

M I N E R A L N U T R I T I O N
A N D T R E E G R O W T H

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INTRODUCTION

The successful application of mineral fertilizers in agriculture and later also in forestry greatly promoted research in mineral nutrition. The problems were so numerous and the methods so specific that plant nutrition soon became an art of its own, specializing in basic research on biochemical and physiological processes of nutrient uptake, translocation and utilization (as recently reviewed by Clarkson and Hanson, 1980) and in applied research describing growth or yield response to fertilizer application. Aside from early attempts to correlate nutritional status of crop plants with water use efficiency (reviews by Biebl, 1958; Linser and Herwig, 1972; Viets, 1962) which were frequently hampered by the then poor understanding of plant water relations, very little effort has been made to study mineral nutrition, carbon nutrition and water relations simultaneously in forest trees (Kramer and Kozlowski, 1979, p.347). The following discussion is an attempt to put more emphasis on aspects of carbon nutrition and water relations in the discussion of mineral nutrition and tree growth.

MINERAL NUTRITION AND CARBON GAIN

F o l i a g e D e v e l o p m e n t
a n d N u t r i e n t U p t a k e

Soon after germination of a seedling, its growth creates a demand for the uptake of mineral nutrients. If this demand is not satisfied, no net carbon gain occurs, the seedling ceases to grow and, in cases of severe mineral deficiency, dies after exhaustion of its carbohydrate reserves (Figure 1).

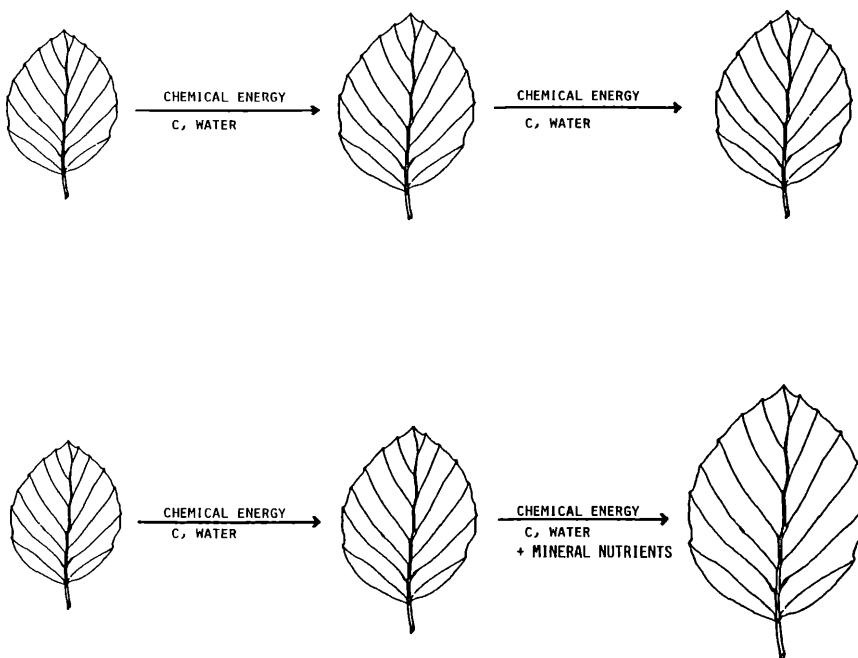


Figure 1. Foliar expansion and uptake of mineral nutrients.

Working with *Betula* seedlings Ingestad and Lund (1979) recently demonstrated very clearly the crucial role of nitrogen uptake for growth. An abrupt reduction of nitrogen supply caused transitional symptoms of nitrogen deficiency by dilution due to overshoot of growth. Later on growth adjusted to rates allowed by the current levels of nitrogen supply ("constant internal nitrogen stress"). These results are not surprising as nitrogen is a major constituent of many organic compounds in living plant cells. The close coupling of nitrogen nutrition and growth is apparently the reason for severe dilution of other essential elements frequently observed when only nitrogen is added as fertilizer (e.g. Glatzel, 1971). It is a common error to describe observed disorders as "nitrogen effect", while often critical dilution of other nutrients is the cause.

