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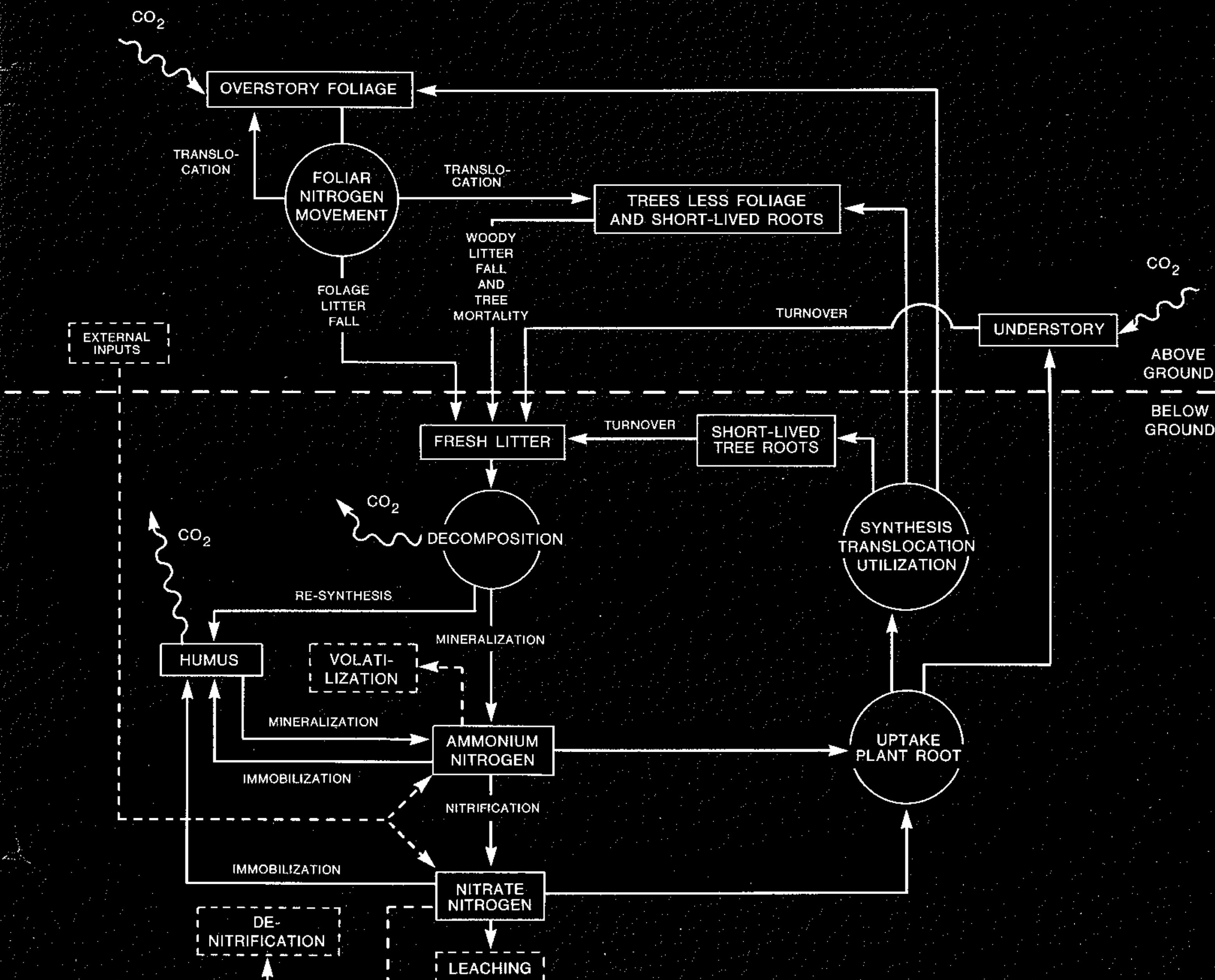
Information Report BC-X-280
Pacific Forestry Centre

NITROGEN AND CARBON ACCUMULATIONS AND MOVEMENT



Shawn: a model of Douglas-fir ecosystem response to nitrogen fertilization and thinning: a preliminary approach

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1986

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ISSN 0830-0453
ISBN 0-662-14709-X
Cat. No. Fo46-17/280E

Abstract

An ecosystem model of the growth of Douglas-fir (*Pseudotsuga* ***menziesii*** (Mirb.) Franco) at Shawnigan Lake, British Columbia has been constructed as part of the Shawnigan project. It depends on nitrogen as the driving force and the ecosystem processes are mediated via environmental factors including carbon-nitrogen ratios. The general purpose of the model is to facilitate understanding at the ecosystem level of the observed responses to thinning and nitrogen fertilization. The model includes the facility for parameter sensitivity analysis, which allows identification of parameters important to the system and thus deserving of careful empirical measurement, as well as the identification of features of the Shawnigan experiment needing further research. The model can also be used as a gaming tool to investigate the effects of alternative stand management options.

This report documents the model's structure and some of its properties. A comparison is made between model predictions after thinning and nitrogen fertilization treatments and the data available from the Shawnigan project. The model correctly predicts the rank order of several variables after various combinations of treatments. No quantitative comparisions of model output with data were made since this is not the purpose of the model. A sensitivity analysis of the model allowed the identification of parameters to which the model was not sensitive, allowing future simplification, and also parameters to which the model was quite sensitive, thus identifying directions for future elaboration of the model.

Resume

Un modèle d'tcosystkme pour la croissance du Douglas taxifolié (*Pseudotsuga* ***menziesii*** [Mirb.] Franco) à Shawnigan Lake (C.-B.) a ttt construit dans le cadre du programme de Shawnigan. La variable d'action est I'azote. Les processus de l'écosystème sont rtgis par des facteurs environnementaux, dont le rapport des concentrations de carbone et d'azote. Le but général du modèle est de faciliter la comprehension au niveau de l'écosystème des effets observes de l'éclaircie et de la fertilisation azotte. Le modèle offre également la possibilite de faire des analyses de sensibilitt afin de determiner les paramètres importants du système qui devraient être mesurés avec attention et les aspects de l'expérience de Shawnigan qui devraient être approfondis. Le modèle peut tgalement servir de moyen de simulation pour I'ttude des effets de divers modes possibles d'amtnagement.

Les auteurs décrivent dans ce rapport la structure du modkle et quelques-unes de ses propriétés. Ils comparent les prévisions obtenues après des traitements d'éclaircie et de fertilisation azotée en utilisant les donntes disponibles du programme de Shawnigan. Le modèle a prevu correctement I'ordre de plusieurs variables après diverses combinaisons de traitements. Aucune comparaison quantitative des rtsultats du modkle avec les données n'a ttt effectute car le modkle n'a pas ttt conçu à cette fin. Une analyse de sensibilitt a permis de determiner les paramètres auxquels le modkle n'était pas sensible, ce qui permettra de le simplifier, et aussi les paramètres auxquels il ttait trts sensible, ce qui a indiqué des directions pour son perfectionnement.

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Introduction

One of the more intensively managed species in British Columbia at present is Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). This species characteristically occupies sites that are acknowledged to be nitrogen deficient. A number of thinning and fertilization trials were established in the 1950s and 1960s throughout the Pacific Northwest. These studies have shown generally positive, though highly variable, growth responses to thinning and to fertilization with nitrogen applied as urea or ammonium nitrate (Gessel *et al.* 1969). These favorable results prompted the establishment in British Columbia of two long-term and complementary projects.

One of these projects was carried out by the Forest Productivity Committee of the B.C. Ministry of Forests. It laid out thinning and fertilization installations over a range of sites and stand types and was designed to provide a data base for the development of managed stand yield tables for Douglas-fir and western hemlock.

The other project, the Shawnigan Lake project, was carried out by the Pacific Forestry Centre of the Canadian Forestry Service. It followed a more intensive approach. A single thinning and fertilization installation was established and supported with a multidisciplinary scientific investigation. It was designed to provide understanding of a fundamental nature and address the site-specific nature and variability of the observed response.

The Shawnigan Lake installation was established in 1971 in a 24-year-old Douglas-fir plantation near Shawnigan Lake, B.C. A complete description of the installation, its experimental design, site characteristics and component studies are documented in the project's establishment report (Crown and Brett 1975).

The installation initially consisted of three levels of thinning for each of three levels of nitrogen fertilization. The three levels of thinning were removal of 0. 1/3 and 2/3 of the basal area, which spanned the range of stocking levels then being considered for management of these stands. The three levels of fertilization were 0, 224 and 448 kg N/ha applied as urea, which spanned the range of fertilizer applications then being used. The installation was later expanded to include higher levels of fertilization with urea (up to 1344 kg N/ha), fertilization with ammonium nitrate, and fertilization combined with removal of the understory vegetation. Extensive monitoring and investigation of different aspects of ecosystem response were carried out through individual studies.

Much effort has gone into forest modelling in recent years in an attempt to understand tree growth and stand dynamics. A variety of modelling approaches have been used, some of which have been reviewed by Munro (1974). One important distinction among forest models is that of single-tree models, such as those by Mitchell (1975, 1980) and Arney (1972), versus whole-stand models, such as DFSIM (Curtis *et al.* 1981) and that of Myers (1971). Another important distinction is that between predictive models, such as those of Clutter (1963) and Goulding (1972), which attempt quantitative prediction of volume growth, and mechanistic models, which incorporate biological and chemical information with a view to generating testable hypotheses regarding tree growth. These mechanistic models facilitate scientific investigation and understanding at the ecosystem level and have recently received considerable attention. Examples of such models are FORCYTE (Kimmins and Scoullar 1982), FORTNITE (Aber and Melillo 1982), and the models of Linder (1981). Our model, SHAWN, is also a mechanistic model.

With all these models in existence why build another one? The dynamics of forest ecosystems are still insufficiently understood to delineate the "best" approach to such modelling, and the various existing models use differing approaches. Furthermore, different models are created for different purposes, and often different purposes dictate different and sometimes mutually incompatible approaches. Also forest models are often species-specific and sometimes site-specific, which again necessitates a multiplicity of models.

Thus as part of the Shawnigan Lake project, a modeling effort was initiated to synthesize the findings of the project's individual studies and evolve a conceptual understanding of ecosystem dynamics. The resulting model is a description of forest site. It describes "site" and "stand" as a network of pools of material linked by biological processes whose individual rates depend upon environmental conditions. It links stand treatment to a change in environmental conditions and, in turn, to changes in the individual rates of biological processes. The model, therefore, is a framework within which site-specific system responses can be examined and understood in terms of underlying physiological and biological processes. The model might most appropriately be classed as a "site" model. It does not approach stand dynamics from a mensurational or biometrics point of view, and it is neither a "tree" nor a "stand" model as these terms are normally understood. In addition, the Shawnigan model does not attempt accurate quantitative prediction of wood volume as do mensurational models.

In addition to facilitating understanding, the model has several specific objectives: (a) to formalize present ideas about coastal Douglas-fir ecosystem processes, (b) to identify research needs and areas of inadequate understanding, (c) to identify processes and parameters to which the model output is particularly sensitive, (d) to explain observed responses to thinning and fertilization in terms of ecosystem processes and responses, (e) to allow qualitative prediction of response to other possible management interventions not pursued in the Shawnigan experiments, and (f) to assist in establishing a site classification which is more theoretically based than those presently available.

