Selection of *Corymbia citriodora* for pulp productivity

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**Abstract**

Evaluation of a series of spotted gum (*Corymbia citriodora*) progeny trials, established in the subtropical region of Queensland, Australia, was undertaken to provide information for the development of advanced generation breeding populations suitable for pulp production. Measurements of growth at two ages were combined with assessments of wood density and pulp yield from a selected sample of provenances to provide comparisons between provenances, to generate genetic parameter estimates and to predict genetic gain potential. While growth at this age was moderate relative to other eucalypts the near infrared predictions of average wood density of 756 kg/m³ and pulp yield of 55% indicate the species has considerable potential as a pulpwood crop. A pulp productivity breeding objective was used to identify production populations using a range of selection trait weightings to determine potential genetic gain for pulp productivity. Genetic parameters indicated: 1) levels of genetic control were moderate for all traits and higher for wood property traits, 2) genetic improvements could be achieved by selection among and within provenances with greater levels of improvement available from selection within populations, 3) genotype by environment interactions were negligible, 4) genetic correlations between traits were favourable, and 5) selection of volume production alone would maximise improvements in pulp productivity.

**Keywords**

*Corymbia citriodora* subsp *variegata*, Genetic parameters, Wood quality, Index selection, Subtropics
Introduction

Natural hardwood forests in the subtropics of eastern Australia have provided a range of wood products for many decades. These forests have been utilised by the forest products industry for many years, however various government policies have reduced the areas available for harvesting forest products. Plantation development programs have since been undertaken to provide an alternative source of forest products. One of the spotted gums, *Corymbia citriodora* ssp. *variegata* (McDonald and Bean 2000) or CCV, has consistently performed well in a range of taxa comparison trials (Lee et al. 2010, Lee et al. 2011, Listyanto et al. 2010). Much of the existing 18,000 hectares of spotted gum plantations established within the subtropics of Australia has been managed for solid wood products (Lee 2007), the high wood density and pulp yield of spotted gum species indicates these plantations may also be well suited for pulpwood production (Clark and Hicks 2003, Gardner et al. 2007).

Selection of individuals for inclusion in seed production orchards or advanced generation breeding populations requires consideration of the range of traits that contribute to the profitability of a species. For the improvement of a species that may be utilised for pulp production, the composite trait of pulp productivity can be calculated directly as the product of three selection traits: volume, wood density and pulp yield. Volume has been extensively studied in progeny trials for a range of tree species, but the wood quality traits of density and pulp yield are more difficult to quantify and their genetic control is typically poorly understood in most tree improvement programs. Near infrared (NIR) spectroscopy has been utilised in a number of species to provide a rapid and inexpensive means of assessing wood quality compared to standard laboratory techniques (Downes et al. 2009). The utilisation of NIR to evaluate the large number of individuals that are required to obtain estimates of genetic parameters has been well documented in the literature (Costa et al. 2009, Stackpole et al. 2010).

This study firstly compares volume production among CCV provenances evaluated in a set of three progeny trials established with seedlings of open pollinated families collected from across the species’ native range in eastern Australia. This is followed by an examination of pulp productivity traits (growth, wood density and Kraft pulp yield) undertaken using families selected to represent a breeding population from a restricted sample of provenances surrounding the Gympie region in order to provide estimates of genetic parameters and predictions of genetic merit. Finally, a deterministic Monte Carlo simulation is used to demonstrate the impact of different selection trait weightings on the level of genetic gain in pulp productivity that may be achieved in subsequent populations based upon selections made from the sampled populations.

Materials and Methods

Three pedigreed populations of CCV were established in open pollinated progeny trials, established using a randomised incomplete-block trial designs as a part of the...
Queensland state government’s tree improvement program (Table 1). Each tree can be traced back to an individual mother tree and provenance within natural stands. The trials differ in the representation of genetic material (families within provenance), incomplete block size and in the number of individuals established in each family line-plot. These trials were managed to convert the progeny trials into seedling seed orchards by removing inferior individuals within multiple-tree plots of each family to rapidly provide a source of improved germplasm for use in plantation establishment.

**Plant materials, genetic tests and assessments**

Extensive natural forests of CCV are found throughout the subtropics of eastern Australia in areas where frosts are light and soils are well drained. Phenotypic selections of large individuals with good form and a seed crop were identified throughout the natural range and open pollinated seed were collected from locations detailed in Figure 1. A description of the early performance and genetic connectivity within these trials has been provided by Brawner et al. (2011). For the purposes of this study, three of the seven available CCV progeny trials (Figure 1) were selected for more detailed examination (Table 1). Families were selected from the geographically narrow sample of populations in the Gympie area for two reasons; 1) production populations have been derived from these sources as they have been shown to be reliable and possess good tolerance to Quambalaria shoot blight across many provenance trials, 2) population structure was undesirable for an association genetics study that also used wood quality data.

**Figure 1 – Locations of seed collected for inclusion in the Corymbia...**

**Table 1 - Description of progeny trials and assessments used to...**

All stems were sampled for diameter at breast height (DBH) and total height at various ages during the course of the field trials. Total height and DBH were used to estimate total tree volume (m$^3$) using a generic conical volume equation ($\frac{1}{3} \times DBH^2 \times \text{Height}$). There was no adjustment of taper or bark thickness differences between populations (Dieters and Brawner 2007). A pair of growth assessments was selected to represent volume production at two points in the life of each trial with two of the three trials measured before and after thinning (Table 1). The average times from trial establishment to the early and later assessment were 37 and 60 months and these traits are hereafter referred to as ‘3-year volume’ and ‘5-year volume’. Wood samples were taken from trial 451C, 451D and 451G at 134, 118 and 95 months after planting respectively. The wood samples were sifted from swarf (shavings or sawdust <1mm) that was produced by drilling into stems, at breast height (~1.3 m), with a 16mm spade bit to a depth of approximately 50 mm following the removal of bark.

