Leaf Life Span and the Mobility of "Non-Mobile" Mineral Nutrients – the Case of Boron in Conifers

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Aphalo, P.J., Schoettle, A.W. & Lehto T. 2002. Leaf lifespan and the mobility of "non-mobile" mineral nutrients – the case of boron in conifers. Silva Fennica 36(3): 671–680.

Nutrient conservation is considered important for the adaptation of plants to infertile environments. The importance of leaf life spans in controlling mean residence time of nutrients in plants has usually been analyzed in relation to nutrients that can be retranslocated within the plant. Longer leaf life spans increase the mean residence time of all mineral nutrients, but for non-mobile nutrients long leaf life spans concurrently cause concentrations in tissues to increase with leaf age, and consequently may reduce non-mobile nutrient use efficiency.

Here we analyze how the role of leaf life span is related to the mobility of nutrients within the plant. We use optimality concepts to derive testable hypotheses, and preliminarily test them for boron (B), a nutrient for which mobility varies among plant species. We review published and unpublished data and use a simple model to assess the quantitative importance of B retranslocation for the B budget of mature conifer forests and as a mechanism for avoiding toxicity.

Keywords boron, conifers, leaf life span, model, needle age, nutrient mobility, toxicity

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Received 30 June 2000 **Accepted** 20 May 2002

1 Introduction

Nutrient conservation is considered to be important for the adaptation of plants to infertile environments (Eckstein et al. 1999). The negative correlation between the distribution of long leaf life spans and the nutrient availability of habitats was noted by Harper in 1914. According to Eckstein et al. (1999) nutrients can be conserved mainly by extending the life span of plant parts or by minimizing the nutrient content of those parts which are abscised. (In this context it is important to distinguish between leaf life span and leaf habit, as evergreenness can be achieved by replacement of short lived leaves several times per year, see Kikuzawa 1991.)

However, there are many possible selection forces favouring long leaf life spans. Chabot and Hicks (1982) list 11 hypothetical advantages, and on a world wide basis mineral nutrient conservation may not be the most widespread. Furthermore, these advantages are not mutually exclusive. Schoettle and Fahey (1994) have reviewed the nature of foliage longevity in pines, and proposed the *ecological light compensation point* as the immediate control on leaf shedding.

Nutrient conservation can be measured through the mean residence time of a nutrient in the plant (Eckstein et al. 1999). However, plant nutrient-use efficiency depends both on mean residence time and nutrient productivity. Nutrient productivity relates dry mass production to instantaneous nutrient content (Berendse and Aerts 1987). Apparently mean residence time and nutrient productivity are negatively correlated (see Eckstein et al. 1999, and references therein).

Plant adaptations and responses to multiple environmental factors are frequently non-additive (Chapin III et al. 1987). The importance of mean residence time and leaf life span has been discussed in the literature mainly in relation to the macronutrients N and P, which are mobile in the plant, and there is convincing evidence that long leaf life spans are in many cases an adaptation to low supply of N or P (Reich 1993). However, only some mineral nutrients are mobile in the plant (i.e. they can be redistributed) while others are not mobile (i.e. they cannot be redistributed). A long life span of the foliage and concomitant long mean residence time improves the use efficiency only for mineral nutrients which can be redistributed within the plant. In contrast, if there is a continuous flux of a ‘non-mobile’ nutrient towards the foliage a long leaf life span decreases its productivity, and does not increase use efficiency.

For phloem mobile nutrients recycling occurs partly within the plant, and decreases possible loss through leaching or immobilization in the soil. In contrast, in the case of nutrients that are not mobile in the plant recycling occurs outside the plant, through the soil, and immobilization can occur by accumulation in old living foliage. In either case use efficiency increases when overall immobilization and losses are decreased.

Boron is a plant micronutrient peculiar in two respects: (1) its mobility varies markedly among plant species, and (2) the range of tissue concentrations spanning from deficiency to toxicity is narrow. This makes it a very good candidate for testing optimality hypotheses because (1) there is genetic variability, and (2) the selective pressure against suboptimal use is strong.