The Shawnigan model was developed in the late **1970s.** Many features of the model represent a considerable simplification compared with reality, since to deal realistically with all the processes would be prohibitively complicated and also often enter the realm of the unknown. For many ecosystem processes hard data are not available and many of the process formulations in the model are based largely on intuition. In retrospect we feel that certain of our formulations will require changes in future versions of the model.

Model structure and assumptions

General description of the model

SHAWN is a model of forest growth and nutrient dynamics. The major characteristics of the model are as follows: (a) nitrogen is assumed to be the only limiting nutrient; (b) growth is based on photosynthesis, which in turn is based on environmental features including available nitrogen; (c) although stand structure does affect growth, it is not considered in the model; (d) the soil is modelled as functional compartments, and spatial structure of the soil is not described by the model; (e) the nitrogen dynamics in the soil are process oriented.

The model consists of the following general compartments: forest floor (L and H layers), mineral soil, understory layer and trees. In each of these, nitrogen resides and transfers occur among compartments. Carbon is also transferred among all compartments except the mineral soil. The nitrogen in the mineral soil consists of nitrate (NO_3^-) and ammonium (NH_4^+) ions while that in the forest floor (litter and humus) and the living compartments is in organic form. The forest floor consists of two components: litter and humus.

The flora of the ecosystem explicitly modelled includes Douglas-fir trees and unspecified understory vegetation. Soil organisms are not explicitly modelled and soil processes are simply represented as first order rate constants modified by external factors. The atmosphere is both a sink and a source for carbon; no other sources or losses of carbon to the system exist. The only sources of nitrogen are constant external inputs (due to precipitation, nitrogen fixation, animal excrement, etc.) of NH_4^+ and NO_3^- every season. Denitrification and leaching are sinks in that they represent permanent losses of N to the system. An overview of the model is shown in Fig. 1.

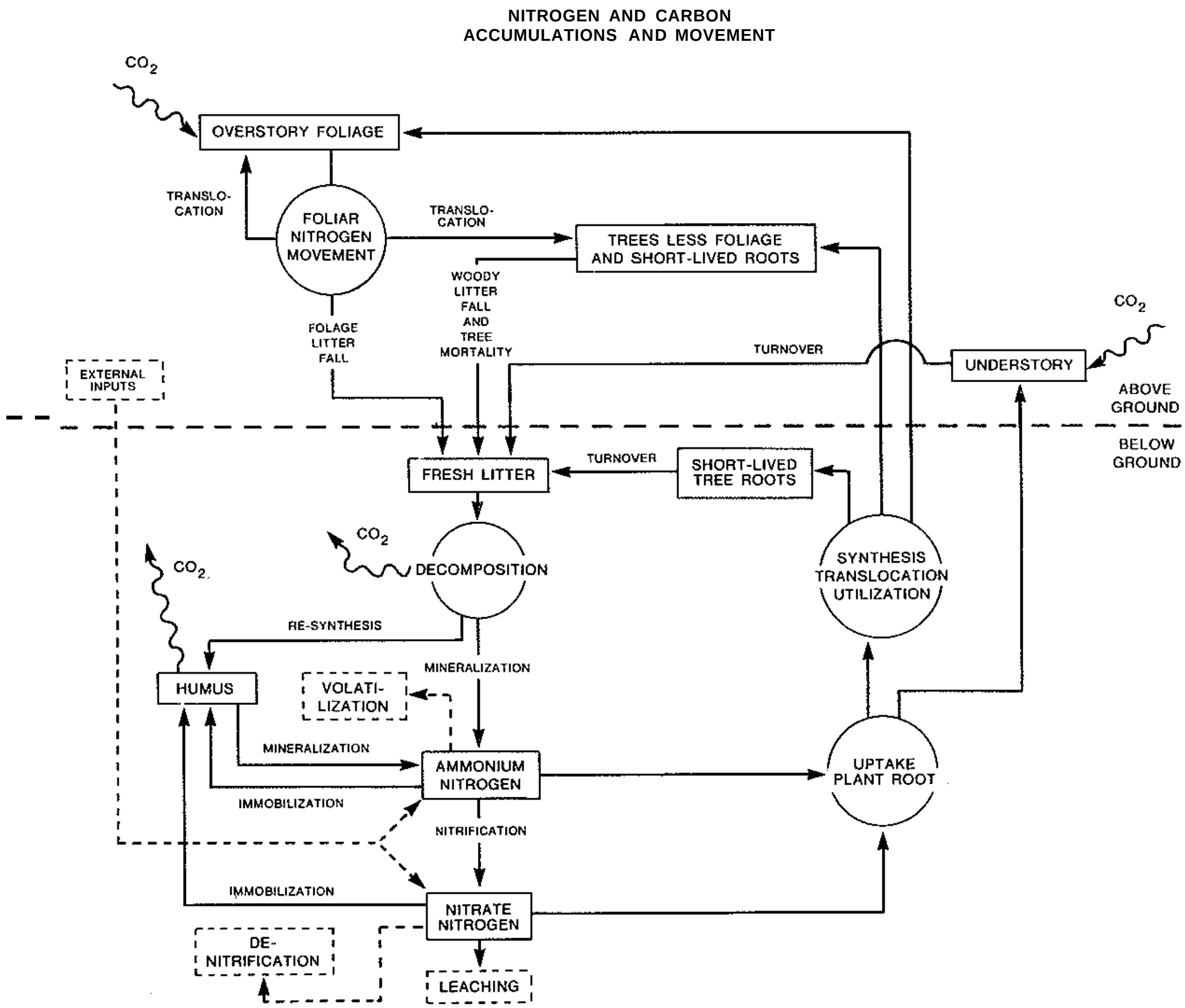


Figure 1. Schematic diagram of the nitrogen cycle on which the model is based

Figure 1 represents the flow of carbon and nitrogen within the system. Nitrogen may take a variety of pathways once it enters the forest floor and soil. For example inorganic soil nitrogen may be immobilized, nitrified, denitrified, leached, volatilized or taken up by the roots. Organic nitrogen in the forest floor may or may not be mineralized, depending on environmental conditions. The trees are divided into foliage, permanent woody parts (including stemwood, branches, hark and large roots), and short-lived roots for accounting purposes. The foliage is further split into six similar age classes, the oldest of which is shed annually.

Overstory foliage loses C as a result of the oldest age class dropping to the litter layer in fall and as a result of tree mortality; loss of foliar N occurs by fall of the oldest age class, by tree mortality, and by translocation of some N from the oldest age class into the other foliage classes and into the stemwood just before falling. Stemwood, bark, branches and larger roots only lose N and C as a result of mortality, which is a constant proportion each year independent, of either density or level of fertilization; there is no translocation out of these components or other losses. Mortality in all components is a constant proportion of what exists; there are no environmental or density effects on mortality.

Several different kinds of characteristics are used in the description of SHAWN. (a) Parametersare quantitative characteristics of the system which are fixed and do not change except under the manipulative control of the modeller. **A** list of parameters appears in the Appendix. (b) Variables quantitatively describe the state of the system at any given time. These relate mostly to amounts of carbon and nitrogen in the various components, and a list of variables is also given in the Appendix. (c) Transfers are a special kind of variables that describe rates of entry to or exit from a given compartment of nitrogen or carbon, and thus represent changes in the values of state variables. (d) Factors are environmental features which indirectly affect the rates of transfer of nitrogen and carbon among compartments. There are eight factors: temperature (T), soil moisture potential (SMP), carbon-nitrogen ratio (C:N), pH, overstory leaf area index (OSLAI), foliage nitrogen concentration (PCN), **total** mineralized nitrogen (TMIN) (NO_3^- and NH_4^+) and a supply-demand (S-D) index. Some of the factors are **thus** also variables since their value depends on the current state of the system. (e) Processes are biogeochemical phenomena the rates of which are directly affected by the environmental factors and are the supposed mechanisms by which nitrogen and carbon transfers occur. There are nine soil-based processes: immobilization, denitrification, leaching, volatilization, root uptake, nitrification, mineralization, decomposition and external inputs. (f) Functions are the relationships between factor-process pairs that define the quantitative effects of each factor on the process in question. There are **27** functions and these are shown graphically in Figs. **2** to 10. **(g)** The numerical output of each function is termed a multiplier since up to five of these are multiplied together to calculate the value of a given transfer, most transfers being affected by several different factors.

One process, for example, is the immobilization of ammonium and nitrate nitrogen. In the model, immobilization, along with the processes of leaching, denitrification and volatilization, compete with the process “plant root uptake” for nitrogen as it is made available by the processes mineralization, nitrification and external input. These particular processes are defined to represent net effects, with respect to the movement or transformation of nitrogen and carbon, of complex and not well-understood biochemical pathways. The factors that were singled out as effectively controlling the rate of immobilization were temperature, soil moisture potential, carbon-nitrogen ratio and pH. Similarly, for each process, the model contains functions which express that process in terms of each factor in its set. An overall process rate is then calculated, for specified factor values, as a simple product of the individual function values (i.e. multipliers) and calibration constant. Fig. 11 provides an overview of the interrelationships among the various functional categories listed above.

Each process is calculated as a product of up to five function values (i.e., multipliers) scaled by a constant. These multipliers describe the individual effects of each environmental factor on the process involved. For example, it can be seen that a process rate will be zero if any one of the factors in its set assumes a value which gives its respective function a zero value.

One ecosystem response of common interest is stand growth. Stand growth is identified in the model as the total capacity of an overstory canopy to carry out photosynthesis, leading to dry matter production. This in turn, is described as the product of total leaf area (measured on a land area basis as leaf area index or LAI) and net assimilation rate per unit of leaf area. Leaf area increases due to leaf growth and decreases due to foliage litter fall and tree mortality. The two plant processes identified here, leaf growth and net assimilation rate, have the same factor set which consists of leaf area index, temperature, soil moisture potential and foliage nitrogen concentration.

A key feature of the model **is** that carbon:nitrogen ratios in various plant and soil components are important in determining several of the processes. A large number of microbiological processes are subsumed under the C:N ratios and in part the success or failure of the model will depend on the validity of this approach.

SHAWN is structured specifically to investigate ecosystem responses of young Douglas-fir stands to thinning and to fertilization with nitrogen applied as urea or ammonium nitrate in specified seasons of the year. Thinned trees are added to the litter component and left to decay. Any trees thinned out are completely representative of those initially present in their N and C contents. In addition, thinning affects soil temperature, certain carbon: nitrogen ratios and soil moisture while fertilization affects soil pH and total mineral nitrogen. These changes affect the various processes which go to determine the rate at which nitrogen is made available for plant uptake and, in turn, the foliage nitrogen concentration. Soil moisture potential and foliage nitrogen concentration are both in the set of factors determining environmental conditions for the processes leaf growth and net assimilation rate. Thus treatment bas affected stand growth by affecting the moisture and nutrient relations governing tree growth. In addition, changing overstory leaf area index also changes the rate of leaf growth and net assimilation rate of the understory vegetation which, in turn, changes bow the overstory and understory will compete for that amount of nitrogen which is being made available by soil processes.

