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Linking changes to breeding objectives and genetic evaluation to genetic gain in New Zealand

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Abstract This article uses the breeder's equation, which predicts genetic gain in breeding programs, to frame a general discussion on breeding objectives, new phenotypic techniques for selection criteria and statistical models as applied to short rotation species. Short-rotation breeding programs are increasingly working on wood quality traits; however, we keep on treating them as if they were growth traits. Understanding tree-level patterns of variation can lead to alternative strategies for evaluation, analysis and inclusion in breeding objectives; which I describe in a pilot application in *Pinus radiata* in New Zealand. Finally I discuss the relationship between the breeder's equation and formulations of linear mixed models, using genotype by environment interaction as example, to show the interplay between genetic evaluation and breeding strategies. There is tension between increasing complexity (and the implicitly promised flexibility), information recovery (as more parameters are poorly estimated) and computational demands. The latter can be tackled through much more computer power (a never-ending endeavor), exploiting features of the problem or moving back to a lower complexity level.

Keywords Early screening · Genetic evaluation · Genotype by environment interaction · Wood properties

Introduction

Genetic evaluation is central for any breeding program, as it provides information to select the best trees, predict genetic gain and manage population structure to maximize the long-term benefits of the program (White 1987). While the role of evaluation is simple, practical implementation gives rise to a number of complications: we have to account for multiple traits and environments, and the vagaries of long-term decisions. Tree breeding is not an

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isolated discipline and, besides its connections to other forestry activities, it is informed by progress in both animal and crop breeding. Tree and crop breeding have in common the heavy use of experimental designs and genetic evaluation based on multiple environments, while tree and animal breeding have in common the large numbers of genotypes under testing. Three points of distinction are that (1) tree breeding deals with much longer-lived and large organisms, which involves (2) a clear distinction between selection criteria and objective traits and (3) testing often focuses on single individuals rather than on the operational unit (a stand).

This article focuses on advances in genetic evaluation—in a wide sense, considering both statistical models and new phenotypic techniques for selection criteria—although with a distinctive 'Kiwi flavor' and an emphasis on the work developed at the University of Canterbury. There are two reasons for this; firstly, it is the work with which I have most familiarity; secondly, we have been working in new approaches to very early wood quality assessment that could be less familiar to many readers. Some of this work is flowing into the current breeding strategy of the New Zealand Radiata Pine Breeding Company (NZRPBC), while other is still in the evaluation stage and, in some cases, it is speculative at best.

It is convenient to frame the discussion of research targeting genetic evaluation on terms of predicted genetic gain per year, which is estimated with the *breeder's equation* as the product of four factors: accuracy of prediction, selection intensity, additive genetic variation and the inverse of generation interval (described in many places, for example Van Vleck et al. 1987). Traditionally the calculation is presented in its univariate, mass-selection form:

$$\Delta G = \frac{i h^2 \sigma_p}{L} \qquad ([1])$$

where i is selection intensity, h^2 heritability for the single trait under selection, σ_p phenotypic variance and L generation interval. This form is useful if one were to start a breeding program, selecting plus trees based on their own phenotypic records for a single trait. However, advanced-generation, modern programs tend to rely on Best Linear Unbiased Prediction (BLUP) breeding values for multiple traits—reflecting selection efforts for quantity and quality characteristics—as well as recognizing that performance in multiple sites can be modeled as multiple traits (going back to Falconer 1952). In this case, a more useful form of the equation is:

$$\Delta G = \frac{i r_{IH} \sigma_H}{L} \qquad ([2])$$

where r_{IH} is the correlation between the index I used for selection and the breeding objective H (accuracy), and σ_H is the standard deviation of the breeding objective. The following discussion will cover three areas: breeding objectives, corewood quality traits, and multiple environments as multiple traits, referring back to effects on the components of Eq. [2].

Breeding objectives and uncertainty

Most operational breeding programs target multiple traits that, if the aim is maximizing commercial value, requires a formal definition of the breeding objective. This involves both identifying traits that have an effect on profit and their relative economic weights.

