Biological Insights Gained from Fertilization - Thinning Trials at Shawnigan Lake, B.C.[1/]

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In silvicultural practices such as site preparation, forest fertilization and juvenile spacing, we attempt to create an environment favorable for tree growth. We often find that a particular practice may be beneficial in some cases but not in others; however, we are unable to explain why this is so. Not enough is known about how our treatments change the environment of trees or how environmental conditions affect tree growth. It has been said that to grow trees successfully we first must know how trees grow (Kramer and Kozlowski 1960). We should also keep in mind that the only way environmental changes resulting from silvicultural practices affect the growth of trees is by influencing their physiological conditions or processes. A basic knowledge of these factors could be of great help in pointing out the best treatments to apply under different stand and site conditions. We have seen an example today of how computer modelling can be a very valuable tool, but we also realize the need to incorporate realistic biological concepts.

I shall briefly discuss some of the important environmental changes brought about by thinning and some of their effects on physiology and growth of trees. Our Shawnigan Lake experiments will form the basis for my discussion. Thinning was done in a 24-year-old Douglas-fir stand and it, therefore, cannot

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be classified as juvenile spacing. This will not be critical for my discussion; at least we will be aware of the situation that faces us if juvenile spacing is not carried out in time. The experiment also involved nitrogen fertilization at different thinning levels; in fact, fertilization was the main object of the study, and I shall deal with some interactions of these two treatments.

Tree Growth

Studies have generally shown that stand thinning, within wide limits, will not affect the total production of our forest (Smith 1962; Assmann 1970); but yield may be increased by increasing the merchantable portion of the products. The primary objective of thinning is to increase the growth rate of the remaining, better trees so that desirable products can be obtained faster. I shall, therefore, concern myself mostly with growth rates of individual trees rather than forest stands in relation to thinning.

The Shawnigan Lake site and treatments have been described in detail (Crown and Brett 1975). Briefly, the basic design involved 3 levels of nitrogen fertilization, i.e., 0, 224 and 448 kg N, as urea, per ha (F_0, F_1, and F_2, respectively) and 3 levels of thinning, in which zero (T_0), approximately 1/3 (T_1) and 2/3 (T_2) of the basal area was removed. Treatments were replicated twice in each of 2 years (1971 and 1972) before the growing season began in 0.08 ha plots with 10-m-wide buffer zones. The stand was situated on a medium to low site (21 m height at 50 yr). In my part of the project, diameter growth was followed by weekly measurements during the growing season, using dendrometer bands at different stem heights, for 6 codominant trees of initial uniform size in each plot (4 plots per treatment). Height growth data were for volume sample trees used in another study (Crown unpubl.). Data were selected to illustrate specific points. The study is still in progress and therefore incompletely analyzed.

Diameter Growth. Thinning increased diameter growth from the first season, with some additional effect in subsequent years. The effect was greater at breast height (BH) than at half the tree height above BH (Table 1). Nitrogen fertilization greatly increased the growth response.

Weekly measurements showed that thinning was effective from the beginning of the first season, even before production of new foliage took place in June (Fig. 1). Though thinning had some effect throughout the growing season, the response was more pronounced early (May-June) than late (Aug.-Sept.) in the season (Figs. 1 and 2). Although this was not the case in 1972, growth is usually impeded by soil drought in unthinned stands in July, as pictured in Fig. 2 for 1975, but thinned stands will continue good growth for part of that month.

Height Growth. Thinning reduced height growth in the first and second year but increased it thereafter (Fig. 3). This initial adverse effect of thinning was overcome by fertilization, and trees in treatment T_2F_2 grew 50% more in height the first year than control trees. Height growth of control trees decreased with time and this was only partly caused by inclusion of height measurement of suppressed trees.

