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5 Incorporating wood quality and deployment traits in *Eucalyptus globulus* and *Eucalyptus nitens*

Carolyn A. Raymond[1,2] and Luis A. Apiolaza[2,3,*]
[1]State Forests of NSW, Technology and Services (R&D, PO Box 46, Tumut NSW 2720 Australia; [2]CRC for Sustainable Production Forestry, GPO Box 252-12, Hobart Tas 7001 Australia; [3]Forestry Tasmania, GPO Box 207, Hobart Tas 7001, Australia
*Email: Luis.Apiolaza@forestrytas.com.au

Abstract

Breeding of E. globulus and E. nitens has evolved from focusing mostly on growth and survival to stressing the importance of wood quality. This shift attempts to align breeding programs with the economic objectives of forest companies. The past decade has seen the development of economic models to formalize breeding objectives, sampling strategies that allow the study of the genetic architecture of wood properties and the popularization of BLUP for genetic evaluation. Future research will put a strong emphasis on wood quality traits, especially for solid wood products. It will also need to deal with compatibility between alternative objectives and will revisit the role of propagation in breeding and deployment.

Correspondence/Reprint request: Dr. Carolyn A. Raymond, State Forests of NSW, Technology and Services, (R&D, PO Box 46 Tumut NSW 2720, Australia. E-mail: carolynr@sf.nsw.gov.au

Introduction

Domestication of eucalypts started over one hundred and fifty years ago [1;2]; however, breeding of eucalypts for traits of commercial importance is a relatively recent development and is linked to the increase in establishment of plantations both within Australia and overseas. Initially, plantations were established with seed collected from wild populations but it soon became evident that considerable variation existed within each species for traits of economic importance such as survival, growth rate and stem form. Domestication and breeding of eucalypts as crop plants for wood production commenced with the aim of improving the quality of seed and subsequent plantations for traits relating to the quantity and quality of wood produced.

Early work concentrated on establishing species and provenance trials to determine suitability of genotypes for particular environments, the degree of variation within each species and provenance by environment interactions. Based on the results from these trials, the most promising species and provenances were selected, extensive seed collections of individual families were undertaken and progeny trials established across a range of sites. These progeny trials formed the base breeding populations for each species and allowed for the estimation of genetic parameters for a range of traits, determination of the magnitude and practical importance of genotype by environment interactions and development of breeding programs. Detailed descriptions of the historical development of the early breeding programs for a range of species are provided in [3].

As tree breeding work progressed, the range of traits assessed increased. Initially, most attention was focused on early growth and survival as these directly influenced the success of the plantation. As the trees grew, other traits relating to tree shape and size, such as stem straightness and branching quality, were included. Following this, more attention was paid to what may be called risk traits, those relating to the ability of genotypes to survive environmental threats such as winter frosts, browsing animals or insects, salinity or drought. Risk traits have attached both a probability of occurrence and a probability of severity. Later still, attention turned to the quality traits.

The need to align breeding programs with the economic objectives of forest companies has stimulated the formalization of breeding objectives. This need has also translated in a larger emphasis on wood properties and their sampling, because they determine the suitability and economic viability of a range of end products.

Limited work on assessing wood quality traits in breeding programs had been undertaken prior to the 1990s for several reasons. In tree breeding programs there is a requirement to assess large numbers of individual trees and families for traits of economic importance. However, traditional methods of assessment for wood quality traits (tree discs) are expensive and restrict the numbers of samples that can be processed. In addition, traditional assessment methods involve the destruction of the sampled trees. For species that do not reliably propagate vegetatively, such as *E. globulus* and *E. nitens*, destructive sampling will result in the loss of valuable genotypes for breeding.

In addition to wood quality, there are other traits that, although with no direct value by themselves, may affect the outcome of a breeding program. The success of breeding relies on the ability to transfer gains from the breeding population to the operational plantations (see, for example, [4]). Thus, there is a direct relationship between the "deployment factor" of genetic material (rate for bulking-up selected material) and the selection pressure possible to apply in the deployment population. While from the uniformity and selection intensity viewpoints clonal deployment is appealing, rooting ability is poor for several temperate eucalypt species (including *E. globulus* and *E. nitens*). Another deployment issue is the coppicing ability of trees. Coppicing can be an appealing silvicultural option, specially for pulp production in marginal sites.