In seedlings growing exponentially, the differences in leaf area due to different nutritional regimes can be extremely large. Even under conditions which curtail growth, such as self shading, increased photosynthate demand by other plant organs, increased maintenance respiration, competition and genetic limitations, crown size is significantly influenced by nutrient regimes (Albrektson et al. 1977; discussion by Tamm, 1979). The larger photosynthetically active surface of trees

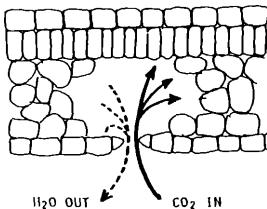
with adequate supply of mineral nutrients contributes very significantly to the improved carbon gain of these trees (Fagerström and Lohm, 1977), but it cannot be the primary because first additional carbon has to be assimilated before additional growth can occur.

E f f i c i e n c y o f P h o t o s y n t h e s i s a n d T r a n s p i r a t i o n

Since the introduction of infrared gas analysis as a tool to monitor CO_2 -exchange of plants, it has become a well established fact that alleviation of mineral deficiencies generally leads to increased leaf area or leaf mass efficiency of carbon gain. Experiments with forest tree species were reviewed by Keller (1967, 1973), who was also the first one to investigate these problems in detail. Concurrent to increased photosynthetic efficiency, improved water use efficiency (units of water transpired per unit carbon gain) was frequently observed. In some cases of heavy nitrogen fertilization, opposite effects were detected, probably due to critical depletion of other elements. At the whole plant level, improved water use efficiency of potted *Picea* seedlings receiving adequate mineral nutrition was determined gravimetrically by Glatzel (1976), and by Bradbury and Malcolm (1977) and for potted *Pinus* seedlings by volumetric determination of water uptake by Heinze and Fiedler (1980). Under field conditions, similar results were obtained by Lützke (1975) employing a lysimeter technique.

Changes in the ratio of CO_2 -uptake to H_2O -loss by transpiration at fixed stomatal apertures can only be due to increased CO_2 -diffusion into the leaf because of more efficient CO_2 -fixation by the mesophyll cells, as a significant influence of nutritional status on water vapor saturation of the air in the substomatal cavity is difficult to conceive. The strong influence of mineral nutrition on the performance of the photosynthetic system and on carbohydrate transport on the cellular and subcellular level is well documented (Natr, 1972). In extreme cases of deficiency, chlorosis is the visible manifestation of low chloroplast counts, low chlorophyll content and consequently high mesophyll resistance.

Improved water use efficiency at optimal mineral nutrition can not be singularly attributed to lower mesophyll resistance. As early as 1932, Mothes demonstrated that mineral nutrition effects leaf morphology and leaf anatomy profoundly. Dry matter concentration, number of epidermal cells and number of stomata per unit leaf area, veination and mesophyll structure of tobacco leaves showed strong negative correlation with nitrogen supply in hydroculture. Mothes noted also higher "relative transpiration" (transpiration per unit leaf area of detached leaves compared to evaporation from a free water surface) in nitrogen deficient leaves.

1. INCREASED EFFICIENCY OF CO₂-FIXATION

INCREASED EFFICIENCY OF CO₂-FIXATION
AND REDUCTION →
STeeper CO₂-DIFFUSION GRADIENTS →
DECREASED MESOPHYLL RESISTANCE

2. INCREASED FOLIAGE AREA

HIGHER LEAF AREA INDEX
DECREASED EVAPORATION FROM THE SOIL SURFACE (BUT ALSO MORE INTERCEPTION)
INCREASED BOUNDARY LAYER RESISTANCE WITHIN DENSER CANOPY

3. IMPROVED STOMATAL CONTROL

IMPROVED SPEED AND PRECISION OF STOMATAL MOVEMENTS
DIFFERENT STOMATAL BEHAVIOR IN MINERAL DEFICIENT PLANTS

Figure 2. Factors contributing to higher carbon gain and improved water use efficiency of trees at optimal mineral nutrition.