Following Borralho et al.'s (1993) work on breeding objectives for *Eucalyptus globulus* there have been several articles defining objectives for short rotation species, with the largest number for radiata pine, sometimes showing large discrepancies in the estimated values (e.g., Chambers and Borralho 1999; Apiolaza and Garrick 2001b; Ivković et al. 2006). There are two terms in Eq. [2] that involve the economic weights: r_{IH} and σ_H (see appendix of Apiolaza and Garrick 2001b for details on their calculation); thus, disagreements in estimated values may result not only in different selected genotypes, but in different predicted genetic gains as well.

There is a fascinating distinction between research on genetic parameters and economic weights. In the case of genetic parameters, it is always possible to invest more on testing to obtain better estimates; in contrast, for breeding objectives and economic weights, uncertainty 40–50 years in the future (1 breeding cycle + 1 rotation) cannot be reduced substantially. If, on top of this, we include shifting environmental conditions due to, for example, climate change, the prospect of deriving 'good' economic weights is daunting.

An alternative to using point-estimates of economic values—often obtained from bio-economic models with large numbers of assumptions—could be the use of 'robust selection', generating broad scenarios of economic weights using Monte Carlo simulation and selecting the genotypes that achieve a high value under a mix of conditions. As an example, Evison and Apiolaza (2013) used unpublished economic weights for the NZRPBC breeding program as the mean for the simulation, while a number of published alternatives were used to define the variability of the simulations. Using this approach, it is possible to select genotypes that perform well on average and are resilient to variability of economic weights; that is, that perform well over a broad set of economic circumstances. In a related problem, Apiolaza and Alzamora (2013) used portfolio analysis to deal with performance instability at the deployment level—due to either GxE interaction or changing economic circumstances—making explicit trade-offs between gain and stability/predictability. This approach could also be used for breeding purposes.

Targeting corewood in short rotation softwoods

As discussed in the introduction, a characteristic feature of tree breeding is the marked distinction between objective traits—which affect profit, are often expensive to assess and observed at rotation age—and selection criteria, which are correlated with objective and are hopefully easier, cheaper and faster to assess. In the case of radiata pine in New Zealand, objective traits like volume, wood stiffness or branching are on average valued at rotation age (average 28 years), while selection criteria like dbh, acoustic velocity and basic density are on average assessed at 8 years. Selection indices targeting the objective require genetic parameters for selection criteria at early age, objective traits at rotation age and correlations linking criteria and traits.

The New Zealand Radiata Pine Breeding program started in the 1950s with an emphasis on tree growth and form. Successive selection efforts extended to nodality (later abandoned) and disease resistance (e.g. *Dothistroma sp.*). All these traits could be easily assessed in large numbers of individuals. In the late 1960s and early 1970s it started to become clear that radiata pine was a poor wood quality species, particularly in the first ten rings (often named corewood). Initially much work was developed on basic density, considered at the time as *the* fundamental wood property, as it displayed strong correlations with other wood properties, and is relatively easy to assess and highly heritable. Nevertheless—at least from a solid wood perspective—modulus of elasticity (MoE) and dimensional stability have larger effects on the performance (and price) of the end-products. The relationship between basic density and MoE changes with time (Chauhan and Walker 2006), showing strong associations in outerwood (wood following the first ten rings) but poor association in corewood (Apiolaza 2009). Unfortunately, tree selection for breeding purposes is done at age eight in radiata pine, when trees contain mostly corewood.

Our research group has proposed a change of philosophy concerning the evaluation of wood quality, letting go of the idea of predicting quality at rotation age (Apiolaza 2009, Apiolaza et al. 2011a, b). Most of the poor wood quality problem in short rotation softwoods relates to corewood, which combined with the gradual increase of quality with age makes targeting rotation age (and therefore juvenile-mature correlations) unnecessary. The problem can then be framed as predicting corewood quality as early as possible, for which we have developed tools and techniques that scale to thousands of genotypes (Chauhan et al. 2013). These range from low-cost and fast devices to assess longitudinal shrinkage in wood samples or splitting tests to estimate growth-strain to purpose-built acoustic velocity and resonance tools developed by the University of Canterbury.

