

CHAPTER 19

## GROWTH-INFLUENCING FACTORS IN DYNAMIC MODELS OF FOREST GROWTH

G. M. J. Mohren and R. Rabbinge

**Abstract.** The effects on forest growth of weather, soil conditions, and disturbances such as those resulting from air pollution and acidification can be analyzed with the aid of dynamic models of plant growth, based on underlying physical, chemical, and biological processes. From the photosynthesis-light response curve for individual leaves, canopy assimilation is calculated using numerical integration methods. Respiration requirements for growth and maintenance are subtracted, and net biomass growth is calculated. The results of a model for Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) growth based on this approach are presented. Secondary disturbances can be modeled on the basis of their direct effects on process rates, or through delayed effects resulting from changes in site conditions due to soil pollution and acidification. Comprehensive explanatory models summarize data, integrate results from different disciplines, and identify gaps in knowledge. After validation and simplification, summary models can be used for predicting system behavior under changing growing conditions, assessing exposure-effect relationships, and evaluating management alternatives and policy strategies.

### INTRODUCTION

Tree growth is the outcome of a series of physical, biochemical, and physiological processes in which, driven by solar radiation, carbon dioxide (CO<sub>2</sub>) from the air is assimilated by the foliage, and the carbohydrates produced by the photosynthetic process are converted into the structural dry matter of the living plant. From germination onwards, living biomass accumulates up to a point when production is compensated for by losses such as the dying of older tissue and subsequent litterfall or root turnover. Stem structural dry matter accumulates during stand development when living sapwood turns into dead supporting heartwood tissue.

Forest growth can be studied in many different ways. A "bottom-up" approach to forest growth starts with detailed analysis of the processes involved and aims at an accurate description of the basic elements, which are then assembled to give a description

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Dr. Mohren is Forest Production Ecologist at the Research Institute for Forestry and Landscape Planning "De Dorschkamp," Bosrandweg 20, P.O. Box 23, 6700 AA Wageningen, the Netherlands. Dr. Rabbinge is Professor of Crop Ecology at the Department of Theoretical Production Ecology, Wageningen Agricultural University, Bornsesteeg 65, P.O. Box 430, 6700 AK Wageningen, the Netherlands. The authors wish to acknowledge the help of A. F. M. Olsthoorn and M. J. Kropff, who commented on an earlier draft of the present paper. An evaluation of problem areas in physiological models of tree and stand growth, together with the feasibility of using these models for the analysis of disturbances as a result of air pollution and soil acidification, was carried out as part of a CEC/COST-612 workshop held December 14-17, 1987, in Gennep, the Netherlands. Discussions and recommendations from this workshop were summarized in Mohren (1988).

of tree and stand performance. The other extreme is a "top-down" approach to primary production and growth. In this case, the analysis starts with an elementary model of the whole stand, which contains as few elements as possible. This general model is subsequently extended to incorporate more growth-influencing factors as these turn out to be relevant.

Such a dynamic model, based on underlying processes, integrates knowledge of the physiological processes involved at the tree level. Modeling provides a way of scaling up from the process level to the level of the stand, and from short-term disturbances to changes in stand growth in the long run. Ecophysiological modeling is especially important in forestry, as stand development takes several decades, and long-term studies are cumbersome and expensive. Model-building and simulation are particularly useful for developing a framework for experimentation (Landsberg, 1986) and the combination of simulation models with field measurements and laboratory experiments allows rapid testing of hypotheses.

### GROWTH-INFLUENCING FACTORS

In a top-down approach, a distinction is made between growth-determining factors, growth-limiting factors, and growth-reducing factors, all of which act as modifiers of primary production. Growth-determining factors set the upper limits for growth and production. The main factors determining photosynthetic production are tree physiology, temperature, and incoming radiation. Thus primary production can be calculated from the amount of intercepted radiation and from the efficiency with which the stand uses photosynthetically active radiation absorbed by the foliage (Jarvis and Leverenz, 1983; Linder, 1985).

