

Introduction

A better understanding of the genotypic variation in foliar nutrient concentrations and their relationships with tree water use efficiency (WUE) and growth under contrasting environmental conditions are required for assessing the potential of using physiological indicators in tree breeding programs for improved productivity. Foliar nutrient concentration has been shown to be a good indicator of nutrient stress in many tree species (Pederick et al. 1984; Nilsson and Winklund 1994; Zas and Serrada 2003) and has potential use in selecting elite clones of exotic pines with greater nutrient and water use efficiency (Prasolova et al. 2005). There is substantial literature showing that radiata pine genotypes differ in their foliar nutrient concentrations as a result of site or nutrient supply effects (Burdon 1976; Pederick et al. 1984; Theodorou and Bowen 1993; Sun and Payn 1999; Carson et al. 2004). However, there are few studies where foliar nutrients have been examined in relation to tree WUE (assessed by carbon isotope composition $\delta^{13}\text{C}$) and growth of radiata pine genotypes under different site conditions, especially in New Zealand.

Through analysing the results of 45 radiata pine genotypes grown at two contrasting sites with different soil nutrient and water availability we aim to (1) quantify the genotypic variation in foliar nutrient concentrations, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in relation to radiata pine growth and (2) determine the genotype by environment interactions for these traits.

Study sites, trial design and analyses

One trial site located at Aniseed Valley in Nelson New Zealand has adequate rainfall (1600 mm), and the (serpentine) soil (Mafic Brown Soil) has high extractable Ca and Mg and low extractable K and Bray-P. Another trial site located at Balmoral in North Canterbury New Zealand has low rainfall (650 mm), and is exposed to fohn-type winds and droughts. The soil (Orthic Brown Soil) at this site has low extractable Ca and Mg but high Bray-P. Both trials were a randomised complete block design. Each of 4 blocks (plots) was randomly planted with 3 ramets of each of 40 radiata pine clones and 2 seedlings of each of 5 control-pollinated families. Both trials were established in July 2002 with stocking of 625 seedlings ha^{-1} .

At both trials, tree height and ground-line diameter (GLD) or diameter at breast height (i.e. DBH at 1.4m) were measured in July 2002, 2005 and 2006. Tree volume was calculated from the measured tree height and GLD or DBH. In late February 2006, current-year needles were sampled from the youngest second-order branches of 45 radiata pine genotypes in each plot, respectively. Samples were oven-dried and then ground for analysis of nutrients, carbon and nitrogen isotope compositions ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$). For tree growth data, analysis of covariance was conducted to determine the effects of site and genotype and their interactions. For foliar nutrient concentrations (including $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), analysis of variance was carried out to determine the effects of site and genotype and their interactions. The statistical analyses for genotype effects were also carried out for each site separately. The relationships among growth variables, foliar nutrient concentrations, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of radiata pine genotypes were examined by Pearson's correlation and stepwise regression analyses for each site separately.

Variation among the genotypes in growth, foliar nutrient concentrations, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$

There were significant differences among the genotypes in tree growth, with some genotypes performing consistently better and some poorer across sites. The interaction of site by genotype was also significant for all growth variables. The site by genotype interaction was mainly due to the considerable growth reduction of some genotypes at Balmoral site. Significant differences

were found among the genotypes in foliar nutrient concentrations, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ across sites. However, larger genotypic variations were found for foliar K, Ca, Mg, B, Mn, Zn and $\delta^{15}\text{N}$ concentrations than N, P, S and $\delta^{13}\text{C}$ at Aniseed Valley and for foliar Ca, B, Mn, Zn and $\delta^{15}\text{N}$ concentrations than for N, P, K, Mg, S and $\delta^{13}\text{C}$ at Balmoral. Significant site by genotype interactions were only found for foliar Ca, Mg and Mn concentrations.

This study confirmed a large genotypic variation within the species in foliar nutrient concentrations, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. This result agrees with the previous observations for foliar nutrients of radiata pine and other pine species (Burdon 1976; Pederick et al. 1984; Beets and Jokela 1994; Xu et al. 2003; Carson et al. 2004; Prasolova et al. 2005). In this study, genotype effect accounted for a major source of variation in determining foliar concentrations of N, P, Ca, Mg, S, Mn, Zn, B and $\delta^{13}\text{C}$, and to a lesser extent foliar K and $\delta^{15}\text{N}$ concentrations.

Relationships among tree growth, foliar nutrient concentration, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$

Significant correlations were found between growth variables and foliar nutrient concentrations or $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ of radiata pine genotypes at both Aniseed Valley and Balmoral. At Aniseed Valley, the significant positive correlations between genotype means of growth variables and foliar N, P, K, S and Fe indicated these nutrients might limit tree growth at this site and fast-growing genotypes could have a greater capacity to uptake, translocate and utilise these nutrients. However, the significant negative correlations between genotype means of growth variables and foliar Mg concentration indicated a possible Mg toxicity on serpentine soil and the fast-growing genotypes could have an ability to maintain a low foliar Mg concentration. This ability of fast-growing genotypes on serpentine soil could be related to specific physiological mechanisms limiting Mg and Ni uptake by their roots or by symbiotic ectomycorrhizal fungi (Jones and Hutchinson 1988; Gabbrielli et al. 1990; Kayama et al. 2005). Stepwise multiple regression analyses of tree growth variables against foliar nutrient concentrations further indicated that P, Fe, Mg, K, S and N were the main nutrients contributing to the different growth of the genotypes at this site.

At Balmoral, the significant positive correlations between growth variables and foliar K, S, Ca, B and Mn concentrations of the genotypes implied these nutrients might limit tree growth at this site. However, this relationship was not well reflected in the genotype means of these foliar nutrient concentrations, which (except foliar S) were well above the critical foliar levels of these nutrients (Will 1985). The highly significant negative relationships between genotype means of growth variables and foliar N concentration should not be caused by the direct effect of N on the growth of these genotypes because foliar N concentrations (1.11-1.47%) were not high enough to cause a detrimental effect on any genotypes. This masking relationship could result from an indirect effect of soil moisture stress on tree growth of these genotypes at this site. A larger reduction of tree growth but possibly smaller reduction of N uptake from soil for certain genotypes sensitive to soil moisture stress could result in higher foliar N concentrations in these genotypes than other relatively soil moisture tolerant genotypes. A significant correlation ($r=0.36$, $P<0.0001$) between foliar N concentration and $\delta^{13}\text{C}$, both of which negatively correlated to tree growth, confirmed the limitation of soil moisture. Stepwise multiple regression analyses of tree growth variables against foliar nutrient concentrations revealed that foliar N, Mn and S were main nutrients contributing to the different performance of genotypes at this site.

Acknowledgements

We thank the numerous forest companies and private owners for providing the sites for the trial

series. We acknowledge the invaluable assistance and hard work of many past and present Scion's staff who have been involved in installing and maintaining these two trials including D. Henley, S. Pearce, L. Garrett and S. Olykan. Many thanks are also due to G. Coker and M. Watt who provided soil and climatic information and help with statistical analysis, and Veritec laboratory staff for soil and plant sample analyses. The project was funded by the New Zealand Foundation for Research Science and Technology under contract C04X0304, 'Protecting and Enhancing the Environment through Forestry'.

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