Simulation Modeling of Growth and Nitrogen Dynamics in a Young Douglas-fir Ecosystem

by

Philip Jerome Riggan

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ABSTRACT

SIMULATION MODELING OF GROWTH AND NITROGEN DYNAMICS

IN A YOUNG DOUGLAS-FIR ECOSYSTEM

By Philip Jerome Riggan

Chairperson of the Supervisory Committee:

Professor Dale W. Cole

College of Forest Resources

A general theory of the control of nitrogen cycling and growth in a developing Douglas-fir plantation was formulated and investigated through field experiments and a simulation model. The theory consists of a set of hypotheses which characterize the control of individual processes in the ecosystem. Included are the following: Uptake rate per unit fine root is a hyperbolic function of soil ammonium concentration. Ammonium moves to the root surface by diffusion from sites of organic N mineralization. Ammonium absorbed by roots is transformed to free amino acids. N incorporation in tissue is primarily protein synthesis, which is positively related to the free amino acid-N concentration. It is most active in expanding and young age classes of foliage. Redistribution of N from old tissue to new is positively related to protein-N concentration and inversely related to free amino acid-N concentration. Growth of foliage consists of components for growth per shoot and the number of developing shoots. Both are

functionally related to new foliage N concentration. The number of developing shoots is additionally influenced by structural limitations on the branching pattern. Stem volume growth is functionally related to the number of developing shoots and the new foliage N concentration. Retention of foliage age classes is related to foliar N concentration.

These hypotheses were incorporated in a simulation model and function parameters and forms were developed from the literature and a series of field experiments. In these experiments, ammonium sulfate was applied to a seven-year-old, high-site-quality Douglas-fir plantation in a replicated block design with four application rates. Foliage growth was measured by whorl and position on a branch and statistical models describing the development of shoot length and needle weight were developed. Total N and free amino acid-N concentrations were measured throughout the growing season and early winter in new foliage. Change in N content for new and old foliage was estimated. Soil exchangeable ammonium and nitrate were measured. Exchangeable ammonium rapidly declines to the level of a control after approximately 120 days. Substantial nitrification occurred and evidence of stimulation of nitrification by previous fertilization is presented.

Volume increments were measured by stem analysis and a 20% reduction in growth occurred the second year following fertilization at high rates.

The simulation model developed from the general theory and field experiments describes N cycling and growth in a developing, N-deficient Douglas-fir stand. It was used to demonstrate the validity of the following system hypotheses:

1. Growth of nitrogen deficient Douglas-fir is determined by the supply of N to growing tissue. This supply is ultimately controlled by (1) current uptake, which is largely determined by the soil mineralization/immobilization rates, and (2) a homeostatic mechanism, redistribution, which integrates over past supply.
2. Following fertilization, the pattern of growth (over several years) is determined by factors controlling N supply to growing tissue. Response is determined by elevated uptake the first year and redistribution of accumulated N thereafter.

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INTRODUCTION

Growth and the nitrogen cycle in the Douglas-fir ecosystem

The productivity of forest ecosystems is contingent upon their ability to acquire and utilize nitrogen. In the Douglas-fir forests of the Pacific-Northwest, N fertilization has been shown to be an effective means for increasing growth and yield. This demonstrates a wide-spread, incipient deficiency of this element. Chlorosis associated with slow growth has also been observed, particularly in regenerating stands. This chlorosis may be indicative of more severe N deficiency.

N input to the forest ecosystem via precipitation and biological fixation is low in relation to amounts required for Douglas-fir growth (Cole et al, 1968). Consequently, the forest remains productive only through efficient use and the cycling of nitrogen among ecosystem components.

Most N in the ecosystem resides in refractory organic compounds with a long residence time. N is made available for uptake by vegetation and loss from the system when these compounds are decomposed to a soluble, ionic form. This release from organic material and cycling to an available form in the soil is slow. Nevertheless,

vegetation and microorganisms are able to actively absorb nitrogen from solutions of low concentration and accumulate appreciable amounts of N. The slow release from insoluble forms and efficient uptake by vegetation and microorganisms combine to maintain low levels of soluble N in the soil. These system-maintained low levels minimize N leaching losses and thereby function as a mechanism of nutrient conservation, but they make plant uptake more difficult.

Thus, the conservative nature of the N cycle (i.e., low rate of loss) is a systemic property, dependent on the individual transfer rates and processes that constitute this cycle. Indeed, the growth and yield of the forest may similarly be under systemic control. Under a different environment, with different rates of input and transfer, a different rate of growth would be expected.

Differences in the way forest stands cycle and accumulate N may be reflected in the amount and pattern of growth response to N fertilization. Nitrogen fertilization in forests commonly produces an increased growth rate, or response, that continues for a number of years following treatment (Gessel and others, 1969; Tamm and others, 1962; Wells and others, 1975).

The pattern of growth following fertilization typically shows a small, or zero increase the first year followed by larger increases (depending on site and stand characteristics) in subsequent years (Miller and Cooper, 1973; Tamm and others, 1962; Miller and Pienaar, 1973; Crossin and others, 1966). Growth in any year appears to be dependent upon physiological activity in buds produced the previous year, which may explain the lack of first-year response (Miller and Cooper, 1973).

However, some first-year growth responses following fertilization have been reported. In particular, foliar growth in the form of increased needle and shoot expansion has been measured in Douglas-fir following N fertilization (Turner and Olson, 1976). Such first year responses are expected to depend on the date of fertilization and subsequent precipitation. Also, first-year growth response may be relatively small and difficult to measure.

A maximum increase in growth rate (relative to an unfertilized stand) may occur within a few years of treatment. In Corsican pine, a maximum basal area growth rate occurred the third year of treatment when N was applied during the growing season for three successive years (Miller and Cooper, 1973). In low site quality (V)

Douglas-fir, peak responses have been measured three or four years following application of 150 kg N/ha. Maximum response occurred after five years with applications of 310 and 460 kg N/ha (Miller and Pienaar, 1973). Crossin and others (1966) presented data from several sites which showed different apparent patterns of height growth response. Depending on site conditions, height growth (1) peaked the third year following application and declined thereafter, (2) peaked the third year and continued undiminished, (3) showed a small but persistent response, or (4) did not respond.

It is uncertain whether a permanent change in growth rate for the stand or individual tree is effected. Duration of response may be defined as the period of time during which treated stand growth rate is greater than that of a control. It has been estimated at 7 to 9 years following fertilization of Douglas-fir on Vancouver Island (Crossin and others, 1966) and at over 10 years in southwest Washington (Miller and Pienaar, 1973). A more quantitative estimate has been made for nitrogen fertilization of Corsican pine (Miller, Miller, and Pauline, 1976). In this study, the time required for growth rates to return to that of the control was estimated from regressions of post-fertilization growth

versus time. For annual fertilizations of 84, 168, 336, and 504 kg N/ha (applied successively for three years), growth rates remain higher than that for a control for 6, 8, 9, and 11 years, respectively.

This observed change in growth response and duration with fertilization rate suggests that the pattern of response is contingent upon the way applied N is distributed and accumulated in the ecosystem. This in turn is a property of system transfers and their control.

Transfers between system components are often a function of the concentration or amount of N in those components. As examples, uptake is a function of the N concentration in the soil solution, while N mineralization in the forest floor increases with increasing amounts of litter and the litter N concentration. Individual transfers and rates may also be functions of the environment. Temperature and moisture may play important roles in this regard. For example, seasonality in nutrient uptake may be temperature controlled, while litter decomposition is strongly influenced by litter temperature and water content.

It may be inferred from systems theory that not all processes are equally important in determining the behavior of system components or the flux of N in the system. Yet no one process is expected to entirely regulate the flux. Consequently, hypotheses concerning the regulation of nutrient flux must be quantitative and consider the relative importance of processes. Since any component is ultimately (if indirectly) linked to every other component or transfer in the system, these hypotheses must be evaluated in the context of the system, not by examining individual steps in isolation. Now, what processes are expected to be important in regulating N flux in the system and, hence, growth and yield?

EXPERIMENTAL HYPOTHESES

N transported within the tree is directed toward areas of high metabolic activity, including growing tissue (Nommik, 1966; Mead and Pritchett, 1975b; Wallace and others,1954). In N-deficient Douglas-fir, this supply to growing tissue originates from both the uptake stream and redistribution from older tissue.

In unfertilized Douglas-fir, redistribution may supply 45% of the nutrients required by growing tissue (Turner, 1977). Under conditions of high uptake, such as following fertilization, N is accumulated in older tissue and may be used in growth during later years (Mead and Pritchett, 1975a). Thus, redistribution may act to maintain homeostasis in the N supply to growing tissue. If this is the case, it may be important in determining the amount and pattern of growth response to N fertilization.

The uptake stream may be characterized as a sequence of events including mineralization of organic N, transport to the root surface by diffusion or mass flow, and uptake across the root surface. Net mineralization in Douglas-fir stands is typically low in relation to the amount of organic N in the forest floor and soil; approximately 1%/yr (Heilman and Gessel, 1963). Also, uptake rate in untreated stands is high in relation to the amount of soil mineral N, which indicates a rapid flux through these forms. Transport to the root surface is thought to be similarly rapid. Therefore, mineralization is likely a limiting process.

On this basis, the following hypothesis is proposed.

1. In nitrogen deficient Douglas-fir, growth and yield are determined by the supply of N to growing tissue. This supply is ultimately controlled by current uptake and N redistribution from older tissue. The most important determinant of current uptake is the soil mineralization rate. The redistribution mechanism is homeostatic and integrates over past supply.

As a corollary to this hypothesis, the following is proposed.

2. Growth response to nitrogen fertilization will be determined by the physiological state of the stand and by factors controlling N supply to growing tissue.

(A) Response over the first several years will be determined by elevated uptake due to N application the first year and redistribution of accumulated N thereafter. The first year N uptake is sensitive to the soil ammonium immobilization rate.

(B) Since growth rates must be consistent with N supply to the tree, maintenance of elevated

growth for several years after fertilization is dependent on a long-term increase in forest floor or soil mineralization.

EXPERIMENTAL APPROACH

These hypotheses may be examined by direct experimentation or by simulation modeling. Experimentation is the most direct method but would have inherent difficulties. Considering the first hypothesis, the direct approach might follow an experimental design that compares uptake by genotypes that possess different N uptake characteristics (root affinity for N or maximum rate of absorption), on soils of different net mineralization rates. Given that the first hypothesis is true, the expected outcome is a tree uptake rate that differs more by soil than by genotype. Evaluating the homeostatic characteristics of the redistribution process would involve a design over several years time. It might include treatments with fertilization in the first of several years, at intervals, or in each year. In succeeding years with no treatment, the supply of N from older tissue to new must then be shown to be a function of stored N in the

old tissue, regardless of treatment. This functional relation must also show that N is supplied at a rate that is substantial enough to effect a prolonged, elevated growth rate.

Considering the second hypothesis, the direct approach must evaluate the proportion of the N supply (following fertilization) from mineralization, uptake of residual applied N, and redistribution for the duration of the growth reponse (assuming a finite response). Also, a long-term change in mineralization rate, if it occurs, must be shown to account for prolonged, increased uptake and growth relative to a control.

The largest problems with the direct approach are (1) coping with the large variance associated with different experimental plots, trees, and measurement techniques, and (2) the time (5-10 years) necessary to complete the experiment. It is also important that manipulations alter only the desired factor, a requisite that is difficult to achieve due to the interaction of processes.

The second approach is to evaluate the hypotheses via a simulation model. The model consists of a set of differential equations describing biomass and N dynamics in the system. It is formulated so that the important mechanisms controlling individual processes (or transfers) are included. It is necessarily limited by our knowledge of these mechanisms, but serves to illustrate the logical consequences of our formulation representing the real system. The validity of a hypothesis test is necessarily dependent upon the incorporated assumptions. Therefore, the model only needs to be plausible and not ultimately determined.

The simulation approach is ideally suited to testing hypotheses that consider the relative importance of processes, such as control of N flux in the system. As in the direct experimental approach, the sensitivity of Douglas-fir N uptake to (1) the characteristics of the root uptake mechanism and (2) the soil mineralization rate may be investigated. A similar experimental design is used, with simulations run for each treatment. Different treatments are represented by changing appropriate parameters in the model functions.

The model is also well suited to evaluating time trends, and the relative importance of N transfers as they affect growth and yield. Regarding the second hypothesis, a simulated fertilization will produce time trends of uptake, redistribution, and growth. The relative contribution of uptake and redistribution may be compared year by year and the duration and timing of response compared with experimental evidence. This analysis may lead to the rejection or substantiation of the experimental hypothesis.

In this dissertation, the above hypotheses will be examined by simulation modeling. A general model structure describing nitrogen cycling and growth as influenced by changing levels of N nutrition will be developed from the literature. This model will then be greatly extended and parameters estimated using data and hypotheses from field experiments conducted in a third-growth plantation of seven-year-old, high site-quality Douglas-fir. These experiments will measure rates of N transfer among system components following several levels of N fertilization. The functional relationships controlling individual processes and rates will be established. It is these relationships that will largely determine model

behavior. The experiments designed to address these relationships should have considerable bearing on our understanding of the autecology of Douglas-fir. The results from the field experiments and model will be discussed and the experimental hypotheses will be evaluated using appropriate model simulations.

GENERAL MODEL STRUCTURE

In order to evaluate the experimental hypotheses, the model structure must have the following features.

(1) It includes the components and transfers that are important in the N cycle.

(2) It describes the accumulation of organic material in the tree and forest floor.

(3) Growth of the tree and transfers of N are sensitive to changes in the amount of N cycling in the system.

(4) It describes changes in state variables (components) on a time scale appropriate to that of the processes involved.

In determining appropriate components, it is important that subdivision of the system not invalidate

the model by neglecting an important process. Yet subdivision should not reach a level of resolution that requires description of processes for which there is no information.

A model running on an annual basis would be inappropriate since important information may be lost. For example, distinct seasonality occurs in growth and N cycling. Also, concentrations in the foliage and soil may change rapidly over a period of days. The annual model might reproduce (via difference equations) nutrient budget data for a steady-state system, but it could not accurately describe transient changes in a real, growing forest.

The components and transfers in the model are shown in figure 1. Of particular importance are specifications of (1) a free amino acid-N component in the Douglas-fir, (2) transfers of N involving individual age classes of foliage, and subdivisions of (3) roots into fine and coarse components, (4) forest floor and soil N into organic and mineral components, (5) soil into zones within or outside the influence of absorbing (fine) roots, and (6) foliage growth into components for the number of new shoots and growth per

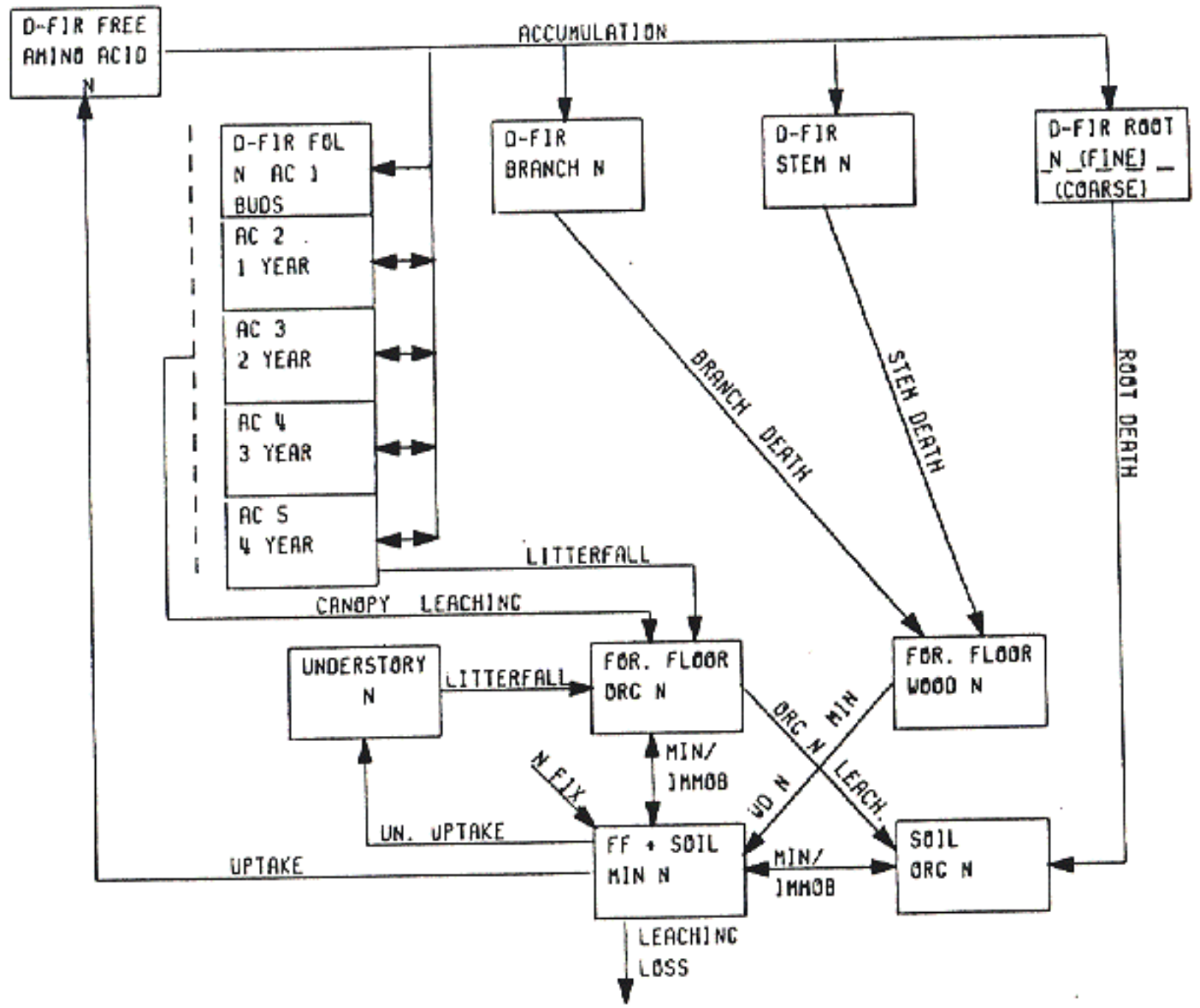


Figure 1. Simulation model flow diagram.

shoot. These features are necessary for an adequate description of the behavior of the system.

processes in the system that are functionally related to the levels of N nutrition and stand development include (1) N uptake by Douglas-fir, (2) net accumulation of N in new and old foliage, (3) growth, (4) litterfall, and (5) forest floor and soil net mineralization. The functional relations involved in each of these transfers will now be discussed.

Nitrogen Uptake

Plants are able to accumulate nutrients to internal concentrations greatly exceeding those found in soil. Thus, nutrient absorption moves ions against a concentration gradient. The mechanism of cation transport across the plasmalemma is not well understood, but there is general agreement on several features of the process (Bowling, 1976; Epstein, 1972). These features include (1) a hyperbolic concentration dependence (at low concentrations), which resembles Michaelis-Menten enzyme kinetics, (2) ion-specific carriers, with some ions showing competitive

inhibition, (3) expenditure of metabolic energy, and (4) an electropotential across the membrane.

N may be absorbed either as nitrate or ammonium ions (or urea following fertilization with that form). Affinities for these ions by Douglas-fir roots are similar (van den Driessche, 1971). The form used may depend primarily on that which is available. In a 43-year-old Douglas-fir plantation growing on glacial outwash soils at Cedar River, exchangeable ammonium and extractable (1N KCl) nitrate are 2.7 ppm and 0.04 ppm, respectively (D.W. Johnson, pers. Comm.). Therefore, ammonium is apparently the major form absorbed, although appreciable nitrification following fertilization (Heilman,1974) could result in increased nitrate uptake. Ebell (1972a) concurs that N uptake in Douglas-fir is primarily from the ammonium form.

The concentration-dependent uptake, UP, may be described by a Michaelis-Menten-type equation:

$$UP = \frac{Vmax*C}{(Km+C)}$$

where Vmax is maximum uptake, C is solution concentration, and Km is a constant representing the

concentration at which uptake is half of the maximum rate. Km is a measure of the affinity of the uptake mechanism for the absorbed ion (Km is inversely proportional to affinity). Values for Vmax and Km for Douglas-fir are not available, but Km was estimated at 0.21 ppm ammonium-N and Vmax was approximately 0.0025 gm N/day-gm root for Pinus radiata seedlings in solution culture (Flewelling, 1977).

This rate of absorption per root must be corrected for the absorbing root surface per tree to calculate tree uptake. This absorbing surface is likely the endodermal layer of the root. A correlative relation between the area of this layer and the surface area of fine roots is assumed. The development of fine root biomass with stand age or the influence of nitrogen upon root mass is not known for Douglas-fir. Fine root biomass (roots < 2 mm diameter) in Douglas-fir stands following crown closure is approximately one to two tons/ha (C.C. Grier, pers. Comm.). Fine root biomass may increase with fertilization. An increase in fine root (<3 mm diameter) biomass of 128% over a control was observed in 1971 in a beech-birch-maple stand following applications of N-P-K fertilizer in 1964 and 1969 (Safford, 1974). Such an increase is expected to

produce a prolonged exploitation of the soil volume. A parallel increase in uptake might not be achieved because of inter-root competition (Baldwin and others, 1972).

N uptake may be influenced by the diffusion rate of ammonium thru soil. By analogy to potassium, which has a similar diffusion coefficient in water (CRC Handbook), fine roots are expected to generate an ammonium depletion zone of approximately 3-5 mm (Farr and others, 1969). Inter-root competition would result if the depletion zones of adjacent roots overlap.

Approximately 80% of N absorbed by roots moves to the roots by diffusion (Ballard and Cole, 1974). Diffusion between cylindrical zones of soil around the root is proportional to the surface area of the zones, and the concentration gradient between them. The flux between two zones, F (gm N/day), is given by:

$$F= (C(i+1)-C(i))*2*Pi*r*L*D*VHC/dr$$

where D is the diffusion coefficient (cm^2/day), VHC is the volumetric water content (ml/gm), C(i) is the solution ammonium concentration for the ith zone (ppm), r is root radius (cm), L is root length, and dr is the radial distance between zones (cm).

Annual N uptake rates have been estimated for Douglas-fir as the change in N content over a one year period. These estimates require knowledge of growth rates, N concentration in new tissue, and the rate of redistribution from old tissue to new. Uptake in low-site-quality Douglas-fir is approximately 6 kg N/ha-yr in a 9-year-old stand and increases to approximately 20-30 kg N/ha-yr in stands older than 20 years (Turner, 1975). With N fertilization in a 42-year-old stand, uptake was 31 and 63 kg N/ha-yr at application rates of 220 and 880 kg N/ha (control uptake was 17 kg N/ha-yr)(Turner, 1977).

Foliage N

Rates of accumulation of N in new foliage through the year have been measured for Douglas-fir. Accumulation is high during the growing season and low or zero during the dormant season. (Ebell, 1972a). Rates of accumulaton are not as rapid as foliage expansion. Typically, N concentrations rise shortly before bud break, drop during rapid shoot growth, and change little thereafter (Ebell, 1972a). N resides in foliage primarily as protein-N. Thus, accumulation is

presumably the result of a net synthesis of protein. The rate of peak synthesis is expected to be timed with the period of most rapid foliage expansion (Loewenberg, 1970).

Fertilization generally results in large increases in foliage N concentration and content. The relation between N concentration in foliage and application rate for 25 to 33 cm dbh trees on fertilizer trial plots at Pilchuck, Washington shows increasing concentration with increasing application up to 440 kg N/ha. Application of 220 kg N/ha has resulted in an average increase in foliar N from 1.3% to 1.8% (data from Brackett, 1964; quoted by Gessel and others, 1969). In low-site stands at Cedar River, N concentration increased from 1.0% to 1.28% following fertilization at 220 kg N/ha (Turner and Olson, 1975).

Fertilization produces large changes in the concentration of free amino acids in foliage (van den Driessche and Webber, 1977a,b; Ebell and McMullan, 1970; Barnes and Bengston, 1968). The concentration increases (approximately 5 fold) may greatly exceed concurrent increase in total N (approximately 1.6 fold) (van den Driessche and Webber, 1977b).

During leaf senescence in deciduous trees, a large proportion of leaf protein and other cellular constituents are degraded to smaller, mobile compounds, such as amino acids and sugars. Mobilized compounds are translocated into phloem tissue and stored there and in roots (Taylor, 1967). Evergreen conifers have been shown via ^{15}N techniques to redistribute N from older to newer foliage (Mead and Pritchett, 1975a). Decrease in N content in older foliage has been assumed to be equivalent to this redistribution. A substantial amount of the supply to new tissue comes from this source (Switzer and Nelson, 1972; Krueger, 1971). In 42-year-old low-site-quality Douglas-fir, 45% of this supply is from redistribution (Turner,1977). N concentration in older foliage begins declining just before bud burst and continues to drop during expansion of new foliage (Krueger, 1971). Thus, redistribution is associated with foliage expansion.

Rates of change in N concentration in older foliage are affected by the state of nutrition in the tree. With fertilization, N accumulates in older foliage, while increased redistribution has been demonstrated in treatments designed to raise the C/N ratio of the forest floor and immobilize available N.

Estimated values of redistribution on plots with fertilizations of 880 and 220 kg N/ha, no treatment (control), and raised C/N ratios, were -13.0, 12.4, 14.0, and 22.4 kg N/ha-yr (Turner, 1977). Thus, as N becomes more available, net redistribution from older tissue appears to decrease.

In the second year following fertilization, N previously accumulated in older foliage is redistributed to new, expanding foliage. In slash pine, losses of 0.57, 0.90, and 1.24 mg N/needle in the senescing foliage age class were measured for control, 56, and 224 kg N/ha fertilizations, respectively (Mead and Pritchett, 1975a). The new foliage formed the second year had N contents of 1.5, 1.7, and 1.9 mg N/needle for these three treatments. Although a strict budget cannot be calculated from these data, if the number of needles is similar between the two years, then it is apparent that an increasing amount of the nitrogen in the second-season growth was acquired from the senescing tissue. Loss for a senescing needle was 38, 53, and 65% of the gain in new foliage in the control, low, and high nitrogen treatments.

Miller, Miller and Pauline (1976) examined the hypothesis that growth response after cessation of fertilizer application depend on N accumulated in the tree. They estimated uptake for the duration of the growth response as the difference between N accumulation and loss for the tree. The duration of response was estimated by regressions of basal area increment versus time. The amount of nitrogen necessary to maintain the growth measured in each treatment was then estimated by dividing stand uptake by the duration of the response. For the three-year applications of 84, 168, 336, and 504 kg N/ha, required mean annual uptake rates of 27, 27, 19, and 19 kg N/ha-yr were estimated. These values are similar to those measured on control plots. Therefore, fertilized trees do not require a larger supply of N from the soil than is supplied on control plots. Increased growth may be due to N accumulated within the tree during the years of fertilizer application.

Growth

The effect of changing nutrition upon growth may be assessed by foliage analysis (Steenbjerg and

Jakobsen, 1963). Foliage is a site of metabolic activity within the tree. Low concentrations of a nutrient element indicate a possible impairment of this activity.

Presumably, N nutrition affects growth via the synthesis of enzymatic protein (Epstein, 1972). N fertilization has been shown to increase levels of foliage protein in Douglas-fir (Ebell and McMullan, 1970). Empirical growth functions of foliar N concentration, G=f(%N), have been developed graphically for Douglas-fir. These functions show rapid increase in growth rate with increasing foliar N concentration until a maximum is reached. Above this point, growth remains high until at high concentrations a slight depression occurs (Ebell, 1972b). Using 5-year diameter increment following fertilization, Gessel, Stoate, and Turnbull (1969) have shown maximum growth to be achieved at a foliage concentration of approximately 1.7%. Ebell (1972b), using 6 levels of fertilization, has shown yearly radial increment versus %N in current foliage for each of four years following treatment. Maximum growth was achieved at approximately 2% N. Growth at 1% N was one-third of the maximum rate.

Foliage growth will respond to changing N supply. An increase in weight/needle may be observed the first year following fertilization. A 15% increase was observed following application of 220 kg N/ha in Douglas-fir at Cedar River (Turner and Olson, 1976). An increased number of growing shoots may result after the first year (Kozlowski, 1972; Brix, 1976).

Litterfall

Several factors affect the return of nutrients to the forest floor via litterfall. These include (1) the length of retention of foliage age classes in the canopy, (2) size of the senescing foliage age class, and (3) nutrient concentration in the litterfall. All three factors are influenced by the level of N nutrition.

The first year following fertilization in a 42-year-old Douglas-fir stand at Cedar River, litterfall decreased, implying an increase in canopy needle retention, and litterfall N concentration increased (relative to a control). In subsequent years, litterfall increases as the larger-biomass

foliage age classes senesce (Heilman and Gessel, 1963). Treatment designed to immobilize soil available N resulted in increased litter mass and decreased N concentration (Gessel and Turner, 1976).

Following fertilization in Corsican pine, increasing rates of N application have led to increasing rates of litterfall and nitrogen transfer in litterfall over a six year period (with fertilizer applied over the first three years). The first year of treatment, litterfall decreased with increasing application rates and in subsequent years litterfall weights increased to over twice the control. The sixth year following initial application, litterfall weights showed no sign of returning to the level of the control. This is partly a reflection of needle weights over this period, which increased with increasing application rates and show, for higher rates of application, no detectable decline towards control levels (Miller, Cooper, and Miller, 1976).

In the same experiment, N concentration in autumn litterfall was closely related to N concentration in top-whorl foliage the previous October (Miller, Cooper,

and Miller, 1976). Top-whorl foliage N concentrations increased with increasing application rates and reached maxima during the last year of fertilization, declining thereafter (Miller and Cooper, 1973). Thus, litterfall N concentration may peak one year following cessation of application.

Mineralization / Immobilzation

Mineralization / immobilization processes are influenced by the amounts of available N and carbon. N mineralization and immobilization are opposing processes. The former is the decomposition of organic N to ammonium and the latter is the incorporation of ammonium into microbial tissue. Following the terminology of Bartholomew (1965), net mineralization is defined as the net release of ammonium from these processes while net immobilization is the net decline in ammonium and increase in organic N. Bartholomew (1965) has reviewed the agricultural literature concerning the mineralization and immobilization processes and makes the following points.

(1) When fresh residues are added to soil, a rapid change (four weeks) in mineralization / immobilization

occurs, after which change is slow irrespective of initial N content.

(2) The direction of the process (towards net formation of inorganic or organic N) depends on whether N is present in excess of the needs of the microbial population.

(3) The initial, rapid population bloom of microbes in fresh residue is followed by a gradual decrease as available food supplies are depleted. Net immobilization does not decline as rapidly.

(4) Plant protein is largely or totally decomposed; compounds resistant to decay are formed by microbes using the liberated inorganic N. Microbial protein becomes associated with products of the plant decomposition, possibly polyphenols. This renders the N relatively inaccessible to further mineralization.

(5) Addition of N fertilizer will lead to increased net immobilization when N is limiting to the development of the decomposing microflora.

(6) Soil organic N and newly immobilized N are mineralized at approximately 2 t0 10% per year.

Net immobilization may be strong in forest litter. Cromack and Monk (1975) show first-year N loss from hardwood litter to be only 12%, while no significant

loss occurred for white pine litter. Percentage weight losses for these two litter types were 50% and 37%, respectively.

In comparison with agricultural residues showing net immobilization (Bartholomew, 1965), Douglas-fir litter has a low N concentration and might be expected to show initial immobilization of inorganic N. Fogel and Cromack (1977) show net immobilization of N in decomposing, green Douglas-fir needles over two years time, while weight loss was 35%.

Net rates of mineralization in forest floor and soil in Douglas-fir stands at Cedar River may be calculated from estimates of plant uptake, leaching loss, and the proportion of uptake from roots in the forest floor (Turner, 1975). Mineralization from forest floor material with a content of approximately 200 kg N/ha is 13 kg N/ha-yr. Soil mineralization is 14 kg N/ha-yr from a pool of 2400 kg N/ha.

