THE CONCEPT OF NITROGEN PRODUCTIVITY IN FOREST GROWTH MODELLING

by

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1. INTRODUCTION

Modern scientific development has taught us that there is no such thing as a unique representation of nature. Indeed, one can only look for the most efficient representation in a given situation. However, there are representations that are more general than others because having the essences of basic principles behind them they apply to more different cases. A particularly well understood example of how different representations must be used in different situations is the wave-particle dualism in quantum mechanics, see e.g. Merzbacher (1961). Forest research has in general not yet reached that stage where the scientist can choose between a selected number of well developed theories as the most appropriate in addressing a particular problem. This means that not only is a lot of work invested in developing a structure for the ideas but also that the comparison between different results, approaches, and ideas is hampered. In this paper, a concept, the nitrogen productivity, is presented which appears to have application for a wide range of situations to be analysed.

I will show that this concept, whose foundation rests upon basic physiological properties (Ingestad 1979, Ågren 1982a) can be used for analysing and understanding a wide range of nutrition experiments and growth responses. It is particular useful under conditions where nitrogen is the most critical element limiting growth as may be the case for many forests (cf. Cole & Rapp 1981, Vitousek 1982). In other cases, for exampple where lack of water is the major constraint or other mineral nutrients are limiting, the basic approach presented should still be useful with slight modifications.

2. THEORY

The nitrogen productivity is defined as the amount of biomass produced per amount of nitrogen in the biomass per unit of time. Thus, given that the amount of nitrogen in the biomass is known, the production rate of new biomass can be calculated. Formally, this is represented by the growth equation

$$\frac{dW}{dt} = g(W,N)\ N - f\ W \qquad (1)$$

where W is amount of biomass, N amount of nitrogen in the biomass, g(W,N) the nitrogen productivity, and f a loss rate of biomass. In principle, g could also be made a function of several other variables. But what makes the nitrogen productivity concept particularly appealing is its mathematical simplicity. In almost all cases, a function may be derived in only W and N. The exact form will depend upon whether laboratory or field studies are being evaluated. Under laboratory conditions, nutrient addition rates are often the controlling variable and results can, for instance, be expressed in terms of relative growth rate, $\frac{1}{W}\frac{dW}{dt}$, and nitrogen concentration, N/W. In an exponential growth phase, commonly maintained in such experiments, these two variables remain constant. Moreover, because laboratory studies are usually conducted for only short periods, any loss of biomass is negligable, f=0. Hence, under such conditions Eq.(1) reduces to:

$$R_G = \frac{1}{W}\frac{dW}{dt} = g(W,N)\ \frac{N}{W} \qquad (2)$$

When both R_G and N/W are constant while W and N increase exponentially, the only functional form possible for g(W,N) is a function in N/W only. Experimentally, Ingestad (1979, 1980, 1981) has demonstrated that R_G is a linear function of N/W.

$$R_G \quad a\ \frac{N}{W} - a' \qquad (3)$$

or

$$g(W,N) = a - a'/(N/W) \qquad (4)$$

Therefore, under laboratory conditions plant growth can be described with only the simple equation

$$\frac{dW}{dt} = a\ N - a'W \qquad (5)$$

Ågren and Ingestad (1982) have explored the properties of this growth equation further.

Under field conditions, in addition to the inclusion of the loss term (fW) some constraint must be applied to recognize that trees can not be made to grow indefinitely by increasing their nitrogen content indefinitely by e.g. fertilization. The nitrogen productivity must therefore be a decreasing function of W (or N). The simplest hypothesis is to assume a linear function such that

$$g(W,N) = a - b\ W \qquad (6)$$

This leads to a simple growth equation

$$\frac{dW}{dt} = (a \quad bW)\ N - f\ W \qquad (7)$$

Moreover, it can be shown that parameter b in Eq.(6) can be related to the photosynthetic performance and the light-extinction properties of the forest stand (Ågren 1982a).

By accepting Eq.(5) and Eq.(7), the problem of modelling tree (forest) growth has been reduced to one of controlling nitrogen uptake. This latter problem is outside the scope of this paper but ways of dealing with it are given by e.g. Bosatta (1980).