In plant stands the denser foliage of well nourished plants restricts water vapor exchange and thus lowers evapotranspiration. This fact is considered to contribute significantly to water use efficiency in crop stands (Viets, 1962). While the effect of denser crowns on over all carbon gain and on evaporation from the soil is undisputable, its impact on the ratio of photosynthesis to transpiration is more difficult to assess. An increase in boundary layer resistance of leaves not only inhibits water loss but also CO₂-uptake.

Conifers which develop their annual foliage growth in brief flushes and retain a large amount of old foliage offer a unique opportunity to exclude the effects of changed canopy structure. By proper timing, it is possible to change the nutritional status after completion of shoot development and thus work with individuals of comparable crown structure and leaf morphology for the rest of the growing season. In experiments with potted *Picea abies* (Glatzel, 1976), substantial increases of net biomass production, stem diameter growth and water use efficiency were observed in adequately nourished plants. Miller and Miller (1976) attributed increased production in a fertilized 36 year old *Pinus nigra* stand to both greater needle area (up to 70 percent) and increased net assimilation rate (up to 60 percent).

Finally, water use efficiency may be influenced by stomatal behavior. The role of mineral nutrients, mainly potassium is well established at the functional level. In addition there is substantial evidence that patterns of stomatal regulation too are influenced by the nutritional status of plants (Atkinson and Davison, 1972; Christersson, 1973; Davies and Kozlowski, 1974; Radin and Parker, 1979). There is still

much confusion and contradiction in the relevant literature (see discussion by Christersson, 1976) but it seems justified to assume that severe mineral deficiencies impair stomatal reactivity. Circumstantial evidence indicates that plants suffering from mineral deficiencies transpire frequently much more than optimally nourished plants. Heinze (1973) pointed out that high calcium contents in the foliage of mineral deficient, slow growing trees are an indication for excessive transpiration, as calcium is chiefly taken up passively with the transpirational stream (Marschner, 1974). Negative correlations between growth and foliar Ca-levels seem to be the rule (Fiedler et al. 1973). In experiments already mentioned (Glatzel, 1976), deficient plants transpired considerably more during the night, when light was too low for photosynthesis and during late afternoon, when optimally nourished plants might have had reached photosynthate saturation. It is tempting to speculate that increased transpiration of deficient trees evolved as a mechanism to increase mass flow of water and dissolved nutrients to the roots and to prevent leaching losses of nutrients in humid climates. (It should be noted here that for some elements diffusion is more important than mass flow in conveying nutrients to the root surface). Until further examinations clarify this matter, stomatal dysfunction must serve as the more conservative explanation.

MINERAL NUTRITION AND CARBON ALLOCATION

Photosynthate allocation in plants has received increased attention during the past years (e.g. Promnitz, 1975; Wareing and Patrick, 1975; Chung and Barnes, 1977; Thornley, 1977; Mooney et al., 1978; Geiger, 1979). Unfortunately information on the role of mineral nutrients in these processes is rather limited. Therefore only a few aspects can be discussed here.

R o o t S h o o t R e l a t i o n s h i p s

The functional equilibrium between shoot growth and root growth has been studied intensely both at the physiological (review by Boote, 1976) and at the statistical-mathematical level (Melzer, 1963; Hunt, 1977). It is a well established fact that this equilibrium can be altered by changing the supply of mineral nutrients (Brouwer, 1962). Every forester concerned with nursery practice knows that unbalanced nitrogen fertilization promotes shoot growth much more than root growth and this leads as planting stock with unwanted high shoot:root ratios (Figure 3).