Population genetic structure was purposefully avoided to allow for a separate genetic association study designed to link single nucleotide polymorphisms with phenotypic traits. Consequently, the wood quality of families from a geographically narrow range
of provenances in the Gympie region (Table 2) was evaluated within these progeny trials using 12, 7, 17, 25, 150 families that represented the provenances of Brooyar, Curra, Home, Wolvi and Woondum, respectively (Figure 1). All available individuals within these families were sampled for wood quality traits across the trials. While the experiment-wise connectivity of 78 families represented on at least two sites is sufficient for the estimation of population wide genetic parameters for stability, this significant level of imbalance in family representation across the three trials led to the exclusion of any inferences on the suitability of a specific family for a specific trial site. As well, imbalance in population representation was evident with a large proportion of the families originating from the Woondum provenance due to this population’s superiority for disease tolerance and associated greater growth rates in other taxa trials (Dickinson et al. 2004). Within the 211 families sampled for wood properties, wood samples were collected from an average of 6.7 stems per family (standard deviation of 2.8, minimum of 3, maximum of 16 trees per family) and scanned with a near infrared spectrometer.

Near Infrared Spectroscopy

Near infrared spectra were acquired on individual samples presented as fines (<1mm) sifted from the breast height wood swarf. Prior work on sampling protocols (data not presented) had determined that consistently sampling outer wood from one side of the stem provided a practical means of obtaining repeatable estimates of wood quality traits. A laboratory based NIR (Bruker MPA, Bruker Optik, Ettlingen, Germany) was used to acquire full range NIR spectra in the range 10,000 – 4,000 cm\(^{-1}\) (1,000 – 2,500 nm) at 8 cm\(^{-1}\) resolution.

NIR spectral analysis was performed using a dedicated multivariate data analysis package, The Unscrambler v9.8 (Camo A/S, Trondheim, Norway). Partial least squares (PLS) calibration models were prepared using spectra transformed with first or second derivatives following the Savitzky-Golay method (Savitzky and Golay 1964), with 15 point windows (all second order polynomial fits). The Kraft pulp yield (KPY) model development process has been previously described for multiple hardwood species across a range of geographic sites by Downes et al. (2009) while the density model (Downes et al. 2011) was developed using fewer eucalypt species including 76 samples of CCV taken from trial 451D at 7.5 years-of-age (Washusen et al. 2009). Wood density refers in this instance to the basic density being the weight of a given volume of dry wood in units of kilograms per green cubic metre and Kraft pulp yield refers to the volume of pulp that can be extracted from a given volume of wood using the Kraft pulping process with units in percent.

Statistical analyses

Provenance performance within each trial was evaluated with a reduced linear mixed model that did not include family level classification. This reduced model included fixed effects for the overall mean, trial, provenance and provenance by trial
interaction as well as random effects for replication within trial and incomplete blocks nested within replications of each trial. Proc Mixed (SAS 2009) was used to determine the significance of design effects and provide estimates of least square means for provenance performance with associated standard errors and the significance of between-provenance contrasts reported in Table 2.

Two mixed linear models were used to estimate genetic parameters and provide best linear unbiased predictions (BLUP) of parental breeding values. Model 1 was used to produce parameter estimates and BLUPs for each of the four analysis traits separately (3-year volume, 6-year Volume, Density and Kraft Pulp Yield), allowing for distinct within trial variances and between trial covariances (Brawner et al. 2010). Model 2 combined all four traits in a single multivariate analysis, allowing for distinct variances for each trait and covariances between traits. Model 1 was used to produce heritability estimates and type-B correlations while Model 2 was used to produce heritability estimates and type-A correlations. All models were fit using the ASReml software (Gilmour et al. 2009).

Model 1 – \( Y_{ijklmn} = \mu + T_i + R_j(T_i) + T_i \times P_k + T_i \times F_l + T_i \times B_m(R_j T_i) + T_i \times E_n, \) where:

- \( Y_{ijklmn} \) is the vector of phenotypic observations,
- \( \mu \) is the overall mean for the trait across all trials,
- \( T_i \) is the fixed effect of trial \( i \),
- \( R_j(T_i) \) is the fixed effect of replication \( j \) nested within trial \( i \),
- \( T_i \times P_k \) is the random effect of provenance \( k \) for trial \( i \),
- \( T_i \times F_l \) is the random effect of family \( l \) for trial \( i \),
- \( T_i \times B_m(R_j T_i) \) is the random effect of incomplete block \( m \) within replication \( j \) of trial \( i \), and
- \( T_i \times E_n \) is the error associated with each individual tree of trial \( i \). Where random effects were crossed with the fixed trial effect, unstructured variance-covariance matrices were fitted that allowed for trial specific variances and between trial covariances. Both the incomplete block and error variance structures were fit as block diagonal matrices as no inter-trial covariance exists between these disconnected effects.