Applied N may be rapidly immobilized in forest soils (Chu and Knowles, 1966). In Douglas-fir stands at Cedar River, exchangeable ammonium concentration two years after fertilization is only a few ppm higher than

control levels (2 ppm) (D.W. Johnson, pers. Comm.). Applied urea fertilizer is largely accounted for in the organic matter of upper soil horizons (Heilman, 1961; Crane, 1972).

The general functional relations between process rates and the level of nutrition may now be summarized.

(1) Uptake rate per unit fine root is a hyperbolic function of soil solution ammonium concentration.

(2) Diffusion of ammonium to the root is proportional to fine root surface area and the concentration gradient that develops around the root.

(3) Accumulation of N in newly formed tissue is low or zero during the dormant season and maximum during rapid growth. It represents a net synthesis of protein from free amino acids, and increases with fertilization. Thus, a functional relation between accumulation and free amino acid concentration is hypothesized.

(4) Redistribution from older to newer foliage is associated with foliage expansion. It increases under conditions of N stress (lowered supply). Accumulation in older foliage occurs with fertilization. Redistribution increases during the year following fertilization. The redistribution from older tissue and the accumulation in that tissue may be viewed as a

net degradation and synthesis of protein, respectively. It is assumed that N release during protein degradation is proportional to protein-N concentration and N incorporation during protein synthesis is proportional to free amino acid-N concentration. Fertilization would produce increased uptake, free amino acid concentration, and accumulation of N in older foliage. Decreased uptake is expected to result in lowered amino acid concentration and loss of N from older foliage. In the year after fertilization, uptake and amino acid concentration will decline and N content in old foliage will be higher than during the previous year, favoring N loss from older foliage.

(5) Foliage growth has two components; growth of individual shoots and production of shoots. Both are increased with increasing foliage N concentration until a maximum is reached. Thereafter, a slight decline may occur.

(6) Litterfall is comprised of approximately one age class of foliage. Increased N supply results in more retention, while decreased N supply produces less retention. Fertilization results in a transient increase in retention with lower litterfall the first few years. As the larger foliage age class reaches its life expectancy, litterfall increases. A return to

pre-fertilization conditions indicates a similar reduction in retention, which would increase litter production.

(7) Mineralization from fresh litter is expected to be proportional to the amount of litter, and to follow an approximately exponential trend with time. Immobilization of applied N is expected to be rapid and proportional to soil exchangeable ammonium.

In order to evaluate the experimental hypotheses, the processes summarized above must be quantified, the form of the functional relations established, and equation parameters must be estimated. An experiment was designed to manipulate a young Douglas-fir stand by N fertilization to achieve these goals.

EXPERIMENTAL DESIGN

An experimental design was established to produce a series of different nutritional regimes by N fertilization at several application rates. In this series, rates to be estimated include (1) immobilization of applied N, (2) nitrate accumulation in soil, (3) N uptake by Douglas-fir, (4) accumulation

of N in new and old foliage (including redistribution), (5) accumulation of free amino acid-N in new foliage, and (6) growth of foliage, branches, and stem.

Variation between plots within a hectare was thought to be due to differences in stand structure rather than micro-environment. Therefore, measurements were made on individual trees. Remeasurement of experimental units (trees, branches, shoots) was made wherever possible to reduce variance, with the intention of employing analysis of covariance techniques.

Site selection and treatments

The primary criterea for site selection were (1) young trees, (2) a well stocked stand, and (3) a fine-textured soil with a minimum of rock. Young trees were desired so that processes in a developing stand could be assessed. Also, in a young stand, complete occupancy of the site might not have been acheived and, hence, the stand may function more as a set of individuals. The trees must be small enough to allow convenient repeated measurement of shoot extension and

collection of foliage samples, yet large enough to sustain repeated foliage collection without overly affecting growth. A fine-textured soil was desired to minimize summer-drought effects and facilitate soil sampling.

These criterea were met by a third-growth Douglas-fir plantation at the Weyerhaeuser Company's Snoqualmie Falls Tree Farm, near North Bend in western Washington. The site is located on nearly level terrain of south-facing aspect, at an elevation of 260 m, in sec. 21, T.24N., R.8E. The soil is a Tokul series, classified as an Entic Xeric Durochrept, developing from glacial till plain deposits overlying an indurated basal till. At nearby Snoqualmie Falls, mean annual temperature is 11.2 degrees C., and mean annual precipitation is 155 cm. The indurated basal till retards water movement below approximately one meter soil depth, and maintains moist soil conditions during the summer drought.

The site index is high; approximately 150' at 50 years. From regional N fertilizer growth response trends, a reduced (from the regional mean) but positive response might be expected (RFNRP, 1976). Mean tree

height at age 7 is 5.8 m, and mean dbh is 8.2 cm. Use of such a high-site-index stand was expected to establish maximum rates for many of the processes investigated.

Treatments were applications of 100, 200, 400, and 600 kg N/ha as ammonium sulfate. These rates were chosen to give both a broad range and small increments between treatments at low rates, so that the form of functions could be established. Ammonium sulfate was chosen so that ammonium would be directly applied, without the pH change or volatilization loss associated with urea, or possible leaching loss associated with nitrate.

Four blocks were established with five plots per block. Plots were of a size that would encompass 6-8 trees per plot, avoiding only obvious openings in the stand or areas of poor stocking. Plots are .003-.005 ha, within a total study area of approximately one hectare, and are a minimum of 5m apart.

Three blocks were treated 5/18/76 to 5/21/76. One block remained untreated. Treatments were randomized within each block. Application was by hand spreading,

with one-quarter of a plot treated at a time to better insure uniformity. One block was refertilized at 400 kg N/ha on 6/2/77. Also at that time, the untreated block had two plots fertilized at 400 kg N/ha, two plots treated with 50 lbs sugar (5/25/77) to raise the C/N ratio and immobilize soil available N, and two plots maintained as controls.

Foliage sampling

Expanding new shoots (1976) were sampled to determine their length, needle dry weight, and N concentrations. Two trees from block 3 were sampled in each of four whorls (referred to hereafter as the intensive sample). An additional two trees in each plot of block 2 and four trees in each plot of block 4 (simple sample) were sampled in the 1973 whorl only (four whorls from the top of the tree).

The following shoot terminology was devised. Lateral shoots expanding at the distal end of a branch (from the base of the terminal leader) are "B laterals". Shoots expanding from a subbranch that formed (as a B lateral) the year before are "C

laterals", and so forth (figure 2). For modeling purposes, positions of new shoots on a branch will later be referenced by their position from the branch base (1,2,3,...) Rather than the tip (B,C,D,...).

Shoot expansion

Expansion of 1976 shoots was measured by whorl and position for two branches per whorl, on six dates during the growing season. The lengths of shoots in prescribed locations were remeasured on each date. Shoots were selected on each branch to encompass a range of expected final lengths. Lengths were measured from the base of the shoot to the base of the new terminal bud on that shoot (if formed).

For the intensive sample, shoots were measured in whorls initiated in 1972, 1973, 1974, and 1975. In each whorl, for two branches, the terminal leader was measured, two B laterals were measured in whorls 1975, and 1973, and three B laterals and four C laterals were measured in whorls 1974, and 1972. For the simple sample, the terminal and two B laterals were measured in the 1973 whorl.

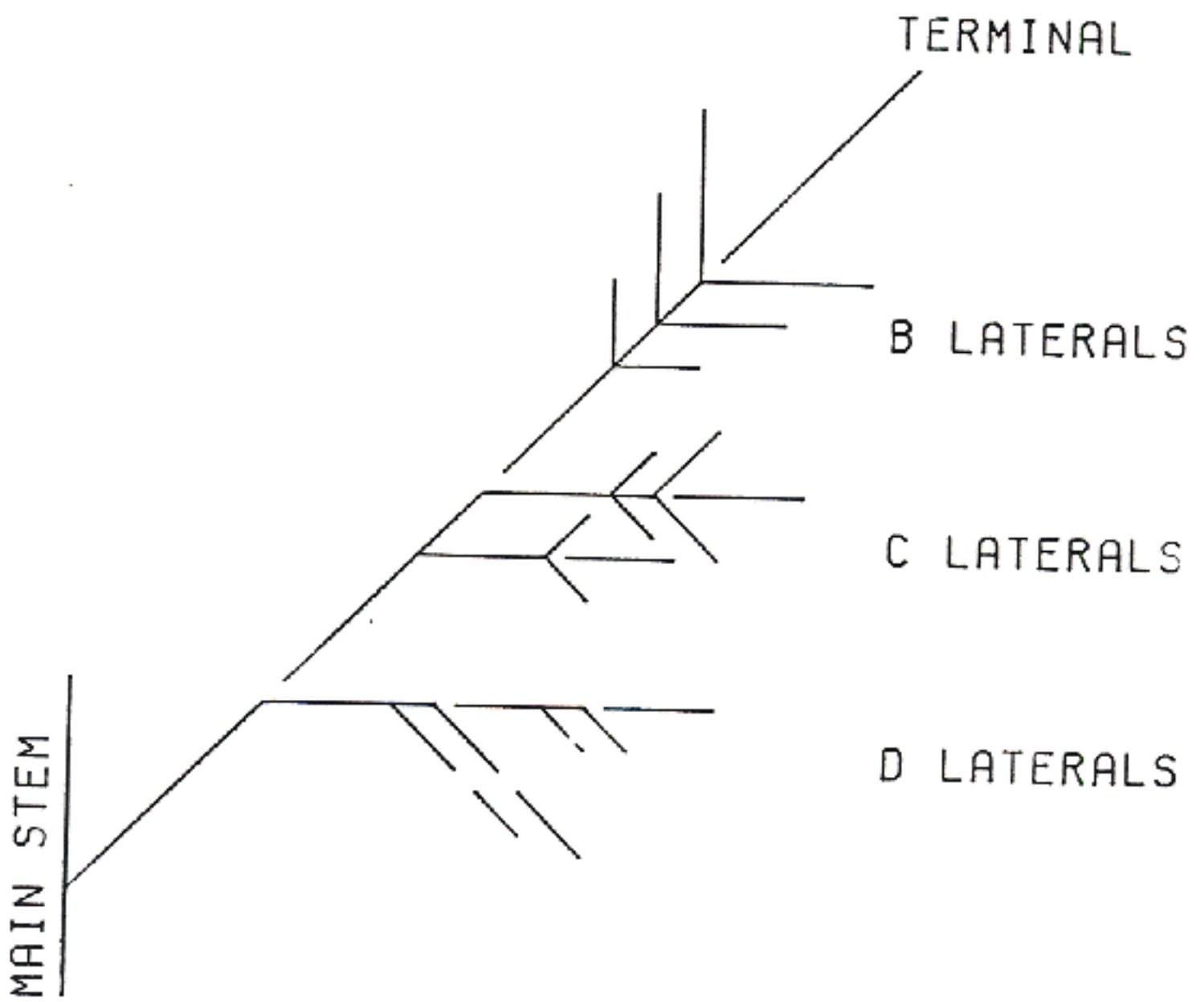


Figure 2. Shoot nomenclature.

Shoot dry weight and N concentration

For each whorl, position, and date that shoot lengths were measured, ten shoots were collected from branches other than those bearing the shoot length sample. For each collected shoot, length was measured, new buds were counted, and all needles were removed, dried, and weighed. Regressions of needle dry weight versus shoot length were computed. N concentration was determined for each measurement tree and date from these foliage samples.

Soil sample collection

Samples were collected at 0, 19, 34, 58, 84, 118, and 180 days following fertilization (1976) on all plots of blocks 3 and 4. Soil was sampled with a 2.5-cm diameter soil corer to a depth of 15 cm. Six composite samples composed of five cores from each of five randomly selected locations were collected from each plot (30 cores / plot). These composite samples were used for chemical analyses.

Laboratory methods

Needles were removed from stems and dried for 24 hours at 75 degrees C before analysis. Total N in both foliage and soil samples was determined by a modified Kjeldahl procedure (Parkinson and Allen, 1975). For foliage, 0.4 gm dry weight was digested with 5 ml of a solution made by combining 350 ml of 30% hydrogen peroxide, 0.42 gm selenium powder, 14 gm lithium sulfate monohydrate, and 420 ml concentrated sulfuric acid. Samples were made to volume and analyzed for ammonium on a Technicon auto-analyzer II.

Free amino acids were determined on samples collected from the 1974 whorl for sample trees from each treatment. Samples were collected at approximately 1:00 PM each sample date to minimize variance associated with diurnal fluctuations. Needles were removed from shoots and frozen with liquid nitrogen in the field. They were stored in polyethylene bottles at -20 degrees C until analyzed. Before analysis, needle samples were ground with liquid nitrogen in an inert mortar and pestle, with a sample removed for determination of water content. Approximately 0.05 gm fresh wt was extracted with 15 ml

of 60% ethanol for one-half hour. One ml aliquots were used for the determination using aspartic acid standards and the ninhydrin procedure of Yemm and Cocking (1955). Standards and unknowns were analyzed on a Bausch and Lomb spectrophotometer.

For analysis of soil exchangeable ammonium and nitrate, soil samples were sieved through a square-mesh 2 mm screen and stored at 2 degrees C until analysis (usually within 2 weeks). Little immobilization or nitrification of ammonium occurred under these storage conditions. An approximately 12 gm fresh weight sample (approximately 8 gm dry weight) was weighed into a 50 ml centrifuge tube. 25 ml of 1N KCl was added, the sample was shaken, centrifuged, and the supernatant decanted through a glass wool plug into a 100 ml volumetric flask. The KCl addition, centrifuging, and filtering was repeated twice with pooling of the supernatant. The combined extracts were made to volume, filtered through glass fiber filter paper and analyzed for ammonium and nitrate on a Technicon Auto-analyzer II.

RESULTS FROM THE FIELD TESTS

Shoot expansion and foliage growth

Measurement of growth as the change in foliage dry weight through the growing season requires destructive sampling. Repeated random sampling would be an insensitive method since a large variance is associated with different shoots at any given time. However, a good estimate of growth is obtained if some other factor associated with this growth is measured repeatedly on the same shoots, and dry weight of the needles is correlated with this factor. Shoot length, L, may be measured without injuring the shoot and it was hypothesized that wt./shoot would be highly correlated with length. Therefore, to estimate growth, shoot length was measured through the growing season on the same sample of shoots. Shoots were randomly selected from a range of positions, whorls, and trees. On separate samples, dry weight of needles per shoot, DW, was measured and regressions of DW=f(L) determined. Length as a function of time, L=f(t), and DW=f(L) may then be combined by position, to give estimates of DW=f(t). These are then weighted by the number of shoots in each position to give DW=f(t) for an average shoot on the tree.

Shoot L=f(t) may be modeled with a sigmoid-shaped Chapman-Richards function (Pienaar and Turnbull, 1973) of the form

$$L(t) = A(1+b*\exp(-kt))^{(1/(1-m))}. \quad [1]$$

The differential form of this function is

$$dL/dt = (k/(1-m))*(A^{(1-m)}*L^{m}-L).$$

In these functions, t is time, A is the asymptotic maximum value, $m^{(1/(1-m))}$ is the fraction of A attained at the inflection point, k is a constant that affects the shape of the curve, and b=exp(k*t0) is an integration constant affecting the position of the curve along the X (time) axis. K/m is the growth rate at the inflection point. Ak/(2m+2) is the mean growth rate.

The intensive sample shoot data were fitted (for each shoot) to the integral form and parameters were examined for differences by position, whorl, and treatment. The positions were branch terminals, B laterals, and C, D, and E laterals combined (referred to hereafter as C laterals).

[1] Exponentiation to base e is represented as exp in these equations.

The parameter A is equivalent to final shoot length and is measured. The data were first fitted with a third-degree polynomial, differentiated twice, and set to zero to solve for the inflection point. M was then estimated from the values for the inflection point and the maximum, via the above relation. The data were then fitted using a linear regression to a transform of the integral form given by

$$\ln(1-(L/A)^{(1-m)}) = \ln(b)-k*t$$

The parameter estimates obtained are biased with respect to the original data, so refined estimates were obtained using non-linear regression (Taylor's series with iteration)(Draper and Smith, 1967).

No trends in the parameters by treatment were evident. No trends in either m or b by whorl or position were apparent. Mean values are m=2.9 and b=127. A Wilcoxin rank sum test across whorls for differences in parameter k by position (A, B, or C) shows $k(A) < k(B)$ and $k(B) < k(C)$. Mean values by position were $k(A)=0.104$, $k(B)=0.130$, and $k(C)=0.148$. Also, k for positions A and B was greater in whorl 1972 than in whorl 1973 .

With m constant among positions, k/m (which is the growth rate at the inflection point) is greatest in less dominant positions and in the lowest measured whorl. This accounts for the observation that position C shoots attain their maximum extension before position B or A shoots.

No differences in final shoot length, A, were evident by treatment.

The shoot length distributions for a given position are skewed to the left, with the most common B position length approximately 7-8 cm. The length distributions for B positions are not stochast.cally different by whorl, as tested by a Kolmogorov-Smirnov two-sample distribution test. The C positions are different (alpha=.01) and shoot lengths in whorl 1972, position B are greater than those in whorl 1974, position C (72B>74C). Therefore, the length distributions by whorl and position may be ranked in the order: 75B=74B=73B=72B>74C>73C>72C.

Values of the relative growth rate at the time of the inflection point, k/m, for shoots in whorl 1974 position B and whorl 1974 position C are 0.045 and

0.051, respectively. The mean growth rates, Ak/(2m+2), for whorl 1974 position B and C are 0.195 and 0.167, respectively. Therefore, B laterals approach their maximum extension more slowly than C laterals, but grow at a higher rate.

Dry weight as a function of length

Simple linear regressions of DW=f(L) were computed by whorl, position, tree, and time. With a linear model, a reasonable fit to the data was apparent given the small sample size (10) per regression, but a consistent pattern was not evident in comparing regressions by time. Grouping the data across time reveals a single sigmoid-shaped trend. Therefore, the data were fitted by tree, position, and whorl using a third-degree polynomial model of the form

$$DW = B1(L)+B2(L^2)+B3(L^3).$$

For this model, regression coefficients are different from zero, and the model was adequate. The models should not be extrapolated beyond the data due to the inherent nature of the polynomial model but are adequate for describing the function within the range of the measured data.

A consequence of the model is that a shoot of given length will bear a particular weight of needles regardless of state of development. A model developed from shoots of different lengths collected at the end of the season would suffice for prediction of DW from lengths measured earlier in the growing season.

No trends in the DW=f(L) models were apparent by treatment. Therefore, the data were pooled across trees and refitted by whorl and position.

Analysis of covariance on the seven models by whorl and position shows significant differences exist among the models (table 1). Evaluating the models for intermediate shoot lengths (20 cm) gives expected values of wt./shoot in the order 75B>74B>74C=73B>72B=72C where, for example, 75B represents shoots in the 1975 whorl, B position (figure 3). Thus, shoots of a given length in upper whorls and B positions generally bear a larger weight of foliage than those in lower whorls and C positions.

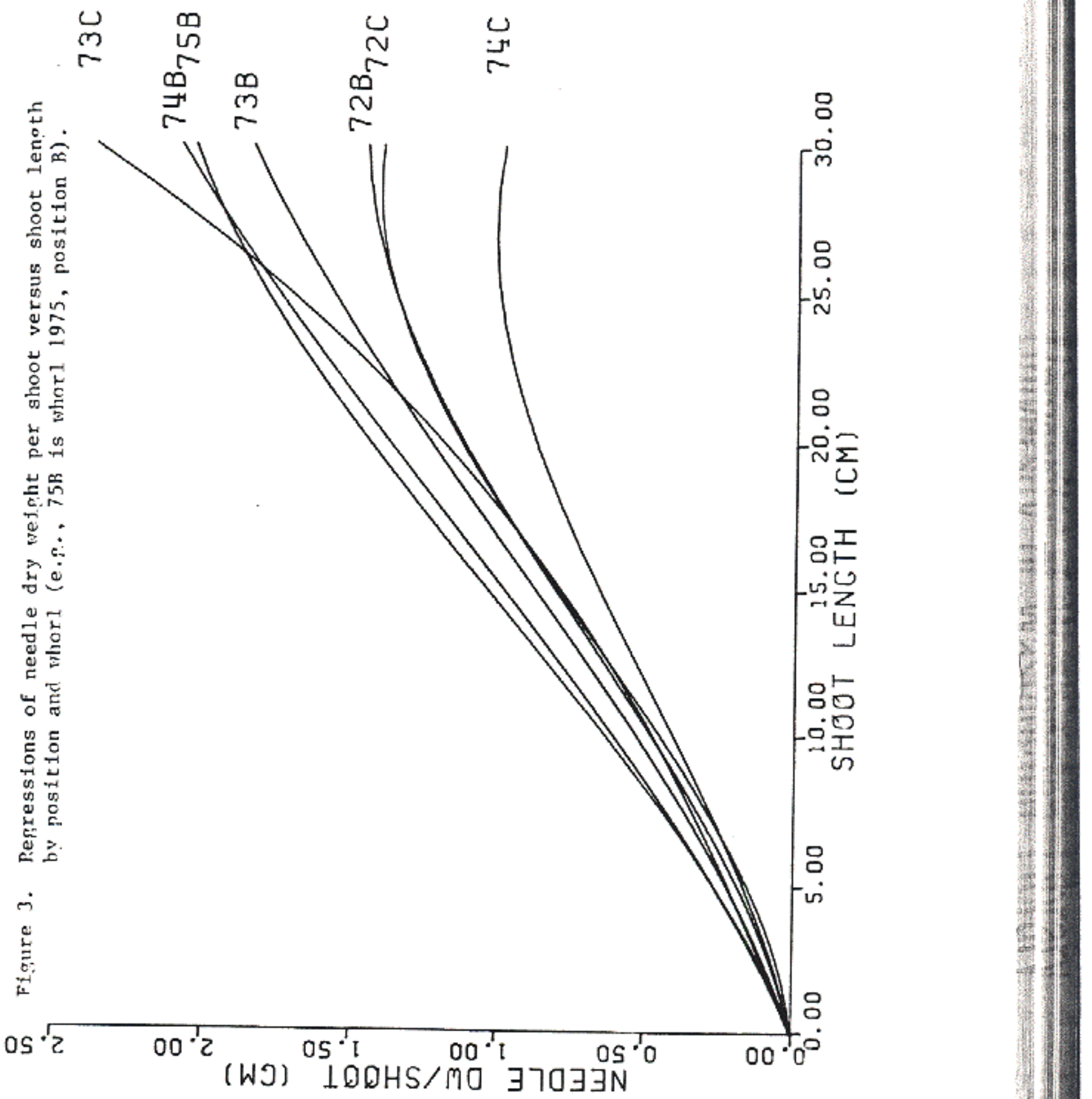


Figure 3. Regressions of needle dry weight per shoot versus shoot length by position and whorl (e.g., 75B is whorl 1975, position B).

Table 1. DW=F(L) regression model by whorl and position.

Regression coefficients

Position	B1	B2	B3
75B	4.011E-2	2.967E-3	-6.806E-5
74B	4.331E-2	2.051E-3	-3.940E-5
74C	2.203E-2	3.502E-3	-7.134E-5
73B	3.361E-2	2.331E-3	-4.684E-5
73C	4.143E-2	1.938E-4	3.515E-5
72B	2.243E-2	3.278E-3	-8.034E-5
72C	1.084E-2	4.423E-3	-1.076E-4

Analysis of variance (ANOVA) for the null hypothesis, H0:no difference among models.

Source	df	ss	ms	
total	932	2355		
regr (full)	21	2254		
(reduc)	3	2233		
hypothesis	18	21	1.17	
residual	911	101	.11	
				F=10.52 reject H0

Dry weight/shoot as a function of time

The regressions for weight/shoot as a function of length, DW=f(L), length as a function of time, L=f(t), and the final length distributions may be combined by whorl and position to give a combined model for weight/shoot through the growing season for the tree, DW=f(t). The equations must be evaluated for a representative sample of shoot lengths, since evaluation for a mean length does not yield a mean weight value. The L=f(t) models were evaluated for every new shoot in the intensive sample (2 branches/whorl, 4 whorls/tree, 10 trees = 6636 shoots) for t= day 150, 165, 180, 195, 210, 225, and 240. The DW=f(L) models were then evaluated for each of these values. The resulting weight/shoot values were then summed by position and whorl for each date and a mean weight/shoot was calculated. These data were then fitted with the Chapman-Richards equation using non-linear regression (table 2, figure 4).

The parameters m, b, and k are similar across whorls for both B and C positions. Mean maximum weight/shoot, A, varies greatly between positions and whorls in the order 75B>74B>73B>72B=74C>73C>72C. Mean

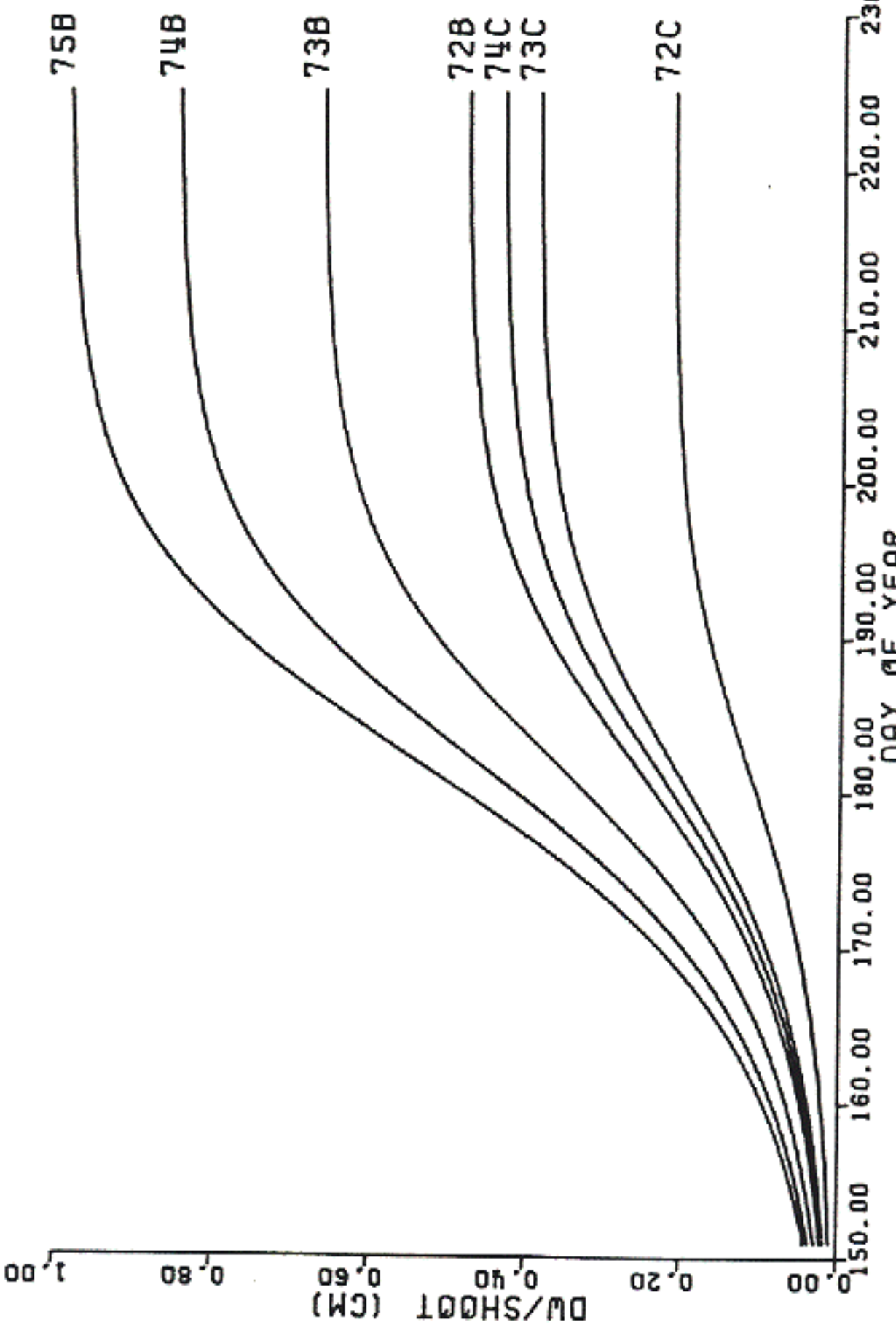


Figure 4. Regressions of needle dry weight per shoot versus the day of the year by position and whorl.

relative growth rates, k/(2m+2), are approximately equal among C positions and among B positions. They are 16% higher for the C positions than for the B positions, indicating the former group reaches a maximum weight/shoot faster.

Table 2. DW=F(t) model parameters by whorl and position. K=-.142 m=2.51 b=139.

Position	Max wt/shoot, A (cm)
75B	0.988
74B	0.848
74C	0.433
73B	0.664
73C	0.388
72B	0.479
72C	0.214

Mean number of new shoots by whorl and position

Considering the 1972 through 1975 whorls, the number of new shoots increases with decreasing whorl, that is, there are more new shoots in lower whorls of the tree (table 3). The proportion decreases: 3.8

times as many shoots are in whorl 74 as in whorl 75, 1.8 times are in 73 as in 74, and 1.2 times are in 72 as in 73. The largest proportion of new shoots are in inferior branch positions (lower subbranches) in lower whorls.

Table 3. Number of new shoots on a branch by position. Mean and standard deviation by tree (n=20).

	Whorl			
position	75	74	73	72
B	18 (4.)	20 (3.)	15 (2.)	13 (2.)
C+D+E		49 (17.)	112 (39)	137 (36)
total	18	69	127	150

Tree dry weight/shoot model

Weighting each maximum dry weight/shoot from the DW=f(t) models with the proportion of shoots in each whorl and position, gives a mean value of 0.40 gm/shoot for the tree. An independent estimate of weight/shoot for the tree may be obtained from the total needle weight of 6253 shoots from the ten tree intensive sample. With a total weight of 2576 gm, mean weight/shoot is 0.41 gm. This value closely agrees

with the above estimate of 0.40 gm.

The derived weight/shoot data used to compute the DW=f(t) models were weighted by the proportions of shoots by whorl and position for each date and fitted with the Chapman-Richards equation. This gives values of m=2.51, b=139., and k=0.142 for a weight/shoot model for the entire tree. Thus, expected mean weight/shoot, DW, is given by

$$DW=0.40(1+139.\exp(-0.142t))^{1/(1-2.51)}$$

where t is the number of days since the beginning of the growing season, day 150.

Proportion of foliage weight by age class and whorl

The distribution of foliage in the canopy was examined with data from four trees that were destructively sampled, with all foliage separated by age class and whorl (table 4). The fraction of the foliage in the most recent age classes is high; 41% is in the 1976 age class and 36% is in the 1975. Increasing weights from older to younger age classes may reflect the expanding branching pattern in the young tree and litterfall loss from older age classes.

The increase in the number of shoots with tree age follows an approximate power function (figure 5). This function is given by $SHN=8.62(AGE)^{3.62}$, where SHN is shoot number and AGE is tree age in years. Little foliage is lost from the two most recent age classes, while increasing amounts are lost from age classes 1974 thru 1971.

Table 4. Foliage dry weight by age class and whorl.