Tölle (1969) found the same effect in full grown Pinus stands. High foliar nitrogen concentrations apparently promote the investment of photosynthates into foliar expansion and shoot growth rather than root growth. The mediation of this process by phytohormones was investigated by Michniewicz et al. (1976). They detected a pronounced effect of nitrogen nutrition on the

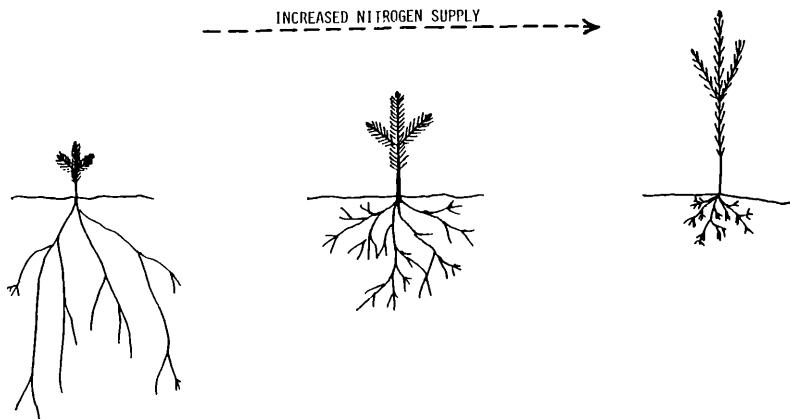


Figure 3. The effect of increased nitrogen supply on the root shoot relationship

activity of several endogenous growth regulators in shoots and roots of *Pinus silvestris* seedlings.

In full grown trees, the situation is much more complex than in herbaceous plants or tree seedlings. In tree seedlings growing exponentially, foliage growth and root growth are highly synchronized and strongly dependant on mineral nutrient supply and current photosynthate production. In full grown trees, only a small fraction of the total carbon gain can be invested in foliage growth. The situation is further complicated by the substantial storage capacity (capacitance) of large trees for photosynthates as well as for mineral nutrients and water, by the fact that in many species foliage growth occurs only during brief periods of the growing season, and by the fact that water stress frequently checks foliar expansion (Sands and Rutter, 1959; Boyer, 1970; Hsiao, 1973). (Fig.4)

The complicated interplay of these factors may be best illustrated by a simple example (Fig.5): If foliar expansion in a fast flushing species such as *Picea abies* is checked by water stress, the needles will remain short and are densely spaced on stunted shoots. The sink for mineral nutrients supplied by utilization of storage and new uptake is therefore much smaller than usual, leading to increased foliar nutrient levels. The potential for increased photosynthetic capacity provided by high nitrogen levels cannot be realized by foliar expansion (as lammas shoots rarely develop in full grown *Picea abies*) but is realized as increased photosynthetic efficiency per unit leaf area in the existing foliage (compare Garret and Zahner, 1973). A similar effect can be produced by partial defoliation (Hodgkinson, 1974; Dyrenkov and Glatzel, 1976). Thus, at the cost of possibly reduced root growth, photosynthate supply for bud formation and storage is assured.

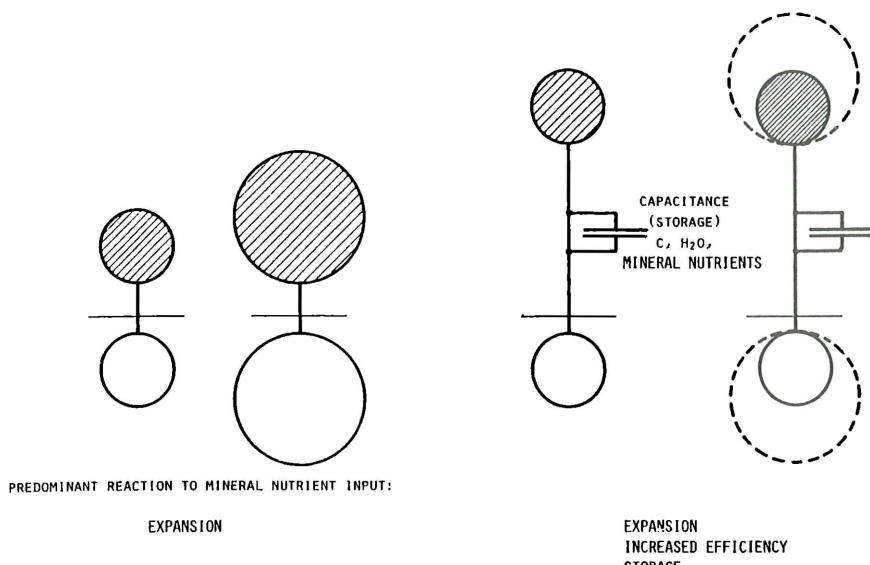


Figure 4. Seedlings and grown trees differ significantly in their reactions to mineral nutrient input

