1 # Selection of *Corymbia citriodora* for pulp productivity

2 J.T. Brawner[1,2], Roger Meder[1], Mark Dieters[2], D.J. Lee[3&4],

3 [1] CSIRO – Plant Industry, 306 Carmody Road, St. Lucia Qld 4067, Australia.

4 Corresponding author - Jeremy.Brawner@csiro.au – Tel - +61 4 1925 3005

5 [2] The School of Land, Crop and Food Sciences, University of Queensland, St. Lucia,
6 Qld 4072 Australia
7 [3] University of the Sunshine Coast, Maroochydore, Qld 4558, Australia
8 [4] Department of Employment Economic Development and Innovation, PO Box 395,
9 Gympie Qld 4570, Australia

10 **Abstract**

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

30 **Keywords**

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

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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 e Silva 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

76   Queensland state government's tree improvement program (Table 1). Each tree can
77   be traced back to an individual mother tree and provenance within natural stands.
78   The trials differ in the representation of genetic material (families within provenance),
79   incomplete block size and in the number of individuals established in each family
80   line-plot. These trials were managed to convert the progeny trials into seedling seed
81   orchards by removing inferior individuals within multiple-tree plots of each family to
82   rapidly provide a source of improved germplasm for use in plantation establishment.

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

97   **Figure 1** – Locations of seed collected for inclusion in the Corymbia… **NEAR HERE**
98
99   **Table 1** - Description of progeny trials and assessments used to… **NEAR HERE**
100
101   All stems were sampled for diameter at breast height (DBH) and total height at
102   various ages during the course of the field trials. Total height and DBH were used to
103   estimate total tree volume (m^3) using a generic conical volume equation ($^1/_3 \times DBH^2$
104     $\times$ Height). There was no adjustment of taper or bark thickness differences between
105   populations (Dieters and Brawner 2007). A pair of growth assessments was
106   selected to represent volume production at two points in the life of each trial with two
107   of the three trials measured before and after thinning (Table 1). The average times
108   from trial establishment to the early and later assessment were 37 and 60 months
109   and these traits are hereafter referred to as '3-year volume' and '5-year volume'.
110   Wood samples were taken from trial 451C, 451D and 451G at 134, 118 and 95
111   months after planting respectively. The wood samples were sifted from swarf
112   (shavings or sawdust <1mm) that was produced by drilling into stems, at breast
113   height (~1.3 m), with a 16mm spade bit to a depth of approximately 50 mm following
114   the removal of bark.

115   Population genetic structure was purposefully avoided to allow for a separate genetic
116   association study designed to link single nucleotide polymorphisms with phenotypic
117   traits. Consequently, the wood quality of families from a geographically narrow range

118 of provenances in the Gympie region (Table 2) was evaluated within these progeny
119 trials using 12, 7, 17, 25, 150 families that represented the provenances of Brooyar,
120 Curra, Home, Wolvi and Woondum, respectively (Figure 1). All available individuals
121 within these families were sampled for wood quality traits across the trials. While the
122 experiment-wise connectivity of 78 families represented on at least two sites is
123 sufficient for the estimation of population wide genetic parameters for stability, this
124 significant level of imbalance in family representation across the three trials led to the
125 exclusion of any inferences on the suitability of a specific family for a specific trial
126 site. As well, imbalance in population representation was evident with a large
127 proportion of the families originating from the Woondum provenance due to this
128 population's superiority for disease tolerance and associated greater growth rates in
129 other taxa trials (Dickinson et al. 2004). Within the 211 families sampled for wood
130 properties, wood samples were collected from an average of 6.7 stems per family
131 (standard deviation of 2.8, minimum of 3, maximum of 16 trees per family) and
132 scanned with a near infrared spectrometer.

133

134 **Near Infrared Spectroscopy**
135 Near infrared spectra were acquired on individual samples presented as fines
136 (<1mm) sifted from the breast height wood swarf. Prior work on sampling protocols
137 (data not presented) had determined that consistently sampling outer wood from one
138 side of the stem provided a practical means of obtaining repeatable estimates of
139 wood quality traits. A laboratory based NIR (Bruker MPA, Bruker Optik, Ettlingen,
140 Germany) was used to acquire full range NIR spectra in the range 10,000 – 4,000
141 cm^{-1} (1,000 – 2,500 nm) at 8 cm^{-1} resolution.