	Age class					
whorl	76	75	74	73	72	total
76	44					44
75	208	36				244
74	371	148	9			528
73	597	556	145	0		1298
72	253	1518	227	73	0	941
71	121	251	222	170	38	802
total	1594	1379	603	243	38	3857
fraction in an age class	.41	.36	.16	.06	.01	

The fraction of new foliage weight in a whorl increases almost linearly from the 1976 whorl to a maximum in the 1973 whorl, declining thereafter (figure 6). This follows increasing branching and number of

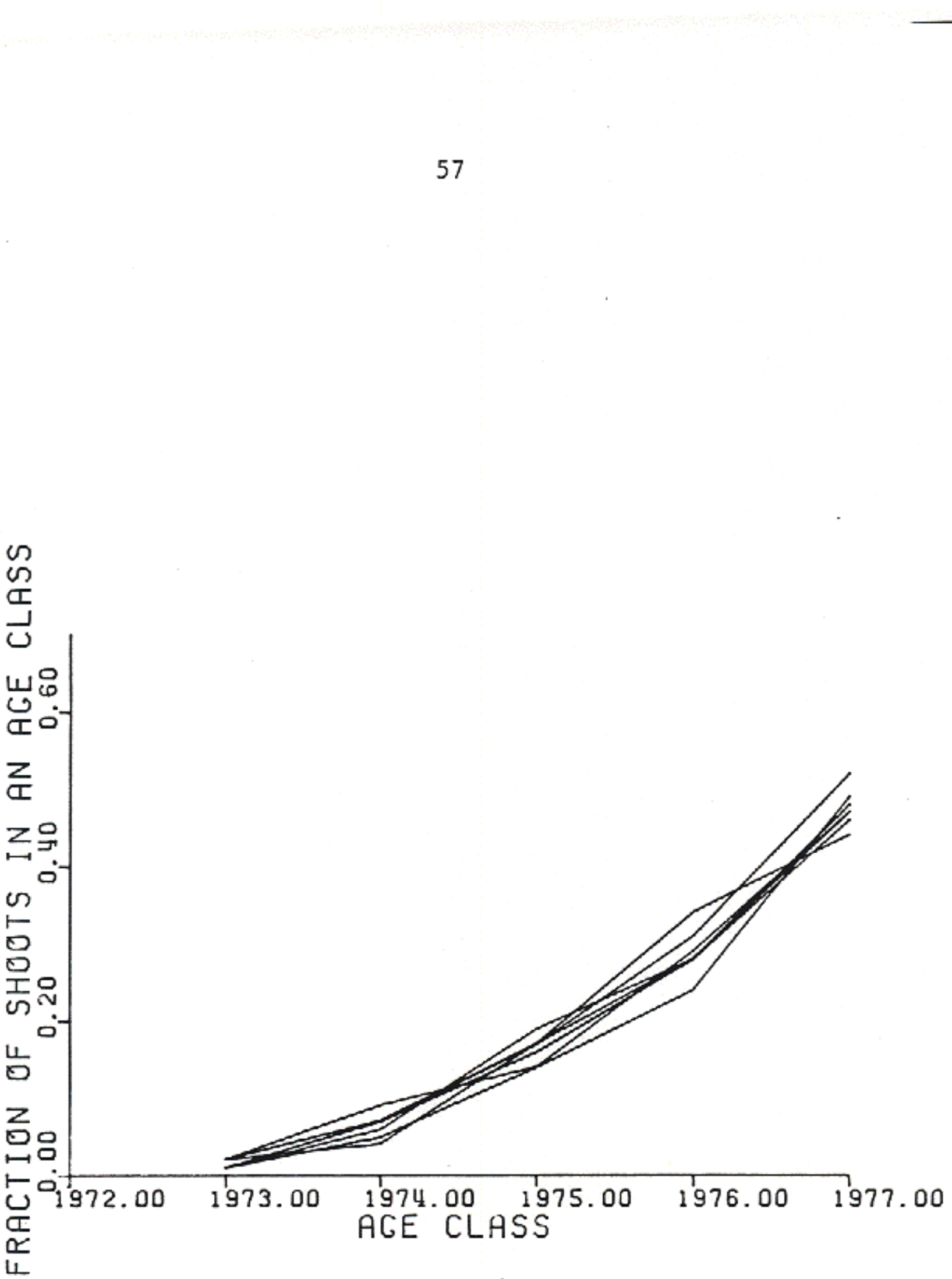


Figure 5. Fraction of new shoots in an age class versus age class for seven trees.

new shoots from the 1976 whorl to the 1973 whorl and a decline in shoot production and shoot size in lower whorls.

Shoot branching

The shoot branching pattern by whorl and position may be examined directly from the ten-tree intensive sample (figure 7). Ratios of the number of new shoots in a position for a given year to the number the year before indicate a relative change in branching. Ratios of shoots produced in any position declines from upper to lower whorls. In the B position, for example, #77buds/#76shoots declines from 3.7 in the 1975 whorl to 2.8 in the 1972 whorl. This shows the declining production of shoots with aging of the whorl. Ratios of shoots produced on any sub-branch declines with age of the sub-branch.

Within the limited number of years given, ratios are similar across years for similar positions in relation to whorl location (from the top of the tree) and sub-branch position (from the base of the branch). These ratios indicate an increase in shoot production

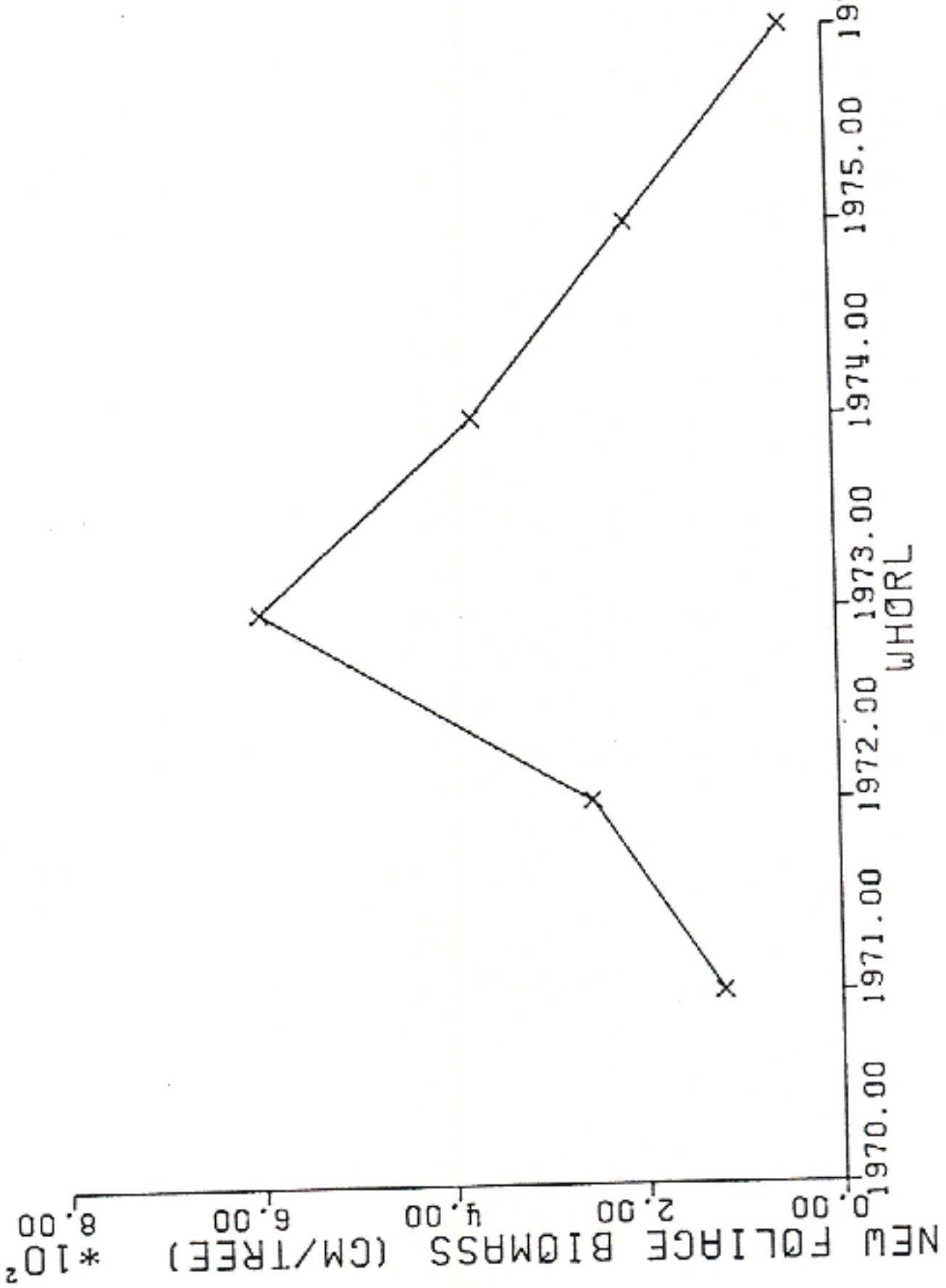


Figure 6. New foliage biomass per whorl (from the destructive sample of four trees).

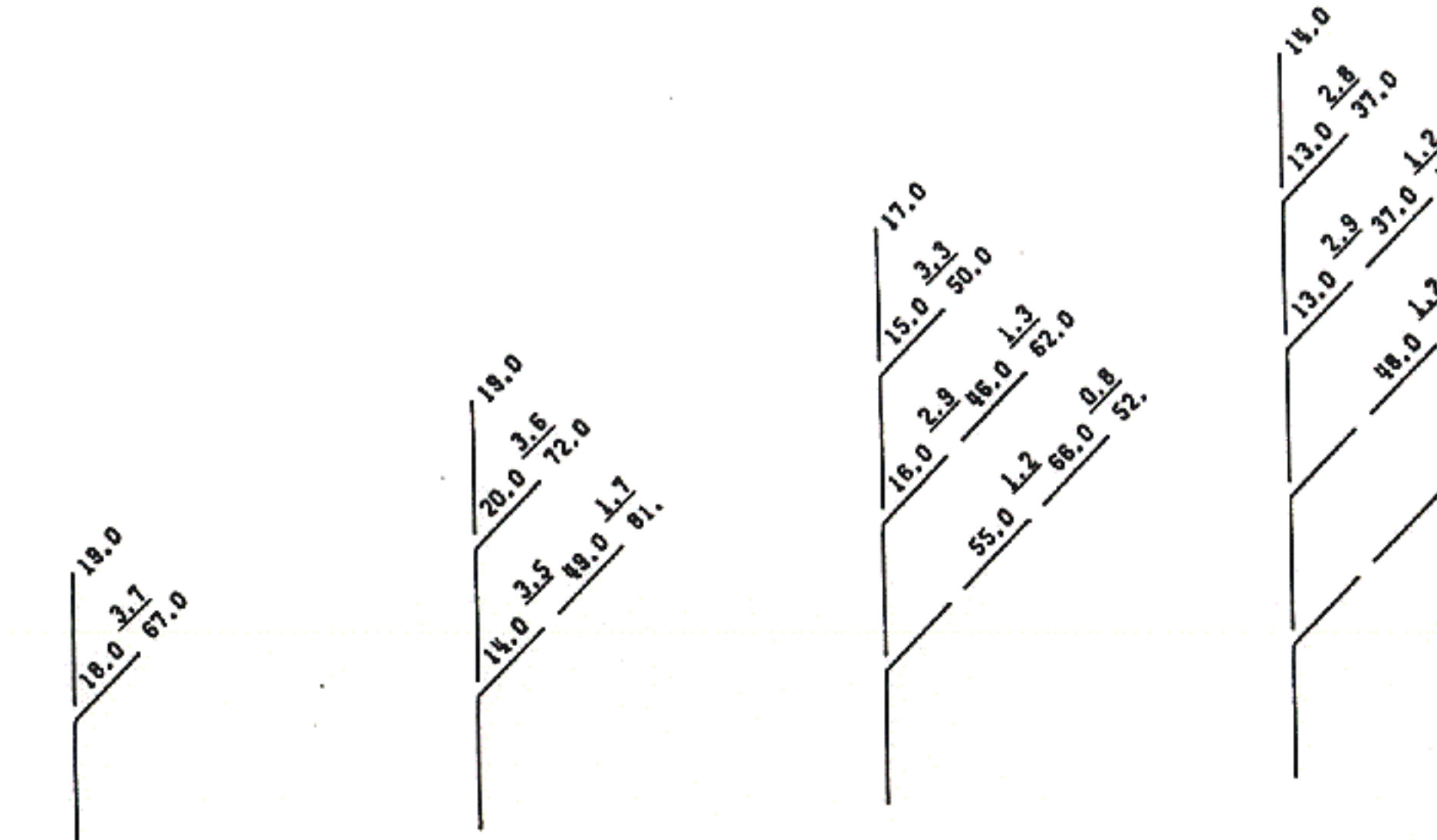


Figure 7. Number of new buds (value at end of sub-branch), number of shoots in a position and age class, and ratios of shoots produced in a year : shoots produced the year before (underlined values).

per sub-branch (ratio > 1) until the sub-branch is four whorls from the top and in the lowest position from the base of the branch.

Foliage biomass per tree

Foliage biomass was estimated (Nov., 1977) for ten control trees and ten trees fertilized over two years. The data were modeled as a function of dbh (inside bark) using the function $Bf = a(dbh)^b$ (figure 8). With total foliage dry weight, Bf, in kg and dbh in cm, the regression coefficients for the control trees are a=0.013 and b=2.83. The relation is not an allometric one; it does not relate relative change in tree components with age, but it shows change as a function of tree size at one age. In comparison with the model of Bf=f(dbh) developed for 40-year-old Douglas-fir at Cedar River (Dice, 1970), this model is considerably different (see figure 8). This suggests that widespread application of such models to other sites and ages is dangerous.

In order to examine the affect of fertilization on foliage biomass, the data were modeled as a function of

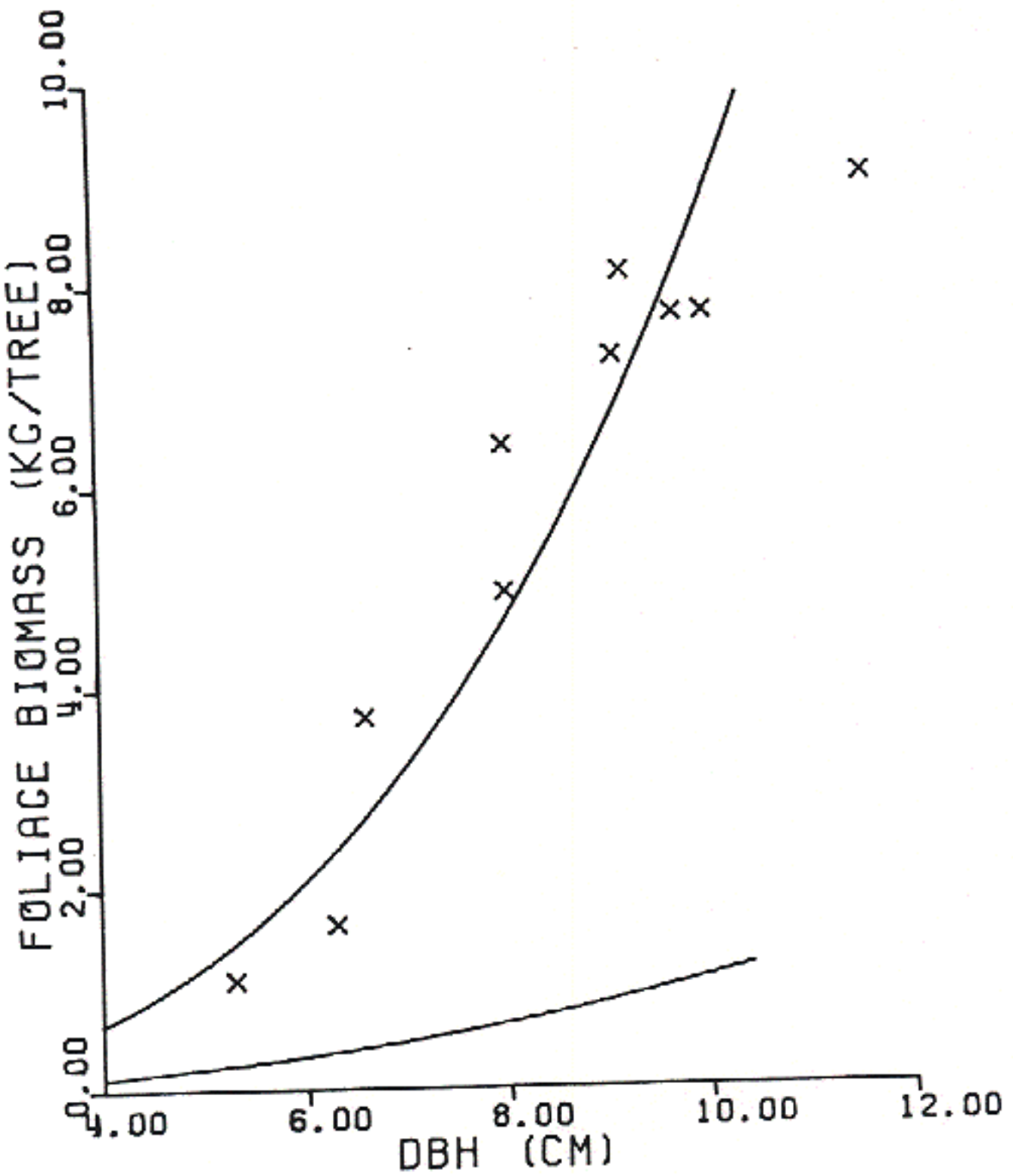


Figure 8. Regressions of foliage biomass per tree versus stem dbh. The lower regression is the model of Dice (1970), which is shown for comparison.

pre-season stem volume. A function of the form Bf=a+b*ln(VOL) was used, where Bf is the 1977 foliage biomass (kg) and VOL is the 1976 stem volume (dm^3). For control trees, the regression coefficients are a=-6.40 and b=5.03, while for fertilized trees the regression coefficients are a=-4.76 and b=4.09. It appears that the foliage biomass of larger trees fertilized over two years may be less than for control trees (figure 9). However, the regressions are not significantly different.

Number of new shoots per tree

The mean 1976 dbh (outside bark) from a sample of 90 trees is 8.2 $\pm$ 1.1 cm, (inside bark dbh=7.6) with the dbh distribution skewed to the right (figure 10). Evaluating the foliage Bf=f(dbh) model for this distribution of diameters (inside bark) gives an expected distribution of foliage biomass per tree with mean Bf=4.11 kg/tree.

Combining this value for foliage biomass with the estimate of 0.41 of the foliage in the 1976 age class yields 1.69 kg foliage in the new age class. Together

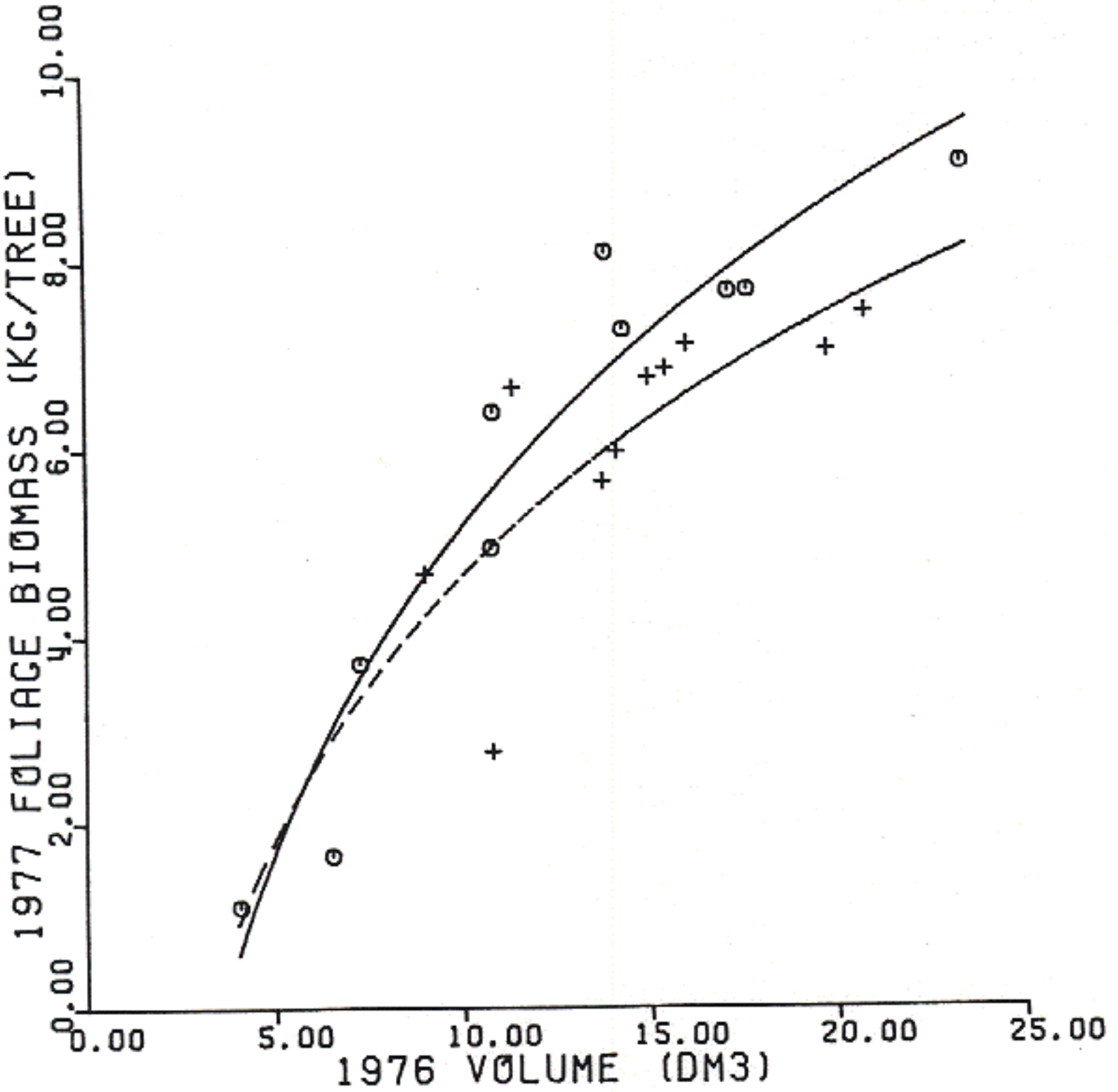


Figure 9. Regressions of foliage biomass per tree (measured after the growing season) versus stem volume (measured before that season). The solid line and circles are for control trees while the dashed line and plus signs are for fertilized trees.

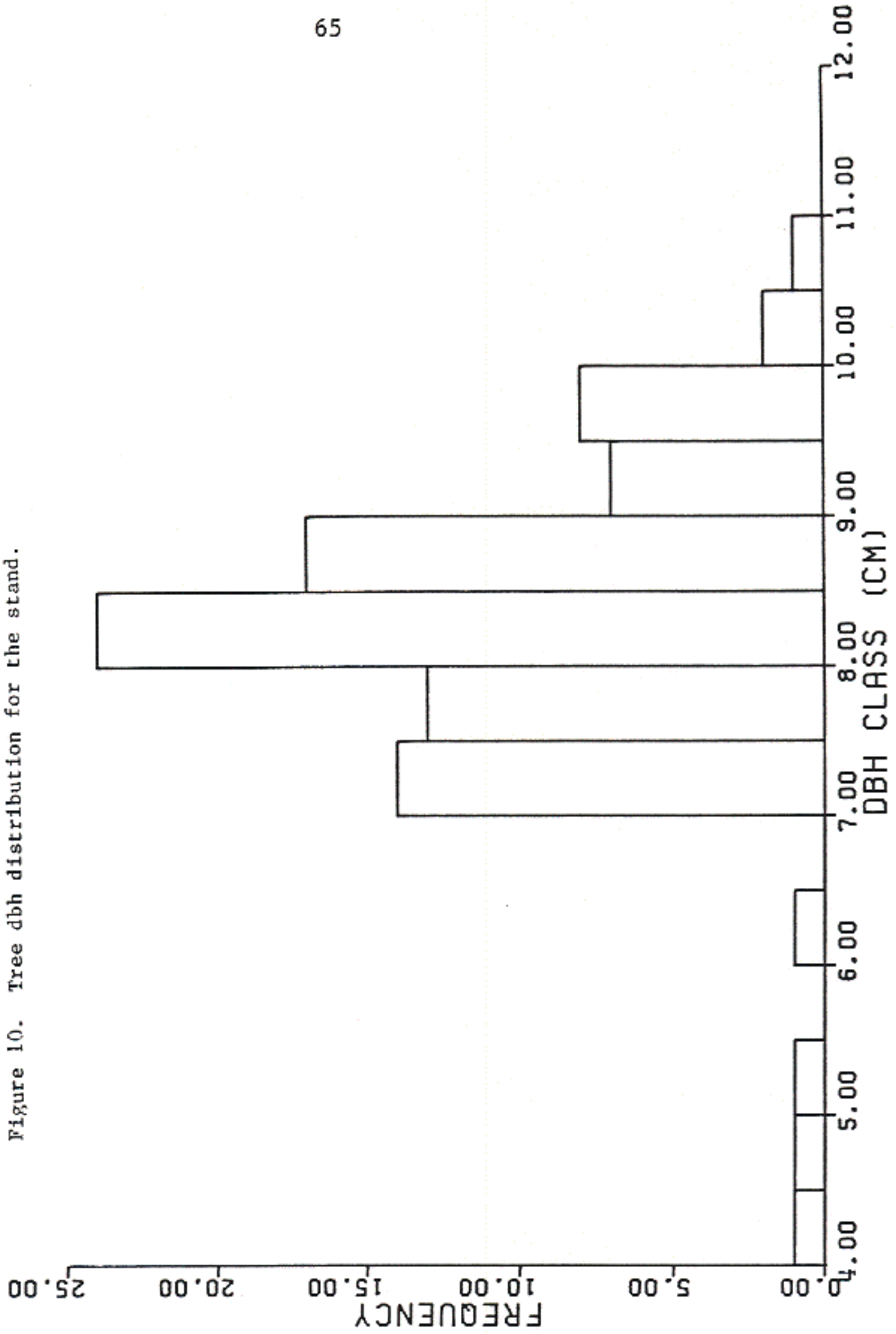


Figure 10. Tree dbh distribution for the st

with the value of 0.40 gm/shoot, this gives 4225 new shoots/tree produced during the 1976 growing season (at an age of seven years). This may be combined with the whole-tree weight/shoot model to estimate new foliage biomass for a mean-dbh tree through the growing season.

N concentration in new foliage

Changes in N concentration (%N) in new foliage with whorl (lower whorls only), position on a branch, shoot length, and time during the growing season were examined. No differences in %N were evident between the 1973 and 1974 whorls where the majority of new foliage biomass is located. Similarly, no differences were found between different positions on a branch and no relation with shoot length was evident.

There is a distinct pattern in the N concentration of new foliage through the growing season (figure 11). Initial concentration in the bud is 3.2% $\pm$ 0.53. The large variance in initial concentration may be due to differences in timing of shoot expansion among trees. All samples collected day 156 may not be in the same state of expansion, and since concentration changes rapidly with expansion at this early stage, a relatively large variance may be expected. A rapid

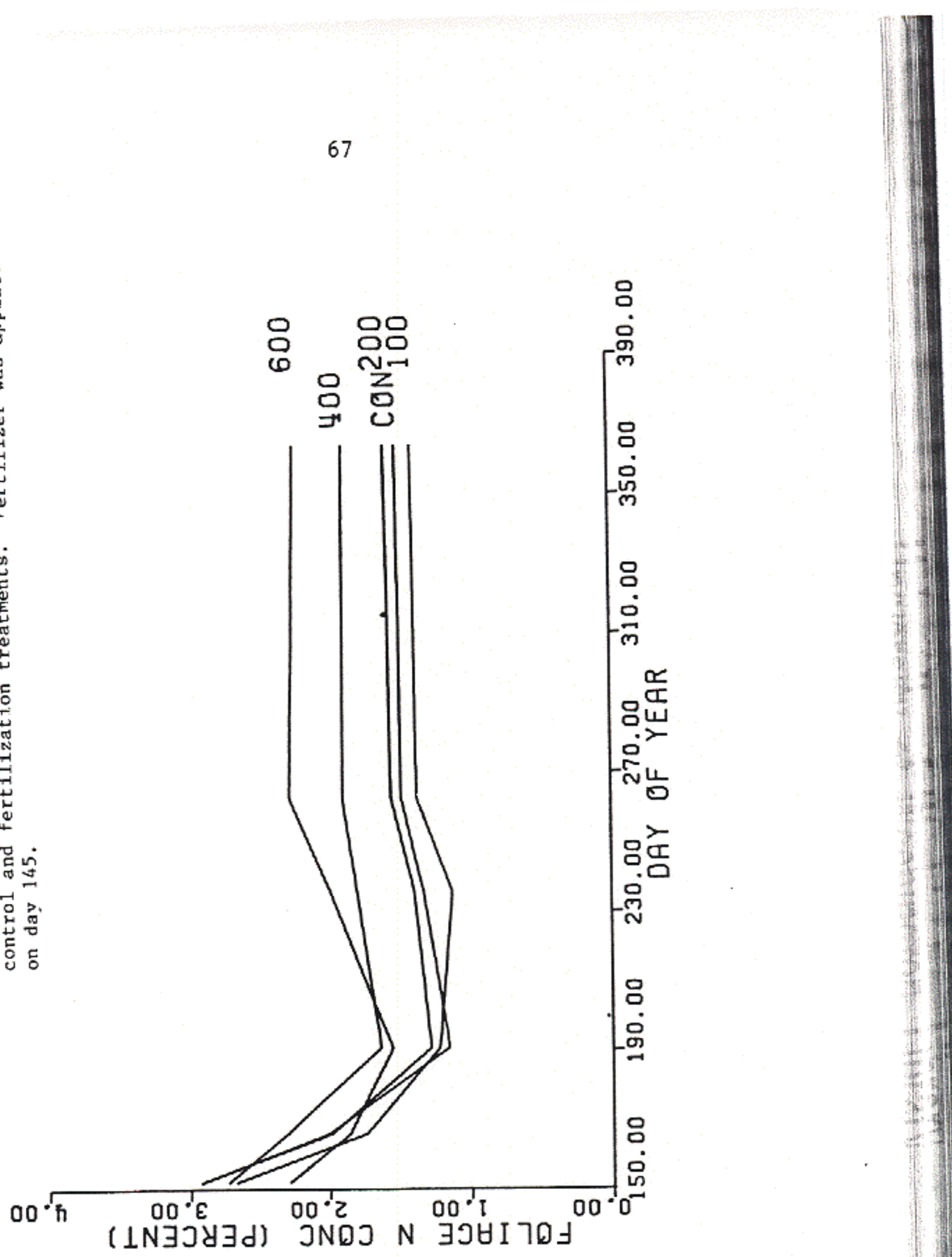


Figure 11. New foliage N concentration versus day of the year for the control and fertilization treatments. Fertilizer was applied on day 145.

decline occurs following bud break; shoot expansion and foliage growth are initially more rapid than N incorporation. From approximately day 190 until day 260, a slow increase in concentration occurs. This increase is more pronounced with fertilization. N concentration is unchanging from day 260 until day 365, and presumably, throughout the dormant period.

The simple and intensive samples were combined (38 trees) to give growing season concentration trends by treatment (table 5). Analysis of variance of the concentrations at day 215 rejects (alpha=0.05) the hypothesis of equal treatment means. Scheffe's multiple comparison test rejects the null hypotheses of no differences between means for the control and 400 kg N/ha fertilization, control and 600 kg N/ha fertilization, and 100 and 400 kg N/ha fertilizations (H0:μ0=μ400, H0:μ0=μ600, and H0:μ100=μ400). It fails to reject all other null hypotheses.

Table 5. New foliage N concentration (38 trees).