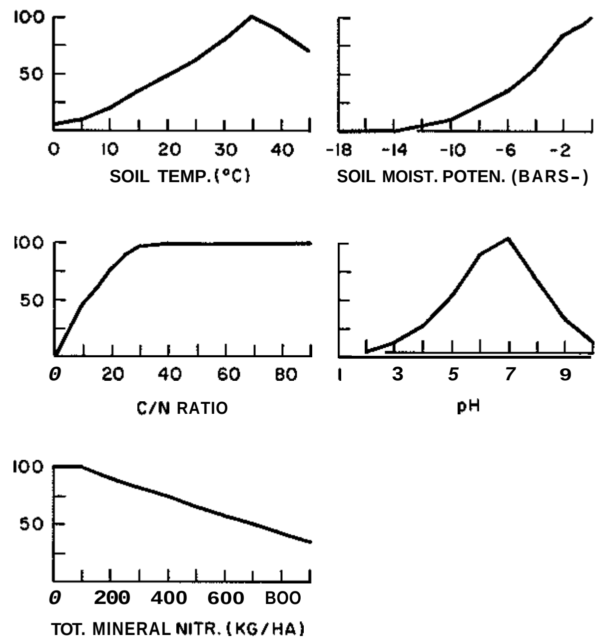


Figure 2. The process immobilization as affected **by** the factors (i) soil temperature, (ii) soil moisture potential, (iii) C:N ratio (iv) pH, **and** (v) total mineral nitrogen.

The main outputs of SHAWN are overstory leaf area index (OSLAI) and net assimilation rate (NAR), with dry matter production (DMP) being the product of these two. Individual trees are not identified nor is the total number of trees, although stemwood, root and branch biomass are updated each season as are nitrogen and carbon contents of each of several compartments. There is a maximum allowable density of OSLAI and both overstory growth and net assimilation rate are depressed as this maximum is approached. The model calculates new values of all variables once for each of the four seasons and continues for a user-specified number of years.

Most of the transfers include modifier constants. Many of the parameter values and the initialization of variable values are under user control. The inclusion of temperature, soil moisture, soil pH, existing **LAI** and nitrogen availability appears to cover the more important features of Douglas-fir ecosystems as they are presently understood. The data required to run the model are obtainable in principle; in practice many of the values can be obtained from the literature with sufficient accuracy for first approximation. The emphasis on processes rather than site-specific growth rates allows generalization across site qualities and habitat types provided the basic processes are similar. The provision of a sensitivity analysis will allow simplification of processes and transfers to which the model is not sensitive and elaboration and refinement of processes to which the model is highly sensitive.

Description of processes

The biogeochemical and growth processes are the heart of the model and require explicit description. In this section each process is described as a function of the set of factors that affect it.

Immobilizaton

Some of the inorganic nitrogen in the soil is taken up by humus. The rate depends on soil temperature, soil moisture potential (SMP), C:N ratio of humus, pH of humus and of the total mineral nitrogen in the soil (Fig. **2,** Table 1).

Denitrification

Some of the NO_3^- in the soil is transformed into gaseous dinitrogen and lost to the atmosphere. The rate at which this process occurs depends on the soil moisture potential, which in turn depends on the season. For the values used in the data definition section of SHAWN, denitrification is maximal in winter and zero in all other seasons (Fig. **3,** Table 1).

Table 1. The ten soil processes and three plant processes as affected by the eight factors and four seasons. An asterisk indicates an effect.

	Process											
Factor	External Input	Nitri-fication	Decom-position	Mineral-ization	Denitri-fication	Immobil-ization	Leaching	Volatil-ization	Root Uptake	Overstory foliage growth	Understory foliage growth	Net Assimiliation Rate
Temperature		*	*	*		*				*		*
SMP			*	*	*	*	*		*	*		*
pH		*	*	*		*						
C/N			*	*		*						
OSLAI										*	*	*
PCN										*	*	*
TMIN						*		*	*			
S-D									*			
Spring	*	*				*		*	*	*	*	*
Summer	*	*	*	*		*		*				
Autumn	*	*	*	*		*		*				
Winter	*	*	*				*	*				

Leaching

Nitrate is a highly mobile ion and can be leached out and lost from the soil profile. Leaching also depends only on SMP via the season, and is maximal in winter and zero in other seasons (Fig. **4,** Table 1).

Volatilization

Some of the NH_4^+ ions in the soil and arising from hydrolysis of applied urea volatilize and are lost to the atmosphere. The rate depends linearly on the total NH_4^+ ions in the soil (Table 1).

Root uptake of nitrogen

The plants take up NO_3^- and NH_4^+ in spring only, and the rate depends on spring soil moisture potential (SMP), the supply-demand (S-D) value and the amounts of NH_4^+ and NO_3^- presently in the soil (Fig. 5, Table 1). Uptake by overstory and understory occurs proportionately according to their relative biomasses. Uptake of N by trees occurs after that by understory and is translocated in constant proportion to (a) overstory foliage, (b) short-lived roots, and (c) stemwood, bark, branches and larger roots.

Nitrification

A fraction of the NH_4^+ in the soil is converted to NO_3^- depending on humus temperature and pH (Fig. 6, Table 1).

Mineralization

A fraction of the organic nitrogen in litter and humus is converted to mineral NH_4^+ and this depends on soil temperature, SMP, C:N ratios in humus and litter, and pH (Fig. 7, Table 1). Constant proportions of the N released from litter go to NH_4^+ and to humus.

External inputs

NH_4^+ and NO_3^- are added to the soil in constant amounts during all seasons via precipitation, nitrogen fixation, animal excreta, etc. **Any** addition of fertilizer occurs at the start of the simulated growth period only.

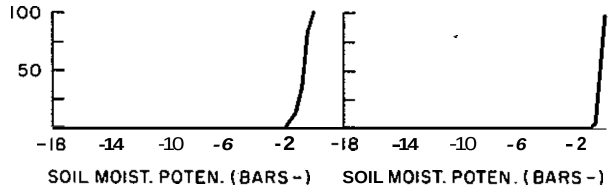


Figure **3.** The process denitrification versus soil moisture potential.

Figure **4.** The process leaching versus soil moisture potential.

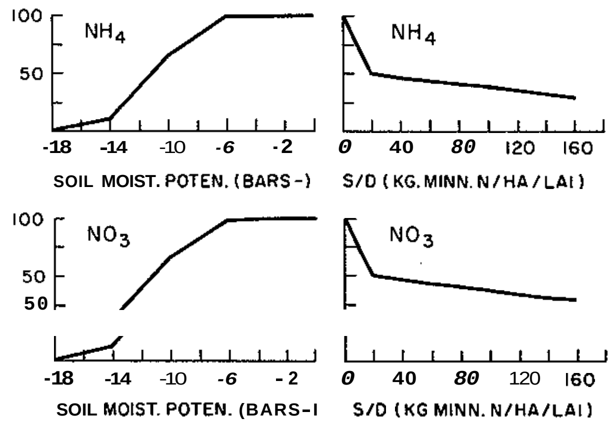


Figure **5.** The process plant uptake of NO_3^- and NH_4^+ versus soil moisture potential and supply-demand.

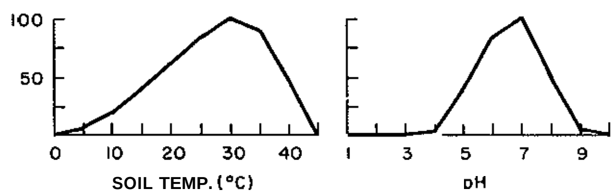


Figure *6***.** The process nitrification versus soil temperature and pH.

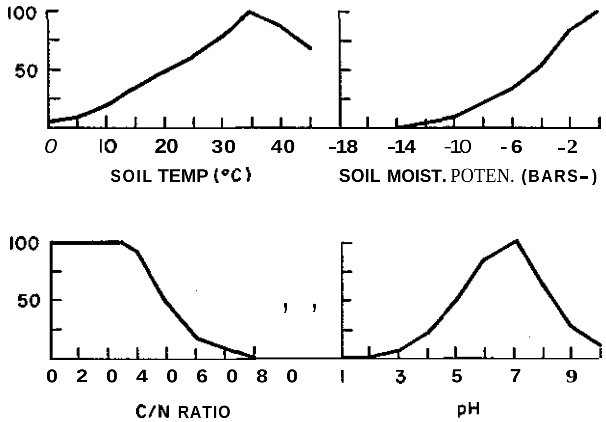


Figure 7. The process mineralization versus soil temperature, soil moisture potential, C N ratio and pH.

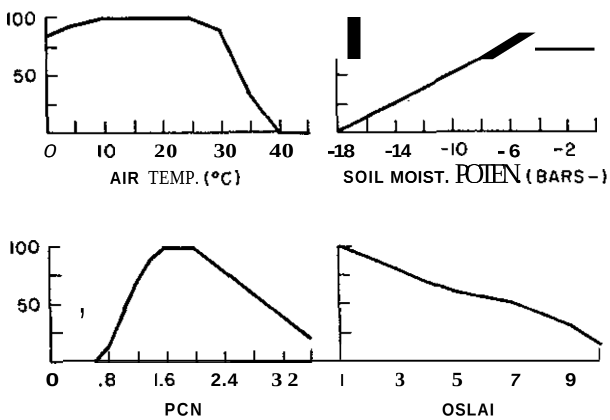


Figure 8. The process overstory foliage growth versus air temperature, soil moisture potential, percent foliar nitrogen and **OSLAI.**

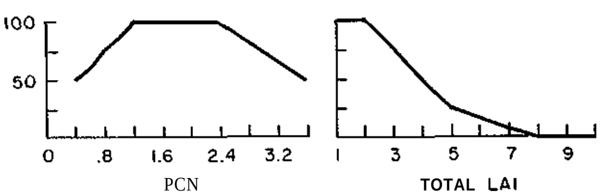


Figure 9. The process understory growth versus foliage percent nitrogen and total LAI.

Decomposition

Decomposition is closely tied to mineralization and is governed by the same factors (Fig. 7). A fraction of the litter breaks down into humus each season and goes from organic to organic form. The carbon being transferred from litter to humus is a simple product of the N transferred and the C:N ratio in humus. Carbon lost as CO_2 from both litter and humus is governed by the same'factors as is the corresponding loss of N except that the C lost is not a function of the C:N ratios.

Overstory foliage growth

This occurs only in spring. Growth is proportional to existing overstory leaf area index (OSLAI) modified by air temperature, soil moisture potential (SMP), percent foliar nitrogen (PCN) and a crowding factor depending on existing OSLAI (Fig. 8, Table 1). Losses occur by dropping old foliage (foliar age class *6)* as well as by tree mortality.

Understory foliage growth

This also occurs only in spring. Growth is proportional to existing understory leaf area index (USLAI) modified by PCN and total leaf area index (Fig. 9, Table 1).

Net assimilation rate

This depends on air temperature, soil moisture potential, percent foliar nitrogen and total leaf area index (Fig. 10, Table 1). Net assimilation rate represents total photosynthesis minus respiration; plant respiration is not explicitly modelled in SHAWN.

Dry matter production

This is the product of OSLAI and net assimilation rate. All growth processes decrease as the total leaf area index approaches its maximum values. The growth of stemwood, bark and large roots utilizes all the **C** left over from net assimilation after foliage, understory and fine root growth have occurred.

