Mechanisms of Response to Fertilization

II Utilization by Trees and Stands

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Abstract

An understanding of the mechanism of tree and stand response to
fertilization is needed to refine our fertilizer prescription and
response prediction for different site and stand conditions. This paper
discusses (1) utilization of fertilizer in relation to stand thinning
using results from the Shawnigan Lake installation as an example, and
(2) the relative importance of foliage area and efficiency in fertilizer
response and how this information can be used to partly explain the
response pattern with time, as well as thinning-fertilization
interactions and refertilization effects. The influence of environmental
conditions on growth response to fertilization is discussed with
emphasis on soil water deficits.

Introduction

Most of the forest fertilization research in the Pacific Region has dealt with establishment of empirical relationships of growth to fertilizer source and application rate for stands of different ages and on different sites. Interaction with stand thinning has also received attention. This background has been sufficient to initiate successful operational fertilization programs in coastal Douglas-fir. Although the average response has been satisfactory, response has varied greatly and this is largely unexplained. More research is therefore needed on the mechanism of the response, and on factors affecting it, in order to refine site and stand selection criteria for optimization of fertilizer operations in Douglas-fir. Even less research has been devoted to the mechanism of the response in other commercial species in the Pacific Region and our discussion will therefore mainly draw examples for Douglas-fir, although the basic principles will be the same for other species.

The first paper on the response mechanism (Marshall, this workshop) dealt with the fate of nitrogenous fertilizers in terms of losses, availability and cycling. The emphasis of the discussion in this second paper will be on outlining the physiological mechanism by which nitrogen fertilization affects tree and stand productivity and on relating this to some important operational variables such as stand density, timing of fertilization following stand thinning, and refertilization. Environmental influences on the response will also be discussed.

Nutrient Utilization

Uptake

Uptake of nutrients from the soil depends on root distribution and on movement of nutrient ions to the root surface by diffusion or mass flow. Most of the ion uptake occurs close to the root tips and involves, for the most part, active, energy-requiring processes before nutrients enter into the xylem sap and are translocated by mass flow in the transpiration stream to the tree crown. In conifers, inorganic nitrogen ions taken up (ammonium and nitrate) are primarily metabolized in the roots to organic forms before being translocated to the crown. Uptake by roots, metabolism in roots, and translocation to crowns depend on environmental conditions, in particular soil moisture and temperature; they therefore vary seasonally and between sites. For example, nutrient uptake may be limited in summer by soil moisture and in winter by soil temperature. Uptake also depends on many stand factors as will be discussed in the following section. Other aspects were dealt with in the previous paper by V. Marshall.

Thinning effect

Thinning affects root distribution and nutrient requirement by reduction in growing stock and can therefore be expected to influence nutrient uptake. Most of the fertilization in B.C. is in recently spaced stands. One concern is that these stands do not have sufficient root distribution and storage capacity to adequately utilize the fertilizer applied, particularly with poorly mobile ions such as ammonium. Indeed, Miller (1986) argued that only the nitrogen taken up during the first year after application will be utilized by the trees and the rest will be immobilized or lost; unless the amount immobilized is large in relation to the soil nitrogen capital it will not have a significant effect on future nitrogen supply. This agrees with the study by Heilman et. al. (1982b) in which most of the fertilizer N uptake in their Douglas-fir stands occurred between 6 and 24 weeks after fertilization. Although fertilizer uptake therefore may be limited in thinned stands as well as in early stages of stand development, Miller (1981) has

suggested that the need for added nutrient supply is greatest before canopy closure. Thereafter much of the nutrients required for growth comes from internal redistribution of stored nutrients as discussed by van den Driessche (1984), and trees are less dependent on external nutrient supplies. However, the substantial growth responses of closed stands of Douglas-fir and of other species in many forest regions to N fertilization demonstrate that N deficiency also occur at later stages of stand development. In any case it is important that the stand is 'ready' to use the fertilizer when it is applied.

For an intensive forest fertilization program, Peterson et al. (1986) identified timing of fertilization in relation to stand thinning as an important question requiring more research. Response to delayed fertilization in three precommercially thinned Douglas-fir stands has been reported (Regional Forest Nutrition Research Project 1986). Only a 2-year delay in stands thinned to 1000 stems/ha was studied and this delay was found to have no effect over an 8-year response period. The Ministry of Forests' lodgepole pine fertilization trials in interior B.C. include a test of the effect of delaying N fertilization two or more years after thinning (Brockley 1986). In addition to studying growth response they are also concerned about possible influences of this delay on stand damage (snow pressure and animals).