Model 2 – \( Y_{ijklmno} = \mu_o + T_{io} + R_{jo}(T_i) + P_{ko} + F_{lo} + B_{mo}(R_j T_i) + E_{ijklmn}, \) where:

- \( Y_{ijklmno} \) is the vector of phenotypic observations,
- \( \mu_o \) is the mean for each trait \( o \) across all trials,
- \( T_{io} \) is the fixed effect of trial \( i \) for trait \( o \),
- \( R_{jo}(T_i) \) is the fixed effect of replication \( j \) nested within trial \( i \) for trait \( o \),
- \( P_{ko} \) is the random effect of provenance \( k \) for trait \( o \),
- \( F_{lo} \) is the random effect of family \( l \) for trait \( o \),
- \( B_{mo}(R_j T_i) \) is the random effect of incomplete block \( m \) nested within each trial replication for trait \( o \), and
- \( E_{ijklmn} \) is the error associated with each individual tree for trait \( o \). As effects are associated with the four assessment traits, unstructured variance-covariance matrices were estimated for each random effect.

Derivation of genetic parameters and prediction of breeding values

Genetic parameters are useful in developing breeding strategies, understanding the effectiveness of progeny trial design, determining the distribution of trials across the
target planting region and assessing the suitability of assessment protocols. In this study, six genetic parameters were estimated to assist with the development of the breeding strategy for CCV: 1) narrow sense heritability, 2) proportion of provenance variation, 3) family trait-trait or type-A correlations and 4) provenance type-A correlations, 5) family site-site or type-B correlations and 6) provenance type-B correlations.

Narrow-sense heritability estimates for each individual site analysis were approximated using the following formulae, which is the ratio of additive genetic variance to the within provenance phenotypic variance:

\[ h^2 = \frac{\hat{V}_p}{\hat{V}_p} = \frac{3\hat{\sigma}_{\text{Family}}^2}{\hat{\sigma}_{\text{Family}}^2 + \hat{\sigma}_{\text{Error}}^2}, \]

where \( \hat{\sigma}_{\text{Family}}^2 \) is the between-family variance, \( \hat{\sigma}_{\text{Error}}^2 \) is the error variance, \( \hat{V}_p \) is the phenotypic variance with each variance specific to trial i or trait o. This heritability estimate assumed the coefficient of relationship was one-third (Eldridge et al. 1993, Griffin and Cotterill 1988) due to mixed mating, rather than one-quarter as is appropriate for true half-sibs.

In order to compare the among-provenance variance and among-family variances, the following statistic, termed the proportion of provenance variance (Hodge and Dvorak 2001), was used,

\[ \hat{P}^2 = \frac{\hat{\sigma}_{\text{Prov}}^2}{\hat{V}_p}, \]

where \( \hat{\sigma}_{\text{Prov}}^2 \) is the provenance variance for trial i or trait o and \( \hat{V}_p \) is the same phenotypic variance used to estimate heritability.

The type-A and type-B additive genetic correlations were estimated as,

\[ r_{\text{Family}} = \frac{\hat{\sigma}_{\text{Family1,2}}}{\sqrt{\hat{\sigma}_{\text{Family1}}^2 \hat{\sigma}_{\text{Family2}}^2}}, \]

with the genetic covariance (\( \hat{\sigma}_{\text{Family1,2}} \)) specific to a pair of traits for type-A correlations or a pair of trials for type-B correlations.

Type-A and type-B provenance correlation were estimated as,

\[ r_{\text{Prov}} = \frac{\hat{\sigma}_{\text{Prov1,2}}}{\sqrt{\hat{\sigma}_{\text{Prov1}}^2 \hat{\sigma}_{\text{Prov2}}^2}}, \]

where \( \hat{\sigma}_{\text{Prov1,2}} \) is the covariance among provenances for either traits or trials.

Breeding value predictions used to identify parents that would be suitable for inclusion in future seed production facilities were produced using Model 2, which included four assessment traits: 1) individual tree volume prior to thinning (3-year Volume (m\(^3\))), 2) individual tree volume after thinning if thinning was undertaken (6-year Volume or Vol (m\(^3\))), 3) NIR-predicted basic density (Den (kg/m\(^3\))) and, 4) NIR-predicted Kraft Pulp Yield (KPY(%)). While early thinning effectively emulates the
The phenotypic data used to generate BLUPs was scaled to have a mean of zero and a standard deviation of one (Z-scores). This standardisation of data effectively removes interaction variance due to scale effects (White et al. 2007) and facilitates convergence of the REML algorithm used by ASReml (Gilmour et al. 2009, Patterson and Thompson 1971, Thompson 2008). Breeding values for maternal parents were calculated as twice the parental BLUP (Falconer and Mackay 1996) plus the BLUP for the provenance to which the family belongs, estimated as the deviation of the assessment trait from the overall mean. Rescaling of the parental breeding values from units of standard deviations to represent the performance of 74 month old progeny at Bakers progeny trial (451D) on the phenotypic scale was undertaken for each parental prediction; these predictions were used for the estimation of genetic gain. The Bakers progeny trial was selected to provide scale (phenotypic mean and variance) for the predictions as this trial was not thinned prior to the later assessment of growth and this more closely resembled the silviculture of stands managed for pulp production. Rescaled breeding value predictions were calculated as the sum of two components: 1) the trait average and 2) the product of the breeding value and the phenotypic standard deviation of the trait.

