

Plant Growth – Stoichiometry and Competition

Theory Development in Ecosystem Ecology

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Abstract

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In four different studies, this thesis addresses issues concerning plant nutrition and growth from a theoretical perspective. Terrestrial plants require nutrients, water, light and space for their existence. All of these resources may be limiting for growth, however in this thesis the main focus is on the nutrients.

The first paper is part of an environmental impact assessment on introducing logdepole pine (*pinus contorta*) as a replacement for the domestic Scots pine (*pinus sylvestris*) in Swedish forests. The long-term development of carbon and nutrient pools was simulated in a mathematical model. Higher yield of *P. contorta* meant higher acidification of the soil. Lower decomposability of *P. contorta* litter had minor impact on the soil carbon pool after one rotation, but lead to significantly larger storage at steady state.

The subject of paper II was plant nutrient ratios. Lab experiments have suggested that nutrients are required in similar proportions for a number of species. We wanted to know if the same proportions could be detected also in the field. We first made the assumption that nitrogen is either limiting growth or when available in larger amounts, only taken up moderately in excess of requirements for growth. Then we found that nutrient ratios determined from field data corresponded well to the optimum ratios determined in the lab.

In paper III we addressed the competitive exclusion principle, which predicts that for plants occupying the same niche and competing for a single limiting nutrient, the stronger competitor will outcompete all the others. The competitive exclusion relies on the assumption that growth is proportional to biomass. However, growth is commonly assumed proportional to the concentration of the limiting nutrient. We showed that it is highly unlikely that potential nutrient uptake increases proportionally to plant biomass, but rather at a slower rate. When this scaling relation is included in a competition model, plants are allowed to coexist without niche separation.

Finally, in paper IV, feedback of carbon was added to plant nitrogen and phosphorus relations in an ecosystem model. For nutrient acquirement, plant carbon can be invested in roots, be exchanged for nutrients in the symbiotic relation with mycorrhiza or exudated, where the exudates stimulate nutrient availability in different ways. We suggest that the plant partly can direct this carbon investment to the nutrient most limiting growth. We also suggest that a smaller fraction of available carbon is invested as nutrient availabilities increase. The model then predicts 1) The plant nutrient ratio partly reflects availabilities and partly plant requirements. 2) When co-limited by N and P, plant growth will increase at increased availability of either of these, because a larger fraction of carbon can be directed for uptake of the more limiting nutrient.

Keywords: nutrient ratios, optimum nutrition, ecosystem ecology, competition, coexistence, ecosystem modelling.

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Appendix

Papers I-IV

The present thesis is based on the following papers, which will be referred to by their Roman numerals:

- I. Ågren G I, Knecht M F. 2001. Simulation of soil carbon and nutrient development under *Pinus sylvestris* and *Pinus contorta*. *Forest Ecology and Management* 141, 117-129.
- II. Knecht M F, Göransson A. 2004. Terrestrial plants require nutrients in similar proportions. *Tree Physiology* 24. 447-460.
- III. Billberger M F K, Ågren G I. 2005. Allometric constraints on nutrient uptake in an ecosystem model allow plants to coexist without niche separation. (Submitted to *Oikos*)
- IV. Billberger M F K, Wetterstedt J Å M, Ågren G I. 2006. Coupling limitations from energy and nutrients on plant growth. (Manuscript).

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Foreword

How did Magnus find his way into ecology?

I must honestly declare that until I started my studies at SLU as a PhD student I had no intent of pursuing a carrier within science and in particular in the field of biology. I started my higher education in mathematics and physics, moving on to hydrology as a means to combine my interest on one hand in mathematics and on the other hand environmental issues and nature in general. Whether it was faith or coincidence I don't know, but as the opportunity arose to obtain a PhD in ecology I decided to take the chance.

The following thesis is based on a collection of four papers on different, but related subjects. The summarising overview is intended to explain the work and place it in the context of humans making use of what nature can provide. Details of background, methods and results will be found in the accompanying papers.

Introduction

How can we be able to build houses and produce food to such extents that we can live in comfort in a country like Sweden where snow and ice cover the land up to five or even six months per year? Indeed, there is no simple answer to such a question, but one of the more fundamental requirements for us being able to live here is our ability to make good use of what nature can provide. I strongly feel that this where the original motivations and reasons that successively have led me to the issues that I address in this thesis.

