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► To cite this version:

Jean-Marc Bouvet, Chrissy Garel Makouanzi Ekomono, Oliver Brendel, Jean-Paul Laclau, Jean-Pierre Bouillet, et al.. Selecting for water use efficiency, wood chemical traits and biomass with genomic selection in a Eucalyptus breeding program. *Forest Ecology and Management*, 2020, 465, pp.118092. 10.1016/j.foreco.2020.118092 . hal-02534416

HAL Id: hal-02534416

<https://hal.inrae.fr/hal-02534416>

Submitted on 22 Aug 2022

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1 **Selecting for water use efficiency, wood chemical traits and biomass with**
2 **genomic selection in a *Eucalyptus* breeding program**

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25 **Highlights**

- 26 • Selecting *Eucalyptus* ideotypes is a major challenge for plantations in dry zones
- 27 • Genomic selection improves selection accuracy of breeding and clonal populations
- 28 • Water use efficiency (WUE), volume, and wood traits are under a strong genetic control
- 29 • Correlations between volume, WUE, lignin and cellulose are low in *Eucalyptus*
- 30 • Index selection can lead to suitable genetic gains to enhance WUE and wood properties

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Abstract

The selection of ideotypes combining high biomass production, high water use efficiency (WUE) and adequate wood properties is a major challenge in improving forest trees for industrial plantations. This issue was addressed in a field experiment evaluating 1130 clones of *Eucalyptus urophylla* * *Eucalyptus grandis*. Genomic selection using 3303 SNPs and the GBLUP model was carried out at age 55 months to select genitors and clones for stem volume (V55), WUE (using stable carbon isotope composition in stemwood, $\delta^{13}\text{C}$, as a proxy transformed into intrinsic WUE, Wi), as well as lignin (KL) and holocellulose (HCEL) contents. The variance components were mainly additive for $\delta^{13}\text{C}$ (Wi), KL and HCEL, while they were highly non-additive for V55 (the ratio of dominance to additive variance was 130%). The narrow sense heritability was higher for Wi ($h^2=0.704$) than for volume and wood traits (<0.5), showing that this trait was under strong genetic control. Additive and total genetic correlations among traits were low (between -0.265 and 0.265]) as were the correlations due to environmental effects (between -0.267 and 0.348), which suggests a rather independence among traits. The equal emphasis and the desired gain index selection methods were used to assess economic weights and to estimate the expected gains. Different breeding objectives were defined with percentages weighting the economic coefficients or the desired gain for the equal emphasis or desired gain method, respectively. When the breeding objective gave emphasis to volume production using the percentages of 70%, 10%, 10%, and 10% for V55, HCEL, KL and Wi, respectively, positive gains were observed in both methods, but the correlation between index rankings were 0.686 and 0.635 for breeding and clonal selection, respectively. With a more balanced breeding objective using percentages such as 25%, 25%, 25%, 25% for V55, HCEL, KL and Wi, respectively, both index methods gave close positive gains and similar rankings, the correlation between index rankings ranging from 0.941 to 0.982 for parent selection and from 0.883 to 0.903 for clone selection. With more contrasted percentages between V55 and Wi, such as (80%, 10%, 10%, 0%) or (90%, 10%, 10%, -10%), the gain increased for V55 and was close to the maximum and decreased markedly for Wi. This study explores the magnitude of economic coefficients for index selection and shows that positive genetic gains can be achieved by associating biomass, a proxy of WUE and wood chemical traits. It provides encouraging results for selecting *Eucalyptus* varieties adapted to dry zones while maintaining good performances regarding other economic traits.

Key words: eucalypt hybrid, growth, water use efficiency, wood chemistry, genomic selection, heritability, genetic correlation, index selection

67

68 1. Introduction

69

70 Forest plantations are viewed as one means of meeting the growing demand for biomass in
71 temperate (Wartelle and Dreyfus, 2010) as well as in sub-tropical and tropical regions (FAO, 2010).
72 Tree breeding programs have been carried out with many tree species to produce varieties
73 presenting high volume and lignin concentration for fuelwood production, or high volume and
74 cellulose concentrations for the pulp and paper market. Such programs are conducted for *Eucalyptus*
75 commercial plantations in many parts of the Mediterranean and tropical zones with intensive
76 silviculture (de Oliveira Castro et al., 2016). However, the duration of drought periods is expected to
77 increase because of the climate change in many regions and *Eucalyptus* plantations are expected to
78 extend to drier areas. Both concerns raise a major threat to the sustainability of intensively managed
79 plantations, for example in Brazil (Booth, 2013) and in South Africa (Albaugh et al., 2013). Selection
80 criteria enhancing the efficiency of water use for biomass production are therefore required to
81 develop genotypes better adapted to water-limited areas making it possible to use less water for the
82 same biomass production. These critical questions related to selection for wood products and water
83 resource use efficiency have promoted research in ecophysiology and genetics, with some efforts to
84 combine them.

85

86 Research in ecophysiology has improved our understanding of tree adaptation by addressing
87 complex traits that play a critical role in adaptation. This is the case of water use efficiency (WUE),
88 which can be defined as the ratio between harvested biomass and the amount of water used to
89 produce this biomass (Hsiao and Acevedo, 1974). At the leaf level, WUE is defined as the ratio
90 between net CO₂ assimilation rate to stomatal conductance for water vapor and is called intrinsic
91 WUE (W_i). Discrimination against ¹³CO₂ during photosynthesis is used as a time-integrated surrogate
92 for W_i (Farquhar and Richards, 1984; Condon *et al.*, 1990). Therefore, differences in W_i among plants
93 are thought to translate into differences in stable carbon isotope composition ($\delta^{13}\text{C}$) of plant organic
94 material. $\delta^{13}\text{C}$ has proven to be robust in predicting differences in WUE in both leaves and whole
95 plants, among plant species or genotypes (Condon *et al.*, 2004), including tree species (Roussel et al.,
96 2009a, b; Rasheed et al., 2013). Similar results were observed for *Eucalyptus* trees (Osorio et al.,
97 1994, 1998; Li et al., 2000). Owing its ease of measurement by isotopic mass ratio spectrometry, $\delta^{13}\text{C}$
98 allows large-scale screening of phenotypes under a range of environments and is therefore a tool for
99 disentangling genotypic and environmental effects using different experimental approaches and
100 models (Chen *et al.*, 2011).

101

102 Although our understanding of the genetic bases of $\delta^{13}\text{C}$ has improved in *Araucaria* (Xu et al., 2003),
103 *Quercus* (Brendel et al., 2008), *Eucalyptus* (Bartholomé et al., 2015), and *Pinus* (Cumbie et al., 2011;
104 Marguerit et al., 2014; Plomion et al., 2016), the factors influencing the variations of this proxy of
105 WUE in breeding populations remain poorly understood. Research is still needed to gain insight into
106 the genetic and environmental effects in phenotype variation and plasticity. The relationships
107 between WUE, growth and wood traits have been little documented, and the results are still partial
108 and sometimes inconsistent. Depending on experiments, biomass production and WUE can be
109 positively correlated (Le Roux et al., 1996), negatively correlated (Monclus et al., 2005) or not
110 correlated (Cumbie *et al.*, 2011). It is difficult to determine whether these divergent results are due
111 to sampling or to species or environmental effects. A meta-analysis showed a positive global intra-
112 specific correlation between $\delta^{13}\text{C}$ and height (Gr= 0.28, P<0.0001), a stronger correlation for biomass
113 than for height (Gr= 0.68, P<0.0001), and a non-significant correlation for diameter (Gr= 0.04,
114 P<0.64) (Fardusi et al., 2016). However, the authors did not study the influence of genetic and
115 environmental effects on these correlations. Better knowledge of genetic and environmental
116 correlations is a key issue in guiding tree breeding programs. This is especially critical when WUE and
117 growth traits are negatively correlated genetically and when increasing genetic gain in WUE leads to
118 a decrease in productivity. Similarly, increased genetic gain in WUE should not be at the expense of
119 wood quality, which will depend on the end use of the wood (high lignin content for fuelwood or
120 high cellulose content for pulpwood). Few data are available for understanding how genetic and
121 environmental conditions are shaping the relationships between WUE, biomass production and
122 wood properties.

