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Heritability of growth strain in *Eucalyptus bosistoana*: a Bayesian approach with left-censored data[§]

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Abstract

Background: Narrow-sense heritabilities of the wood properties of 2-year-old *Eucalyptus bosistoana* F.Muell. were estimated from 623 stems.

Findings: Heritability estimates were calculated for the following: growth strain (0.63), density (0.54), diameter (0.76), volumetric shrinkage (0.29), acoustic velocity (0.97) and stiffness (0.82). A modified version of the splitting test for detecting growth strain is described. The modified rapid-testing procedure resulted in left-censored growth strain data, so a Bayesian approach was implemented to reduce errors associated with censored data sets.

Conclusions: Correlations between wood properties are presented and discussed, as well as trade-offs when shifting trait means by selective breeding.

Keywords: *Eucalyptus bosistoana*, Heritability, Growth strain, Wood properties

Findings

Introduction

The main use of plantation-grown *Eucalyptus* species is the production of biomass for the pulp and paper and bioenergy industries. These trees are fast growing and can potentially produce high-quality timber for appearance, structural and engineered wood products. Unfortunately, this potential is hindered by the frequent presence of large growth strains, which are associated with log-splitting, warp, collapse and brittle heart, imposing substantial costs on processing.[1]

A few technological mitigation strategies have been developed to reduce the incidence of wood defects caused by growth strain, but they are costly and only partially effective.[1] An alternative approach to the problem is to rely on the genetic control of the growth strain—shown in this article to be highly heritable—to select and grow individuals with low growth strain. However, measuring growth strains in large numbers of

trees (as needed for a successful breeding programme) has been difficult, time consuming and expensive until now. As an example, the largest reported studies to date assessed only 164 (Murphy et al. 2005) and 216 (Naranjo et al. 2012) trees.

The University of Canterbury has developed and implemented a rapid growth strain-testing procedure, based on the work by Chauhan and Entwistle (2010) and Entwistle et al. (2014). In order to minimise the time taken to measure the growth strain on each tree, the rapid-testing procedure does not account for negative values, where the wood in the centre of the stem is under tension rather than compression, assigning instead a zero that results in left-censored data sets.

Left-censored data are common in research areas where detection limits are high compared to the measured values, such as testing for the presence of drugs in an animal. There are many approaches to deal with censoring (Senn et al. 2012), and in this article, we use a Bayesian framework to impute the missing data from known data, reducing the error induced by zero inflation. A Bayesian approach makes it easier to include model complexity (e.g. censoring) while accounting for the hierarchical nature of the data. In addition, one can easily obtain complex distributions of functions of

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covariance components, like heritabilities, as a byproduct of the estimation process (Cappa and Cantet 2006). There are several examples of Bayesian applications in forest genetics, for example: univariate analysis of growth traits (Soria et al. 1998); multivariate analysis of growth traits (Cappa and Cantet 2006); and multivariate analysis of early wood properties (Apiolaza et al. 2011).

We ran a pilot study consisting of two *Eucalyptus bosistoana* F.Muell. progeny tests from both seed- and coppice-grown stems, which included 623 individual stems from 40 half-sibling families. Our estimates of narrow-sense heritability were obtained from left-censored growth strain data and other wood properties, utilising a Bayesian approach. These results were used to design a much larger evaluation of the *E. bosistoana* breeding population currently underway.

Materials and method

An *E. bosistoana* open-pollinated progeny trial was established at an irrigated nursery site in Harewood, Christchurch, New Zealand. The trial represented 40 families from two provenances, for a total of 423 seedlings planted into 100-L bags, which were coppiced after the first harvest, giving a total of 623 tested samples. Two separate plantings (or trial sections) occurred in 2010 and 2012. The 2010 families originated from South East Australia, were harvested and coppiced in 2012 and harvested again in December 2014. The 2012 families originated from higher elevation in New South Wales and were harvested in 2013 (these data were not included in the analysis, due to the magnitude of errors induced by small, malformed stems) and again in October 2015 (at age 2). All seedlings were established following a completely randomised design.

