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The longevity of Norway spruce responses to boron fertilisation

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ABSTRACT

Effects of boron (B) and nitrogen (N) fertilisation on Norway spruce (*Picea abies*) were studied. The general hypothesis was that N further exacerbates the leader dieback induced by B deficiency whilst B corrects it. After 13 years needle B concentration was 8.4 μg g^{-1} in fertilised trees and 2.6 μg g^{-1} in controls. About half of the trees had growth disorders (leader dieback) before the fertilisation. The occurrence and severity of this was significantly reduced in B fertilised trees, yet the fertilised trees had some leader dieback. Therefore, B deficiency should be verified by needle B analysis. Boron did not affect condensed tannins; B deficiency – induced tannin accumulation does not appear to be a cause for the growth disorder. The dry mass of spruce fine roots was lowered by N fertilisation, possibly because of an increase in soil pH by the urea fertiliser and therefore locally low B availability. Boron eliminated the negative effect of N on fine roots. Boron clearly increased height growth and the effect was not declining by the end of the 13-year study period. The increase in growth did not lead to dilution effect on other nutrients, but magnesium and copper concentrations were increased by B.

1. Introduction

Boron (B) deficiency in forest trees is now known to be common in Fennoscandia, as well as in many other regions in the world (Stone, 1990; Lehto et al., 2010a). Despite this, B deficiencies remain elusive and under-diagnosed. As B is needed for the formation of the primary cell walls, a continuous supply of B is needed during bud formation (Sutinen et al., 2007). Needle B concentrations vary both between years and during the same growing season (White and Krause, 2001). The variability in precipitation is one of the main reasons for this, as B is unavailable in dry soil, and its transport within the plant is reduced when transpiration is reduced (Möttönen et al., 2005; Sutinen et al., 2006). In low-B areas, this variability may lead to temporary B deficiency (Bell, 2000; Sutinen et al., 2007). Moreover, within a stand, typically only a part of the trees are affected by the most obvious symptoms, leader dieback and consequent bushy appearance (Lehto et al., 2010a). In Finland, B fertilisation is a common practice both in peatland and upland forests, but still deficiencies often remain unnoticed, which leads to economic loss; in many parts of the world, forest B fertilisation is not practiced despite low B levels (Lehto et al., 2010a). Removing the cutting residue and small-diameter stems for bioenergy is increasingly common and this further increases the likelihood of deficiencies (Luiro et al., 2010; Tamminen et al., 2012).

Reduced growth of roots and reduced formation of mycorrhizas are frequently the first macroscopic symptoms of B deficiency in plants, including Norway spruce [*Picea abies* (L.) Karst.] (Dell and Huang, 1997; Möttönen et al., 2001; Räisänen et al., 2007). At a later stage, apical buds are affected and in severe B deficiency when needle B concentrations are less than 4 μg g^{-1}, they will be completely deformed. These symptoms have been suggested to be partly due to reduced frost hardiness caused by B deficiency in boreal forests. However, the frost hardiness of buds was shown to be reduced only slightly by B deficiency, unless the deficiency was so acute that bud structure was already damaged (Räisänen et al., 2006, 2007). Nevertheless, the bud dieback caused by frost can be difficult to distinguish from B deficiency symptoms, particularly after months or years since the damage has taken place. The same applies to bud dieback caused by invertebrate and vertebrate herbivores. Hence, although the linkage between B deficiency and bud dieback has been shown in Norway spruce (Saarsalmi and Tamminen, 2005; Sutinen et al., 2006), it still remains to be assessed quantitatively, how reliable the leader dieback symptom is as an indicator of B deficiency.

Above-ground, earlier studies have shown that B deficiency affects mainly the height growth of trees, both via leader dieback and independently of dieback (White and Krause, 2001; Brockley,

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2003; Saarsalmi and Tamminen, 2005). The effect of a single B fertilisation on needle B concentration lasted for 10 years in two Norway spruce stands, although the response was very variable. Volume growth was still positively affected by fertilisation in the more fertile stand (Möttönen et al., 2003). However, the long intervals between growth measurements did not allow assessing whether the increase in growth in B fertilised trees was already diminishing, and the longevity of the B-fertilisation responses in boreal forests is still not known.

In field studies, the growth of tree fine roots (diameter < 2 mm) has not always been strongly affected by B fertilisation on sites low in B, even though B fertilisation can increase the proportion of live roots of all fine roots (Möttönen et al., 2003). In recently fertilised experiments, a lack of effects may be caused by the fact that some of the roots were grown prior to the treatment, and these older roots increase the error in the estimation of fertilisation effects. The root ingrowth core method allows studying fine roots that have grown and possibly died after the application of the treatment. Root ingrowth core studies have not been previously reported from B fertilisation experiments.

Before the occurrence of visible symptoms, the effects of B deficiency can be observed at microscopic level. In earlier studies on B deficient conifer tree needles the formation of sclerenchyma cells has been negatively affected (Raitio, 1983; Jokela et al., 1995; Sutinen et al., 2006, 2007; Sutinen and Saarsalmi, 2008). The main function of the sclerenchyma is to support tissue structure; the cell walls of mature sclerenchyma cells are extremely thick and the cell cavity or lumen is very small or it may disappear completely. Moreover, the cross-sectional area of central cylinders of needles has been found to be larger in B fertilised trees (Sutinen and Saarsalmi, 2008). It is not certain if these cellular level changes occur already in the year of B fertilisation, and how N fertilisation affects them.