123

124 Several questions must be addressed, especially for *Eucalyptus* species planted in marginal zones
125 where water availability may become a critical issue (Stape et al., 2010, Christina et al., 2016). What
126 is the contribution of additive and non-additive gene effects in the expression of WUE, biomass
127 production and wood property traits? What is the magnitude of the genetic and environmental
128 correlations between WUE and other traits? Can we carry out an effective index selection combining
129 suitable performances for biomass production, WUE and wood property traits? Using a field
130 experiment with clones from *Eucalyptus* hybrid families planted in humid tropical conditions on a
131 soil with a low water holding capacity, the objectives of our study were: (i) to gain insights into the
132 genetic and environmental components controlling $\delta^{13}\text{C}$, stem volume and wood chemical traits, (ii)
133 to assess the genetic and environmental correlations between those traits, (iii) to analyze the effect
134 of multi-trait selection on the genetic gain for the traits of interest, and (iv) to draw the
135 consequences in terms of selection of ideotypes for different breeding objectives.

136

137

138 **2. Material and methods**

139

140 **2.1. Field experimental data**

141 The study was conducted using a *Eucalyptus* progeny trial located east of Pointe-Noire (11°59' 21" E,
142 4°45' 51" S) in the Republic of the Congo. Rainfall averaged 1200 mm/year. The soils were deep
143 Ferralic Arenosols characterized by low water retention, a very low level of organic matter and poor
144 cationic exchange capacity (Mareschal et al., 2011). The plant material resulted from controlled
145 pollination crosses of thirteen *Eucalyptus urophylla* S.T. Blake females and nine *Eucalyptus grandis*
146 Hill ex Maid. males according to a factorial mating design. [Parents of each species came from
147 different provenances in order to maximize the variability. No clear genetic structure was detected
148 using molecular information \(data not shown\). The membership of a group was not considered in
149 genetic analyses.](#) These crosses generated 69 full-sib families and 1415 progenies. Each of the 1415
150 progenies was replicated three times using cuttings and a clonally replicated progeny test was
151 planted at a stocking density of 833 trees ha⁻¹. The field experiment was a complete block design
152 with three replications. Twenty-five trees replicated in three blocks represented each full-sib family.
153 The total number of trees used in this study was reduced to 3596, representing 1130 clones, because
154 of natural mortality.

155

156 **2.2. Measured traits**

157 Total tree height (HT) and circumference at breast height (C) were measured 55 months after
158 planting and used to calculate a proxy of the total tree volume (V₅₅) using the cylinder formula with
159 a stem form factor of 0.3 (Schröder et al., 2013). To avoid difficulties in statistical mixed model
160 convergence and variance estimation, the volume data were normalized using a logarithmic
161 transformation.

162 Wood samples were collected at age 55 months from 1690 trees for near-infrared spectroscopy
163 (NIRS) analyses. The wood chips were collected by drilling each tree to the heart of the stem at a
164 height of 1.3 m. The wood chips were dried and ground (particle size 4 mm) and NIRS models were
165 used to estimate Klason lignin (KL) and holo-cellulose content (HCEL). We used existing NIRS models
166 of multiple *Eucalyptus* species that included samples from this study (Denis et al., 2013). The model
167 was built using about 3,000 wood samples collected from six *Eucalyptus* species and hybrid
168 plantations of ages ranging from 5 to 30 years located in Congo, Senegal and Brazil. One hundred
169 samples were selected using the Mahalanobis distance calculated from spectral information to
170 measure wood chemistry traits through wet chemistry (Chaix et al., 2015), then spectral and wet
171 chemistry data were used to calibrate NIRS predictions (Denis et al., 2013).

172

173 Stable carbon isotope composition ($\delta^{13}\text{C}$) of wood was measured on the same samples as those used
174 for NIRS after grinding them to a fine powder (<0.1 mm). One mg of the powder was enclosed in a tin
175 capsule and analyzed with an elemental analyzer (Carlo Erba, NA 1500-NC, Milan, Italy) coupled to an
176 isotope-ratio mass spectrometer (Finnigan, Delta S, Bremen, Germany). $\delta^{13}\text{C}$ was expressed
177 according to the international standard (Vienna Pee Dee Belemnite, VPDB). The accuracy of the
178 analyses (standard deviation below 0.2‰) was assessed by repeated measurements of several
179 laboratory standards. Due to the large number of sampled trees (1690), $\delta^{13}\text{C}$ was measured on wood
180 rather than on cellulose. Cellulose has the advantage of being more homogeneous chemically and is
181 produced with fewer biochemical steps from transported phloem sugars, therefore providing a less
182 noisy integration of the isotopic leaf signal than wood. The difference between wood and cellulose
183 $\delta^{13}\text{C}$ might be mainly impacted by variations in the content of lignin, which is isotopically lighter
184 (Bowling et al., 2008). Therefore, on a subsample of 100 trees, cellulose and lignin were extracted
185 using the methods of Chaix et al. (2015) and isotopic analyses were done as described above. The
186 linear regression between wood and cellulose $\delta^{13}\text{C}$ was highly significant ($p < 0.001$) and strong
187 (adjusted R^2 was 0.97). The $\delta^{13}\text{C}$ of extracted lignin was on average 2.9‰ more negative than the
188 values for cellulose, which is close to the offset observed by Benner et al. (1987) of 4 ‰ to 7 ‰ for
189 other forest tree species. However, the difference between $\delta^{13}\text{C}$ in wood and $\delta^{13}\text{C}$ in cellulose was
190 steady and not related to the amount of lignin in the wood. The genotype ranking was similar using
191 $\delta^{13}\text{C}$ measured either on cellulose or on bulk wood. These results showed that wood $\delta^{13}\text{C}$ was a
192 robust estimator of cellulose $\delta^{13}\text{C}$ in our dataset.

193

194 Because the CV of $\delta^{13}\text{C}$ cannot be calculated, as $\delta^{13}\text{C}$ is not an absolute value but a deviation from a
195 standard (Brendel, 2014), we converted the $\delta^{13}\text{C}$ of each tree into intrinsic WUE (W_i) using the
196 Farquhar equation (Farquhar and Richards, 1984): $W_i = \text{Ca} (1 - (\delta^{13}\text{C}_{\text{air}} - \delta^{13}\text{C} - 4.4)/22.6)/1.6$ with $\text{Ca} =$
197 400 ppm and $\delta^{13}\text{C}_{\text{air}} = -8 \text{ ‰}$. It must be stressed that W_i is a linear transformation of $\delta^{13}\text{C}$ for statistical
198 purposes and not a robust estimate of intrinsic WUE which would have required use of a more
199 complex set of equations for which we did not have all the parameters required.