142 NIR spectral analysis was performed using a dedicated multivariate data analysis
143 package, *The Unscrambler* v9.8 (Camo A/S, Trondheim, Norway). Partial least
144 squares (PLS) calibration models were prepared using spectra transformed with first
145 or second derivatives following the Savitzky-Golay method (Savitzky and Golay
146 1964), with 15 point windows (all second order polynomial fits). The Kraft pulp yield
147 (KPY) model development process has been previously described for multiple
148 hardwood species across a range of geographic sites by Downes *et al.* (2009) while
149 the density model (Downes *et al.* 2011) was developed using fewer eucalypt species
150 including 76 samples of CCV taken from trial 451D at 7.5 years-of-age (Washusen et
151 al. 2009). Wood density refers in this instance to the basic density being the weight
152 of a given volume of dry wood in units of kilograms per green cubic metre and Kraft
153 pulp yield refers to the volume of pulp that can be extracted from a given volume of
154 wood using the Kraft pulping process with units in percent.

155 **Statistical analyses**
156 Provenance performance within each trial was evaluated with a reduced linear mixed
157 model that did not include family level classification. This reduced model included
158 fixed effects for the overall mean, trial, provenance and provenance by trial

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159 interaction as well as random effects for replication within trial and incomplete blocks
160 nested within replications of each trial. Proc Mixed (SAS 2009) was used to
161 determine the significance of design effects and provide estimates of least square
162 means for provenance performance with associated standard errors and the
163 significance of between-provenance contrasts reported in Table 2.

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

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

175 Y_{ijklmn} is the vector of phenotypic observations, μ is the overall mean for the trait
176 across all trials, T is the fixed effect of trial i, $R_j(T_i)$ is the fixed effect of replication j
177 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
178 random effect of family l for trial i, $T_i{\times}B_m(R_jT_i)$ is the random effect of incomplete block
179 m within replication j of trial i, and $T_i{\times}E_n$ is the error associated with each individual
180 tree of trial i. Where random effects were crossed with the fixed trial effect,
181 unstructured variance-covariance matrices were fitted that allowed for trial specific
182 variances and between trial covariances. Both the incomplete block and error
183 variance structures were fit as block diagonal matrices as no inter-trial covariance
184 exists between these disconnected effects.

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

186 $Y_{ijklmno}$ is the vector of phenotypic observations, μ_o is the mean for each trait o across
187 all trials, T is the fixed effect of trial i for trait o, $R_{jo}(T_i)$ is the fixed effect of replication j
188 nested within trial i for trait o, P_{ko} is the random effect of provenance k for trait o, F_{lo} is
189 the random effect of family l for trait o, $B_{mo}(R_jT_i)$ is the random effect of incomplete
190 block m nested within each trial replication for trait o, and E_{ijklmn} is the error
191 associated with each individual tree for trait o. As effects are associated with the
192 four assessment traits, unstructured variance-covariance matrices were estimated
193 for each random effect.

194

195 **Derivation of genetic parameters and prediction of breeding values**
196 Genetic parameters are useful in developing breeding strategies, understanding the
197 effectiveness of progeny trial design, determining the distribution of trials across the

198   target planting region and assessing the suitability of assessment protocols. In this
199   study, six genetic parameters were estimated to assist with the development of the
200   breeding strategy for CCV: 1) narrow sense heritability, 2) proportion of provenance
201   variation, 3) family trait-trait or type-A correlations and 4) provenance type-A
202   correlations, 5) family site-site or type-B correlations and 6) provenance type-B
203   correlations.

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

207   [1] $\hat{h}^2 = \dfrac{\hat{V}_A}{\hat{V}_P} \approx \dfrac{3\hat{\sigma}^2_{Family}}{\hat{\sigma}^2_{Family} + \hat{\sigma}^2_{Error}}$, where $\hat{\sigma}^2_{Family}$ is the between-family variance, $\hat{\sigma}^2_{Error}$ is

208   the error variance, $\hat{V}_P$ is the phenotypic variance with each variance specific to trial i
209   or trait o. This heritability estimate assumed the coefficient of relationship was one-
210   third (Eldridge et al. 1993, Griffin and Cotterill 1988) due to mixed mating, rather than
211   one-quarter as is appropriate for true half-sibs.

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

215   [2] $\hat{P}^2 = \dfrac{\hat{\sigma}^2_{Prov}}{\hat{V}_P}$, where $\hat{\sigma}^2_{Prov}$ is the provenance variance for trial i or trait o and $\hat{V}_P$ is

216   the same phenotypic variance used to estimate heritability.

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

218   [3] $r_{Family} = \dfrac{\hat{\sigma}_{Family_{1,2}}}{\sqrt{\hat{\sigma}^2_{Family_1}\hat{\sigma}^2_{Family_2}}}$, with the genetic covariance ($\hat{\sigma}_{Family_{1,2}}$) specific to a pair of

219   traits for type-A correlations or a pair of trials for type-B correlations.