**Selection index weights**

Selection of individuals for establishment in a clonal seed orchard using an index that combines growth and wood quality traits requires index weightings for each trait; these weights can be deduced using a variety of methods (Borralho et al. 1993, Greaves et al. 1997). In this study, the approach used to compare selection index weights relies on the ability to use relative weightings since standing-tree pulp productivity is calculated as the product of the three selection traits: volume, density and Kraft pulp yield. A deterministic simulation was used to iteratively estimate genetic gain for various combinations of selection index trait weightings. Index weights were varied in 10% increments so that the relative importance for each of the three traits varied from 0 to 100% with the sum of the three traits driving pulp productivity always being set equal to 100% (Sanhueza et al. 2002).

Genetic gain for each of the selection indices was estimated as the ratio of the average of the top 10% of the parent’s breeding values (37 of 374 total parents in trial) to the population average assuming selections could be placed in an isolated clonal seed orchard and allowed to interbreed at random. While selection of the parents for seed orchards is infeasible as parents were not captured as grafted ramets at seed collection, the backwards selection strategy using more reliable

parental predictions rather than individual tree progeny predictions was utilised to provide approximations of the genetic gain.

Results

Considerable differences among provenances for the three selection traits (p < 0.01) were detected at each trial site using the reduced linear model (Table 2). Of note were the considerable differences between provenances; relative to the trial mean, the difference between individual tree volume estimates of the largest and smallest provenances were 148, 73 and 67 percent greater than the trial mean for 451C, 451D and 451G, respectively. Relative to the wood quality traits, variation was large for volume production at both ages. A much broader range of provenances were sampled for volume production than were sampled for wood quality traits (Table 2). This sub-sampling must be kept in mind when making conclusions about either the relative importance of variation at the population and family level or the impact of selection traits on a composite trait.

Table 2 demonstrates important changes in the ranking of provenances across sites (provenance by site interaction p < 0.01). Nevertheless, the provenance level correlation estimates for individual tree volume generated by Model 1 were high across sites (Table 3). Provenances originating from Queensland that consistently grew well were Home and Woondum (Table 2), which were two of the five provenances selected for wood property sampling. The other three provenances selected for wood property sampling (Wolvi, Brooyar and Curra) were less productive. Although Wolvi grew well, particularly in 451G, Brooyar and Curra were not significantly different from the trial mean or one another for volume production when grown together in 451G (p<0.65). Some of the provenances from New South Wales grew well at all sites; Grange and Kangaroo ranked 1 and 2 in trial 451C, Kangaroo and Dalmorton ranked 2 and 3 in trial 451D and Richmond Range and Cherry Tree ranked 1 and 4 in 451G, respectively. Families from Grange, Kangaroo and Dalmorton were selected using data collected from an earlier progeny trial that was not included in this study so that comparisons are therefore limited for these sources.

Table 2 – Least square means, with standard errors in parenthesis...

For the geographically narrow range of provenances sampled for wood quality evaluation with near infrared spectroscopy, there were significant differences among populations for both density and KPY (p < 0.01). While density showed significant rank changes between sites (p < 0.01), no rank changes were evident for KPY (p<.73). The significance of differences between provenances could be attributed to Brooyar. Across sites, Brooyar was significantly more dense than all other provenances (p < 0.01) and there were no differences between the other populations (p > 0.1). Conversely, Kraft pulp yield for Brooyar was significantly lower than that of
all other provenances \((p < 0.01)\) and again there were no differences among the other populations \((p > 0.1)\). Gardner et al (2007) found in other \textit{Corymbia} species grown in South Africa on a similar site (False Bay) lower absolute values with density of \textit{C. henryi} = 658 kg/m\(^3\) and \textit{C. citriodora} ssp. \textit{citriodora} = 672 kg/m\(^3\) with KPY \textit{C. henryi} = 53.3 kg/m\(^3\) and \textit{C. citriodora} ssp. \textit{citriodora} = 53.5. Compared to these estimates, the average wood density of 756 kg/m\(^3\) and pulp yield of 55% found in these trials indicate the species has considerable potential as a pulpwood crop when grown in southeast Queensland.

Model 1 was used to generate narrow-sense heritability and provenance proportion of phenotypic variance estimates for each trial site as well as between-site type-B correlations. These parameters indicated substantial levels of genetic control for the assessment traits for most trials with differing patterns of across-site stability (Table 3). Coefficients of variation for the assessment traits were much higher for volume compared to wood properties: 1.01, 0.83, 0.05 and 0.04 for 3-year volume, 6-year volume, density and KPY respectively. The stability of both family and provenance ranking across sites was relatively high for volume and consistently increased from the early to later assessment. Both density and KPY exhibited high levels of stability at the family level. However, provenance rankings for density were inconsistent, although this may have been related to the low number of provenances sampled and differences in family within provenance representation across sites rather than true interactions.

Table 3 – Performance statistics for each trait assessed in each trial.... NEAR HERE

The single multivariate analysis undertaken using Model 2 included all trial data simultaneously and provided estimates of narrow-sense heritability, proportion of provenance variance and type-A genetic correlations. Heritability estimates for volume were lower and wood quality estimates were larger than the average of estimates generated with Model 1. As was the case for estimates generated with Model 1, proportion of provenance variance estimates were consistently lower than estimates of heritability indicating a greater level of genetic control within populations rather than among populations.