Growth-limiting factors depend on site conditions and define the attainable production level. They include the availability of water and nutrients. Under the conditions in the Netherlands, the total potential transpiration of a closed Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) stand is about 400–500 mm; total nitrogen (N) and phosphorus (P) requirements can be around 100 kg/ha for N and some 10 kg/ha for P. These amounts have to be available for uptake by the roots or may be supplied in part by redistribution of the N and P already incorporated in the biomass. If the supply falls below the minimum demand, growth is retarded. Additional growth-reducing factors include a range of agents causing deviations from the attainable production level for a particular site. Examples of growth-reducing factors are incomplete canopy closure, the occurrence of air pollution, and pests and diseases. The incorporation of these factors in an ecophysiological model will be illustrated later in this paper. Various production situations may be discerned on the basis of different combinations of growth-determining, growth-limiting, and growth-reducing factors (Table 1).

**Table 1.** Production situations that may be discerned on the basis of growth-determining and growth-limiting factors (assuming a completely closed canopy and the absence of pests, diseases, weeds, or other growth-reducing factors).

1	Potential growth with abundant water, N, and minerals: closed canopy. Growth determined by weather and tree physiology only.
2	Growth limited by the availability of moisture in the soil during part of the growing season.
3	Growth limited by the availability of water and N and/or P during at least part of the growing season.
4	Growth limited by the availability of water, N and/or P, and other minerals during at least part of the growing season.

As indicated in production situation 1 in Table 1, potential growth is realized when water and nutrients are in ample supply, the canopy is completely closed, and disturbances are absent. In this situation, growth is solely a function of temperature and incoming radiation, as well as the physiological, geometrical, and optical characteristics of the crop that determine the photosynthetic light-use efficiency of the whole stand and the amount of incoming photosynthetically active radiation that is absorbed by the foliage. In the second production situation, available water falls short of demand during at least part of the growing season. Water deficit in the soil limits root uptake and causes the stomata to close, thereby reducing the uptake of  $\text{CO}_2$ . Shortage of N or P occurs in addition to the water shortage in production situation 3; while in production situation 4 shortage of water, N, and P may occur in combination with a shortage of other minerals such as magnesium (Mg), potassium (K), or calcium (Ca) during at least part of the growing season. Growth reductions induced by disturbances are superimposed on these production situations.

So far, models have been developed mainly for production situations 1 and 2 (e.g., De Wit et al., 1978) and to some extent for production situation 3, involving N (e.g., Van Keulen and Seligman, 1987). Some preliminary models for the effects of P on growth do exist (e.g., Mohren, 1986), but models dealing with other minerals (production situation 4) are still in the stage of infancy (see overview by Penning de Vries, 1983).

The top-down approach views the forest stand as a closed green canopy. The main state variables consist of foliage biomass (with foliage area derived from it), root biomass (usually separated into fine and coarse roots), and stem and branch biomass. Reproductive structures such as flowers and seeds usually are not taken into account in primary production models, especially when applied to coniferous forests. In typical seed-crop years, this may lead to an overestimation of bole increment, as diameter growth may be suppressed by 15–20% due to cone production (Eis et al., 1965). This effect is ignored in most general stand-growth models.

When studying the relationship between environmental conditions and stand growth using an explanatory model based on tree physiology, it is not necessary to take individual trees into account. Their contribution is encompassed through the calculation of stand properties such as horizontal canopy closure. This leads to relatively little detail in the description of stand structure in process models of tree growth. In general, it is preferable to study closed stands instead of individual trees; it is much easier to determine the resources available for a stand when a one-dimensional model is used than it is to determine the resources available to individual trees in the stand when a three-dimensional individual-tree model is used. It has been shown (Van Gerwen et al., 1987) that a stand-level model allows the calculation of individual-tree growth in the stand by taking into account competition among the trees. This will not be considered here, as incorporation of individual tree growth merely adds complexity to the model.

## DYNAMIC INTERACTIONS OF CARBON, WATER, AND NUTRIENTS

Figure 1 gives an elementary representation of primary production in plants, redrawn from Mohren (1987). It is based on the production and consumption of assimilates in the plant. The diagram portrays potential production, because canopy assimilation was considered merely a function of weather conditions, i.e., solar radiation and temperature, and leaf area index (LAI). The physiological processes involved—photosynthesis, respiration, and transpiration—can be considered identical in all  $\text{C}_3$  plant species, including most trees. Maximum values for photosynthetic rates and respiration requirements, together with the relationship of these processes to temperature, have to be