In the model volatilization, immobilization of NH_4^+, nitrification and (in spring) root uptake of NH_4^+ are each calculated independently of the

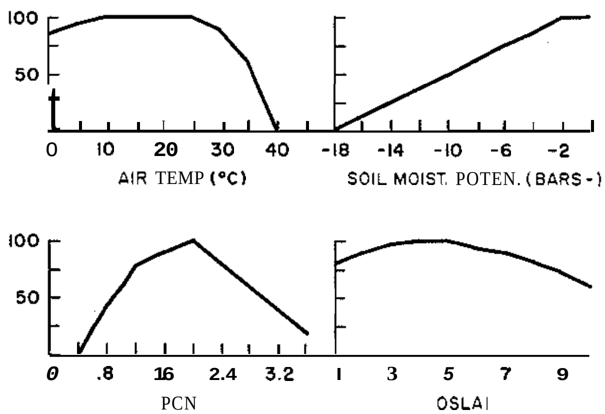


Figure 10. The process net assimilation rate versus air temperature, **soil** moisture potential. foliage percent nitrogen and **OSLAI.**

others and then prorated to lower levels if the total exceeds the total available nitrogen. Similarly, immobilization of NO_3^-, denitrification, leaching and (in spring) uptake of NO_3^- are treated in the same manner.

In addition to the above processes which depend on the factors (listed below), several other plant-based processes occur which do not depend on the factors. These include tree mortality, translocation of nitrogen throughout the plant, annual death of all fine roots, annual **loss** of the oldest foliage age class and death of the understory.

Description of factors

The environmental factors that govern the rates of the various processes are themselves influenced by the state of the system and by initial treatment. Since information on the nature of the interactions of factors in determining process rates is unavailable, their combined action is taken as the simple product of their individual actions.

Temperature (T)

The temperature of the various ecosystem compartments depends on the season, the overstory leaf area index, and thus also on the extent of thinning. Humus and litter temperature are increased by thinning in summer and decreased in winter; in spring and autumn the humus and litter temperature are independent of leaf area index.

Soil moisture potential (SMP)

The soil moisture potential also depends on season and total leaf area index, and thus also on thinning. Soil moisture increases after thinning unless total LAI before thinning <5, in which case SMP is affected only by season.

Carbon:Nitrogen ratio (C:N)

The C:N ratio for each component is simply the

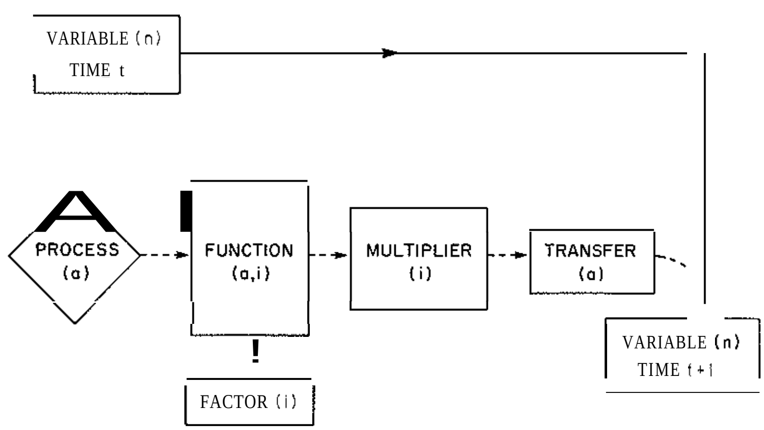


Figure 11. Relationships of the various quantities involved in the model calculations. The effects of process a and factor i on variable n are shown schematically.

ratio of total carbon to total nitrogen present in that component.

pH

The pH of both litter and humus is modified only by the addition of NO_3^- or NH_4^+ ions as urea or ammonium nitrate. If fertilization has occurred, then the pH in each returns to normal (5.5) slowly over the next several years.

Overstory leaf area index **(OSLAI)**

This is used as a modifier in calculating the growth of **OSLAI** sincespace limitations are present when crown closure occurs. Thus **OSLAI** has a maximum value imposed by itself.

Foliage nitrogen concentration (PCN)

The percentage of nitrogen in the foliage determines the internal transfers of N both within foliage age classes and also from foliage to other parts of the tree, as well as N lost via leaf fall. PCN is determined by nitrogen uptake by the overstory.

Total mineralized nitrogen (TMIN)

The total mineral nitrogen in the soil (NH_4^+ plus NO_3^-) helps to determine the rates of several of the biogeochemical processes as well as root uptake and subsequent growth. The level of mineral nitrogen is a balance of the removal processes and the supply processes.

Supply and demand index (S-D)

This is defined as the total available mineralized nitrogen divided by the total leaf area index and is used to determine the amount of uptake of NO_3^- and NH_4^+ by the trees and understory.

Effects of fertilization and thinning

At the start of a run of the model, the user can fertilize and/or thin the stand. This occurs only at the initiation of a model run. Thinning consists of the removal of a given proportion of foliage and wood material from the stand and adding it to the litter, where the dead roots of the thinned trees also accumulate. Fertilization consists of the addition of a given amount of urea or ammonium nitrate, but not both, to the soil.

Fertilization and thinning affect the state of the system in many ways. In the model the effects act on the variables, processes and environmental factors as follows. Thinning directly decreases all components of the tree biomass by removal of growing stock. Thinning also directly increases the temperature of the overstory foliage, the litter and humus as well as increasing the soil moisture potential of litter and humus horizon.

In addition, removal of overstory foliage decreases the depressive effect on the growth of overstory and understory foliage and on the net assimilation rate and the supply and demand factor since overstory foliage explicity reduces the rates of each of these processes. Somewhat less directly, the fraction of nutrients available for uptake by the understory is also increased.

Fertilization increases the available nitrogen pool (but only if fertilization occurs in spring before growth) as well as affecting litter and humus pH. Addition of urea increases the pH of both litter and humus while ammonium nitrate decreases the pH of both compartments.

Sensitivity analysis

Due to the extent of the linkages amongst the various processes in the model the causal paths are difficult to trace. This makes understanding the effects of anv intervention correspondingly difficult. One way of approaching an understanding of the dynamics of an ecosystem is via parameter sensitivity analysis on a model of the ecosystem. This consists of varying a parameter incrementally for a specified set of values of the parameter and running the model once for each parameter value used. At the end of each run the values of the state variables are stored and later compared graphically against those parameter values. This allows easy assessment of the importance of a given parameter for the final status of a given variable. For example, a horizontal line indicates that the parameter has had no effect within the range of variation on the final state of the variable.

The sensitivity analysis of a model is equivalent to experimental manipulation of the parameters of the corresponding real system. The implicit assumption is that if the model is a good one, the results of model manipulation should reflect those of the manipulation of the real system. Since the parameters of the real system are often expensive and difficult to determine, model sensitivity is often used to determine which links in the real system warrant intensive investigation.

Model behavior

Changes over time

Figure 12 shows the progress of 36 variables (listed in the Appendix) annually for 100 years following (null) treatment. The time step for the model is one iteration per season (i.e., four per year). In all cases the values are averages over the four seasons. This indicates general trends in variables after an undefined set of initial conditions.

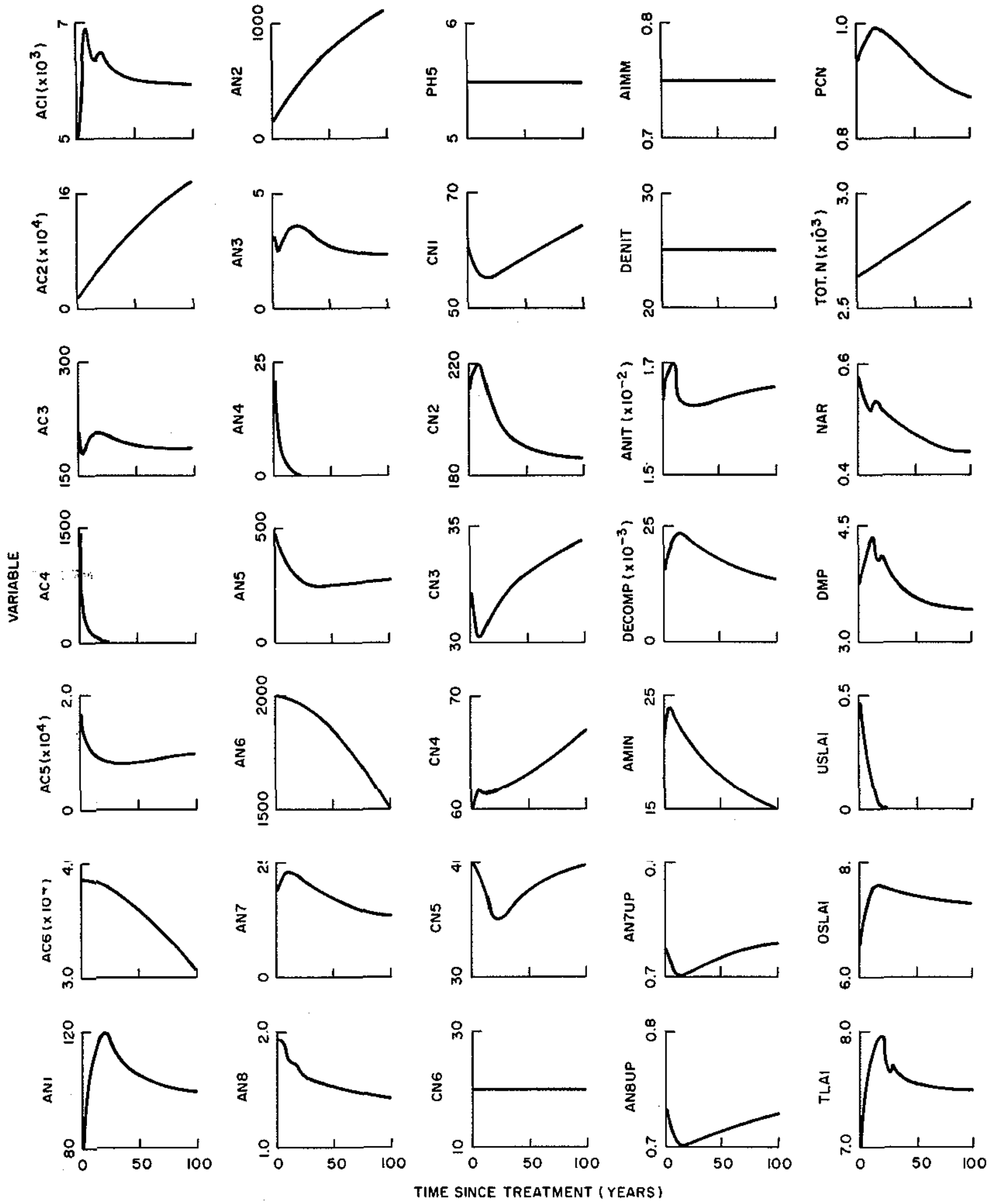
Each variable is scaled so that the graph limits coincide with the minimum and maximum values of that variable over the 100 years with the exception that if the total variation of a variable was not more than 10% of its median value, the upper limit is 10% greater than the lower limit (if it is positive).

Initial conditions are apparently such that the system receives an initial pulse of nitrogen, accounting for the large increase in overstory carbon (AC1), nitrogen (AN1), and leaf area index (OSLAI) as well as increased decomposition activity (DECOMP). This could be removed by adjusting the initial values of the variables, but it might require considerable searching for an appropriate set. In addition, the overstory carbon, nitrogen and LAI decline after this initial pulse, indicating that an overshoot of steady state has occurred. These initial conditions were estimated as being roughly appropriate for the 24-year-old stand if no treatment was applied.