Some results from the Shawnigan installation address questions on the possible inadequate utilization of nitrogen fertilizer in recently thinned stands. The net gain in above-ground nitrogen contents over a 9-year period following nitrogen fertilization has been greater in thinned than in unthinned plots, i.e., 63 versus 27 kg N/ha (Pang et. al 1987). The greater net gain in N in thinned stands is related to increased crown expansion and lower N losses in litterfall following thinning. The total N uptake in above-ground biomass during this period was calculated as net gain in N content of biomass plus N content of litterfall (Table 1). Fertilization in unthinned stands resulted in an N uptake of 57 kg N/ha and in thinned stands 71 kg N/ha. This is 13 and 16%, respectively, of the 448 kg N/ha applied. It was previously calculated that urea fertilization at Shawnigan resulted in an increase

of 38 kg N/ha in foliar N content after the first growing season in
unthinned stands (Dangerfield and Brix 1979). This then would account
for the major part of the uptake during a 9-year period even without
consideration to possible increases in N content of other tree
components. Uptake in other tree components amounted to 45% of the total
uptake in the study by Heilman (1982b). Using this figure we would
conclude that all N uptake resulting from fertilization in unthinned
stands occurred in the first year. Considering the reduction in growing
stock biomass with thinning (two-thirds) (Pang et al. 1987) and the
finding that thinned and unthinned stands had the same foliar N
concentration in the fall following the spring fertilization (Fig.1), we
can estimate that N uptake in thinned stands was only about one-third of
the uptake in unthinned stands during the first year. A greater
proportion of the total N uptake over the 9-year period must therefore
have become available subsequently in thinned stands, possibly as a
result of a fertilizer "priming" effect on N mineralization of native
organic soil N. Another possibility is that the immobilized N fertilizer
is remineralized more rapidly in thinned stands and becomes available
with expansion of the root system in subsequent years. Studies with the
use of N-15 are needed for a better interpretation of the source of the
N supply. The priming effect was studied with N-15 in Douglas-fir stands
by Heilman et al. (1982a). Their data indicated a short-term effect on
soil mineral N content (50 kg N/ha) and not a substantial effect on
foliar N concentration. They pointed out that it is not presently known
how long this side effect of fertilization will continue.

The Shawniga data show that in thinned stands root absorption
capacities and N requirements were adequate to utilize the N fertilizer
and the N that may have become available presumably through the priming
effect or by remineralization over the 9-year period. Similarly our
growth response to fertilization has been as good as or better in
thinned as in unthinned stands, in spite of the initially lower growing
stock (Barclay and Brix 1985). Our stocking after spacing (900 trees/ha)
was twice as high as has been used in some operations and the concern of
fertilizer timing and utilization is still valid with very low stocking.
If the fertilizer is applied shortly after a heavy spacing the response

would appear to be greatly dependent on the magnitude and duration of the fertilizer priming effect or on remineralization, because the direct uptake of fertilizer N would be low.

Understory

Delay in fertilization after thinning could increase the capacity of the stand for nutrient uptake but, on the other hand, could have the detrimental effect of a build-up of an understory competing for the fertilizer. Nutrients taken up by the understory, however, can represent a reservoir that eventually may be more readily available to the trees following litter mineralization than fertilizer elements which would otherwise have been immobilized in the soil or lost. The amount of N tied up in the understory at Shawnigan was small and not likely to have significantly affected the tree growth response to fertilization. The increase in N content of the aboveground understory (bracken fern and salal) at Shawnigan 5 years after fertilization with 448 kg N/ha was 8.1 kg N/ha in unthinned stands and 14.6 kg N/ha in thinned stands (Stanek et al. 1979), or the equivalent of 1.8 and 3.3%, respectively, of the fertilizer applied. In addition, the removal of the understory in one experiment did not have a detectable effect on tree foliar N concentrations (Brix, unpubl.).

Foliage Area and Efficiency

The most important factors affecting dry matter production of plants are foliage area (mass), rates of photosynthesis per unit of foliage area, rates of respiration of all living tree components, and dry matter distribution to different tree components. By studying fertilizer effects on these properties we can therefore learn much about how dry matter production is affected and controlled. This information will also provide a basis for studies of fertilizer interactions with site and stand conditions.

Foliage efficiency

The rate of photosynthesis has been shown to be affected by foliage N concentration (Brix 1971,1981b) with an optimum rate at 1.74% N and a decrease with higher N concentrations (Fig. 2). The gain in photosynthetic rate from a foliage concentration of 1.0% to optimum was about 30%. Following fertilization with 448 kg N/ha this optimum concentration was reached during the first year, and the N concentration diminished thereafter to close to control level by year 4 (Fig. 1). Fertilization had a similar effect on foliage N concentration in thinned stands. Some increase in rate of respiration of shoots has also been recorded in response to fertilization thus reducing the net carbon gain (Brix 1971).

Crop production is often analysed in terms of dry matter production of the total plant (or components thereof) per unit of foliage weight (or area) and unit of time. This rate is usually termed net assimilation rate (E) but will also be referred to here as foliage efficiency. The net assimilation rate integrates the rate of photosynthesis over time and also takes into account losses in dry matter associated with respiration of plant components under consideration. Furthermore, if E is calculated on the basis of a component of the plant such as stem or aboveground plant rather than total plant, the allocation of the total plant production to that component will affect the rate.

