TREE FORM AND THE ROLES OF BORON AND CALCIUM IN HARDWOODS

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A balanced nutrition is essential for the healthy growth and form of tree species. In the absence of the micronutrient boron (B) and/or the macronutrient calcium (Ca) loss of apical dominance occurs rapidly resulting in the onset of poor tree form. Knowledge of specific roles of these elements helps to explain their importance and why tree form deteriorates when their supply becomes limited.

ROLES OF CALCIUM AND BORON

Calcium and B have essential roles in the binding of pectin in the primary cell wall of all cells within the tree. The primary cell wall is a three dimensional network of: cellulosic microfibrils bundled together as macrofibrils; hemicellulose; and pectin. The pectin is a network of polysaccharide chains bound together with a series of loops. There are three types of polysaccharide chains that make up pectin, namely homogalacturanon, rhamnogalacturonan I (RGI) and rhamnogalacturonan II (RGII). The homogalacturanon has been referred to as the smooth regions and the latter two as the hairy regions of pectin chains (de Vries *et al*., 1982; Grant Reid, 1997). The role of Ca in the pectin network is through the formation of Ca-bridges between chains of homogalacturanon. The role of B has been isolated to the formation of a borate-diester bond in the RGII region of the pectin network as a dimer (dRG-II-B) (Kobayashi, *et al*., 1996; Ishii and Matsunaga, 1996; O'Neill, *et al*., 1996). These bonds between homogalacturanon and RGII units are thought to be critical for the formation of loops to bind the pectin network with the cellulose microfibrils (Fry, 1986), thereby providing strength and flexibility to the cell wall. Calcium has additional roles in forming Ca-bridges in the middle lamella (between cells) and along with B in stabilising the cell membranes. Boron has a secondary role in the synthesis of lignin for rigidity of the secondary cell wall (Marschner, 1995). Thus in the absence of Ca and/or B, growth of the apical shoots slow or cease due to impaired cell wall development, setting up the tree for a loss of apical dominance.

SUPPLY OF CALCIUM AND BORON

A number of factors influence the supply of Ca and B for growth. Firstly, Ca and B are passively taken up by the plant, meaning that they are naturally absorbed into roots with the uptake of water and moved around the plant in the xylem. Thus, actively transpiring tissues receive greater amounts of these elements than shoot tips and reproductive structures. They then become trapped in the target tissues with little or no retranslocation to areas of need such as rapidly growing shoot and root tips. There is an exception to this rule for B amongst a small number of species that have evolved with a defacto system of remobilisation of B through cis-diol bonds with sugar alcohols (Brown and Hu, 1996). Therefore in the vast majority of species, disruptions to water uptake and/or nutrients in the soil solution result in rapid effects on cell wall growth in growing tissues such as shoot and root tips.

Soil types vary considerably in both B concentrations and their B availability to trees. Soils with sandy loam A horizons (classified as Chromosols, Kurosols and Kandosols under Isbell, 1996) only required 0.4-0.6 mg B kg^{-1} Hot $CaCl_2$ extractable soil B for adequate foliar B in avocados compared to 7.2-11.2 mg B kg^{-1} Hot $CaCl_2$ extractable soil B for Ferrosol soils (as classified under Isbell, 1996) (Smith, 2004). Variations in B supply between soil types are due to factors such as clay content, sesquioxides (iron and aluminium oxides), organic matter, soil pH and soil water. Thus, soil type differences need to be accounted for when interpreting soil chemical data and determining fertilizer application rates.

IMPLICATIONS FOR WOOD QUALITY

We are not necessarily going to see declines in vegetative tree growth with marginal or temporary deficiencies of these elements as they are not major drivers of metabolic reactions for growth, like elements such as nitrogen and phosphorus. However, declines in tree form and wood quality are the most likely factors to be affected by shortfalls in these elements through direct effects on cell walls. Wood quality assessments are currently being planned to assess the effects of treatments on a range of hardwood species growing in Ca and B field trials.

In our experiments to date there have been -B treatment effects on tree form in *Corymbia citriodora* sub sp. *variegata*, *Eucalyptus pilularis* (Plates 1a & 1b, respectively and Figures 1&2, respectively), and *E. nitens* (Plate 1c) and -Ca and -B treatment effects on tree form of the *Corymbia* complex hybrid (Plate 2).

(a) (b) (c)

Plate 1: Loss of dominance effects on (a) *Corymbia citriodora* sub sp. *variegata* at Tingoora, Qld (b) *E. pilularis* at Blackbutt, Qld and (c) *E. nitens* at Nowendoc, NSW in –B treatments

Boron deficiencies are likely in the Queensland hardwood plantations due to low total and available soil B levels along the east coast of Australia, and the greater adsorption of B on Ferrosol soils leading to low plant available B. Unless this issue is addressed through corrective fertilizer additions, then tree form issues are likely to undermine the continued success of these plantations and the value of products at harvest. Similarly, areas of low Ca need further investigation regarding wood quality issues.