Priority areas for research in selection of eucalypts wood quality over the past decade have been: (a) developing breeding objectives for different production systems; (b) developing non-destructive sampling methods for wood properties; (c) evaluating alternative surrogate criteria or methods for use as indicators for traits that are more expensive to assess; and (d) assessing the degree and structure of genetic variation for these traits. While the potential number of traits to improve is quite large, we will focus the discussion into wood quality and deployment traits.

Breeding objectives, markets and products

Basics of breeding objectives

The aim of tree breeding programs is to increase the competitiveness of forestry organizations, usually through profit maximization. Profit is often a function of multiple traits, and is improved by way of increased income, reduction of costs, or a combination of both. A simple definition of breeding objective is the answer to the question "what are we breeding for?" In more formal terms, a breeding objective is a mathematical function of breeding values (**a**) and economic weights (**w**):

$$H = f(\mathbf{a}, \mathbf{w})$$

This function is often expressed in linear terms; thus $H = a_1 w_1 + a_2 w_2 + \ldots + a_n w_n$, where the subindex refers to each of the traits included in the objective. In this way, the definition of the objective encompasses two problems: firstly, what are the biological traits that drive the production system influencing profit and, secondly, what is the relative importance of these traits.

While breeding objectives theory is straightforward and has been available since the work of Smith [5] and Hazel [6], tree breeders side-stepped their definition for several decades, preferring instead to use non-economic alternatives (e.g., [7]). Although there were several attempts to value the contribution of breeding to industry profit (e.g., [8]), it was not until the work of Borralho et al. [9] that tree breeders formalized the objective in economic terms. Borralho et al. [9] modelled a vertically integrated forest growing and pulp processing business. Subsequently, Greaves et al. [10] included stem form and made improvements to the unbleached kraft pulp component. When extending these models to more complex industrial systems (see Greaves [11] and Apiolaza and Garrick [12] for examples in *Pinus radiata*) it is evident that the number of traits influencing profit increases.

In forestry, most of the traits will be expressed at harvest age, with the exception of traits affecting mid-rotation income (e.g., thinning yield). However, breeding programs often rely on early assessments of progeny tests, usually less than one third of rotation age. In addition, many traits (specially wood quality ones) are too expensive and time consuming to assess. A common solution is to assess surrogate characters, nominated selection criteria, which are genetically correlated with the objective traits and that are easily included as part of the evaluation protocol of trials.

Most advanced breeding programs make use of BLUP (Best Linear Unbiased Prediction, [12]) for the prediction of breeding values for selection criteria. However, the aim of breeding is to maximise profit for a linear function of the objective traits, not the selection criteria. This optimisation is achieved using an index $I = b_1 a_{s1} + b_2 a_{s2} + ... + b_m a_{sm}$, where a_s refers to breeding values for selection criteria, and the index coefficients (b) maximise the association between the index and the breeding objective. Index coefficients are calculated using $\mathbf{b} = \mathbf{G}_{ss}^{-1} \mathbf{G}_{so} \mathbf{w}$; thus, they take into account: i) the genetic association between selection criteria ($\mathbf{G}_{ss}$), ii) the genetic association between criteria and objective traits ($\mathbf{G}_{so}$), and iii) the relative economic importance of objective traits (**w**) (see [13] for details). Once the objective traits and the selection criteria have been identified, the next step is to determine the genetic parameters and geographic structure of the traits.

The traits included in the objective will depend on the system being modelled (e.g. forest grower, or integrated grower and processor), while the economic weights depend on the cost-income structure, which is particular to each organization. Therefore, we will only discuss issues related to traits and selection criteria but not economic weights.