In our analysis of tree response to fertilization and thinning at Shawnigan, we have calculated E for yearly intervals based on stem as well as total aboveground production (Brix 1983). Data for E for unthinned, fertilized plots are shown in Fig. 3. We have no information on root production. Considering that fertilization only increased the rate of photosynthesis to a maximum of 30%, we can only explain some of the increase in E, which was as high as 100%, by effects on photosynthesis. Fertilization increased respiration (Brix 1971) so this cannot be the reason for the high E response which was 45% above control in the first year and 100% in the second year based on aboveground production. An alternative explanation is that fertilization affected

distribution of dry matter with a higher allocation to stem and
aboveground tree parts and a lower allocation to roots. This appeared to
be a temporary effect during the first 3 or 4 years; thereafter, E
values are what one would expect from changes in rates of photosynthesis
alone. As discussed later, the low E values in years 6 and 7 are
attributed to increased mutual shading in the crown with increase in
foliage. The distribution effect has apparently had a considerable
influence on stem and aboveground production during the first few years
and conceivably more than doubled the production which can be attributed
to effects on the rate of photosynthesis alone. The interpretation given
here is consistent with studies by Grier et al. (1981) and Keyes and
Grier (1981) which show that a considerable proportion of net primary
production (up to 67%) may be allocated to fine root production and that
this allocation decreases with improvement in site nutrient status. It
is not known what governs this partitioning. If it is soil N
availability the effect is likely to last only 1 to 2 years following
fertilization; if it is internal tree N status the effect may last a few
more years; if it is total carbohydrate production the effect may last
the entire growth response period.

Production and foliage area

Dry matter production at the stand level can be expected to increase
linearly with an increase in leaf area during early stand development.
As crown closure is approached production will diminish because of
increased mutual shading of foliage. With further increase in foliage,
dry matter production will level off to a plateau or possibly decrease
in production (Fig.4). This decrease in production with increase in
foliage may not be the usual pattern for most crops. However, the
addition of foliage and branches will result in higher respiration
which, on account of low light, may not be compensated for by an
increase in the rate of photosynthesis. An effect of fertilization on
foliage area or mass will therefore have varying influences on tree
production depending on the initial foliage area before fertilization;
spaced stands are therefore more likely to benefit from an increase in
foliage area than are closed stands. It may be for this reason that only
thinned stands of radiata pine (Pinus radiata) respond to N

fertilization and that the response diminishes when fertilizer is
applied more than 3 years after thinning (Woollons and Will 1975).

The relationship between leaf area index (LAI, projected leaf area per
unit of land area) and aboveground dry matter production (stems and
total) at Shawnigan is shown in Fig.5. The Shawnigan stand, which had
reached crown closure (LAI 5.9) at the time of treatment, was still able
to respond in dry matter production to the increase in foliage mass
resulting from fertilization although with a 20% decrease in foliage
efficiency (production per unit foliage), as seen in Fig.3. In fact, it
was shown that the main effect of N fertilization on the Douglas-fir
stem growth response was a result of influences on foliage area (mass);
63% of the response in unthinned stands and 73% of the response in
thinned stands over a 7-year period was accounted for by an increase in
foliage mass. The rest was caused by an increase in foliage efficiency
(Brix 1983). Nitrogen deficient stands of Douglas-fir would appear then
to have insufficient foliage even after crown closure for effective
light utilization. This suggests that light measurement below closed
canopies could be used to indicate stand N deficiency and potential
growth response to increases in foliage following fertilization.

Pattern of response
An analysis of the relationship of fertilizer growth response to
increases in foliage mass and efficiency can be used to explain the
pattern and the mechanism of the response over time. Using Shawnigan
data as an example it was shown that the stem growth response to
nitrogen fertilization in the first and second years resulted primarily
from an increase in foliar efficiency as a result of increases in foliar
nitrogen concentration (Fig.6) (Brix 1983). In the next 3 years foliar
efficiency decreased and leaf mass increased. By year 5, foliar N
concentration and efficiency was back to control level, and the growth
response was entirely attributable to the build up of foliar mass. The
influence of fertilization on foliar efficiency thus provided for the
initial, short-term, growth response and enabled an increase in foliage
mass that sustained the growth response over a longer period. Nitrogen
fertilization also affects the distribution of total production to the

different parts of the tree with a higher proportion being allocated to foliage production in Douglas-fir (Brix 1983) and apparently also to aboveground biomass. The duration of the growth response will be influenced by the longevity of the foliage. Douglas-fir at Shawnigan retain their foliage for approximately 6 years so an increase in foliage production in 1 year will be effective for tree production for the following 5 years. In contrast, species with short-lived foliage will have a faster percentage increase in total foliage mass with an increase in current foliage, and therefore a quicker growth response, but the duration of the response, by the same token, will be reduced. To illustrate this point we have used the Shawnigan data for N effect on total foliage mass over time for Douglas-fir (Brix 1981a) and compared this to the reponse of trees with 3-year needle longevity but using the same N effect on current foliage production as shown for Douglas-fir (Fig.7). The resulting two types of growth response to N fertilization can be recognized in the study by Möller (1974) with Scots pine (Pinus sylvestris) and Norway spruce (Picea abies); the latter has longer-lived needles and a growth response with a pronounced plateau of longer duration.