An initial decrease in height growth following thinning has been commonly observed for various tree species and is referred to as a shock effect (Staebler 1956; Miller 1961; Berry 1969). Possibly some growth reduction may be caused by increased respiration induced by a temperature increase of trees in the more exposed situation (Smith 1962). However, this does not explain how diameter growth of these trees is increased at the same time. A change in increment distribution to various tree parts appears to take place for some years following thinning, with the low-stem position taking preference. Some evidence for this dates back to the last century when a German researcher, Robert Hartig, pointed out that this change in increment distribution was caused by the effect of wind (Assmann 1970). A likely explanation is that mechanical stress in the lower stem, developed by increased swaying of the tree, will stimulate growth in that part of the stem, presumably by pressure-induced hormonal action. With a limited food (photosynthate) supply, height growth will suffer. With an increased photosynthetic capacity some years following thinning, or as a result of fertilization, the food supply will suffice to maintain or even increase height growth.

Explanation of Growth Responses

To explain the improvements in growth rate, we should first investigate changes in the tree environment and, thereafter, the resulting changes in physiological conditions of trees.

The important improvements in environment will arise from a reduced competition for light, soil water and soil nutrients. With regard to physiological aspects, we should recall that the most important physiological process determining growth and dry matter production is photosynthesis, since trees for about 75% of their weight are comprised of carbohydrates which are direct products of this process (Kramer and Kozlowski 1960). Photosynthates also form the basis for all other organic compounds synthesized by the trees. Minerals taken up from the soil, although essential in tree metabolism, comprise only a few per cent of the tree's dry weight. Some of the products of photosynthesis are later expended in the process of respiration whereby energy is released for maintenance of living tissues and for growth. The rate of net dry matter production is determined by the difference in rates of these two processes.

The photosynthetic capacity of a tree depends on (1) the size of the crown (vertical and horizontal), (2) the structure of the crown (spacial arrangement of branches and foliage), (3) the amount of foliage, and (4) the photosynthetic efficiency of the foliage. The latter is determined by their water status, mineral nutrient status, light and temperature conditions under which the foliage is grown and by the demand for photosynthates (sinks) in other parts of the tree. In respect to efficiency, I will deal only with the factors of water and nitrogen status since little information is available on the importance of the other factors.

What are the changes in environment caused by thinning and how do they affect the photosynthetic capacity of trees?

<u>Light</u>. Light intensity was measured in 18 locations in tree crowns of thinned and unthinned stands, i.e. on the top of main branches in nodes 6, 9 and 12 at 3 equal distances from the stem and for branches on the north and south sides of trees. A special light probe measured only radiation in the photosynthetically active spectrum. Using the relationship found between radiation and rate of

photosynthesis (Fig. 4), we converted our measurements into rates of photosynthesis expressed as a percentage of the rate we would have under optimum light conditions (Fig. 5). Though this does not account for all the light and tree factors involved, such as a different reaction of foliage grown in the shade versus in the light, it appears that thinning had no effect on photosynthetic conditions in the upper one-third of the crown but drastically improved it further down.

Based on measurements of crown dimensions and crown competition in the stand, we will be able to calculate improvements in light regimes at different tree spacings during different times of the day and the year for various 'open space' light conditions.

Water. Soil water probes (thermocouple psychrometers) were placed at different soil depths and distances from trees in the various treatment plots. Thinning has greatly improved the soil water conditions for most of the growing season, although it has not been at the optimum at all times (Fig. 6).

The improved soil water conditions is reflected in the reduced leaf water deficit in the thinned stands but only in the early morning (Fig. 7). During the night, water in soil and trees reach more or less an equilibrium, but the higher radiation load on exposed trees in thinned stands and the resulting increase in transpiration increases their water deficit to the control level later in the morning. Note that the deficit of trees in thinned stands which have been fertilized remain lower than that of control trees.

Water deficit of foliage affects the rate of photosynthesis (Brix 1972) so thinning has had some effect in this way for a short period of the day.