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

221   [4] $r_{Prov} = \dfrac{\hat{\sigma}_{Prov_{1,2}}}{\sqrt{\hat{\sigma}^2_{Prov_1}\hat{\sigma}^2_{Prov_2}}}$, where $\hat{\sigma}_{Prov_{1,2}}$ is the covariance among provenances for either

222   traits or trials.

223   Breeding value predictions used to identify parents that would be suitable for
224   inclusion in future seed production facilities were produced using Model 2, which
225   included four assessment traits: 1) individual tree volume prior to thinning (3-year
226   Volume (m^3)), 2) individual tree volume after thinning if thinning was undertaken (6-
227   year Volume or Vol (m^3)), 3) NIR-predicted basic density (Den (kg/m^3)) and, 4) NIR-
228   predicted Kraft Pulp Yield (KPY(%)). While early thinning effectively emulates the

229 silviculture of stands managed for solid wood production and is appropriate for the
230 production of improved seed, this silvicultural intervention complicates genetic
231 analyses and can lead to biased genetic parameter estimates (Hadfield 2008). To
232 adjust for the thinning effect, a multivariate approach was used to include data from
233 an early assessment of growth (3-year volume) undertaken prior to thinning and a
234 later assessment of growth (6-year volume) undertaken after thinning (Wei and
235 Borralho 1998).

236 The phenotypic data used to generate BLUPs was scaled to have a mean of zero
237 and a standard deviation of one (Z-scores). This standardisation of data effectively
238 removes interaction variance due to scale effects (White et al. 2007) and facilitates
239 convergence of the REML algorithm used by ASReml (Gilmour et al. 2009, Patterson
240 and Thompson 1971, Thompson 2008). Breeding values for maternal parents were
241 calculated as twice the parental BLUP (Falconer and Mackay 1996) plus the BLUP
242 for the provenance to which the family belongs, estimated as the deviation of the
243 assessment trait from the overall mean. Rescaling of the parental breeding values
244 from units of standard deviations to represent the performance of 74 month old
245 progeny at Bakers progeny trial (451D) on the phenotypic scale was undertaken for
246 each parental prediction; these predictions were used for the estimation of genetic
247 gain. The Bakers progeny trial was selected to provide scale (phenotypic mean and
248 variance) for the predictions as this trial was not thinned prior to the later assessment
249 of growth and this more closely resembled the silviculture of stands managed for
250 pulp production. Rescaled breeding value predictions were calculated as the sum of
251 two components: 1) the trait average and 2) the product of the breeding value and
252 the phenotypic standard deviation of the trait.

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

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

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

273

Results

275 Considerable differences among provenances for the three selection traits ($p < 0.01$)
276 were detected at each trial site using the reduced linear model (Table 2). Of note
277 were the considerable differences between provenances; relative to the trial mean,
278 the difference between individual tree volume estimates of the largest and smallest
279 provenances were 148, 73 and 67 percent greater than the trial mean for 451C,
280 451D and 451G, respectively. Relative to the wood quality traits, variation was large
281 for volume production at both ages. A much broader range of provenances were
282 sampled for volume production than were sampled for wood quality traits (Table 2).
283 This sub-sampling must be kept in mind when making conclusions about either the
284 relative importance of variation at the population and family level or the impact of
285 selection traits on a composite trait.

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

302 **Table 2** – Least square means, with standard errors in parenthesis... **NEAR HERE**

303 For the geographically narrow range of provenances sampled for wood quality
304 evaluation with near infrared spectroscopy, there were significant differences among
305 populations for both density and KPY ($p < 0.01$). While density showed significant
306 rank changes between sites ($p < 0.01$), no rank changes were evident for KPY
307 ($p<.73$). The significance of differences between provenances could be attributed to
308 Brooyar. Across sites, Brooyar was significantly more dense than all other
309 provenances ($p < 0.01$) and there were no differences between the other populations
310 ($p > 0.1$). Conversely, Kraft pulp yield for Brooyar was significantly lower than that of

311   all other provenances (p < 0.01) and again there were no differences among the
312   other populations (p > 0.1). Gardner et al (2007) found in other *Corymbia* species
313   grown in South Africa on a similar site (False Bay) lower absolute values with density
314   of *C.henryi*=658 kg/m^3 and *C.citriodora* ssp. *citriodora*=672 kg/m^3 with KPY
315   *C.henryi*=53.3 kg/m^3 and *C.citriodora* ssp. *citriodora*=%53.5. Compared to these
316   estimates, the average wood density of 756 kg/m^3 and pulp yield of 55% found in
317   these trials indicate the species has considerable potential as a pulpwood crop when
318   grown in southeast Queensland.

