Nutrition and growth of forest trees

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Application of small, repetitive doses of fertilizer shows promise as an efficient and environmentally sound technique for increasing plant growth.

Inorganic fertilizers have proved to be one of the most effective means of improving crop production. However, the widespread use of this technical application has been founded on a shortsighted and empirical basis. It is remarkable that a unifying theory linking nutrition and growth has never been developed.

The underlying relationships between nutrition and growth have eluded discovery largely because of the assumption that fertilizer concentration—a static concept—is the driving force in a plant/soil ecosystem that is quite dynamic. The practice of applying fertilizer in large doses at widely spaced time intervals is aimed at increasing nutrient concentrations in the soil. However, this approach overlooks the continuous weather- and season-dependent processes of soil fertility and nutrient uptake.

This paper introduces several time-dependent and theoretically related parameters for nutrient addition, nutrient uptake, and plant growth. The new and fundamental concepts developed using this approach can be used either to model plant growth or as treatment variables. While the proposed model is quite different from the traditional view, the experimental results show a high general validity, striking similarity between laboratory and field observations, and unexpectedly high growth and production responses to fertilization.

Plant nutrients

Green plants have the unique ability to combine solar energy and inorganic elements to synthesize organic matter and life. Carbon, oxygen, and hydrogen are the skeleton-forming elements of the organic compounds. Nitrogen also is a main constituent in the proteins. Different amounts of many other so-called mineral nutrients are taken up from the soil by the plant roots. These minerals, listed in **Table I**, are required by the life processes for structural or functional purposes (*3*, *4*). In general, the lack of one or more nutrients limits plant development and growth under natural as well as husbandry conditions.

The practice of adding nutrients via inorganic fertilizers began more than a century ago. This is probably the single most important factor in changing the human condition from one of recurrent periods of starvation to the situation today, where surplus food is produced in many developed countries. The increase in plant production has largely been proportional to the increased use of fertilizers (*5*).

Environmental concern

The success of this development—and the immense production of cheap fertilizers—has led to excessive and careless use of fertilizers at a low level of precision. We tend to use too much fertilizer at the wrong occasion. During the past few decades, environmental concern has called this practice into question (*6*). However, the urge of a shortsighted practical and economic agenda has superseded the demand for the objective scientific research that would deepen our understanding of the ecological problems. Our knowledge about the fundamental principles is, therefore, very limited and far from sufficient to answer new and unexpected questions regarding the misuse of fertilizers.

We need much more knowledge if we are to use our natural resources with care, efficiency, and finesse. Unfortunately, public discussion of these issues has been obscured by other considerations. To some extent, the current state of confusion is due to the failure of the natural sciences to describe and explain plant-soil interrelationships and functions in general and realistic terms and on an ecological scale. One serious deficiency is the failure to identify and quantify the inherent capacity and limitations of crop production.

Insufficient information

The maximum production capacity of crop plants, where nutrition is nonlimiting, is unknown within both forestry and agriculture. Without such an elementary reference for comparison and for evaluation of current production and fertilization methods, it is reasonable to question the basis of the current culture methods.

Similarly, knowledge about the factors that limit crop production is greatly impeded by insufficient understanding and control of plant nutrition. Fundamental relationships, such as that between light and growth, are poorly known (*7*, *8*), and many other causes of growth limitation have generally been confused because of inadequate

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I. Weight proportions (nitrogen = 100) for nutrients taken up by tree seedlings* (*1, 2*)

Macro nutrients		*Micro nutrients*	
Nutrient	*Relative value*	*Nutrient*	*Relative value*
Nitrogen	100	Iron	0.7
Potassium	65	Manganese	0.4
Phosphorous	13	Boron	0.2
Sulfur	9	Zinc	0.06
Magnesium	8.5	Copper	0.03
Calcium	7	Molybdenum	0.007

*Later investigations indicate that the lowest relative amounts necessary to obtain maximum growth are generally lower, at least under strictly controlled conditions (Ericsson, T., and Goransson, A., personal communication). The proportions listed here are safe to use under field conditions, since control is then less accurate and uptake is usually comparatively high (Aronsson, A., personal communication). Na and Cl, although not shown to be necessary nutrients, are supplied in small amounts as salts with molybdate and copper, respectively.