Mankind's harvest of nature's good

For our mere existence we must rely on what nature provides us in terms of food and shelter. However, as a species we have been quite successful in satisfying these basic needs and moved further to provide ourselves with more than just that. In a very condensed description we could say that we have went from survival to welfare through increasingly effective ways of harvesting nature's goods. But we should of course not forget the tremendous boost our development has received from our utilisation of fossil energy resources. Among the more important areas we have managed to control is how to cultivate plants to provide food, fuel and building material. Here we have always focussed on increasing and maximizing yield; and rather at an as low cost as possible.

How to maximize the return from our efforts

Harvest of nature's goods requires efforts in cultivation, maintenance and it lies naturally in our interest to maximize the return from our efforts. Considering terrestrial plants, we know that they are limited in growth basically by availabilities of light, water and nutrients. Further aspects are competition for these resources and also competition for space. Constraining our efforts is the fact that we are quite specific about which species we like to cultivate. We are aware that different species have different potential of productivity. This leaves us with a quite complex task of maximizing the productivity of certain species in given climatic and environmental conditions. Essential for maximizing plant production is to identify the factors that limit growth and how such limitations can be overcome.

Understanding ecology

Already in man's early days of cultivation it must have become obvious that supplying crops with water could be essential for survival and that appropriate irrigation would increase yield, but also that too much water could in the worst cases drown the crop. Another early observation must have been that manure could stimulate growth. During the first half of the 19th century German the agricultural chemists Carl Sprengel and Justus von Liebig were part of the pioneering work that lead to the development of the theory of mineral nutrition of plants; Liebig has given name to the law of the minimum, although this principle probably first was formulated by Sprengel (van der Ploeg & Kirkham, 1999). The science of ecology successively developed over the years from roots in agriculture but also from basic

sciences as botany and zoology. Tansley (1935) thoroughly reviewed concepts and terms of ecology and with Hutchinson (1959) the ideas of competition and niches had become central concepts as well as the idea of ecosystems (e. g. Odum, 1969). Of course ecology has continued to develop as a science with new concepts and ideas being introduced (Odum, 1990).

Mass balance approach - biogeochemistry

Investigating nature and specifically how plants function can be done from several different approaches. Scientist may address individuals, communities or entire ecosystems, with emphasis on for example interaction between individuals and species or as is the case of this thesis – mass balance. The mass balance approach is based on the fact that matter cannot be created neither can it be destroyed. A carbon atom that enters a plant through photosynthesis will remain in the plant until it is released in for example litterfall or respiration (Schlesinger, 1997). I have in this thesis mainly focused on the mass balances of carbon, nitrogen and phosphorus of terrestrial plants and investigated issues concerning the competition for mineral nutrients. In this context I have not considered carbon, hydrogen and oxygen as mineral nutrients.

Nutrient requirements of terrestrial plants

It has been known for a long time that plants require certain elements for their existence; these are referred to as essential nutrients (e. g. Mengel & Krikby 2001). The availability of essential nutrients sets constraints for plant well-being, growth and even survival. For growth a simple relationship between plant relative growth rate and the concentration of the nutrient limiting growth exists (Ågren 1985, 1988):

$$R_G(c_n) = \begin{cases} 0 & [0, c_{n,min}] \\ P_n \cdot (c_n - c_{n,min}) & [c_{n,min}, c_{n,opt}] \\ P_n \cdot (c_{n,opt} - c_{n,min}) & [c_{n,opt}, c_{n,tox}] \end{cases} \quad (1)$$

where R_G is the relative growth rate, P_n is a proportionality constant (the nutrient productivity) relating relative growth rate to nutrient concentration, $c_{n,min}$ is the minimum concentration required for growth, and at $c_{n,opt}$ the relative growth rate has reached its maximum. When experiments with *Betula pendula* were analysed, this relation could be clearly verified for nitrogen (Ingestad 1979) and phosphorus (Ericsson & Ingestad 1988). Deficiency symptoms developed initially when the seedling growth was limited by potassium, but once growth had stabilised these symptoms rarely reappeared and again growth followed Eqn (1) (Ericsson & Kähr 1993). Deficiency symptoms were similar or even more pronounced for zinc (Göransson 1997), iron (Göransson 1993) and manganese (Göransson 1994) suggesting that the growth relationship might be more complicate than suggested by Eqn (1), see also Ågren (2004).