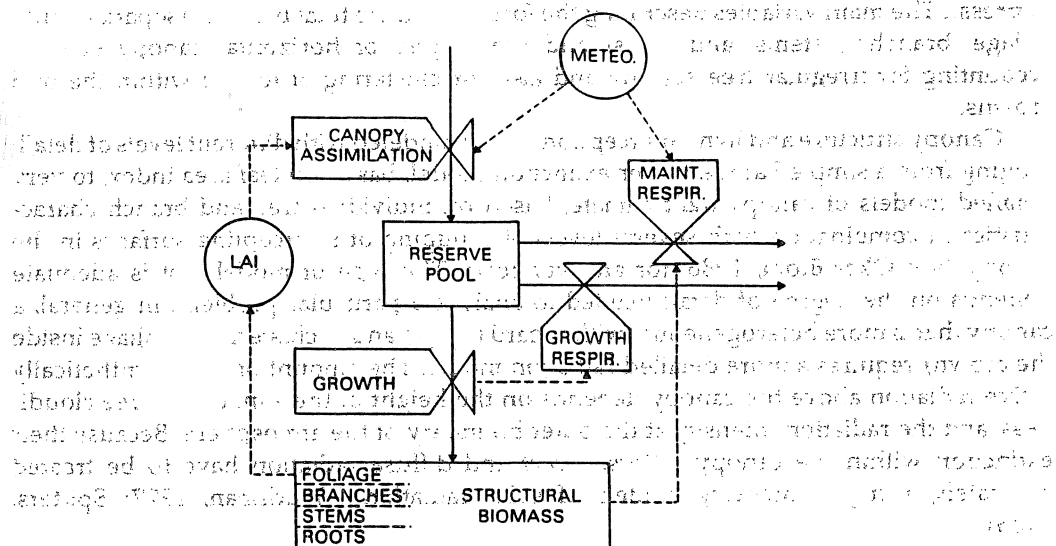


Figure 1. Diagram of an elementary summary model of plant growth. Boxes represent state variables, circles contain intermediary variables or driving functions, and valve symbols represent rate variables.

determined for a particular plant species. Based on these underlying principles, a general simulation approach has been developed at the Department of Theoretical Production Ecology of Wageningen Agricultural University (De Wit et al., 1978; Spitters et al., in press) and applied to forest stands by Mohren (1987).

A generalized growth equation for the individual biomass components in these models is

$$G_i = DWC_i \times DC_i \times (P_g - R_m) - L_i \quad (\text{kg/ha/year}) \quad (1)$$

where  $G_i$  is the net annual dry weight increment of biomass component  $i$  in kg/ha/year;  $DWC_i$  the corresponding dry weight conversion in kg dry weight per kg carbohydrates ( $\text{CH}_2\text{O}$ );  $DC_i$  the distribution coefficient for the carbohydrates available for growth;  $P_g$  the gross canopy assimilation in kg  $\text{CH}_2\text{O}$ /ha/year, calculated on a daily basis from light absorption and photosynthesis-light response of individual leaf layers;  $R_m$  the total maintenance respiration of the living tissue; and  $L_i$  the rate of litter loss for biomass component  $i$  in kg/ha/year.

Based on a gross  $\text{CO}_2$  assimilation rate of 15 kg/ha/h and a light-use efficiency for  $\text{C}_3$  species of 0.4 kg  $\text{CO}_2$ /ha/h/J/m<sup>2</sup>s, or 11.2  $\mu\text{g}$   $\text{CO}_2$ /J, total gross photosynthesis of a closed forest canopy varies from some 30  $\text{CH}_2\text{O}$ /ha/d during winter to a maximum of about 350 kg  $\text{CH}_2\text{O}$ /ha/d during June and July, using Dutch weather data for the calculations. For coniferous stands such as Douglas fir in temperate, maritime climates in western Europe, the annual total for  $P_g$  is around 60,000 kg  $\text{CH}_2\text{O}$ /ha/year. Maintenance requirements may amount to some 45% of this total, leaving 33,000 kg  $\text{CH}_2\text{O}$  for dry weight increment. The coefficient for conversion of assimilates to structural dry matter is around 0.65, giving a potential dry matter production of some 21,500 kg/ha/year. Half this is stemwood; using a value of 450 kg/m<sup>3</sup> for specific gravity, this gives a value for the potential annual stem volume increment of 24 m<sup>3</sup>/ha/year. Typical values for the parameters used can be found in Mohren et al. (1984) and Mohren (1987).