Refertilization

The foliar efficiency at Shawnigan decreased from the second year after fertilization until it was reduced to control level at year 5 (Fig.3). This is due to a decrease in foliar N concentration (Fig.2) and the resulting effects on rate of photosynthesis (Fig.1), and on dry matter distribution. Annual refertilization would appear to be needed to maintain maximum foliar efficiency. This is the objective of Weetman and Fournier (1984, 1986a) in their optimum nutrition trials with jack pine, lodgepole pine and Douglas-fir (unpublished) in which elements other than N are also supplied. Examination of Figure 6 suggests that refertilization at year 5 would provide for the optimum combination of a large foliar mass coupled with a high foliar efficiency and therefore produce the maximum growth response to fertilization. However, refertilization of a closed stand at this time would probably not provide the best biological efficiency and ecomonic return from fertilizer investment. The foliar mass would be close to optimum at year

5 so the benefit from fertilizer effect on foliar mass would be small. Refertilization of some plots at Shawnigan was done after 9 years when foliar biomass was still high. The resulting volume growth over the next 3-year period was increased by 34% in unthinned stands (Barclay and Brix 1985). This is the effect one would expect on the basis of an increase in foliar efficiency alone (Fig.3). The response in thinned stands was 71%, indicating that an increase in foliar mass contributed to the response.

Foliar graphical diagnostic technique

This technique (Timmer and Morrow 1984, Weetman and Fournier 1986b) is currently being tested for several tree species in B.C. as a means of detecting fertilizer requirement on different sites. The method utilizes changes in foliage weight, size, nutrient content and nutrient concentration one growing season following fertilization to interpret and predict possible tree growth responses over time. To assist in this interpretation it would be helpful to know how the response of the tree species in question will depend on changes in foliar efficiency and foliar mass. Only the Douglas-fir response has been analysed in this way and similar studies for other species are needed.

Environmental Influences

A main objective of forest fertilization research is to arrive at site specific precriptions, and to accomplish this, we must know how various edaphic and climatic factors affect tree response to fertilization.

Periodicity of growth and physiological processes

To properly evaluate environmental influences on growth and responses to N fertilization we should know the activity in growth in various tree organs and in important physiological processes throughout the year. For instance, a drought in July and August will not affect height growth in the same year since this is completed in June but it may affect diameter growth which continues to the end of August. Similarly, fertilization in

the spring may affect needle size in the first year but not the number
of needles on a shoot since this is determined during bud formation the
previous year. This is one example of how environmental conditions in
one year can therefore affect growth in the next year. The timing of
growth and some important physiological processes for Douglas-fir at
Shawnigan Lake is given in Fig.8 and is probably applicable, with some
modification, to other coastal B.C. regions.

Other nutrient elements

Besides the fertilizer element applied, other nutrient elements may
limit growth on a particular site and influence the growth response to
fertilization. Interactions with other soil deficient mineral elements
such as P and S in growth response to N have been well demonstrated
(Turner 1979) and fertilization with N may induce deficiency of these
elements (Gill and Lavender 1983b, Radwan and Shumway 1984). These
aspects will be discussed in other presentations at this workshop.

Climatic influences

These influences are likely important but they have not received much
attention (Brix, in press). Some fertilizer projects have covered a wide
geographic range but growth responses have not been related to climatic
variations (Weetman and Krause 1979, Möller 1983, Peterson et al. 1984).
With regard to climatic influences on growth, we are inclined to
consider climate only during the growing season. However, as pointed out
by Waring and Franklin (1979), the climate in the coastal Pacific region
is favorable for photosynthesis for much of the rest of the year. During
that time the photosynthetic capacity remains high especially after
N fertilization when shoots are exposed to favorable light and
temperature conditions (Brix 1971). The effect of improved nutrition,
however, is not evident at low light (Brix 1971) and this, rather than
low temperature, may limit N effect in the 'off-season'. This question
deserves further study.

As a step towards evaluating climate, season, and associated site effects on tree response to N we have studied rates of photosynthesis for N fertilized and unfertilized Douglas-fir trees in relation to temperature and water stress (Brix, 1971, 1972, 1981b).

Soil water deficit

Water deficit is common in many regions of B.C. and precipitation and other factors affecting the soil and tree water status is therefore of special interest in relation to fertilizer response. The role of water deficit in fertilizer response has been the subject of some studies but more are needed before its overall significance can be evaluated (Brix 1979, in press). A highly significant interaction between summer irrigation and N fertilization in the growth of 23-year-old Douglas-fir over a 2-year period was obtained with increases in growth over the control of 15, 16 and 59% by irrigation (25 mm water per week), 448 kgN/ha fertilization, and irrigation and fertilization combined, respectively (Brix 1972). This indicates that growth response to N would be best in years and on sites with favorable soil water conditions. In an attempt to explain this interaction, the treatment effect on rates of photosynthesis, leaf growth and leaf mineral nutrient concentrations were studied. There was an interaction between the two treatments in leaf mineral concentrations whereas water stress had similar effects on rate of photosynthesis for unfertilized and fertilized trees.

A water-fertilization interaction on height growth has been demonstrated on the Shawnigan site. Here growth-limiting soil water deficits usually begin in June which is the month when height growth occurs (Fig.8). A June precipitation below 40 mm will affect height growth as well as the response to N fertilization (Brix, in press).