Mineral Nutrition. Effect of thinning on soil nutrition is studied by other researchers in the project. Suffice it to say that with less trees sharing the available soil nutrients, the possibility for improved nutrient uptake exists. Since the main limiting element for growth in this region is nitrogen, we studied thinning and nitrogen fertilization effects on nitrogen concentration of the foliage (Table 2). In a previous study, we showed that nitrogen fertilization and the resulting increase in nitrogen concentration of the foliage increases their photosynthetic efficiency (Brix 1971). It appears that thinning has not had sufficient effect on nitrogen concentration to enhance the rate of photosynthesis, whereas nitrogen fertilization has been effective in this regard (Table 2). Considering the increased growth as a result of thinning, for which nitrogen was used, more nitrogen must have been taken up by these trees than by control trees just to maintain the same nitrogen concentration. The conclusion would be that the improved soil nutrition for the remaining trees has permitted a better growth, but it has not caused it.

Crown Size. An expansion of the crowns of open-grown trees would improve light interception and, therefore, the rate of photosynthesis. However, branch elongation was not enhanced for the first 2 years, only thereafter (Fig. 8). Similarly, Reukema (1964) found that thinning in a Douglas-fir stand tended to reduce crown expansion. This could, therefore, not account for the increased stem growth. Branch elongation was promoted when thinning was combined with fertilization (Fig. 8).

Lower branches stayed alive longer following thinning, extending down to node 16 in the 5th season versus node 14 for control trees. Combined with the improved light condition this could have some effect on growth.

Crown Structure. The arrangement of branches and foliage within the crown will likely affect the light regimes of the leaves and the flow of CO_2 to them. The importance of leaf arrangement has been well demonstrated for the productivity of some agricultural crops (Evans 1975). The role of crown structure in forest productivity has received some attention by Japanese researchers (Kira *et al.* 1969; Satoo 1971). One index of foliage arrangement that I can present is the number of branches produced in relation to thinning (Table 3). Other aspects of crown structure are under study. Thinning had no effect on the number of branches (shoots) produced until the fourth year, but addition of nitrogen fertilizer had a marked effect from the second year on.

Foliage Amount. The relationship between amount of foliage and productivity of forest stands has been studied primarily by European and Japanese workers (Assmann 1970; Satoo 1971). Up to a point, we can expect an increase in productivity with increase in foliage mass but, thereafter, the mutual shading of leaves becomes so severe that additional foliage will not have sufficient light to be effective photosynthetically. As we have seen from our light studies, thinning has created an effective light regime even in the lower part of the crown, so additional foliage of spaced trees will contribute to productivity.

Thinning did not increase the number or the area of leaves produced for the first 2 years but, thereafter, they increased and had more than doubled in the fifth year (Figs. 9, 10). Fertilization had an even more marked effect and the area of leaves increased from the first year on. Calculated on the basis of a 6-year persistence of leaves on the branches and for branches on node 9 only, trees in thinned stands would have a 40% greater leaf area by 1975 -- 5 years after thinning.

Respiration. It was mentioned earlier that respiration is an important factor in net production and it will commonly consume 30-50% of the photosynthetic products (Kramer and Kozlowski 1960). A major reason for a low productivity in old dense stands is that the amount of living tissues in leaves, branches, stem and roots, which has to be maintained by energy released in respiration, is high in relation to the amount of photosynthesizing tissues. In our case, a higher net production for released and fertilized trees is unlikely caused by a decreased respiration, since all the changes in growing conditions listed in the following summary (Table 4) will probably increase the rate.

Changes in Growing Conditions: A Summary

Changes in environment and in trees following thinning are listed for unfertilized (T_2F_0) and for fertilized (T_2F_2) trees (Table 4). The study is still in progress and is incompletely analyzed so I will describe the changes only in broad terms. They have been classified as beneficial (+), detrimental (-) or nil (0).

The primary reason for growth response in the first 2 years following thinning was a marked improvement in light conditions for the lower 2/3 of the crowns (Table 4 and Fig. 5). The only other improvement noted was in the water status of the foliage, but this occurred only for part of the day during part of the growing season. In another study, irrigation during the growing season accounted for only a 15% increase in diameter growth (Brix 1972). The additional growth increase for trees in thinned plots from the first 2 to the last 2 years was caused by an increase in amount of foliage being produced and in the size and structure of the crowns.