In the model used here, gross canopy assimilation ( $P_g$ ) is calculated from the distribution of photosynthetic active radiation over the foliage, using a gaussian technique to integrate over the day and over the layers within the canopy (Goudriaan, 1986; Spitters et al.,

in press). The main variables describing the forest stand are total biomass (separated into foliage, branches, stems, and roots) and the degree of horizontal canopy closure, accounting for irregular tree spacing and also for clustering of foliage within the tree crowns.

Canopy structure and light interception can be modeled with different levels of detail, ranging from a simple Lambert-Beer extinction model, based on leaf area index, to very detailed models of canopy light climate, based on individual tree and branch characteristics in combination with several levels of grouping of intercepting surfaces in the canopy (see Oker-Blom, 1986, for an overview). The type of model that is adequate depends on the degree of detail needed to analyze a particular problem. In general, a canopy that is more heterogeneous (with regard to gaps and to clustering of foliage inside the crown) requires a more detailed radiation model. The amount of photosynthetically active radiation above the canopy depends on the height of the sun, the degree cloudiness, and the radiation intensity at the outer boundary of the atmosphere. Because their extinction within the canopy differs, direct and diffuse radiation have to be treated separately, using elementary models of solar radiation (Goudriaan, 1977; Spitters, 1986).

The uptake of  $\text{CO}_2$  is coupled to leaf transpiration, and the conversion of carbohydrates into structural dry matter is coupled to the uptake of N and mineral elements such as P, K, Ca, and Mg. This further implies that the processes of canopy assimilation and transpiration are closely coupled, with the degree of coupling determined by canopy roughness and the vapor pressure deficit of the air. When the vapor pressure deficit is low, more  $\text{CO}_2$  can be taken up per unit of water transpired, and drought is less likely to occur. At the same time, dry matter increment and nutrient availability are linked. The ratio between the separate processes is determined by the physiological characteristics of the plant and by prevailing environmental conditions. Most nutrients are taken up by the roots and transported by the transpiration flux through the xylem tissue. Soil moisture in the root zone allows root uptake of nutrients by providing the link between the root surface and the mineral soil; when the soil is dry, nutrients cannot be taken up. Nutrient uptake may be further modified by soil conditions such as pH, the aluminum (Al) concentration and the root surface, and the presence or absence of mycorrhizae.

The nutrient content of the plant tissue is not only directly coupled to the basic requirement for incorporation in newly formed dry matter (minimum nutrient content per unit of dry matter formed), but also to the rates of the basic physiological processes. Nitrogen occurs mainly in proteins such as enzymes; process rates that depend on the amount of enzymes available are related to N content. An example of this is the high correlation between N content of leaves and the maximum net photosynthesis rate at light saturation (Van Keulen and Seligman, 1987, p. 47). Phosphorus, in the form of  $\text{P}_2\text{O}_4$  in organic complexes such as adenosine triphosphate (ATP), is an important part of the energy metabolism of plant cells. Both N and P are, within narrow limits, stable biomass components. They are required in minimum amounts in the living tissue, and they cannot be taken up beyond a certain maximum concentration. For Douglas-fir, minimum and maximum amounts for N are 0.8 and 2.0% of dry weight respectively; and for P, minimum and maximum amounts are 0.08 and 0.30% of dry weight (Mohren et al., 1986). Other elements, such as K, are involved in transport processes within the plant and are more mobile, with high concentrations in meristematic and newly formed tissue.

At the stand level, this coupling between tissue concentration and growth is usually less clear than the interactions at the biochemical process level, because at the stand level a number of other interactions may be involved. The total amount of N and P taken up, however, is highly correlated with total net primary production, indicating that on the average 200 kg of dry matter are formed per kg of N taken up. The corresponding figure for P is

2000 kg dry weight per kg of P taken up (Miller, 1984). At a net primary production of 20,000 kg/ha/year, this leads to estimates of N and P requirements of some 100 kg/ha/year and 10 kg/ha/year, respectively.