Exponential growth and nutrient supply

When setting up an experiment where plants are supposed to grow at a constant relative growth rate R_G , it is necessary to appreciate that as plants grow larger, they will require continuously increasing amounts of nutrients in order to be able to maintain constant nutrient concentrations and thereby constant R_G . Plants growing at constant relative growth rate will increase in size according to an exponential function and need nutrients accordingly supplied at an exponential increasing rate (Ingestad & Lund 1986, Ingestad & Ågren 1988). The requirements for maintaining a constant R_G are relatively easy to satisfy in the laboratory, but are equally important under field conditions (Ingestad & Ågren 1988).

Nutrient relations in terrestrial plants

Redfield (1958) concluded that ratios of carbon, nitrogen and phosphorus in phytoplankton were in a statistical sense uniform and about 106:16:1 (on molar basis), generally referred to as “the Redfield ratio”. Geider & La Roche (2001) investigated this relation further and argued that the Redfield ratio should not be understood as the critical N:P ratio (the ratio when N and P are limiting growth simultaneously), which they indicate is in the range 20-50. However, they confirmed patterns of constrained N:P ratios in both overall observations and in estimated critical ratios. Can similar patterns be found in terrestrial plants? Based on the law of the minimum (Liebig 1840, 1855) we can conclude that it should be possible for plants to be limited in growth by several mineral nutrients simultaneously. In this situation nutrients are present in the plant in certain ratios, which I define as optimum nutrient ratios.

The nitrogen to phosphorus ratio in particular has been suggested as a tool for analysing nutrient limitations and determining fertiliser requirements in agriculture and forestry (Güsewell *et al.* 2003, Koerselman & Meuleman 1996, Tessier & Raynal 2003). More extensive analyses, including additional nutrients have also been made (Bailey *et al.* 1997, Montañés *et al.* 1993, Sinclair *et al.* 1997, Walworth & Sumner 1987). Optimum nutrient ratios at maximum relative growth rate have been determined for a number of species in laboratory experiments, where it has been found that the nutrient proportions required at maximized R_G are similar for a range of species (Ericsson 1995). A plant physiological approach suggests the possibility for similar optimum nutrient ratios for most plant species, carbon excluded. (Sterner & Elser, 2002, Elser *et al.* 1996). In contrast to animals, plants are much less sensitive to nutrient imbalances allowing nutrient concentrations to sometimes vastly exceed the levels required for growth. This needs to be taken into account when plant nutrient ratios are analyzed.

Nutrient availabilities

It is of course unlikely that nutrients in nature are available in the optimal proportions of plants. Although highly available in earth’s atmosphere, nitrogen is the nutrient most commonly limiting growth in terrestrial ecosystems. Phosphorus limitation is also quite common and limitation by other elements also occurs (Vitousek & Howarth 1991). Hedin (2004) and Reich & Oleksyn (2004) reported

global patterns with nitrogen limitation at high latitudes and phosphorus limitation more common close to the equator. Nutrients, apart from nitrogen, which also may be acquired through fixation from the atmosphere (*e. g.* Pastor & Binkley 1998, Rastetter *et al.* 2001) and lost through denitrification, are mainly cycled within the ecosystem (*e. g.* Schlesinger 1997). In addition the soil community has an important impact on nutrient availabilities (Bever *et al.* 1997). To satisfy their nutritional needs plants have developed various properties that enhance their ability to acquire nutrients from the soil. Symbiotic relationship with mycorrhizas can drastically increase the amount of soil that can be explored (Cornelissen *et al.* 2001, Read 1991). Root exudates can constitute a significant part of plant carbon flows and are assumed to enhance weathering and mineralisation (Bertin *et al.* 2003, Grayston *et al.* 1996, Nardi *et al.* 2002). Plants generally show high plasticity in root-shoot allocation, increasing the amount of carbon invested for roots at low nutrient availabilities. (Ågren & Franklin 2003). Further, a significant part of plants nutrient requirement can be supplied through resorption from senescing leaves (Aerts 1996, 1997, Killingbeck 1996).