200

201 **2.3. Statistical model**

202 We used a linear mixed model combining genetic and environmental effects to analyze the data.
203 Different models were tested using AIC criteria (Aikake, 1974), especially using autoregressive
204 functions to take into account spatial effects and competition. Finally, the following model was
205 implemented:

206

$$y = X\beta + Z_{col}col + Z_{r.b}r:b + Z_c a_f + Z_c a_m + Z_c d + \epsilon \quad [model (1)]$$

207 Where \mathbf{y} was the vector of the phenotypic variable (V55, $\delta^{13}\text{C}$, W_i , KL and HCEL measured at 55
 208 months), $\boldsymbol{\theta}$ was the vector of fixed effects due to the general mean and blocks, $\mathbf{col} \sim N(\mathbf{0}, \sigma^2_{\text{col}}\mathbf{Id})$ was
 209 the vector of random spatial environmental effects due to the field design column, with σ^2_{col} being
 210 the variance related to the spatial effects, \mathbf{Id} was the identity matrix, $\mathbf{r:b} \sim N(\mathbf{0}, \sigma^2_{\text{r:b}}\mathbf{Id})$ was the vector
 211 of random spatial environmental effects due to field design row by block interaction, with $\sigma^2_{\text{r:b}}$ being
 212 the variance related to the spatial effects. The genetic effects were defined by: $\mathbf{a}_f \sim N(\mathbf{0}, \sigma^2_{\text{af}}\mathbf{A}^{\text{H}}_{\text{fg}})$, \mathbf{a}_m
 213 $\sim N(\mathbf{0}, \sigma^2_{\text{am}}\mathbf{A}^{\text{H}}_{\text{mg}})$ and $\mathbf{d} \sim N(\mathbf{0}, \sigma^2_{\text{d}}\mathbf{D}^{\text{H}}_{\text{G}})$ with $\mathbf{A}^{\text{H}}_{\text{fg}}[\text{c,c}]$ and $\mathbf{A}^{\text{H}}_{\text{mg}}[\text{c,c}]$ the molecular-based female and
 214 male additive relationship matrices, $\mathbf{D}^{\text{H}}_{\text{G}}[\text{c,c}]$ the dominance relationship matrix.

215 \mathbf{X} , \mathbf{Z}_{col} , $\mathbf{Z}_{\text{r:b}}$, \mathbf{Z}_p , and \mathbf{Z}_c were the incidence matrices connecting the fixed and random effects to the
 216 data. The female and male additive molecular marker-based coancestry matrices $\mathbf{A}^{\text{H}}_{\text{fg}}[\text{c,c}]$ $\mathbf{A}^{\text{H}}_{\text{mg}}[\text{c,c}]$
 217 were derived from the haplotypes of each progeny according to Van Raden's estimator using 3303
 218 single nucleotide polymorphism markers, see details in Bouvet et al. (2016). The variance component
 219 estimation based on the REML method and the BLUP calculations were done using the ASReml
 220 version 3 package (Gilmour *et al.*, 2006) implemented in R software (R Development Core Team,
 221 2011).

222

223 Narrow- and broad-sense heritabilities were defined by $h^2 = \sigma^2_{\text{a}}/\sigma^2_{\text{p}}$ (eq. 1) and $H^2 = \sigma^2_{\text{g}}/\sigma^2_{\text{p}}$ (eq. 2).
 224 The dominance variance ratios representing the part of dominance variance in total variance was
 225 defined by $d^2 = \sigma^2_{\text{d}}/\sigma^2_{\text{p}}$ (eq. 3). These ratios were calculated with σ^2_{a} , σ^2_{g} and σ^2_{p} defined as the
 226 additive ($\sigma^2_{\text{a}} = \sigma^2_{\text{am}} + \sigma^2_{\text{af}}$) (eq. 4), the total genetic ($\sigma^2_{\text{g}} = \sigma^2_{\text{am}} + \sigma^2_{\text{af}} + \sigma^2_{\text{d}}$) (eq. 5) and the phenotypic
 227 variances ($\sigma^2_{\text{p}} = \sigma^2_{\text{am}} + \sigma^2_{\text{af}} + \sigma^2_{\text{d}} + \sigma^2_{\text{e}}/2$) (eq. 6).

228

229 The correlation estimates were obtained using model (1) in the multivariate formulation
 230 (Rambolarimanana et al., 2018). The correlations related to genetic and environmental effects
 231 between traits 1 and 2 were calculated with the following formulas:

232 the additive genetic correlation $\rho_{\text{a}} = (\text{cov}_{\text{a}(1,2)})/(\sigma_{\text{a1}}) (\sigma_{\text{a2}})$ (eq. 7)

233 the dominance correlation $\rho_{\text{d}} = (\text{cov}_{\text{d}(1,2)})/(\sigma_{\text{d1}}) (\sigma_{\text{d2}})$ (eq. 8)

234 the total genetic correlation $\rho_{\text{g}} = (\text{cov}_{\text{g}(1,2)})/(\sigma_{\text{g1}}) (\sigma_{\text{g2}})$ (eq. 9)

235 the residual (environmental) correlation $\rho_{\text{e}} = (\text{cov}_{\text{e}(1,2)})/(\sigma_{\text{e1}}) (\sigma_{\text{e2}})$ (eq. 10)

236 where $\text{cov}_{(1,2)}$ is the covariance between traits 1 and 2 and σ_1 , σ_2 are the standard deviations of traits
 237 1 and 2, respectively. Approximate standard errors for linear functions of variance components were
 238 calculated using the pin.R function. This function, proposed by Ian White (2013)
 239 (<http://www.homepages.ed.ac.uk/iwhite/asreml/>), applies the delta method for the estimation of
 240 approximate standard errors (Oehlert, 1992).

241

242 The best linear unbiased predictors (BLUP) related to the additive (BLUP_u) and total (BLUP_g) genetic
243 effects were computed by solving the mixed model equations. The BLUP_u was calculated by the
244 addition of male and female random coefficients estimated with the ASReml package. The BLUP_g was
245 calculated with the addition of male, female and male by female interaction random coefficients
246 estimated with the ASReml package.

247

248 **2.4. Index selection and genetic gain**

249 We investigated the multiple trait selection combining four traits: V55, HCEL, KL and W_i. We
250 considered the breeding context of massal selection starting from a breeding population composed
251 of the 1130 hybrid clones. Two genetic gains were calculated: i) the additive genetic gain based on
252 breeding values, resulting from selection and crossings of the selected parents in successive
253 generations, and ii) the total genetic gain based on total genetic values for dissemination of clones as
254 varieties.

255 The approach was derived from the index selection method (Smith 1936; Hazel 1943). We
256 considered the breeding objective (Hazel 1943), also defined as the aggregate breeding value “H”
257 (Hazel et al., 1994) and developed in tree breeding (Cotterill and Dean, 1990; Berlin et al., 2012). It
258 was calculated using the additive BLUP for the four traits of a tree “l” defined by the vector “u_i” or
259 total genetic BLUP for the four traits “g_i” estimated with model (1) and economic weights a₁, a₂, a₃
260 and a₄ for V55, W_i, KL, HCEL, respectively. For an individual *i*, **H** was defined as $\mathbf{H}_{ui} = \mathbf{u}_i \mathbf{a}_u$. (eq. 11)
261 based on additive values and $\mathbf{H}_{gi} = \mathbf{g}_i \mathbf{a}_g$ (eq. 12) based on total genetic values where **a_u** or **a_g** are the
262 vectors of economic coefficients for parents and clone selection, respectively.