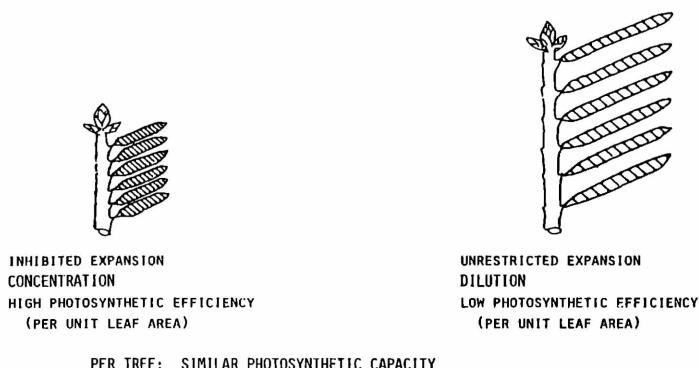


Figure 5. Influence of the seasonal weather regime on foliar nutrient levels and photosynthetic efficiency.

The opposite effect can be observed in wet springs: Optimal water supply permits full expansion of the foliage. Mineral nutrients in the needles are diluted and photosynthetic

leaf area efficiency is low, while the over all efficiency of the crown may be little changed. The partial desynchronization of root: shoot processes in trees may be a very important mechanism to dampen the effects of the seasonal weather regime and to assure long term stability of growth.

S t e m G r o w t h

Even though stem growth is the most important aspect of carbon allocation as far as practical forestry is concerned, information of possible direct influences of nutritional status on photosynthate allocation is more than scarce. Radial growth of stems reacts generally more sensitive than longitudinal growth to changed photosynthate availability and thus to fertilization. But it is not clear to what extent nutritional status determines partitioning directly. Sterba (1978) observed different distribution of radial increment along the bole of fertilized and unfertilized trees. But this could also be explained by different crown size and photosynthate availability as a comparison of radial growth in free standing and suppressed trees suggests. As cambial activity is influenced by phytohormones (Larson, 1962) and mineral nutrition influences phytohormone synthesis and distribution (Michniewicz et al., 1976) direct effects of mineral nutrition on photosynthate allocation for radial growth are likely and should be investigated.

O t h e r E f f e c t s

Keller (1969) found increased respiration in *Picea abies* due to abnormal nutritional status. It is reasonable to assume that mineral nutrition influences the ratio of photosynthates used for maintenance respiration to photosynthates used for biomass increment. Because of low enzymatic efficiencies increased maintenance respiration can be expected in mineral deficient or unbalanced supplied plants. Photosynthate allocation for seed production is another aspect to be considered. Fertilization frequently increases or even induces seed production (e.g. Wenger, 1953) but it is currently not clear whether this is an indirect effect of increased photosynthate availability or a direct effect of nutritional status mediated by phytohormones.

OUTLOOK

The development of reliable models of tree growth has become a major challenge to forest ecophysiology. Until now even advanced models like Ceres (Dixon et al., 1978) accept no direct information on the nutritional status of trees. The effect of

mineral nutrition is frequently considered to be constant at a given site. Unfortunately this assumption is incorrect. The nutritional status of the foliage and hence its photosynthetic performance and its water use efficiency may vary considerably both in time and crown space. Even though changes in nutritional status occur at lower time frequencies than changes of water status or CO_2 -exchange, nutritional status is a dynamic parameter, correlated not solely to edaphic factors.