Trees that were fertilized, in addition to being released, benefitted in several ways in the first season and thereafter (Table 4). This was also reflected in the diameter growth response which was about twice that of trees in plots that were thinned only (Table 1). In addition to the improvement in light resulting from thinning, fertilization provided the trees with bigger crowns and with more foliage in the first season. The water status of the foliage was even better than for trees in plots thinned only, and the nitrogen status of foliage was improved sufficiently to increase their photosynthetic efficiency. The relative importance of these factors for growth changed from the first to the last season, with an increasing effect of crown size, crown structure and foliage amount and a decreasing effect of water and nutrient status. By 1975, the per cent nitrogen of foliage was back to the control level, yet the benefits from other sources yielded the best growth rate in that year.

By these examples, I have shown that the response of trees to thinning results from many changes in the tree's environment and in the condition of the trees which affects their photosynthetic capacity. Some changes are most important in the early response, while others will have more effect some years after the treatment. A good understanding of tree growth will better equip us to prescribe the optimum management practices for various site and stand conditions.

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Table 1. Diameter growth at breast height (DBH) and at half the height above BH (½ H above BH) expressed as a percentage of growth of control trees for different thinning (T) and fertilizer (F) regimes; 1972 plot trees.

Growth in DBH

	F_0				F_2			
Treatment	1972	1973	1974	1975	1972	1973	1974	1975
T_0	100	100	100	100	158	199	226	285
T_1	139	135	150	151	224	273	290	333
T_2	187	189	205	245	355	341	413	544

Growth in D ½ H above BH

	F_0				F_2			
	1972	1973	1974	1975	1972	1973	1974	1975
T_0	100	100	100	100	159	213	215	210
T_1	119	132	133	128	186	245	236	241
T_2	138	147	146	166	243	284	285	279

Table 2. Nitrogen concentration of leaves, per cent of dry weight, in the fall for 1972 plot trees.

	Year			
Treatment	1972	1973	1974	1975
T_0F_0	1.03	1.06	0.99	0.85
T_2F_0	0.95	1.10	1.14	0.98
T_2F_2	1.93	1.54	1.26	0.85

Table 3. Number of branches (shoots) produced in different years on a mainbranch in node 9; 1971 plot trees.

Treatment	1970	1971	1972	1973	1974	1975
	Year					
T_0F_0	9	27	40	65	67	67
T_2F_0	8	22	42	65	89	107
T_2F_2	8	31	66	165	235	242

Table 4. Changes in growing conditions compared to control for T_2F_0 and T_2F_2 trees in 1972 plots.

	T_2F_0				T_2F_2			
	1972	1973	1974	1975	1972	1973	1974	1975
Environment								
light	+*	+	+	+	+	+	+	+
soil water	+	+	+	+	+	+	+	+
soil nutrients	+	+	+	+	+	+	+	+
Crown size	–	0	+	+	+	+	+	+
Crown structure	0	0	0	+	0	+	+	+
Foliage amount	0	0	+	+	+	+	+	+
Foliage efficiency								
water status	+	+	+	+	+	+	+	+
nutrient status	0	0	0	0	+	+	+	0
light	+	+	+	+	+	+	+	+