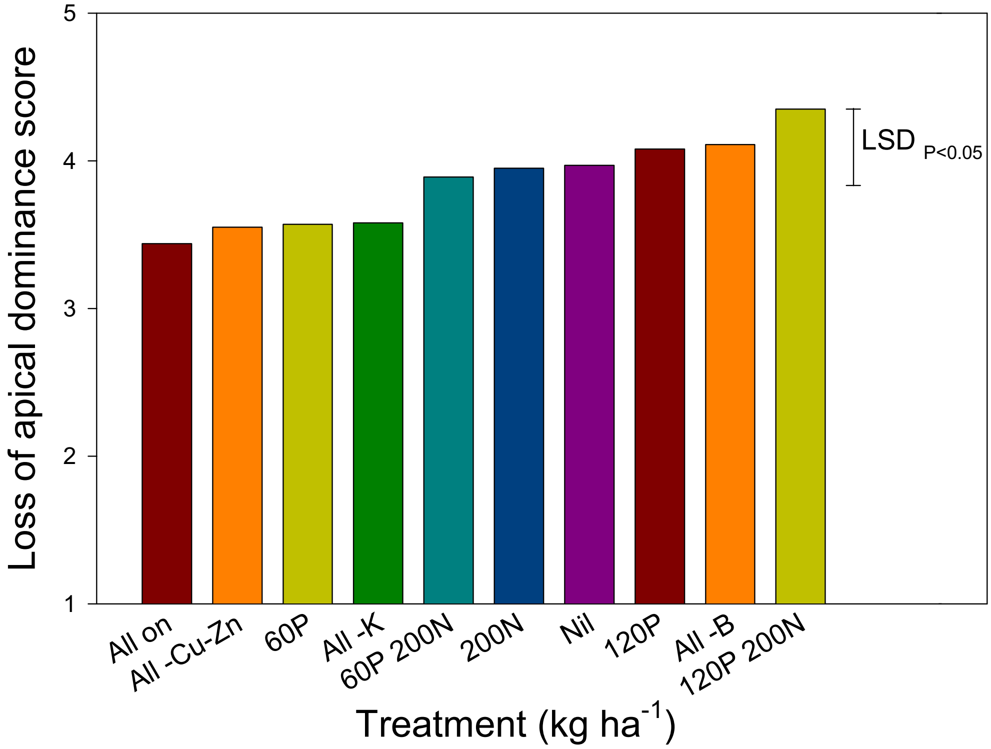

Figure 1: Loss of apical dominance (LAD) in *Corymbia citriodora* sub sp. *variegata* in low B treatments at age 2 years. Score: 1 = 0 LAD, 5 = Severe LAD

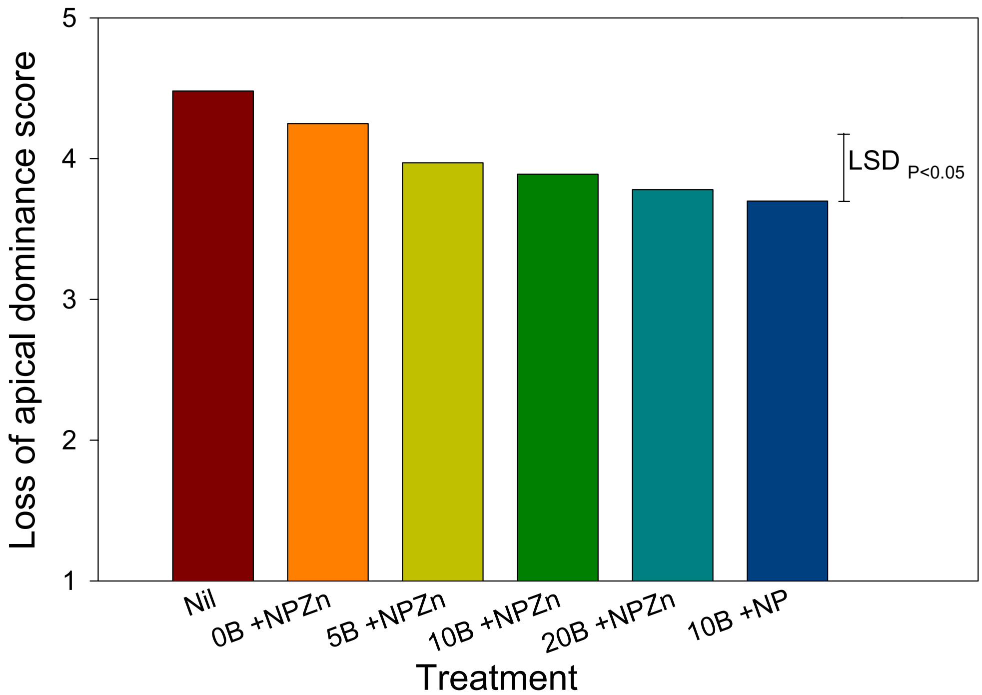

Figure 2: Loss of apical dominance (LAD) in *E.pilularis* in low B treatments at age 2 years. Score: 1 = 0 LAD, 5 = Severe LAD

(a) (b) (c)

Plate 2: Loss of dominance effects in the *Corymbia* complex hybrid grown in (a) complete (All), (b) All –Ca and (c) All –B hydroponic solution treatments at age 5 months

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