Reframing the problem also affects the breeding objective, as the trait we are breeding for (corewood quality) is expressed much earlier. Another related issue is how to integrate very early screening in the breeding strategy. Despite our efforts, we have not scaled evaluation beyond 3,000 trees (6,000 samples), which is enough for establishing basic genetic parameters, but not sufficient to screen our breeding population. Instead, we suggest targeting screening the deployment populations (particularly clonal ones), which are much smaller than breeding populations and already present superior growth and adaptation. Alternatively, breeders could target elite breeding populations, in which assessing 5–10 ramets/genotype would prove very valuable. This process could be expanded to tackle non-key traits; e.g. heartwood/resin content using NIR to provide a comprehensive coverage of wood properties.

Probably the biggest problem when working with wood quality is how expensive is assessment, which leads to very small sample sizes reducing selection intensity in Eq. [2] and potentially reduced accuracy of selection. Table 1 shows a simplified view of the number of samples required to estimate parameters; most of the wood quality literature deals with tens of samples and, in some cases, as little as a single tree.

The unsuitability of small sample sizes of large trees to support breeding for wood properties led us to propose an alternative: measure small trees—even seedlings—as they are much cheaper and faster to assess. This makes some key assumptions: (1) poor quality trees by age 2 will tend to have poor quality corewood and take longer to produce acceptable timber outerwood; (2) the price discount between the lowest framing and appearance grades, and reject material (~50 %) is far greater than the difference with premium grades (~10 % for engineering and finishing); and (3) there is no need to delay selection because the poorest wood is at the center of the tree, with a gradual improvement with age. That is, if corewood meets a quality threshold the outer rings will also meet it, and therefore there is no need to worry about age–age correlations for wood quality. This approach makes a conscious trade-off between reduced accuracy of selection, and higher selection intensity and lower generation interval in Eq. [2].

Very early screening of wood quality is both a change of selection criteria and a change of objective traits, as we move to two classes of products: industrial (low value) and ‘good enough’ for structural and appearance purposes. In New Zealand, at the average rotation of 28 years, about 50 % of the volume of radiata pine is low quality (and value) corewood (Van Wyk 1990; Cown 1992 and Gaunt 1998). ‘Fixing’ corewood has the greatest financial benefit in short rotation softwoods as it upgrades product quality and potentially allows for

Table 1 Number of samples required to obtain a good estimate parameters

Estimated parameter	Number of samples
Mean	Tens
Variance	Hundreds
Correlation	Thousands

shorter rotations. We have strong evidence for these assumptions, and the NZRPBC has established two ‘sister trials’ that will be grown until 8 years to compare the results from very early screening with traditional selection techniques.

The reader might be wondering why do we worry about early screening genotypes that have *already* been selected for the breeding and deployment program considering growth, form and basic density. Figure 1 provides a good answer, plotting the predicted breeding values for the parents of a radiata pine clonal seed orchard, considering wood stiffness (MoE in GPa) in the X-axis, longitudinal shrinkage (a measure of dimensional stability, in percentage) in the Y-axis and basic density (in kg m^{-3}) as circle area, based on a genetic trial using 2-year old seedlings. Selection of the orchard parents focused on wood *quantity* but ignored solid wood *quality*.

Considering only MoE and shrinkage, the best parents would be at the bottom-right of the graph (high stiffness, low shrinkage), while the worst parents would be at the top-left (low stiffness, high shrinkage). Some of the most abundant parents in the orchard, chosen because adequate or high density, are among the worst performing parents for wood quality. Using this type of very early screening trial we can further rogue deployment populations for solid wood quality, without waiting for the typical selection age.

In parallel to studying very early screening, our research group has developed high-resolution acoustic tools, including a disk and a core scanner. The main drivers for this effort were to improve our understanding of within-tree variation, to improve the link between very early screening and overall tree performance, and to convince breeders and end-users that once a quality threshold is achieved wood quality does not deteriorate. These tools can provide assessments every few mm, producing large amounts of data, which is mostly useless from a selection viewpoint. SilviScan—an X-ray diffraction/densitometry tool for increment cores—also generates similar datasets providing excellent *research* data, but it is overkill for *breeding* purposes. As researchers many times we become fascinated by high-resolution data, which due to time and cost restrictions can be obtained for very small samples, often targeting only our best genetic material. We have to be careful to extend conclusions from non-random, potentially biased samples to our overall breeding populations.