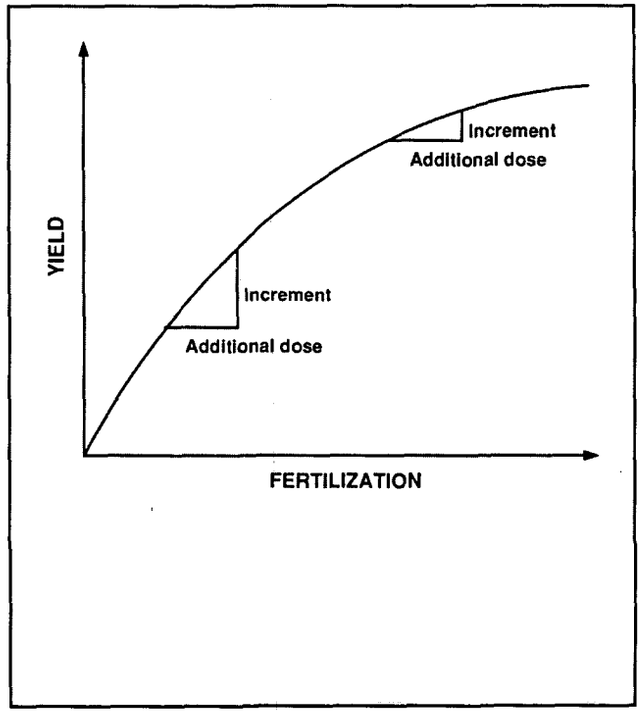
quantitative definition of both nutrition and growth. Consequently, diagnosis and prediction of production limitations are rough and uncertain, and recommended measures become inefficient.

Soil fertility and fertilization

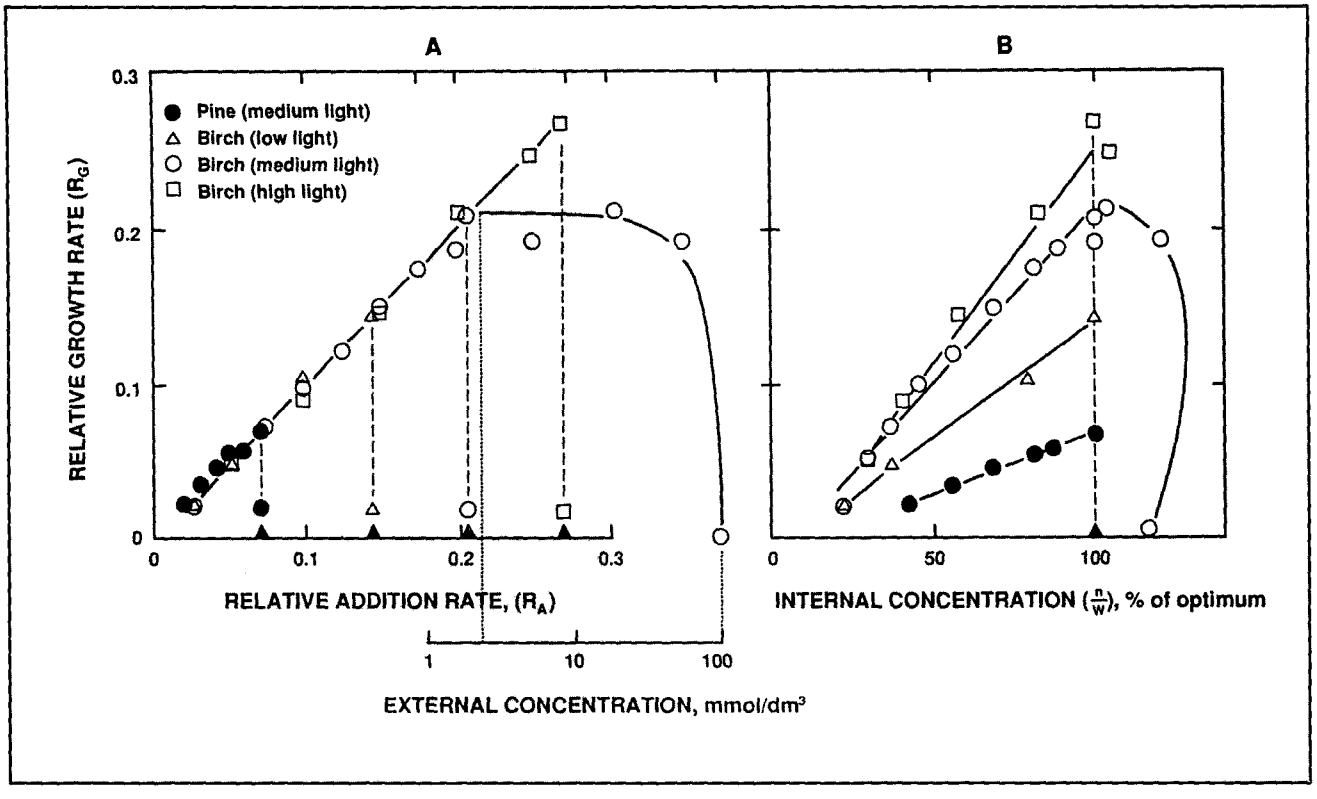
The practice of applying fertilizers in a few large doses has little to do with the continuous, natural processes that take place in the soil and determine its fertility. These processes vary from day to day within a given season because of climatic influences such as humidity and temperature. The amount of nitrogen mineralized is in the order of up to a few kilograms per hectare per day, and the uptake capacity of the vegetation is of the same order. Natural ecosystems are generally in balance, and the amount of nutrient retained in the system changes slowly. Thus the soil contains little nutrient in the form of soluble salts, and little is leached out. This is, of course, a prerequisite for the long-term existence of the ecosystem. It also is the normal case in rich ecosystems, as long as external conditions are not drastically changed (e.g., by climatic changes, forest fire, heavy harvesting).