Plants competing for nutrients

When resources are limited plants will have to compete for them to satisfy their needs. When Lotka (1925) and Volterra (1926) investigated the dynamics of competition using mathematical models they came to the conclusion that species competing for a single limiting resource cannot coexist. Gause (1932) confirmed their statement in experiments with yeast thereby establishing the competitive exclusion principle (Hardin 1960). However, when applying this principle to terrestrial plants competing for nutrients, the principle seems difficult to reconcile with the high diversity of species often observed in a given area. Species, which seem to compete for the same nutrient resources, coexist and efforts to understand and explain this have been extensive (Palmer, 1994). Spatial heterogeneity (Huston & DeAngelis 1994, Grace 1995) and niche separation (Hutchinson 1959) are two well-established examples. Tilman (1990) presented models, which specifically address plants competing for nutrients, and predicted that the species that could lower the limiting resource to its lowest value would outcompete the others. However when extended to incorporate spatial heterogeneity the models predict coexistence instead (Pacala & Tilman 1994).

More recently Rastetter & Ågren (2002) suggested that some of the assumptions in models describing plant competition need to be revised. They argue that the growth function should be a nonlinear, downward concave function of biomass. This change allows species to coexist even if there is only one limiting resource. The nonlinearity between growth and biomass can be explained by the allometric scaling of plants as they increase in size (Niklas & Enquist 2001, 2002). Niklas' & Enquist's results also indicate that the amount of soil exploited by plant roots does not increase proportionally with total plant biomass, but rather as the power 3/4.

Modelling an ecosystem

During my years as a PhD student in ecology I have often encountered scepticism about the use of models in ecology. Typically, people argue that systems of mathematical equations are unable to describe an ecosystem satisfactorily. A discussion initiated by Aber (1997, 1998) shows that my experiences are by no means unique (see also Dale and Van Winkle, 1997 and Van Winkle and Dale, 1998). My general perception of the critique has led to two conclusions: (i) the critics find it difficult to understand the mathematical expressions and (ii) to a great extent they use models themselves. The use of models is one of the cornerstones of science in order to understand the consequences of, and reasons for observed relationships. In this thesis the modelling is mainly focused on plant growth and forest productivity.

The most powerful use of models is obtained when observations or theory can be translated into mathematical expressions. These expressions can then be rewritten and processed to produce new logical consequences - results. These results in turn need to be interpreted and translated back to understandable formulations. A translation to a model is of course a matter of approximation and there is also plenty of room for mistakes for example in the method used (*e. g.* Hoffman & Poorter, 2002) or in numerical evaluation (Seppelt & Richter, 2005). I consider it a modeller's duty to realise such limitations and to keep them in mind when presenting results.

Getting on to the papers of this thesis

Which are the specific questions addressed in this thesis? Initially I was presented with Redfield ratios and the question arose whether these might have their counterpart in terrestrial ecosystem. But until I could give this matter its fair attention I had to unravel some of the mysteries of ecosystem ecology. What do we know about plants and ecosystems? How can we synthesise our understanding of specific issues to make up the whole? And what do we need in order to be able to make predictions of what will happen if we interfere with the ecosystem in one way or the other? I started out by learning a lot about ecology and especially about the concept of the ecosystem. The complexity of nature easily becomes too difficult for us to handle in terms of simple cause and effect as many parts are interlinked. A disturbance may cause chain reactions such that we cannot reasonably foresee all the effects. Instead we need to bring out our little toolbox and pick up one of the scientists' most useful tools – mathematics (Ågren & Bosatta 1998). We translate our ecological understanding from English, Swedish or whatever natural language we prefer and form mathematical expressions. Mathematical expressions can be analysed, specific questions asked and answers be given. A more difficult part of our work can be to interpret these results and to translate them back to the original language.

Paper I: Simulation of soil carbon and nutrient development under *Pinus sylvestris* and *Pinus contorta*

As a part of an extensive environmental impact assessment I contributed with a modelling exercise to estimate long term consequences of the introduction of *Pinus contorta* (lodgepole pine) in Swedish forestry.

The introduction of foreign species to Swedish ecosystems has become a matter of increasing interest over the last 30 or so years. Several examples have shown how vulnerable an ecosystem may be to the introduction or invasion of foreign species. This has led to an increased awareness and a legal framework that calls for carefulness in this matter. Plantations of *P. contorta* in Sweden have indicated that this species has the potential to increase yield compared to *P. sylvestris*. Much less is clear about possible impacts on for example other species in the ecosystem and on the carbon and nutrient pools and dynamics, especially over longer time periods. To estimate the possibilities of long term effects, the impact on carbon and nutrient pools was simulated in a mathematical model. The model was based on conventional yield models for the two species from which litter production was calculated. The decomposition of litter and accumulation of soil organic matter for the two species was then compared. Data about the two species were derived from the literature and when not available, roughly estimated. We evaluated the sensitivity of the model to uncertainties in parameters by using the Monte Carlo method. The higher productivity of *P. contorta* resulted in higher yield and thereby also larger removal of base cations acidifying the soil. For a single rotation the soil carbon stores differed little for the two species, but lower decomposability of *P. contorta* litter lead to significantly higher carbon storage at steady state.