A study with Douglas-fir in Oregon found only an additive effect of the two treatments and not an interaction (Strand 1964). A water-nitrogen interaction may well depend on the degree of water and N deficiency, and on other growth limiting factors, e.g. other deficient nutrient elements, but this has yet to be explored (Brix, in press). Another

possibility is that N fertilization affects the water use of trees and
the importance of this for growth would depend on site water conditions.
By increasing foliar biomass (area) transpiration could be increased and
on dry sites or dry years the water stress of soil and trees may be
increased to the extent at which no response or even a negative response
to N would occur. For example N fertilization of radiata pine in
Australia increased growth the first year but the increase in foliage
that year combined with drought the following year increased the water
stress of the trees to the extent that growth was reduced in the second
year compared to unfertilized trees (Landsberg 1986). This possible
problem has been addressed for Douglas-fir at Shawnigan where tree and
soil water stress has been recorded over a 10-year period since
fertilizer-thinning treatments in 1972. Fertilization did not have any
significant adverse effect on soil and tree water stress in spite of
large increases in leaf area, possibly because of better stomatal
control of transpiration (Brix and Mitchell 1986). Although some effect
of June precipitation on height growth response to fertilization has
been demonstrated, good volume responses have been found even in dry
years so the severe problem experienced with radiata pine did not occur
in our experiment with Douglas-fir.

The possibility that nitrogen fertilization may induce a critical water
stress in western hemlock is presently being studied by us. We have seen
examples of hemlock mortality some years after fertilization in mixed
Douglas-fir hemlock stands where Douglas-fir has responded well to
fertilization. In addition to increasing foliar biomass, fertilization
may also aggravate the water balance problem by reducing fine root
production, as shown by Friedman-Thomas with Douglas-fir (Regional
Forest Nutrition Project 1986), and by increasing root mortality (Gill
and Lavender 1983a). It also seems possible that the growth reductions
in hemlock following fertilization, which have been the average response
recorded in young coastal stands in Oregon and Washington under the
Regional Forest Nutrition Research Project (1982), may have been caused
by induced water stress, as was the case with radiata pine (Landsberg
1986). Our preliminary study at Mt. Prevost, Vancouver Island, however,
did not demonstrate a detrimental effect of urea fertilization on the

water stress of western hemlock 3 years after treatment but further studies are warranted.

Stand thinning

Thinning will influence the tree environment, i.e., water, light, temperature, nutrients, and thereby possibly the response to fertilization. Interactions of thinning and nitrogen fertilization on growth have been clearly demonstrated in the Shawnigan studies (Barclay and Brix 1985) but not in others (Regional Forest Nutrition Project 1980). It is of importance to the forest manager to know the conditions promoting this interaction and there are several possibilities in addition to those already discussed. For example, thinning has improved the soil and tree water status during part of the growing season at the Shawnigan site (Brix and Mitchell 1986) and thus provided a basis for a better fertilizer response. However, on more moist sites this contribution from thinning would be less important. Similarly, thinning may affect the requirement for other nutrient elements and their availability on different sites could modify the response to N. Although not studied, the relationship of biomass production and leaf area index (LAI) shown in Fig. 5 presumably is influenced by the light regime of a site. If this is the case N fertilization effects will also be influenced by light regime. The lower the light the less the effect of N on productivity at any one LAI. This is because increases in foliage by fertilization will have less influence on productivity. Additionally, the effect of N nutrition on the rate of photosynthesis is reduced at low light (Brix 1971).

Conclusion

Some studies have shown that the applied N fertilizer is only available for tree uptake during the first year and will have little or no effect on N supply thereafter (Heilman et al. 1982b, Miller 1986). This raises the question of how a heavily thinned stand with sparse root distribution and with little requirement and storage capacity for N immediately after thinning is able to utilize the N fertilizer. In the years following thinning the N requirement will likely increase in these stands to facilitate crown development but by then the N applied may have been immobilized or lost. To address this question, N uptake at Shawnigan over a 9-year period was estimated for thinned and unthinned stands both with and without N fertilization. This was done on the basis of changes in N content of aboveground biomass at the beginning and at the end of the 9-year period plus the N content of litterfall over this period. Estimates of N uptake during the first growing season after thinning and fertilization were made on the basis of changes in foliage N content.

Thinned and unthinned stands had similar N uptake as a result of N fertilization over the 9-year period. However, in the unthinned stands, all uptake appears to have occurred during the first year, while in thinned stands the greatest amount was taken up following the first year. It is speculated that the pattern of N uptake in thinned stands resulted from the so-called 'priming' effect of fertilizer N, which increased N mineralization of native soil organic matter, or from remineralization. Although the N utilization in thinned stands at Shawnigan with the stocking of 900 trees/ha was satisfactory, one would still be concerned about utilization of aerial applied fertilizer in stands thinned operationally to levels as low as 400 trees/ha. Here the N availability would depend even more heavily on the uncertain supplies of N resulting from the fertilizer priming effect or remineralization.

Operational fertilization is practiced in stands at different stages of development before and after canopy closure, as well as in stands in

which stocking and canopy density are regulated by thinning. To interpret and predict responses in stands with different canopy development and foliage areas, the most useful initial analysis of growth responses in physiological terms is probably the relative contribution of fertilizer effects on foliage efficiency and foliage area (mass) during the period of the growth response. If this is known it will assist in explaining and predicting the pattern of the response over time, the difference in response in stands with different canopy closures, and the effects of refertilization at different fertilization intervals. To enable a further interpretation and prediction of responses, we should know the relationship between rate of photosynthesis and foliar N concentration and how this concentration changes with time after fertilization. With regard to foliage area, we should know the relationship of stand productivity to foliage area (leaf area index). Examples based on data from the Shawnigan project with Douglas-fir are presented.