When harvested, each sample was processed for growth strain, volumetric shrinkage (displacement method, before and after drying), stem diameter (measured under bark using digital callipers), basic density (mass and displacement method) and dry acoustic velocity (resonance). Growth strain was measured using a modified version of the Chauhan and Entwistle (2010) and Entwistle et al. (2014) log-splitting methods. The newly developed "rapid splitting test" substantially reduces measurement time, enabling larger numbers of samples to be processed. The modified method involves stripping the bark and measuring the under-bark large-end diameter of a clear section of the stem, giving an overestimate of the average diameter used by Chauhan and Entwistle (2010). The sample is then cut lengthwise, with the slit length determined by the length of clear wood and diameter of the sample. The diameter and slit length are measured, recorded and the stem cut. The small end of the sample is left intact with the large end free to distort, which removes the need to

clamp the two halves together. Finally, the opening is measured and recorded. The calculation of strain is unchanged (with the exception that the average radius is now the large-end radius) from Chauhan and Entwistle (2010) and calculated using Eq. 1. It is important to note that the overestimate of radius slightly reduces the strain value but does so linearly over all samples.

$$Y_u = \frac{0.87\epsilon L^2}{R} \qquad (1)$$

where Y_u is the deflection, ϵ is the strain, L is the cut length and R is the big-end cross-section radius.

All specimens were grown on the same site; however, they were grown during different time periods which are confounded with the effect of the two provenances and hence are included as a trial effect. The tree effect accounts for the measurement unit, as the same trees were assessed as both seedlings and coppice.

The analyses used a Bayesian approach to estimate the posterior distributions for the heritability of the growth strain and other wood properties. We implemented a hierarchical model where y_{ijklm} follows a left-censored normal distribution $N(\omega_{ijklm}, \tau_{j|i})$ with predicted value ω_{ijklm} and a trial-dependent precision $\tau_{j|i}$. The precision (reciprocal variance) $\tau[x_1]$ for each trial was given a vague gamma prior $\Gamma(0.01, 0.01)$.

The predicted value for the ith assessment is modelled as a function of an overall intercept, the effect of the jth trial, kth coppicing level, lth family and mth tree (to account for repeated assessment pre- and post-coppicing):

$$\omega_{jklm|i} = \mu + \alpha[x_{1j|i}] + \beta[x_{2k|i}] + \gamma[x_{3l|i}] + \delta[x_{4m|i}] \qquad (2)$$

where x_1, x_2, x_3 and x_4 represent indicator variables for the levels of the factors.

The overall intercept (μ) and individual-level coefficients for coppicing (α_j) and site (β_k) were given vague normal prior distributions:

$$\begin{aligned} \mu &\sim N(0.5, 10^{-12}) \\ \alpha &\sim N(0.5, 10^{-12}) \\ \beta &\sim N(0.5, 10^{-12}) \end{aligned} \qquad (3)$$

The family (γ_l) and tree (δ_m) effects were assumed to come from normal distributions $N(0, \tau_f)$ and $N(0, \tau_t)$, with vague gamma priors $\tau_f \sim \Gamma(0.01, 0.01)$ and $\tau_t \sim \Gamma(0.01, 0.01)$, respectively. The statistical model is also presented graphically following Kruschke (2014) in Fig. 1.