* + beneficial, - detrimental, 0 nil

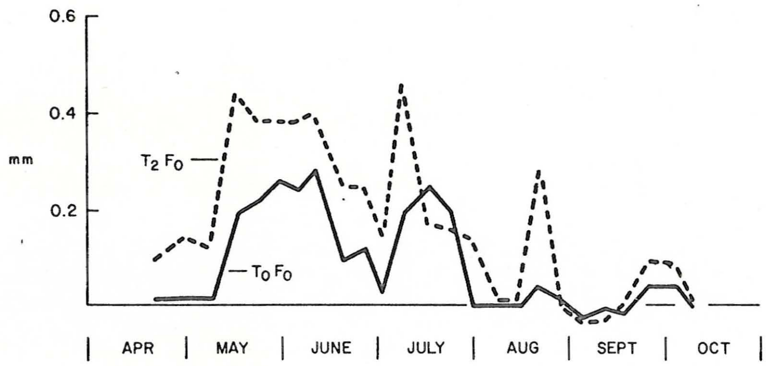

Fig. 1 Weekly DBH increments in 1972 for 1972 plot trees

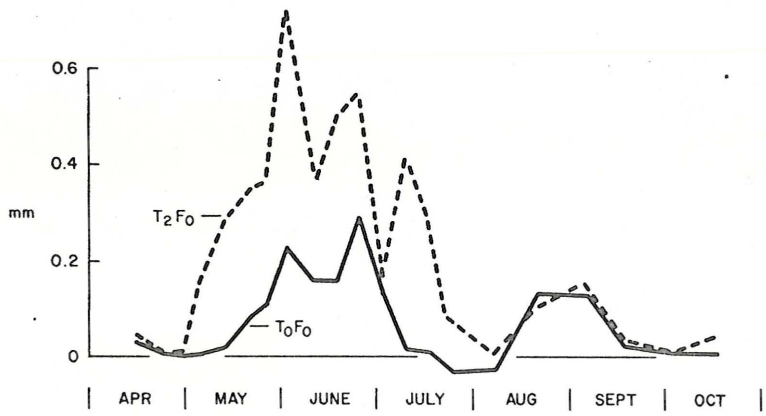

Fig. 2 Weekly DBH increments in 1975 for 1972 plot trees

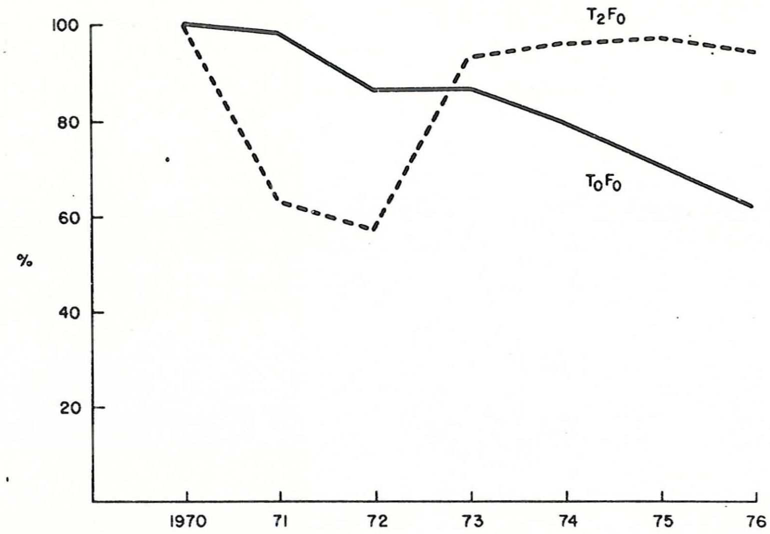

Fig. 3 Height growth as a percentage of average growth in 1969-70; 1971 plot trees