Table 4 – Genetic parameter estimates a single multivariate across-site….NEAR HERE

Very high age-age correlations for volume indicate small changes in both family or provenance rankings occurred between the two assessments of DBH and height. As well, high correlations between KPY and volume predictions of provenance performance were indicative of positive correspondence between these traits. On the other hand, correlations between density and other traits at both the family and provenance level were moderate and estimates of between-trait provenance correlations were associated with very high standard error estimates. With the exception of the correlations between volume production, all standard errors

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associated with provenances were larger than those that were associated with families, which is likely related to the small number of provenances (4-5) assessed for wood properties.

On average, trees within this population produced 20.9 kg of pulp when scaled to represent 6-year volume and wood property assessments from trial 451D. The simple volume equation used to calculate tree volume uses a form factor of 1/3, which is similar to unpublished form factors for under-bark wood production and therefore indicative of harvestable pulpwod volume exclusive of bark. Nevertheless, predictions of genetic gain in pulp productivity for a range of selection strategies are presented as the percentage of the maximum genetic gain that could be achieved if selection was dedicated to the trait of interest to facilitate comparisons (Figure 2). With breeding values scaled to represent the mean and variance of the population sampled in trial 451D, the maximum genetic gains achievable using this sampling and selection strategy are: 59.8, 54.2, 3.8 and 2.5 percent for pulp productivity, 6-year volume, density and KPY, respectively.

Estimates of genetic gains indicated substantial improvements in the objective trait of pulp productivity (PP) could be realised following selection on indices designed to identify the top 10% of the parents within this base population of CCV. It is evident in Figure 2.3 that selection for volume is the primary driver of PP; this can be partially explained by the high coefficient of variation for growth traits as the heritability and proportion of provenance variation are generally smaller for volume relative to either wood trait. Within the small selected populations of 37 trees identified as superior using selection indices, density and KPY are unrelated with increases in one trait resulted in comparable decreases in the other trait. The positive between-trait correlations across the population that are specified in Table 4 are reflected in the selected population with increasing selection pressure directed to 6-year volume leading to positive increases in wood quality traits.

Discussion

_Corymbia citriodora_ subsp. _variegata_ is an important species for plantation development in lower rainfall areas of the Australian subtropics (Nichols et al. 2010) and this has led to three genetic improvement programs within Australia (Lee 2007). As this study is the first to provide multi-site genetic parameter estimates for a range of traits in a _Corymbia_ species, comparisons are made with other hardwood species. The coastal provenances of CCV that were sourced from native forests geographically close to the three progeny trials (Woondum, Home, and Wolvi) and several provenances from New South Wales (Grange, Cherry Tree, Kangaroo and Richmond Range), grew well in these trials. Similar findings were reported by Johnson et al (2009) where Richmond Range, Home, Wolvi and Woondum were superior for growth traits in one trial established in Northern New South Wales.
Interestingly, in the NSW trial Grange was reported to perform poorly while Brooyar and Wondai were reported to perform well; the opposite was found in these trials. The reported superiority of the coastal provenances from Queensland has been associated with higher levels of tolerance to the fungal pathogen *Quambalaria pitereka* (Dickinson et al. 2004, Lee et al. 2009, Pegg et al. 2005) and this resistance has been associated with provenances originating from higher rainfall coastal areas (Johnson et al. 2009). The poor performance of the families from the South African clonal seed orchard, which grew significantly less than all provenances but Esk (p<0.05), may have been the result of an increased early incidence of a shoot blight fungi (Brawner et al. 2011) or intense selection for a distinct environment.

Estimates of wood density and pulp yield were high and these findings concur with other studies that have compared the wood properties of *Corymbia* species with other species (Clark and Hicks 2003, Gardner et al. 2007). Although the sample of provenances selected for wood property assessment was small and the geographic range was purposefully limited, significant differences among provenances were found for both traits. Across all trials, Brooyar was significantly (p < 0.01) less dense and had a significantly lower pulp yield than three of the four other provenances. Of the provenances sampled, Brooyar represents the provenance with the lowest mean annual rainfall. In the single trial where least square means were estimable for all five provenances sampled (451G), Curra was inferior for both wood quality traits (p<0.05) and is also from a lower rainfall area in Southeast Queensland. These inconsistencies in provenance rankings are typically not the case when wood property traits are evaluated as low levels of genotype by environment interaction are often reported for wood property traits (Borralho et al. 1992, Cornelius 1994, Costa e Silva et al. 2009).

Single-site heritability estimates for volume using Model 1 (Table 2) were similar to those presented by Johnson et al (2009) for DBH and height and are similar to those reported for many forest tree species (Cornelius 1994). Typically, heritability estimates based on single trials are biased upward due to the inability to partial out variance due to genotype by environment interactions (Hodge and White 1992), however Model 1 accounts for between trial covariance and theoretically provides less biased estimates. Heritability estimates for wood properties were consistently greater than heritability estimates for volume, which has also been reported for a range of other forest tree species. When compared with other hardwood species parameters for growth data, the among-provenance variance of the CCV populations evaluated in these trials is high: \( \hat{P}^2 = 0.03 \) for *E. urophylla* (Hodge et al. 2001) and \( \hat{P}^2 = 0.10 \) for *Gmelina arborea* (Hodge and Dvorak 2004). For volume at the early or later age of assessments, these results indicate differences between populations will be more important in CCV breeding than in other forest tree species and strengthen the case for selecting individuals from many populations rather than focusing on a few local populations. Type-B correlations between these trials indicate genotype
by environment interactions are of little importance. While the three sites differed in climatic and edaphic characteristics, this result may have been expected as the sample of environments was geographically limited. The notable exception to this general trend was for density, which has been frequently cited as a stable trait in forest tree populations.