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

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

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

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

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

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

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

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

378 **Figure 2** – Percent of maximum gain achievable … **NEAR HERE**

379 **Discussion**
380 *Corymbia citriodora* subsp. *variegata* is an important species for plantation
381 development in lower rainfall areas of the Australian subtropics (Nichols et al. 2010)
382 and this has led to three genetic improvement programs within Australia (Lee 2007).
383 As this study is the first to provide multi-site genetic parameter estimates for a range
384 of traits in a *Corymbia* species, comparisons are made with other hardwood species.

385 The coastal provenances of CCV that were sourced from native forests
386 geographically close to the three progeny trials (Woondum, Home, and Wolvi) and
387 several provenances from New South Wales (Grange, Cherry Tree, Kangaroo and
388 Richmond Range), grew well in these trials. Similar findings were reported by
389 Johnson et al (2009) where Richmond Range, Home, Wolvi and Woondum were
390 superior for growth traits in one trial established in Northern New South Wales

391   (NSW). Interestingly, in the NSW trial Grange was reported to perform poorly while
392   Brooyar and Wondai were reported to perform well; the opposite was found in these
393   trials. The reported superiority of the coastal provenances from Queensland has
394   been associated with higher levels of tolerance to the fungal pathogen *Quambalaria*
395   *pitereka* (Dickinson et al. 2004, Lee et al. 2009, Pegg et al. 2005) and this resistance
396   has been associated with provenances originating from higher rainfall coastal areas
397   (Johnson et al. 2009). The poor performance of the families from the South African
398   clonal seed orchard, which grew significantly less than all provenances but Esk
399   (p<0.05), may have been the result of an increased early incidence of a shoot blight
400   fungi (Brawner et al. 2011) or intense selection for a distinct environment.

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

416   Single-site heritability estimates for volume using Model 1 (Table 2) were similar to
417   those presented by Johnson et al (2009) for DBH and height and are similar to those
418   reported for many forest tree species (Cornelius 1994). Typically, heritability
419   estimates based on single trials are biased upward due to the inability to partial out
420   variance due to genotype by environment interactions (Hodge and White 1992),
421   however Model 1 accounts for between trial covariance and theoretically provides
422   less biased estimates. Heritability estimates for wood properties were consistently
423   greater than heritability estimates for volume, which has also been reported for a
424   range of other forest tree species. When compared with other hardwood species
425   parameters for growth data, the among-provenance variance of the CCV populations
426   evaluated in these trials is high: $\hat{P}^2 = 0.03$ for *E. urophylla* (Hodge et al. 2001) and

427   $\hat{P}^2 = 0.10$ for *Gmelina arborea* (Hodge and Dvorak 2004). For volume at the early or
428   later age of assessments, these results indicate differences between populations will
429   be more important in CCV breeding than in other forest tree species and strengthen
430   the case for selecting individuals from many populations rather than focusing on a
431   few local populations.   Type-B correlations between these trials indicate genotype

432 by environment interactions are of little importance. While the three sites differed in
433 climatic and edaphic characteristics, this result may have been expected as the
434 sample of environments was geographically limited. The notable exception to this
435 general trend was for density, which has been frequently cited as a stable trait in
436 forest tree populations.

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

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

464 In figure 2, the trade-offs in gain maximisation arising from changes in the
465 importance of selection traits are consistently presented with respect to the gain that
466 may be achieved in pulp productivity. Figures 2.1 and 2.2 clearly demonstrate the
467 importance of volume production in realising improvements in pulp productivity. The
468 relative importance of these traits will likely change in advanced generations as less
469 productive populations and families are culled. As well, the end-product or
470 processing may place restrictions on the rate at which some traits are allowed to be
471 changed in the genetic improvement program. For example, in a South African
472 study that included *Corymbia* species, the species' wood density was found to be
473 higher than the optimal range desired for local pulp mills but quite suitable for a chip

474 export markets (Gardner et al. 2007). Using the results presented in Figure 2,
475 changes in density could be minimised without unduly limiting pulp productivity
476 improvement by applying a selection index that places a weight of 70% on volume
477 and 30% on KPY. Nevertheless, due to the positive correlation between volume and
478 density, selection for volume production alone is expected to increase the density of
479 resulting plantations by less than two percent.

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

490

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

509

510 **Acknowledgements**

519 **Appendices**

520 **A1 – Summary of NIR Calibration**
521 The summary statistics for the NIR calibration models used in the prediction of Kraft
522 pulp yield and density are:

523

|	R^2 (calib.)	r^2 (valid)	RMSEP[1]	Factors	Treatment	
Density (kg/m^3)	0.71	0.70	44	8	1st deriv.	unpublished
Kraft pulp yield (%)	0.94	0.83	0.95	5	2nd derive.	(Meder et al. 2011)

526 [1]RMSEP: Root-mean-square-error-of-prediction, where the mean error for prediction of density is ±44
527 kg/m^3 and for Kraft pulp yield is ±0.95. For example, a NIR-predicted Kraft pulp yield value of 52.0 %
528 the value is in the range 51.05 – 52.95 %.