Paper II: Terrestrial plants require nutrients in similar proportions

When cultivating plants we perform various activities to enhance the quality and the yield from our efforts. Some effective ways of increasing yield are irrigation and fertilisation. Of course, too much water or too much fertiliser is detrimental to the plant or to downstream sites from runoff water. To avoid excessive fertilisation nutrients should be applied in amounts required to maximize growth but without causing leaching of nutrients from the ecosystem (Linder 1995). Economic aspects may also be invoked in terms of maximizing the payoff from fertilisation.

Extensive laboratory experiments with carefully controlled nutrient supplies have indicated similar nutrient proportions of a wide number of species; care has however to be exercised in such experiment or the plants might take up nutrients in larger amounts than required for growth. We define nutrition as optimal when plant growth is maximal and no nutrient has been taken up in excess. Optimum nutrient ratios can also be considered a logic consequence of the law of the minimum (or Liebig's law). The law of the minimum states that growth is limited by the nutrient in least supply in relation to plant requirements. If different nutrients may be limiting in different cases, then it comes logically that several nutrients under the

right conditions can be limiting growth simultaneously. In this case the limiting nutrients are in optimum ratios according to our definition.

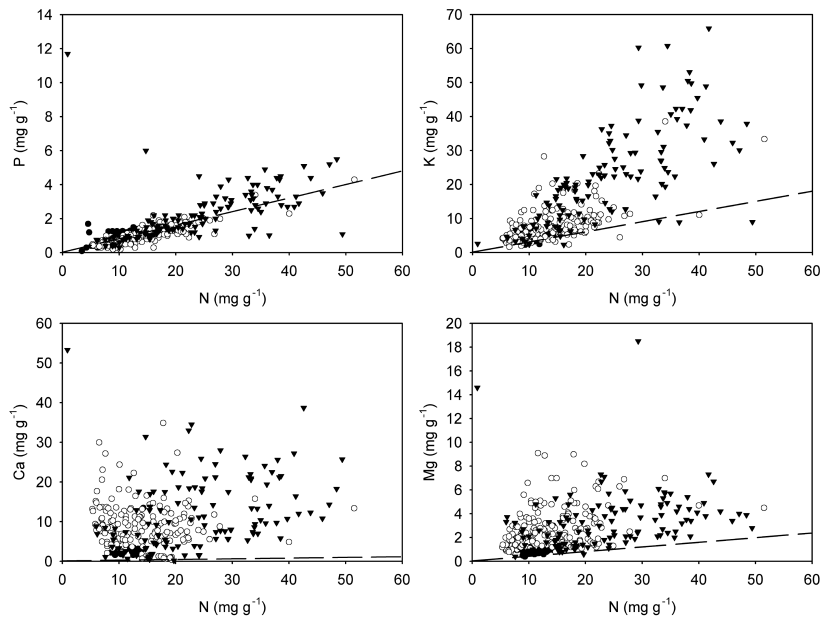


Figure 1. Phosphorus, potassium, calcium and magnesium concentrations versus nitrogen in foliage of coniferous (filled circles), deciduous (open circles) and herbaceous (filled triangles) species as found in the literature. The dashed lines represent the optimum nutrient ratios.

To determine if the similarities in nutrient ratios can be extended to terrestrial plant species in general, we investigated data sets from the literature for field grown plants. From these data sets we calculated nutrient ratios for different plant species not subjected to fertilisation or intensive management. The analysis was complicated by the fact that when available, plants take up nutrients in excess of their requirements. Standard statistical methods did therefore not exist for testing our hypothesis that terrestrial plants in general require nutrients in similar proportions. Instead we made the following assumptions: 1) Most terrestrial ecosystems are limited in growth by either nitrogen or phosphorus (Vitousek, 1991). 2) Nitrogen is available in relatively sparse amounts even when not limiting growth such that the room for excessive uptake of nitrogen is limited. 3) Plants do not take up nitrogen in amounts considerably larger than required for the current relative growth rate. Based on these assumptions we hypothesised that the ratios of nutrients, excluding phosphorus, relative to nitrogen generally should be larger than predicted from the optimal ratios determined in the laboratory.