Narrow-sense heritability at the trial level for all properties was calculated using Eq. 4. The constant of 2.5 used was suggested by Griffin and Cotterill (1988) due to the unknown proportions of selfing, full-siblings and
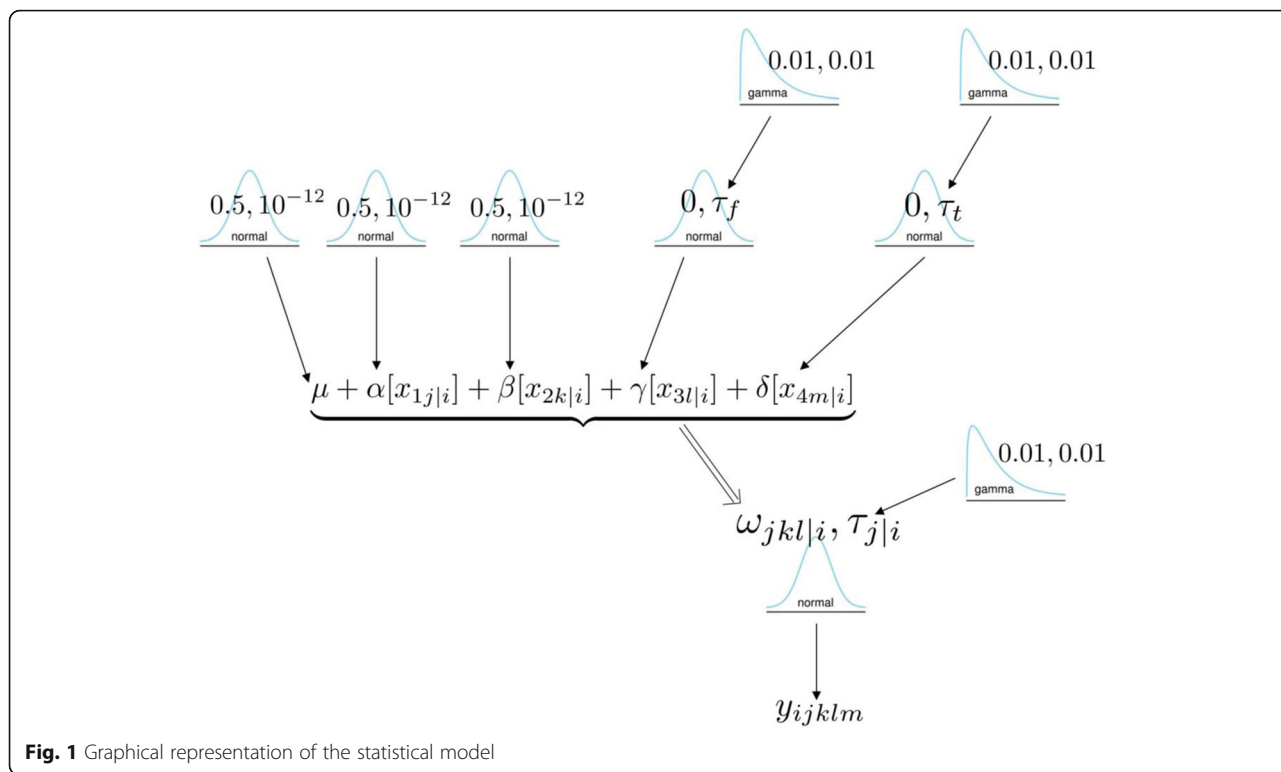
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Fig. 1 Graphical representation of the statistical model

half-siblings within the open-pollinated families (loosely referred to as half-sibling families in this article).

$$h^2 = \frac{2.5 \times \sigma_f^2}{\sigma_f^2 + \sigma_t^2 + \sigma^2} \tag{4}$$

where the σ^2 variances were obtained as the reciprocal of the precisions (τ) mentioned in the model description.

All the models were fitted using rjags, an R (R Core Team 2016) interface to JAGS (Just Another Gibbs Sampler (Plummer 2015)) which uses Gibbs Sampling to estimate the marginal posterior distributions for the parameters of interest. Approximately 35% of the strain data was left-censored, and missing values due to censoring were imputed by JAGS as a random value below the limit of detection (using the function dinterval; for details, see Lunn et al. 2013) but above −1.5 (equivalent to a negative strain of 1500 micro-strains). We used a family model instead of an animal model as, for the purposes of a simple one-generation pedigree, the models are equivalent (sensu identical expected values and variance (Henderson 1985)), while the family model is much less computationally intensive. The R/JAGS code is available as supplementary material.

Results and discussion

While the study was larger than preceding attempts, the sample number was still small when considering heritability calculations. The paucity of data resulted in wide 95% credible intervals (Table 1), which require more samples to tighten. The heritability indicates that growth strain can be influenced by breeding and are in line with the 0.32 reported by Murphy et al. (2005) but are significantly higher than the 0.02 value reported by Naranjoi et al. (2012). Density, diameter at age 2 (growth), volumetric shrinkage, acoustic velocity and stiffness all have significantly large heritability, suggesting that breeding for these traits is achievable. The heritabilities are similar to those reported for other eucalypt species

Table 1 Narrow-sense heritability of measured wood properties, calculated as per Eq. 1

Property	Heritability	95% credible regions
Strain	0.63	0.28–0.98
Density	0.54	0.11–0.97
Diameter	0.76	0.42–1.0
Volumetric shrinkage	0.29	0.13–0.45
Acoustic velocity	0.97	0.60–1.0
Stiffness	0.82	0.48–1.0

(Hung et al. 2014; Hein et al. 2012; Blackburn et al. 2010; Blackburn et al. 2014; Hamilton et al. 2008).