Sensitivity analysis

The effects of each of the 54 parameters capable of independent manipulation were tested against each of *36* variables in a sensitivity analysis. Each parameter in turn was assigned 21 different values ranging from 50% to 150% of its preassigned value. In cases where this preassigned value was 0, the limits were $\pm$ 1.0. A run of the program was made for 50 years for each of these 21 values. At the end of each run the value of the parameter and the final value of each of the variables were tabulated for later use in graphing. Each of the graphs in Figs. 13-15 represents the set of 21 such pairs of numbers for a given parameter and a given variable.

Although **54** $\times$ 36 $=$ 1944 graphs were so generated, only a subset of 12 parameters and 12 variables were chosen to represent the model's behavior. These represent the parameters with greatest effect on the system and the variables of major interest. Of the 12 parameters of greatest importance, all except two yield similar trends in the 12 variables, although they differ in the percent variation that they cause in the variables. The 10 parameters yielding similar trends are: (i) annual external inputs (excluding fertilization) of NH_4, (ii) annual external inputs (excluding fertilization) of NO_3, (iii) spring humus temperature at LAI$=$5, (iv) changes in spring humus temperature for **LAI $\neq$ 5,** (v) spring and fall soil moisture potential maximum (vi) spring and fall SMP minimum, (vii) fresh litter initial pH, (viii) the percentage of the N from decomposing litter which becomes mineralized to NH_4 as opposed to being retained in the humus; (ix) a scaling constant for decomposition; and (x) a scaling constant for mineralization. An increase in any of these parameters increases stemwood carbon, **(AC2)**, nitrogen in both foliage (AN1) and stemwood **(AN2)**, mineralized NH_4 (AN7) and **NO_3** (AN8), overstory foliage (OSLAI) and percent N in this foliage (PCN), the net assimilation rate (NAR) and the rate of decomposition (DECOMP). On the other hand, an increase in any of these 10 parameters causes a decrease in the uptake of NH_4 (AN7UP) and NO_3 (AN8UP). Figure 13 shows the sensitivity analy-


VARIABLE
AC1 (x10^{3})
AC2 (x10^{4})
AC3
AC4
AC5 (x10^{4})
AN1
AN2
AN3
AN4
AN5
AN6
AN7
AN8
PH5
CN1
CN2
CN3
CN4
CN5
CN6
AIMM
DENIT
ANIT (x10^{-2})
DECOMP (x10^{-3})
AMIN
AN7UP
AN8UP
PCN
TOT. N (x10^{3})
NAR
DMP
USLAI
OSLAI
TLAI
0 50 100
TIME SINCE TREATMENT (YEARS)

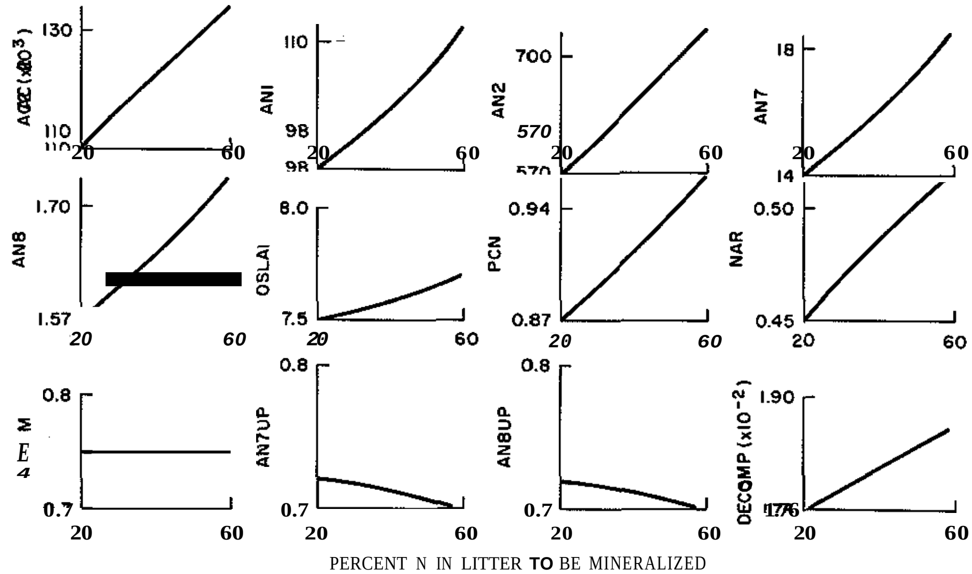


Figure 13. Sensitivity analysis of the percentage of N in litter that is mineralized upon decomposition (as opposed to remaining in humus).

sis for the percent N being mineralized from litter. The remaining two parameters exhibit a different pattern. The percentage of the N in oldest foliage that ends up in litter, as opposed to being translocated to other parts of the plant prior to falling, acts similarly to the above 10 parameters except that an increase in that percent causes decreases in stemwood carbon and nitrogen (Fig. 14). None of these 11 parameters affect immobilization rate (AIMM) of nitrogen. The remaining parameter is a scaling constant for the increase of overstory foliage and its actions are quite different from the previous 11.

An increase in this constant decreases stemwood C and N, mineralized NH_4^+ and NO_3^-, percent N in *OS* foliage, net assimilation rate, rate of N immobilization, uptake of NH_4^+ and NO_3^- and decomposition rate; increases occur in overstory foliage and total foliar nitrogen (Fig. 15). These decreases appear to be mediated via decreases in temperature and soil moisture which accompany an increase in OSLAI.

An idea of the quantitative effects of this 3-fold variation in each parameter may be obtained from Fig. 16. For each of the 1944 parameter-variable combinations, an index was computed to describe the amount of variation in the variable (at the end of a 50 year run) resulting from a 3 fold variation in the parameter. This index was the total range of the variable divided by the value of the variable at the midpoint of the range. Since all variables were always greater than or equal to zero, this index varies between zero, for no variation, and **2.0,** if the lower limit of the range is zero. However, those variables which exhibited the greatest proportional variation were usually the smallest in magnitude. Thus in addition to the indices, which are presented graphically in Fig. 16, an idea of the size of the variable can be obtained from the number in the last column. ?his number is an exponent of 10, say n, such that the maximum value of the variable in each sensitivity analysis lies between 10^n and 10^{n+1}. Bars over these numbers indicate negative exponents. These exponents are averages over all parameters, but the variation in these exponents was minimal for all except a few of the variables, and these receive comment below. The scale of the graphs of the sensitivity indices is from 0.0 to 1.0. In the few cases where the index was > 1.0, i.e., where the maximum:minimum is greater than 3:1, the graph was fixed at

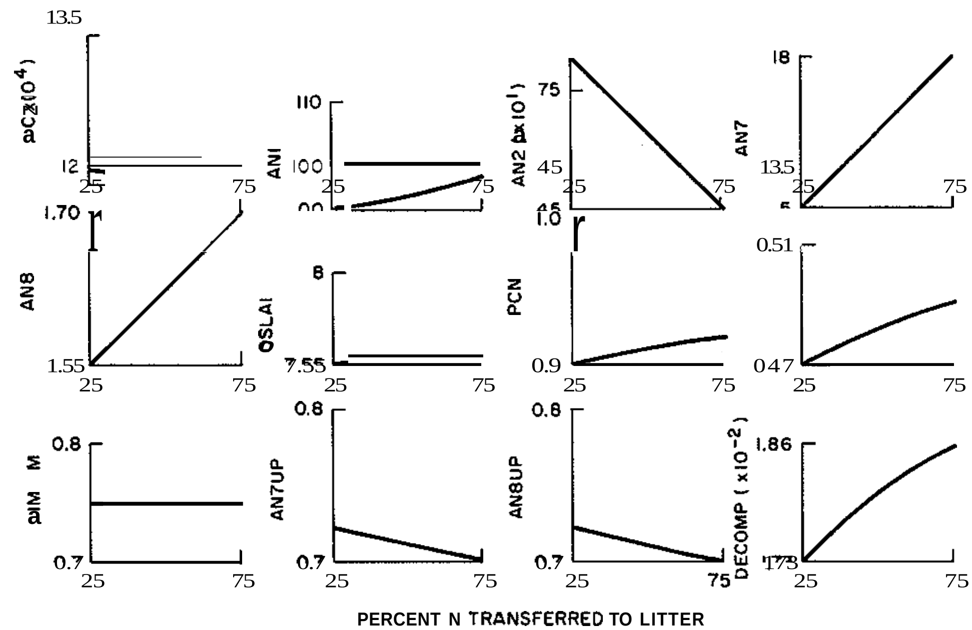


Figure **14.** Sensitivity analysis of the percentage *of* N in the oldest foliage which is transferred to litter.

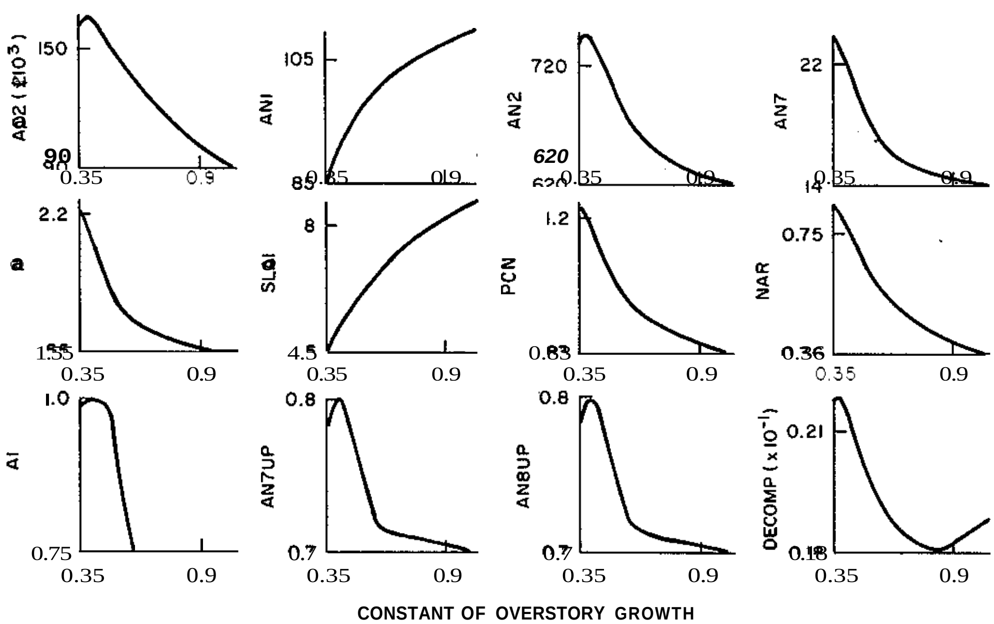


Figure 15. Sensitivity analysis of the overstory growth scaling constant

1.0. This occurs mainly for understory LAI, C and N; these three variables are also the only ones for which significant departure occurred from the mean exponent. The conditions causing such departure were variation of the mean lifetime of understory vegetation and of the overstory growth rate in the sensitivity analysis of that parameter. The understory LAI, C and N appeared to be sensitive to nearly all the parameters and as such are probably the best indicator variables regarding the state of the system.

Ten of the parameters had no detectable effect on any of the variables; these were fresh litter summer temperature, overstory foliage temperature in summer, fall, winter and changes in these temperatures, rate of return of pH to normal, changes in pH with urea and ammonium nitrate, and the constants of immobilization and volatilization. This was due in most cases to the parameter not being functionally incorporated into the system under the conditions of the model runs. For example, changes in pH with urea and NH_4NO_3 could have no effect since the sensitivity analysis was conducted for unfertilized treatments. One parameter had an effect which was detectable on a few of the variables but too small to be graphed in Fig. 16; this was a constant relating to immobilization of NO_3. These 11 parameters were omitted from Fig. 16.