529
530

531   **Figures**

532   Figure 1 – Provenances of *Corymbia citriodora* subsp. *variegata* sampled for
533   inclusion in the spotted gum breeding program and evaluated for growth and wood
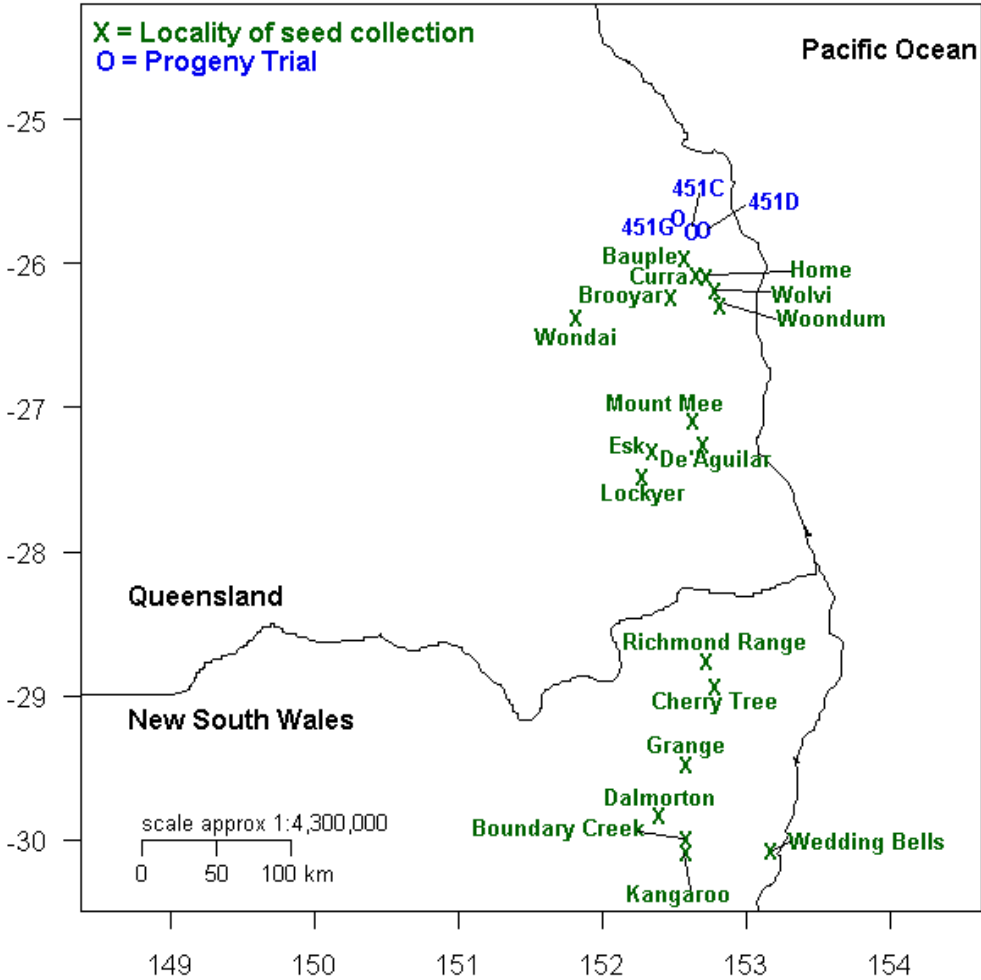534   properties in three progeny trials established in southeast Queensland
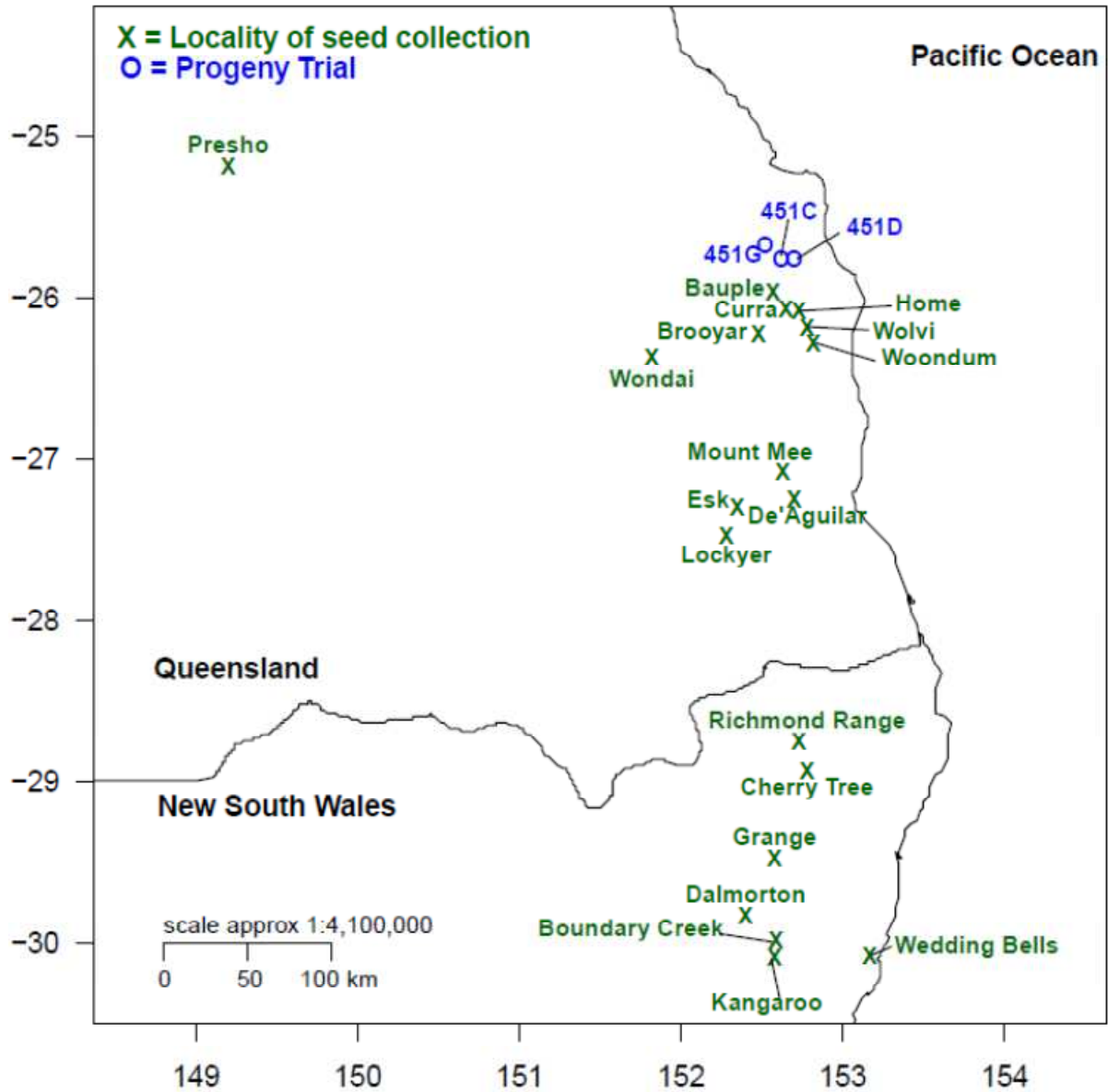