We found that observed nutrient ratios corresponded well to our predictions, here illustrated by graphs with concentrations of phosphorus, potassium, calcium and magnesium plotted against nitrogen (figure 1). In these graphs we have added

the line representing optimum ratios determined under laboratory conditions. In agreement with our predictions most data points lie above the optimum line. For phosphorus versus nitrogen, the data points are scattered on both sides of the optimum line, which is in agreement with assumption 1) above. The scatter in the N-P relation is also considerably less than for other elements. Our investigation showed rather strong support for our hypothesis, but not sufficiently for invariable confirmation. A stronger test of our hypothesis would in addition to nutrient concentrations require determination of which nutrient that was limiting growth in each case.

Paper III: Allometric constraints on nutrient uptake in an ecosystem model allow plants to coexist without niche separation

We have in this paper addressed plants competing for mineral nutrients. The general concept taught in ecology textbooks is that plants competing for the same (growth-) limiting resource cannot coexist unless certain additional criteria are met, *e.g.* occupation of different niches or competition for light. This is generally referred to as the competitive exclusion principle, the Volterra principle or the Gause principle. An expected consequence of this principle is limited species diversity. However, the high diversity of plants often observed in nature seems to contradict the principle. Many different explanations have been proposed (for a review, see Palmer 1996). The continuous stream of papers still addressing this issue indicates that the currently available explanations for coexistence embraced by the competitive exclusion principle are not satisfactorily.

Rastetter & Ågren (2002) suggested that the connections between plant growth and turnover rate and plant size had not been considered properly. Based on the model they presented we have further investigated the consequences of different models for nutrient uptake. We show that geometry sets constraints on how a plant may increase its potential nutrient uptake. We show also that it is highly unrealistic that the soil volume that a plant's root system can exploit is proportional to plant biomass. It is much more likely that the soil volume accessed by roots increases slower than proportionally to plant biomass. Extensive allometric investigations by *e. g.* Enquist & Niklas (2002) indicate that root surface area might increase with the $\frac{3}{4}$ power of biomass.

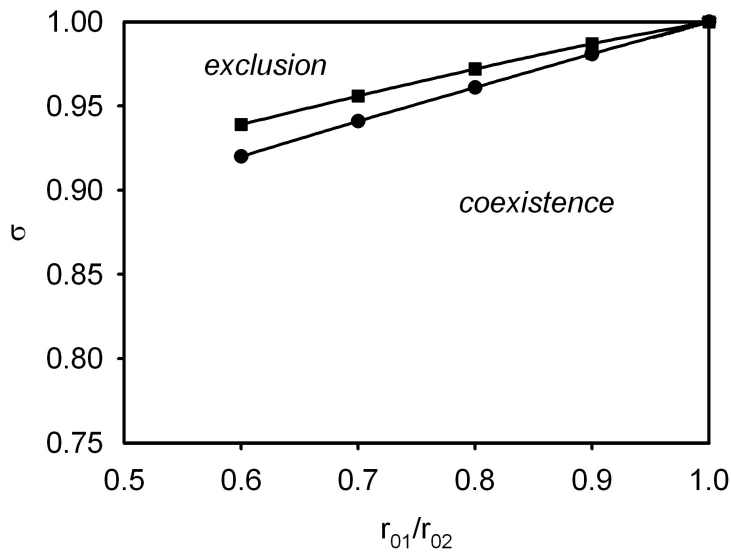


Figure 2. Coexistence regions for two competing species. Parameter combinations above the lines lead to exclusion and below the lines to coexistence. In this example, species differ in their ability to resorb nutrients before litterfall, expressed by the parameter r_0 (nutrient concentration in litter).

We inserted a scaling relation between plant nutrient uptake potential and plant biomass in a simple plant competition model to investigate how sensitive the outcome of competition was to this modification. Figure 2 illustrates that as soon as we chose a scaling factor (σ) less than proportionality ($=1$) coexistence becomes possible. We found a relatively high sensitivity, indicating a strong negative feedback of plant size on potential for sustaining constant relative nutrient uptake rate.

Paper IV: Coupling limitations from energy and nutrients on plant growth.

