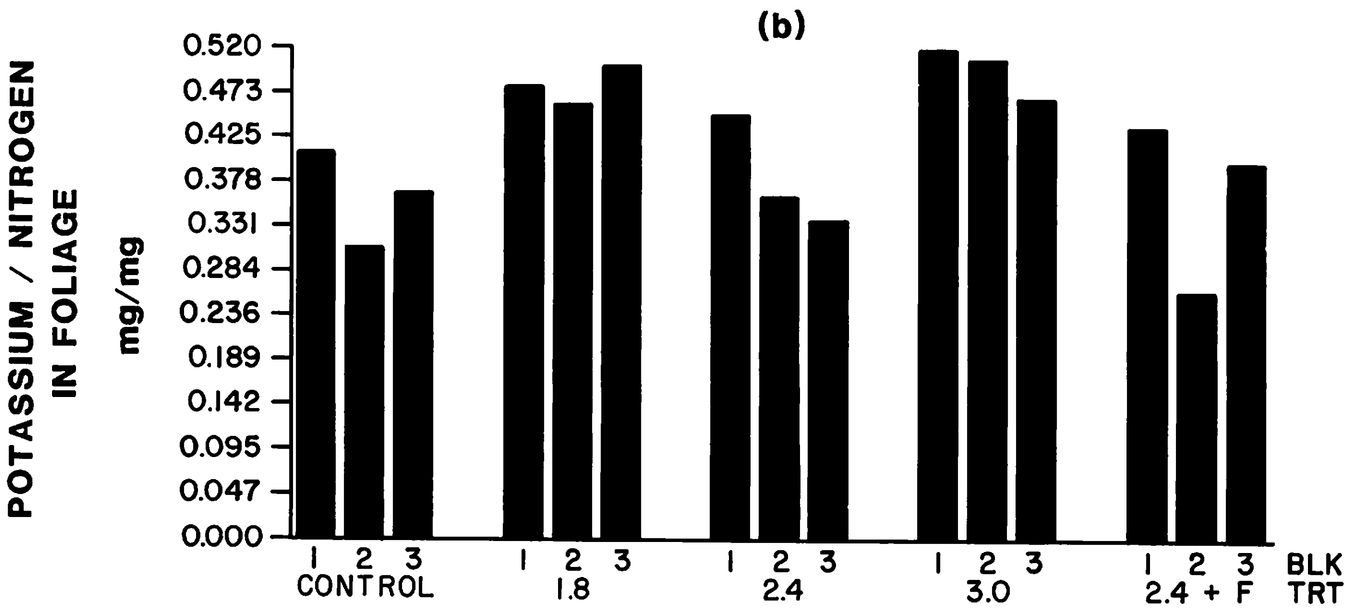


Figure 8. Comparisons of foliar concentrations of other nutrients to the foliar concentrations of nitrogen for foliage collected in October 1985 from thinned, fertilized and unthinned plots. (a) Phosphorous, (b) potassium.

plots (Equation 6). Higher rates of uptake per unit of foliar weight were partly responsible for higher rates of stemwood production per tree in thinned plots. The search for an optimal spacing must evaluate the long-term balance between the opposing effects of treatment, which on the one hand reduces stem growth rate per hectare but on the other hand increases rates of stem growth per unit of foliar weight.

The additional time taken to return to maximal foliar weight per hectare by canopies of plots thinned to wide spacings can be inferred by comparing their rates of net foliar production per kilogram of foliage to those of plots thinned to close spacings (Table 1). Canopies of plots thinned to wide spacings will return to maximal foliar weight earlier than if their relative foliar growth rates only equalled those for canopies of plots thinned to close spacings. Relative foliar growth rates are greater in canopies with less foliage principally because more light penetrates to lower branches giving them higher rates of foliar production than the lower branches of canopies with more foliage (Siemon *et al.* 1976; Ilonen *et al.* 1979; Brix 1981a).

Nitrogen fertilization increased the rates at which canopies were recovering from thinning (Table 1). Similar results have been observed for other conifer species by Brix (1981a) and Mead *et al.* (1984). Thinning and fertilization have complementary effects on foliar production: fertilization increases foliar production of well-lighted portions of canopies more than of heavily shaded portions of canopies, and thinning increases the proportion of the remaining canopy that receives high light intensities (Brix 1981a). The additional site occupancy contributed significantly to the increased stem production in response to the combined treatment (Figure 1). Miller (1981) concluded that fertilizers are optimally applied in circumstances where they can hasten completion of canopy development, which is the case in recently thinned stands.

Rates of Resource Acquisition by Individuals and Stands

Higher rates of annual stemwood production per kilogram of foliage (Figure 4) were primarily responsible for greater stemwood production rates per tree in thinned plots compared to unthinned plots (Figure 2) as predicted by Equation 7. Annual rates of stemwood production per kilogram of foliage were greater in plots containing less foliar weight per hectare. Similar observations were made by Waring *et al.* (1981), Brix (1983) and Mitchell *et al.* (1983). However, slopes of this relationship have varied widely among these studies, so other factors are probably modifying the exact relationship between foliar quantity and rate of stemwood production per unit of foliar weight.