Fertilization effect on aboveground dry matter production per unit of foliage during the first 3 or 4 years at Shawnigan was more than double the production that can be accounted for by the increases in rates of photosynthesis. It is conceivable that this additional fertilizer effect is caused by a shift in dry matter distribution with a reduction in allocation to fine roots and an increase to aboveground components. Fine roots are short-lived and it is therefore considered unlikely that the initial reduction in fine root production will necessitate a subsequent increase in dry matter allocation to fine roots to compensate for this initial reduction.

The opinion is sometimes voiced that all we may be accomplishing in forest fertilization is an acceleration of stand development, but apart from that we do not increase stand productivity. Before crown closure, N fertilization will speed up crown development and thereby increase productivity and maximum current annual increment (CAI) in volume will be attained sooner. This also means that the subsequent decrease in CAI will occur sooner, as will the culmination of the mean annual increment. Miller (1981) therefore cautioned that the response achieved before

maximum CAI is attained will give us an overly optimistic view of the benefits of fertilization. By decreasing the time to culmination of the mean annual increment, the rotation age is reached earlier. However, this is not all that N fertilization will mean to stand productivity and stand management. According to the knowledge we have from the Shawnigan project with Douglas-fir and the evidence I have presented here, the fertilizer response is not restricted to an acceleration of crown development. In addition, in both thinned and unthinned closed-canopy stands there was an increase in aboveground production per unit of foliage (foliage efficiency) during the first 4 years. This was accomplished partly by an increase in the rate of photosynthesis and partly, it appears, by a shift in dry matter allocation from roots to increase stem and aboveground production. Even in the closed canopy, unthinned stands did productivity increase after fertilization by increasing the foliar area from a maximum LAI of 6 without fertilization to a LAI of 9. These unthinned stands had reached their maximum CAI and fertilization effect on productivity apparently was not accomplished by speeding up stand development.

A knowledge of the influence of various edaphic and climatic factors on growth response to N fertilization is needed to provide guidance in response prediction on different sites. Few studies have dealt with this aspect in sufficient detail, particularly the physiological mechanisms involved, to provide guidance in response prediction. Since soil water deficit is a common occurrence in many forest regions in British Columbia, it is especially important to characterize the water-nitrogen interaction in growth. Although a considerable interaction has been demonstrated in one study with Douglas-fir (Brix 1972), the magnitude of the interaction will probably depend on the degree of limitation of these as well as other growth limiting factors on a particular site and this has yet to be studied. A good growth response to N fertilization has been obtained with Douglas-fir on the dry Shawnigan site, although height growth was reduced in years with a below normal June rainfall. It has been encouraging to find that N fertilization did not aggravate the water deficit problem in Douglas-fir in the Shawnigan study, in spite of an increase in foliage mass with fertilization. Other species may react

differently and experience this problem, as was the case with radiata pine in a study in Australia, and this should be considered in future studies.

Acknowledgement

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Figure Legends

Fig. 1. Foliar nitrogen concentration (% of dry weight) in years since nitrogen fertilization (F2 :448 kg N/ha as urea) and stand thinning (T2: 2/3 of BA removed); FO and TO are control treatments. Data means with same letters in any one year are not statistically significant (p=0.05).

Fig. 2. The rate of net photosynthesis (Pn) for current shoots of Douglas-fir in relation to foliar nitrogen concentration using trees fertilized in different years. Rates are expressed as a percentage of the highest treatment mean which was obtained with 448 kg N/ha as ammonium nitrate (from Brix, 1981b).

Fig. 3. Net assimilation rates (E) by years following N fertilization based on aboveground and stemwood dry matter production. Rates are expressed as a percentage of rates for control trees. (Data from Brix 1983).

Fig. 4. Hypothetical relationship of dry matter production to leaf area index (LAI) showing a plateau (a) and an optimum (b) type of response.

Fig. 5. Total above ground and stemwood biomass production of Douglas-fir at the Shawnigan Lake installation in relation to leaf area index. Data are based on Brix (1981a, 1983) with (a) for thinned plots (T2) after thinning shock was overcome (year 3), (b) for untreated control plots (year 7), and (c) for unthinned, fertilized plots (TOF2) when foliar nitrogen concentration had returned to control level (year 7).

Fig. 6. Stemwood growth response to TOF2 treatment (no thinning, 448 kgN/ha), percent above control, and contribution of foliar efficiency (E) and foliage biomass to the response in years following treatment (from Brix, 1983).

Fig. 7. Pattern of nitrogen fertilization effect on total foliage mass in years since fertilization for trees with 3-year and 6-year needle retention but with the same effect on current foliage production, i.e. effect shown by Brix (1981a) for Douglas-fir (trees with 6-year needle retention).

Fig. 8. Periodicity of growth and of some physiological processes of Douglas-fir as related to the Shawnigan Lake, B.C. location (activities # 1 and 5 have not been determined there). Solid lines indicate highest activity. Low activities in 5, 6, and 8 during July and August are caused by high soil water deficits.

