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Drivers of genotype by environment interaction in radiata pine as indicated by multivariate regression trees

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ABSTRACT

Productivity of forest tree plantations can be maximized by matching genetically adapted planting stock to environments where they perform best. We used multivariate regression tree (MRT) analysis with environmental predictors to quantify and characterize the nature of genotype by environment interactions (G × E) of radiata pine diameter at breast height (DBH) grown in New Zealand. The analysis was carried out for 21 provenance trials, and 48 progeny trials of second-generation selections that are widely used in plantation forestry today. To quantify the maximum variance explained by G × E, we used unconstrained clustering of genotypes based on their performance across all sites. Subsequently, the clustering was constrained by climate and soil variables, i.e. the putative causes for G × E. Unconstrained clustering explained 62% and 58% of the observed G × E variance in provenance and progeny trials, respectively. Constrained clustering explained approximately 50% and 25% of the G × E variance in provenance and progeny trials, respectively. Minimum temperature was identified as an important driver of G × E in both provenance and progeny trials. Environments can be grouped into warm humid sites, where most second-generation selected genotypes performed better, and cold sites, where specific genotypes performed best. Based on the progeny trials, only marginal (ca. 3%) gains can be made by targeted deployment to warm humid sites, but more substantial (approx. 20%) genetic gain can be made on cold sites, compared to current deployment strategies.

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1. Introduction

Commercial plantations of radiata pine (*Pinus radiata* D. Don) are the basis for forest industry in New Zealand, and likewise are also important in Australia and Chile. Over the past five decades, radiata pine resources have been expanded and consolidated as a major provider of domestic and export solid-wood and pulp products. This has largely been achieved through long-term investments in tree breeding and silviculture. Significant progress has been made in understanding the genetic control of growth, form and wood quality traits of radiata pine. Based on data from genetic field trials, substantial gains of up to 32% in volume have been achieved (Mead, 2013, Table 6.3). However, an important obstacle to the realization of this genetic gain in commercial plantations lies in suboptimal matching of selected germplasm to varied environments of different regions and planting sites within regions. The New Zealand Radiata Pine Breeding Company (RPBC) programme aims to breed and provide germplasm for deployment across New Zealand, the Central and Southern Tablelands of New South Wales and Tasmania in Australia (Cullis et al., 2014). At present, RPBC produces a single set of breeding values for each trait. These breeding values are calculated including data from all available test sites, making the assumption that genotype by environment interaction (G × E) is not important.

Genotype by environment interaction (G × E) is a phenomenon in which different genotypes respond differently to variations in environment. It can consist of heterogeneous genetic variances across environments, and/or genetic correlations between expressions of a trait in different environments being low with changes of genotype rankings. The options that are available when dealing with G × E depend upon the predictability of the role of environment in generating G × E (Kang, 2002). The environments in which radiata pine grows in New Zealand have some predictable components and it is possible to exploit G × E. Johnson and Burdon, (1990), in a study of radiata pine in the New Zealand regions of Northland were able to select families for which regionalisation

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improved predicted genetic gain to 25% as compared to 22% from non-regionalisation. Carson (1991) also found an increase in expected genetic gain for diameter through regionalisation of seed orchards from 11.2% for a non-regionalised programme to 14.4% for a site-specific selection. It should be noted, however, that Johnson and Burdon's (1990) study included only four sites, whereas Carson (1991) reported findings from 11 sites with progeny derived from a set of just 25 parents. As a result, the conclusions drawn from these studies are probably insufficient to discount the need for regionalisation. Burdon et al. (1997) investigated the relative performance of three provenances from California and three land races across 21 sites throughout New Zealand. Strong differences among sources in their relative performance on different site categories were reported. A recent large G × E study by McDonald (2009) reported that genetic correlations for diameter at breast height growth between sites averaged 0.50. The study also reported evidence for heterogeneous genetic variances (i.e. level of expression) for diameter growth across different regions in New Zealand.

For multi-site progeny trials in forestry, site–site genetic correlations (also called type-B genetic correlations) were usually estimated using linear mixed models (Burdon, 1977). Since 1980s, Singular Value Decomposition (SVD) was employed to describe G × E patterns (Gauch, 1992), initially applied for agronomic crops using Additive Main effects and Multiplicative Interaction model (AMMI), and later on in forestry trials (Wu and Ying, 2004). More recently, factorial regression using a mixed model approach (Factor Analytic method) was introduced to explore G × E patterns for multi-environment trials (Smith et al., 2001; Costa e Silva et al., 2006; Beeck et al., 2010; Cullis et al., 2010) and to relate underlying factors to the causes of G × E interactions (Costa e Silva et al., 2006; Cullis et al., 2010; Hardner et al., 2011; Cullis et al., 2014). Beside linear and non-linear fixed and mixed models using parametric approaches to decompose the G × E interactions, Multivariate Regression Trees (MRT) are a method to analyse G × E that can also handle categoric as well as ordinal environmental variables (Sheaves et al., 2007; Chen et al., 2010; Hamann et al., 2011). The method has been originally developed for ecological research, to analyze interactions between environmental variables and species abundance in ecological communities (De'ath, 2002; Larsen and Speckman, 2004). The method is a recursive binary partitioning algorithm that assigns objects of the response matrix (species in inventory plots, or genotypes in genetic test plantations) to homogenous groups, with partition criteria being sourced from a separate data matrix (environmental variables for each site or plot).