Small changes in family and provenance rankings between the two volume assessments were suggested by the very high age-age correlations (Table 3). Adjustments to 6-year volume breeding value predictions achieved through inclusion of early-age data (Stackpole et al. 2010, Wei and Borralho 1998) would therefore be small. This also indicates that either thinning would not drastically alter selections made from these trials or that the thinning interval was insufficient to allow for the expression of changes. Interestingly, the genetic correlation between growth and density was positive and large; small to significantly negative genetic correlations are typical in forest tree populations (Cornelius 1994). It should be reiterated that all genetic parameter estimates for density were associated with large standard errors.

As the breeding objective of standing-tree PP is the product of the three selection traits, improvement in a pulp-productivity breeding objective is related to both the level of genetic control and the phenotypic variance in the selection traits. Theoretical gain estimations may also be calculated as product of the heritability, phenotypic variation and the selection intensity. Selection intensity was held constant at 10 percent in this study. Although the heritability for both wood property traits was greater than for volume, the coefficient of variation was 17 to 21 times larger for age-6 volume than for density or KPY, respectively. Recommendations for sampling strategies developed from this study are applicable for identifying improved parents for seed production populations within this study population and the relative importance of each trait on the level of genetic gain achievable is likely to vary considerably in different populations. Maximum genetic gains achievable using the indices described above were 59.8, 54.2, 3.8 and 2.5 percent for PP, 6-year volume, density and KPY, respectively. Selection of 37 parents for the composite trait of pulp productivity would lead to plantations producing 33.4 rather than 20.9 kg of pulp per tree at 74 months of age; this should provide significant improvements to the profitability CCV plantations managed for pulp production.

In figure 2, the trade-offs in gain maximisation arising from changes in the importance of selection traits are consistently presented with respect to the gain that may be achieved in pulp productivity. Figures 2.1 and 2.2 clearly demonstrate the importance of volume production in realising improvements in pulp productivity. The relative importance of these traits will likely change in advanced generations as less productive populations and families are culled. As well, the end-product or processing may place restrictions on the rate at which some traits are allowed to be changed in the genetic improvement program. For example, in a South African study that included Corymbia species, the species’ wood density was found to be higher than the optimal range desired for local pulp mills but quite suitable for a chip
export markets (Gardner et al. 2007). Using the results presented in Figure 2, changes in density could be minimised without unduly limiting pulp productivity improvement by applying a selection index that places a weight of 70% on volume and 30% on KPY. Nevertheless, due to the positive correlation between volume and density, selection for volume production alone is expected to increase the density of resulting plantations by less than two percent.

*Corymbia citriodora* subsp. *variegata* is a species with considerable potential for areas in the subtropics that have historically been considered marginal for profitable plantation forestry. The species ability to survive in difficult conditions, tolerate endemic pests and diseases, its high wood density and acceptable Kraft pulp yield makes it a less risky and more profitable option for the production of a commodity crop in Australia’s subtropics (Lee et al. 2011). Compared to other eucalypts commonly grown for pulpwood crops, the superior wood properties of *Corymbia* (Gardner et al. 2007) merits further study by the pulp and paper industry. As well, the excellent quality of the species for solid wood products provides further value-adding opportunities and silvicultural challenges.

**Conclusions**

Evaluation of a set of trials for volume production and wood properties indicates that selection from within this base population for a pulp production breeding objective would primarily rely on selection for improvement in volume production and correlated improvements in wood property traits. Forest managers sourcing seed from base populations that have been intensively selected for volume production would realise most of the genetic improvement that could be obtained through a more complex selection strategy targeting the composite trait of pulp productivity. This strategy should be generally applicable for base populations of CCV with advanced generations requiring adjustments to selection indices as the elimination of inferior families and provenances would reduce the coefficient of variation for the main driver of pulp productivity, individual tree volume. Genetic parameters suggest moderate levels of genetic control for pulp productivity traits, little genotype by environment interaction, high age-age correlations and beneficial trait-trait correlations. Genetically improved seed from selections made within superior families identified in these progeny trials are expected to provide an increase in the profitability of plantation forests managed for pulp production across the extensive areas of marginal land that may be available for afforestation within the subtropics.

**Acknowledgements**

We would like to thank the Queensland government for supporting the establishment, maintenance and assessment of these field trials, and specifically for the research grant from the Department of Employment, Economic Development and
Innovation that provided the financial support for the Smart Forest Alliance. The University of the Sunshine Coast is also acknowledged for the provision of facilities that facilitated this multi-organization collaboration. Comments and suggestions from two anonymous reviewers as well as the Southern Forests editorial panel were used to improve this manuscript.
Appendices

A1 – Summary of NIR Calibration

The summary statistics for the NIR calibration models used in the prediction of Kraft pulp yield and density are:

<table>
<thead>
<tr>
<th>Factors</th>
<th>Treatment</th>
<th>$R^2$ (calib.)</th>
<th>$r^2$ (valid)</th>
<th>RMSEP$^1$</th>
<th>Density (kg/m$^3$)</th>
<th>Kraft pulp yield (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>0.71</td>
<td>0.70</td>
<td>44</td>
<td>0.71</td>
<td>0.94</td>
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<td></td>
<td></td>
<td>1$^{st}$ deriv.</td>
<td>unpublished</td>
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<td>0.83</td>
<td>0.95</td>
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<tr>
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<td></td>
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<td></td>
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<td>5</td>
<td>0.70</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2$^{nd}$ deriv.</td>
<td>(Meder et al. 2011)</td>
</tr>
</tbody>
</table>

$^1$RMSEP: Root-mean-square-error-of-prediction, where the mean error for prediction of density is ±44 kg/m$^3$ and for Kraft pulp yield is ±0.95. For example, a NIR-predicted Kraft pulp yield value of 52.0 % the value is in the range 51.05 – 52.95 %.
Figures
Figure 1 – Provenances of Corymbia citriodora subsp. variegata sampled for inclusion in the spotted gum breeding program and evaluated for growth and wood properties in three progeny trials established in southeast Queensland.
Figure 2 – Percent of maximum gain achievable for target traits following selection of the top 10% of the *Corymbia citriodora* population using an index with weights incremented by 10% for each selection trait and restricted to sum to 100% for pairs of traits including individual tree volume (Vol), basic density (Den) and Kraft pulp yield (KPY). The composite trait of Pulp productivity is also included. Indices on X axis indicate percent weighting applied to the selection traits Vol, Den and KPY.
Table 1 - Description of progeny trials and assessments used to evaluate *Corymbia citriodora* ssp. *variegata* populations

<table>
<thead>
<tr>
<th>Trial</th>
<th>Location</th>
<th>Established</th>
<th>Material(^a)</th>
<th>Design(^b)</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Assess(^c)</th>
<th>Thin(^d)</th>
<th>Total stems</th>
<th>WQ stems(^e)</th>
</tr>
</thead>
<tbody>
<tr>
<td>451c</td>
<td>Taipo Camp</td>
<td>Mar-99</td>
<td>14 (122)</td>
<td>8, 5, 2</td>
<td>25.78º S</td>
<td>152.63º E</td>
<td>32, 53</td>
<td>34 (51)</td>
<td>1520</td>
<td>128</td>
</tr>
<tr>
<td>451d</td>
<td>Bakers</td>
<td>Jul-00</td>
<td>14 (242)</td>
<td>7, 21, 4</td>
<td>25.76º S</td>
<td>152.68º E</td>
<td>37, 74</td>
<td>No thin (92)</td>
<td>7247</td>
<td>994</td>
</tr>
<tr>
<td>451g</td>
<td>St Mary's</td>
<td>May-02</td>
<td>12 (138)</td>
<td>5, 12, 4</td>
<td>25.67º S</td>
<td>152.52º E</td>
<td>43, 89</td>
<td>50 (48)</td>
<td>2880</td>
<td>296</td>
</tr>
</tbody>
</table>

\(^{a}\) Genetic material established in trials with number of provenances followed by number of open pollinated families in parentheses

\(^{b}\) Design lists number of replications, incomplete blocks per replication and trees per contiguous family plot, respectively

\(^{c}\) Age of diameter at breast height and total tree height assessments in months from planting

\(^{d}\) Age of thinning(s) in months from planting with percent of trees remaining at second assessment in parentheses

\(^{e}\) Number of stems assessed for wood quality
Table 2 – Least square means, with standard errors in parenthesis, for provenances of *Corymbia citriodora* evaluated in provenance trials for 6-year-old volume growth (the latter of two assessments), basic density and Kraft pulp yield

<table>
<thead>
<tr>
<th>Provenance</th>
<th>6-year Volume (dm$^3$)</th>
<th>Density (kg/m$^3$)</th>
<th>Kraft pulp yield (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bauple</td>
<td></td>
<td></td>
<td>0.42 (0.06)</td>
</tr>
<tr>
<td>Boundary Creek</td>
<td>1.00 (0.19)</td>
<td>0.52 (0.05)</td>
<td>1.66 (0.13)</td>
</tr>
<tr>
<td>Brooyar</td>
<td>0.72 (0.08)</td>
<td>0.39 (0.04)</td>
<td>1.40 (0.10)</td>
</tr>
<tr>
<td>Cherry Tree</td>
<td></td>
<td></td>
<td>1.89 (0.05)</td>
</tr>
<tr>
<td>Curra</td>
<td></td>
<td></td>
<td>1.45 (0.07)</td>
</tr>
<tr>
<td>De’Agular</td>
<td></td>
<td></td>
<td>0.96 (0.05)</td>
</tr>
<tr>
<td>Dalmorton</td>
<td>0.80 (0.26)</td>
<td>0.54 (0.07)</td>
<td>1.67 (0.18)</td>
</tr>
<tr>
<td>Esk</td>
<td>0.33 (0.07)</td>
<td>0.25 (0.06)</td>
<td></td>
</tr>
<tr>
<td>Grange</td>
<td>1.25 (0.26)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Home</td>
<td>1.01 (0.07)</td>
<td>0.59 (0.04)</td>
<td>1.66 (0.09)</td>
</tr>
<tr>
<td>Kangaroo</td>
<td>1.10 (0.10)</td>
<td>0.55 (0.06)</td>
<td></td>
</tr>
<tr>
<td>Lockyer</td>
<td>0.39 (0.07)</td>
<td>0.34 (0.08)</td>
<td></td>
</tr>
<tr>
<td>Mount-Mee</td>
<td></td>
<td></td>
<td>1.26 (0.05)</td>
</tr>
<tr>
<td>Richmond Range</td>
<td>0.77 (0.26)</td>
<td>0.51 (0.05)</td>
<td>2.04 (0.10)</td>
</tr>
<tr>
<td>SA-CSO$^1$</td>
<td>0.14 (0.08)</td>
<td></td>
<td></td>
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<tr>
<td>Wedding Bells</td>
<td></td>
<td></td>
<td>0.48 (0.05)</td>
</tr>
<tr>
<td>Wolvi</td>
<td>0.86 (0.06)</td>
<td>0.55 (0.03)</td>
<td>1.94 (0.07)</td>
</tr>
<tr>
<td>Wondai</td>
<td>0.46 (0.09)</td>
<td>0.47 (0.12)</td>
<td></td>
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<tr>
<td>Woondum</td>
<td>0.88 (0.05)</td>
<td>0.52 (0.03)</td>
<td>1.89 (0.04)</td>
</tr>
</tbody>
</table>