3. RESULTS

In the previous section, two equations, Eq.(3) and Eq.(6), were introduced as a basis for the analysis of the nitrogen productivity concept. In this section I will apply these two equations to both field and laboratory data. In the laboratory, Ingestad has performed a series of nutrition experiments in which both the relative growth rate and the nitrogen concentration remained constant (Ingestad 1979, 1980, 1981, pers. comm.). Testing Eq.(3) on these experimental data gives extremely high

r^2-values, Table I. Although in several of the experiments only a few data points were available, they covered the entire range of nitrogen concentrations proper for the species. Moreover, such experiments are highly reproducible so the general agreement shown between predicted and observed values should also be expected on other data sets.

I have tested the general validity of Eq.(6) for the leaf production of five coniferous species as summarized in Table II (Ågren 1982a). In this case, data were obtained from the literature representing a wide range of stand conditions, soils, and climates. In view of the very different conditions from which the data were derived, it is not surprising that the r^2-values are not as high as from the laboratory studies. Yet, they are sufficiently good to illustrate the wide utility of Eq.(6). A systematic variation in the two parameters a and b occurs among the species, Fig. 1, supporting our general classification into shade-tolerant or intolerant classes. The intolerant pine species all have high values of a, i.e. indicating that they are efficient at low canopy densities (LAI). They also have high values of b, indicating that the decrease in nitrogen productivity with increasing needle biomass is steep. This means that productivity will decrease quickly with decreasing availability of light. The spruce and Douglas-fir, both more shade-tolerant species have lower values of both a and b.

4. DISCUSSION

From this point on, I will apply the nitrogen productivity concept only to the growth of the leaf biomass. Then, already the simple growth equation, Eq.(7), permits us to predict certain properties of forest stands. Considering a stand with a stable, closed, canopy, Eq.(7) reduces to:

$$W^* = \frac{a}{b} - \frac{f}{b(N/W)^*} \qquad (8)$$

where * denotes a stable canopy density. From Eq.(8) the stable needle biomass can be estimated from knowledge of the nitrogen concentration in the needle biomass alone. This simplification was tested in a Scots pine stand by Axelsson (1982a) with good result when the needles were sampled during the growing season. Conventional foliar sampling during the dormant season gives misleading information because there is little demand for nutrients when tree growth stops. In fact, substituting autumn foliar analysis into Eq.(8) gives completely uninterpretable results. The time of the year for sampling is therefore critical and should match the maximum growth rate (Waring & Youngberg 1972). Another advantage of Eq.(8) is that it allows the estimation of the potential needle biomass for a species under optimal conditions (Ågren 1982a).

If the growth equation, Eq.(7), is supplemented with an equation describing the nitrogen uptake, a series of further predictions about forest stands can be made. Restricting the analysis to situations near maximum canopy development ($\frac{dW}{dt} \approx 0$), the mineralization rate of soil nitrogen can be described with first order kinetics. Hence, if the total nitrogen pool divided between trees and soil is T, the nitrogen uptake by the trees can be formulated as:

$$\frac{dN}{dt} = q(T - N) \quad pfW \qquad (9)$$

where q is the mineralization rate per year and p the nitrogen concentration in abscissing needles. This model is analyzed in more detail by Ingestad et al. (1981). With this model a forest stand is characterized by four measurable tree parameters (a, b, f, and p) and two soil properties (q and T). High values of q and T corrspond to high soil fertilities. With this model I have demonstrated (Ågren 1982b) that coniferous forests subject to acid precipitation will in certain cases soon not be able to absorb all the deposited nitrogen. This problem seems much more urgent than the decrease in microbial decomposition due to high concentrations of nitrate. In another paper I have analyzed other internal stability properties of coniferous forests (Ågren 1982c) and how they vary with the producitivity of the forest. These stability analyses are quite different from those where interspecific interactions can cause instabilities when enriching a system, "the paradox of enrichment" (Rosenzweig 1971, Riebesell 1974).

It is common in nutrition studies to express the relation between response and added amount of nutrients in terms of the Mitscherlich curve and in that way trying to achieve a theoretical foundation for the results.