263 As we did not have any appropriate bio-economic data or economic function linking traits to
264 economic values, we used the following two methods to define economic weights (Cotteril and
265 Jackson, 1985). The first was based on equal emphasis (Shelbourne and Low 1980). The economic
266 weight for the trait “t” was defined by $a_t = s_t / \sigma_{at}$, where *s_t* is a coefficient related to the relative
267 importance of the trait “t” and σ_{at} is the additive standard deviation of the trait “t”. The economic
268 weights for different economic breeding objectives were calculated using a set “s” (s₁, s₂, s₃, s₄) of
269 percentages giving the relative importance of the trait in the index (the different values “s_t” are given
270 below).

271 The second method was based on the desired gain (Pesek and Baker 1969). The economic
272 coefficients were calculated by $\mathbf{a}_u = \mathbf{G}_u^{-1} \mathbf{P} \mathbf{G}_u \mathbf{d}$ (eq 13), where **G_u** is the additive variance-covariance
273 matrix among traits, **P** is the phenotypic variance-covariance matrix among traits and **d** the vector of
274 desired gain. The set of relative importance “s” was used to estimate the desired gain of the trait “t”
275 $d_t = s_t * \Delta G_{u_{max,t}}$ as the proportion of the maximal gain for each corresponding trait in the index.
276 $\Delta G_{u_{max,t}}$ was defined using equations 14 and 15 (see below).

277

278 For both approaches, we used a set of percentages “s” defining the relative importance of each trait
279 in the breeding objective. This first set was 70%, 10%, 10%, 10% for V55, W_i, KL, HCEL, respectively,
280 which provided a major influence of volume production on the selection index. The second set tested
281 was 40%, 40%, 10%, 10% for V55, W_i, KL, HCEL, respectively, which emphasized volume production
282 and water use efficiency. The third set tested was 30%, 30%, 30%, 10% for V55, W_i, KL, HCEL,
283 respectively, which emphasized volume production, with good water use efficiency for charcoal
284 production. The fourth set tested was 30%, 30%, 10%, 30% for V55, W_i, KL, HCEL, respectively, which
285 emphasized volume production, with good water use efficiency for pulp production. The fifth set
286 tested was 25%, 25%, 25%, 25% for V55, W_i, KL, HCEL, respectively, with a balanced weight among
287 the traits.

288 To facilitate comparison among methods, economic weights were presented as actual values as well
289 as transformed so that V55 has a relative weight of 10 m⁻³.

290

291 To estimate the relative genetic gain in each trait induced by these different breeding objectives as
292 the consequence of selection on index, the following formulas were used (White et al., 2007):

293
$$\Delta G_u = \frac{\frac{1}{n} \sum_1^n (BLUP_{a_{sel}})}{\bar{y}} \text{ (eq. 14)}$$

294

295
$$\Delta G_g = \frac{\frac{1}{n} \sum_1^n (BLUP_{g_{sel}})}{\bar{y}} \text{ (eq. 15)}$$

296 where BLUP was the best linear unbiased predictor estimated using the model 1, BLUP_{a/g_sel} being the
297 BLUP_{a/g} of the selected trees using the index or independent culling level method, n was the number
298 of selected trees and μ was the overall mean. The additive relative genetic gain ΔG_u was calculated
299 using the BLUP_u. The total relative genetic gain ΔG_g was calculated using BLUP_g. The gains were
300 calculated using two selection intensities (the proportion of selected individuals to the total number
301 of trees in the population) of 10 % for parent selection and 1% for clone selection.

302

303

304

305 **3. Results**

306

307 Phenotypic variabilities were highly variable depending on the traits (Table 1). The log-transformed
308 volume stood out with a coefficient of variation (CV) of 18.9%, whereas the wood property traits
309 showed CVs around 5%. The $\delta^{13}C$ values converted to WUE (W_i), showed a CV of 9%. The distribution

310 of V55 showed a marked skewness and the distribution of the three other traits was close to normal
311 (Figure 1).

312

313 **3.1. Variance components and variance ratios**

314 Variance components were well estimated by the linear mixed model, without convergence
315 problems (Table 1). The female and male variance (σ_{af}^2 and σ_{am}^2 , respectively) showed close
316 estimates for V55 and $\delta^{13}\text{C}$ (and W_i), whereas σ_{af}^2 was much higher than σ_{am}^2 for HCEL and KL. This
317 result suggested a higher variability of the *E. urophylla* parent set than the *E. grandis* parent set for
318 these latter traits. The variance ratios showed clear differences between V55 and the other traits.
319 The V55 variable was characterized by a large part of the dominance variance as shown by d^2/h^2
320 $=1.379$. On the other hand, we noted the absence of dominance variance for $\delta^{13}\text{C}$ (and W_i), KL and
321 HCEL with d^2/h^2 equal to zero.

322

323 As expected, the narrow sense heritability (h^2) was smaller than the broad sense heritability (H^2),
324 except when the dominance variance was null. This was the case for $\delta^{13}\text{C}$ (and W_i), KL and HCEL with
325 similar values of h^2 and H^2 . Differences in heritability estimates were high among traits. Narrow sense
326 heritability was the smallest for HCEL ($h^2=0.290$) and the highest for $\delta^{13}\text{C}$ ($h^2=0.704$). This trend
327 changed markedly for broad sense heritability where V55 showed the highest estimate as a result of
328 the marked dominance variance ($H^2=0.727$).

329

330 **3.2. Correlations**

331 Globally, our results stressed the low to moderate genetic and environmental correlations between
332 traits (Table 2). We noted small positive additive genetic correlations ($\rho_a < 0.300$) between V55 and
333 wood chemical traits and low negative additive genetic correlations between V55 and $\delta^{13}\text{C}$ ($\rho_a \approx$
334 -0.265 (or -0.260) for W_i). Similarly, correlations between wood chemical traits and $\delta^{13}\text{C}$ (or W_i) were
335 not strong and negative estimates were observed ($\rho_a = -0.101$ and $\rho_a = -0.192$ for HCEL and KL,
336 respectively). The correlations due to the dominance effect were null for all the combinations of $\delta^{13}\text{C}$
337 (or W_i), KL or HCEL because the estimates of the dominance variance were null. As a result, the total
338 genetic correlations were equal to the additive genetic correlations. Most of the environmental
339 correlations were small ($\rho_e < 0.200$ in absolute value), except between V55 and KL ($\rho_e = 0.348$).
340 Similar patterns were noticed for phenotypic correlations.