SUMMARY

The scope of this review was the discussion of interdependencies between mineral nutrition, carbon nutrition, and water relations of trees.

To a limited, and from element to element varying degree, foliar expansion can occur independently from concurrent uptake of mineral nutrients. This provides for deficiencies as well as overconcentrations of essential elements in leaves.

Mineral nutrient availability effects carbon gain and water relations of trees in many ways:

- + The ratio of stomatal water loss to CO_2 -uptake at given stomatal apertures depends on the efficiency of CO_2 -fixation in mesophyll cells (mesophyll resistance) which is strongly correlated with nutritional status.
- + Additional carbon gained is partly invested to increase foliage area.
- + Stomatal behavior may be affected by nutritional status.

Carbon allocation is also correlated with mineral nutrition. Root: shoot ratio is one example. Under conditions of ample nutrient supply (especially nitrogen), foliage expansion is favored, while deficiencies lead to increased carbon allocation for root system expansion.

In fast flushing species and grown trees, foliar expansion is strongly influenced by soil water supply and weather conditions. In this situation, storage (capacitance) of mineral nutrients becomes very important. Changes in nutrient supply after foliage expansion is completed, can only be realized as changes of photosynthetic efficiency per unit leaf area.

In assessing metabolic performance of trees it is important to bear in mind that nutritional status is a dynamic parameter, varying considerably both in time and in crown space.

ZUSAMMENFASSUNG

Im vorliegenden Bericht wurden anhand ausgewählter Literatur Zusammenhänge zwischen Baumwachstum und Mineralstoffer-

nährung, Kohlenstoffernährung und Wasserhaushalt diskutiert. Die wichtigsten Aspekte sind im folgenden zusammengefaßt.

In beschränktem und von Element zu Element wechselndem Maß kann das Blattwachstum unabhängig von der parallellaufenden Nährstoffaufnahme stattfinden. Nährstoffmangelzustände aber auch Nährstoffüberkonzentrationen in den Blättern entstehen auf diese Weise.

Der Mineralstoffernährungszustand beeinflußt die Kohlendioxydassimilation und den Wasserhaushalt der Bäume auf verschiedene Weise:

- + Das Verhältnis zwischen dem stomatären Transpirationsfluß aus den Blättern und dem CO_2 -Fluß in die Blätter hängt bei konstantem Spaltöffnungszustand von der Effizienz der CO_2 -Fixierung durch die Mesophyllzellen ab. Diese wiederum ist mit dem Ernährungszustand stark korreliert.
- + Aufgrund höherer Nettophotosyntheseraten erworbener Kohlenstoff kann teilweise zur Vergrößerung der Blattfläche verwendet werden.
- + Das stomatäre Regelungsverhalten ist vom Mineralstoffernährungszustand abhängig.

Die Verwendung der gebildeten Photosynthate hängt ebenfalls vom Ernährungszustand ab. Ein Beispiel ist das Sproß-Wurzelverhältnis. Bei ausreichender Nährstoffzufuhr (insbesondere Stickstoffzufuhr) wird die Kronen- und Sproßentwicklung gefördert. Bei Nährstoffmangel werden Photosynthate vermehrt in die Ausbreitung des Wurzelsystems investiert.

Bei Arten, die ihre Blattmasse in kurzen Schüben ausbilden, hängt das Flächenwachstum der Blätter in hohem Maße von der Bodenwasserverfügbarkeit und den Witterungsbedingungen zur Zeit des Austriebes ab. Änderungen der Nährstoffverfügbarkeit nach Abschluß der Blattentwicklung können von diesen Arten nur durch Änderungen der Flächeneffizienz der Photosynthese und durch Speicherung bzw. Vorratsausschöpfung begegnet werden.

Bei allen Bemühungen, Stoffwechselvorgänge von Bäumen zu modellieren, sollte berücksichtigt werden, daß der Ernährungszustand ein dynamischer Parameter ist, der sowohl im zeitlichen Ablauf als auch im Kronenraum erheblich variieren kann.

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