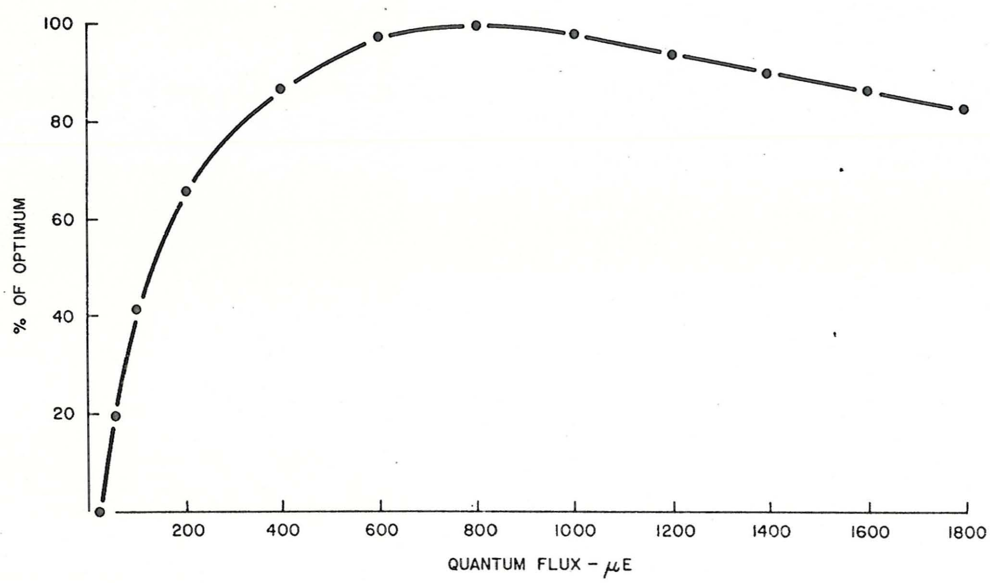

Fig. 4 Rate of photosynthesis as a percentage of the maximum rate in relation to light intensity

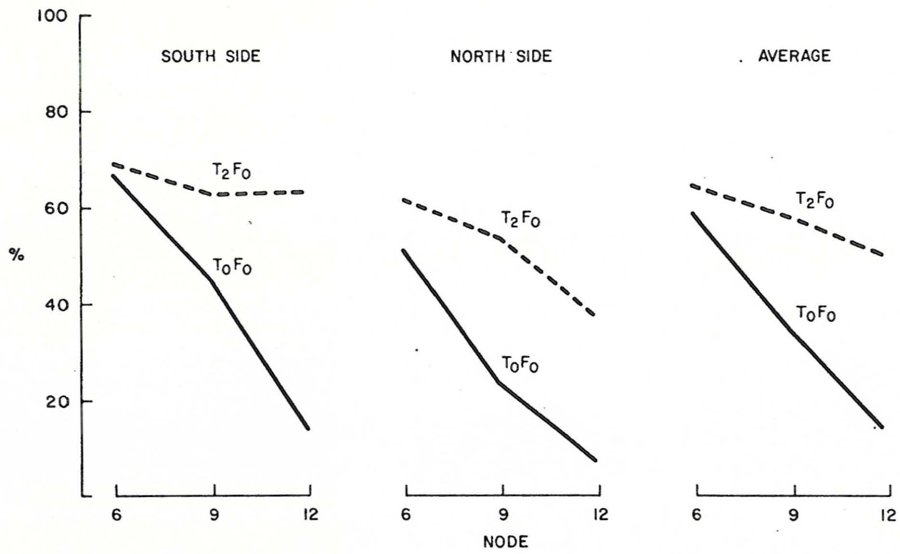

Fig. 5 Photosynthesis in tree crowns in relation to light regimes in the crowns, expressed as a percentage of the rate under optimum light intensity; data from a sunny day in July 1973