Table 1. Net gain in N content of aboveground biomass
during 9 years after treatment and N content
of litterfall over that period (kg N/ha). The sum of
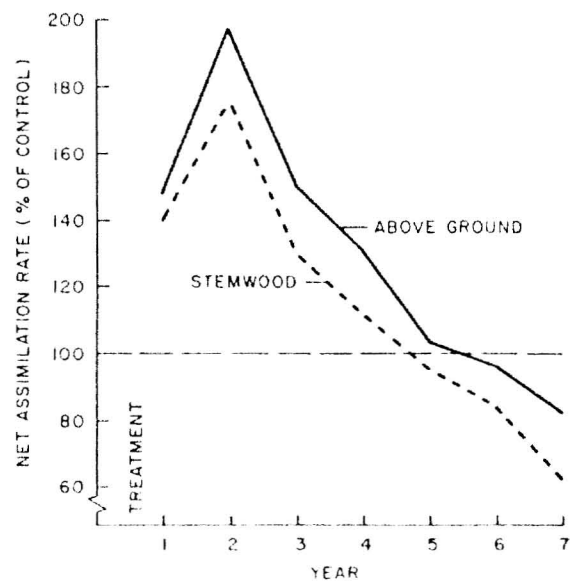these values is taken as aboveground tree uptake of N.

Treatment*	Biomass net N gain	Litterfall N content	Total N uptake	Total less control
ToFo	106	61	167	0
ToF2	133	91	224	57
T2Fo	128	30	158	-9
T2F2	191	38	229	62

* To and Fo: control; T2: thinned with 2/3 of basal area removed;
  F2: fertilized with 448 kg N/ha.