Markets, products and economic drivers

Currently, the major market for eucalypt wood is the pulp and paper industry with the major product classes being newsprint from cold soda pulping or fine writing and photocopy paper from kraft pulping. In recent years, there has been increasing interest in using plantation eucalypts for producing sawn timber, veneers and reconstituted wood products.

Breeding objectives have been developed for unbleached kraft pulp [10] and for newsprint [14] but not for solid or reconstituted wood products. Table 1 presents a summary of the economic drivers, in addition to volume growth, for a range of markets and products (from [10;14;15]).

Table 1. Markets, products and economic drivers

Market	Product class	Products	Economic drivers
Pulp and paper	Kraft pulp	Photocopy paper Fine writing paper	Chemical consumption, pulp yield, paper quality
	Mechanical pulp	Newsprint	Energy consumption, paper quality
Solid timber	Sawn timber	Furniture Flooring Structural	Recovery (green and dry), grade, drying cost, drying degrade, sawing productivity
Composites	Veneers	Furniture Laminated veneer lumber	Recovery, grade, degrade during drying, glue usage
	Composites	Medium density fibre board Oriented strand board	Resin/glue usage, energy consumption

Once the economic drivers are defined, the next step is to determine their relationship to desirable tree, wood, processing and product characteristics so that the key wood properties may be defined for each product. Table 2 presents a summary of our current perceptions of which wood properties should be assessed for a range of products [10;15;16]

Table 2. Key wood properties for a range of product classes

Pulp and paper	Sawn timber	Composites
Wood properties	Wood properties	Wood properties
Basic density	Basic density and	Basic density
Pulp yield / cellulose	gradient	Lignin content
content	Microfibril angle	Extractives content
Fibre length		Cellulose content
	Shrinkage and collapse	Product properties
	Tension wood	Strength and stiffness
	Knot size	Durability
	Incidence of decay,	Gluability
	spiral grain and end	Hardness
	splits	
	Product properties	
	Strength and stiffness	
	Dimensional stability	
	Lack of internal	
	checking, crook and bow	

The traits included in Table 2 require the breeder to prioritise the research efforts, and decide on the number of traits included in the objective. Including all traits will be more costly, while the information available for some traits may be limited, or the payment system in the industry may not include a premium for their improvement. Alternatively, leaving out important traits will hold back the breeding efforts.

Assessment issues for selection criteria

Non-destructive sampling

Estimation of genetic parameters and breeding values always involve population sampling. While the sample for growth and form traits often includes all trees of a progeny trial, other traits (e.g., wood properties) are too expensive to evaluate on an individual tree basis, making subsampling a necessity [17]. The medium to high heritability of wood properties (see Figure 1) allows the judicial use of relatively small number of individuals to estimate genetic parameters. In addition, the use of non-destructive techniques is preferable, because it permits further use of the trees in the breeding program.

In the early 1990s a motor-driven coring system for removing 12 mm wood cores from standing trees was released onto the market [18]. This development made it feasible to non-destructively sample the relatively large numbers of trees required for assessing wood properties in tree breeding trials. However, little information was available, for any wood property, to indicate where the samples should be taken from to obtain a representative estimate of the whole tree wood properties.

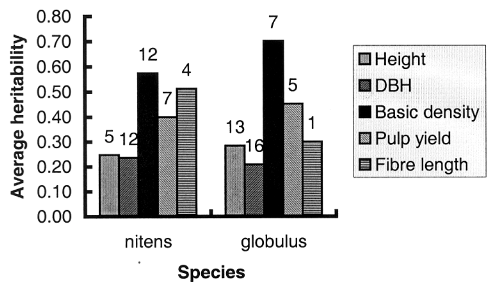

Figure 1. Summary of published within provenance heritability estimates for a range of traits in *E. nitens* and *E. globulus*. Bars represent mean of published estimates and the number of estimates included is given above each bar [38].