341

342 **3.3. Index economic coefficients and genetic gains**

343 The method used greatly influenced the estimation of economic coefficients (Table 3). The equal
344 emphasis method provided coefficients whose values were proportional to the percentage set "s"

345 expressing the relative importance of each trait in the breeding objective. For example, with a
346 breeding objective favoring gain in volume, $s=(70\%;10\%;10\%;10\%)$, the transformed economic
347 weights with the equal emphasis method were $a_1=10 \text{ m}^{-3}$, $a_2=1.45 (\mu\text{mol mol}^{-1})^{-1}$, $a_3=1.48 \text{ \%}^{-1}$ and
348 $a_4=1.34 \text{ \%}^{-1}$, while they were $a_1=10 \text{ m}^{-3}$, $a_2=-1.12 (\mu\text{mol mol}^{-1})^{-1}$, $a_3=-0.21 \text{ \%}^{-1}$ and $a_4=0.73 \text{ \%}^{-1}$ with the
349 desired gain method for V55, HCEL, KL and Wi, respectively. The difference between the two
350 methods was greater for an equal percentage of each trait in the breeding objective,
351 $s=(25\%;25\%;25\%;25\%)$, with $a_1=10 \text{ m}^{-3}$, $a_2=9.90 (\mu\text{mol mol}^{-1})^{-1}$, $a_3= 9.80 \text{ \%}^{-1}$ and $a_4=1.98 \text{ \%}^{-1}$ for the
352 equal emphasis method, while they were $a_1=10 \text{ m}^{-3}$, $a_2=30.42 (\mu\text{mol mol}^{-1})^{-1}$, $a_3= 32.67 \text{ \%}^{-1}$ and
353 $a_4=7.25 \text{ \%}^{-1}$ with the desired gain method for V55, HCEL, KL and Wi, respectively. Regarding the
354 additive genetic gain ΔG_u , both methods provided similar estimates, except for
355 $s=(70\%;10\%;10\%;10\%)$. In that case, ΔG_u for Wi was 0.2% with the equal emphasis method and 7.1%
356 with the desired gain method (Table 3). In consequence, the Spearman correlation was the lowest
357 with $s=(70\%;10\%;10\%;10\%)$ ($r=0.686$), while it was close to one with the other sets “s”.

358

359 The same approach was used for clonal selection considering a selection intensity of 1% and
360 including non-additive effects (Table 4). As expected, the total genetic gains ΔG_g were higher than
361 additive genetic gains, especially for V55, KL and Wi. There was a marked difference between
362 methods with $s=(70\%;10\%;10\%;10\%)$ for ΔG_g estimates, leading to the smallest correlation between
363 indices ($r=0.635$). With the other sets “s”, both methods led to close estimates of ΔG_g , r varying
364 between 0.883 and 0.903. We noticed that ΔG_g for V55 was far from the maximum gain (23.2%),
365 which was particularly marked for the desired gain method with ΔG_g smaller than 7% for V55.

366

367

368 **4. Discussion**

369 The approach developed in this study was based on a large sample of 1130 eucalyptus clones
370 belonging to 69 full-sib families that were connected through the crossing of 13 females and 9 males.
371 Each clone was represented by three ramets, allowing the estimation of genetic and environmental
372 variations. Measurements were conducted at 55 months of age, which is a relevant stage for the
373 prediction of adult performance in the context of fast-growing *Eucalyptus* species (Bouvet et al.,
374 2009a). Our genetic and statistical models used relationship matrices estimated from a dense
375 genome-wide genotyping with SNPs. This genomic information leads to better estimates of the
376 variance components than classical pedigree approaches (Bouvet et al., 2016). Variance components
377 and correlations of important traits made it possible to estimate gains with different strategies of
378 index selection and breeding goals.

379

380 **4.1. Part of additive, dominance and environmental effects in trait variation**

381 Volume, Klason lignin and holocellulose presented the means and coefficients of variation usually
382 observed in experiments in similar conditions with the same *Eucalyptus* hybrid (Denis et al., 2013).
383 Very few experiments to our knowledge have measured the variability of $\delta^{13}\text{C}$ based on a large
384 *Eucalyptus* clonal population. In our study, $\delta^{13}\text{C}$ varied between -31 and -27‰; the range was quasi-
385 similar to the one found in a nearby *Eucalyptus* stands based on a single full-sib family in the Congo
386 (Bartholomé et al., 2015) and close to the range reported in *Eucalyptus grandis* trees in a Brazilian
387 experiment (between -26 and -28‰, Epron et al., 2012). A similar range was reported for 49 wild
388 genotypes of *Hevea brasiliensis* in Northern Thailand (Kanpanon et al., 2017), in a full-sib family with
389 *Quercus robur* (Brendel et al., 2008) and in progeny trial of *Pinus pinaster* (Marguerit et al., 2014).
390 This similarity can be explained by the variation of the intrinsic WUE, and hence of $\delta^{13}\text{C}$, which is
391 physiologically constrained by the gradient of CO_2 concentrations between the atmosphere and the
392 intercellular air space (Farquhar et al., 1982).

393 The additive and dominance variance components in this study, as well as their relative magnitude,
394 were consistent with previous genetic studies carried out on *Eucalyptus*. They showed a marked
395 dominance variance for volume and stressed a preponderance of the additive variance for physical
396 and chemical wood traits (Bouvet et al., 2009b). The narrow sense heritability was higher for wood
397 chemical traits than for volume, which was consistent with other studies estimating this parameter
398 for lignin (Poke et al., 2006; Stackpole et al., 2011; Hein et al., 2012; Mandrou et al., 2012; Makouanzi
399 et al., 2017) and holocellulose (Rambolarimanana et al., 2018). The pattern was different for the
400 broad sense heritability (H^2), with higher values for V55 than for wood traits. [This might result from](#)
401 [the preponderance of dominance variance in complex traits such as V55 and from the inability of the](#)
402 [model to take into account inter-tree competition. This effect may have been captured by the male-](#)
403 [by-female interaction inflating the dominance variance. A previous study showed that the](#)
404 [dominance variance for volume increases with tree age and competition in Congolese *Eucalyptus*](#)
405 [plantations \(Bouvet et al., 2003\).](#)

406

407 Our results stressed the high heritability of $\delta^{13}\text{C}$ (W_i) and were consistent with previous findings,
408 although the plant tissue and the heritability magnitude differed: in *Pinus sp.* with needles (Cumbie
409 et al., 2011; Correia et al., 2008) and wood (Marguerit et al., 2014), in *Populus sp.* with leaves and
410 wood (Monclus et al., 2005; Verlinden et al., 2015), in *Araucaria cunninghamii* with branchlets (Xu et
411 al., 2003), and in *Quercus suber* with leaves (Ramirez-Valiente et al., 2009). For *Eucalyptus*, studies
412 addressing the genetic determinism of $\delta^{13}\text{C}$ are scarce: two showed a high genetic variability among

413 tree populations (e.g. Li and Wang, 2003), or among provenances of *E. microtheca* at the nursery
414 stage (Li, 2002). Li and Wang (2003) and Li (2002) were based on $\delta^{13}\text{C}$ measurements in leaves.
415 However, most of the studies were carried out on a very small number of genotypes (Olbrich et al.,
416 1993; Le Roux et al., 1996; Nunes et al., 2016). Other studies analyzed the genetic architecture
417 through quantitative trait loci of carbon isotope composition in stem wood (Bartholomé et al., 2015)
418 but did not give any estimation of the variances. Very few studies have addressed the variance
419 components of wood $\delta^{13}\text{C}$ using a large population in field conditions. Marguerit et al. (2014) using
420 about 1900 individuals of *Pinus pinaster* distributed at three sites is among the rare studies in the
421 literature. As far as we know, our study is among the first for *Eucalyptus* using more than 1000 clones
422 in field conditions.

423

424 **4.2. Correlation among traits**

425 The additive correlations between V55 and wood chemical properties (KL, HCEL) were weak but
426 positive (Table 2). Similar results were recently reported for *Eucalyptus robusta* (Rambolorimanana
427 et al., 2018), but previous studies showed that wood chemical traits and volume are generally poorly
428 correlated in *Eucalyptus* (Hein et al., 2012; Denis et al., 2013). More generally, results on other
429 species show small to moderate correlations between $\delta^{13}\text{C}$ and growth traits in, for example,
430 *Araucaria cunninghamii* (Xu et al., 2003), *Pinus sp.* (Cumbie et al., 2011; Marguerit et al., 2014) and
431 *Populus sp.* (Verlinden et al., 2015).