535
536   PDF File

537

538   BMP file

539

540 **Figure 2** – Percent of maximum gain achievable for target traits following selection
541 of the top 10% of the *Corymbia citriodora* population using an index with weights
542 incremented by 10% for each selection trait and restricted to sum to 100% for pairs
543 of traits including individual tree volume (Vol), basic density (Den) and Kraft pulp
544 yield (KPY). The composite trait of Pulp productivity is also included. Indices on X
545 axis indicate percent weighting applied to the selection traits Vol, Den and KPY.
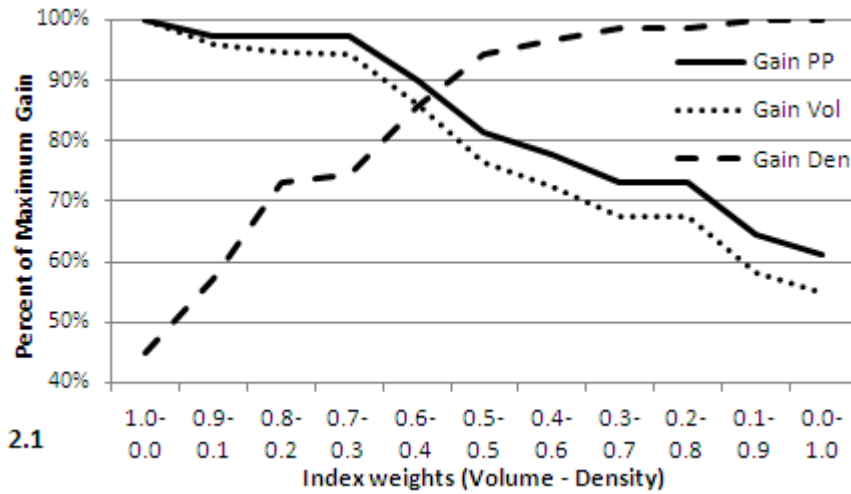
546
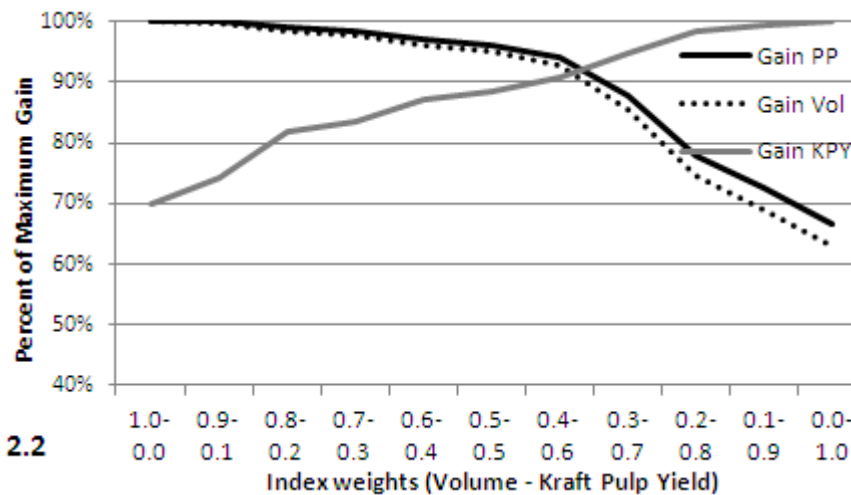
547
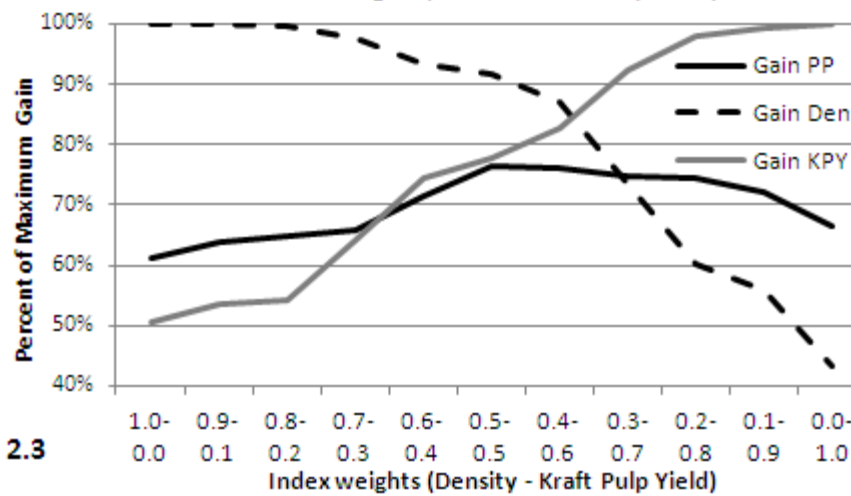
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551

552 **Tables**

553 **Table 1** - Description of progeny trials and assessments used to evaluate *Corymbia citriodora* ssp. *variegata* populations

Trial	Location	Established	Material[a]	Design[b]	Latitude	Longitude	Assess[c]	Thin[d]	Total stems	WQ stems[e]
451c	Tairo Camp	Mar-99	14 (122)	8, 5, 2	25.78⁰ S	152.63⁰ E	32, 53	34 (51)	1520	128
451d	Bakers	Jul-00	14 (242)	7, 21, 4	25.76⁰ S	152.68⁰ E	37, 74	No thin (92)	7247	994
451g	St Mary's	May-02	12 (138)	5, 12, 4	25.67⁰ S	152.52⁰ E	43, 89	50 (48)	2880	296

554 a. Genetic material established in trials with number of provenances followed by number of open pollinated families in parentheses
555 b. Design lists number of replications, incomplete blocks per replication and trees per contiguous family plot, respectively
556 c. Age of diameter at breast height and total tree height assessments in months from planting
557 d. Age of thinning(s) in months from planting with percent of trees remaining at second assessment in parentheses
558 e. Number of stems assessed for wood quality
559

560

561 **Table 2** – Least square means, with standard errors in parenthesis, for provenances of *Corymbia citriodora* evaluated in
562 provenance trials for 6-year-old volume growth (the latter of two assessments), basic density and Kraft pulp yield