Humus and litter pH are assigned and do not vary unless fertilizer **is** applied, so they were sensitive to only the initial assignment. Leaching and denitrification occurred only in winter with the parameter values given, so they are sensitive only to winter soil moisture potential. The following list of parameters had only slight effects on the variables: mean stem lifetime, fresh litter temperature at LAI=5 in winter and spring and the fresh litter SMP in winter and **SMP** minimum in summer. The parameters which had a strong effect on overstory leaf area index (OSLAI) were overstory specific gravity, humus pH and the OSLAI growth parameter; those strongly affecting net assimilation rate (NAR) were overstory specific gravity, litter pH, and constants relating to mineralization and OSLAI growth. Leaf specific gravity (Kg/ha/unit OS) will not vary much in nature. The litter and humus pH may vary considerably among habitats but are likely fairly constant within a habitat. The constants of mineralization and foliage growth are likely to be system-specific constants which are not very manipulable. Thus litter and humus pH appear to be the only parameters of great importance to production which are capable of control.

The sensitivity analysis performed on the parameters was done around a single point in the 54-dimensional parameter space. Due to the number and complexity of the processes in the model (involving thresholds in some cases), the analytic methods of sensitivity analysis described by Tomovic (1963) could not be used and numerical methods were required. Since the value of a parameter may easily determine its relative sensitivity and since numerical methods were used, the sensitivity indices obtained (Fig. 16) will almost certainly not be valid for different values of the parameters. Specifically, some of the parameters judged to be not important in the present system would likely become important under different conditions. **For** example, since the sensitivity analysis was done without fertilization or thinning and since pH is only changed by fertilization, neither the change in pH with urea nor the time taken to return to normal could have any effect. If fertilization had been done, the change in pH resulting would certainly have had an effect on growth. In addition, the various maximum and minimum values (e.g. temperature and soil moisture) would become important under more extreme conditions.

A sensitivity analysis provides **us** with several important pieces of information on each parameter: (a) how important **is** the parameter in the dynamics of the system, (b) how important are errors of measurement of the parameter to our predictive abilities, (c) how much effort should be expended in estimating the parameter, (d) how much variability of system behavior among habitats can be expected due to variation in the parameter, (e) how important **is** stochastic variation in the parameter over time (Tomovic 1963). In a real forest system, some parameters will be relatively invariant from habitat to habitat (such as probably leaf specific gravity). Thus even if a sensitivity analysis indicates considerable sensitivity of many variables to a given parameter, if its variation from habitat to habitat or over time is slight then this variation need not seriously be considered in judging the state of the system, although the parameter must be carefully estimated. A parameter which may vary widely over habitats but which has little effect on the system may be virtually ignored. The parameters of particular

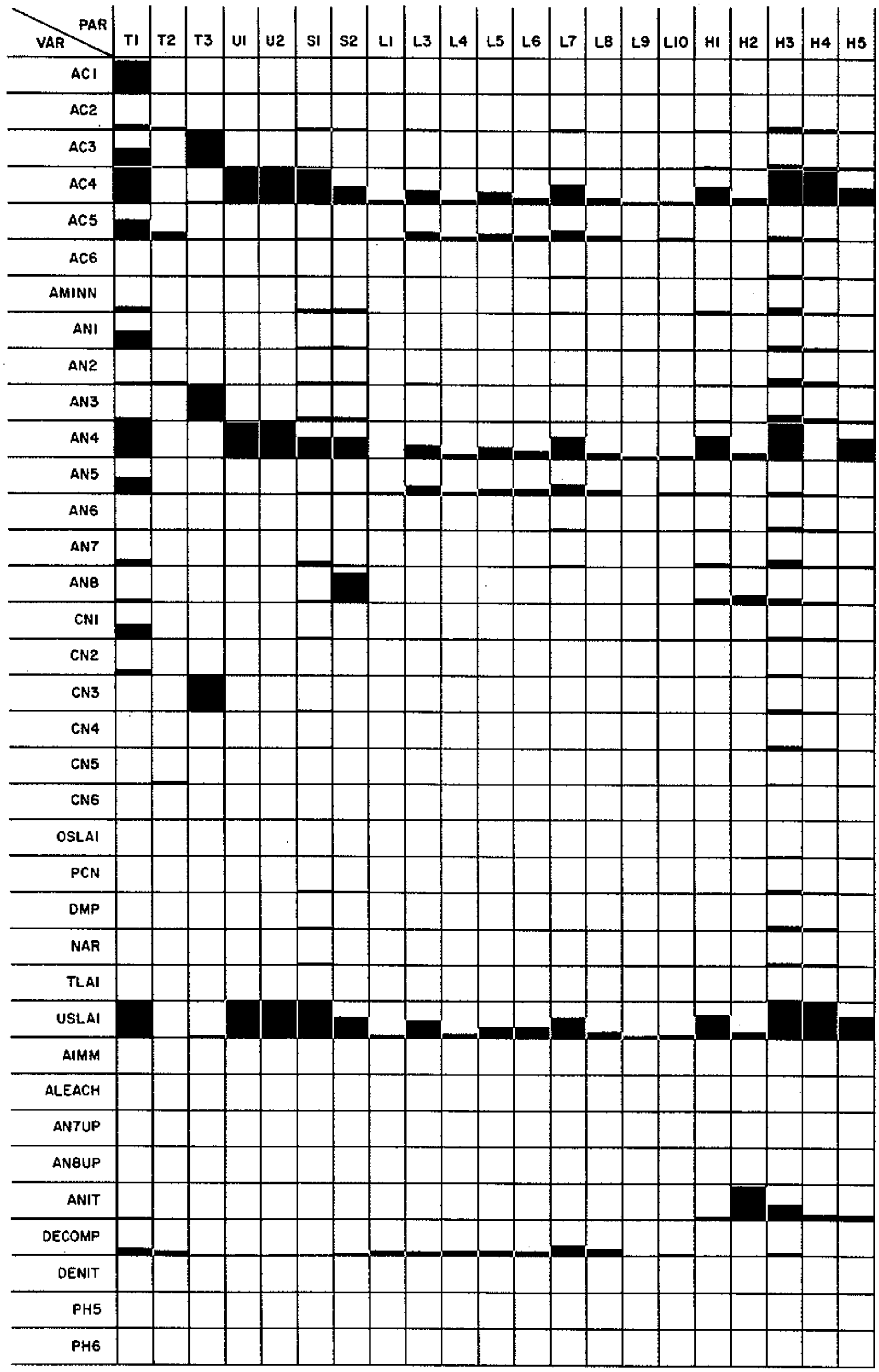
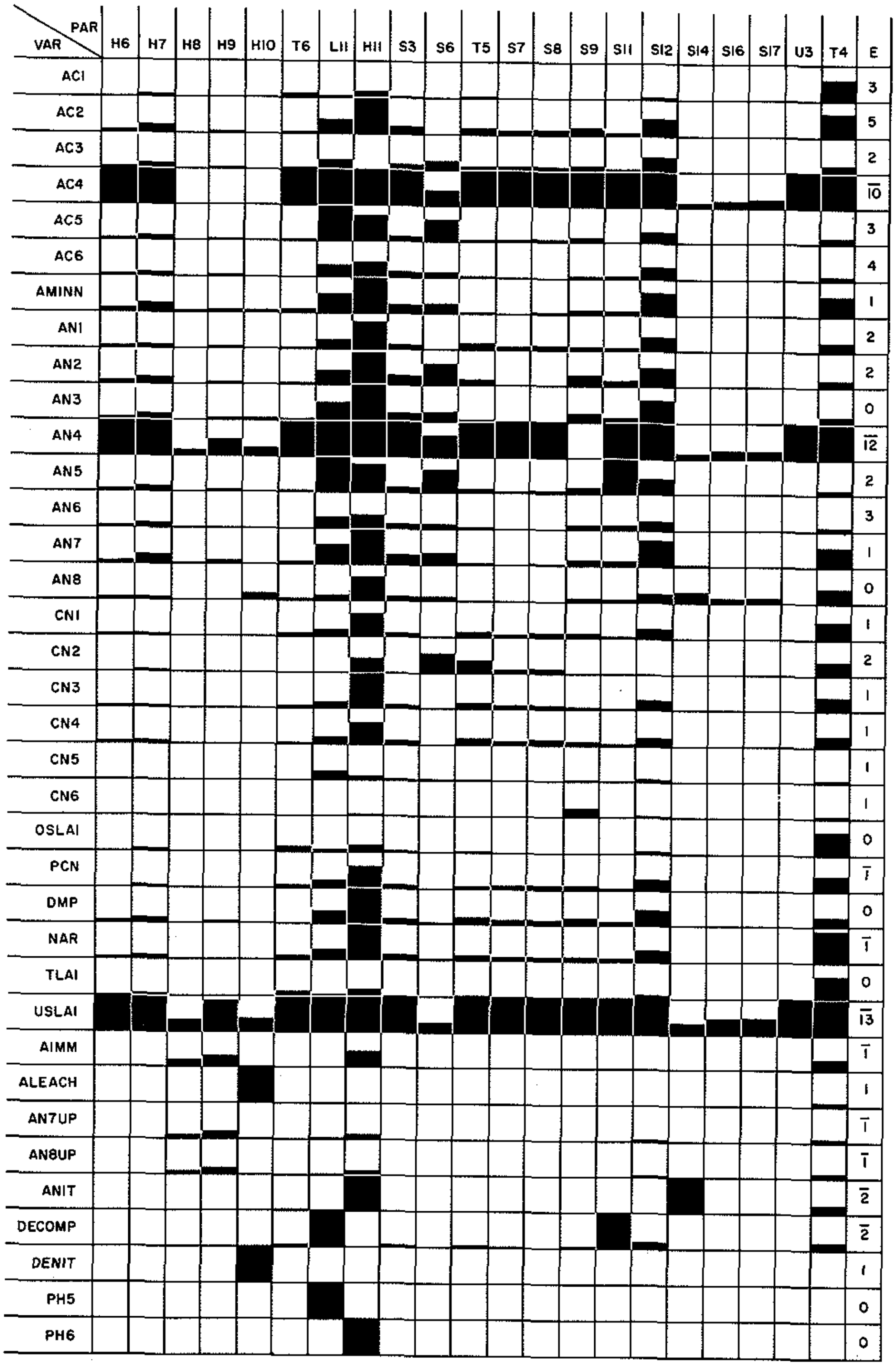


Figure 16. Sensitivity indices for each parameter on each variable. These indices range between 0 and 2 (see text) but are only graphed from 0 to 1; any greater than 1 are graphed as 1. Relative magnitudes are also shown in the right hand column as exponents of 10 which result in numbers near the upper limit of the variables (see text). Twelve parameters had little or no effect, and these are not included here. See Appendix for parameter and variable names.


PAR
VAR
H6 H7 H8 H9 H10 T6 L11 H11 S3 S6 T5 S7 S8 S9 S11 S12 S14 S16 S17 U3 T4 E
AC1 3
AC2 5
AC3 2
AC4 10
AC5 3
AC6 4
AMINN 1
AN1 2
AN2 2
AN3 0
AN4 12
AN5 2
AN6 3
AN7 1
AN8 0
CN1 1
CN2 2
CN3 1
CN4 1
CN5 1
CN6 1
OSLAI 0
PCN 1
DMP 0
NAR 1
TLAI 0
USLAI 13
AIMM 1
ALEACH 1
AN7UP 1
AN8UP 1
ANIT 2
DECOMP 2
DENIT 1
PH5 0
PH6 0

interest are those which are both unpredictable and important to the system.