As a result of the interactions mentioned above, site differences in water and nutrient availability may lead to entirely different responses to fertilization or irrigation which cannot be easily separated on the basis of field data only. These interactions become even more important when additional effects of air pollution and soil acidification are investigated, as the effects of water and nutrient availability usually cannot be separated from the effects of abiotic and biotic disturbances. In addition, the effects of disturbances may differ markedly in various production situations. Under these circumstances, explanatory models in which the effects of water, nutrient, and growth disturbances on process rates are quantified separately, are very useful. Such models help to define the problem properly and may be used to formulate critical hypotheses and facilitate the design of field studies and laboratory experiments.

### A MODEL OF WHOLE-STAND GROWTH

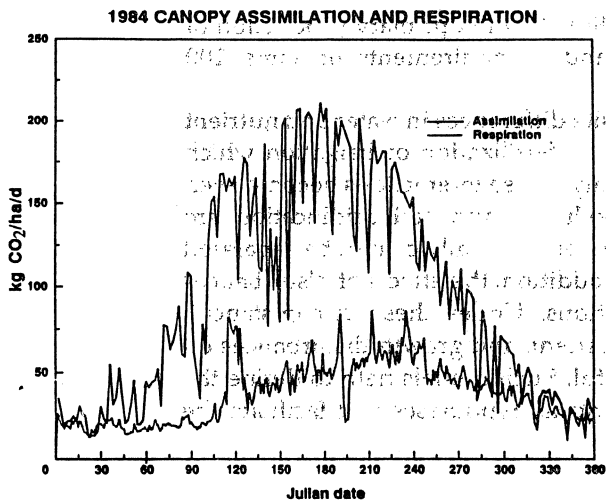
Since the mid-1960s, many physiological growth models have been developed. They range from very detailed models that explain individual physiological processes such as photosynthesis (Farquhar et al., 1980) or the functioning of roots (De Willigen and Van Noordwijk, 1987; Luxmoore and Stolzy, 1987), through single-tree models (Ågren, 1980) and models for stand growth (Mohren, 1987; Mäkelä, 1988), to models for forest micrometeorology (Goudriaan, 1977, 1979) and models for large-scale forest dynamics and succession (Shugart, 1984). Most ecophysiological simulation models, however, have been developed for agricultural crops (Penning de Vries, 1983).

An example of the outcome of a physiological stand growth model is shown in Figures 2, 3, and 4. The figures are the results of a general model based on Equation 1; a detailed description is found in Mohren (1987). The model simulates canopy assimilation, respiration, and transpiration with time-steps of one day to account for seasonal variation. Using historical weather records, stand development can be simulated for several decades to allow comparison of the simulation results with measurement series from permanent field plots. Input data for this model consist of daily weather variables such as solar radiation, air temperature, vapor pressure of the air, wind speed, and precipitation.

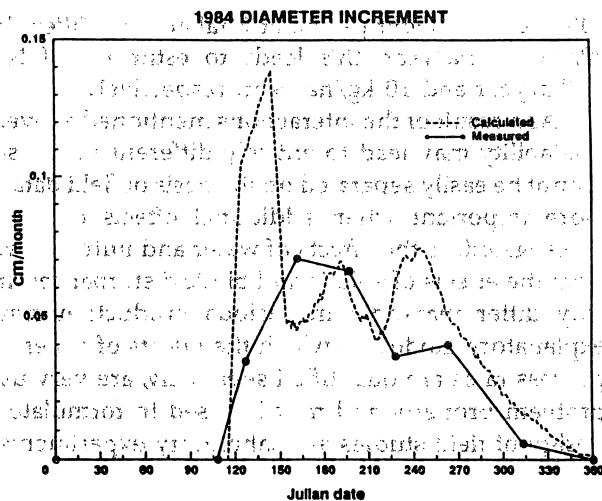
The soil is characterized by the water-holding capacity of the rooting zone, based on wilting point and field capacity of the soil, and by the total amounts of N and P in the rooted soil profile. The availability of N and P in the soil are based on a distinction between stable and unstable pools of these nutrients. Also taken into account is cycling of elements, through litterfall and decomposition of organic material, and rates of atmospheric deposition (see Mohren, 1986, for a full description of the nutrient cycle model).

In Figure 3, the model's overestimation at the beginning of the growing season is due to the assumption in the model that stem growth is distributed evenly over the bole, whereas in reality growth of diameter at breast height (dbh) will lag behind diameter increment higher up the trees. Total growth is somewhat overestimated by the model in this case, as can be inferred from the area underneath the curves. For this particular plot, this is due to model overestimation of horizontal canopy closure.