In contrast to the continuous natural fluxes of nutrients, typical fertilizer dosages are very large. The practice of applying large doses of fertilizer is based on empirical studies that were designed for economic evaluation.

1. Mitscherlich-type dose-response curve (*4*). With increasing fertilization, there is a diminishing return with each additional dose.



2. A: Dose-response curve under steady-state conditions (constant internal nutrient status and relative growth rate) for different species and light conditions (*13*). Dashed vertical lines represent optimum R_A (nutrient saturation) for each species and light condition. R_G closely equals R_A (and thus R_U), in agreement with the purely theoretical relationships expressed in Eqs. 1 and 2. Genome and light influence the maximum R_G and the corresponding optimum R_A. At suboptimum R_A, the observed external concentrations are extremely low, generally <1 μM (*12*). Increasing R_A above the potential maximum R_G produces no corresponding uptake or growth response, although there is an increased nutrient accumulation in the root medium. B: R_G as a function of internal nutrient concentration. Dashed vertical line at 100% represents optimum n/W. The slopes of the strong linear relationships express the growth rate per unit of nutrient multiplied by a nutrient productivity factor, P_n, which is species and light dependent. The downward curves represent supraoptimum nutrition, i.e., high internal concentrations (n/w) caused by high external concentrations which ultimately become lethal.



Dosages are related to crop yield in Mitscherlich-type (diminishing return) dose-response curves, depicted in **Fig. 1**. However, this relationship is empirical, and its validity is thus restricted to the specific method used.

There are no general theories about plant nutrition (*9*). It is remarkable that this enormously important and widespread enterprise has such a weak scientific basis. One of the main reasons for this is that applied research has been restricted to endless repetition of existing methods. There have been few investigations where the continuous processes, such as the nutrient fluxes in the soil, are experimentally controlled and varied (*10*).

Nutrient availability

External concentration

Nutrient availability is commonly measured in terms of nutrient concentration in the root medium (*3*). This is a universal practice, manifested all the way from field analysis of soil to basic research, where fundamental theories on ion uptake are based on nutrient concentration in solution.

There are several reasons why nutrient concentration has proved to be an unfortunate choice as the driving variable for nutrition.

1. Concentration, while reflecting quantity, is a secondary variable that is influenced by at least two time-dependent processes: addition rate and uptake rate.
2. The required concentration levels for optimum uptake rate are extremely low (*11, 12*). Consequently, the amount of nutrients required to be available is small in relation to the amount required to be taken up over a short period of time. The time-dependent processes thus have much greater influence on the uptake rate than does concentration.
3. Concentration has no time dimension, which is an important characteristic for nutrient uptake as well as for growth. Relationships between external concentration and uptake or growth can, therefore, only be empirical.

Relative addition rate of nutrients

To obtain a better understanding of the fundamental relationships between nutrition and plant performance, we must formulate entirely new criteria where soil and crop characteristics are given a sufficient quantitative resolution over time (*13*). Thus, dynamic concepts of soil fertility, plant nutrition, and plant growth are needed to develop methods that can combine reasonable production goals with environmental considerations.