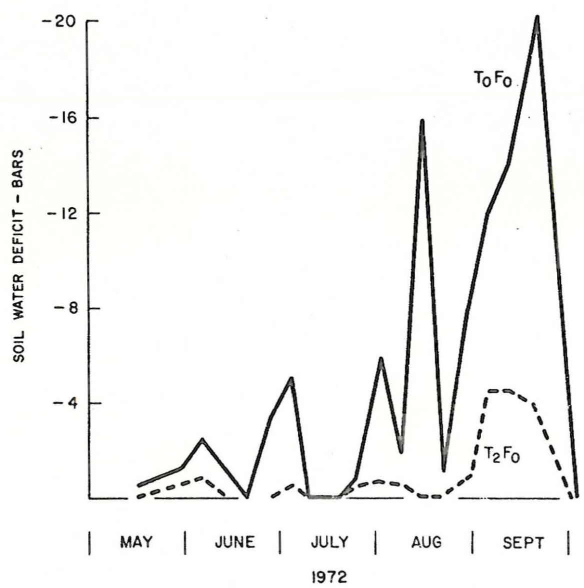

Fig. 6 Soil water deficits in 1972 on 1972 plots

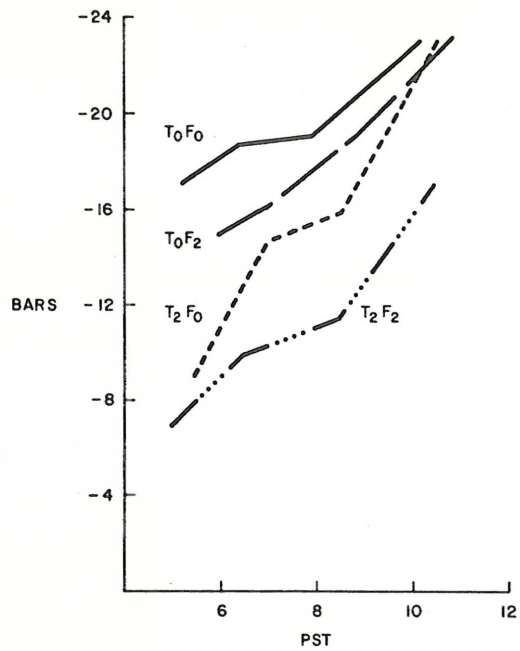

Fig. 7 Leaf water deficits for 1972 plot trees, Sept. 6/72

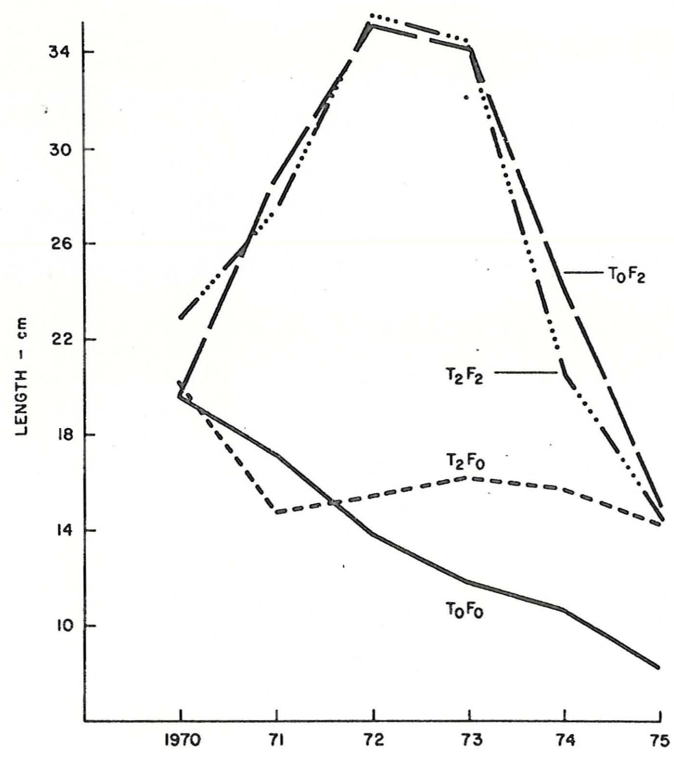

Fig. 8 Yearly growth in length of mainbranches, node 9, for 1971 plot trees