Wood processors pay premiums for stable and stiff timber, while forest growers often prefer to have fast-growing trees as to shorten rotation lengths increasing profitability. The preferences are not always aligned, particularly within wood properties. Stiffness, used for grading logs, is positively correlated with growth strain with a correlation of 0.61, an unfavourable correlation requiring a trade-off between the two traits. While zero growth strain is desirable to be economically viable to process, some unknown maximum value below which little economic loss is experienced exists. Stiffness is already used for log grades, and structural timber in New Zealand requires 8 GPa (Buchanan et al. 2005). To meet these stiffness grades at age 2, some compromise with the level of growth strain in the stems is needed.

All stems measured within each family were averaged to give correlations between properties at the family level (Table 2). A very strong positive relationship is evident between growth strain and stiffness at the family level. This means that reducing growth strain will require reducing wood stiffness at the population level. On the positive side, some *Eucalyptus* species have such high wood stiffness that a reduction would not have practical implications from a wood-processing viewpoint.

We have made some alterations to the original Chauhan and Entwistle method to convert it from a research to an operational technique, but the effect of these changes should be negligible. The linear error introduced by using the large-end diameter rather than the average diameter of the stem will result in a slight reduction of all reported strains over the original method. Leaving the small end intact (that is, not cutting it as in the original splitting test) does not release as much strain as the original method, again lowering the growth strain value over all samples, however, given that a single measurement is now taken, rather than two, measurement error is reduced. Further work is required to determine the accuracy and precision of both tests and to separate natural within-stem variability from variability between stems.

Heritabilities presented here are for *E. bosistana* at age 2; at later ages, these heritabilities may change. From a breeding perspective, these values are from a wild, unimproved population, and hence, there is considerably larger variability than in older breeding programmes. Even if heritability reduces with time, by removing the worst performing individuals from the breeding population going forward, budgets can be more efficiently spent only assessing the trees with a higher chance of producing a premium quality product in the longer term, rather than substantially more expensive breeding programmes.

Genetic gain per unit of time for a breeding programme depends on four elements: variability for the trait under selection, selection intensity (proportion of individuals selected), accuracy of prediction (proportional to heritability) and time required for turning a breeding cycle. New phenotyping techniques, like rapid growth strain-testing, increase selection intensity (as more trees are able to be assessed) and reduce selection time (as trees can be less than 2 years old when tested). As far as we are aware, variability for early wood properties is not smaller than at typical selection age and the degree of genetic control is also similar (Apiolaza et al. 2011).

Conclusion
The modified rapid-screening test for growth strain captured population variability in *E. bosistoana* which is under genetic control. Narrow-sense heritability of the growth strain was estimated to be 0.63, with a 0.28–0.98 95% credible interval. This suggests that a breeding programme could effectively reduce growth strain in the population.

Heritabilities for wood density, stem diameter, volumetric shrinkage, acoustic velocity and wood stiffness are also presented. All of them are within the range described in previous publications. A strong, unfavourable correlation between growth strain and stiffness indicates that tree selection will have to deal with a trade-off between those traits when breeding for overall wood quality in *E. bosistoana*.

Table 2 Pearson correlation between average family values for measured wood properties

	Density	Volumetric shrinkage	Acoustic velocity	Stiffness	Strain
Diameter	−0.17 [−0.46, 0.15]	−0.43 [−0.66, 0.14]	0.27 [−0.04, 0.54]	0.25 [−0.07, 0.52]	0.19 [−0.12, 0.48]
Density		0.27 [−0.04, 0.54]	−0.20 [−0.48, 0.11]	0.01 [−0.30, 0.32]	−0.12 [−0.41, 0.20]
Volumetric shrinkage			−0.59 [−0.76, −0.34]	−0.55 [−0.73, −0.28]	−0.47 [−0.68, −0.17]
Acoustic velocity				0.98 [0.95, 0.99]	0.80 [0.65, 0.89]
Stiffness					0.79 [0.64, 0.88]

95% confidence intervals in brackets

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This pilot study demonstrated the feasibility of implementing rapid growth strain-screening at a speed and reliability that would scale up to an operational breeding programme.

Endnote

[1]Yamamoto, H. (2007). *Tree growth stress and its related problems. Compromised wood workshop.* Canterbury, New Zealand: University of Canterbury.

Authors' contributions
ND designed and carried out the experimental work, data analysis and paper preparation. LA handled data analysis and paper preparation. MS designed and carried out the experimental work. All authors read and approved the final manuscript.

Competing interests
The authors declare that they have no competing interests.

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