Non-destructive sampling methods for wood properties must be developed based on knowledge of patterns of variation within the tree for the property of interest [18]. When developing an effective and efficient sampling strategy several key questions must be addressed, including: how does the wood property change up the stem and is this pattern consistent across sites and ages, what is the best height to remove a core, which side of the tree should be sampled, how well will the core predict the whole tree value, how many trees should be sampled and should trees be stratified based on tree size? As the sampling strategy will be applied to a large number of trees it has to be rapid and easy to use in the field and result in minimal damage to the tree.

Each of the above questions was addressed in a large study on sampling methods for basic density, fibre length, fibre coarseness and pulp yield in *E. globulus* and *E. nitens* [19;20;21]. Ten trees of each species were sampled from each of five sites, sectioned and optimum sampling methods determined – see Raymond et al. [21] for a summary of their sampling recommendations.

Assessment techniques

The search for cost-effective selection criteria for assessing wood properties in breeding programs has been a major field of research over the last 10 years. Much interest centred on evaluating alternatives to kraft pulp yield, including using near infrared reflectance analysis [21;22;23], raman spectroscophy [24] and secondary standards, such as other chemical wood components, including hot water extractives content [25] or cellulose content [23]. In recent years there has been a large increase in interest in the assessment of solid wood properties. Current information on available assessment methods is summarised below in Table 3.

Of the alternative methods evaluated for assessing kraft pulp yield, hot water extractives content cannot be recommended [25] due to the low correlation with pulp yield. However, cellulose content of wood, as measured using an acid diglyme digest [26], is strongly correlated with pulp yield in temperate eucalypts [27;28] as shown in Figure 2.

While using this method increases the numbers of samples that may be processed, it still relies on wet chemistry, which can be time consuming and costly. A large increase in the numbers of samples processed would be possible if an indirect method, such as use of near infrared reflectance (NIR) analysis or raman spectroscopy, could be used for

Table 3. Methods available for assessing a range of wood properties, together with whether the method uses core samples and can be used for non-destructive testing

	Assessment method	Core sample?	Non-destructive?
Basic density	Gravimetric assessment Pilodyn (indirect assessment)	✓	✓
Density variation Density gradient	X-ray densitometry	✓	✓
Microfibril angle	X-ray diffraction Confocal microscopy	✓	✓
Pulp yield	Digestion of wood chips to given residual lignin level		
Cellulose content Lignin content Extractives	Chemical analysis of ground wood Near infrared reflectance analysis Raman spectroscophy	✓	✓
Fibre length	Optical measurement of separated fibres	✓	✓
Growth Stresses	Displacement of markers after release of stress		✓
Modulus of Elasticity	Mechanical testing of boards or clear sections Acoustic/stress wave Prediction from SilviScan based on density and microfibril angle variation	✓	✓
Shrinkage	Measurement of green and dry boards		
Tension Wood	Histological assessment		
Incidence and extent of decay	Requires tree to be felled and sectioned unless decay is sufficiently severe for cell breakdown to occur. If so then timing of stress wave transmission or a Resistograph may be used for non-destructive assessment		
Knot size	Measurement of branch size and incidence		✓

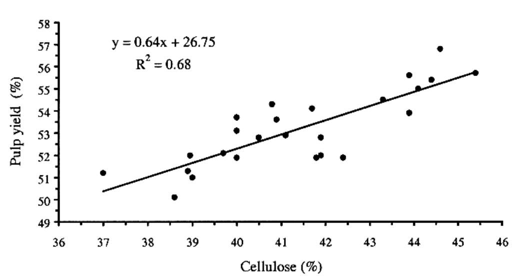

Figure 2. Relationship between cellulose content of cores at 0.9 m height and whole tree pulp yield at kappa 18 for 14 year old *E. nitens* [28].

prediction of kraft pulp yield or cellulose content. For these methods the wood sample is ground to produce wood meal, which is then measured in a spectrophotometer. The analyses rely on developing a calibration that relates the spectra of a large number of samples to their known chemical constitution, for example pulp yield or cellulose content. This calibration is then used to predict the pulp yield or cellulose content of further samples based on their NIR spectrum. It is implicit in this technique that the "training" sets on which the calibrations are based contain the whole range of variation in the samples to be analysed. NIR analysis has recently been used to predict pulp yield [29;30;31] and cellulose content [29;32;23]. Raman spectroscopy has also been used for prediction of wood constituents, including holocellulose, α-cellulose, lignin and extractives [24].