In the present study, we explore whether multivariate regression tree analysis can be applied to identify and quantify environmental drivers of G × E in radiata pine grown in New Zealand. We first re-analyze archival data from previously published work (Burdon et al., 1997) which found strong G × E across a wide range of test environments, to investigate if the technique can reliably replicate these results using a recursive algorithm to identify the primary environmental drivers of G × E. Second, we applied the MRT analysis to a large data set from 48 second- and third-generation radiata pine progeny trials established by the RPBC, with some of the genotypes in these trials widely deployed in New Zealand for commercial plantation forestry. The main objective of this paper is to investigate if we can identify environmental drivers of G × E that could be translated into straightforward guidelines to plant particular sets of genotypes under different planting-site environments. Lastly, this study contributes a broad comparison of how unimproved provenances or land races (Burdon et al., 1997) compare to genetically improved second- and third-generation selections (RPBC material) in their response to different environments.

2. Materials and methods

2.1. Radiata pine provenance trial data

Twenty-one provenance trials planted across New Zealand provide the experimental basis for the first part of this study, site information being provided in Table 1. Seventeen trials represented provenances as 6-tree row plots with 12 replicates in randomized complete blocks. At the sites Pouto, Riverhead, Rotoehu, and Kaingaroa, 6 × 6-tree plots with 10 replicates were used, and 6 × 6-tree plots with five replicates were used at the sites Berwick and Longwood. Tree spacing varied among trials with 16 trials with a typical spacing of 4 × 3 m (see Table 1 for details).

Three seed origins from California, as well as three land races of naturalized New Zealand sources were planted at all provenance trials. California collections of radiata pine (Eldridge, 1978) included an average of 40 seed parents from each of 13 local subpopulations but are analyzed here as three main populations Año Nuevo (four localities), Monterey (six localities) and Cambria (three localities). The breakdown into subpopulations was disregarded, as previous studies reported subpopulation differences being negligible (Burdon et al., 1992, 1997; Raymond and Henson, 2009). The three regional land-race stocks, Kaingaroa, Nelson and Southland were collected mostly from select-trees found in unimproved stands (Burdon et al., 1997). The landrace seedlots were representative of 15 stands in Kaingaroa, six in Southland, and one large commercial stand in Nelson (Burdon et al., 1997). For simplicity, we refer to all genetic entries as provenances.

Assessments were carried out when provenance plantations reached 7–10 m in height, which varied among sites and led to measurements being carried out between 5 and 15 years (Burdon et al., 1997). Diameter at breast height (DBH) was chosen as the variable to study because it has two advantages: (i) having been measured with good precision throughout, and (ii) often DBH is more sensitive to maladaptation than height growth (e.g., Rais et al., 2014). DBH data had already been subjected to spatial adjustments where possible, as in Gapare et al. (2012) for microsite differences to reduce residual error as recommended by Costa e Silva et al. (2001) and Dutkowski et al. (2002, 2006). To standardize measurements from different ages and different site types, we subtracted the mean of individual-tree DBH in cm at each test site and divided by the test site standard deviation, so that each individual-tree DBH is expressed in units of standard deviations from a site mean of zero. Best Linear Unbiased Estimates (BLUEs) were obtained for each provenance and site, treating provenances as fixed effects using the software ASReml (Gilmour et al., 2009). We note here, that standard errors were slightly larger for the land races (0.14–0.15) than for the Californian origins (0.09–0.10), for standardized BLUEs that ranged from −0.82 to +0.82. However, this should not influence the G × E analysis presented in this paper other than producing a residual error variance.

2.2. Radiata pine progeny trial data

The second dataset we used in this study contains 48 field trials of the RPBC. The trial design was in most cases, randomized complete block designs, with two trials having incomplete blocks. Most trials were planted with restricted randomization of families in disconnected sets that were randomised in main plots within replicates, and then families were randomized within sets. The numbers of plots, blocks, family-sets-in-blocks and parents varied among trials and are provided in Table 2. Thirty-three trials contained controlled-pollinated (CP) families and the remaining 15 contained open-pollinated (OP) families.

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