	Day of the year			
treatments	156	177	192	215
control	3.57	2.25	1.63	1.35
100	3.11	2.19	1.73	1.49
200	3.38	2.34	1.82	1.62
400	3.04	2.41	2.02	1.82
600	2.83	2.21	1.86	1.85

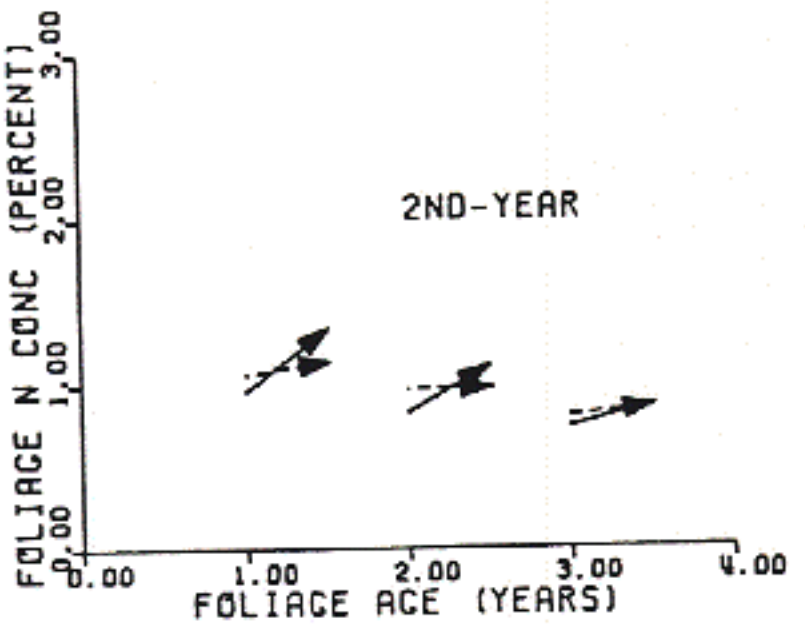
Old foliage N concentration

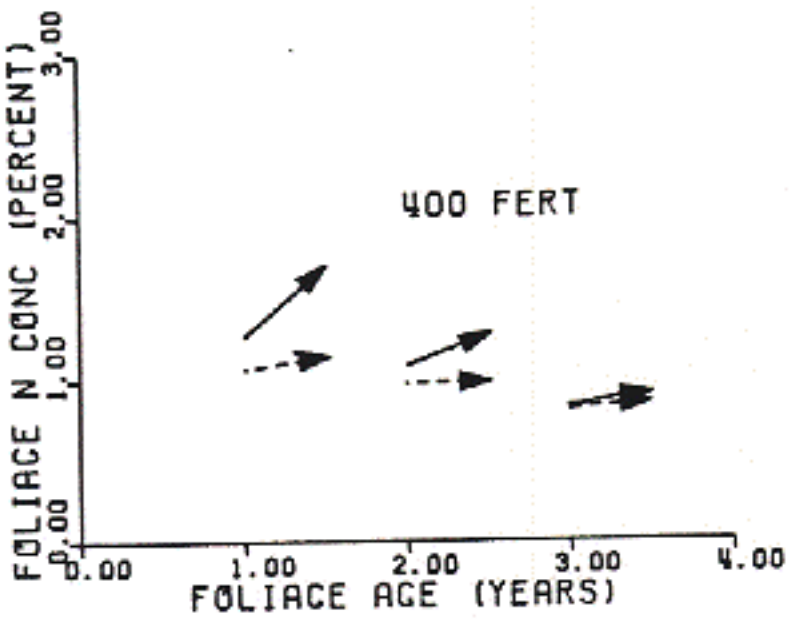
At any one time, the N concentratiion in older foliage decreases in the sequence from 1- to 3-year-old foliage. Average decrease in N concentration per age class is 0.15%.

Since old foliage N concentration declines during the growing season, presumably supplying N to new foliage (Krueger,1971), and since fertilizer-induced changes are expected during this period, concentrations were measured before (May 1977) and after (Oct. 1977) the growing season. The change in old foliage N concentration was estimated by age class and tree for trees that were untreated, fertilized at 400 kg N/ha in

May 1976, fertilized May 1977, or fertilized both years.

Changes in N concentration over the 5-month period (figure 12) were analyzed by 2-way analysis of variance with treatment and age class as factors (table 6). The arrows in figure 12 show the time trends in N concentration for each age class and treatment.





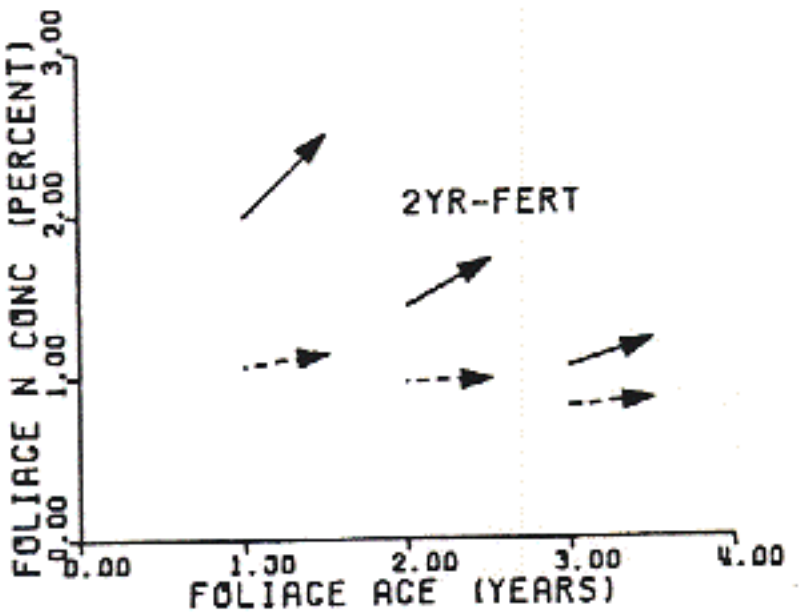


Figure 12. Change in old foliage N concentration with time for the different age classes. Shown are measured values for the first (400 fert) and second (2nd-year) years, and for fertilization over both years. Control values are shown as dashed lines for comparison.

Table 6. Old foliage N concentration changes over the growing season.

Change in N conc (%)					new foliage N conc (%)
	age class				
treatment	76	75	74	n	77
control	.10	.06	.02	10	1.27
fert at 400	.39	.31	.13	5	1.52
2nd yr after fert at 400	.42	.19	.08	3	1.26
2-yr fert	.52	.28	.14	5	1.92

ANOVA for change in N conc.

Source	df	ss	ms	f
total	71	5.6352		
mean	1	2.3657		
hypothesis	11	1.6163		
treatment	3	.8392	.2797	9.99
age cl.	2	.5484	.2742	9.79
tr x age cl.	6	.2287	.0381	1.36
residual	59	1.6532	.0280	

The interaction of factors was not significant, while both main effects were significant. Thus, the

change in concentration over the growing season was influenced by both treatment and age class.

For control trees, the concentration changes over the growing season by age class are not different. Across treatments, the mean N concentration for 1976 foliage is greater than that for 1975 foliage as well as 1974 foliage. The hypothesis of equal concentration between 1975 and 1974 foliage was not rejected. Across age classes, N concentration in foliage of trees fertilized at 400 kg N/ha was greater than that of control trees. N concentration for trees fertilized over two years was similarly higher than for controls. Hypotheses of equal concentration between trees fertilized at 400 kg N/ha and trees fertilized over two years, and between the second year after fertilization and any other treatment were not rejected.

These analyses may be interpreted as follows. The change in old foliage N concentration for high-site controls is positive and small (+0.062%) over the five-month period. No differences among age classes is indicated. In the year of fertilization, there is a large accumulation of N in older foliage, especially in the 1-year-old age class. No difference between the 2-

and 3-year-old age classes is indicated. N continues to accumulate at this high rate if fertilizer is applied a second time.

Analysis of variance on the Oct. 1977 N concentration in new foliage by treatment shows that the mean for the two year fertilization is greater than those for the 400 kg N/ha fertilization, the control, or the second year after fertilization. The mean for the 400 kg N/ha fertilization is greater than that of the control, while the hypothesis of equal means between the second year and control was not rejected. This indicates a continued elevation of N concentration in new foliage with a second fertilization. Also, the N concentration in new foliage expanding the second growing season following fertilization cannot be discerned from similar foliage on control trees, but it is lower in concentration than that in the first year after fertilization.

New foliage free amino acid-N

Concentrations of free amino acid-N were measured throughout the growing season and early dormant period

for each treatment (figure 13).

The concentration in the bud at the beginning of the growing season is 0.082% ± 0.022. Thereafter, the concentration may be affected by changes in the content of free amino acid-N in the shoot and possibly by the rapid change in shoot dry weight during expansion. In trees that were untreated or fertilized at low rates, the concentration initially falls, while in trees fertilized at high rates, concentration rises continually during the growing season.

Concentrations attained by day 364 by trees fertilized at 600 kg N/ha (0.15%) were 6.7 times higher than those of control trees (0.023%). Total-N concentration of these fertilized trees (2.22%) was only 1.5 times that of controls (1.50%). Thus, the free amino acid-N concentration is much more sensitive to changes in N supply to the tree than is the total-N concentration.

The high free amino acid-N concentrations observed with 400 or 600 kg N/ha fertilizations could possibly be due to a secondary nutrient deficiency that is induced or aggravated by N application. For example,

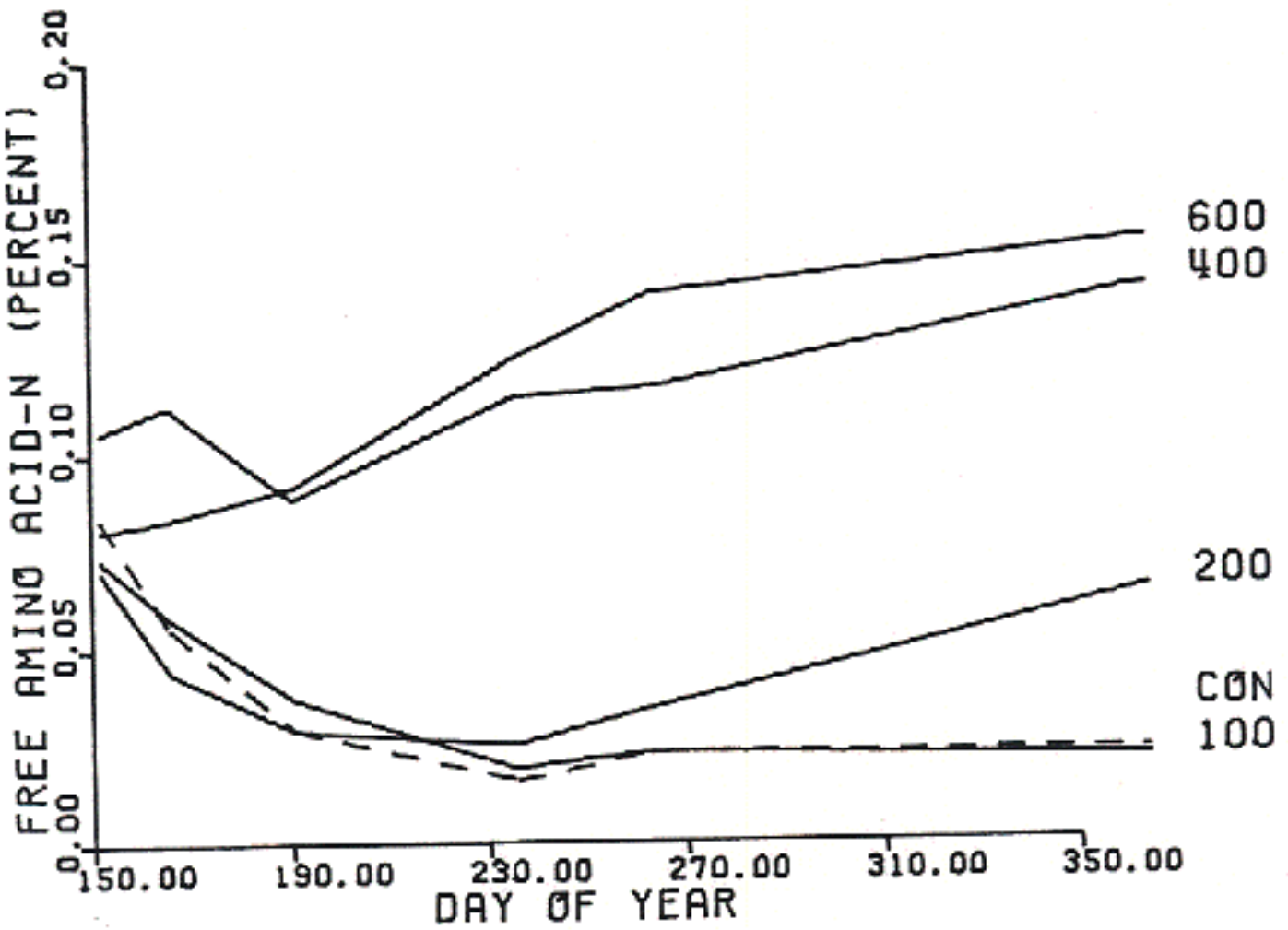


Figure 13. New foliage free amino acid-N versus the day of the year by treatment.

sulfur deficiency has been implicated as the cause of some low growth responses to N in western Washington. With sulfur deficiency, protein synthesis is limited by a lack of S-containing amino acids. Amino acids then accumulate as a result (Coleman, 1957). Induced sulfur deficiency is unlikely as a cause of amino acid accumulation here because an ammonium sulfate fertilizer was used. Other nutrient deficiencies could have a similar secondary effect (Steward, 1974). However, foliage nutrient analysis indicates sufficient levels of other elements (Turner, Lambert, and Gessel, 1977).

Soil exchangeable ammonium

Exchangeable ammonium concentration in untreated soil was 5.01 $\pm$ 2.93 ppm. No trends in concentration from May through December were evident.

Applied ammonium fertilizer is rapidly depleted with concentrations declining exponentially as shown by fitted regressions (figure 14). Presumably, this decline is primarily due to immobilization by soil microorganisms. Also contributing are uptake by

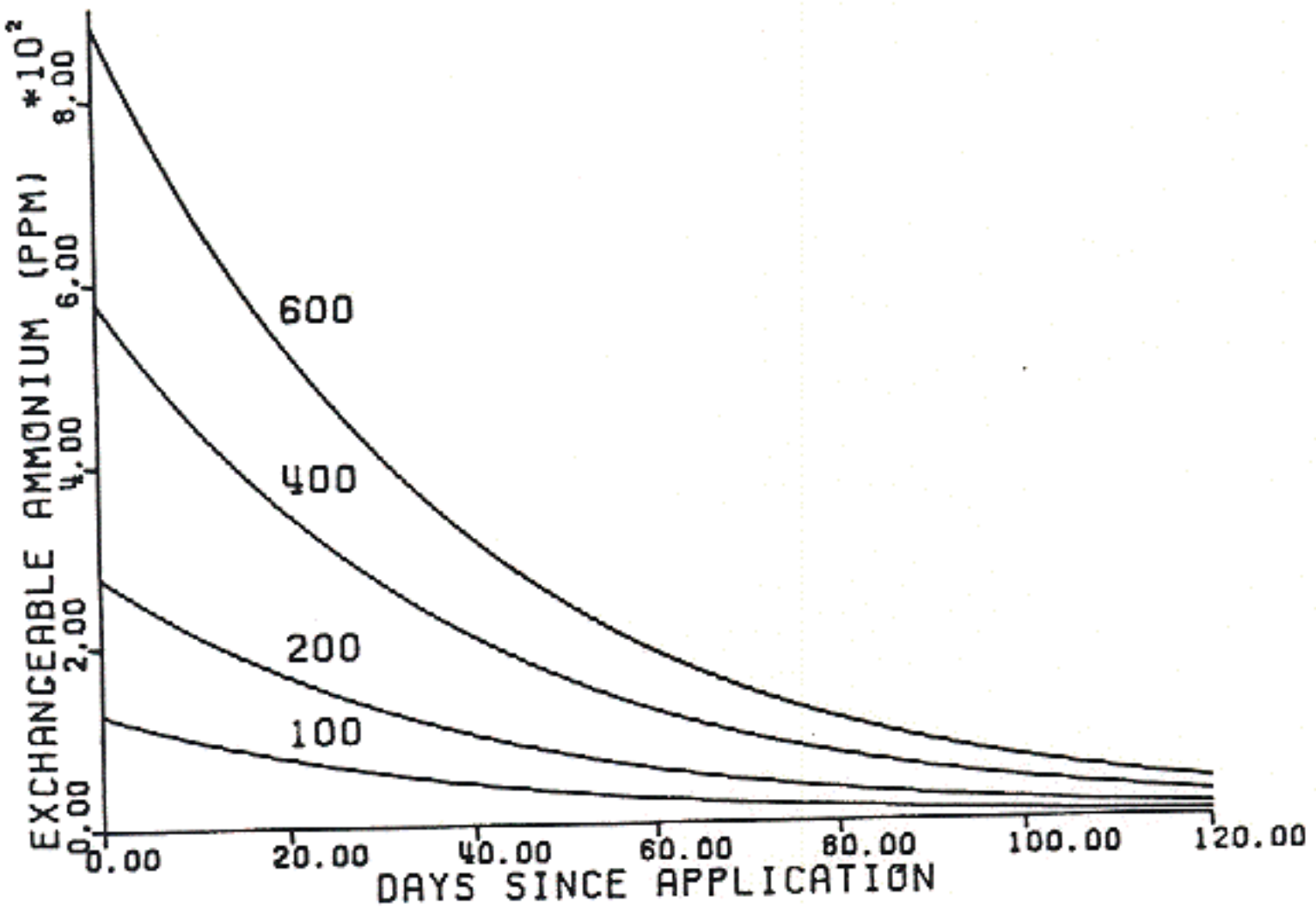


Figure 14. Regressions of soil exchangeable ammonium concentration versus time since application for the different fertilizations.

vegetation and nitrification. Exchangeable ammonium concentration may be described as a function of time by the relation

$$exNH4=a*exp(-b*t)$$

where exNH4 is the concentration in ppm, t is time in days since application, and "a" and "b" are fitted constants. The parameter "a" represents the concentration immediately following application, while "b" may be interpreted as the relative rate of change of ammonium with time, since

$$d(exNH4)/dt= -a*b*(exp(-b*t),$$

$$d(exNH4)/dt* (1/exNH4)=-a*b*exp(-b*t)/(a*exp(-b*t))=$$

$$-b.$$

The hypothesis of equal "b" parameters by treatment was rejected, but there is no monotonic trend with the application rate, and differences in "b" are small, so differences are likely due to plot differences rather than treatment. The parameter "b" for pooled data = -0.0257. The parameter "a" shows a good linear relation to application rate, APPL (kg N/ha). These results give the model for exchangeable ammonium concentration as a function of time since fertilization as (with a bias correction):

$$exNH4=(-26.0+1.51*(APPL))*\exp(-0.0257*t). \quad R^2=0.84$$

Soil nitrate

The nitrate concentration in unfertilized soil is 3.5 $\pm$ 3.3 ppm. There is no uniform pattern during the growing season. Soil nitrate concentration on the 600 kg N/ha fertilization plot remained low until after day 164, at which time it increased rapidly to a measured maximum of 50.6 ppm on day 263 (figure 15). The concentration then declined to 28.3 ppm by day 364. The intermediate level fertilization plots show nitrate concentrations on day 263 intermediate to the control and 600 kg N/ha treatment plots.

Nitrate concentration is a function of nitrification, leaching loss, and uptake. A relative increase in nitrification or decrease in nitrate uptake or leaching loss with fertilization would result in a nitrate concentration increase with respect to a control. Since uptake and leaching loss are expected to be proportional to concentration, an increase in concentration with fertilization is most likely due to accelerated nitrification. Therefore, these data show

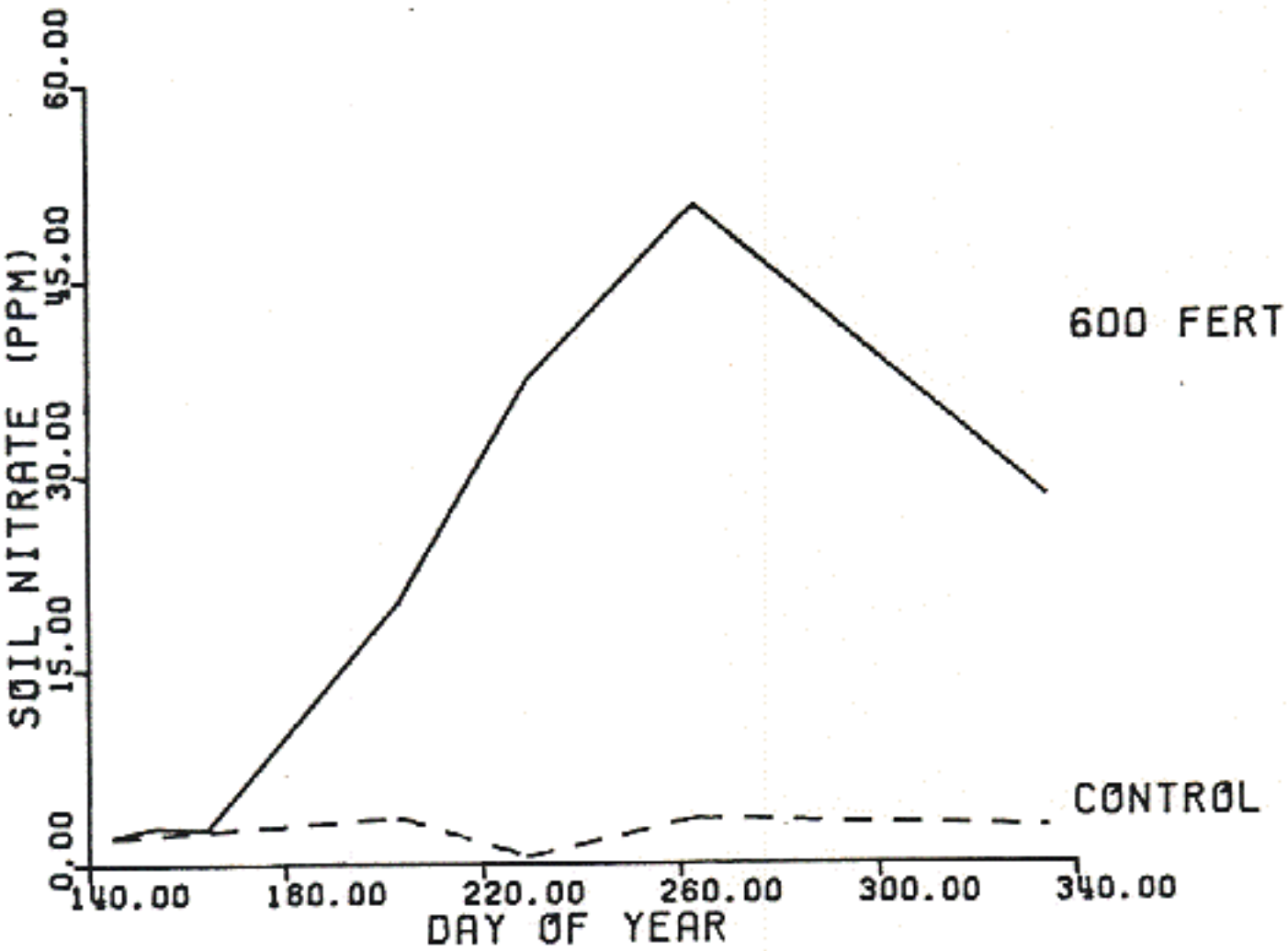


Figure 15. Soil nitrate concentration versus the day of the year for a control and 600 kg/ha fertilization.

a high rate of nitrification is possible on the high site-quality Tokul soil. High levels of nitrate accumulation may accompany fertilization, increasing with increasing rates of application.

These data lend support to the hypothesis that nitrification is substrate (ammonium) limited, since nitrate concentration increases with increasing application rate and declines late in the year when exchangeable ammonium concentration has returned to control levels. The data also suggest that high rates of nitrification are dependent on a large population of nitrifiers, since nitrate concentration remains low for at least 20 days after fertilization. This would result if nitrification is not immediately concentration dependent but requires population growth.

An experiment was designed the second year to further test the substrate limitation hypothesis and test the hypothesis that the response in nitrification to applied ammonium depends on any previous stimulation of nitrification. For this experiment, two plots were untreated, two were treated with sugar at 4500 kg sugar/ha, two were fertilized at 400 kg N/ha, and individual plots fertilized at 100, 200, 400, or 600 kg

N/ha the first year were refertilized at 400 kg N/ha the second year. The increased C/N ratio brought about by sugar addition is expected to stimulate microorganism activity, including immobilization of soil ammonium. If the substrate limitation hypothesis is correct, lower soil nitrate concentration should result.

The sugar addition and control plots had similar nitrate concentrations at the beginning of the experiment on day 145 (table 7). The higher value for nitrate on plot 3 on day 145 is consistent with higher initial exchangeable ammonium concentration for this plot. Over the three month measurement period, control plot nitrate was 3.85 $\pm$ 4.3 ppm while the sugar treated plots had 0.18 $\pm$ 0.12 ppm. Thus, the sugar treatment resulted in a markedly reduced soil nitrate concentration, which is consistent with the substrate limitation hypothesis.

Table 7. Nitrate and exNH4 concentrations on control and sugar addition plots.

NO^3 conc (ppm)

	day of year			
treatment	145	174	214	249
plot number				
control				
3	1.94	3.22	6.90	1.5
7	1.07	13.6	.86	.82
sugar				
6	.86	.15	.05	.30
10	.78	.15	.11	.39

NH^4 conc (ppm)

control				
3	22.0	15.8	15.2	16.5
7	4.0	7.5	7.8	4.8
sugar				
6	2.8	1.2	0.9	2.0
10	2.9	1.6	2.8	1.6

The effects of previous fertilization on nitrification may be examined by comparing nitrate concentrations on plots fertilized over two years with

plots fertilized for the first time during the second year. The independent variable is ammonium applied the first year. If the hypothesis is correct, increased nitrate would be expected on the plots fertilized at higher rates the first year.

The plots fertilized at 200, 400, or 600 kg N/ha the first year show large accumulations, with a maximum (approximately 100 ppm) on day 217 (figure 16). Plots fertilized at 100 kg N/ha the first year, or unfertilized the first year show considerably lower accumulations. Thus, the hypothesized stimulation of nitrification by prior fertilization has been shown to occur.

Litter N mineralization

Senesced foliage (before litterfall) was collected from nine trees, both untreated and fertilized. Litter bags with 5 gm dry weight litter were prepared keeping samples from individual trees separate.

Data from litter bags from four trees measured four times each over a four month period, show a decrease in N content of 17% of the initial content over the first 140 days. However, combined nine tree

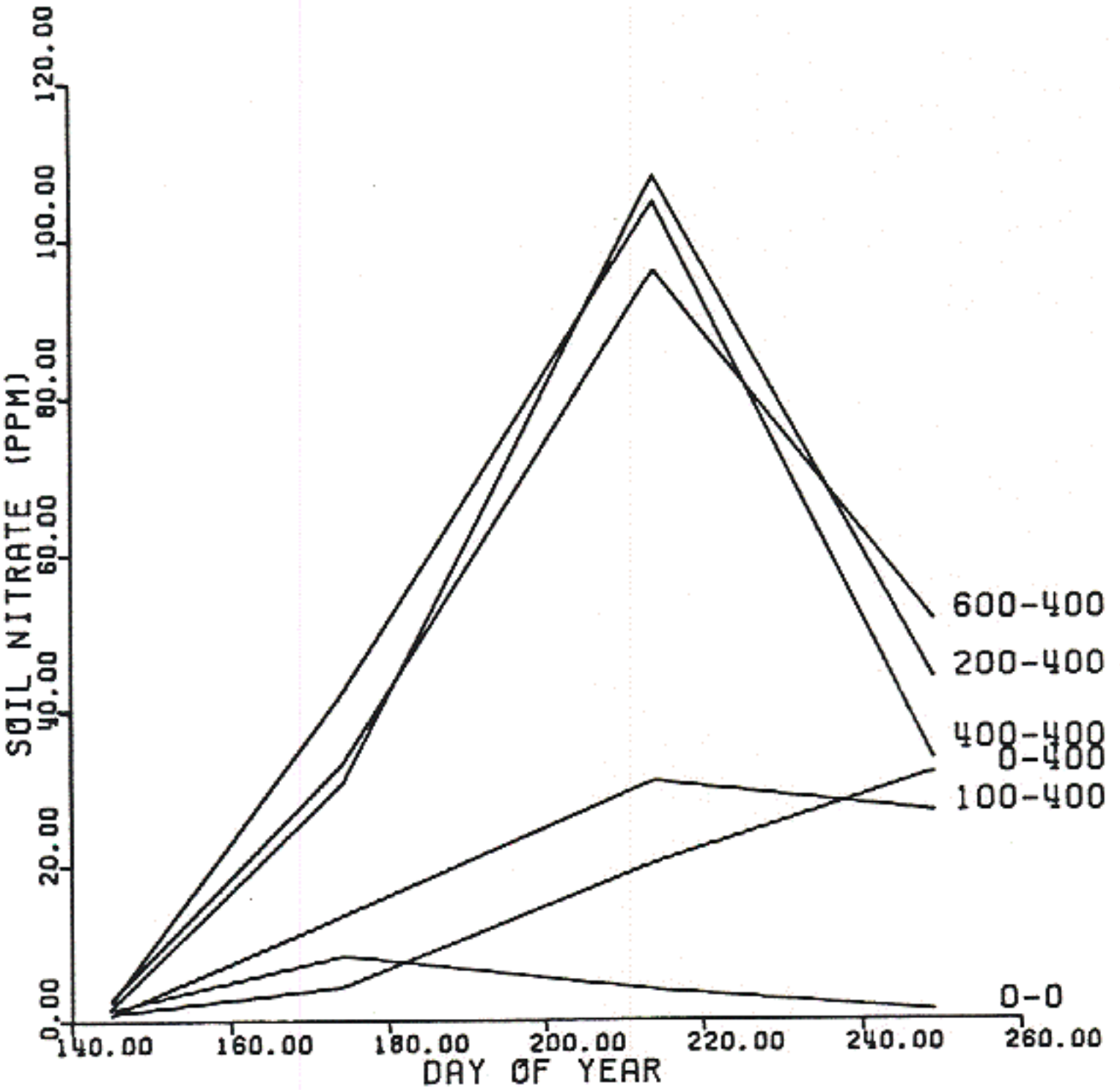


Figure 16. Soil nitrate concentration versus the day of the year for fertilizations over two years. The data are labeled by the first and second year application rates.

data for one year shows a mean increase in litter N content of 4.9%. The increase in litter N content must be due to larger inputs than output (from mineralization). Since N content was decreasing over the first 140 days, a net mineralization must occur initially. The net increase in content is likely from decomposition of subsequent litterfall (the next Summer) and canopy leaching. Thus, new litter must be considered both as an initial source of mineral N and as an absorbing material that may immobilize N.

Stem volume increment

Stem volumes and volume increments were determined for ten control trees, ten trees fertilized at either 800 or 1000 kg N/ha over two years, and eight trees fertilized at 100 kg N/ha the first year only.

Simple linear regressions of volume increment, VI, in one year as a function of volume increment in the same tree the year before, for each treatment (pooling across plots) were calculated: $VI(t)=a+b*VI(t-1)$. These regressions fit the data well and account for a high proportion of the observed variance ($r^2=0.95$).

Thus, volume increment in a tree is a good predictor of volume increment the following year (in relation to the population).

Trees from different plots follow the same relation between volume increments in successive years, even though the plots may differ considerably. As an example, plot 3 (control) contains more open, and larger trees relative to the population, while plot 23 (control) is more dense, with smaller trees exhibiting evidence of suppression (small diameters, loss of foliage, and a lack of branching, relative to the population). Yet trees from both plots exhibit the same trends in volume increment, and the same regression is suitable.

Considering regressions by treatment of the volume increment of a tree the year following fertilization versus that of the year before, 1976 VI =f(1975 VI), and making use of the extra-sum-of-squares principle (Draper and Smith, 1967), analysis fails to reject the null hypothesis of equal y-intercepts and slopes, h0:a1=a2=a3; b1=b2=b3 (table 8). Thus, the regressions are not different and one regression may be used to predict growth the first year following treatment,

regardless of treatment (figure 17). This indicates a lack of growth response the first year.

Table 8. Volume increment regressions.

1976VI=a+b(1975VI)

Parameters			Hypothesis Anova			
				df	ss	ms
	a	b	total	28	1362.7744	
control	.32	1.79	model	6	1358.4583	
100 kg fert	1.00	1.62	hyp	4	.9302	.2326
2-yr fert	-1.12	2.17	resid	22	4.3161	.1962

F=1.18
fail to reject H0

1977VI=a+b(1976VI)

Parameters			Hypothesis Anova, control and 2-yr fert.			
				Df	ss	ms
	a	b	total	20	1561.6389	
control	-.207	1.369	model	4	1558.2688	
2-yr fert	1.373	1.308	hyp	2	12.3445	6.1723
			resid	16	3.3701	.2106

F=29.3
reject h0.