	6-year Volume (dm^3)			Density (kg/m^3)			Kraft pulp yield (%)		
	451C	451D	451G	451C	451D	451G	451C	451D	451G
Bauple		0.42 (0.06)							
Boundary Creek	1.00 (0.19)	0.52 (0.05)	1.66 (0.13)						
Brooyar	0.72 (0.08)	0.39 (0.04)	1.40 (0.10)	756 (12)	770 (5)	798 (8)	53.8 (0.8)	54.0 (0.4)	54.6 (0.6)
Cherry Tree			1.89 (0.05)						
Curra			1.45 (0.07)			749 (7)			54.3 (0.4)
De'Aguilar			0.96 (0.05)						
Dalmorton	0.80 (0.26)	0.54 (0.07)	1.67 (0.18)						
Esk	0.33 (0.07)	0.25 (0.06)							
Grange	1.25 (0.26)								
Home	1.01 (0.07)	0.59 (0.04)	1.66 (0.09)	732 (7)	759 (4)	764 (8)	55.9 (0.5)	55.1 (0.3)	55.7 (0.5)
Kangaroo	1.10 (0.10)	0.55 (0.06)							
Lockyer	0.39 (0.07)	0.34 (0.08)							
Mount-Mee			1.26 (0.05)						
Richmond Range	0.77 (0.26)	0.51 (0.05)	2.04 (0.10)						
SA-CSO[1]	0.14 (0.08)								
Wedding Bells		0.48 (0.05)							
Wolvi	0.86 (0.06)	0.55 (0.03)	1.94 (0.07)	746 (7)	753 (4)	767 (7)	54.9 (0.5)	55.2 (0.3)	55.5 (0.4)
Wondai	0.46 (0.09)	0.47 (0.12)							
Woondum	0.88 (0.05)	0.52 (0.03)	1.89 (0.04)	758 (5)	754 (3)	762 (4)	55.2 (0.4)	55.2 (0.2)	55.9 (0.3)

563 [1] South African clonal seed orchard bulk

564

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

	3-year Volume (dm^3)			6-year Volume (dm^3)			Density (kg/m^3)			Kraft Pulp Yield (%)		
	451C	451D	451G	451C	451D	451G	451C	451D	451G	451C	451D	451G
Performance statistics												
	0.19	0.13	0.28	0.70	0.52	1.58	749 (34)	755 (37)	764 (37)	55.16	55.1 (2.4)	55.6
	(0.22)	(0.11)	(0.25)	(0.61)	(0.46)	(1.02)				(2.2)		(2.4)
Family genetic parameter estimates												
451 C	**0.33**			**0.43**			**0.12**			**0.15**		
	(0.07)			**(0.11)**			**(0.28)**			**(0.30)**		
451 D	0.84	**0.25**		1.00	**0.23**		0.95	**0.46**		0.87	**0.38**	
	(0.11)	**(0.03)**		(0.13)	**(0.03)**		(1.19)	**(0.10)**		(0.92)	**(0.09)**	
451 G	0.96	0.66	**0.20**	0.92	0.95	**0.25**	0.84	0.94	**0.79**	0.74	0.97	**0.33**
	(0.26)	(0.19)	**(0.04)**	(0.34)	(0.18)	**(0.07)**	(1.15)	(0.19)	**(0.20)**	(1.38)	(0.33)	**(0.18)**
Provenance genetic parameter estimates												
451 C	**0.17**			**0.21**			**0.13**			**0.13**		
	(0.08)			**(0.09)**			**(0.15)**			**(0.16)**		
451 D	0.94	**0.02**		1.00	**0.07**		-0.13	**0.02**		0.99	**0.06**	
	(0.16)	**(0.01)**		(0.03)	**(0.03)**		(1.06)	**(0.03)**		(0.30)	**(0.07)**	
451 G	0.78	0.94	**0.04**	0.94	0.92	**0.15**	0.48	0.79	**0.07**	0.99	1.00	**0.13**
	(0.29)	(0.22)	**(0.03)**	(0.11)	(0.12)	**(0.08)**	(0.80)	(1.00)	**(0.11)**	(0.28)	(0.20)	**(0.12)**

571

572

573

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

	3-year volume m^3	6-year volume m^3	Density kg/m^3	Kraft Pulp Yield %
Family				
3-year volume	**0.25 (0.03)**			
6-year volume	0.98 (0.01)	**0.22 (0.02)**		
Density	0.42 (0.10)	0.39 (0.10)	**0.51 (0.08)**	
Kraft Pulp Yield	0.45 (0.11)	0.48 (0.11)	0.26 (0.14)	**0.32 (0.07)**
Provenance				
3-year volume	**0.07 (0.03)**			
6-year Volume	0.98 (0.01)	**0.10 (0.04)**		
Density	0.09 (0.88)	-0.10 (0.89)	**0.01 (0.03)**	
Kraft Pulp Yield	0.82 (0.21)	0.92 (0.14)	-0.47 (0.90)	**0.11 (0.07)**

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