Alternative assessment methods for solid wood products have concentrated on assessment of peripheral growth stress as an alternative to end splitting or board deflection during sawing; using acoustic methods for assessing stiffness; and alternatives for assessing drying degrade (shrinkage and collapse). For growth stresses, non-destructive sampling techniques are available [33;34] but it is unclear whether these techniques, as currently applied around breast height in standing trees, are actually representative of the whole tree values for the wood property in question. Use of acoustics techniques (stress or sound wave transmission) for assessing stiffness of sawn timber is a growing area of research, which appears promising. Assessment of density variation, density gradient and microfibril angle are now possible using X-ray densitometry and analysis of diffraction patterns. For example, SilviScan-2 [18] generates radial profiles of air-dry density and microfibril angle.

Genetic variation

There is substantial genetic variation with a geographic structure for many traits of *E. globulus* and *E. nitens* [35;36], and wood quality traits would not be an exception. Nevertheless, for many wood quality traits there is still little or no information available about the degree of genetic variation or the heritability of the trait. Most data is available for the easier to measure traits, such as basic density. The limited data available indicates that the wood properties generally exhibit different patterns of genetic variation and much higher heritabilities (after provenance effects are removed) than those found for other traits (Figure 1). For example, a recent large genotype by environment interaction study in *E. globulus* [37;22] found very different patterns of genetic variation for diameter, wood density, and pulp yield, predicted using near infrared reflectance analysis. For diameter there was relatively little difference amongst the provenances and a low heritability (h^2 of 0.16 to 0.33). For pulp yield, the provenance differences were small but the heritabilities moderate (h^2 of 0.33 to 0.58). In contrast, wood density had very large provenance differences together with high heritability (h^2 of 0.67 to 1, Figure 3). Genotype by environment interactions were evident for all traits but without practical importance for operational breeding programs.

One important issue when designing a breeding strategy is the relationship between tree growth rate and wood quality. Many breeding programs have based their selection in early generations predominantly on growth and survival, without considering wood quality. For most wood properties there is little or no information about the relationship with tree growth. Most data is available for tree diameter and basic density, where

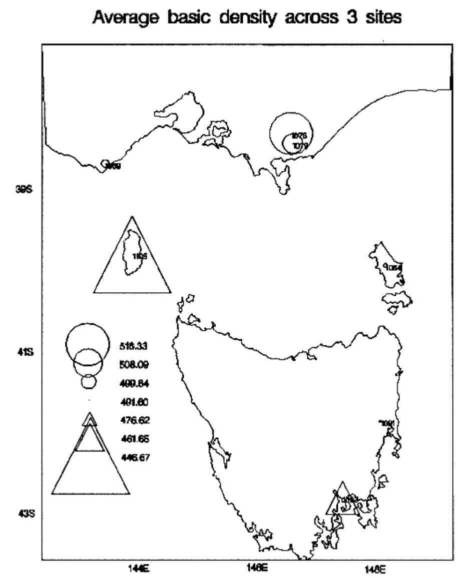

Figure 3. Average basic density (kg/m^3) across 3 sites for seven subraces [37].

published estimates for genetic correlations are variable but often close to zero, and there is no evidence for a strong negative relationship. These two traits appear to be largely independent and thus may be improved simultaneously.

Alternative breeding objective traits

While this chapter emphasises the role of wood quality, there are other traits that can have a large impact on the amount of gain delivered by the breeding program. For instance, deployment traits like rooting ability directly affect the selection intensity applied in the deployment population [39].

In principle, there are at least two options to deal with propagation problems: tandem selection for deployment and including propagation ability as a breeding trait. The former involves ranking the trees for genetic-economic value in a first stage, and then screen the trees for propagation ability. Only the trees with propagation ability over a threshold (defined on terms of economic feasibility) are used for deployment. The later option implies expanding the breeding objective to include propagation ability.