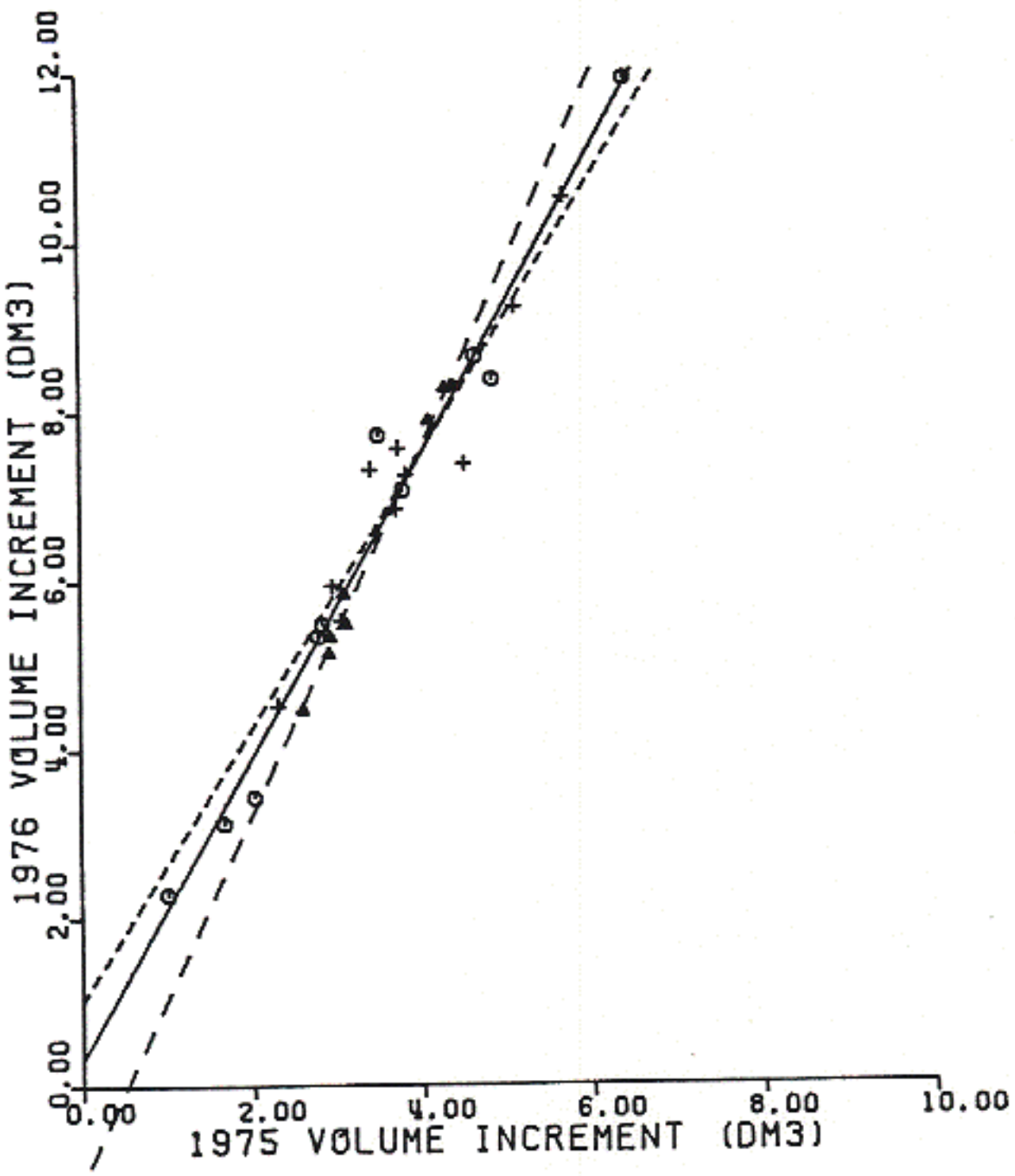


Figure 17. Regressions of stem volume increment the year following fertilization versus volume increment the year before. The solid, heavy dashed, and light dashed lines are the control, 100 kg/ha, and high rate (800 or 1000 kg/ha over two years) fertilizations, respectively.

Considering the regressions of volume increment the second year after initial fertilization versus that the first year after fertilization, 1977 VI=f(1976 VI), the two-year fertilization regression is significantly different from the control, while the 100 kg N/ha (1st year) regression is not (figure 18). The slopes of the control and fertilization regressions (two-year) are similar but the y-intercepts are not: control=-0.207 and fertilized=-1.37. For an intermediate-sized tree with a 1976 volume increment of 7 dm^3, the two-year fertilization resulted in a 20% reduction of stem volume increment.

Thus, fertilization at high levels in a high-site quality stand of Douglas-fir has been shown to reduce growth substantially (20%). This effect may be direct, perhaps due to ammonium toxicity, or it may be indirect. Increased litterfall due to high ammonium levels might result in a smaller, less productive canopy. Also, an interaction with the abnormally dry conditions observed the second growing season is possible. If foliage growth was stimulated the first year, high water stress in cambium and foliage would be induced with resultant decrease in cambial growth and increased litterfall during the second, drier year.

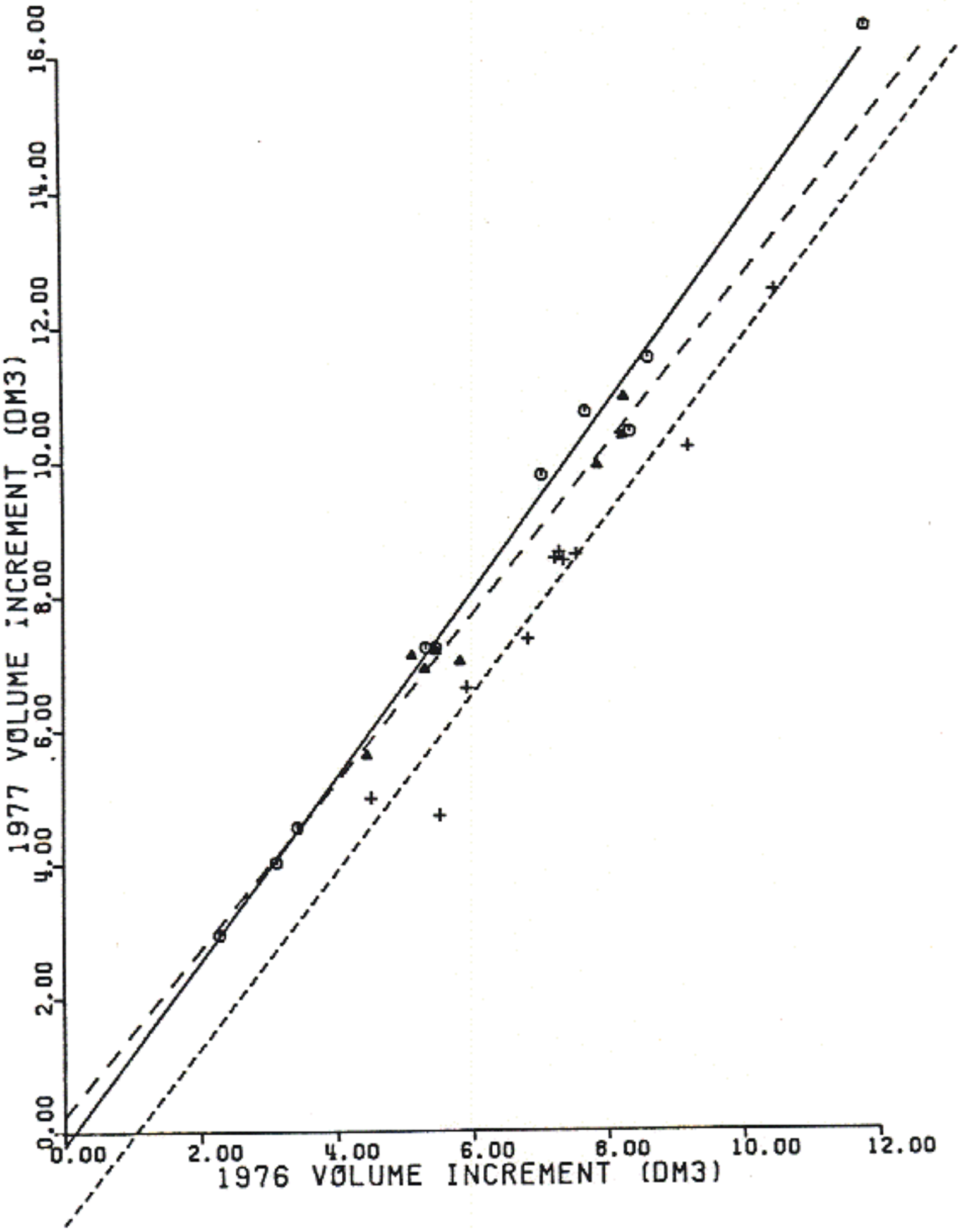


Figure 18. Regressions of stem volume increment the second year following fertilization versus volume increment the first year after. The solid, heavy dashed, and light dashed lines are the control, low rate, and high rate fertilizations, respectively.

Analysis of stem growth by this single-tree technique demonstrates that growth response to treatment may be measured with statistically significant results using relatively few trees and plots.

Foliage biomass is also a good predictor of volume increment for a tree. Volume increment (dm^3) was related to foliage biomass, Bf (kg), measured at the end of the 1977 growing season (figure 19) by the regression

$$1977VI = 2.51(1977Bf)^{0.187},\ r^2=0.90.$$

This relation will be used later to develop a volume increment model.

Stem volume and volume increment are well correlated with dbh (inside bark)(figures 20,21). For the stem analysis trees (including 14 harvested and measured in 1976), dbh was estimated by interpolating measured cross-section areas to breast height (1.3m) and assuming a circular cross-section. 1976 stem volume and dbh were related by the regression,

$$VOL=-1.73+0.31(dbh)^2,\ r^2=0.96,$$

while 1976 volume increment and dbh were related by

$$VI=0.80(dbh)^{2.273},\ r^2=0.96.$$

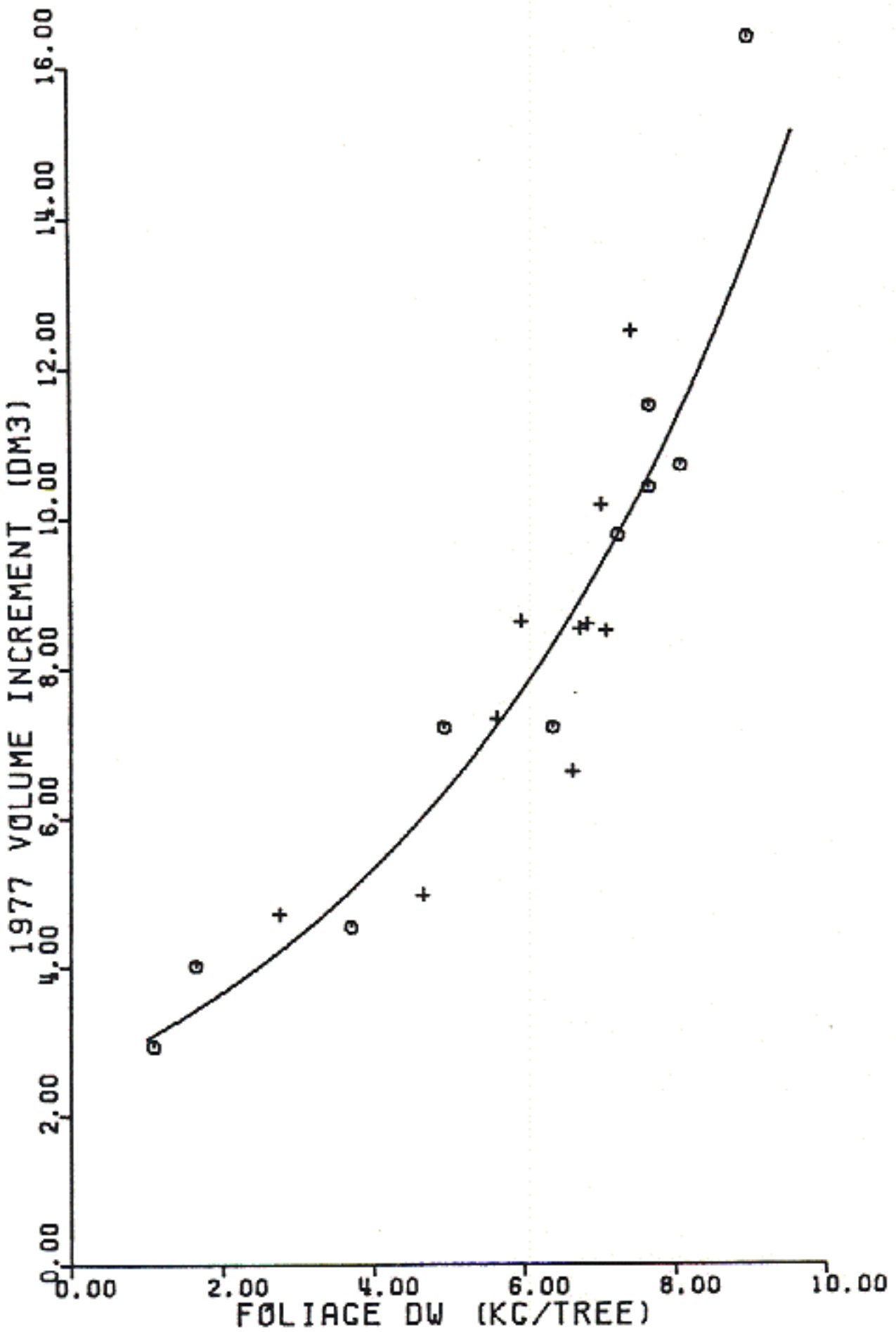


Figure 19. Regression of volume increment versus foliage dry weight for pooled control (o) and high rate fertilization (+) data.

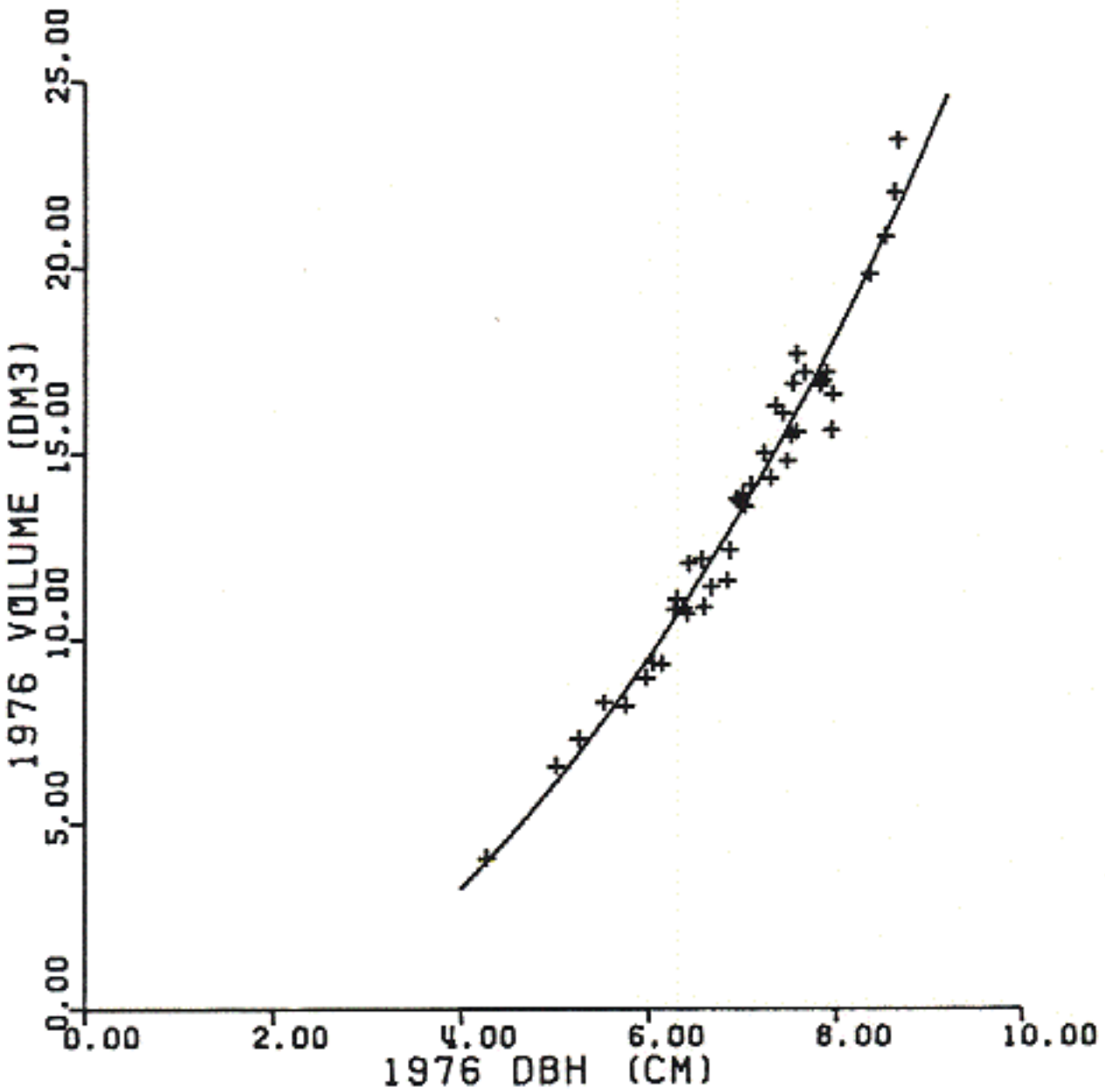


Figure 20. Regression of stem volume versus stem dbh.

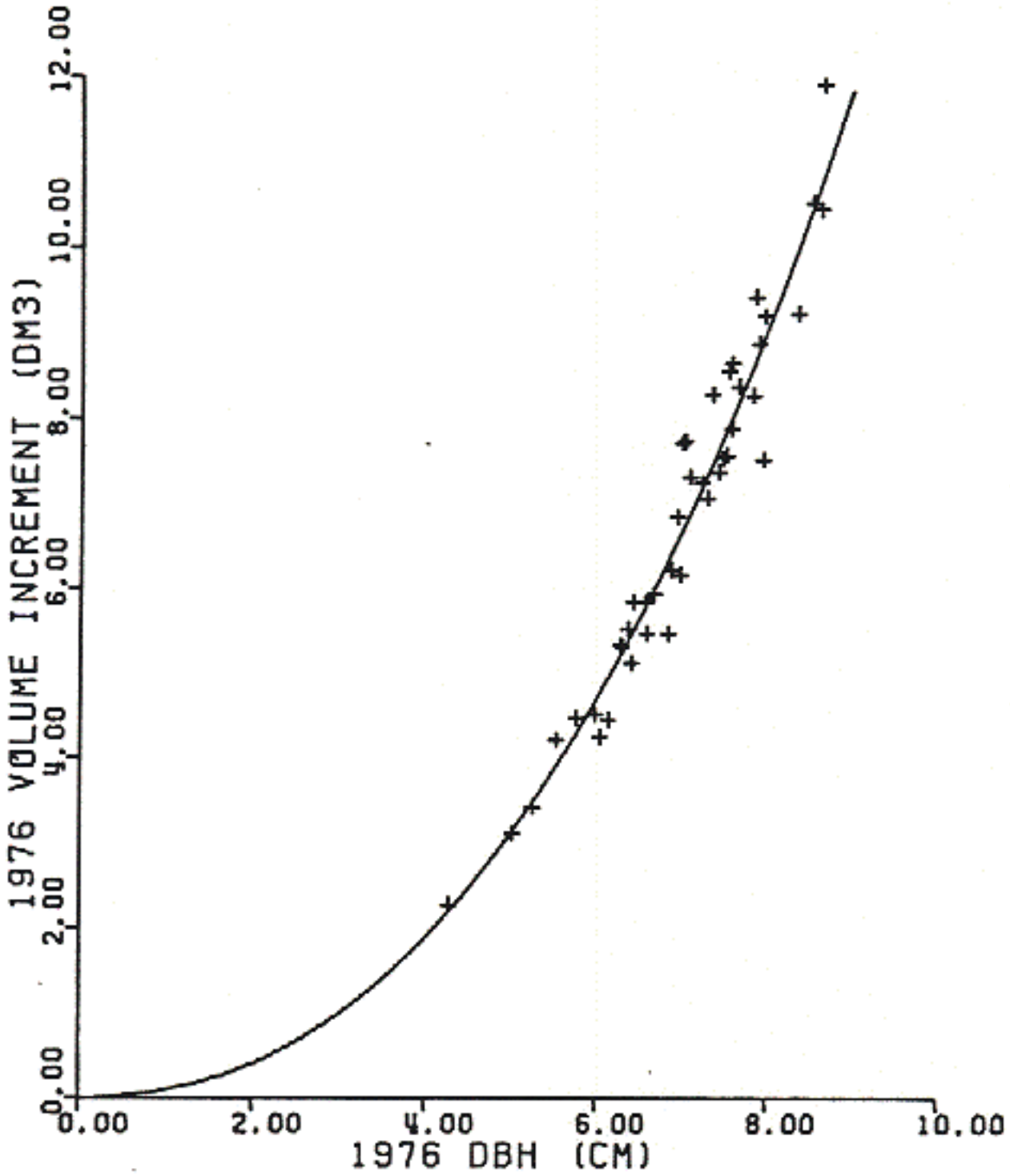


Figure 21. Regression of stem volume increment versus stem dbh before the growing season.

It should be noted that this relates volume increment during the growing season to dbh after the season and is used to estimate volume increment from end-of-season dbh measurements.

Estimates of mean volume and volume increment for 1976 may be obtained by evaluating these equations with the dbh distribution of a representative sample of trees. This procedure gives an estimate of mean volume increment =8.32 ($\pm$ 2.48, n=90) dm^3/year for 1976 and mean volume =16.6 ($\pm$ 4.87, n=90) dm^3. Mean volume before the 1976 season (computed as the difference) is 8.3 dm^3(dbh=5.7 cm).

Progressions of VI(t)=f(VOL(t-1)) over time may be used to investigate tree growth as a function of size. Regressions using the stem analysis data were done for t=1974, 1975, 1976, and 1977 for control trees and for t=1977 for trees fertilized over two years (figure 22). For the control, these represent growth in the fifth through eighth growing seasons. Linear regressions were adequate and a test failed to reject the hypothesis: H0: a1=a2=a3=a4=a5=0. Therefore, the regressions were recomputed using the model Y(t)=bX(t-1). All five regression coefficients (b's)

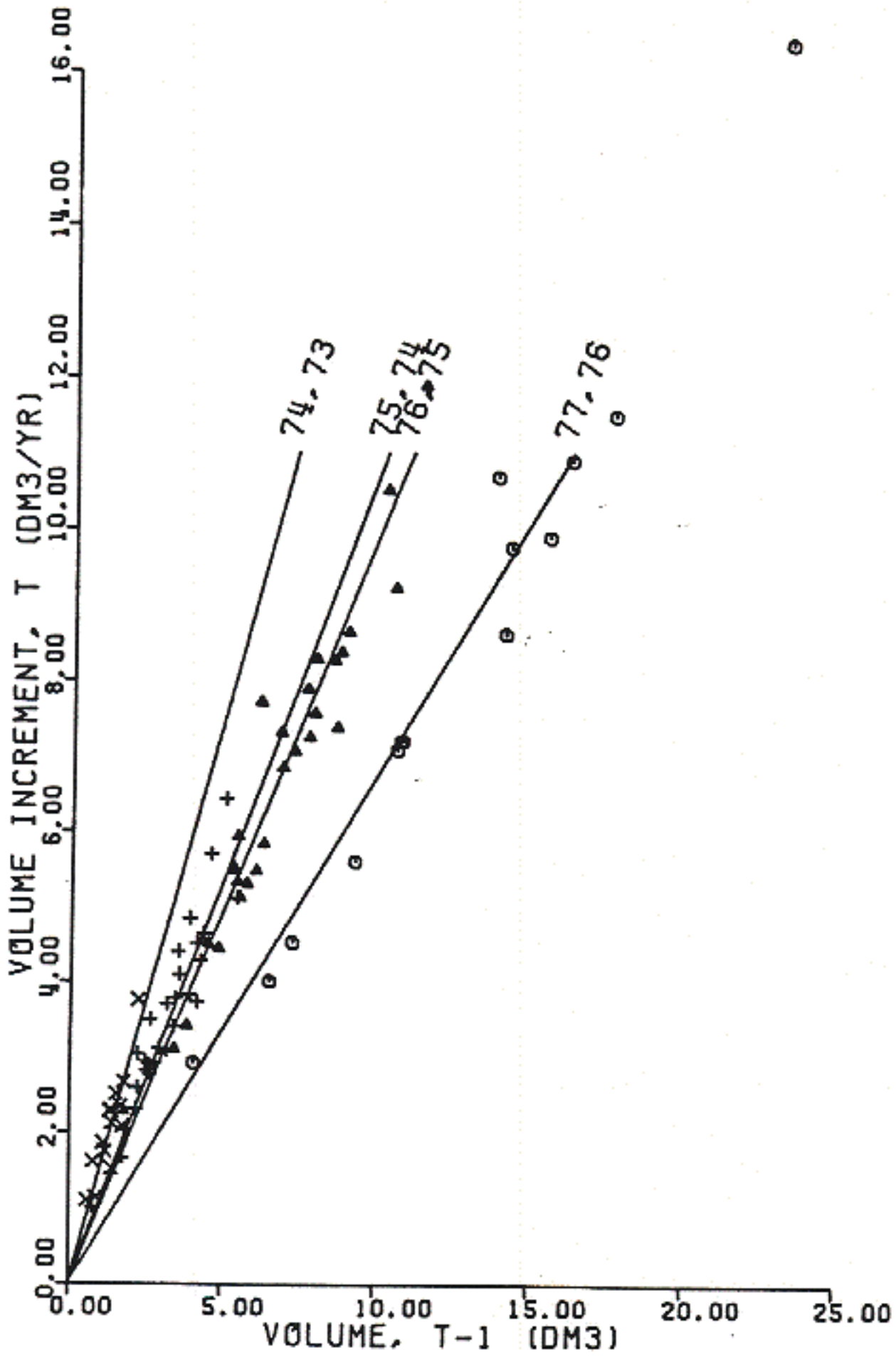


Figure 22. Regressions of stem volume increment versus stem volume before the growing season. Labels represent the year of increment and volume, e.g., 74,73 is 1974 volume increment versus 1973 volume.

were significantly different (table 9), and of relative size $b_{74,73} > b_{75,74} > b_{76,75} > b_{77,76} > b_{77,76\text{-fert.}}$, where for example, $b_{74,73}$ represents the coefficient for the regression of 1974 volume increment versus 1973 volume.

Table 9. Regression coefficients for volume $increment_{(t)}$ versus $volume_{(t-1)}$ functions.

	B	r^2
1977vs1976	0.676	0.97
1977vs1976fert	0.583	0.86
1976vs1975	0.992	0.88
1975vs1974	1.075	0.85
1974vs1973	1.512	0.78

Thus, stem volume increment for a given size tree is age dependent; an older tree will grow more slowly than a younger tree of comparable volume. For example, a four-year-old tree with stem volume= 6.0 dm^3, is expected to grow 9.1 dm^3 in the following growing season, while a seven-year-old tree of comparable stem volume is expected to grow 4.1 dm^3.

The computed coefficients are dependent upon the confounding of tree age with the year of growth, since

all samples were of equal age. However, year-to-year variation is expected to be random, and the regression coefficients show a constantly declining trend, suggesting a true age-dependent effect.

Branch growth

Growth of branches was not measured directly, but total branch weight was measured on the 20 trees used for destructive stem analysis. Branch dry weight at the end of the 1977 growing season, Bb (kg/tree), shows a good correlation with stem volume, VOL (dm^3) (figure 23); this relation is described by

$$Bb=0.12(VOL)^{1.35},\ r^2=0.81.$$

In terms of stem diameter, this relation is

$$Bb=-8.93+1.97(dbh),\ r^2=0.82.$$

Mean branch biomass/tree in 1976 is 6.06 kg/tree (using mean dbh76=7.6 cm).

If an allometric relation between branch weight and stem volume is assumed (i.e., their relative growth is proportional,

$$\frac{d(Bb)}{dt}\cdot\frac{1}{Bb} = k\cdot\frac{d(VOL)}{dt}\cdot\frac{1}{VOL}$$

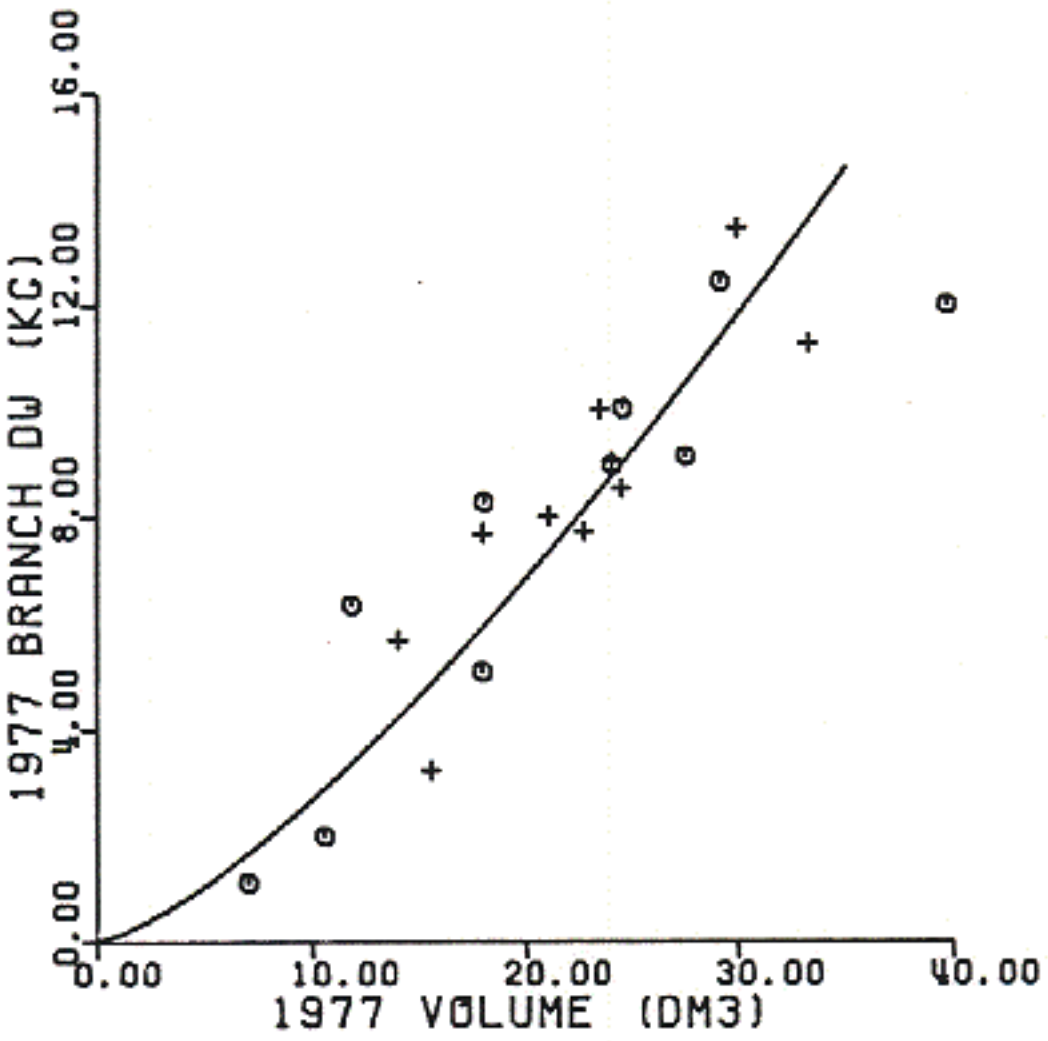


Figure 23. Regression of branch dry weight versus stem volume.

and if the allometric constant in this relation is assumed to be similar to that in the Bb=f(VOL) regression, then 1976 branch growth may be approximated as d(Bb)/dt= 1.35*2.15*8.32/8.3=2.91 kg/tree-year.

N content

The N content of new foliage may be calculated by combining (1) the weight/shoot=f(t) model, (2) the estimate of the number of new shoots per tree, 4225, and (3) measured N concentrations (table 10). This calculation shows increasing content through the growing season, with highest incorporation during the early period of expansion. The incorporation rate for the period from day 156 to day 215 is 18.6 gm/tree for controls and 27.8 gm/tree, or an increase of 50%, for trees fertilized at 600 kg N/ha.

Table 10. Computed N content of new foliage (1976 age class).