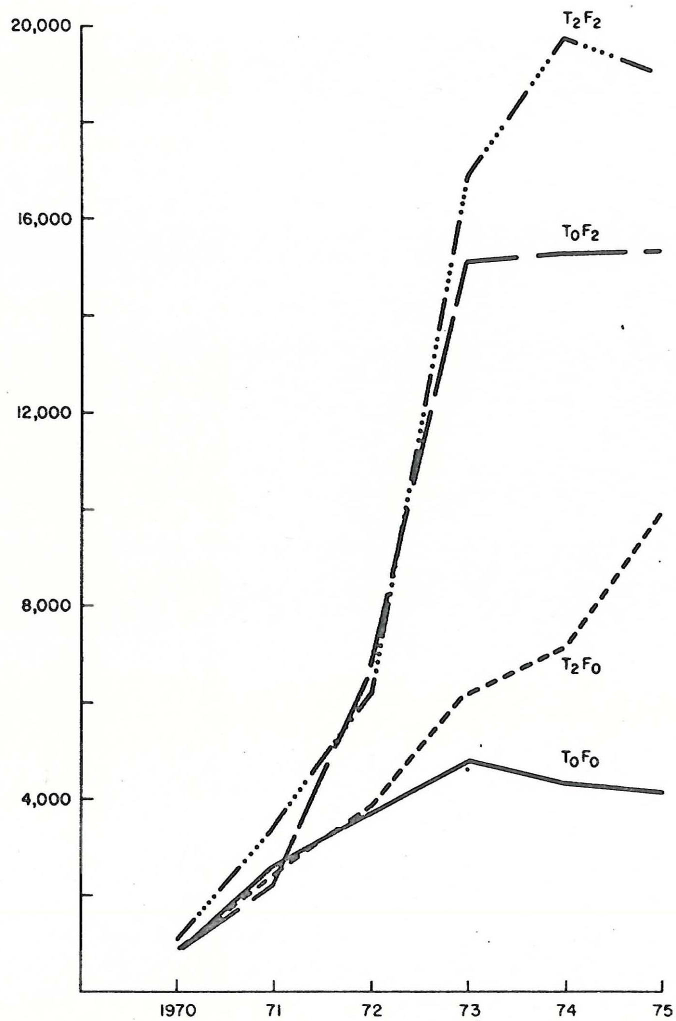

Fig. 9 Number of leaves produced in different years on a mainbranch, node 9; 1971 plot trees

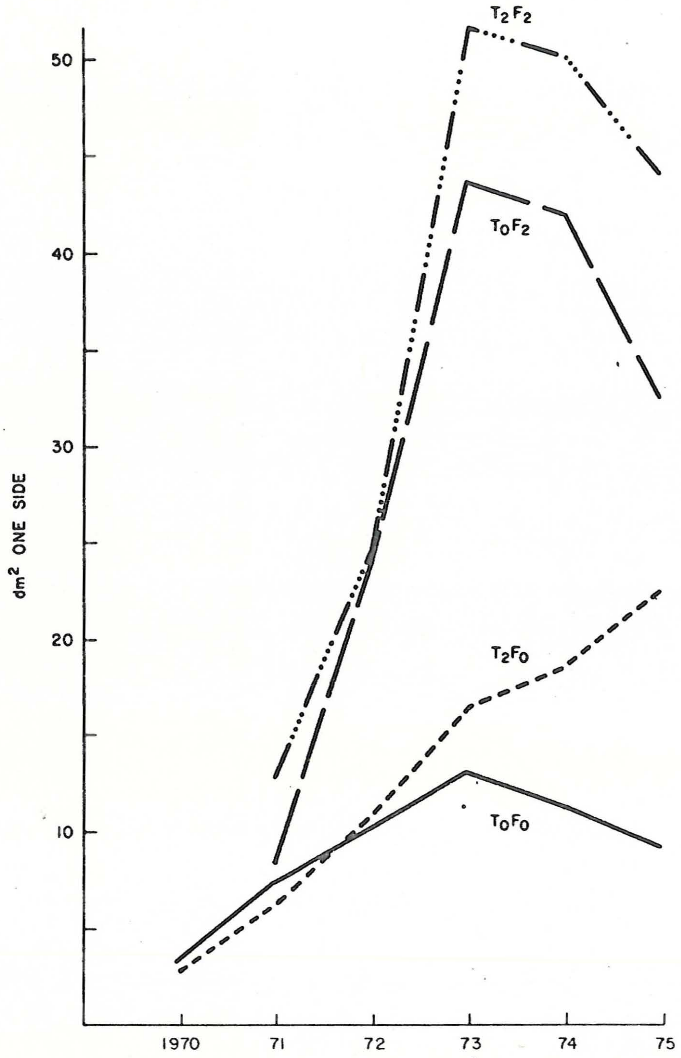

Fig. 10 Leaf area (one side) of leaves produced in different years on a mainbranch, node 9; 1971 plot trees