Figure 4 shows a simulation of the effect on value of selected trees of the correlation between a breeding objective (modified from [10]) and propagation ability. It is clear that larger requirements for minimum propagation ability lead to larger losses in the breeding objective. While there is some information on the degree of genetic control of vegetative propagation in *E. globulus* and *E. nitens* (e.g. [40;41]), there is only anecdotal information for the genetic correlation between propagation and productive traits. Here we simulated a range of correlations, but it is obvious that the effect of tandem selection will most of the time be detrimental in terms of deployed gain from the breeding program. For instance, for a 75% minimum propagation, any degree of negative correlation will lead to propagated trees with economic value under the population average.

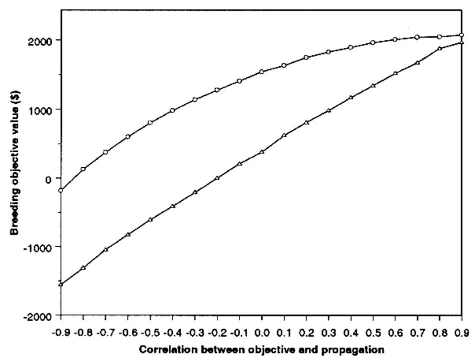

Figure 4. Effect of correlation between propagation ability and breeding objective on the population mean ($) deployed to the field, considering two minimum propagation thresholds: 50% (—o—) and 75% (—Δ—).

Another trait that is receiving increasing attention is coppicing ability (e.g., [42]). This trait presents moderate heritability (h^2 ~ 0.15), but there is plenty of variation between subraces in the number of coppices per stem. In addition, genetic correlations between coppicing and growth traits are positive, making the trait compatible with current breeding objectives.

Challenges for the future

Several areas that offer significant challenges for the future development of breeding strategies for the improvement of eucalypts are discussed below (from [38]):

1.) Breeding objectives for products other than pulp. Development of breeding objectives relies on determining the relationships between end product properties and tree and wood properties. Such information is currently limited but is essential to allow identification of key traits and for developing economic weights.
2.) Determining compatibility of alternative breeding objectives, markets and products. At present there is a degree of uncertainty about the proposed market for many eucalypt plantations and, almost certainly, markets will change and new markets will emerge. One important question is whether breeding for the ideal wood properties for one product or market will produce a log that is suitable for a competing market. Are the desired wood properties compatible for the different alternative markets? A related question is whether to breed for a specific market or to produce a "general-purpose" tree that may be suitable for a range of markets?
3.) Reliable genetic parameter estimates for expensive or difficult traits. Development of a breeding strategy relies on good estimates of genetic parameters. For the more expensive or difficult to measure traits, obtaining parameter estimates based on a sufficiently large sample size is extremely expensive. One alternative may be to determine the phenotypic correlations between the indicator and desired traits and then obtain parameter estimates for indicator traits.
4.) Inclusion of multiple products and traits in a breeding program. For any product class, there is more than one wood property considered to be important. If it is

desired to breed for multiple products, the problem is magnified, particularly if there are adverse genetic correlations between the traits.

5.) Allocation of assessment resources. The issue of how to best use limited resources for assessing the wood properties on large numbers of trees is an important issue. Alternatives include prioritising the traits for assessment, subsampling or only testing those trees considered to be elite based on other desired traits, such as tree growth rate. However, if only the elite trees are tested, the genetic parameter estimates obtained may be biased and not reflect the true values for the whole population.

6.) Consideration of the effect of propagation traits on the deployment strategy. There might be a need for including propagation in the objective. Some pending questions are: What is the correlation of deployment traits with other traits in the objective?, What is the economic impact of rooting ability? and do we need to breed for these traits?

7.) Incorporation of quantitative trait loci and marker based selection. One important question to be resolved is how to incorporate these technologies into a breeding program in a cost-effective manner.

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