Day of year	wt/shoot (gm)	wt/tree (kg)	N content/shoot (mg)				
			cont	100	200	400	600
156	.026	.11	.95	.82	.90	.81	.75
177	.160	.67	3.59	3.49	3.73	3.85	3.53
192	.327	1.38	5.33	5.65	5.95	6.60	6.08
215	.396	1.67	5.35	5.91	6.42	7.45	7.33

The change in N concentration for older foliage over the growing season may be combined with estimates of foliage biomass by age class to give the change in content, redistribution (table 11). A control tree of mean foliage biomass is expected to accumulate 1.9 gm N in older foliage while a tree treated with 400 kg N/ha will accumulate 8.1 gm N. Thus, an accumulation of N in older foliage was estimated for both control and fertilized trees; so redistribution in these trees was by definition -1.9 and -8.1 gm N/tree, respectively. Redistribution was not measured for the other treatments, but if the accumulation of N in older tissue is assumed to parallel that in new foliage (i.e., table 10) redistribution is expected to be -3.8, -5.0, and -7.9 for trees fertilized with 100, 200, and 600 kg N/ha, respectively.

Table 11. Change in N content of old foliage.

	Age Class			
	1975	1974	1973	total
fraction of foliage biomass	.36	.16	.06	
foliage wt/AC (kg/tree)	1.48	.66	.25	
beginning of 1976 growing season				
foliage N conc (%)	1.15	1.07	.89	
content of N/AC (gm)	17.02	7.06	2.23	
change in N conc (%)				
control	.103	.060	.023	
400 fert	.386	.310	.130	
end of 1976 growing season				
content of N/AC (gm)				
control	18.50	7.46	2.28	
400 fert	22.73	9.11	2.55	
change in N content/AC (gm)				
control	1.48	.40	.05	1.9
400 fert	5.72	2.05	.32	8.1

The N concentrations of branch and stem in a site-quality IV, 9-year-old Douglas-fir plantation are 0.39% and 0.19%, respectively (Turner, 1975). Combining these values with the estimates for biomass give approximate N contents (1976) of new branch N= 11.3 gm, branch N= 23.6, new stem wood N=7.3 gm, and

stem wood N= 14.5 gm.

The change in content of the tree, or yearly uptake may be estimated by summing the accumulation of N in new and old tissue (redistribution). For a mean control tree in 1976, this gives 39.1 gm N/tree-year, or for 2000 trees/ha, uptake is 78 kg N/ha-yr. This value is very large in relation to the 17 kg N/ha-yr uptake in site quality IV Douglas-fir stands at Cedar River (Turner, 1977), and reflects the high level of N nutrition in this high-site plantation.

MODEL FUNCTION DEVELOPMENT

Having begun with a general theory of N cycling and the effect of N upon growth, a set of field experiments have been conducted to further develop the theory and provide data for estimates of function parameters. Statistical models have been applied to measured growth and N concentration data to succinctly describe their trends with time and N supply, and test for differences among treatments. The N contents of system components were then calculated from estimates of growth and N concentration. The simulation model

functions may now be developed using these statistical models and estimates.

Growth functions

A hypothetical growth function is proposed that (1) is a function of N concentration in new foliage, (2) has a maximum at high concentrations, and (3) shows a reduction in growth at low concentrations. Specifically, a function is sought that gives growth that is 90% of the maximum rate at 1.75% N, and is 40% of maximum at 1.0% N. These conditions are met by the equation:

$$G=A(1-\exp(-2.31(\%N-0.75)))$$

where G is growth rate in kg/tree-day, %N is new foliage N concentration, and A is the maximum growth rate (figure 24). This growth function is consistent with data from the literature and is used to develop model functions for growth of wt/shoot, number of shoots, and stem, branch, and root biomass.

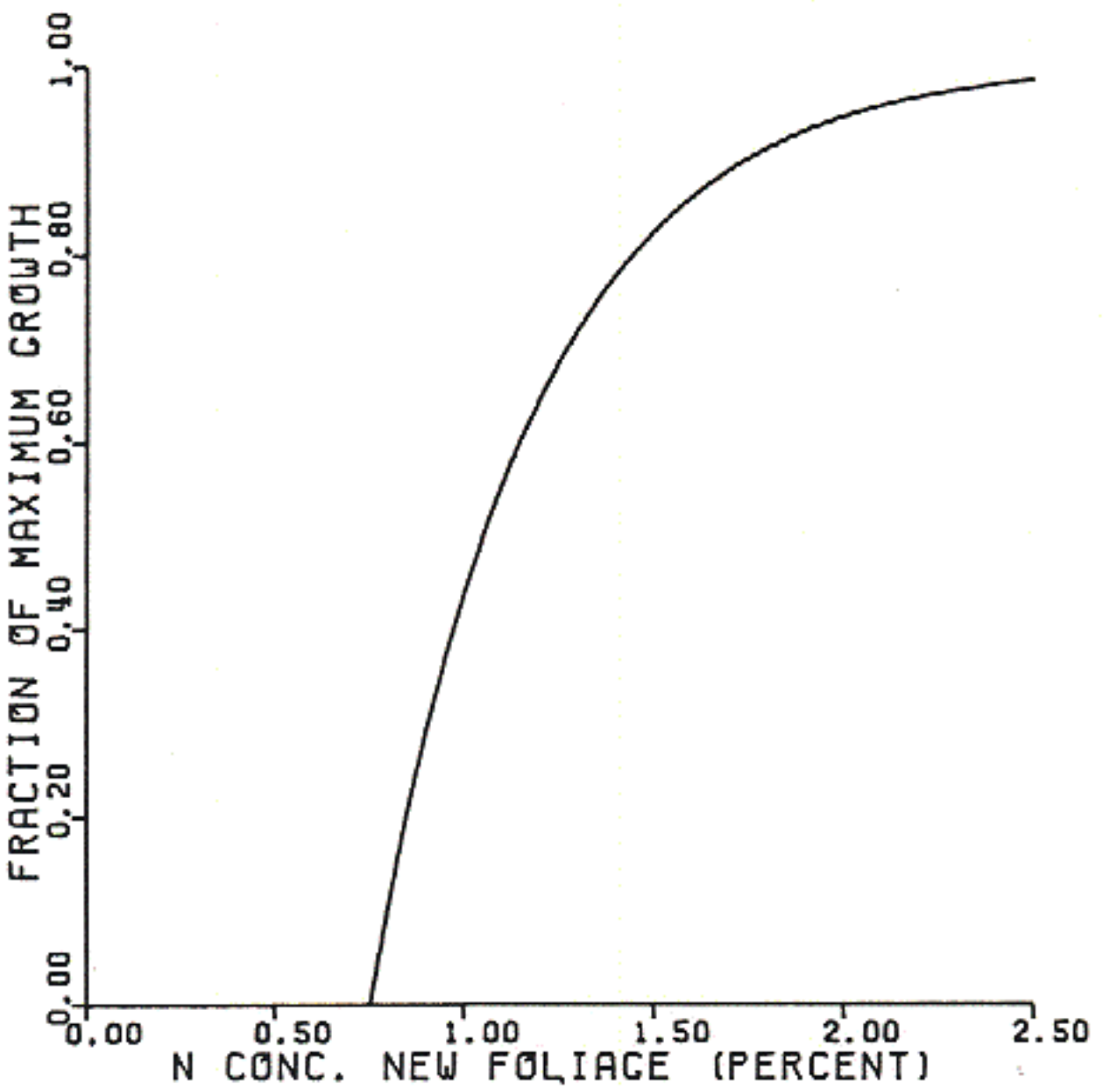


Figure 24. Hypothetical growth function developed from the literature.

Growth per shoot

Foliage growth per shoot, DW, has been statistically modeled for the high-site Douglas-fir as

$$DW = 0.40(1+139.(\exp(-0.142t)))^{-0.66}$$

where t is the number of days since day 150. A function is needed that combines this time trend in development with the G=f(%N) relation (hypothetical growth function). Furthermore, it is assumed that growth may reflect changes in nutrition during the growing season. Therefore, the seasonal progression of %N in new foliage must also be considered.

Evaluating G=f(%N) by the high-site dormant season %N value gives an expected growth rate that is 93% of maximum. Therefore, the above weight/shoot growth function is assumed to be the time course of growth that is 93% of maximum. The growth rate is given by the differential form of this expression.

If total foliage growth (growth per tree) follows the hypothetical growth function, and total growth is composed of terms for weight/shoot and the number of shoots, both of which are related to %N, then each component may follow a relation such as

$$G = A*SQRT(1-exp(-2.31(\%N-0.75)))$$

Thus, growth per shoot is expected to be a function of new foliage N concentration and time of the form

$$dDW/dt=-0.10(3.99DW^{2.51}-DW)(1-exp(-b(t)(\%N-X0(t))))^{0.5}$$

where DW is needle wt/shoot in gm at time t, and b(t) and X0(t) are functions of t.

Now, the seasonal growth of a stand that has a dormant-season N concentration of 1.2% may be estimated from the G=f(%N) relation. It is assumed that the time course of this growth is the same as that for the high site, and the seasonal %N pattern is proportional to that of the high site. The functions b(t) and X0(t) may be estimated using data (1) generated from these assumptions and (2) from the high site. Values for b and X0 are calculated at a range of times, using regression and the transformation $\ln(1-(G/At)^2)=b*X0-b*N$, where G is the growth rate at time t and At is maximum growth rate (with no N limitation) at time t. These values follow trends given by the polynomial regressions

$$b(t)= 1.37-6.12x10^{-3}(t)+1.40x10^{-3}(t^2)-1.17x10^{-5}(t^3)$$

$$X0(t)=1.95-1.07x10^{-2}(t)-7.05x10^{-4}(t^2)+9.28x10^{-6}(t^3).$$

Growth function behavior is illustrated in figure 25.

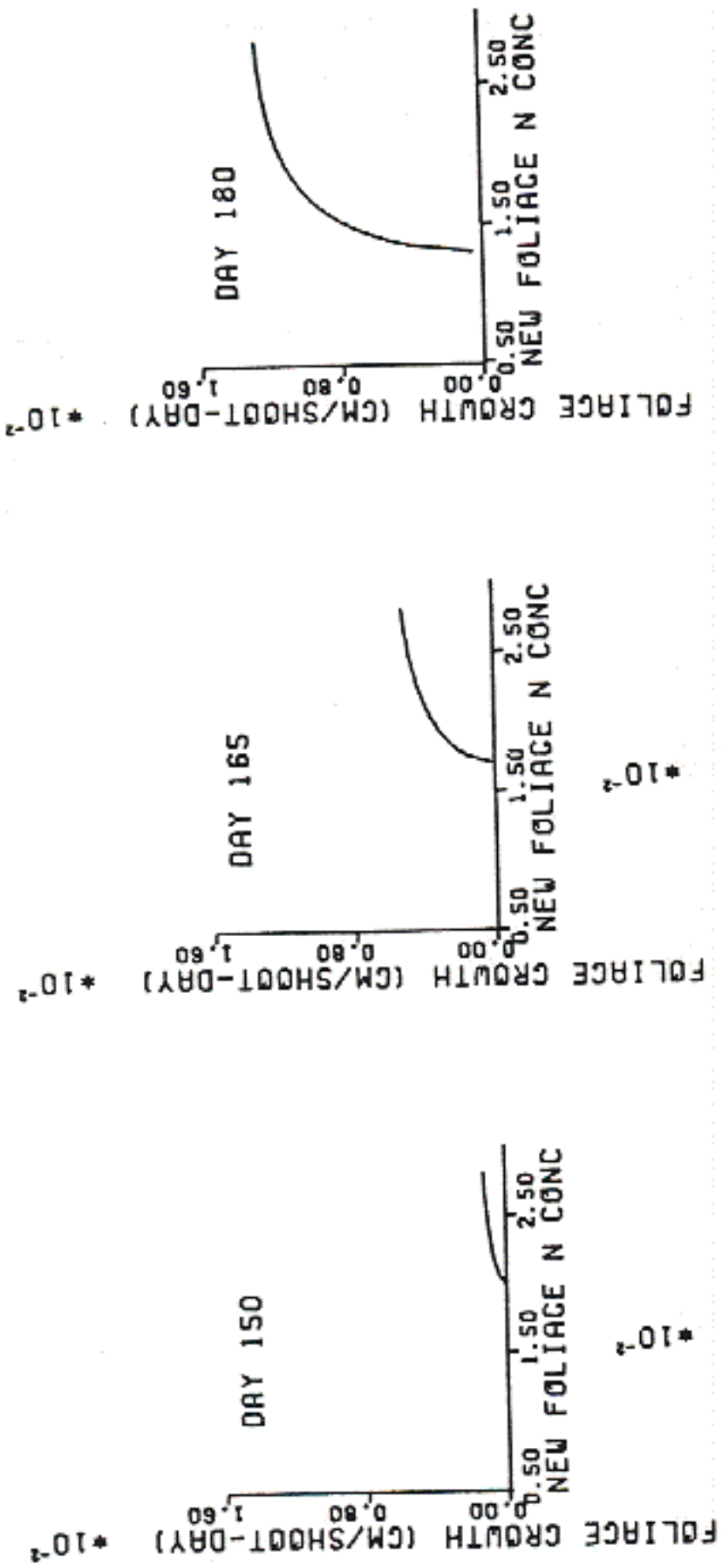


Figure 25. Modeled foliage growth as a function of new foliage N concentration and the day of the year.

Number of developing shoots

The number of shoots produced on a tree is a function of age, or branching development, and the level of N nutrition, presumably early in the growing season when the next season's buds are initiated. It is proposed that the number of shoots produced in a given position is determined by the number of existing shoots in that position, the location of the whorl from the top of the tree, and the location of the position from the end of the branch.

The relative pattern in branching by whorl and position on a branch was examined for the young, high-site trees. The relative pattern is given by ratios of the number of new shoots to the number of existing shoots (figure 7). These ratios are the basis for the shoot branching model. The data are extended by assuming a progression of decreasing ratios with increasing distance from the top of the tree and the end of the branch.

The number of new shoots produced in each position (by whorl and along a branch) on the tree is computed as the product of the existing number in that position,

the appropriate ratio of new to old shoots, and the N limitation computed from the N growth function.

Stem growth

Annual volume increment shows a good functional relation with foliage biomass when comparing different-sized trees. This relation was described for the high-site as

$$Av=2.51\exp(0.187*Fb)$$

where Av is 1977 stem volume increment (dm^3) and Fb is the foliage biomass (kg/tree) measured at the end of the growing season.

Foliage growth may respond to fertilization the year following application by a change in weight/shoot, but volume increment responds only the second season. The number of new shoots, SHN, similarly responds the second year only, suggesting that volume increment is related to the number of new shoots (perhaps via a growth regulator), and not necessarily foliage biomass.

A function VI=f(t,SHN) may be derived if Fb in the above relation is replaced by SHN. Fb and SHN were

earlier found to be related by

$$Fb=9.75\times10^{-4}(SHN).$$

Combining these relations gives

$$VI=2.51\exp(1.82\times10^{-4}(SHN)).$$

This relation is assumed to similarly describe volume increment as a function of SHN across different ages (as well as different-sized trees). Also, the timing of growth during the year is assumed to follow a Chapman-Richards equation with parameters similar to those for foliage growth. Thus, volume growth, Gv (dm^3/tree-day), is given by

$$Gv=-0.094(Av^{-1.51}*VOL^{2.51}-VOL)$$

where VOL is new stem volume (dm^3). Stem biomass growth, Gs (kg/tree), is given by Gs=Gv*DENS, where DENS is stem wood density (=0.46 kg/dm^3).

Branch growth

An allometric relation between annual branch growth, Ab, and volume increment is assumed, i.e.,

$$Ab=a*Bb*VI/VOL,$$

where Bb is branch biomass (kg/tree), VOL is stem volume, and "a" is an allometric constant. The allometric constant is assumed to have a value similar

to the constant, 1.35, from the branch biomass versus volume equation developed earlier. If the timing of branch growth is assumed to parallel that of foliage growth, then branch growth, Gb (kg/tree-day), is given by

$$Gb=-0.094(Ab^{-1.51}*Bn^{2.51}-Bn)$$

where Bn is new branch biomass.

Large root growth

A function analogous to that used for branch growth is used to simulate large root growth. Presumably, large root growth, which accounts for sizable amounts of N incorporation in roots, occurs during the growing season. An allometric relation with above-ground biomass is assumed. The allometric constant (0.9) is assumed to be similar to the value in the relation between root biomass, Br, and above-ground biomass, ABG, given by Dice (1970):

$$Br=0.29(ABG)^{0.9}$$

Thus, large root growth, Gr (kg/tree-day), is given by

$$Gr=-0.094(Ar^{-1.51}*Br^{2.51}-Br)$$

where Ar=0.9*Br*Ag/ABG, with Ag equal to the annual above-ground biomass increment.

Fine root growth

Fine root biomass is modeled using the following assumptions.

1. During any year, maximum fine root biomass is approximately 8/3 of the minimum (Harris and Todd, 1972).
2. Minimum biomass at age 6 is approximately 1 ton/ha.
3. Fine root production is from late April through early September.
4. Mortality removes only part of the year's production in a developing stand (equal to the previous year's production).
5. Mortality is from August 1 to November 1 with the rate following a parabolic function with time.
6. Production is proportional to the number of new shoots developing.

From the simulated biomass, fine root length per tree is calculated by assuming: absorbing root radius =0.04 cm, specific gravity (dry wt. basis) =0.2gm/cm^3 (C. Grier, pers. Comm.), 2000 trees/ha, and a 30 cm rooting depth. A one ton/ha biomass gives $5.x10^{+5}$cm root/tree. 75% of this is assumed to be in the top 15 cm, and 18% is in the 15-30 cm depth

(Roberts, 1976). An exponential distribution of rooting density with depth is assumed.

N uptake

Uptake by the tree is dependent on the amount of absorbing roots and uptake per unit root. As discussed earlier, uptake per unit root follows Michaelis-Menten kinetics at low concentration ranges. Uptake at high concentrations may be approximated by an equation of similar form. If uptake in the two concentration ranges is additive, a combined, empirical equation of a similarly hyperbolic form will describe the uptake process.

While roots absorb ammonium from the solution phase, a much larger reservoir of exchangeable ammonium is in direct equilibrium with the solution phase, and on a time scale of days, represents the pool from which roots draw N.

Thus, tree uptake, UP (kg N/tree-day), is described by the relation

$$UP = f(R)*Vmax*exNH4/(Km+exNH4)$$

where f(R) is a function of absorbing root biomass and Vmax is maximum uptake per unit absorbing root.

The constants Vmax and Km for whole-tree uptake may be estimated from the high-site fertilization data. Change in N content for the tree for a given time interval, dN, is the integral over time of the combined instantaneous uptake rate equation and exchangeable ammonium time course, i.e.,

$$dN=\int Vmax*f(exNH4)dt/(Km+f(exNH4)$$

where f(exNH4)= a*exp(-bt). It is assumed that absorbing root biomass is relatively stable over the time interval studied. Integration for each of the fertilizer treatments and control will yield a series of equations in Vmax and Km, the intersection of which will give an estimate of these parameters (figure 26).

Using dN (whole tree estimates) for day 156 to 215, the soil exchangeable ammonium model, and integrating, the above equation becomes

$$dN = Vmax/b *\ln((Km+a*exp(-65b))/(Km+a*exp(-6b))).$$

The uptake equation parameter estimates that give consistent agreement with the results for the control, 400, and 600 kg /ha treatments are Vmax=1.24 gm N/tree-day and Km=4 ppm.

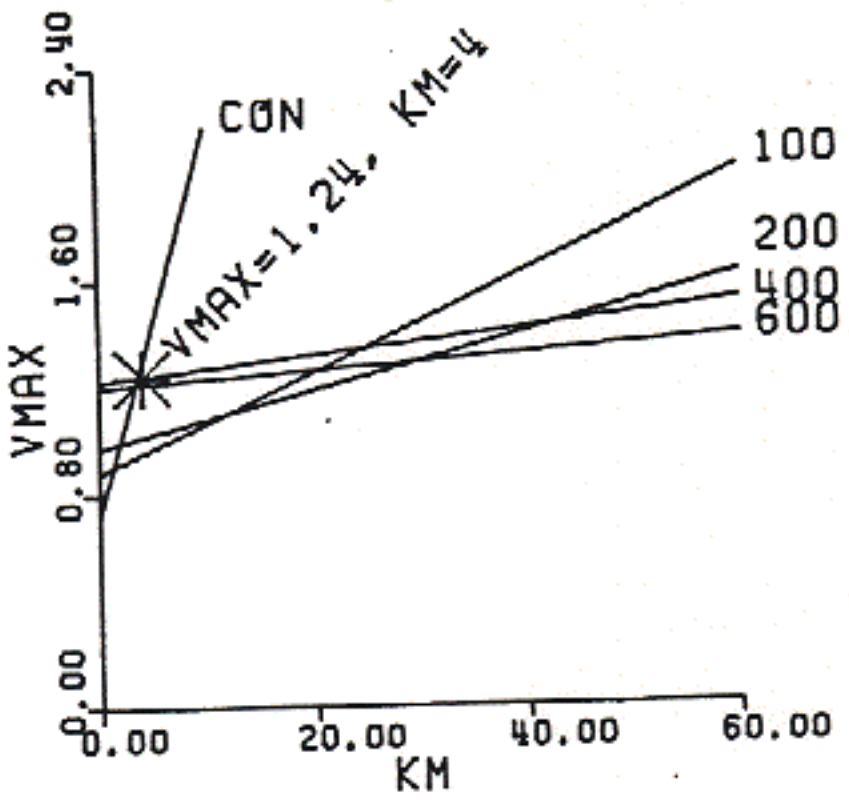


Figure 26. Simultaneous equations for the uptake equation parameters: Vmax as a function of Km.

This Km (ppm exchangeable ammonium) value corresponds with a Km in terms of solution ammonium concentration of approximately 0.2 ppm, since the ratio of exchangeable ammonium concentration to solution ammonium concentration is about 20:1 (D.W. Johnson, pers. Comm.). This compares favorably with the value of 0.21 given for Pinus radiata (Flewelling, 1977). Assuming a 500 gm fine root biomass per tree and the Vmax value (per gm root) estimated for Pinus radiata , Vmax (per tree) is 1.25 gm N/tree-day. This compares well with the estimate just made for Douglas-fir, 1.24.

The expected change in N content by treatment for these parameter values may be compared with the experimental data (figure 27). The expected values show a rapid rise for this time period with application of 100 or 200 kg N/ha. Applications at higher rates will not greatly alter this change in N content.

Given a low value of Km, higher rates of application saturate the uptake mechanism and little difference in uptake among treatments is expected. Over a longer period of time, a larger difference may occur since a higher application rate will maintain elevated soil exchangeable ammonium longer than a lower

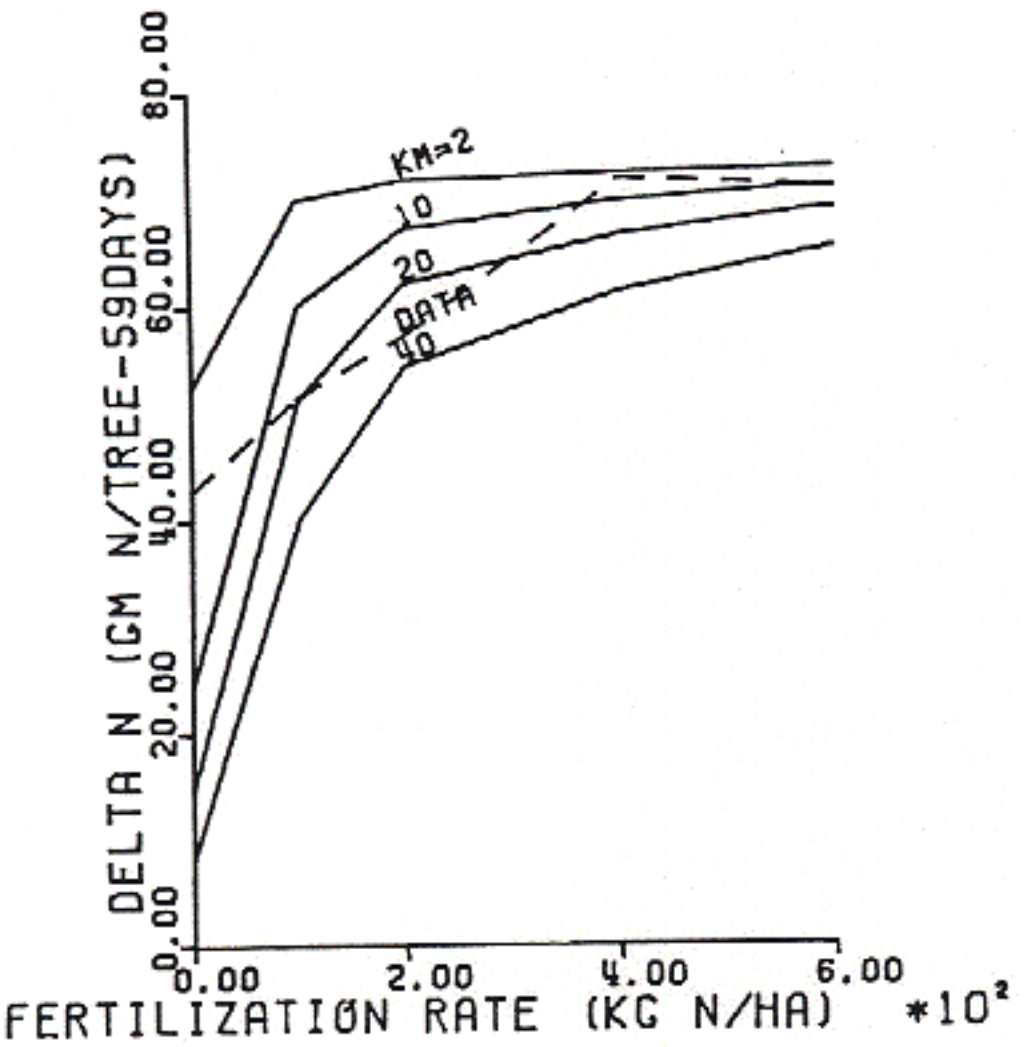


Figure 27. Expected and measured values of N uptake over 59 days versus the fertilization rate.

one.

This uptake model should be adequate for the short periods of time needed to estimate parameters. However, it is inadequate for multi-year simulations, since it inherently assumes that exchangeable ammonium is equally available to both absorbing fine roots and microorganisms. This assumption is invalid since ammonium diffusion through the soil is slow and zones of depletion will develop about the root. Therefore, an uptake model accounting for changes in fine root density and ammonium diffusion to the root surface must be developed.

In this expanded model, the ammonium content of cylindrical increments of soil about a root of given length is simulated. Flux between cylindrical increments is given by the diffusion equation developed earlier, and uptake from the inner-most cylindrical increment. The length of root simulated is the length per cm^2 of ground area in a depth increment of soil.

The number of cylindrical increments simulated depends on their width and the average amount of soil about the root. As fine root length increases, the

average amount of soil about a cm of root decreases. The growing root is assumed to encounter soil with an ammonium concentration of the outermost increment. Conversely, fine root death and a decreasing root length removes ammonium from the vicinity of the root surface.

A temperature dependence for the uptake rate with a Q_{10} value of 2.0 is assumed; the rate will double for each 10 degree C increase in temperature:

$$Up=Up,19.6 * Q_{10}^{0.1(T-19.6)}$$

where Up,19.6 is the uptake rate at a temperature, T, of 19.6 degrees C. Average temperature is given by

$$T=Tyr+0.5(Tmx-Tmn)*\sin(0.0172(DAY-92-k1),$$

where Tyr is the annual mean temperature =12.5, Tmx is maximum daily mean temperature = 20., Tmn is minimum daily mean temperature =5., k1 is the number of days after July 1 when the maximum occurs =10., DAY is the day of the year, 92 is a timing factor in days, and 0.0172 is 2Pi radians/ 365 days.

N accumulation in new foliage

N accumulation in expanding foliage is essentially protein accumulation and is assumed to be functionally related to the concentration of free amino acids in that foliage. Presumably, this concentration-dependent accumulation is complicated by compartmentation within the cell, and developmental changes in the ribosomes. In particular, the whole-tissue free amino acid concentration may not be equivalent to that at the site of protein synthesis (ribosomes). Development of cell walls and other cellular constituents may change whole-tissue concentrations with unknown effects upon concentration at the ribosomes. Also, the determinate growth pattern will require synthesis of different proteins, and different amounts of protein, as development proceeds. Therefore, the model will describe an inherent (although empirical) pattern of N accumulation that is functionally related to whole-tissue free amino acid-N concentration.

The accumulation of N in new foliage at the high site was estimated from the weight/shoot model and interpolated N concentration data. Control tree data was used as a base, and concentrations for other

treatments by time were calculated using the proportional differences measured on day 215, and an assumed starting concentration of 3.4% (on day 150). The change in N content, dN/dt (mg N/shoot-day), for 10 day intervals from day 150 through day 260 was plotted versus interpolated values of free amino acid-N concentration, Cam. It was assumed that dN/dt=0 when Cam=0. Thus, the model

$$dN/dt=A(t)*(1-\exp(-b*Cam))$$

was assumed, where A(t) is the maximum rate as a function of time (figure 28). Assuming the highest application rate produces accumulation that is 95% of the maximum, the parameter "b" was determined by fitting the data for each date in figure 28. The model is insensitive to the small changes in "b" among dates, so a mean value of 32.0 is used. The maxima, A(t), follow a parabolic function of time. Combining these functions with the number of expanding shoots, SHN, and converting from mg to gm, gives a function for new foliage accumulation, ACN(2) (gm/tree-day), given by

$$ACN(2)=(0.20-3.57\times10^{-4}(t-24.5)^2$$
$$*(1-\exp(-32.*Cam))*SHN/1000,$$

where t is the number of days since day 150. This function is subject to the conditions that for $25<t<110$, and $ACN(2)<0.034$,

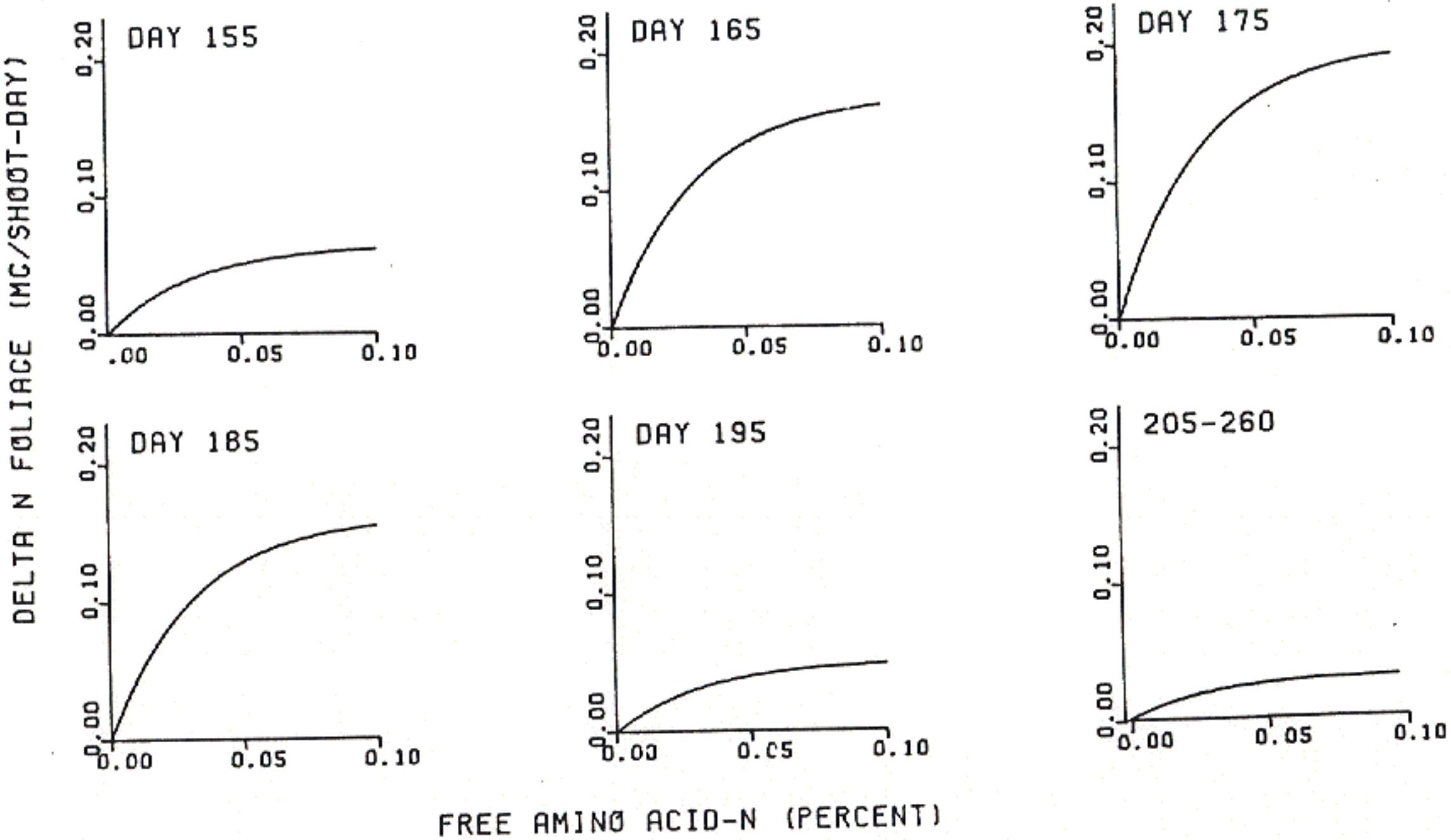


Figure 28. Modeled new foliage N accumulation as a function of free amino acid-N concentration and the day of the year.