In species in which boron moves mainly in the xylem sap it accumulates and concentrations increase as the foliage grows older. In those species in which at least part of the boron in the foliage is retranslocated through the phloem to other tissues (e.g. roots, inflorescences, seeds, etc.) its concentration in the foliage tends to remain constant (see Brown and Shelp 1997).

When there is B retranslocation through the phloem, it depends on the formation of complexes with sugar alcohols such as mannitol, sorbitol, and possibly pinitol (see Brown and Shelp 1997). Recently B-sorbitol and B-mannitol, and also B-fructose complexes have been demonstrated to occur in the phloem sap of B-retranslocating species (Hu et al. 1997). Further evidence of the importance of sugar alcohols was obtained from transgenic tobacco plants, in which the induction of sorbitol formation gave the new ability to mobilize B within the plant (Brown et al. 1999).

Given a long leaf life span (e.g. as adaptation to low availability of a mobile macronutrient such as nitrogen), optimal use of B when availability is low, or toxicity avoidance when availability is high, should favour individuals with the ability to redistribute B away from ‘old’ foliage and towards growing tissues.

However, boron retranslocation is not the only strategy that may have evolved in plants for coping with low or high B availability: grasses have very low B requirements (Dugger 1983), and other species like sunflower can tolerate high B concentrations in their tissues using an unknown mechanism to avoid toxicity (Dannel et al. 1999). However, conifers like most species with long lived foliage have woody tissues which require B for their structural integrity.

2 Hypothesis

From the above discussion a hypothesis can be formulated, which, like most hypotheses related to evolution, can be tested in the sense of finding or not a satisfactory *historical narrative* explanation rather than proving or falsifying a proposed *causal law* (see Mayr 1997, Chapter 4).

We hypothesize that in the absence of retranslocation of a particular nutrient, there is a deadlock, because any improvement in the use of mobile nutrients through longer leaf life-spans would increase the immobilization of nutrients with low mobility. Under strong selective pressure for long leaf life spans, a concurrent selective pressure favouring boron redistribution should develop when this element’s availability is restricted (or high), which should have as a consequence that: *Species with very long-lived leaves are able to redistribute B from old to young tissues.*

3 Evidence from the Forest

It was earlier postulated that B moved only in the xylem, accompanying bulk water flow, accumulating in old leaves (Dugger 1983). If this was true for conifers, then B flow towards needles would be roughly proportional – discounting seasonal and year to year variation in soil availability – to the accumulated volume of water transpired, and over several years B concentration would increase several times compared to that at the time when needle expansion ended. Consistent with Dugger’s (1983) ideas Wikner (1983) suggested that B was not mobile in Norway spruce. In contrast, it has been suggested that B is mobile in Scots pine (Helmisaari 1990b, Wikner 1983) and Monterey pine (Hopmans and Clerehan 1991). In this section we reassess published data for these species, and present previously unpublished data for lodgepole pine. Leaf life spans are up to 4 years for Scots pine and Monterey pine, up to 22 for lodgepole pine (see Schoettle and Fahey 1994, and references therein), and up to about 14 years for Norway spruce (Leena Finér, pers. comm.). Mean leaf life spans are much shorter than the values for oldest needles given above, and additionally for a given species actual leaf life spans vary widely among sites.

3.1 Norway Spruce

In Norway spruce (*Picea abies*) silicon behaves as expected for a non-mobile element: its concentration increases between years linearly with needle age, and within years much faster during the growing season than during the rest of the year (Wyttenbach et al. 1991), suggesting that transpiration does not decrease much with needle age. On the other hand, some decrease in transpiration rate is expected to happen because of increased shading of ageing needles (e.g. Schoettle and Fahey 1994), and because of restrictions to water flow by a more lignified xylem (Ülo Niinemets, pers. comm.).

In this species, Finér (1989) observed a decrease in B concentration ($r = -0.94$, $P = 0.002$), and a steady increase in Ca concentration ($r = 0.98$, $P < 0.001$) with needle age (Fig. 1). This indicates that at this drained peatland site B was much more mobile in the trees than Ca.