1

2

$Y = -8.3 + 124.7 X - 35.9 X^2$

$r = 0.59, n = 75, P < 0.01$

- 1975 DATA
- 1976 DATA
▲ 1978 DATA

3

4

T_0F_2 TREATMENT

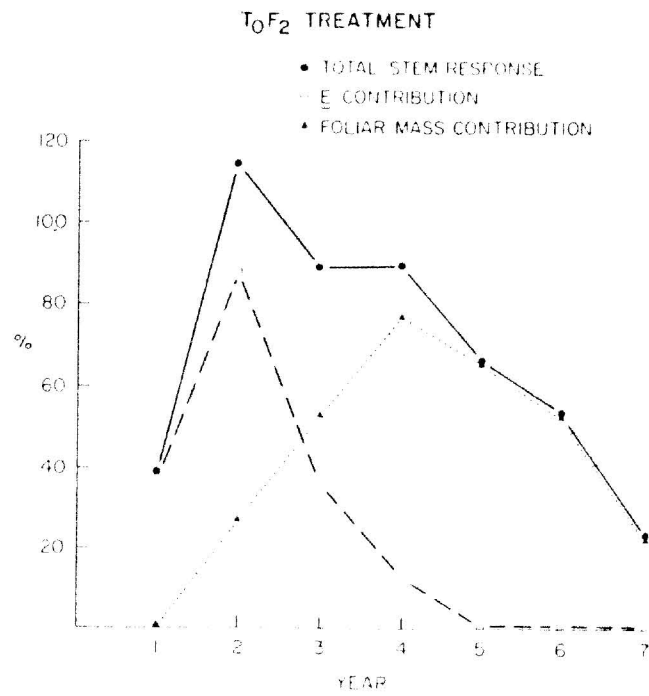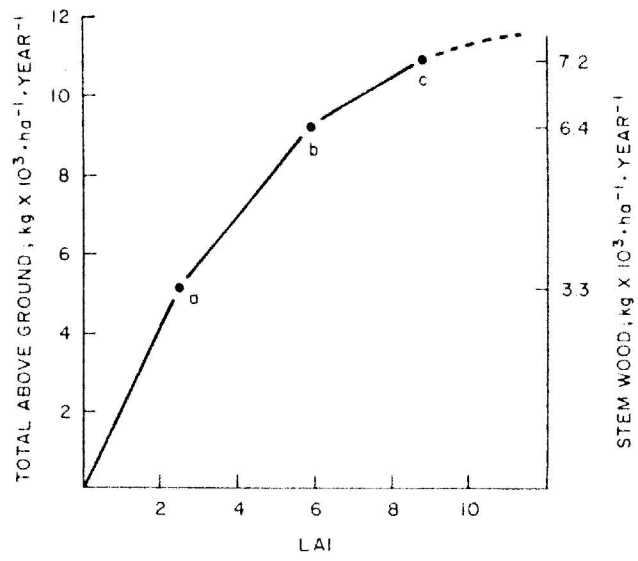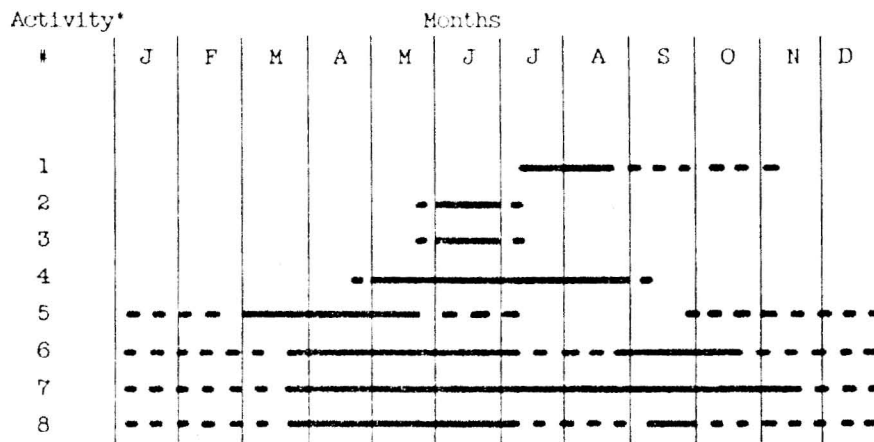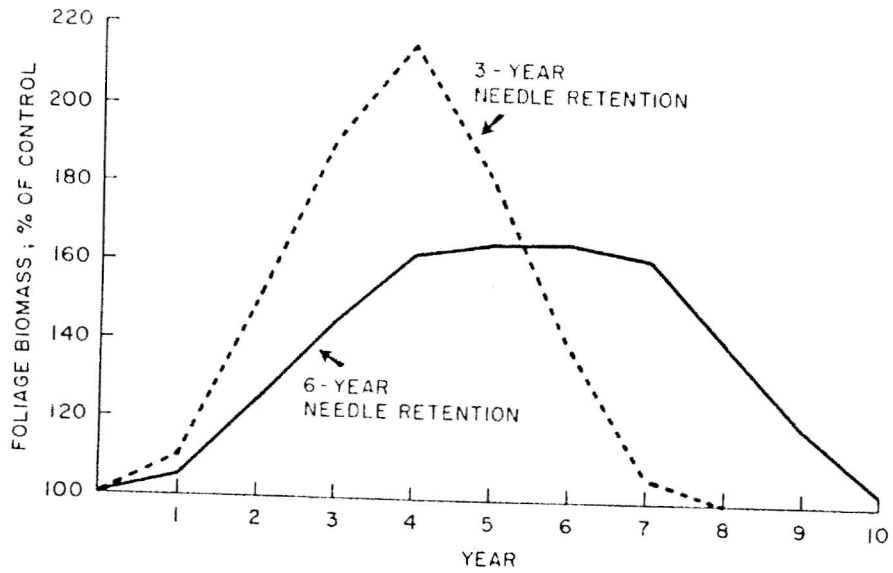- TOTAL STEM RESPONSE
- E CONTRIBUTION
- FOLIAR MASS CONTRIBUTION
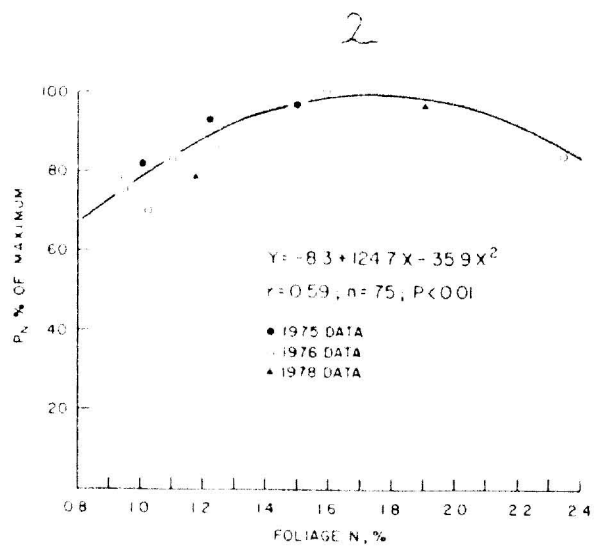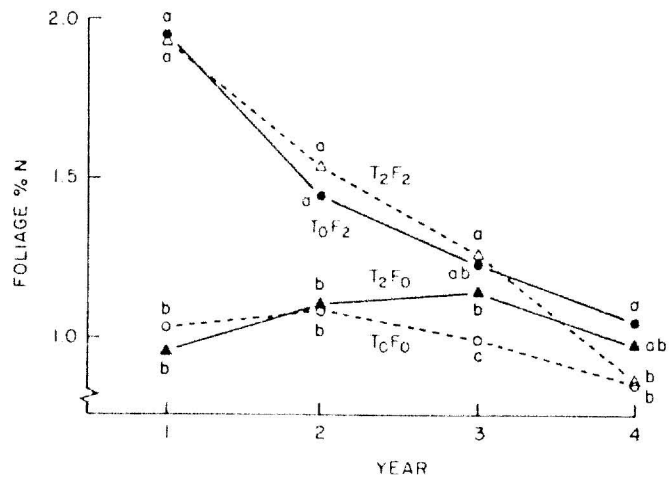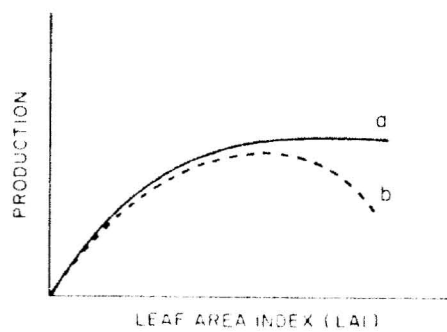
* 1: Initiation of needle primordia (Owens 1968)
  2: Shoot elongation
  3: Needle elongation
  4: Stem diameter growth
  5: Root growth (Kurz,Kimmins,in press)
  6: Photosynthesis
  7: Respiration
  8: Transpiration