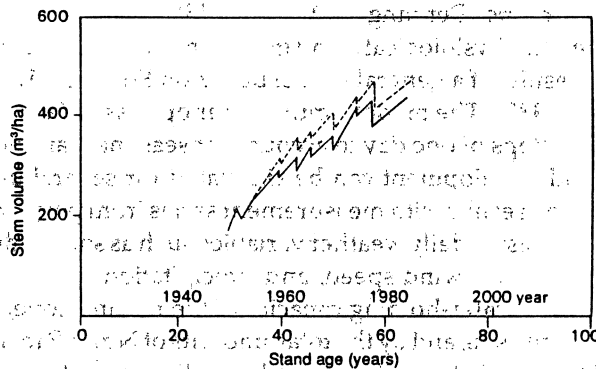
Figure 4 gives the simulated and measured stem volume from the same permanent plot. For the simulation runs presented in Figures 2, 3, and 4, effects of pollution or soil changes due to acidification were not taken into account, because the simulations were mainly concerned with a series of historical data.



**Figure 2.** Simulation of daily assimilation and respiration of a Douglas-fir stand during 1984. The plot is located in the center of the Netherlands in the Veluwe area. In 1984, the trees were 65 years old, with an average height of 28 m. Stocking density was 360 trees per ha, with mean dbh of 37 cm. For the calculation, a value of 6 m<sup>2</sup>/m<sup>2</sup> was assumed for leaf area index.



**Figure 3.** Simulated (daily) and measured (monthly) diameter increment during 1984 in a Douglas-fir stand. Model estimates are compared to data measured in a field plot located in the center of the Netherlands. Calculated current annual increment during 1984 equals 11.5 m<sup>3</sup>/ha, resulting in an average diameter increment of 0.4 mm/year. Total simulated dry weight production amounted to about 13 t/ha. The overall pattern of model results agrees with experimental data.



**Figure 4.** Simulation of total stem volume in a Douglas-fir stand. Solid line (—): measurement series. Broken line (---): simulation results. (Redrawn from Mohren, 1987.)

### MODELING GROWTH DISTURBANCES

Incomplete canopy closure and the effects of growth disturbances are superimposed on and intertwined with growth limitations induced by insufficient water and nutrient availability. A general classification scheme for growth-reducing agents is given in Table 2. Disturbances can be grouped according to their effect, which may be continuous and direct (e.g., when rates of physiological processes such as photosynthesis, respiration, and aging are changed) or delayed in time (e.g., when morphological development is

disrupted by means of changes in assimilate distribution or in hormonal balances). Discontinuous catastrophic disturbances occur, for instance, when windthrow or frost causes physical damage to the canopy. Examples of different effects of growth reductions caused by air pollution and soil acidification are given in Table 3. In the state-rate modeling approach used in Figures 1, 2, 3, and 4, these growth disturbances can be modeled by quantifying their effects on process rates, or quantifying the changes they impose on the state-variables in the model.

**Table 2. Growth reductions that may be superimposed on the production situations outlined in Table 1.**

- Direct effects on process rates (e.g., direct effects of air pollution on photosynthesis and transpiration).
- Changes in forcing functions or driving variables, such as effects of soil acidification on availability of nutrients for uptake, which affect soil conditions for growth.
- Delayed response to continuous disturbing agents such as changes in assimilate allocation and aging of plant tissue.
- Irregular canopy damage (injured or reduced live, functional tissue) from wind, frost, insect attack, or diseases.

**Table 3. Examples of the effects on tree and stand growth of air pollution and acidification, and their classification into direct and delayed effects (after Kohlmaier et al., 1984).**

Direct effects on the process level (instantaneous effects):

- Photosynthesis at light saturation, light-use efficiency, and carboxylation resistance.
- Stomatal resistance, transpiration.
- Excess respiration as a result of tissue damage.
- Assimilate translocation, increased flowering and disturbances in morphological developments.
- Root uptake.
- Aging of foliage and roots.

Delayed effects resulting from tissue damage and changes in carbon partitioning:

- Increased aging of foliage or roots: lower leaf area index → decreased light interception; decreased root uptake capacity → water and nutrient shortage.
- Increased transpiration induced by change in stomatal resistance → increases in water deficit and effects of drought.