The law of the minimum (Liebig's law) predicts that the relative growth rate of a plant is solely determined by the availability (or internal concentration) of the limiting nutrient. Considering nitrogen and phosphorus this relation can be illustrated as in figure 3A (sharp corners) where the iso-lines represent different levels of relative growth rates. In reality the iso-lines for relative growth rates look more like in figure 3B (soft corners), with soft transitions when limitation goes from one nutrient to the other. A possible interpretation of this observation is that one nutrient may, to a limited extent substitute for the other. A direct substitution of that kind is however not supported by current plant physiological knowledge. An alternative and probably more likely explanation for the observed relation is an ability of plants to increase allocation of resources for uptake of the nutrient that is limiting growth. The resources to consider here are the carbohydrates produced by photosynthesis that can be used to fuel plant metabolism, build plant structures, be

exchanged for nutrients in the symbiosis with mycorrhizas or for root exudates that may enhance nutrient availability. In a simple conceptual model we show that a feedback mechanism selecting for the most limiting nutrient produces the “soft corners” instead of “sharp corners” as in figures 3A and B.

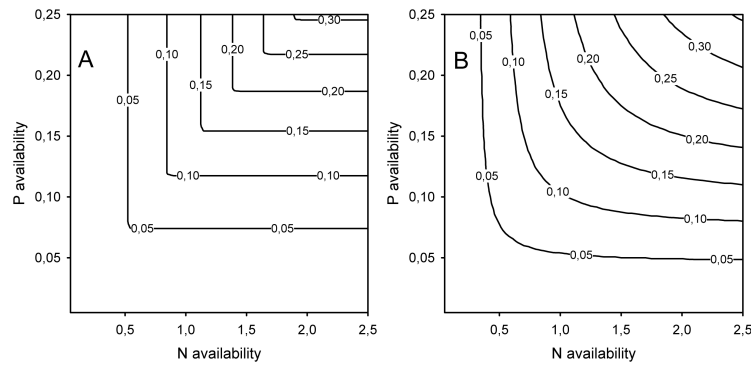


Figure 3. Illustration of iso-lines representing relative growth rates resulting from different nitrogen and phosphorus availabilities. A: strictly according to the law of the minimum only one nutrient limits growth at a time. B: Typical observed relation between nutrient availabilities and relative growth rate.

To further investigate this idea we extended an established model that considers a chain of interactions between nitrogen and phosphorus to also include carbon dynamics. In this model we observed several, previously not easily explained traits of plant nutrient relations.

In a stand of fertilized pine forest autotrophic respiration was reduced. Our model explains this as less carbon is allocated for nutrient uptake. A plant co-limited in growth by N and P responds to increased availability of either of these two. Our model explains this as more carbon available for acquiring the nutrient that becomes the limiting one.

Conclusions and possible implications

For the first paper the application is quite obvious as that study was part of an extensive environmental impact assessment of the introduction of lodgepole pine to Swedish forests. Our estimates indicate higher yield, but also larger soil carbon pools and higher acidity as long-term effects. It may be possible to verify our conclusion of higher yield by investigating some of the stands of lodgepole pine that already exist in Sweden and of which some may be ready to harvest.

Based on the logic of the law of the minimum (Liebig’s law) I have suggested the definition of “optimum nutrient ratios” as the case when all nutrients are limiting growth simultaneously. In the lab similar (but not identical) optimum nutrient ratios were determined for many different species. However, the lab results also showed that the optimum nutrient ratios could vary depending on the relative growth rate. The analysis of nutrient ratios calculated from literature data provided

support for the hypothesis of similar optimum nutrient ratios, but could not ultimately confirm it.

Plants limited in growth by N or P and with an N:P ratio close to 10 are stimulated in growth by addition of either of these two nutrients. We explain this apparent substitution between the nutrients by invoking a feedback of internal nutrient relations on nutrient uptake. When the availability of one nutrient increases, the plant can invest a larger fraction of its available carbon for uptake of the other nutrient. Thereby an increased availability of *e.g.* N will lead to increased uptake of both N and P.

Nutrient uptake is not only limited by the amount of nutrient available but also by the amount of soil that the plant is able to exploit. Especially when several plants are present they will have to compete for the available nutrients. Geometric constraints will in relative terms allow smaller plants to take up more nutrients than larger plants. This invokes a negative feedback on competition allowing plants competing for the same nutrient to coexist. This finding may explain the apparent contradiction between the competitive exclusion principle and the often observed high diversity of plant species in many terrestrial ecosystems.

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