Instead of using nutrient concentration as the critical variable, we can now focus on the nutrient flux required

to maintain concentration unchanged, although, in fact, this is not an important aim in itself. The grower's aim in adding fertilizer is to maintain the nutrient status within the plant constant at a satisfactory level. The flux of nutrients must, therefore, be related to the uptake rate required to maintain the internal concentration at steady state. Stated more formally, the nutrient amounts added [dn/dt, amount of nutrient (n) per unit of time (t)] must be adjusted to maintain internal nutrient concentration (n/W, where W is biomass) constant over time. Fortunately, although not previously recognized, these relationships are theoretically simple and clear (*1, 9*). For purely formal reasons, it follows from the condition of a constant internal concentration [$d(n/W)/dt = 0$] that:

$$(1/n)(dn/dt) = (1/W)(dW/dt) \quad (1)$$

where

$(1/n)(dn/dt)$ = relative uptake rate of nutrients = R_U

$(1/W)(dW/dt)$ = relative growth rate = R_G

No assumptions about plant species or other growth-determining variables are made. Consequently, steady-state nutrition requires, independent of other conditions, that the relative uptake rate of nutrients, R_U, must equal the relative growth rate, R_G, and must therefore be covered by an equal flux or relative addition rate [$R_A = (1/n)(dn/dt)$] in the root medium.

Nutrition/growth relationships

We now have a theoretical and generally valid quantitative expression for the relationships among nutrient addition rate, nutrient uptake rate, and biomass growth rate:

$$R_A \doteq R_U = R_G \quad (2)$$

Figure 2A shows the experimental results obtained when R_A is applied as the treatment variable. This relationship is quite different from the generally accepted dose-response relationship depicted in Fig. 1. The measured relative growth rate (R_G) is, with high precision, equal to the treatment variable (R_A), in agreement with the theoretical equality described in Eqs. 1 and 2. This relationship is valid independent of tree species or climatic conditions. **Figure 2B** shows that, under these conditions, the internal nutrient concentrations remain very stable over time and are linearly related to the relative growth rate. The linear relationship between R_G and internal nutrient concentration can be written as follows:

$$R_G = (1/W)(dW/dt) = a(n/W) - a' \quad (3)$$

The intercept with the x-axis is small (Fig. 2B), so a' is approximately zero. Thus Eq. 3 can be rewritten as:

$$R_G = P_n(n/W) \quad (4)$$

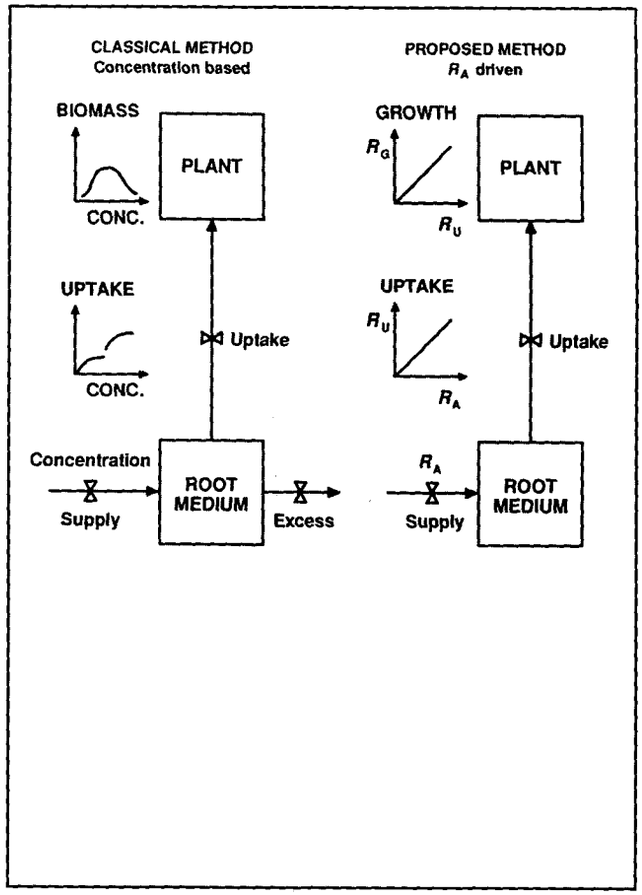
and

$$dW/dt = P_n\, n \quad (5)$$

where

P_n = nutrient productivity

3. Classical model views external concentration of nutrients as the driving force for plant growth. The proposed model explains growth as a function of R_A (*15*). Nutrient flux in the classical model is infinitely large and exceeds uptake rate so that internal nutrient concentration is maintained at constant level. The flux (R_A) in the proposed model is equal to R_U *and* R_G *for purely formal reasons (Eq. 1), and there is no excessive addition of fertilizer. Plant responses, which are merely empirical in the classical method, support the proposed model.*



In other words, biomass growth rate is closely proportional to the nutrient amount in the plant multiplied by a productivity factor (*9, 14*). Thus the first-order nutritional problems, best illustrated under steady-state nutrition, can for the first time be directly studied, and Fig. 2A shows that the usual biological variability in the observed relationships has virtually disappeared.