Comparison with Shawnigan data

Any comparison of model output and data from the Shawnigan experiment is complicated by the fact that the inaccuracy of the initial conditions of the model causes initial variation in many of the variables (Fig. 12). This necessitates the running of the model for sufficient time that the output is relatively independent of initial conditions. Against this must be balanced the fact that the Shawnigan experiment is still only 15 years old and 12-year growth data are the latest available. In addition, only a few of the variables of the model were measured in the experiment. With these caveats, the following comparisons can be made.

Stemwood growth per hectare without and with heavy thinning (T_0 and T, respectively) and without and with heavy fertilization (F_0 and F_2) after 100-year runs of the model were ranked $T_0F_2 > T_2F_2 > T_0F_0 > T_2F_0$; before 50 years T_0F_0 was greater than T_2F_2 (Fig. 17). The results from Shawnigan Lake were identical with the first of these orders 12 years after treatment (Barclay and Brix 1985). The final (100-year) values for the overstory leaf area index from the model were ranked $T_2F_2 > T_0F_2 > T_2F_0 > T_0F_0$. The order at Shawnigan Lake seven years after treatment was $T_0F_2 > T_2F_2 > T_0F_0 > T_2F_0$ (Brix 1981). The values for foliar percent N from the model were ranked $T_2F_2 > T_0F_2 > T_2F_0 > T_0F_0$. The order from the Shawnigan data was identical for the first four years, after which the differences disappeared and in fact all treatments were slightly less than control by seven years (Brix 1983). Net assimilation rate after 100 years from the model were ranked $T_2F_2 > T_0F_2 > T_2F_0 > T_0F_0$, which is identical with the initial ordering from the data (Brix 1983); however these experimental differences decreased quickly and after four years all treatments had roughly the same net assimilation rate.

Understory LAI rapidly went to zero for all model treatments. Where the graphs are readable, however, the order is $T_2F_0 > T_2F_2 > T_0F_0 > T_0F_2$, which is identical with the order given by Stanek *et al.* (1979) five years after treatment. Data on litterfall indicate that mean litter fall from 1980-1984 was ranked $T_0F_2 > T_0F_0 > T_2F_2 > T_2F_0$ (Pang[3], unpublished). From the model output, total carbon in fresh litter was ranked $T_2F_0 > T_0F_0 > T_2F_2 > T_0F_2$ after 100 years, whereas in the first 20 years following treatment, the order was $T_0F_2 > T_0F_0 > T_2F_2 > T_2F_0$. This latter ordering is identical to that found at Shawnigan Lake. Data from Shawnigan Lake taken in 1982 on mineralized NH_4^+ in the mineral soil were ranked $T_0F_2 > T_0F_0 > T_2F_2$ (Pang[3], unpublished). Data for T_2F_0 are not available. Mineralized NH_4^+ from the model run 100 years after treatment was ranked $T_2F_2 > T_0F_2 > T_2F_0 > T_0F_0$, which only partly corresponds to the Shawnigan data above.

A feature of the model which differs from the experimental data is the length of time the differences amongst treatments persist. Accumulations of C can be expected to persist in perpetuity, but not of N; yet the model predicts that 100 years after treatment such differences still persist in mineralized NH_4^+ (AN7) and net assimilation rate (NAR) for all treatments except control (Fig. 17). In making modifications to the model, small changes were often seen to have profound consequences for some of the variable values. Thus it is important to be sure of the exact biological processes operating at each step of the nitrogen cycle. As an example of the sensitivity of the model to a process formulation, a change was made in the decomposition module. The existing formulation makes the mineralization of N from litter depend on the C N ratio in humus. If one instead makes this process depend on the C:N ratio in litter, the results for some variables are quite different. Figure 18 compares six of the variables over 100 years for these two formulations. While neither formulation is correct biologically, the former appears to be an acceptable approximation, given the nature of microbial action. Since many of the model processes are presently known only crudely and their representation in the model is even more crude, development of this model will be ongoing within the Shawnigan project and this documentation should be viewed as only a tentative approximation to the final state of the model or to reality.

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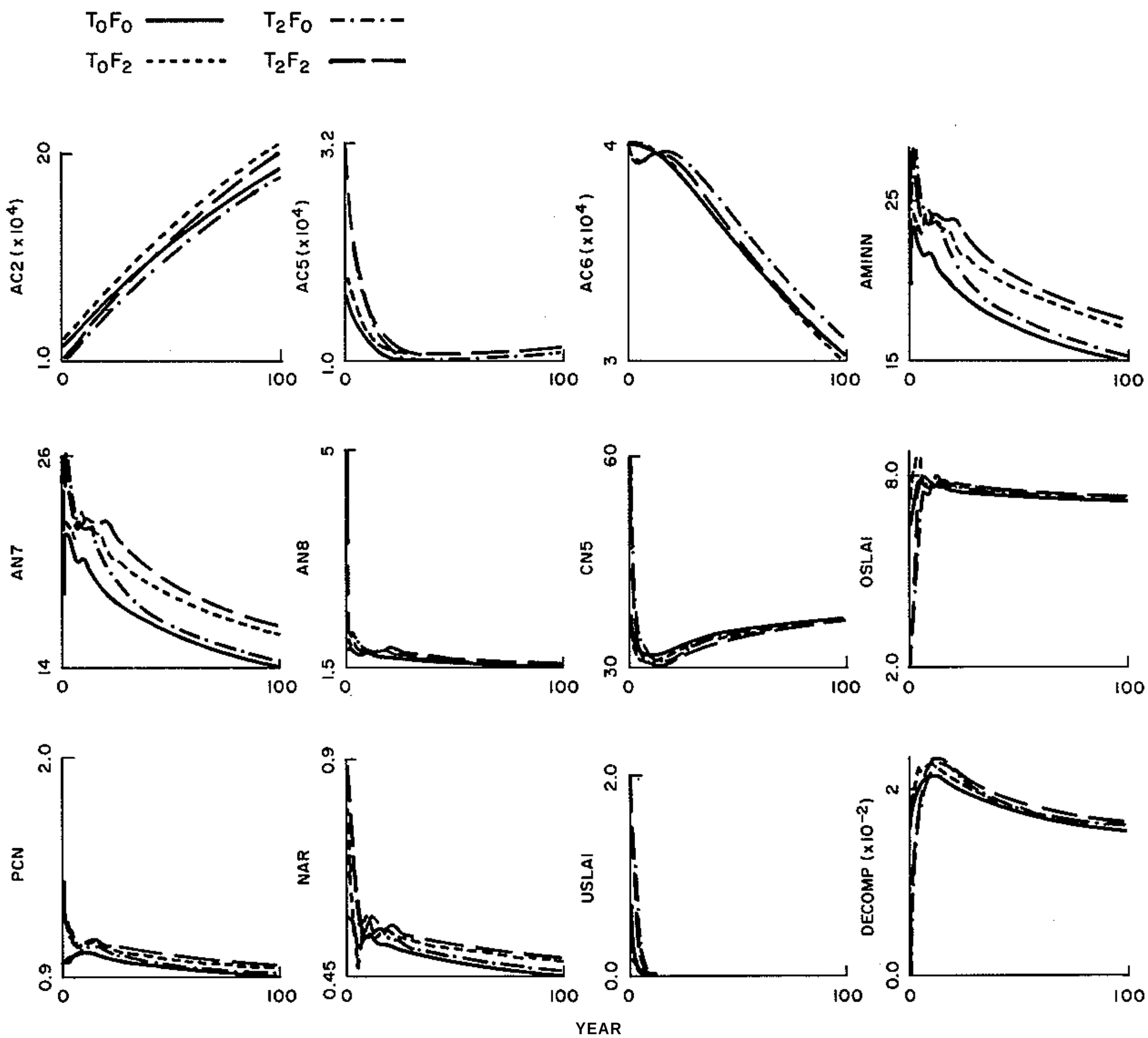

Figure 17. Time graphs (100 years) of 12 variables for each of the four extreme treatments: 1 — T_0F_0, 2 — T_0F_2, 3 — T_2F_0, 4 — T_2F_2 where T_0 is no thinning, T_2 is heavy thinning, F_0 is no fertilization, F_2 is heavy fertilization.

Nevertheless, certain features of the model output do reflect reality as the above comparisons show. The major value of a model such as SHAWN lies in its power to investigate hypotheses regarding system behavior under several plausible sets of alternative process formulations. It should not be used for quantitative prediction since there are still too many unknowns reflected in its structure.

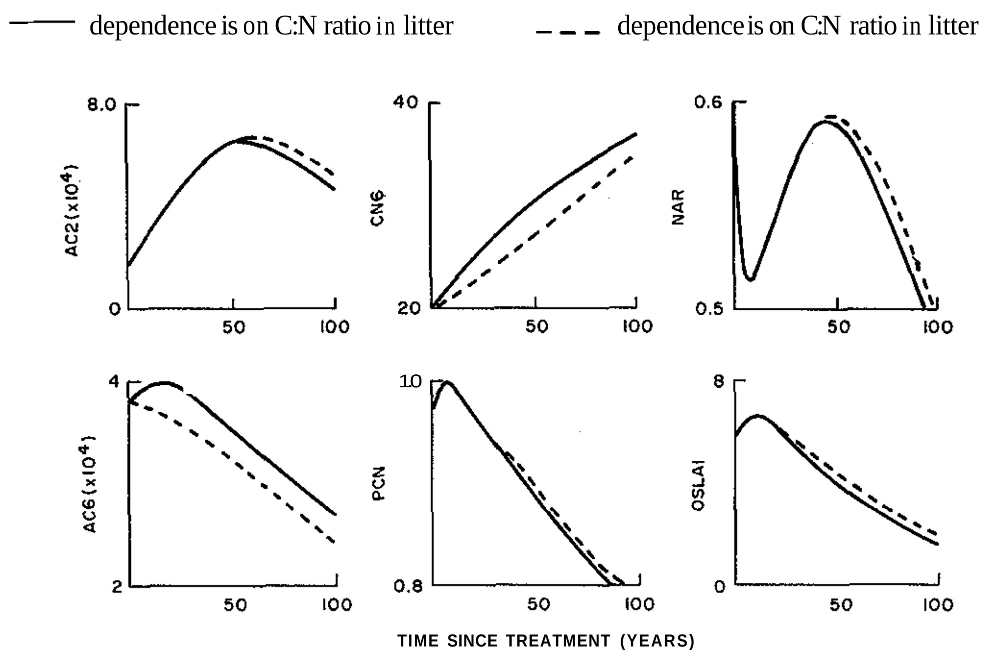

Figure 18. Time graphs (100 years) of six variables showing the differences resulting from two formulations for the transfer of nitrogen from litter to humus.

Conclusions

Potential uses of the model

The SHAWN model, based on a mechanistic representation of biogeochemical processes, can be used in a variety of ways. Perhaps the major areas of use are: (a) to point out deficiencies in available information and thus suggest further experimental work to be undertaken; (b) to identify parameters to which the system is particularly sensitive for the purpose of either accurately measuring or manipulating the parameters; (c) to examine the long-term effects on productivity and nutrient status of various alternative management options. Only the first two of these uses are discussed here since this report consists of preliminary documentation of a model which will change as more data becomes available from the Shawnigan experiment.