Also in Norway spruce, Lehto and Mälkönen (1994) studied the nutrient concentrations in the four youngest needle classes (older classes were also present but not sampled). They observed little accumulation of boron with increasing needle age after the second winter, and a similar pattern for Ca (Fig. 2). This suggests redistribution of both B and Ca, which does not agree with the data in Fig. 1 in which Ca concentration increased almost linearly with needle age. However, Wyttenbach et al. (1995) observed an almost linear increase for calcium only at sites with high Ca availability in the soil, but little accumulation after the first year in sites of low availability. So although Ca is frequently given as an example of a non-mobile nutrient, in Norway spruce Ca can in some situations behave as a partially mobile element (Wyttenbach et al. 1995).

After fertilization, B concentrations increased in all needle classes, even those which had grown beforehand (Fig. 2). This indicates that the lack of increase of B concentrations with needle age is not related to inability to translocate the B recently acquired from the soil to old needles.

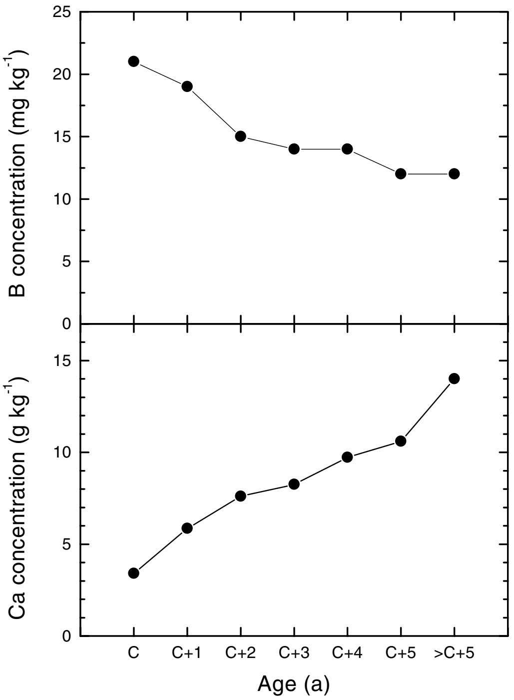

Fig. 1. Changes in boron (B) and calcium (Ca) concentrations in Norway spruce needles with needle age. Sampled in winter 1985, seven branches spanning the whole crown, per each of nine unfertilized trees. Drawn from data of (Finér (1989), Appendix 24). Data points are means. Boron: S.E.≤2.3 mg kg^{-1}. Calcium: S.E.≤1.26 g kg^{-1}.

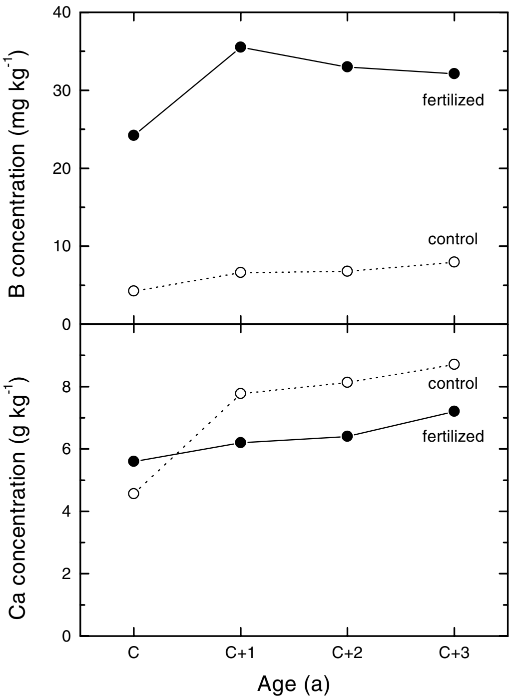

Fig. 2. Changes in boron (B) and calcium (Ca) concentrations in Norway spruce needles with needle age. Sampled in February 1991, from the upper crown and southern exposure. Fertilized with 1.5 kg ha^{-1} of B in June 1989, applied as borax. Drawn from data of Lehto and Mälkönen (1994). Data points are means from two plots. Boron: S.E.≤4.6 mg kg^{-1}. Calcium: S.E.≤0.93 g kg^{-1}.