Delayed effects mediated by soil acidification and disturbances of soil microbial activity (plant response resulting from delayed effects of pollution on soil conditions):

- Changes in nutrient supply to the roots: leaching of nutrients as a result of increased nutrient mobility, increased supply of competing nutrients.
- Change in chemical root environment (e.g., pH) resulting in decreased root uptake of nutrients.
- Changes in biological activity in the soil: decomposition processes, mycorrhizae, etc.

The effects on various processes can be determined through detailed studies carried out in controlled laboratory environments. Changes in process rates thus determined can afterwards be incorporated into simulation models to study their consequences for growth and production of a whole forest stand. The effects on processes can be incorporated by modifying rate variables. Moreover, delayed effects on state variables can be simulated as resulting from altered process rates. Delayed effects on growth induced by changes in site conditions as a result of soil pollution and acidification can be simulated by changing driving variables in the soil.

Several models are now available for studying the effects of air pollution and acidification on the environment for plant growth, such as models of changes in soil processes resulting from proton input, changes in acid-neutralizing capacity, and changed cation-exchange capacity as related to acidification (Van Grinsven et al., 1987; review by Reuss et



al., 1986). Micro-meteorological models are available to estimate the deposition of air pollutants in terrestrial ecosystems from the concentrations in the air at some height above the canopy in combination with canopy roughness and the total amount of potentially intercepting surface. Some of these models apply to particular sites or stands only; others apply to regional scales (e.g., Alcamo et al., 1985). In combination with physiological growth models, these can be used to study the effects of air pollution and soil acidification at the level of the ecosystem.

Detailed models concerned with individual physiological processes are available for evaluating the effects of pollutants on photosynthesis (e.g., the model published by Kropff, 1987). A number of descriptive models have been published that aim to evaluate the ecosystem effects of disturbances on a larger scale, for example, with regard to succession (Harwell and Weinstein, 1983; Kercher and Axelrod, 1984; Shugart and McLaughlin, 1986). Recent reviews in this field have been published by Reuss et al. (1986), on soil acidification, and by Krupa and Kickert (1987), on the response of vegetation to pollution. Models with different levels of detail should be used to evaluate the effects on the process level or on the system level. Process models investigate biochemical aspects such as the effects on enzymatic processes or on membrane activity. In contrast, single-tree and stand-level models are used to evaluate the effects of disturbances at the process level on total production and growth. Finally, ecosystem and succession models are used to investigate the effects of changes in productivity on biomass dynamics, species composition, and ecosystem development.

#### PROBLEM AREAS IN ECOPHYSIOLOGICAL MODELING OF FOREST GROWTH

Assimilates produced by canopy photosynthesis are used in a variety of physiological processes in the plant. Assimilate allocation depends on the developmental stage of the plant, on growing conditions, and on supply and demand within the plant. So far, these basic processes are not well enough understood to construct comprehensive mechanistic simulation models, and most models contain empirical partitioning functions for dry matter which are based on measurements of biomass distributions in the field. This is cumbersome, because sufficient data are usually lacking, and distribution keys are either chosen to fit the field data or built around speculative elements. As disturbances and growth reductions may act upon assimilate distribution, this is an important research area. At present, the analysis of assimilate distribution based on a functional balance between biomass components in relation to environmental factors seems most likely to yield the desired results (Mäkelä, this volume; Valentine, this volume).

When modeling the effects of growth reductions as a result of air pollution, aging of photosynthetic tissue is very important. As with assimilate distribution, the process of aging is not well understood. Experimental data indicate that increased aging of assimilatory organs, leading to a lower leaf area index (in the case of evergreen conifers) or to a shorter growing period (in annual crops), results in a considerable decrease in total canopy assimilation (Kropff, 1987).

Models of dry matter accumulation can be used in combination with data on nutrient concentration in the biomass to estimate the nutrient requirements of the growing forest in a demand-oriented approach (Mohren, 1986). To analyze the effect of soil conditions on tree growth, soil nutrient availability and root uptake capacity must be known. To date, it has generally not been possible to estimate soil nutrient availability with sufficient accuracy to ascertain whether or not deficiencies and thus growth limitations will occur. In addition, root dynamics are not well understood.

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