The 12 parameters that most strongly affect the system fall into three groups, one of which contains 10 parameters that act very similarly. Thus the effects of parameter variation on the system are generally quite predictable. This allows general predictions of the changes in behavior of the system across site classes and as a result of other types of variability. Measurement costs can be concentrated on those parameters that both strongly affect the system and that also may vary from site to site or over time as a result of succession or habitat change. A knowledge of these parameters may also affect decisions on management intervention, since some of the parameter values may be amenable to control. In addition, since many important parameters yield very similar system behavior upon variation, effort can be concentrated on those parameters most easily measured.

The processes which drive the model will ultimately determine its behavior. The importance of the exact formulation of the processes is not revealed by a parameter sensitivity analysis since the processes are unchanged by changes of parameters. However if alternative formulations of all the processes were introduced, as is represented in Fig. 18 for mineralization of NH_4^+ from litter, the results would undoubtedly he dramatic in the case of some processes. Two implications of the foregoing treatment are clear: (a) certain parameters need to be estimated rather precisely to achieve realistic estimates of the variable values over time; (b) the biology of the various processes must be well understood and well formulated before any claim to quantitative accuracy is justified. It appears that the parts of the model relating to nitrogen transformation in the soil need further elaboration. Since the model to a certain extent reflects the status of our knowledge, it appears that much more experimental work needs to be done at Shawnigan in order to establish values of parameters relating to transfers of nitrogen in the soil and also to better characterize mechanisms involved in these transfers. Both appear to he important in determining short- and long-term behavior of the system.

Comparison **of** model and experimental results

Only a comparison of the rank ordering of results from various treatments is presented in this report since accurate quantitative results are not expected from a mechanistic model unless the mechanisms modelled are very well understood. The rank orderings of results for the four extreme treatments (T_0F_0, T_0F_2, T_2F_0, T_2F_2) from the model generally agree well with those from the Shawnigan experiments for stemwood growth, foliage growth, percent N in the foliage, net assimilation rate and understory vegetation. However, the effects of fertilization and thinning on model results among the four extreme treatments persist much longer than one would expect. This is probably due to inadequacies within the algorithms relating to the degradation **of** nitrogen in litter and humus.

Acknowledgements

The Shawnigan model was constructed in consultation with the other members of the Shawnigan research group: Drs. Holger Brix, Jim Dangerfield, Valin Marshall and Patrick Pang. Without their cooperation the model would not have come into existence. We also thank Don Friesen for providing the graphics capability to the model.

References

Aber, J.D., and J.M. Melillo. 1982. FORTNITE a computer model of organic matter and nitrogen dynamics in forest ecosystems, 24 PP.

Arney, J.D. 1972. Computer simulation of Douglas-fir tree and stand growth. Ph.D. thesis. Oregon State University, Corvallis, **Ore.** 19 pp.

Barclay, H.J. and H. Brix. 1985. Fertilization and Thinning effects on a Douglas-fir ecosystem at Shawnigan Lake: 12 year growth response. Can. For. Serv., Pac. For. Cent., Inf. Rep. BC-X-271.34 pp.

Brix, H. 1981. Effects of thinning and nitrogen fertilization on branch and foliage production in Douglas-fir. Can. J. For. Res. 11: 502-511.

Brix, H. 1983. Effects of thinning and nitrogen fertilization on growth of Douglas-fir: relative contribution of foliage quantity and efficiency. Can. J. For. Res. 13: 167-175.

Clutter, J.L. 1963. Compatible growth and yield models. For. Sci. 9: 354-371.

Crown, M. and C.P. Brett. 1975. Fertilization and thinning effects on a Douglas-fir ecosystem at Shawnigan Lake: An establishment report. Can. For. Serv., Pac. For. Res. Cent., Inf. Rep. BC-X-110, 45 pp.

Curtis, R.O., G.W. Clendenen and D.J. de Mars. 1981. A new stand simulator for coast Douglas-fir: DFSIM User's guide. U.S.D.A. For. Serv., Tech. Rep. PNW-128.79 pp.

Gessel, S.P., T.N. Stoat and K.J. Turnbull. 1969. The growth behavior of Douglas-fir with nitrogenous fertilizer in western Washington. 2nd report, Institute of Forest Prod., College of Forest Resources, Univ. Wash. Contrib. No. 7.

Goulding, C.J. 1972. Simulation techniques **for** a stochastic model of the growth of Douglas-fir. Ph.D. thesis, University of B.C., Vancouver, B.C. 234 pp.

Kimmins, J.P and K.A. Scoullar. 1982. FORCYTE-10, a users manual. University of B.C., Vancouver, B.C.

Linder, S. (ed) . 1981. Understanding and predicting tree growth. Studia Forestalia Suecica, No. 160, Swedish Univ. Agric. Sci., Coll. **of** Forestry, Uppsala, Sweden, 87 pp.

Mitchell, **K.J.** 1975. Dynamics and simulated yield of Douglas-fir. For. Sci. Monogr. 17, 39 pp.

Mitchell, K.J. 1980. Distance dependent individual tree and stand models: concepts and applications. In. Forecasting Forest Stand Dynamics, pp. 100-137 (K.M. Brown and F.R. Clarke, eds.). School of Forestry, Lakehead University, Ontario.

Munro, D.D. 1974. Forest growth models – a prognosis. **In.** Growth models for tree and stand simulation (J Fries, ed), Institutionen for Silogsproduktion, Dept. For. Yield Res., Res Notes No. 30, Stockholm, Sweden, 379 pp.

Myers, C.A. 1971. Field and computer procedures for managed stand yield tables. U.S.D.A. Res. Paper RM-79, 24 pp.

Stanek, W., D. Beddows and D. State. 1979. Fertilization and thinning effects on a Douglas-fir ecosystem at Shawnigan Lake on Vancouver Island: Some observations on salal and bracken fern undergrowth. Can. For. Serv., Pac. For. Res. Cent., Inf. Rep. BC-R-1, 11pp.

Tomovic, R. 1963. Sensitivity analysis of dynamic systems. McGraw-Hill Book Co., New York, 142 pp.

Appendix

List of parameters and variables by compartment in SHAWN

(a) Tree-related quantities:

(i) Parameters

T1	Dry weight in overstory foliage (kg/ha/unit OS)
T2	Mean lifetime for stems (years)
T3	Mean lifetime for short-lived roots (years)
T4	Growth of OSLAI constant
T5	Exponent of foliage to foliage transfer
T6	Overstory foliage temperature at OSLAI = 5; Spring (0°C)
TI	Overstory foliage temperature at OSLAI = 5; Summer
T8	Overstory foliage temperature at OSLAI = 5; Fall
T9	Overstory foliage temperature at OSLAI = 5; Winter
T10	Change in overstory foliage temperature for OSLAI ≠ 5

(ii) Variables

AC1	Accumulated carbon in overstory foliage
AC2	Accumulated carbon in stemwood, bark, and roots
AC3	Accumulated carbon in short-lived roots
AN1	Accumulated nitrogen in overstory vegetation
AN2	Accumulated nitrogen in stemwood, bark, and roots
AN3	Accumulated nitrogen in short-lived roots
CN1	C N ratio in overstory foliage
CN2	C:N ratio in stemwood, bark, and roots
CN3	C:N ratio in short-lived roots
OSLAI	Overstory leaf area index
PCN	Percent nitrogen in overstory foliage
DMP	Dry matter production
NAR	Net assimilation rate
TLAI	Total leaf area index

(b) Understory-related quantities

(i) Parameters

U1	Dry weight in understory foliage (kg/ha/unit US)
U2	Mean lifetime for understory vegetation (years)
u 3	Growth of USLAI (units/year)

(ii) Variables

AC4	Accumulated carbon in understory vegetation
AN4	Accumulated nitrogen in understory vegetation
CN4	C:N ratio in understory vegetation
USLAI	Understory leaf area index

(c) Litter-related quantities

(i) Parameters

L1	Fresh litter temperature at total LAI = 5, Spring (0°C)
L2	Fresh litter temperature at total LAI = 5; Summer
L3	Fresh litter temperature at total LAI = 5; Fall
L4	Fresh litter temperature at total LAI = 5; Winter
L5	Change in fresh litter temperature for TLAI ≠ 5
L6	Fresh litter maximum soil moisture potential for Spring and Fall
L7	Fresh litter mininimum soil moisture potential for Spring and Fall
L8	Fresh litter maximum soil moisture potential for Summer
L9	Fresh litter mininimum soil moisture potential for Summer
L10	Fresh litter soil moisture potential for winter
L11	Fresh litter unmodified pH
L12	Number of seasons for pH to return to normal
L13	Change in pH for addition of urea (/100 kg N/ha)
L14	Change in pH for addition of ammonium nitrate

(ii) Variables

AC5	Accumulated carbon in fresh litter
AN5	Accumulated nitrogen in fresh litter
CNS	C N ratio in fresh litter
PHS	Fresh litter pH
DECOMP	Fraction of nitrogen in fresh 'litter to decompose

(d) Humus-related quantities

(i) Parameters

H1	Humus temperature at total LAI = 5; Spring (0°C)
H2	Humus temperature at total LAI = 5; Summer
H3	Humus temperature at total LAI = 5; Fall
H4	Humus temperature at total LAI = 5; Winter
H5	Change in humus temperature for TLAI ≠ 5 (0°C/unit)
H6	Humus maximum soil moisture potential for Spring and Fall
H7	Humus mininimum soil moisture potential for Spring and Fall
H8	Humus maximum soil moisture potential for Summer
H9	Humus mininimum soil moisture potential for Summer
H10	Humus soil moisture potential for Winter
H11	Humus unmodified pH

(ii) Variables

AC6	Accumulated carbon in Humus
AN6	Accumulated nitrogen in Humus
CN6	C:N ratio in humus
PH6	Humus pH

(e) Mineral soil related quantities

(i) Parameters

S1	Annual constant increase in NH_4^+ (kg/ha/year)
S2	Annual constant increase in NO_3^-
S3	Percentage of nitrogen from decomposition to NH_4^+
S4	Percentage of nitrogen taken up by tree to overstory foliage
S5	Percentage of nitrogen taken up by stem wood
S6	Percentage of nitrogen from oldest foliage to fresh litter
S7	Threshold for percentage nitrogen
S8	Exponent for perceniage nitrogen
S9	Threshold for volatilization and immobilization of NH_4^+
S10	Threshold for immobilization of NO_3^-
S11	Constant in decomposition equation
S12	Constant of mineralization
S13	Constant of immobilization
S14	Constant of nitrification
S15	Constant of volatilization (percentage)
S16	Constant of denitrification
S17	Constant of leaching

(ii) Variables

AN7	Accumulated nitrogen in mineral NH_4^+
AN7UP*	Fraction of NH_4^+ taken up by roots
AN8	Accumulated nitrogen in mineral NO_3^-
AN8UP*	Fraction of NO_3^- taken up by roots
ANIT*	Fraction of NH_4^+ to nitrification
DENIT*	Fraction in denitrification
AIMM*	Fraction of nitrogen immobilized
ALEACH*	Factor in leaching of NO_3^-
AMINN	Total mineral nitrogen (AN7 + AN8)
TOTALN	Total nitrogen in the ecosystem

* Fractions may not add to one due to readjustment