The value of using stemwood production per unit of foliar weight or surface area to investigate causal relationships is well recognized (see reviews by Satoo and Madgwick 1982, and Waring 1983). Rates of stemwood production per kilogram of foliage is a function of rates of photosynthesis per unit of foliar weight, proportions of acquired resources allocated to stems, rates of stem respiration and surface area of stems but only photosynthesis is performed by foliage and involved with acquiring resources. Because the other factors controlling rate of stemwood production per unit of foliar weight affect the use of acquired resources, the rate of stemwood production per kilogram of foliage cannot be used simply as a measure of rate of resource acquisition.

Thinning can raise average photosynthetic rates in the years immediately following treatment by increasing light intensities reaching foliage in the lower canopy (Kellomaki *et al.* 1980) and, therefore, can raise rates of annual stemwood production per kilogram of foliage during those years (Equation 6).

Brix (1971, 1981b) and Kellomaki *et al.* (1982) found that fertilization increased maximal rates of photosynthesis in proportion to increases in foliar nitrogen concentration. Differences in photosynthetic rates were insignificant in low light intensities but large in high light intensities. In an investigation of the interaction of light and nitrogen, Reed *et al.* (1983) found that more nitrogen was required to produce healthy foliage on seedlings growing in high light intensities than on seedlings growing in low light intensities. It appears that thinning can increase the effects of fertilization on average rates of photosynthesis per unit of foliar weight. Therefore, higher rates of stem production per unit of foliar weight by individuals in the thinned and fertilized plots (Figure 4) can partly be explained by higher photosynthetic rates in comparison to those of trees in plots that were only thinned (Equation 6).

As the canopies close the advantage in thinned plots due to higher average photosynthetic rates will decrease. Consequently, this effect of treatment benefits trees in plots thinned to wider spacings for a longer time than it does trees in plots thinned to closer spacings. This is one of the benefits of wider spacings that offsets the loss of production per hectare through incomplete site occupancy, and therefore must be considered when seeking an optimal spacing.

Differences in Use of Acquired Resources

The amounts of stem surface area per unit of foliar weight increase continuously throughout the life of trees at rates that vary with the current balance between net foliar production rate and stemwood production rate. Higher stem surface area per unit of foliar weight causes lower conversion rates (Equation 6). The stem surface area per unit of foliar weight increased more slowly in thinned plots than it did in unthinned plots (Table 2). This is because the reduction in site occupancy by thinning increased relative foliar growth rates (Table 1) more than it increased rates of stemwood production per kilogram of foliage (Figure 4).

Brix (1983) demonstrated that lower stem surface area per unit of foliar weight became increasingly responsible over time for the increased annual stemwood production rates in response to thinning during the seven years after thinning in a young Douglas-fir stand. Trees in thinned plots will have lower ratios of stem surface area to foliar weight than trees in unthinned plots for the remainder of the rotation. Also, trees in plots thinned to wide spacing will have lower ratios than trees in plots thinned to close spacing. Hence, this advantage for growth of individuals from thinning is longlasting, and therefore probably the most important benefit of thinning.

Rates of converting acquired resources into stemwood depend on rates of stem respiration per unit of stem surface area, in addition to stem surface areas per unit of foliar weight (Equation 6). Lavigne (1985) reported higher rates of stem respiration in a recently thinned balsam fir stand in comparison to an adjacent unthinned stand. Consequently, conversion rates of thinned stands were lower than those of unthinned stands. Differences in stem respiration rate arose partly because rate of stemwood production per unit of stem surface area was greater in thinned stands. This aspect of resource use will continuously reduce conversion rate of thinned plots more than unthinned plots for the remainder of the rotation, countering to some extent the advantage of lower ratios of stem surface area per unit of foliar weight.

Conclusions

The optimal spacing strikes the best balance over the life of the stand between those effects of thinning that tend to reduce stem growth rates per hectare and those which increase stem growth rates per tree. The counterproductive effects of thinning include loss of resource acquisition during the years that stands do not completely occupy the site and reduction in conversion efficiency by raising respiration rates per unit of stem surface area. Both of these effects of thinning are unavoidable outcomes of concentrating stemwood production on fewer trees. To the benefit of the production of merchantable timber, thinning increases rates of resource acquisition per unit of foliar weight during the years that the site is not fully occupied and causes ratios of stem surface area per unit of foliar weight to be lower than otherwise for the remainder of the rotation. Therefore, the optimal spacing is a function of the tradeoffs between maximal photosynthetic production per hectare versus higher rates of photosynthesis per unit of foliar weight, and between higher ratios of stem surface area per unit of foliar weight versus higher rates of stem respiration rate per unit of stem surface area.

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