3.2 Scots Pine

In Scots pine (*Pinus sylvestris*), Helmisaari (1990b) similarly observed a fast decrease in boron concentrations during the first year and a slower decrease after the first year ($r = -0.76$, $P < 0.001$, Fig. 3). The boron content of the needles further decreased during senescence. The annual course displayed a small transient increase in B concentration in the spring. In contrast concentrations of Ca increased in time ($r = 0.92$, $P < 0.001$), nearly doubling between the time when needles were one and two years old, and almost trebling one year later. This increase took place mainly during the summer, when presumably the trees were actively transpiring. This is evidence that boron was much more mobile than Ca at this site. Helmisaari (1990a) concluded that boron is intermediately mobile in Scots pine.

3.3 Lodgepole Pine

In lodgepole pine (*Pinus contorta* ssp. *latifolia*), A. Schoettle (unpublished) observed that B concentration in needles slowly increased with age in trees where the concentration in current needles was very low ($r = 0.95$, $P < 0.001$), but remained almost unchanged in current plus one and older needles in those trees with slightly higher concentrations ($r = 0.65$, $P = 0.03$, Fig. 4). Concurrently, Ca concentration increased steadily with needle age in all trees ($r = 0.93$ and 0.95, $P < 0.001$). In this case all needle age classes present were

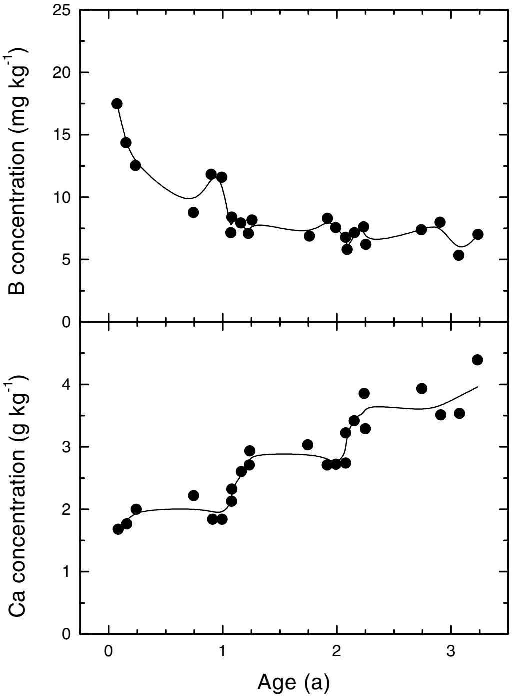

Fig. 3. Changes in boron (B) and calcium (Ca) concentrations in Scots pine needles with needle age. Sampled on three needle classes between June 1983 and September 1984, from a pole stage stand. Lines are B-splines. Redrawn from data in Helmisaari (1990b). Data points are means of 5 to 24 trees. Boron: S.E.$\leq$2.6 mg kg^{-1}. Calcium: S.E.$\leq$0.6 g kg^{-1}, except for measurements taken in September for which S.E.$\leq$1.4 g kg^{-1}.

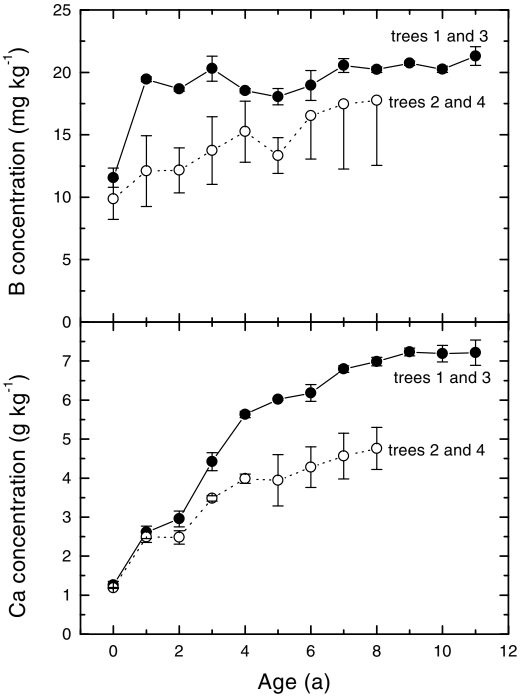

Fig. 4. Changes in boron (B) and calcium (Ca) concentrations in lodgepole pine needles with needle age. Means of two trees ± S.E. Sampling date was August 1987. Two branches (N and S exposure) from the middle crown of each tree from an 80-year old monospecific stand near Fox Park, Wyoming, U.S.A. Site described by Schoettle and Smith (1999) and analysis methods by Barrick and Schoettle (1996).

sampled, and fewer age classes were present in the two trees with lower B concentrations.