432 Studies addressing the correlation between wood $\delta^{13}\text{C}$ (Wi) and growth traits are scarce, and
433 differences between hardwood and softwood species are still poorly documented. The origin of
434 correlation, pleiotropy or linkage disequilibrium (statistical association) remains unknown. With our
435 data, the additive correlation between Wi ($\delta^{13}\text{C}$) and V55 was negative (-0.260) and the
436 environmental correlation was positive (0.195). The sign inversion between additive and
437 environmental correlations suggested a correlation due to linkage disequilibrium (Gallais, 1990), i.e.
438 random gene association resulting from a sample effect. However, the estimates were small with
439 high standard error and further studies are needed to draw relevant conclusions.

440

441 **4.3. Implication for index selection**

442 One of the objectives of our study was to address the selection of *Eucalyptus* ideotypes for different
443 breeding objectives in a context of decreasing water availability. The novelty was the combination of
444 traits related to biomass, wood chemical properties and water use efficiency, the latter trait having
445 not yet been included, to our knowledge, in the multi-trait selection of *Eucalyptus*. Because we did
446 not have any economic information, such as the net profit or net worth of a tree, to estimate
447 economic weights, as done in previous studies for *Eucalyptus* (Greaves et al., 1997; Wei and

448 Borralho, 1999) and softwood species (Aubry et al., 1998), we used two methods based on trait
449 variation and co-variation (Cotteril and Jackson, 1985). Each method produced different sets of
450 economic weights and the consequences were analyzed comparing relative genetic gains. In the
451 following section we mainly focus the discussion on V55 and W_i due to the importance of both traits
452 in sustainable plantations.

453
454 Except in the case of $s=(70\%;10\%;10\%;10\%)$, for both index methods, the genetic gain in V55 was
455 lower than the genetic gain in W_i and much lower than the maximum gain $\Delta G_{u \max}$ or $\Delta G_{g \max}$ (Tables 3
456 and 4). In the case of genetic additive gain (Table 3), the economic weights for V55 were higher than
457 for W_i ; this can be easily noticed with the transformed coefficients equal to 10 m^{-3} for V55 when it
458 varies from 0.23 to $7.25 \text{ } (\mu\text{mol mol}^{-1})^{-1}$ for W_i , whatever the index method. With this higher
459 economic weight, we may have been expected to achieve a greater additive genetic gain in V55
460 compared to the other traits and especially W_i , but this was not the case (Table 3). This pattern might
461 result from both the same selection intensity on W_i and V55, and from the negative genetic and
462 phenotypic correlations between W_i and V55 (Table 2).

463 By imposing more contrasted percentages between V55 and W_i in the vector s , for example
464 $s=(80\%;10\%;10\%;0\%)$ or $s=(90\%;10\%;10\%;-10\%)$, we obtained much higher coefficients for V55 than
465 for W_i with both index methods (Table 5). As a result, the additive and total genetic gains were much
466 higher for V55 than for W_i (Table 5). Moreover, negative additive genetic gain on W_i were achieved
467 with the equal emphasis method when the gains remained positive with the desired gain method
468 (Table 5).

469 These new sets “ s ” highlighted the impact of the different methods on the genetic gains resulting
470 from selection. Our results showed that the desired gain method, even with contrasted coefficients,
471 yielded contrasted but positive gains among traits. This can be attributed to the method that used all
472 the genetic information i.e. the genetic and phenotypic co-variation among traits, to estimate the
473 index coefficients. In addition, this method is generally more intelligible for breeders than the equal
474 emphasis method or methods based on economic function, because breeders are used to dealing
475 with the concept of genetic gain. With methods using economic function, the difficulty is to define
476 the net worth of a tree given that it may change according to the user. For example, the net profit for
477 the *Eucalyptus* grower can be quite different from that of the pulp companies and sawmill companies
478 (Berlin et al., 2012). However, the desired gain method provides coefficients with errors correlated
479 with the accuracy of the variance co-variance matrix that may influence the quality of ranking. The
480 equal emphasis method is simpler, but does not use the all the genetic information (only variances
481 and not co-variances). Whatever the method, the reliability of economic coefficient estimates
482 depends on the quality of the estimation of genetic parameters.

483

484

485 **5. Conclusion**

486 *Eucalyptus* is an important genus for forest plantations in marginal zones unsuitable for agriculture
487 where many commercial companies have made great efforts to optimize biomass production. The
488 assessment of WUE is crucial for expanding *Eucalyptus* plantations to dry zones or coping with the
489 consequences of climate change. Although recent research has stressed the need to improve the
490 measurement of $\delta^{13}\text{C}$ as a proxy of whole plant WUE based on aboveground biomass (Battie-Laclau
491 et al., 2016; Fernandes et al., 2016; Konate et al., 2016, Bogeat-Triboulot et al., 2019), from a
492 technical point of view the measurement of $\delta^{13}\text{C}$ in wood can be done in large-scale breeding
493 populations. However, it is not yet routinely implemented in *Eucalyptus* improvement programs. Our
494 study provides new data on the heritability of wood $\delta^{13}\text{C}$, its relationship with other major traits and
495 the issues raised by trade-offs in index selection. [We implemented two index selection methods to](#)
496 [explore the set of economic weights for contrasting breeding objectives. We showed that index](#)
497 [coefficients can be determined to achieve positive gains for each trait. Our findings are encouraging](#)
498 [and show that inclusion of wood \$\delta^{13}\text{C}\$ in the selection process may lead to *Eucalyptus* varieties](#)
499 [adapted to marginal zones still presenting good performance for biomass and wood chemical traits.](#)
500 [Although the present study was based on a substantial number of clones, further studies involving](#)
501 [other *Eucalyptus* genetic backgrounds are needed to better assess the inclusion of WUE in breeding](#)
502 [objectives.](#)

503

504

505 **Acknowledgements**

506 We are particularly grateful to the field team of the Centre de Recherche sur la Durabilité des
507 Plantations Forestières (CRDPI) in the Congo for the collection of wood cores and the measurement
508 of the growth traits. We are also grateful for the laboratory assistance of the UMR AGAP for the NIRS
509 measurements, especially Sophie Nourrissier-Mountou and Gilles Chaix for the extraction of cellulose
510 and lignin from $\delta^{13}\text{C}$ samples, and Pierre Epron for his technical support in the laboratory. Isotope
511 analyses were carried out at the Technical Platform for Functional Ecology (PTEF OC 081) of UMR
512 SILVA.

513

514 **Funding**

515 This work was partly supported by the WUEtree project (ANR-13-ADAP-0012) and by funding from
516 the different partners associated with the project: Cirad, Université de Lorraine and CRDPI. UMR

517 SILVA is supported by a grant overseen by the French National Research Agency (ANR) as part of the
518 Investissements d'Avenir programme (ANR-11-LABX-0002-01, Lab of Excellence ARBRE).
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773 nitrogen isotope composition and nutrient concentration of 11-year-old hoop pine families in relation to tree
774 growth in subtropical Australia. For. Ecol. Manage., 186, 359–371.
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778 Table 1: Mean and variance components for additive female (σ^2_{af}), additive male (σ^2_{am}), dominance (σ^2_d) and residual (σ^2_r) effects and variance ratios for the
 779 traits measured at age 55 months: the individual tree volume (V55), the stable carbon isotope composition ($\delta^{13}C$), the intrinsic water use efficiency
 780 (W_i), the klason lignin content (KL) and the holo-cellulose content (HCEL). Standard errors of the estimations (SE) and coefficients of phenotypic
 781 variation (CV) are indicated.