If the relation between response, W*, and added amount of nitrogen, T, is calculated from this model, the following response curve is obtained:

$$W^* \quad \{bqT + qf + fap - [(bqT + qf + fap)^2 - 4pfbqaT]^{1/2}\}/(2pfb) \quad (10)$$

Now, making a least-squares fit of a Mitscherlich type curve, W^* $W_a(1-e^{-cT})$, with the parameters W_a and c yields two almost indistinguishable curves. Indeed, with the parameter values for Scots pine needles and Eq.(10), the largest deviation between Eq.(10) and the Mitscherlich curve was 21 kg dw ha^{-1} which should be compared with the optimal value of 12 000 kg dw ha^{-1} in the stable needle biomass. Under these circumstances it is clear that any attempt to separate these two curves by using data is most likely to fail. It would require extremely large amounts of very accurate measurements to obtain a statistically significant difference. However, the curve form is an artefact due to an experimental technique based on giving a single dose of nitrogen rather than continously supplying the tree with its requirement of nitrogen. If this latter form of dosage is used, an essentially linear relationship between dose and response obtains (Axelsson 1982b, Ingestad 1982). In essence this shows that the fit of the Mitscherlich curve to experimentally obtained data is a result of the flexible curve-form rather than a consequence of its theoretical foundation. Of course, it is still a useful tool for curve-fitting.

The ideas in this paper nas partly been derived from ongoing field studies (Aronsson & Elowson 1980) and partly from laboratory studies (e.g. Ingestad 1979, 1981). The applicability of them to practical forestry is now being tested both in young vigorously growing Scots pine and Norway spruce stands as well as in an old stagnating Scots pine stand (Axelsson 1982c). These ideas also seem to have the potential of yielding interesting results with respect to competition between species. Studies of this and related problems are under way.

5. ACKNOWLEDGEMENT

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6. SUMMARY

This paper introduces a concept for evaluating forest productivity, the amount of biomass produced per unit of nitrogen present in the foliage. This "nitrogen productivity concept" provides a unifying framework for interpreting growth of forest stands or individual trees. Moreover, it is applicable to both laboratory and field conditions. Because it leads to very simple growth equations it applies well to integrative system models or simple indices of productivity.

Nitrogen productivity can be related to more traditional variables such as nitrogen concentration. Key variables required in the analysis are: total needle biomass, production rate of new needle biomass, nitrogen content in the needle biomass, nitrogen concentration in abscissing needles. Under field conditions, a decrease in nitrogen productivity with increasing needle biomass is predicted as a result of reduced irradiance required for photosynthesis. Coupling this nutrient dependent growth model with a simple soil fertility model allows analysis of impact of acid rain, fertilization, factors affecting soil fertility, and stability properties of forest ecosystems.

Key-word: Nitrogen productivity, Nitrogen cycling, Needle biomass, Needle biomass growth, Growth model.

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RESUME

On introduit une notion pour l'évaluation de la productivité des forets, la quantité de biomasse produite par unité d'azote presente dans le feuillage. Cette notion de "productivité d'azote" offre une structure unificatrice pour l'interpretation de la croissance des peuplements d'une foret ou d'un arbre individuel. En plus, elle s'applique aussi bien aux études dans le laboratoire que celles dans la foret. Parce qu'elle mène à des équation de croissance très simples elle sert très bien dans des modèles de système integrale ou pour des indices simples de productivité.

La productivité d'azote peut etre relier à des variables traditionels comme la concentration d'azote. Les variables clé nécessaire dans l'analyse sont: la biomasse totale du feuillage, la taux de production de nouvelles feuilles, la contenu d'azote dans le feuillage et la concentration d'azote dans des feuilles mortes. Pour des foret, une décroissement de la productivité d'azote est calculée quand la biomasse du feuillage accroit à cause de la réduction d'irradiation à la photosynthèse. Si ce modèle de croissance est couplé à un simple modèle de la fértilité du sol, on peut analyser des effets de la precipitation acide, d'engraissement, des facteur controllant la fértilité du sol et des proprietés de stabilité des écosystèmes forestiers.