3.4 Monterey Pine

In Monterey pine (*Pinus radiata*) Hopmans and Clerehan (1991) found that B concentrations were slightly higher in older needles than in current year needles of trees with little boron (4–7 mg kg^{-1}) ($r=0.79$, $P=0.42$), but in B-fertilized trees, the concentrations were lower in older needles than in current needles ($r=-0.99$, $P=0.008$, Fig. 5). Based on these data Hopmans and Clerehan (1991) postulated that there was internal redistribution of boron in trees of this species.

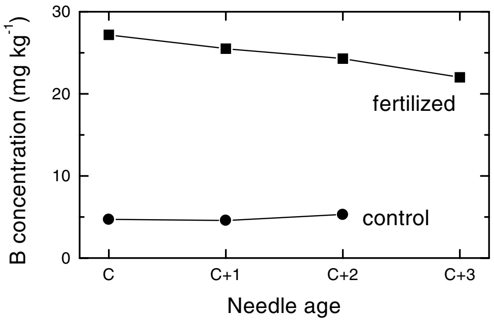

Fig. 5. Changes in boron (B) concentration in Monterey pine needles with needle age. Sampling from the middle crown, in June, six years after fertilization with borax. Means of 4 trees. Drawn from data of Hopmans and Clerehan (1991).

3.5 Caveats and Further Evidence

Although the field data for the four species examined support the hypothesis of boron mobility, there are big differences among the data sets. As at least some of these differences could be caused by differences among sites or sampling dates, it is too early to conclude which species have a greater ability to redistribute B.

Even if nutrient content per needle does not change, nutrient concentration on a dry weight basis will decrease slightly with age because leaf dry weight can increase as a result of increased lignification and secondary phloem formation (Ewers 1982). However, any such effect would equally affect boron and calcium, and consequently the comparison between these nutrients remains valid.

An alternative explanation for a non-increasing boron concentration with needle age could be leaching with rain throughfall. However, at least for Norway spruce there is strong evidence against this alternative hypothesis, as it has been observed that throughfall is *depleted* in boron compared to rainfall (Atteia and Dambrine 1993).

The lack of accumulation of B in old tissues could be also explained by a very efficient sequestration of B by stem tissues, with old needles receiving B-depleted xylem sap, but this would not account for the accumulation of B in growing tissues, or for the marked increase in B concentrations in old needles after fertilization (Fig. 2).

In experiments using the stable isotope ^{10}B as a tracer it was demonstrated that boron is translocated from the foliage to roots of both Scots pine and Norway spruce seedlings (Lehto et al. 2000). This gives further support to the hypothesis that B redistribution indeed occurs in these species, as translocation in the phloem is a limiting step in this process.

4 A Simple Model

The question remains as to *why* are all these conifers able to retranslocate B, an ability considered until now limited to only a few dicots (Brown and Shelp 1997). In this section we use a very simple quantitative model of the B budget of the tree foliage in a pure mature stand to assess the hypothesis stated above. In other words, we try to gain insights into why retranslocation may be an important evolutionary advantage in conifers to have been so consistently selected.

We will use the model to answer the questions: 1) *How much more B would a coniferous forest need without B retranslocation within trees?* 2) *How is the maximum possible life span of needles affected by B retranslocation?*

The model is similar to that used by Wyttenbach and Tobler (2000) to discuss the mobility of other elements in Norway spruce. It assumes no nutrient losses from the foliage other than by mobilization and retranslocation, and no gain other than by xylem flow driven by transpiration or retranslocation. It further assumes that all needle classes have the same transpiration rate. In real trees old needles can be less exposed to sunlight, and their transpiration rate can be slower. However, as discussed above data for Si accumulation suggests that the decrease in transpiration with age is small. Furthermore we assume that the trees are old enough for the foliage biomass to remain approximately constant from year to year.