ACN(2)=0.034(1-exp(-32.*Cam))*SHN/1000.

Change in N content in old foliage

The accumulation of N in old foliage with fertilization and the redistribution from older to newer foliage, are a net synthesis and net degradation of protein, respectively, and are considered here as the same process. Accumulation should be responsive to changes in nutrition during the growing season. It is assumed that the change in content for, say one-year-old foliage, ACN(3) (gm N/gm dry wt-day), is a function of free amino acid-N concentration, %N in the one-year-old age class, and time. Free amino acid-N concentration in new foliage is used as an index of concentration of that component of tree N. %N is assumed to be proportional to foliage protein concentration. An inherent pattern of accumulation during the growing season is assumed. Furthermore, accumulation is assumed to be a linear function of Cam and of %N, and a quadratic function of time. Thus, a general function of the form

ACN(3)=a(t,%N)+b(t)*Cam

is assumed, with

$$a(t,\%N)=a2+b2*\%N,\ b(t)=a3+b3(t-30)^2$$

$$a2=c2+d2(t-30)^2,\ b2=c3+d3(t-30)^2.$$

These are combined to yield

$$ACN(3)=c2+d2(t-30)^2+\ (c3+d3(t-30)^2)*\%N\ +$$

$$(a3+b3(t-30)^2)*Cam$$

As a constraint, each parabolic function of time is assumed to be zero at t=0 and 60 (day 150 and 210), that is, ACN(3)=0 before and after the growing season. Thus, d2=-c2/900, d3=-c3/900, and b3=-a3/900. Rearranging,

$$ACN(3)=c2*t(60-t)/900\ +\ c3*t*\%N(60-t)/900\ +$$

$$a3*t*Cam(60-t)/900.$$

The assumed changes in N content (using the differences in N concentration between successive age classes) over the 60-day period for the high-site control, high-site fertilization at 400 kg N/ha, and an intermediate-site control, are $-1.45x10^{-3}$, $3.9x10^{-3}$, and $-1.15x10^{-3}$ (gm N/gm dry wt-60 days), respectively. Using these values and the assumed parabolic trend with time, values of ACN(3) were calculated. Multiple regression of these values on interpolated Cam and %N data yield regression coefficients of $c2=-8.0x10^{-5}$, $c3=-2.4x10^{-5}$, and $a3=2.3x10^{-3}$.

The model should relate accumulation to the level of nutrition and not necessarily changes in concentration due to a dilution effect from growth or redistribution in the older tissue. Despite the parabolic model, the simulated changes in content will not show such a time trend unless the inherent patterns in concentration of free amino acid-N and total N are considered. Therefore, these concentrations were related to those of the high-site control at the beginning of the season via polynomial regressions:

$$\%Nr=\%N-(100*(-3.63x10^{-5}t+4.03x10^{-8}(t^3/3-30t^2+900t)))$$

$$Cam,r=Cam+0.082-(0.016+8.92x10^{-6}(t-86.)^2).$$

These relative concentrations, Cam,r and %Nr, are used as independent variables in the accumulation model. The rate of change in N content, ACN(3), with time for high- and low-site controls, and high-site fertilization are shown in figure 29.

Mineralization / immobilization model

It was shown earlier that soil exchangeable ammonium following fertilization may be described by the function

$$exNH4=a*exp(-b*t)$$

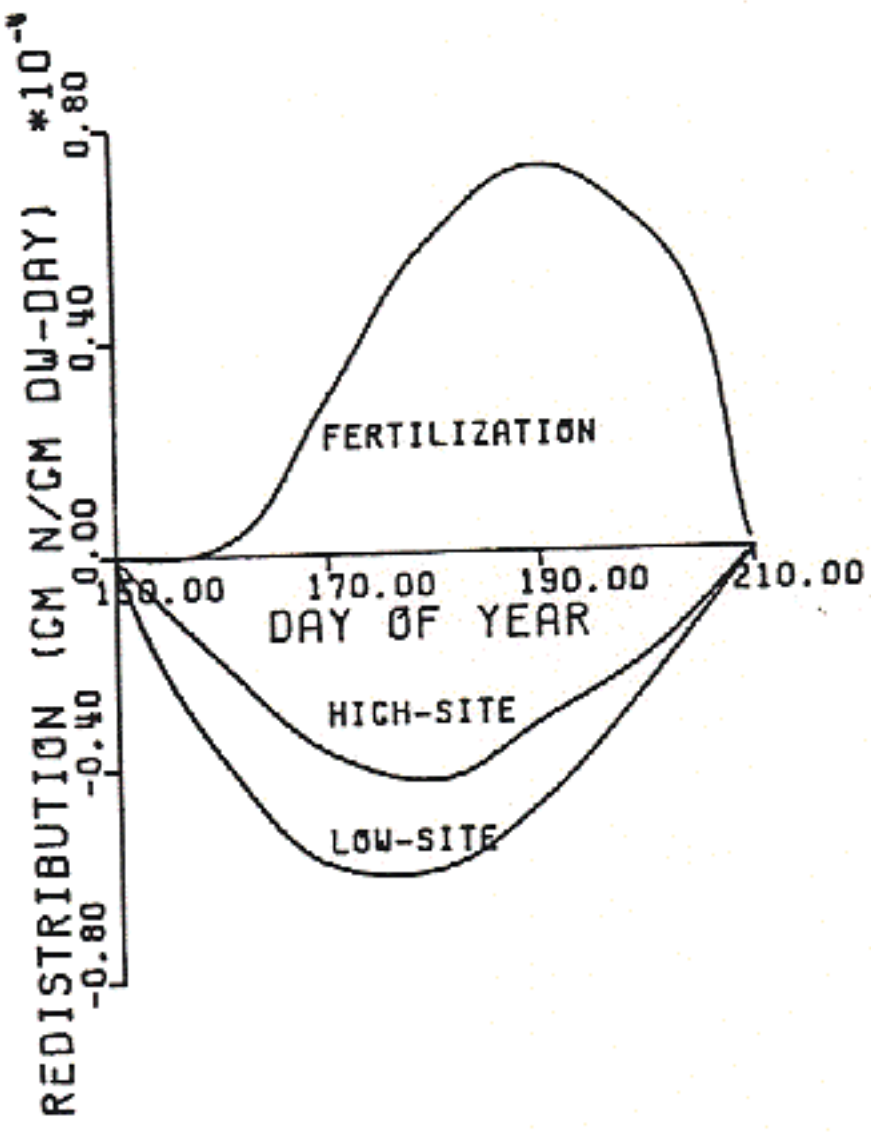


Figure 29. Modeled redistribution of N from old foliage to new.

where "a" is a treatment specific constant representing initial concentration and b=0.026 is the relative rate of change in ammonium with time,

$$d(exNH4)/dt=-b(exNH4).$$

This expression is approximately the rate of immobilization of applied N, since in comparison with the decline in exchangeable ammonium, expected rates of uptake and mineralization are small.

Mineralization of N from fresh litter may be rapid initially with subsequent decline as readily mineralized compounds are exhausted. Presumably, the majority of organic N compounds in old litter and soil are decomposition-resistant and release mineral N slowly. Changes in this pool of slowly-available-N are small over a few years time, so mineralization from this material is expected to be relatively constant. This is reinforced by the observation that over a range of different-aged stands older that 22 years, the increasing forest floor N contents are a linear function of stand age and litter inputs are constant, so that net mineralization may be inferred to be relatively constant (Turner, 1975).

Thus, the net mineralization / immobilization rate is composed of two terms. The positive term represents a constant mineralization rate of fairly resistant organic N compounds, and a mass-dependent rate for fresh litter. The negative term is the concentration-dependent ammonium immobilization rate:

$$d(exNH4)/dt=[K1+K2(Lf)]-0.026(exNH4).$$

Litterfall

Following senescence of old foliage and litterfall (about Sept. 20), at least 3 age classes of foliage are retained in young Douglas-fir (high-site). No senescence is observed in the most recent two age classes. Senescence of needles in the third age class occurs for those needles attached to the main axis of a branch. Little senescence occurs for those needles attached to internodes of higher-order branching. Loss of needles in the fourth age class removes most remaining needles from that age class.

In 42-year-old Douglas-fir at Cedar River, retention is approximately one year longer and may be increased by fertilization (as calculated from

litterfall measurement and estimates of foliage biomass and the weight/age class)(Gessel and Turner, 1976). Assuming 2040 kg foliage /ha in an age class, biomass =9080 kg/ha, and that all but the last age class is complete, retention may be described as a function of %N in one-year-old foliage by the relation:

$$FR=4.9(1.-\exp(-3.15(\%N-0.39))).$$

For the younger stand, one less age class is retained than in the 42-year-old stand, so 1.0 is subtracted from this expression. Litterfall may be simulated as the difference between the current number of age classes (on day 265) and the number retained, multiplied by the foliage weight in each fractional age class lost.

SIMULATIONS AND DISCUSSION OF THE EXPERIMENTAL HYPOTHESES

These model functions (rate equations) are combined to yield differential equations for each of the state variables. These equations are the sum of inputs and outputs for each state variable as shown in figure 1. For example, the rate of change in whole-tree amino acid-N with time is dy/dt=UP-ACN. The

differential equations are solved numerically; a first-order Euler solution with 0.05 day time step is used for soil processes and a second-order Adam's method with 0.5 day time step is used for other state variables. N concentrations throughout the system are calculated at the end of each time step.

N uptake and accumulation in new and old tissue and whole tree amino acid trends during the dormant season are uncertain. Rates of transfer are low during this time but preliminary simulations show that N accumulation during the growing season depends not only on current uptake and old foliage N redistribution but on supply from other storage sources within the tree. N absorbed from the soil during the dormant season is probably distributed and accumulated at these storage locations. In the model this source is the free amino acids and some storage protein. Therefore, a preliminary simulation was made with new foliage amino acid-N concentration forced via a regression equation. The whole-tree amino acid state variable was simulated and its initial condition varied until its seasonally-minimum value was equal to the minimum new foliage concentration. New foliage amino acid concentration was then correlated with this variable.

This correlation was used in further model simulations; new foliage amino acid-N concentration is calculated as 0.46 of the whole tree amino acid-N concentration.

The soil process equations (diffusion, uptake, mineralization/immobilization) were isolated from the overall model and examined under conditions of constant root density to evaluate the experimental hypothesis that uptake is largely determined by the soil mineralization rate. This evaluation consists of a series of sensitivity analyses in factorial design with three factors; maximum uptake, Vmax (gm N/tree-day); the gross mineralization rate; and fine root length, Rl. The gross mineralization rate given earlier as K1+K2(Lf) was simplified to a constant rate, Cmn (kg N/ha-day), for this analysis.

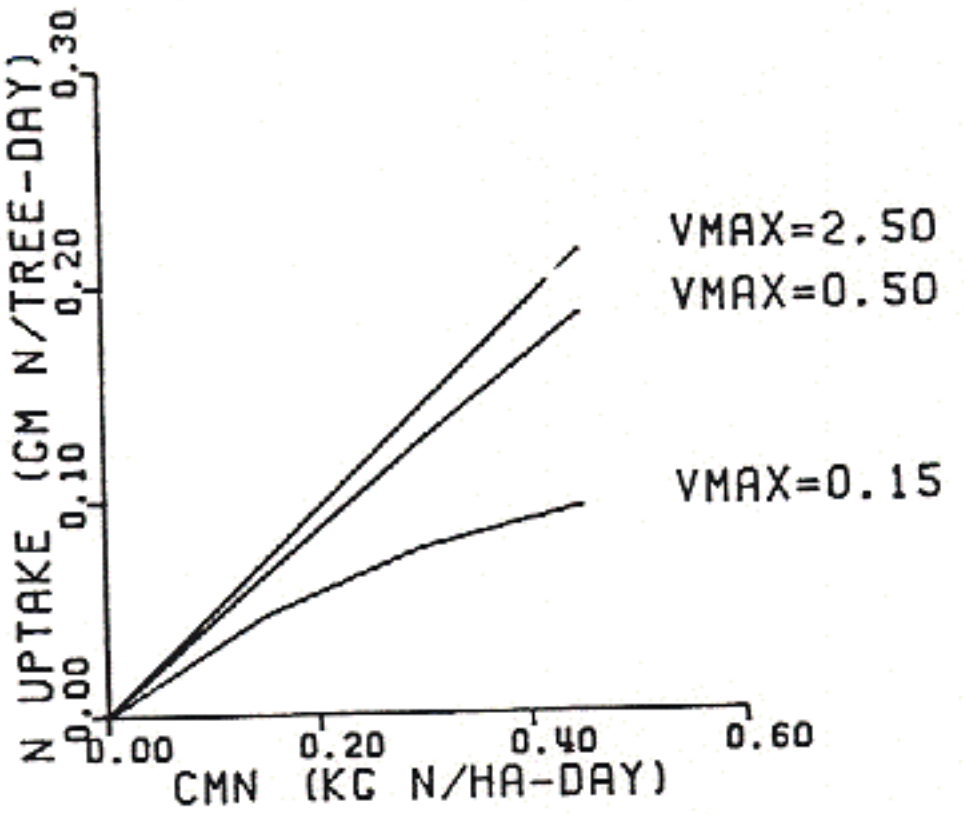
This evaluation considers the relative importance of the inherent maximum uptake rate, Vmax, and the gross mineralization rate at a range of rooting densities. If tree uptake is sensitive to changes in Cmn and relatively insensitive to changes in Vmax, the hypothesis is substantiated. Conversely, relative insensitivity to Cmn rejects the hypothesis. Again, this evaluation depends on the values of other

parameters in the model (such as root density), and the result is applicable to the system that these values describe.

For the high-site-quality stand, simulations indicate that a growing-season uptake rate of approximately 0.18 gm N/tree-day may be expected for a soil exchangeable ammonium concentration of 5 ppm. Given Vmax=1.25, values of Cmn=0.35 and $Rl=1.1x10^{6}$ may be inferred from this sensitivity analysis.

The results of this analysis show that tree uptake is extremely insensitive to changes in Vmax over the range from 0.5 to 2.5 (the best estimate is 1.25) regardless of rooting density or gross mineralization rate. Over this same range in Vmax, tree uptake is an approximately linear function of Cmn and is sensitive to changes in that parameter; doubling the mineralization rate doubles tree uptake (figure 30).

This analysis also shows that increasing root length (and density) results in rapidly increasing tree uptake for root lengths less than about $1.x10^{6}$cm/tree (figure 31). This rate of change in uptake per change in root density, d(Up)/d(Rl), is larger at higher



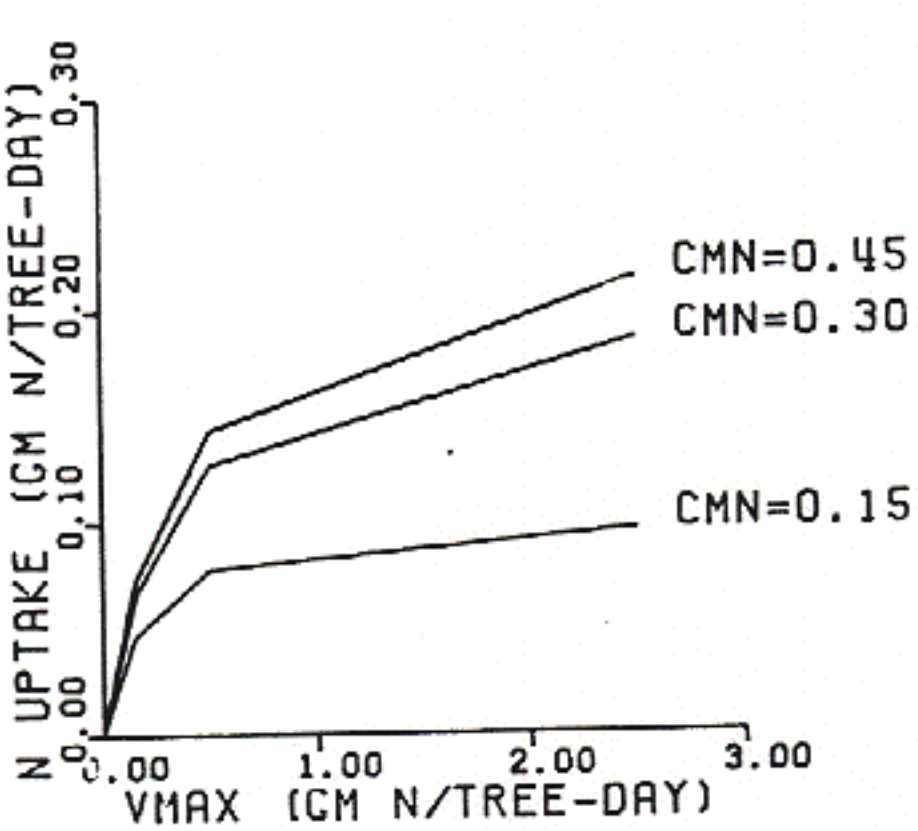


Figure 30. Simulated N uptake as a function of maximum instantaneous uptake rate, Vmax, and the mineralization rate constant, Cmn.

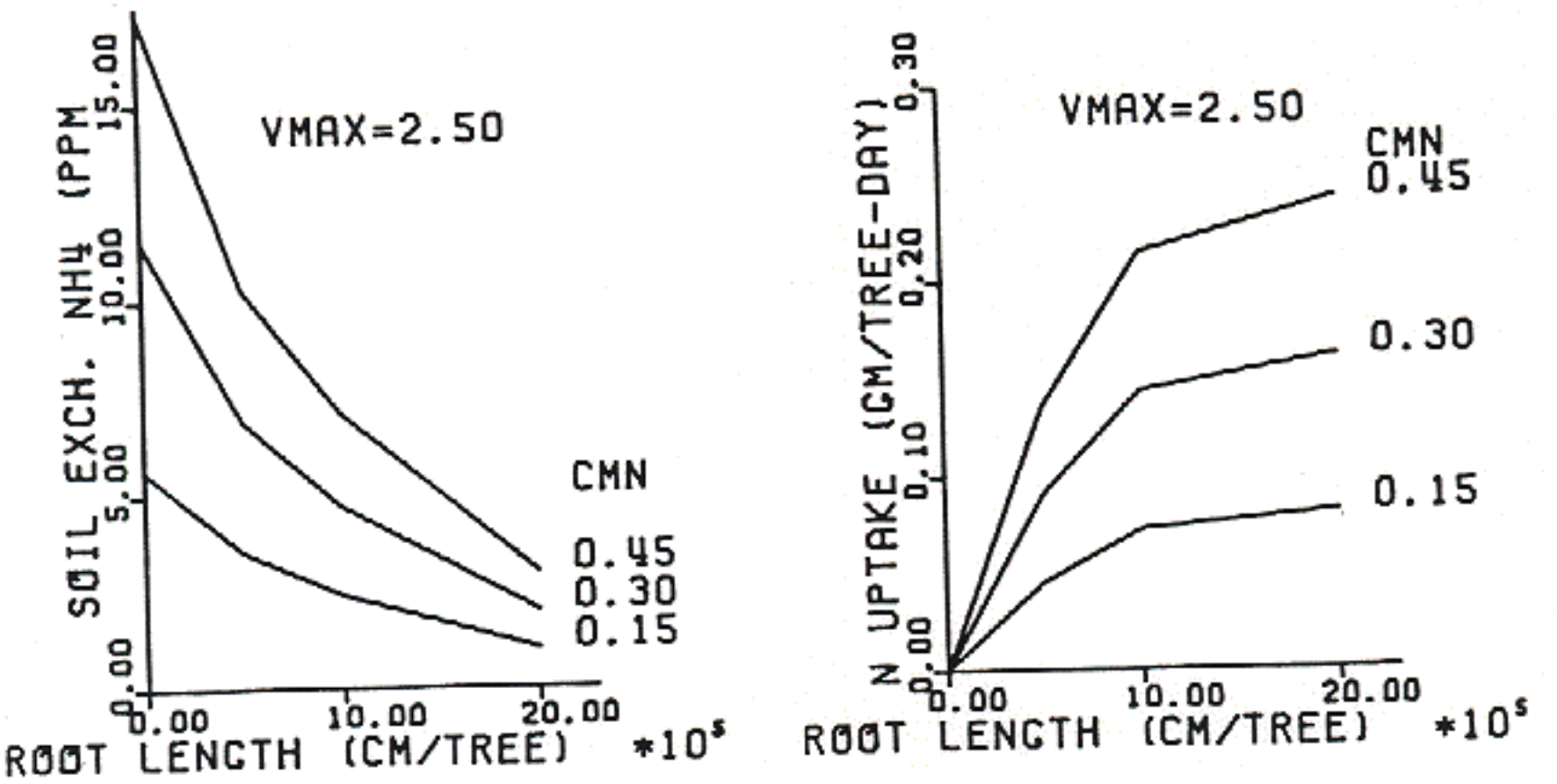


Figure 31. Simulated N uptake and soil exchangeable ammonium concentration as a function of Vmax, Cmn, and root length.

values of Cmn. Thus, at high mineralization rates, an increase in root density produces a larger margin of return in sorbed N than would a similar increase at low mineralization rates. However, as length increases beyond about $1.x10^{5}$, d(Up)/d(Rl) approaches zero.

Thus, the experimental hypothesis that tree uptake is effectively controlled by the soil mineralization rate has been substantiated. With mineralization producing soil ammonium, and immobilization, uptake, and leaching loss via nitrification (which is small) removing ammonium at rates proportional to its concentration, steady-state uptake will approximate net mineralization.

Considering trees with different maximum uptake rates, perhaps genetically determined, a higher Vmax will produce a higher uptake rate. However, as Vmax increases beyond a low value, the ammonium concentration at the root surface will approach zero and the gradient about the root will approach a maximum, as will the tree's uptake rate. Similarly, increasing root density will intensify competition with microorganisms for newly mineralized N and subsequently increase uptake. But as density continues to increase,

uptake will increase more slowly as depletion zones overlap more severely, reducing the gradient about the root. Both a high Vmax parameter and a high root density will be associated with a high energy and material cost to the plant and will supply only a diminishing return in acquired N.

The full model was used to simulate two young, intermediate-site-quality stands with different levels of (gross) soil N mineralization (Cmn=0.4 or 0.25), and a fertilization of 400 kg N/ha in the low mineralization stand. These simulations will allow the examination of the homeostatic properties of the redistribution mechanism, and the effect of system N transfers on the tree's growth response to N fertilization. All simulations begin with the same initial conditions for a seven-year-old stand and simulate nine years of growth.

Since these hypothesis tests are contingent upon the model's plausibility, the model functions must combine to produce a stable system, and reproduce the known behavior of the forest stand. Unrealistic model behavior may suggest inadequacies in the conception of the forest system. Given the model's validity,

multi-year simulations will show the long-term consequences of hypotheses incorporated in the model.

New foliage N concentration is a sensitive indicator of model stability. It responds to changes in rates of N uptake and accumulation (including redistribution), and indicates the nutritional status of the tree. The simulated first year pattern for the low mineralization stand shows a decline from the 3% initial condition to 1.32% as foliage expands, while an end-of-season concentration of 1.46% is shown for the higher mineralization rate.

In a developing stand, simulation indicates that the dormant-season new foliage N concentration will decline until around age 11. Thereafter, it stabilizes at 1.19% under low mineralization conditions and at 1.36% with higher mineralization (figure 32).

Free amino acids are a transfer point linking uptake and N distribution within the tree. This component has high turnover relative to its size and achieves a quasi-steady-state (figure 33). A rapid decline during the growing season with a return to a dormant-season maximum is indicated. This suggests

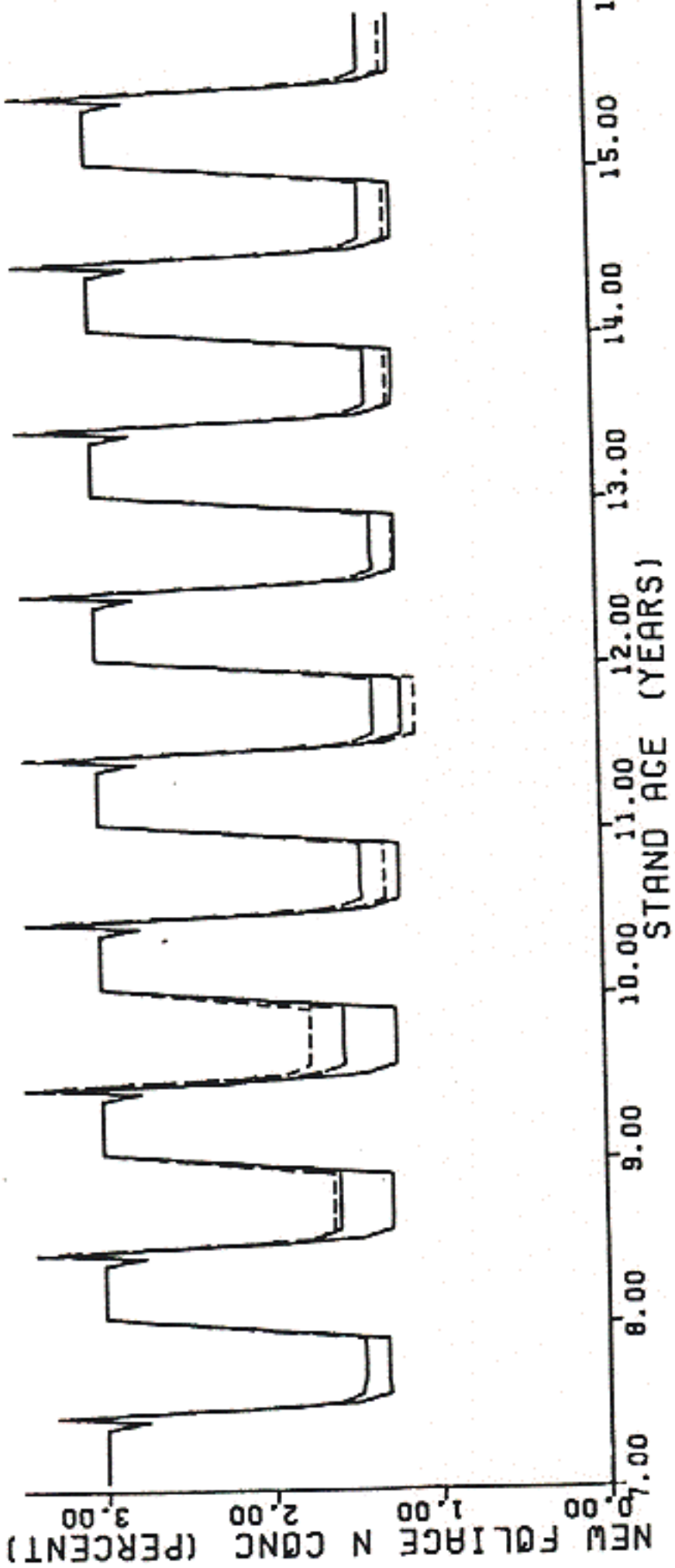


Figure 32. Simulated new foliage N concentration versus time for a low mineralization rate (solid line), high mineralization rate (heavy dashed line), and fertilization (light dashed line). Fertilization is at year 8.5.

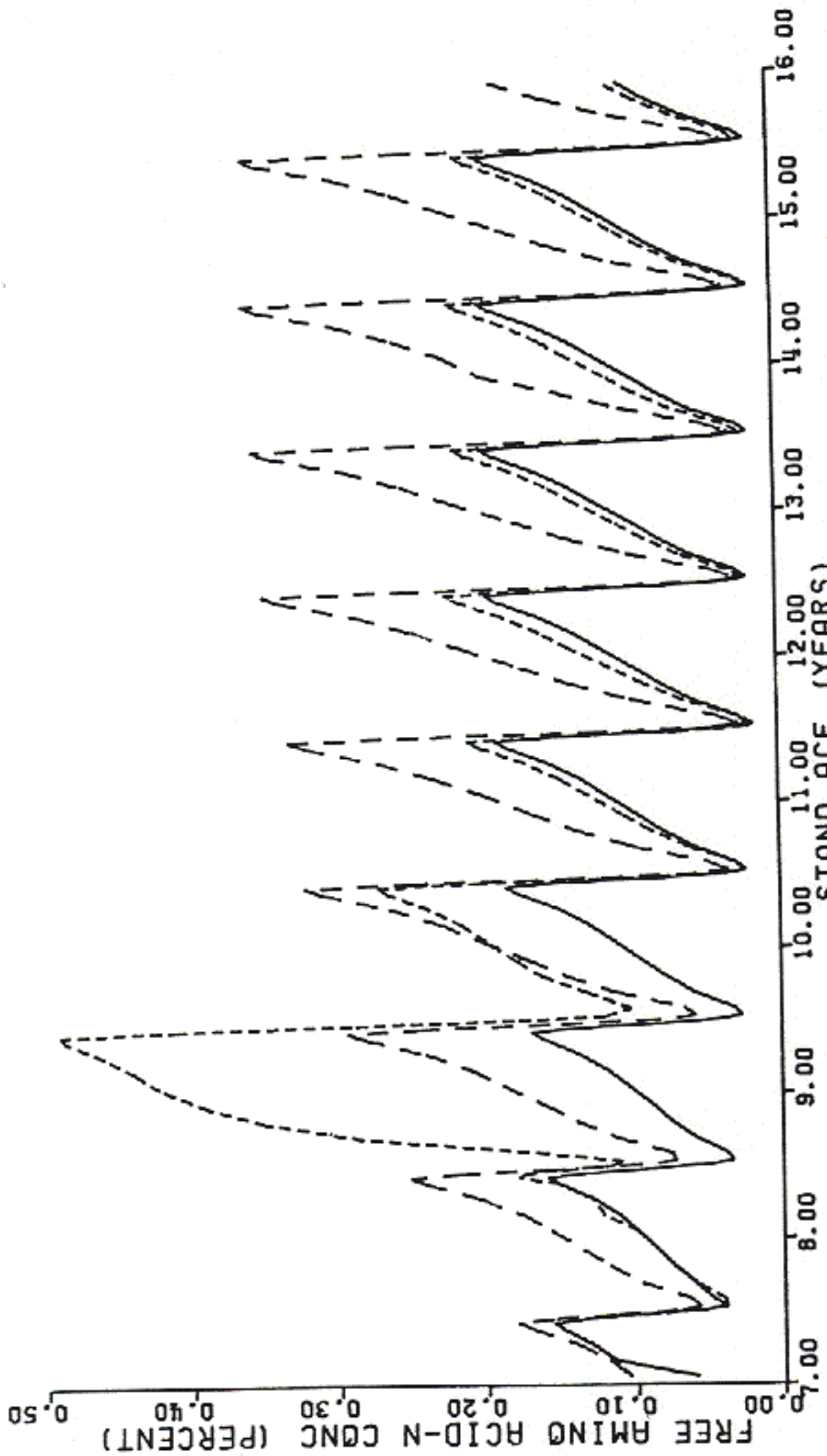


Figure 33. Simulated free amino acid-N concentration versus time for a low mineralization rate (solid line), high mineralization rate (heavy dashed line), and fertilization (light dashed line). Fertilization is at year 8.5.

that the measured decline in new foliage amino acid-N concentration is due to conversion to a protein form rather than a dilution effect with foliage expansion.