Multiple environments as multiple traits

Until last century most genetic evaluations considered a univariate genetic evaluation, where phenotype would be modeled as a function of site, within-site experimental design features and family structure. On terms of methodology, breeders moved from ANOVA to BLP (e.g. White and Hodge 1989) to BLUP (e.g. Borralho 1995) and increasing software sophistication permitted fitting heterogeneous residuals.

Falconer (1952) posited that the expression of a trait in multiple environments could be considered as multiple traits. This view permits treating the range of analyses for multiple environment trials as a continuum from a univariate approach assuming compound

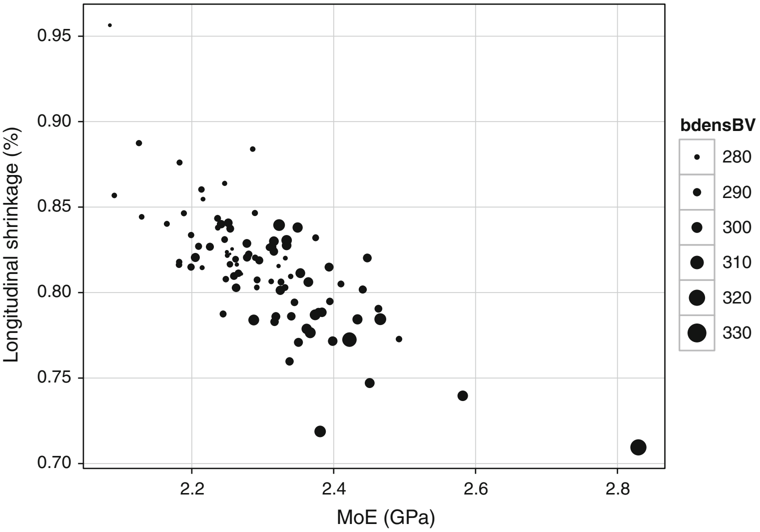

Fig. 1 Predicted breeding values for wood properties for parents of a radiata pine clonal seed orchard

symmetry (i.e. homogeneous variances and correlation) to an unstructured multivariate model (i.e. heterogeneous variances and correlations), affecting the accuracy of the predictions (r_{IH} in Eq. [2]). In a univariate approach we predict a single value across environments, which is adjusted by site differences; in contrast, in a multivariate approach we predict breeding values *for each* environment. The latter is consistent with treating environments as fixed effects in univariate analyses.

This expansion of analytic options has relied on the use of linear mixed models, which permit (1) accounting for sampling and randomization processes in progeny trials, and (2) modeling the covariance structures of the random effects (see Smith et al. 2005 for a review), in many cases relying on highly optimized software like ASReml (Gilmour et al. 2002). Using a multivariate approach often offers worthwhile insights on both degree of genetic control and across-site stability; however, increasing the number of environments (n) creates statistical and computational problems, as the number of covariance components to be estimated is n (n + 1), so there is a decreasing amount of data for each component (Table 2).

Often one can reduce the number of estimated parameters in multivariate analyses by exploiting features of the problem. For example, in the case of longitudinal analyses (when each tree is assessed multiple times at different ages; e.g. for height or ring-level wood properties) the order of the measurements creates patterns of variability, which in some cases—like an autoregressive process—require less than half of the parameters compared to the original unstructured genetic covariance matrix (e.g. Apiolaza and Garrick 2001a).

In the case of multiple environments some patterns are obvious; for example, residuals in one environment are independent of residuals in another one, as a tree can only be in a single site. A similar logic applies to experimental design features like replicates and plots. This makes blocked identity matrices (using a direct sum or product operation) the obvious choice for the covariance matrices of residuals and within-site factors. The situation is more complex when modeling genetic effects, as there is no obvious pattern to exploit in

Table 2 The number of variance components to be estimated in a multivariate linear model treating *n* different environments as different trait is n (n + 1)