Figure 3 compares the traditional empirical method based on external concentration with the proposed theoretical method. There is little resemblance between the results. The proposed method has a strong control variable and clear relationships. The classical method clearly is based on experimental artifacts that are obtained only under the special conditions of the experimental methods, where control of plant nutrition is inadequate.

For instance, the textbook curves (*3, 4*) describing optimum nutritional effects in Figs. 1 and 3 are artifacts. When plant nutrition is in steady state, optimum nutrition and maximum growth are represented by a discrete point, as seen in Fig. 2, and not by a range. The measured maximum growth is much higher, and the restriction of growth caused by stable nutrient stress is much more pronounced than previously observed and described by

4. Birch seedlings under steady-state nutrition, at optimum (R_A = 26%/day) or at strong nitrogen stress (R_A = 10%/day). Classic symptoms of nitrogen deficiency (yellowing leaves) are observed only in the beginning of the stress treatment, when the plant's nitrogen content is dropping. Symptoms disappear under steady-state conditions, as they do in nature. The typical increase of the root/shoot ratio occurs because roots and shoots have different R_G during the non-steady-state period of nitrogen stress. However, this ratio remains constant at stable stress nutrition, since R_G for the different plant parts then becomes equal.

optimum-nutrition curves. Growth rate is, in fact, proportional to the amount of nutrient in the plant all the way up to maximum growth (Fig. 2, Eq. 5).

Even visual observation of symptoms of nutrient deficiency are artifacts caused by the method and are rarely observed in nature. **Figure 4** shows that when nitrogen deficiency is maintained constant over time, the acute symptoms (yellowing leaves, etc.) disappear, just as they do under natural conditions, where vegetation almost always is green and where nutrient status generally changes slowly. The plants look about the same at stress and optimum conditions except that the roots are relatively larger and longer at nitrogen stress. There are no reports of this phenomenon in the literature, indicating that steady-state nutrition has never been established previously. The many artifacts and misinterpreted measurements and observations in the classical experiments can be explained by the failure to control nutrition and maintain a constant nutrient status. The fact that the classical laboratory experiments were carried out without taking time-dependent concepts into account makes their results suspect and divergent from the real world.

Nutrient cycling

The concepts and relationships presented here were developed in the laboratory. Nevertheless, they are applicable to field conditions. **Figure 5** shows how the concept of nutrient cycling can be translated to a forest ecosystem. Nutrient availability can be described as a nutrient flux density (D_n) in the soil, expressed in amounts per area of soil and per unit of time. This flux is determined by the mineralization rate (M) and can be influenced by the fertilization rate (F). The flux is utilized by uptake by the crop (U) or by other organisms and can be made unavailable by chemical immobilization in the soil. Thus, the nutrient flux density quantifies the residence time of available nutrients in the soil. Uptake rate (U) is determined by crop activity, especially by root growth rate, and the resulting interception with the nutrient flux in the soil. Nutrients are lost by leakage if the flux density (D_n) is higher than the uptake processes.

There are strong feedbacks between soil fertility (D_n) and crop development, since crop growth rate is proportional to the amount of nutrient within the plant (Eq. 5). The litter fall is another strong feedback mechanism in the recycling of nutrient resources. The magnitude of the feedback

depends on crop nutrition and growth. This is the basis for the hypothesis, illustrated in **Fig. 6**, that fertilization with small and repeated supplies may contribute to a long-term increase of soil fertility and crop production (*10, 13*). If the fertilizer nutrients are efficiently taken up and stored in organic matter (i.e., prevented from leaching), they are recycled at an increased rate when growth is increased. Nutrient status also is improved because of the increase in litter quality and decomposition rate.

Results from Swedish field experiments—started by Tamm in the 1960s and continued by the SWECON (Swedish Coniferous Forest) project in the 1970s—strongly support this hypothesis and open the possibility of radically increasing forest production with a minimum of environmental hazards (*13, 16*). The experiments were conducted under hard climatic conditions, and observed tree growth was extremely high. The results were far beyond the production levels predicted from the results of traditional fertilization experiments such as those presented in **Table II**. The hypothesis of an efficient recycling is further supported by the fact that even very rich ecosystems can exist for long periods of time under high turnover rates for nutrients, which implies no long-term net losses by leaching.