ZUSAMMENFASSUNG

In diesem Aufsatz wird ein Begriff enigeführt, den man bei der Auswertung der Waldproduktion anwenden kann: "die Menge an Nadelbiomasse, die pro Zeiteinheit und pro Stickstoffmenge der Nadelbiomasse produziert wird". Der "Produktivität des Stickstoffes"-Begriff ergibt eine einheitliche Nomenklatur für die Beschreibung vom Zuwachs des Waldes und einzelner Bäume. Diese kann ausserdem sowohl under Laboratoriums- als Feldverhältnissen angewendet werden. Da dies zu sehr einfachen Zuwachsmodellen führt, ist es anwendbar in zusammengesetzten Systemmodellen oder für einfache Produktivitätsmasse.

Die Produktivität des Stickstoffes kann zu gewöhnlicherweise gemessen Variabeln, wie Stickstoffkonzentration relatiert werden. Die Schlüsselvariabeln, die für die Analyse gefordert wereden, sind: die totale Nadelbiomasse, die Produktionsgeschwindigheit der neuen Nadelbiomasse, der Stickstoffgehalt der Nadelbiomasse, die Stickstoffkonzentration in toten Nadeln. Die Abnahme der Produktivität des Stickstoffes, bei zunahmender Nadelbiomasse wird unter Feldverhältnisse als eine Folge des abnahmenden Lichtzuganges für die Photosynthese vorausgesagt. Wenn man dieses nahrungsabhängige Zuwachsmodell mit einem einfachen Modell vom Nahrungsangebot der Erde zusammenkoppelt, können Effekte von sauren Niederschlägen, Düngung, Einfluss auf das Nahrungsangebot der Erde und Stabilitätseigenschaften der Waldökosysteme studiert werden.

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Species	Range of nitrogen concentration, % of plant dw	r^2	n
Birch[a]	0.94 - 4.24	0.989	9
Birch[b]	1.18 - 3.83	0.970	4
Grey alder[c]	1.54 - 4.28	0.946	5
Grey alder[b]	1.64 - 3.42	0.888	4
Scots pine, southern[d]	0.66 - 2.66	0.998	4
Scots pine, northern[d]	0.59 - 2.41	0.994	4
Lodgepole pine[d]	0.72 - 2.36	0.995	4
Norway spruce, southern[d]	0.74 - 1.95	0.871	4
Norway spruce, northern[d]	0.76 - 2.08	0.828	5

Table I. Coefficients of determination in linear regression of relative growth rate on nitrogen concentration in seedlings of different species grown under different conditions, Eq.(3). *a*) Ingestad (1979). *b*) Ingestad (1981). *c*) Ingestad (1980). *d*) Ingestad (pers. comm., preliminary investigations).

Species	Regression equation	r^2	n
Norway spruce	y 18.4 - 0.000377 x	0.251	24
Douglas-fir	y = 34.4 - 0.00117 x	0.480	5
Corsican pine	y = 50.2 - 0.00184 x	0.953	5
Red pine	y = 55.7 - 0.00241 x	0.869	6
Scots pine	y = 41.4 - 0.00204 x	0.465	38

Table II. Regression of nitrogen productivity, y in kg dw $(\text{kg N})^{-1}\text{y}^{-1}$, on needle biomass, x in kg dw ha^{-1} From Ågren (1982a).

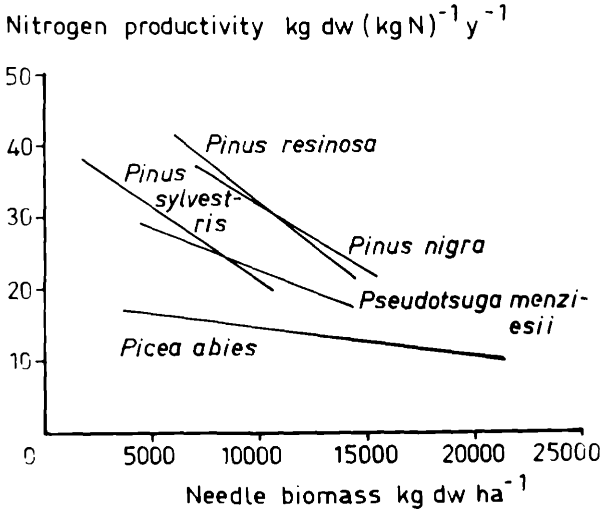

Figure 1. The regressions of nitrogen productivity on needle biomass for five coniferous species. The extension of the regression lines indicates the variation in the needle biomass in the data set. From Ågren (1982a).

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