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Trait	Mean	Min	Max	CV %	Variance components								Variance ratios						
					σ^2_{af}	SE	σ^2_{am}	SE	σ^2_d	SE	σ^2_r	SE	h^2	SE	d^2	SE	H^2	SE	d^2/h^2
V55 (m ³) ^a	3.95	-4.00	5.89	28.83	0.302	0.139	0.236	0.138	0.742	0.283	0.882	0.048	0.306	0.096	0.422	0.123	0.727	0.046	1.379
$\delta^{13}C$ (‰)	-29.37	-31.14	-27.24	nd ^b	0.081	0.022	0.096	0.023	0.000	0.000	0.121	0.006	0.704	0.027	0.000	0.000	0.704	0.027	0.000
W_i ($\mu\text{mol mol}^{-1}$)	62.31	42.70	85.84	9.32	9.891	2.709	11.768	2.810	0.000	0.000	14.851	0.747	0.704	0.027	0.000	0.000	0.704	0.027	0.000
KL (%)	27.73	20.98	34.74	6.32	0.817	0.215	0.383	0.196	0.000	0.000	1.397	0.068	0.460	0.045	0.000	0.000	0.460	0.045	0.000
HCEL (%)	67.19	58.93	76.32	3.64	1.079	0.319	0.444	0.299	0.000	0.000	2.369	0.115	0.290	0.045	0.000	0.000	0.290	0.045	0.000

783 h^2 : narrow sense heritability, H^2 : broad sense heritability and d^2 : proportion of dominance variance to additive variance.

784 ^a The average of V55 without logarithmic transformation was 0.079 m³ and its coefficient of variation was 74%.

785 ^b The coefficient of variation for $\delta^{13}C$ cannot be calculated (see Brendel, 2014).

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788 Table 2: Genetic, environmental and phenotypic correlations between the different traits (the volume (V55), the intrinsic water use efficiency
 789 (W_i), the klason lignin content (KL) and the holo-cellulose content (HCEL). Standard errors of the estimations (SE) were estimated using model
 790 (1).

Traits		V55		HCEL		KL	
		estimate	SE	estimate	SE	estimate	SE
HCEL	ρ_a	0.118	0.126				
	ρ_d	0.000	0.000				
	ρ_g	0.118	0.126				
	ρ_e	-0.267	0.031				
	ρ_p	-0.125	0.039				
KL	ρ_a	0.238	0.092	-0.257	0.112		
	ρ_d	0.000	0.000	0.000	0.000		
	ρ_g	0.261	0.146	-0.257	0.112		
	ρ_e	0.344	0.030	0.023	0.031		
	ρ_p	0.298	0.036	-0.079	0.035		
W_i	ρ_a	-0.260	0.088	-0.101	0.100	-0.192	0.085
	ρ_d	0.000	0.000	0.000	0.000	0.000	0.000
	ρ_g	-0.260	0.088	-0.101	0.100	-0.192	0.08
	ρ_e	0.195	0.033	-0.045	0.032	0.104	0.032
	ρ_p	-0.034	0.039	-0.065	0.036	-0.038	0.036

791 $\rho_a, \rho_d, \rho_g, \rho_e, \rho_p$ are the additive, dominance, total genetic, residual (environmental) and phenotypic genetic correlations (eq. 7) to (eq. 10)

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794 Table 3: Expected relative additive genetic gain (ΔG_u) following selection on indices using economic weights determined either by the equal
 795 emphasis method or by the desired gain method. The expected gains were calculated for an intensity of selection of 10%. Economic weights
 796 were estimated using different sets of percentages “s” representing the relative importance of each trait in the breeding objective. Single trait
 797 selection indicates the maximum relative gain for each trait.

Selection method	s(%)	Equal emphasis method				Desired gain method				Observed relative gain ΔG_u (%)				R: Spearman correlation ^b				
		economic coefficients ^a				Index economic coefficients				V55	HCEL	KL	W _i					
Multitrait	70;10;10;10	0.95, 0.08, 0.09, 0.02 ^c 10.00, 0.85, 0.96, 0.23 ^d				12.0	0.5	1.4	0.2	1.86, -0.01, 0.14, 0.19 10.00, -1.12, -0.21, 0.73				7.2	-0.1	0.42	7.1	0.686
	40;10;10;40	0.54, 0.081, 0.09, 0.08 10.00, 1.49, 1.67, 1.58				5.1	0.1	0.4	8.1	1.52, 0.36, 0.57, 0.35 10.00, 2.37, 3.75, 2.35				3.0	0.0	0.8	8.7	0.982
	30;30;10;30	0.41, 0.24, 0.09, 0.06 10.00, 5.94, 2.23, 1.58				5.3	0.8	0.2	6.5	0.71, 1.02, 0.86, 0.29 10.00, 14.34, 12.17, 4.09				3.3	0.6	1.5	6.4	0.903
	30;10;30;30	0.41, 0.08, 0.27, 0.06 10.00, 1.98, 6.69, 1.58				5.3	-0.1	2.6	5.7	0.79, 0.72, 1.13, 0.31 10.00, 9.12, 14.21, 3.84				3.2	0.2	2.1	6.5	0.966
	25;25;25;25	0.34, 0.20, 0.23, 0.05 10.00, 5.94, 6.69, 1.58				6.2	0.6	2.3	4.2	0.37, 1.13, 1.21, 0.27 10.00, 30.42, 32.67, 7.25				3.2	0.6	2.2	5.0	0.941
Single trait	$\Delta G_{u \text{ max}}$					13.0	1.7	4.4	10.3					13.0	1.7	4.4	10.3	

798 ^aUnits for the index coefficient were: m⁻³, (μmol mol⁻¹)⁻¹, %⁻¹ and %⁻¹, for V55, HCEL, KL and W_i respectively

799 ^b Spearman correlation for the index ranking.

800 ^c actual economic weights; ^d transformed economic weights

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803 Table 4: Expected relative total genetic gain (ΔG_g) following selection on indices using economic weights determined by either the equal
 804 emphasis method or the desired gain method. The expected gains were calculated for an intensity of selection of 1%. Economic weights were
 805 estimated using different sets of percentages “s” representing the relative importance of each trait in the breeding objective. Single trait selection
 806 indicates the maximum relative gain for each trait.