Fertilization model

The critical factor in the ecosystem model of mineral nutrition is the balance between the nutrient flux density in the soil (D_n), the uptake rate of the crop (U), and the immobilization by competitive uptake and chemical binding (Fig. 5). Given this balance, it is obvious that fertilizer should be entered into the system as continuously as possible as a supplement to the mineralization process. The rate of addition should be calculated to increases D_n to the level of, but never above, the potential rates of the uptake and binding processes. This condition is far from the criteria used in the present fertilization practice. Wider application will require the development of new techniques, both with regard to fertilizer distribution as well as chemical problems.

To be able to survey the possibilities and settle the practical and economic conditions for development of a highly productive and environmentally acceptable cultivation technique, a research program must be conducted where the nutrient fluxes are controlled with the highest possible accuracy. This may be accomplished by using a computer-controlled irrigation system that injects nutrients in calculated quantities according to crop properties and weather measurements. This technique is being used in several experiments.

The first step in calculating fertilization is to estimate the potential uptake rate of the crop. It follows from Eq. 1 that the uptake rate at steady-state optimum nutrition can be written:

$$U = dn/dt = R_G\, n \tag{6}$$

Substituting R_G from Eq. 4, we get

$$U = P_n\, n^2 \tag{7}$$

Equation 7 is general, but R_G and P_n are not constant over time. Rather, they decrease because of self shading and aging. This decrease may be assumed to be proportional to plant biomass, i.e.:

$$P_n = P_{n,max} - (bW) \tag{8}$$

where

$P_{n,max}$ = nutrient productivity during exponential growth

b = aging factor

The aging factor b can be estimated from Eq. 8 when biomass has reached its maximum ($W = W_{max}$ and $P_n = 0$). In other words,

$$b = P_{n,max}/W_{max} = R_G/n_{max} \tag{9}$$

where

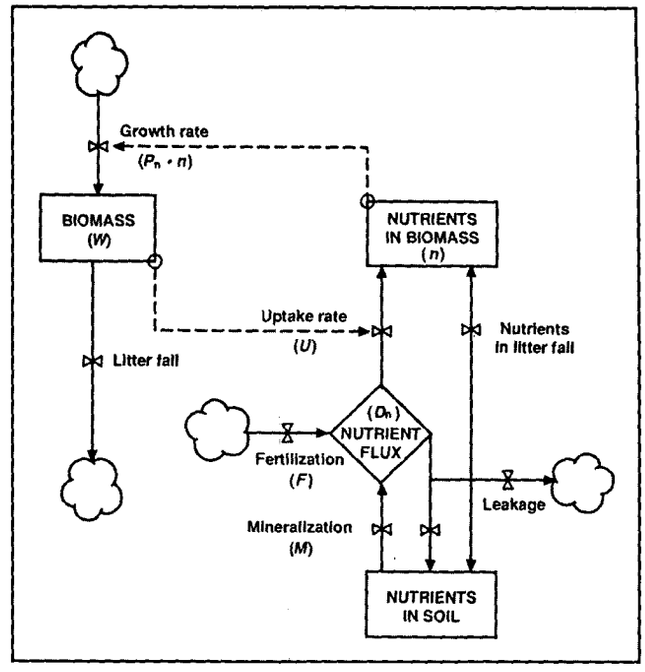
n_{max} = maximum amount of the nutrient that can accumulate in the crop.

From Eqs. 8 and 9, we can estimate the potential uptake rate of the crop:

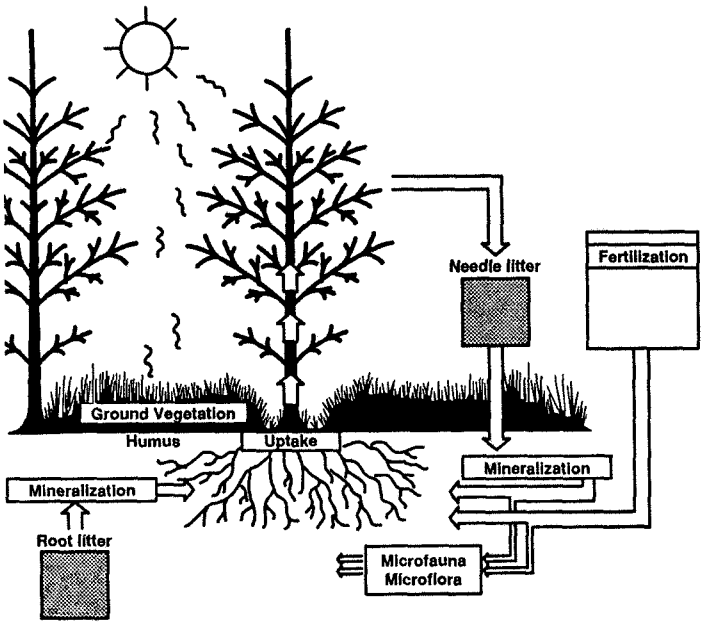
$$U = R_G\, n[1-(n/n_{max})] \tag{10}$$

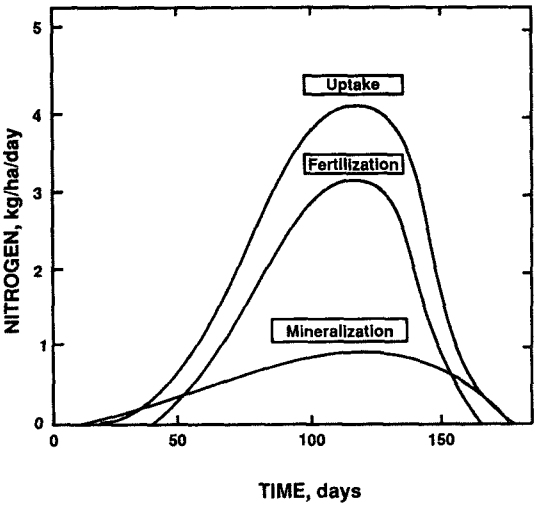
In this simple expression, R_G represents the highest relative growth rate of the species. R_G can be made weather dependent according to the clear dependence of, for instance, light, as demonstrated in Fig. 2 (*16*). There are only two further parameters in the equation: the current nutrient amount in the crop (n) and the maximum amount it can accumulate (n_{max}). Fertilization dosage can be calculated by subtracting such additions as mineralization or deposition from the atmosphere.□

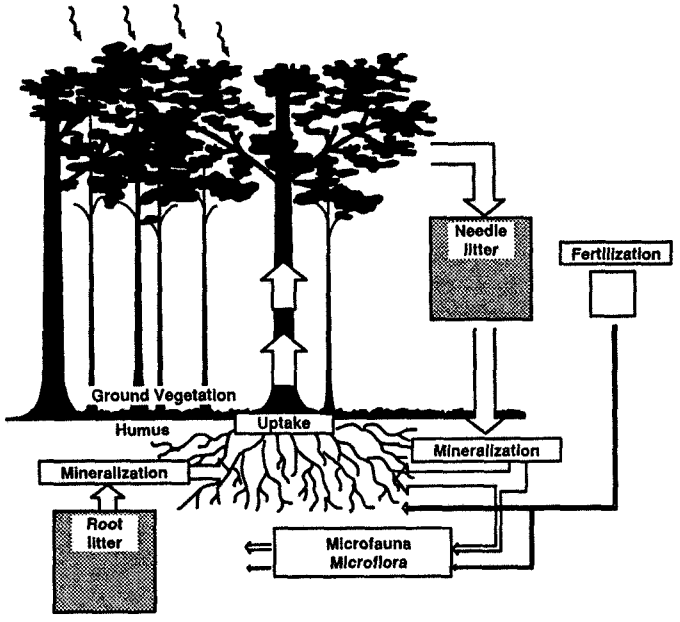
5. Schematic model of nutrient cycling in a forest ecosystem (*10, 13*)

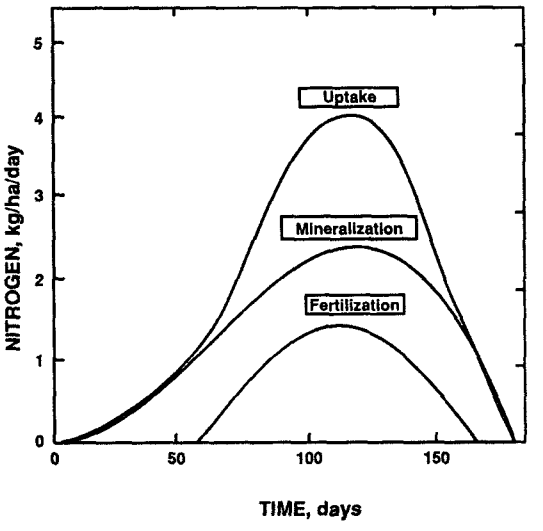


6. *Fertilization with small, repetitive doses may contribute to a long-term increase of soil fertility and crop production. If the fertilizer nutrients* are efficiently taken up and stored in organic matter (i.e., prevented from leaching), they are recycled at an increased rate when growth increases.