4.1 Boron Use

For assessing how much retranslocation affects the amount of boron needed for foliage growth, we assume two hypothetical species with mean leaf life spans of 2.5 years and of 5 years, and compare the cases of retranslocation at a rate able to keep B concentration in needles constant from year to year, versus no retranslocation (linear increase in concentration with needle age). In the first case we further assume that 50% of the B is recycled during senescence while in the second case we assume that all the B remains in the abscised needles. We assume a concentration in

Table 1. Boron uptake needed for foliage growth and maintenance in conifers: an assessment of the effect of mobility in the tree.

	Example 1	Example 2	Example 3
Mean leaf life span (years)	2.5	5	5
New foliage biomass (kg ha^{-1})	2000	2000	1000
New foliage boron (g ha^{-1})	20	20	10
Total foliage biomass (kg ha^{-1})	5000	10000	5000
With retransloation and 50% resorption			
Total foliage boron (g ha^{-1})	50	100	50
Annual B uptake needed for new foliage (g ha^{-1})	10	10	5
Without retransloation or resorption			
Total foliage boron (g ha^{-1})	125	500	250
Annual B uptake needed for foliage (g ha^{-1})	50	100	50
Annual uptake of B needed without retranslocation / annual uptake of B needed with retranslocation	5	10	10

needles of 10 mg kg^{-1} of B at the end of the first year in both cases. This assumption aims at calculating how much boron would be needed by the trees to keep B concentration in the foliage just above growth-limiting deficiency by the end of the first year of a needle's life.

Because of the assumptions, calculations are extremely simple: with retranslocation the B needed for foliage growth is equal to half the boron content of the new needles (the other half is assumed to come from resorption). With no retranslocation the B uptake needed for needles is equal to the annual increase in boron concentration (assumed equal for all needle classes) times the total needle biomass.

Mean residence time is increased by retranslocation: for the foliage of both hypothetical species, it is doubled under the assumptions used in the model. Mean B concentration over the different age classes is decreased because we assumed equal concentrations at the needle age of 1 year. If we had instead assumed equal amounts of B taken up, in the extreme case where all redistribution takes place between needles of different age classes, the mean B concentration in the foliage as a whole would remain unchanged.

Retranslocation reduces annual requirement of B by foliage by 80% in the first example, and by 90% in the second example (Table 1) compared to no retranslocation. This is an extremely large difference.

As within a given pine species differences in growth environment tend to alter leaf life span maintaining similar total foliage biomass (Schoettle and Fahey 1994) a third example in which total foliage biomass is the same as in the first example but mean leaf life span is 5 years as in the second example was studied. With retranslocation and 50% resorption annual B need for foliage growth decreased to half with a doubled leaf life span, while without retranslocation annual B use remains unchanged (Table 1, Example 3).

For assessing how much needle biomass affects the results, a fourth example with 50% more biomass, and 5 years of mean leaf life span was considered. The relative effect of retranslocation does not change, but annual B need and foliage B content increase proportionally (data not shown). Unsurprisingly, species with higher needle biomass (like Norway spruce) both with and without retranslocation use more B than species with low needle biomass (like Scots pine). For this fourth example and with retranslocation, the total amount of B in the foliage (150 g ha^{-1}) is comparable to the total B in the 6 cm deep humus layer (135 g ha^{-1}) in a Norway spruce forest stand on a low B mineral soil (calculated from data in Lehto and Mälkönen 1994, Lehto 1995). Furthermore, B in the humus layer is only partly available to plants while that in deeper layers is mostly unavailable (Wikner 1983).

Finér (1989) measured the quantity of B fixed in the above- and below-ground tree biomass of a 100 year-old Norway spruce stand on peatland in eastern Finland: the biomass contained nearly 700 g ha^{-1} of B, of which about 120 g ha^{-1} was in live needles. The needle biomass was 7900 kg ha^{-1} at this site. The quantity of B fixed in the biomass over a century is much more than that available to plants in the soil at a given time. At this site B deposition at a rate of approximately 7 g ha^{-1} a^{-1} (Wikner 1983) adds up over a century to a quantity of B of the same order of magnitude as the B fixed in the biomass of the forest. The ecosystem B cycle is probably partly open, specially when wood is removed, with forest growth dependent both on B deposition and B release in the soil by decomposition.