Selection method	s (%)	Equal emphasis method	Observed relative gain ΔG_g (%)				Desired gain method	Observed relative gain ΔG_g (%)				R: Spearman correlation ^b
		Index economic coefficients ^a	V55	HCEL	KL	W_i	Index economic coefficients	V55	HCEL	KL	W_i	
Multitrait	70;10;10;10	6.18, 0.89, 0.91, 0.81 ^c 10.00 1.44 1.47 1.31 ^d	20.4	0.4	2.2	4.8	0.72, 0.48, 0.66, 0.20 10.00, 6.65, 9.21, 2.75	6.6	-0.18	4.4	13.1	0.635
	40;10;10;40	1.77, 0.41, 0.46, 1.76 10.00 2.32 2.60 9.94	11.2	0.0	3.0	13.6	0.58, 0.95,,1.21, 0.45 10.00, 16.17, 20.73, 7.79	6.3	-0.15	4.6	13.6	0.885
	30;30;10;30	1.76, 1.70, 0.59, 1.72 10.00 9.66 3.35 9.77	12.1	0.3	2.2	12.9	0.17, 1.91, 1.56, 0.40 10.00, 108.99, 89.43, 22.96	6.5	0.03	4.3	13.1	0.849
	30;10;30;30	1.76, 0.57, 1.73, 1.72 10.00 3.24 9.83 9.77	7.1	-0.3	4.7	13.4	0.29, 1.36, 1.96, 0.42 10.00, 46.30, 66.67, 14.35	5.2	-0.2	4.9	13.2	0.883
	25;25;25;25	1.77, 1.78, 1.73, 1.72 10.00 10.06 9.77 9.72	7.5	-0.1	4.4	13.3	0.05, 1.97, 2.04, 0.39 10.00, 339.09, 349.25, 66.76	5.5	-0.1	4.6	13.1	0.903
Single trait	ΔG_{gmax}		23.2	3.0	6.9	15.0		23.2	3.0	6.9	15.0	

807 ^a Units for the index coefficient were: m^{-3} , $(\mu mol mol^{-1})^{-1}$, $\%^{-1}$ and $\%^{-1}$, for V55, HCEL, KL and W_i respectively

808 ^b Spearman correlation for the index ranking.

809 ^c actual economic weights; ^d transformed economic weights

810 Table 5: Economic coefficients, expected relative additive (ΔG_u) and total genetic gain (ΔG_g) following selection on indices using economic
 811 weights determined by the desired gain method. The expected gains were calculated for an intensity of selection of 10% and 1%. Economic
 812 weights were estimated using two sets of percentages “s” representing contrasted trait importance. Single trait selection indicates the maximum
 813 relative gain for each trait.

Selection method	Equal emphasis s (%)	economic coefficients ^a	Observed relative gain ΔG_u (%)				Desired gain method Index economic coefficients	Observed relative gain ΔG_u (%)			
			V55	HCEL	KL	W_i		V55	HCEL	KL	W_i
Multitrait	80;10;10;0	1.09, 0.08, 0.09, 0 ^c 10.00, 0.74, 0.84, 0.00 ^d	12.7	0.5	1.6	-3.8	1.97, -0.13, 0.03, 0.14 10.00, -0.69, 0.02, 0.69	9	-0.1	0	5.8
	90;10;10;-10	1.2, 0.08, 0.09, -0.02 10.00, 0.66, 0.74, -0.17	12.5	0.5	1.6	-5.6	2.01, -0.26, -0.14, 0.08 10.00, -1.25, -0.67, 0.38	11	-0.1	-0.4	3.6
Single trait	$\Delta G_{u\max}$		13	1.7	4.4	10.3		13	1.7	4.4	10.3
Selection method	Equal emphasis s (%)	economic coefficients	Observed relative gain ΔG_g (%)				Desired gain method Index economic coefficients	Observed relative gain ΔG_g (%)			
			V55	HCEL	KL	W_i		V55	HCEL	KL	W_i
Multitrait	80;10;10;0	0.70, 0.08, 0.09, 0 10.00, 0.66, 0.74, -0.17	22.3	0.6	1.8	-3.5	0.76, 0.33, 0.48, 0.11 10.00, 4.21, 6.27, 1.45	9.5	-0.1	4	13.2
	90;10;10;-10	0.79, 0.08, 0.09, -0.02 10.00, 1.02, 1.15, -0.27	21.9	0.2	1.9	-7.9	0.81, 0.17, 0.30, 0.02 10.00, 2.05, 3.65, 0.30	17.8	0.2	5	2.1
Single trait	$\Delta G_{g\max}$		23.2	3	6.9	15		23.2	3	6.9	15

814 ^aUnits for the index coefficient were: m^{-3} , $(\mu mol\ mol^{-1})^{-1}$, $\%^{-1}$ and $\%^{-1}$, for V55, HCEL, KL and W_i respectively

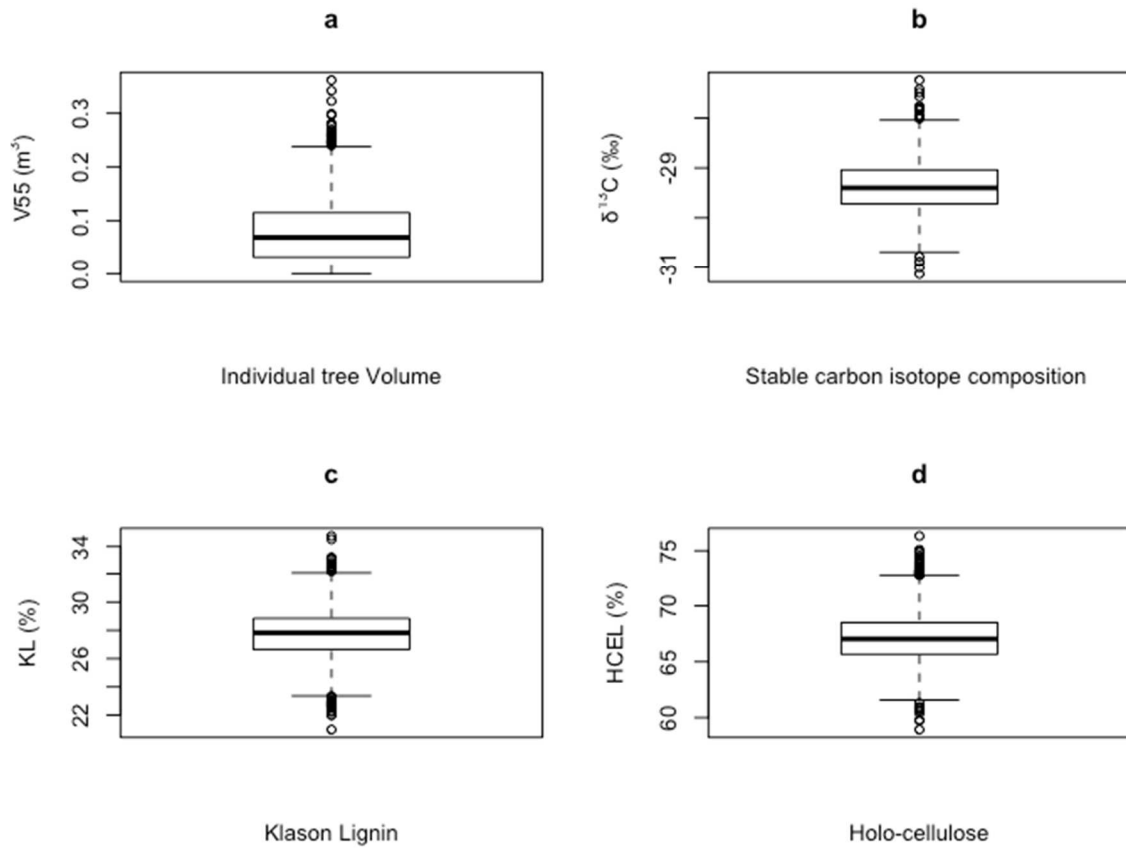
815 ^c actual economic weights; ^d transformed economic weights

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817 Figure 1: Box plots showing the distribution of the studied traits: a) the individual tree volume
818 at age 55 months (V55 in m³) represented before log transformation, b) the stable isotope
819 composition ($\delta^{13}\text{C}$ in ‰), c) the lignin content (KL in %) and d) the holo-cellulose content
820 (HCEL in %).

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