Over several years the seasonal maxima are quite stable. The magnitude of the concentration reflects the mineralization rate; the maximum on the high mineralization stand is about 1.8 times that of the low mineralization stand.

The number of developing shoots, modeled by simple assumptions concerning branch development as a function of age, position, and nutrition, shows a sigmoid-shaped trend with time (figure 34). A maximum production of 5200 new shoots per year is reached at the low mineralization rate while a maximum of 7000 is attained at the high rate. The model, which is based on extrapolated data from the young high-site-stand, will allow about 18 live whorls of foliage to be accumulated.

This sigmoid-trend is a logical result of the assumptions incorporated in the shoot development model. This model integrates over, and is responsive to changes in the nutritional environment, yet produces

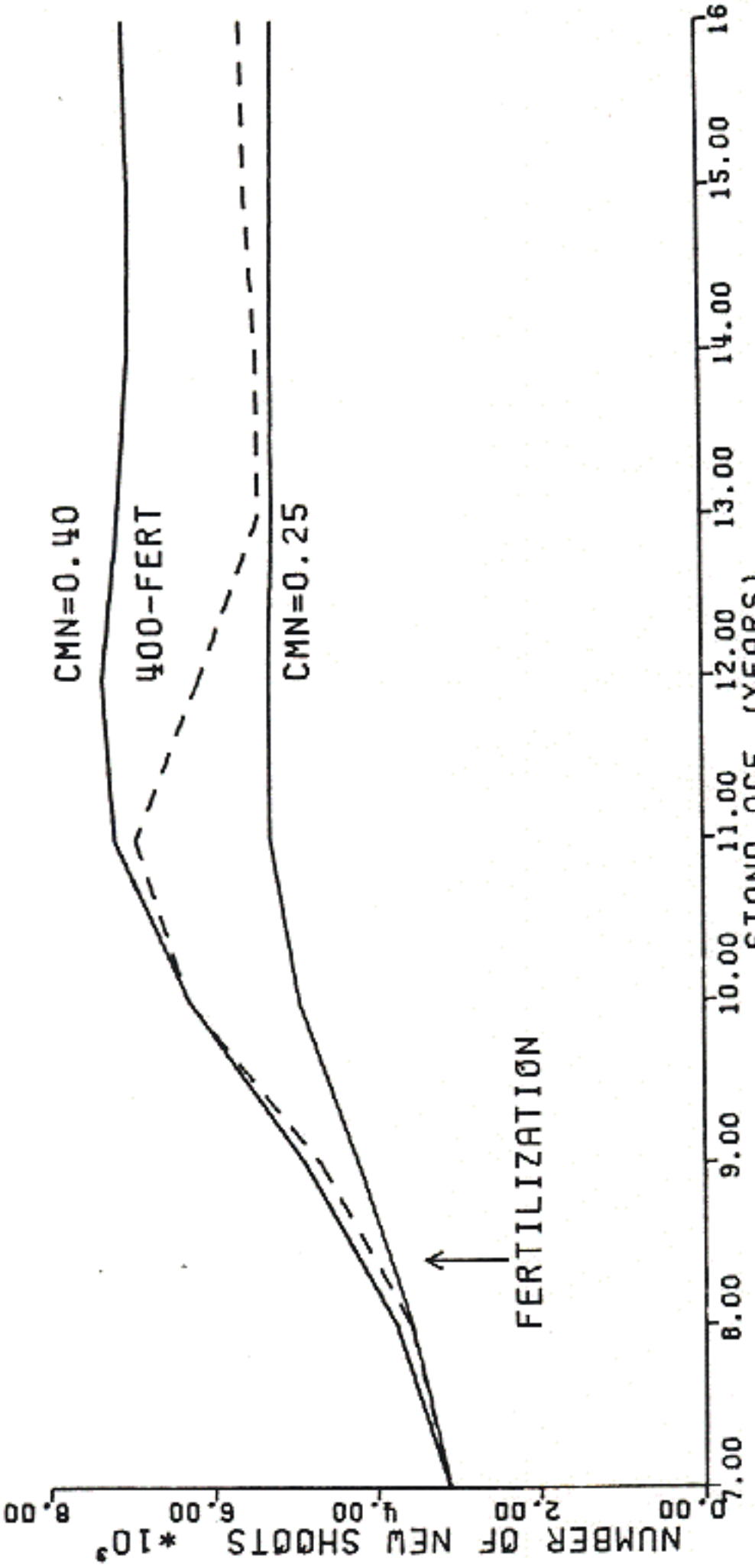


Figure 34. Simulated number of developing shoots per tree versus time for low and high mineralization rates and a fertilization.

the expected long-term trend. It may be inferred that physical limitations on shoot branching and meristem longevity (or development-related effects on production such as self-shading) are responsible for the sigmoid pattern of development. Nutrition may effect rate of growth and maximum productive capacity of the tree.

Simulated soil exchangeable ammonium concentration shows a small growing season depression. For example, dormant-season concentration is 1.13 times as large as the growing-season minimum in year 15 for the low mineralization simulation (figure 35). Both mineralization and uptake rates show a temperature dependence, so that during the growing season both are elevated. Although a large depression in exchangeable ammonium concentration due to plant uptake does not materialize, the flux of N through the soil ammonium component does change markedly. The seasonal maximum uptake (year 15, low mineralization stand) is 2.4 times the seasonal minimum.

Over the age span of 7 to 15 years in the low mineralization stand, exchangeable ammonium concentration declines from a dormant-season level of 6.2 ppm to 4.0 ppm. This reflects the developing root

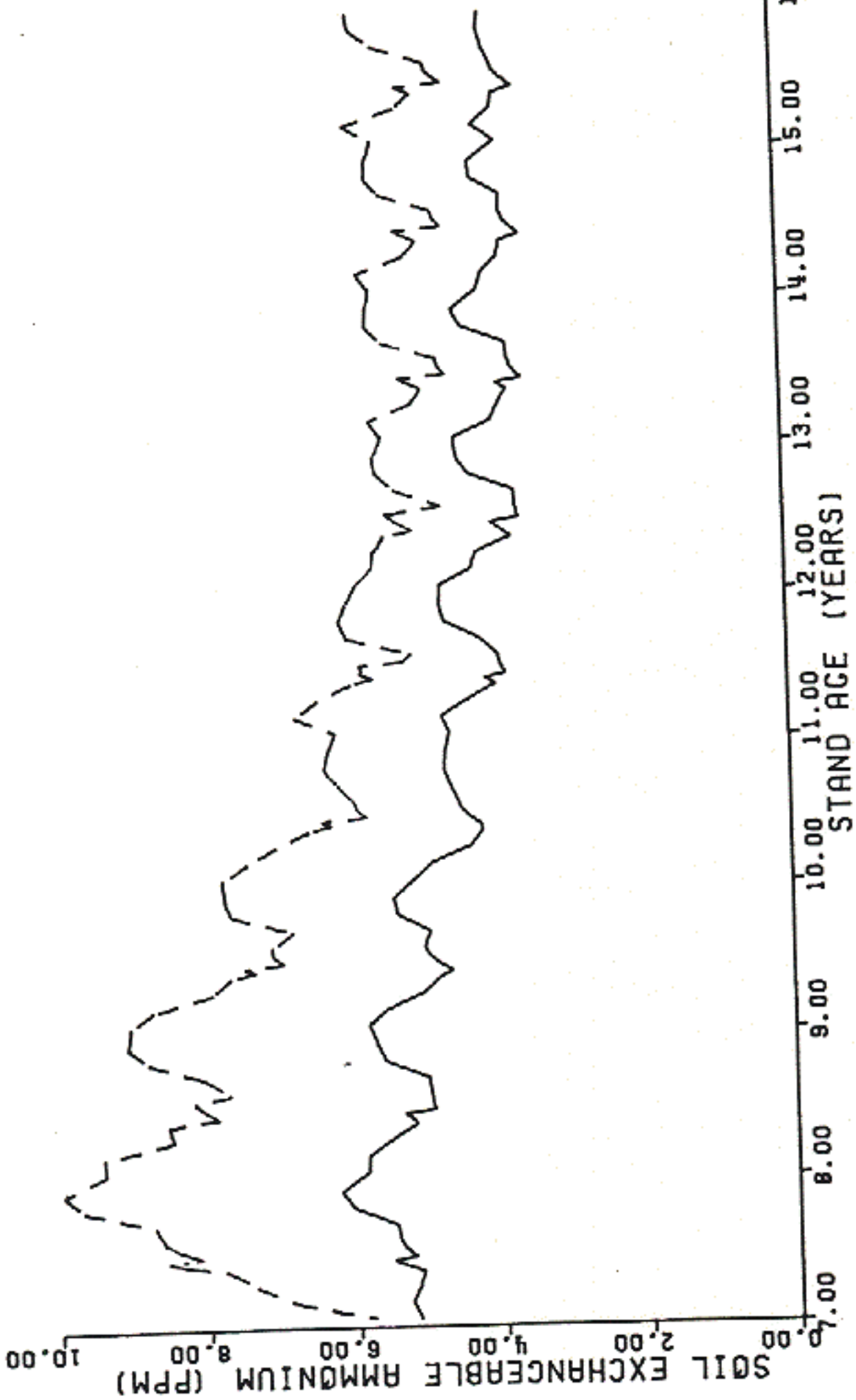


Figure 35. Simulated soil exchangeable ammonium concentration versus time for low (solid line) and high (dashed line) mineralization rates.

system in the young stand.

Uptake rates also change with root system development. In this same age sequence, yearly uptake increases from 21.7 to a steady-state level of 35 gm N/tree-yr (figure 36). The effect of increasing root density upon N uptake examined earlier is operative in this case. Increasing fine root biomass elevates uptake by the tree until depletion zones severely overlap. Thereafter, a small return in N uptake is realized by further increases in root density.

Simulated trends in soil exchangeable ammonium and uptake in the high mineralization stand are similar to the low mineralization condition but are of a different magnitude. Consistent with the higher N supply rate, (0.4/0.25=1.6 times higher), uptake reaches a steady-state level of 61 gm N/tree-yr, which is 1.7 times larger than in the low mineralization stand. Soil exchangeable ammonium levels are also elevated (growing season minimum =4.5 at age 15) but the increase (1.3 times the low mineralization condition) is smaller that the change in uptake.

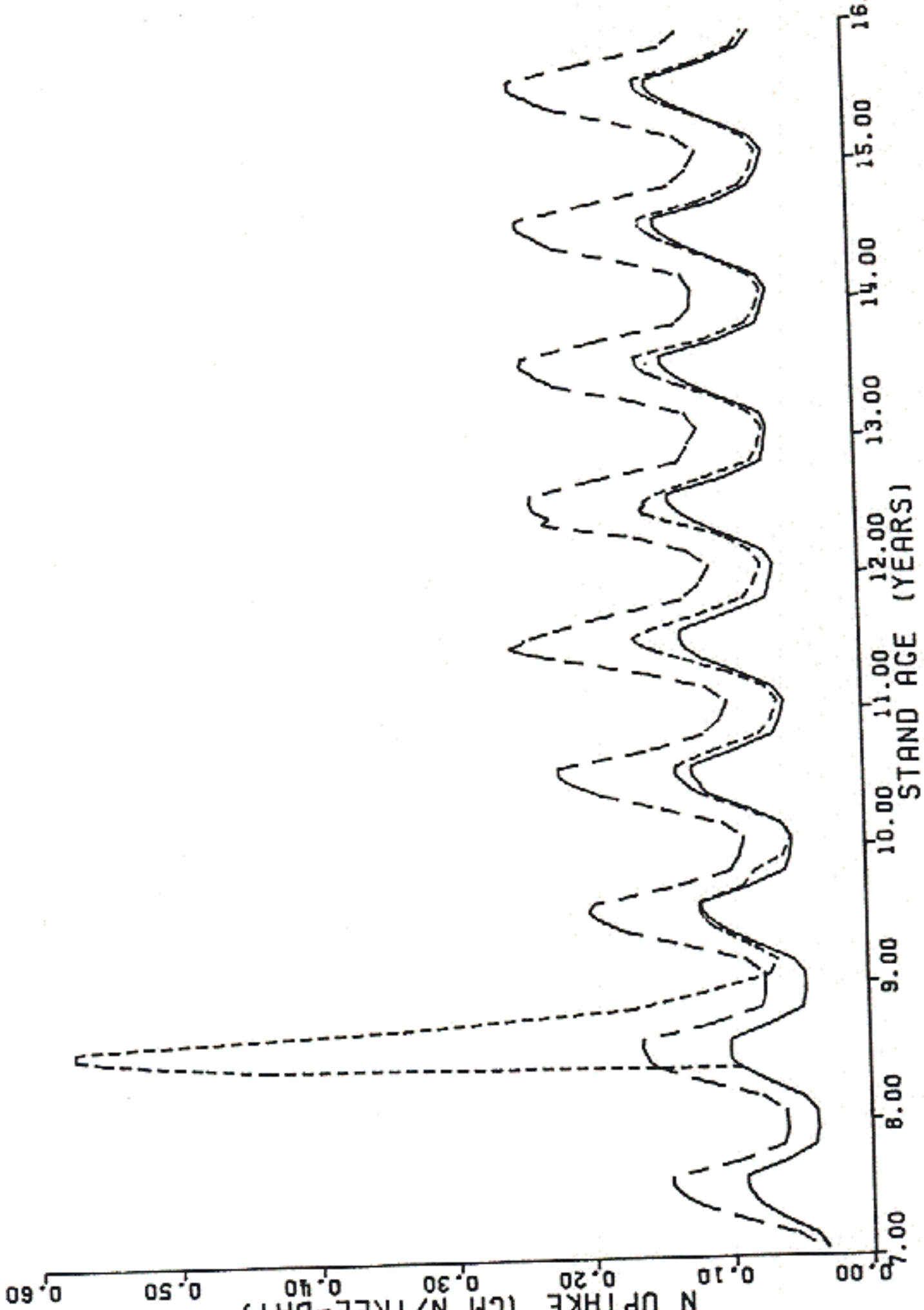


Figure 36. Simulated N uptake versus time for a low mineralization rate (solid line). high mineralization rate (heavy dashed line), and fertilization (light dashed line).

If the simulated exchangeable ammonium concentrations are used to calculate an instantaneous uptake rate for the two mineralization conditions (assuming equal root density and Km=4 ppm in the uptake equation), the high rate is only 1.12 times the low mineralization rate. This is a considerably smaller difference than that for the realized yearly uptake rates.

Thus, it is apparent that the difference between exchangeable ammonium concentrations for different stands is not necessarily indicative of the difference in N flux through that pool. In this case, a small difference in concentrations is associated with a much larger difference in flux. However, the differences in mineralization are quite comparable to those for N uptake.

Redistribution of N from old foliage to new foliage is affected by the supply of N to the tree. With the low mineralization rate, redistribution increases from 4.4 gm N/tree-yr at age 7 to a steady-state level of 12 gm N/tree-yr as foliage biomass and uptake rates reach maximum values. The higher mineralization stand similarly reaches a

constant year-to-year redistribution rate, but at a lower value, 8.5 gm N/tree-yr. The proportion of N supplied to growing tissue in the low mineralization stand (26%) is roughly twice that in the high mineralization stand (12%).

The patterns of nutrient flux and accumulation demonstrated by these simulations suggest that a developing stand under N deficiency conditions is subjected to an increasing N stress. The growth of the tree is directly limited by its N supply, and as root density increases, the tree more fully occupies the site and maximizes the proportion of the gross N mineralization that it acquires. As yearly uptake reaches a constant maximum value, supply to growing tissue from redistribution and production are similarly maximized and reach steady-state. The inverse relation between supply via uptake and redistribution suggests that the latter process functions both as a nutrient conservation mechanism and a homeostatic mechanism.

This system behavior is reflected in the response of growth and nitrogen flux to fertilization. The simulated fertilization of the low mineralization stand in May of the eighth year will now be examined.

Applied N is rapidly immobilized in the soil. Exchangeable ammonium concentration returns to control levels within the first year following application. Simulation results indicate that 70% of that applied remains in the top 4 cm of the soil (figure 37). This agrees reasonably well with field results from urea application, where 83% remained in the top 4 cm (Crane, 1972). Thus, only a portion of the Douglas-fir roots are exposed to high levels of ammonium, and these levels remain for less than one year.

As a result of this temporal distribution in soil exchangeable ammonium concentration, tree uptake is high for the first year only, and returns toward the level of the control thereafter (figure 36). Slightly elevated uptake in subsequent years may result from stimulation of root growth.

With elevated uptake, the tree free amino acid-N concentration rises and remains high through the second year following fertilization. This accelerates accumulation of N in both new and old foliage with new foliage N concentration rising to a maximum of 1.76% in the second year. This elevated concentration produces elevated production of new shoots (figure 34) and stem

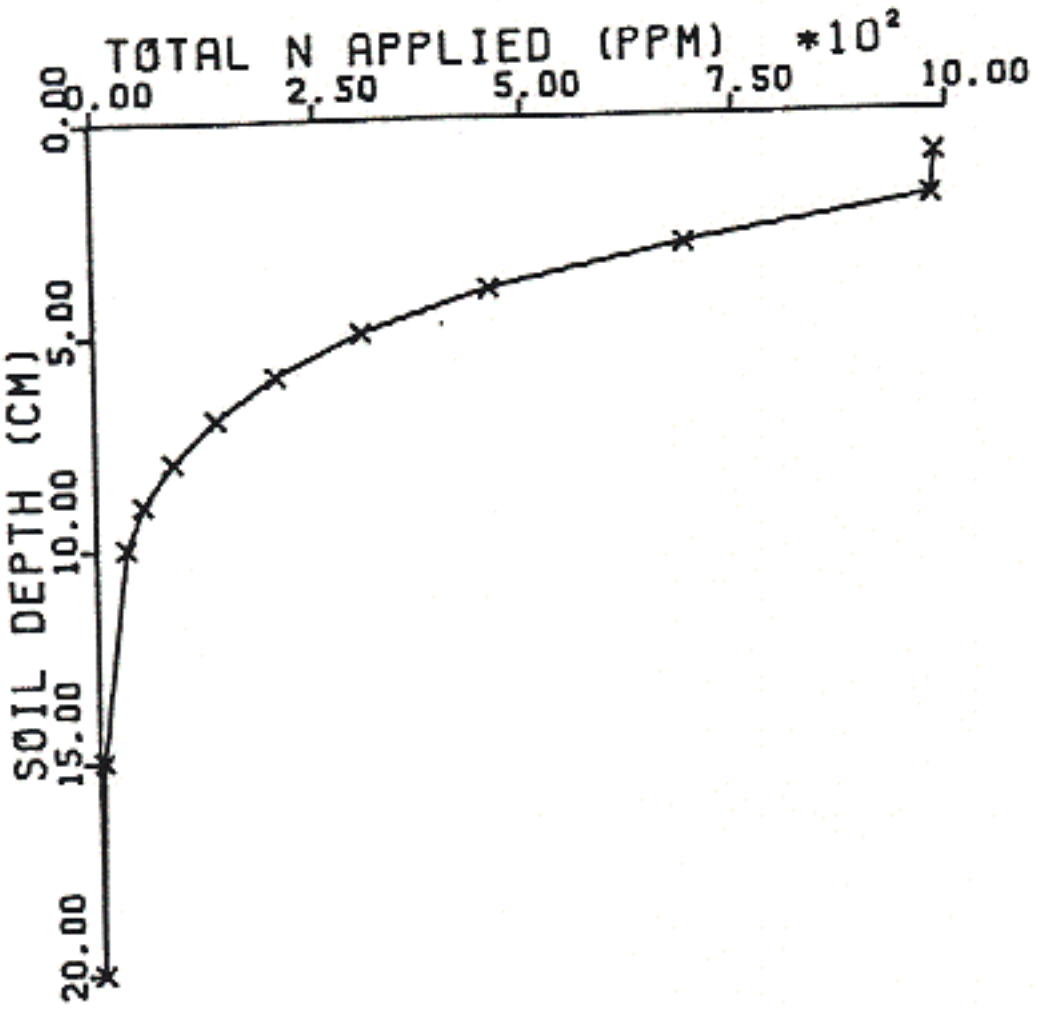


Figure 37. Simulated distribution of applied N with depth after one year.

wood (figure 38) the second growing season following application. Production approaches the level of the high mineralization condition stand and returns to the control level in year 13, a response duration of 4 years.

N accumulates in old foliage the first and second growing seasons following fertilization and is partially redistributed to growing tissue in subsequent years. Elevated N concentrations in new tissue are maintained by supply from the free amino acid-N component and redistribution after the first growing season. Since uptake returns to the level of a control after the first year, and shoot production remains high through the fourth year, new foliage N concentration is maintained at levels equal to or above the control only by supply from these stored forms.

Thus, the second experimental hypothesis is valid; fertilization elevates tree uptake the first year, and supply from stored forms in the tree maintains elevated new foliage N concentration in subsequent years. Production follows the time trends in foliage N concentration with a one year time lag. If the gross mineralization rate of soil organic N remains

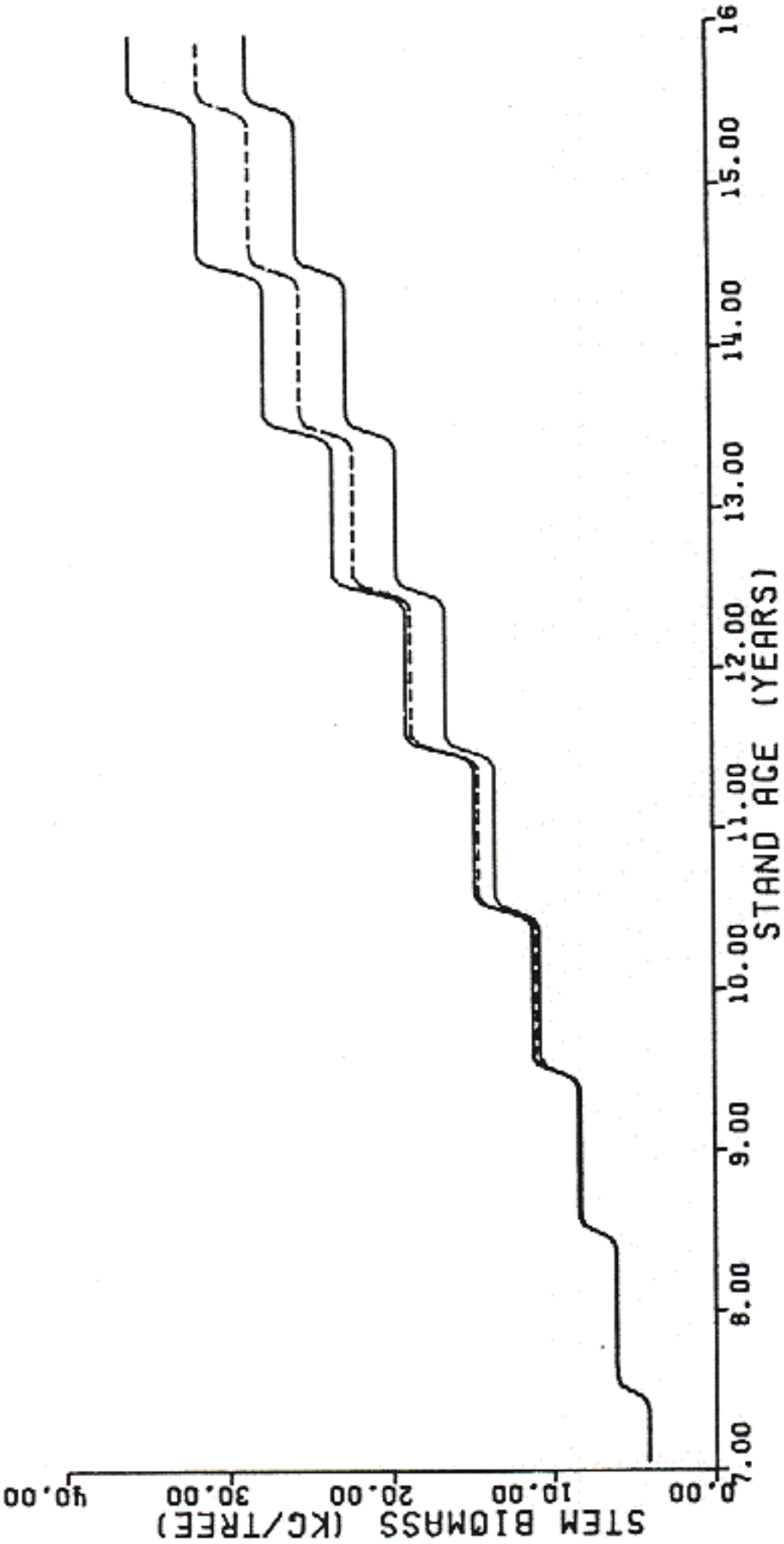


Figure 33. Simulated stem biomass versus time for a low mineralization rate (solid line), high mineralization rate (heavy dashed line), and fertilization (light dashed line).

unchanged, uptake and foliage N concentration will return to the level of a control. Long-term shoot production will similarly return to those levels. Since foliage production does not remain elevated, foliage biomass and the degree of self-shading and inter-tree shading will not remain elevated. Therefore, long-term production should be the same as for a control. If a permanent change in the mineralization rate were effected by fertilization, the fertilized stand would continue to have accelerated growth comminsurate with the higher rate of supply. Such a permanent change may be determined only through soil microbiological studies; the model will estimate the effect of the change upon tree growth and yield.

Several processes involved in the model are only poorly conceptualized or mathmatically described (due to a lack of understanding of the process or specific data).

(1) A strict accounting of N transfers within the tree during the dormant season, and throughout the year following fertilization is needed. Uptake is expected to be small but positive during the dormant season, yet foliage N concentration is thought to remain constant during that period. If N is being stored, is it in the

xylem, phloem, or roots, and is it in a free amino acid or protein form? Following a dormant season fertilization, where is N accumulated within the tree, and in what form is it?

(2) A number of functions in the model assume a relationship with tree size, and then use this function over a range of ages. These functions should be developed in terms of development of a particular size of tree through time (a true allometric relation).

(3) The foliage weight per shoot simulated in the model was developed from high-site data, and it appears to be higher than expected and insensitive to changes in nutrition. This function should be investigated over a range in site conditions.

(4) Redistribution of N from old tissue to new was modeled using annual data and assumptions concerning expected amino acid-N levels. This transfer should be measured throughout its active period (the growing season) and manipulated via different timings and rates of fertilization over several years to ascertain the effects of amino acid-N, protein-N, and foliage age.

(5) The development of fine root density by depth and stand age, the rate at which the soil volume between young trees is explored by the developing root system, and seasonal dynamics in fine root biomass should be

functionally related to soil nutrient and water levels. (6) The development of stand structure, including tree mortality and segregation of individuals into different age classes, should be considered. An empirical relation between stocking and tree size (dbh) (King, 1970) was included in the model in order to simulate mortality, but simulated tree size in these young stands remained below the level at which mortality begins.

CONCLUSIONS

This study has formulated a general theory of the control of N flux and growth and yield in a developing Douglas-fir plantation. This theory consists of a set of hypotheses concerning N transfer among components of the forest ecosystem, and the influence of the state of tree development and N nutrition upon growth. It includes the following.

(1) Uptake per unit fine root is a function of the soil exchangeable ammonium concentration.

(2) N accumulation in new tissue is primarily net protein synthesis, and is proportional to the free amino acid-N concentration.

(3) N redistribution from older to newer tissue is a source-sink relationship; net synthesis of protein in old tissue is favored by high free amino-acid concentration and net degradation is favored by high protein levels.

(4) Growth of new foliage depends on the number of expanding buds and the needle growth per shoot, both of which are proportional to the protein concentration.

(5) The number of new buds expanding is set the growing season before expansion. It is functionally related to the branching structure of the growing canopy.

(6) Stem growth is functionally related to the number of expanding shoots.

These hypotheses were incorporated in a simulation model and the model parameters were estimated using data from N fertilization experiments in high-site-quality Douglas-fir. These experiments have shown the following.

(1) Shoot expansion (length) follows a sigmoid-shaped trend with time. Shoots in more superior positions (the ends of branches and top whorls) grow at a higher rate than do those in inferior positions, but they approach their maximum extension more slowly.

(2) Needle dry weight per shoot is well correlated with

shoot length and follows a sigmoid-shaped trend with length. The same function is applicable throughout the growing season. For a shoot of given length, shoots in more superior positions have a larger needle weight.

(3) The fraction of a tree's new foliage in an individual whorl increases linearly from the top to a maximum in a four-year-old whorl.

(4) Branching complexity initially increases with age for any position on a branch. Shoot production on a sub-branch increases until the sub-branch is four whorls from the top and in the lowest position from the base of the branch.

(5) No response in foliage production was evident following N fertilization.

(6) At age 7, needle weight per shoot was 0.40 gm, 41% of the tree foliage is in the most recent age class, foliage mass is 1.7 kg, and there are 4225 shoots produced per tree.

(7) N concentration in new foliage declines with foliage expansion and remains stable through the fall months. N concentration increases with fertilization, indicating an increased incorporation of N.

(8) Old foliage N accumulation over the growing season for a high-site control is positive and small. With fertilization, N accumulates in old foliage, especially

the one-year-old age class. N continues to accumulate at this high rate following a second fertilization.

(9) New foliage free amino acid-N concentration is sensitive to changes in N uptake. In untreated trees, concentration declines during the growing season, while in trees fertilized at 600 kg N/ha, concentration rises continually to a dormant season level which is 6.7 times higher than a control.

(10) Exchangeable ammonium in untreated soil is 5.1 ppm. Applied ammonium is rapidly immobilized; concentration declines exponentially. With an application of 400 kg N/ha, exchangeable ammonium concentration has declined from 600 ppm to 40 ppm after 120 days.

(11) Nitrate concentration in untreated soil is 3.5 ppm. Following fertilization at 600 kg N/ha, nitrate accumulated to a measured maximum of 51 ppm after 120 days and declined thereafter. The hypothesis that nitrification is substrate limited was further supported by a soil ammonium immobilization experiment. Refertilization the next year at 400 kg N/ha produced a maximum nitrate accumulation of 100 ppm, demonstrating a substantial stimulation of nitrification by previous activity.

(12) Stem volume increment for any year is highly

correlated with the increment of that tree the previous year. Stem analysis of 20 trees by this individual-tree technique showed a statistically significant, 20% reduction in growth the second year of high-level fertilization (800 or 1000 kg N/ha applied over two years).

(13) Tree N uptake was related to soil exchangeable ammonium levels and parameter estimates of Vmax=1.25 gm N/tree-day and Km=4 ppm (exchangeable ammonium) were made.

(14) N incorporation rates (change in content) were shown to be correlated with foliage free amino acid-N concentration.

The N cycling and production model developed from the general theory and field experiments has proven to be stable and useful in testing hypotheses concerning the control and behavior of this forest system. These hypothesis tests have shown the following: Production in a N-deficient forest is under systemic control and is sensitive to the state of tree development and the supply of N to growing tissue. This supply comes both from uptake and internal storage sources. The internal sources serve not only to effect efficient use of a limiting resource, but to maintain homeostasis in the

supply of that resource in a fluctuating environment. Uptake is primarily determined by the soil mineralization rate, and given the existing characteristics of the uptake mechanism, is insensitive to changes in those characteristics.

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VITA

Philip J. Riggan
born: September 5, 1951, San Diego, California
parents: Mr. and Mrs. Royce B. Riggan
education: 1969 graduated from Hilltop High School
Chula Vista, California
1973 Bachelor of Science, Chemistry
San Diego State University
1979 Doctor of Philosophy
University of Washington
professional: 1978 Soil Scientist
USDA Forest Service
Pacific Southwest Forest and Range
Experiment Station
110 N. Wabash Ave.
Glendora, California 91740