II. Annual increment in stem volume in several forest fertilization experiments

Tree species	Country	Years of treatment	Annual increment, m^3/ha/year		Literature cited
			No fertilizer	Fertilizer	
Norway spruce	Sweden	20	7.2	23	*13, 17*
Scots pine[a]	Sweden	13	5.3	12	*18*
Monterey pine[a]	Australia	4	17.8	55	*19*
Tasmanian blue gum[a]	Portugal	2	5.8	16	*20*
Willow clones[a]	Sweden	2[b]	...	49	*21*

[a]Irrigation for fertilized trees. Irrigation alone increased growth, partly because of increased nutrient turnover rate and improved nutrition.
[b]Four-year-old plants, cut after two years.

Literature cited

1. Ingestad, T., and Lund, A.-B., Scand. J. For. Res. 1: 439(1986).
2. Ingestad, T., and Kahr, M., Physiol. Plantarum 65: 109(1985).
3. Epstein, E., Mineral Nutrition of Plants: Principles and Perspectives, John Wiley and Sons, New York, 1972, ISBN 0-0471-24340-X.
4. Mengel, K., and Kirkby, E. A., Principles of Plant Nutrition, 3rd edn., International Potash Institute, Berne, Switzerland, 1982.
5. Evans, L. T., Am. Scientist 68: 388(1980).
6. Carter, A. D., Palmer, R. C., and Monkhouse, R. A., Mapping the vulnerability of ground water to pollution from agricultural practice, particularly with respect to nitrate, in Vulnerability of Soil and Groundwater to Pollutants (W. van Duijvenbooden and H. G. van Waegeningh, Eds.), Proceedings and Information No. 38, The Hague, 1980, pp. 333-42, ISBN 90-6743-109-5.
7. Linder, S., and Rook, D. A., Effects of mineral nutrition of carbon dioxide exchange and partitioning of carbon in trees, in Nutrition of Forest Trees (G. D. Bowen and E. K. S. Nambiar, Eds.), Academic Press, Orlando, Fla., 1984, pp. 211-36, ISBN 0-12-190980-6.
8. Ingestad, T., and McDonald, A. J. S., Physiol. Plantarum 77: 1(1989).
9. Agren, G. I., Physiol. Plantarum 64: 17(1985).
10. Ingestad, T., Aronsson, A., and Agren, G. I., Studia Forest. Suecica 160: 61(1981).
11. Olsen, C., Physiol. Plantarum 3: 152(1950).
12. Ingestad, T., and Agren, G. I., Physiol. Plantarum 72: 450(1988).
13. Ingestad, T., Geoderma 40: 237(1987).
14. Ingestad, T., Physiol. Plantarum 45: 149(1979).
15. Ingestad, T., Quantitative mineral nutrition of forest trees, Acceptance lecture for The Marcus Wallenberg Prize, Marcus Wallenberg Foundation, Falun, Sweden, 1989.
16. Ingestad, T., Scand. J. For. Res. 3: 157(1988).
17. Tamm, C. O., and Aronsson, A., Optimum nutrition of some nonfood plants, in Optimizing Yields—The Role of Fertilizers, Proc. 12th Congr. Int. Potash Institute, Berne, Switzerland, 1982, pp. 181-96.
18. Linder, S., Responses to water and nutrients in conifer ecosystems, in Ecological Studies (E.-D. Schulze and H. Zwolfer, Eds.), Vol. 61, Springer Verlag, Berlin, 1987, pp. 180-202.
19. Linder, S., Benson, M. L., Myers, B. J., and Raison, R. J., Can. J. Forest Res. 17: 1157(1987).
20. Pereira, J. S., Linder, S. Araujo, M.C., and Pereira, H. *et al.*, Optimization of biomass production in *Eucalyptus globulus* plantations—A case study, in Biomass Production by Fast-Growing Trees (J. S. Pereira and J. J. Landsberg, Eds.), Kluwer Academic Publishers, 1989, pp. 101-21.
21. Christersson, L., Tree Physiology 2: 261(1986).