Number of environments	Number of (co)variance components
2	3
4	10
10	55
20	210
50	1,275

the covariance structure. A relatively common approach used during the last decade has been to model genetic effects with a factor analytic (FA) decomposition (Smith et al. 2001, Thompson et al. 2003). An example of successful application is the genetic evaluation for some Australian crops (e.g. Kelly et al. 2007) and some tree breeding analyses (e.g. Costa e Silva et al. 2006; Hardner et al. 2010). Nevertheless, as previously pointed out, tree breeding evaluates many more genotypes than crop breeding and even using an FA decomposition of the genetic effects turns to be computationally too expensive. At this point it is possible to borrow an older approach from animal breeding: the reduced animal model (RAM, Quaas and Pollak 1980; Blair and Pollak 1984). RAM is useful when there is a large proportion of individuals that do not have their own progeny, so their individual breeding values are a function of their parental values and their own assessment. In 2011 Brian Cullis proposed to combine RAM and FA to produce a computationally feasible approach for multivariate tree breeding evaluation (Jefferson and Cullis 2012). This model is used for the annual NZRPBC genetic evaluation.

Breeders test genetic material in multiple environments and analyze the results with multivariate models because we suspect genotypes interact with (at least some of) the environments; that is, they display Genotype by Environment interaction (GxE). One extreme assumption when considering GxE interaction is that there is none whatsoever, so testing in any site will produce pretty much the same ranking. This is a tempting assumption because, if true, a breeder can run very cheap breeding and deployment programs. This was the default position for over 15 years in New Zealand, since the early 1990s. The other extreme assumption is that every environment is interacting significantly—rankings are not stable across any environments—and we require as many breeding and deployment programs as environments. This will likely make breeding financially unfeasible. Therefore, a practical solution will sit in between the two extremes, which makes necessary to collapse the results of a multivariate evaluation to a manageable number of environments. The current genetic evaluation of radiata pine in New Zealand uses over 70 environments, which are then collapsed using a modified version of cluster analysis. The number of breeding regions and the covariance structure used when collapsing sites into regions will affect both the accuracy of selection and selection intensity in Eq. [2]. At the moment, the resulting groups in New Zealand are being considered from the deployment point of view, but there is still a single breeding strategy. Explaining the patterns of interaction is still open to interpretation for several traits. For example, there are relatively clear latitudinal and altitudinal trends (most likely temperature is the underlying variable) for basic density (Apiolaza 2012). However, the situation for growth traits is, in general, much more complex and work by McDonald (2009) and Raymond (2011) most likely does not have environmental information at the right resolution to provide definitive answers. In addition, poor genetic connectedness between trials makes large-scale grouping of trials very difficult.

Final remarks

Breeding programs are sustainable only if they continue producing and, more importantly, deploying genetic gain. I have reviewed a number of changes to the methodologies used in genetic evaluation and the techniques to generate abundant phenotypic data for wood properties, relying on the breeder's equation to connect their effects.

When combining the implementation of breeding objectives involving multiple traits, the feasibility of the assessment of several wood quality traits and treating multiple sites as multiple traits we end up with large numbers of observations: around 80 sites for dbh, 20 sites for density and quality traits (stiffness, dimensional stability) in 2–3 sites and non-key traits in a similar number. Throw in a combination of half-sibs, full-sibs and clones in the evaluation, subsampling of traits, etc. and we have big system of equations to be solved.

Breeders need to maintain operational simplicity on the face of this statistical complexity. Large numbers of environments require collapsing into a much smaller number of breeding regions; repeated assessments of wood properties provide insight on the changes of wood quality with age, but we still want a single optimal selection age; models of the economic effects of breeding have to be simplified for implementation on the breeding program. That is, research allows exploring the complexity of trees, but we have to extract simple rules that can be translated into superior material deployed in plantations.

Despite all the progress, one of the big problems faced currently by breeding organizations is to demonstrate their 'value proposition' to industry members. That is, how much better off is industry by investing in breeding? At a basic level we often struggle with the way we conduct genetic testing, using single-tree plots (because of statistical considerations) but propagating specific families or clones at the stand-level. We know that superiority expressed at the individual-tree level has an imperfect correlation with stand-level performance (e.g. Vergara et al. 2004) but, particularly in New Zealand, there is little information on the strength of that correlation.

Some companies in New Zealand want to include genetic gain in their forest estate valuation. However, valuation experts will only consider growth and yield inventory plots as a valuation standard. For all the sophistication of new methodologies we have to still take care of genetic gain trials; seed mixes tend to be close to useless to demonstrate realized gain. Forest valuators will only take inventory plots representing the material being deployed.

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