Furthermore, B availability can affect the phenol metabolism of trees, although possibly to a lesser extent than found in herbaceous plants (Camacho-Cristóbal et al., 2008; Lehto et al., 2010a). Rummukainen et al. (2007) found that in needles of Norway spruce seedlings the main effect of B deficiency on phenols was an increase in condensed tannins which are the predominant group of phenols in this species. Accordingly, in microscopy studies there were more numerous tannin-accumulating living cells in the primordial shoots of buds and in the differentiating needles both in B-deficient Norway spruce seedlings and in mature trees in the field (Sutinen et al., 2006, 2007). However, tannin concentrations on whole-needle level have not been determined in field-grown Norway spruce trees previously. An excess of tannins can be toxic and eventually lethal to cells (Cakmak and Römheld, 1997) and it might contribute towards the leader dieback.

In this study we report tree and soil responses to B and N fertilisation in an uneven-aged Norway spruce dominated stand. The general hypothesis for this study is that N fertilisation in forest stands with low B levels further exacerbates the B deficiency symptoms and B fertilisation corrects the symptoms both in trees with and without N fertilisation. The specific objectives are:

1. To assess the longevity of B and N fertilisers on needle nutrient concentrations.
2. To assess if there is a substantial decrease in condensed tannins caused by the fertilisers.
3. To assess if fertilisation affects the structure of sclerenchyma cells and central cylinder already on the first year.
4. To quantify the fertiliser effects on fine root growth.
5. To quantify the occurrence of leader dieback and the B and N fertiliser effects on it.
6. To assess the longevity of the B fertiliser effects and its interaction with N on stem height, diameter and volume growth.

2. Materials and methods

2.1. Study site and fertilisation treatments

The experimental site was located in Hammaslahti, Joensuu, Finland (62°24.9′N, 29°54.9′E), with an area of about 1.5 ha. The topography was undulating, causing variability between microsites. The site type was herb-rich forest (Cajander, 1949), which is the most productive site type in the region. The soil was a cambic podzol (FAO, 1988) developed on glacial till. The Norway spruce (*P. abies*) stand was planted in 1979 with 2-year-old seedlings, and thus the trees in the upper canopy layers were 35 years old in the year 2012. However, the seedling survival was rather poor because of competition of ground vegetation, and complementary seedlings were planted two times afterwards. Therefore, the stand was not very even. The overstorey shelter trees and part of understorey trees were cut in the first thinning in 1991. In the beginning of the study in 2000 there were smaller broadleaf trees in the stand, mostly silver birch (*Betula pendula*), grey alder (*Alnus incana*) and rowan (*Sorbus aucuparia*). In the second thinning in early 2012 the alders, rowans and a part of the birches and spruces were cut. Preliminary analyses before the study showed B concentrations of 2–6 $\mu g\ g^{-1}$ in five Norway spruce trees, and there were trees with leader dieback in the stand.

For the fertilisation experiment, 148 trees of 3–6 m height were selected. The minimum distance between two experimental trees was 7 m. The selected trees were grouped into 18 blocks of eight trees and a block with four trees (Räisänen et al., 2006, 2009). The treatments were factorial combinations of B and N fertilisation, hence the treatment combinations were 0 (control), B, N and N + B, denoted NB. The fertilisers were applied to circular plots of 2.5 m radius around individual Norway spruce trees. After the thinning in early 2012 there were 81 sample trees: 19, 21, 17 and 24 trees in control, B, N and NB treatments, respectively.

Nitrogen was applied as urea at a rate of 180 kg ha^{-1}, and B was applied as borax at a rate 2 kg ha^{-1}. Care was taken to spread the fertilisers evenly in the plots; the borax was applied using a kitchen spoon. The fertilisers were spread on 6th–7th June 2000, when the budburst was commencing.

2.2. Soil and needle sampling and element analysis

The first soil sampling was done as a line survey within each block before fertilisation in June 2000. A sampling line was allocated in the middle of the block in an open area not under tree canopies. Samples were taken on the line at 1 m distance between samples. Sixteen to eighteen cores, 3 cm in diameter and on average 5.5 cm in depth were taken from each block ($n = 18$) from the mixed topsoil. The second set of soil samples was taken under 10 trees per treatment, 10 cores per tree, 75 cm from trunks in June 2001; these soil cores with 5 cm diameter and 5 cm in height were taken from the locations where the root ingrowth cores were set (see Section 2.5 below). The 10 samples per tree were pooled for chemical analysis. Third, compound samples were taken of the soil used for filling the root ingrowth cores in 2001: soil (0–5 cm depth) was collected from a non-fertilised edge of the study site, homogenised and treated with the fertilisers corresponding to the treatments. The fertilisers were mixed in the soil. The fourth sampling in 2003 comprised part of the root ingrowth cores; they were sampled as the cores for fine root analysis, but used for chemical analysis, $n = 3$ for treatments 0 and NB, $n = 5$ for treatment B and $n = 4$ for treatment N.

Soil samples were air dried at room temperature for 2 weeks and sieved through a 2-mm sieve. For the three latter samplings, B and N concentrations, pH in 0.01 M $CaCl_2$ and soil organic matter content