At a more fertile site in Sweden Nykvist (1971) measured a needle biomass of 14 900 kg ha^{-1} for another 100 years-old Norway spruce forest. This is similar to the needle biomass used for the fourth example assessed with the model.

4.2 Toxicity

To assess how the maximum possible leaf life span is affected by B retranslocation, we assume a maximum leaf life span of 5 and 10 years for two hypothetical species. As above we compare no retranslocation (linear increase in concentration) to retranslocation effective enough to keep concentration constant after the first year. We assume that the range of concentrations between deficiency and toxicity spans one order of magnitude.

If there is retranslocation, B concentration remains constant through the life span of the needles, and the effective range remains at one order of magnitude or 10×. If B concentration increases linearly throughout the life span of the needles the effective range which can be realized without deficiency in young needles or toxicity in old needles shrinks. Under the assumptions stated above, the effective range of possible B concentrations for healthy one year old needles (which could attain the maximum life span) would be without retranslocation $10 \div 5 = 2$ times instead of 10 times in the first case, and only $10 \div 10 = 1$ in the second case, which implies a single point instead of a range of possible needle B concentrations in one-year-old needles. This is a simple calculation on an annual basis, but most likely the minimum threshold has to be already attained earlier, during needle expansion.

For a given leaf life span, such a reduction in possible needle B concentrations would drastically reduce the range of tolerated boron availability in the soil and would in turn severely restrict the distribution area of the species. Conversely, maintaining tolerance to a wide range of soil B availability without retranslocation would force short leaf life spans.

4.3 Caveats

A whole-tree B budget would better assess the importance of B retranslocation. However, conclusions should not change much because the growth of new stems, branches and thick roots uses less than half of the total B required for new growth, although in old trees a large proportion of B (70–80%) is immobilized in lignified stems and roots (see data in Finér 1989). The role of fine roots in the budget is an important unknown.

The seasonal changes in B concentration observed by Helmisaari (1990a) suggest that translocation to young tissues is intense in the spring. Using a finer time scale in the model would provide new insights, but requires currently unavailable data on the same scale, and would not affect the long term conclusions reached here.

5 Conclusions

Our analysis shows that the possibilities for conservation of mobile nutrients through long leaf life spans are constrained by the accumulation of non-mobile nutrients. Accumulation can either immobilize a scarce resource or cause toxicity. Passive accumulation in old foliage does not increase whole plant use efficiency.

The constraint imposed is especially tight if the range of concentrations between deficiency and toxicity is narrow as simulated for B, but it must also exist for other non-mobile nutrients. This constraint should originate a chain of selective forces: 1) selective pressure for mobile nutrient conservation by means of long leaf life spans, and subsequently 2) selective pressure for mobility of the usually non-mobile nutrients. In fact any selection for long leaf life spans will be equally constrained by accumulation of non-mobile nutrients.

From the viewpoint of the ecosystem nutrient budget, retranslocation can be also very significant in conifers which have long leaf life spans, and a large standing biomass. Suboptimal boron availability is common in large parts of the distribution areas of Scots pine and Norway spruce and other conifers, and the phenomenon of B retranslocation, which drastically reduces B requirements, may make it possible for these trees to grow in sites, which otherwise might not sustain their growth.

Even with good B availability in the soil, if B would keep accumulating in the old needles passively with the transpiration stream, without any retranslocation, a very large part of the plant-available B of a site would end up immobilized in the foliage of trees, and possibly B concentration would increase enough for B to become toxic in old needles. Obviously, this is not the case as these species exist and thrive over wide areas with soils of varying B availability. The explanation is in their ability to redistribute B within the plant.

The data available for Scots pine, lodgepole pine, Monterey pine and Norway spruce showing their ability to retranslocate B is compatible with the hypothesis of strong natural selection for the ability to retranslocate B under the constraint of long leaf life span. Furthermore, the assessment with the model shows that species would be able to thrive only in a small range of habitats, if they were not able to retranslocate B. The importance of B retranslocation for ecosystem function and for species distribution are challenging subjects for future research.

Acknowledgements

We thank Leena Finér for helpful discussion. The workshop made this collaboration possible and we thank the organizers for the stimulating and enjoyable time at Hyytiälä.

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