$^1$ South African clonal seed orchard bulk
**Table 3** – Performance statistics for each trait assessed in each trial (trial average with standard deviation in parentheses) and genetic parameter estimates from separate across-site analyses undertaken for each trait assessed within the three *Corymbia citriodora* progeny trials. Family parameter estimates include narrow-sense heritability on the diagonal (bold) and between-site type-B additive genetic correlations below the diagonal. Provenance parameter estimates include proportion of phenotypic variance on the diagonal (bold) and between-site type-B provenance correlations below the diagonal. Parameter estimates are derived from Model 1. Standard errors of estimates are provided in parenthesis.

<table>
<thead>
<tr>
<th></th>
<th>3-year Volume (dm$^3$)</th>
<th>6-year Volume (dm$^3$)</th>
<th>Density (kg/m$^3$)</th>
<th>Kraft Pulp Yield (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>451C</td>
<td>451D</td>
<td>451G</td>
<td>451C</td>
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<tr>
<td><strong>Performance statistics</strong></td>
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<tr>
<td></td>
<td>0.19 (0.22)</td>
<td>0.13 (0.11)</td>
<td>0.28 (0.25)</td>
<td>0.70 (0.61)</td>
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<tr>
<td><strong>Family genetic parameter estimates</strong></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td></td>
<td>451C</td>
<td>0.33 (0.07)</td>
<td>0.43 (0.11)</td>
<td>0.12 (0.28)</td>
</tr>
<tr>
<td></td>
<td>451D</td>
<td>0.84 (0.11)</td>
<td>0.25 (0.03)</td>
<td>0.95 (0.19)</td>
</tr>
<tr>
<td></td>
<td>451G</td>
<td>0.96 (0.26)</td>
<td>0.66 (0.19)</td>
<td>0.20 (0.04)</td>
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<tr>
<td><strong>Provenance genetic parameter estimates</strong></td>
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</tr>
<tr>
<td></td>
<td>451C</td>
<td>0.17 (0.08)</td>
<td>0.21 (0.09)</td>
<td>0.13 (0.15)</td>
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<tr>
<td></td>
<td>451D</td>
<td>0.94 (0.16)</td>
<td>0.02 (0.01)</td>
<td>-0.13 (0.03)</td>
</tr>
<tr>
<td></td>
<td>451G</td>
<td>0.78 (0.29)</td>
<td>0.94 (0.22)</td>
<td>0.04 (0.03)</td>
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</tbody>
</table>

571
Table 4 – Genetic parameter estimates from a single multivariate across-site analysis of three *Corymbia citriodora* progeny trials undertaken for four traits. Family parameter estimates include narrow-sense heritability on the diagonal (bold) and between-trait type-A additive genetic correlations below the diagonal. Provenance parameter estimates include proportion of phenotypic variance on the diagonal (bold) and between-site type-A provenance correlations below the diagonal. Parameter estimates are derived from Model 2. Standard errors of estimates are provided in parentheses.

<table>
<thead>
<tr>
<th></th>
<th>Family</th>
<th>Provenance</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>3-year volume</td>
<td>6-year volume</td>
</tr>
<tr>
<td></td>
<td>m³</td>
<td>m³</td>
</tr>
<tr>
<td>3-year volume</td>
<td></td>
<td></td>
</tr>
<tr>
<td>6-year volume</td>
<td>0.25 (0.03)</td>
<td>0.98 (0.01)</td>
</tr>
<tr>
<td>Density</td>
<td>0.42 (0.10)</td>
<td>0.39 (0.10)</td>
</tr>
<tr>
<td>Kraft Pulp Yield</td>
<td>0.45 (0.11)</td>
<td>0.48 (0.11)</td>
</tr>
<tr>
<td>Provenance</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3-year volume</td>
<td>0.07 (0.03)</td>
<td></td>
</tr>
<tr>
<td>6-year Volume</td>
<td>0.98 (0.01)</td>
<td>0.10 (0.04)</td>
</tr>
<tr>
<td>Density</td>
<td>0.09 (0.88)</td>
<td>-0.10 (0.89)</td>
</tr>
<tr>
<td>Kraft Pulp Yield</td>
<td>0.82 (0.21)</td>
<td>0.92 (0.14)</td>
</tr>
</tbody>
</table>
Literature Cited


