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Genetic and environmental determinants of relationships between wood properties, water use efficiency and biomass production

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Background and purpose

The possibility of reconciling the objectives of increasing wood production and resource use efficiency is one of the challenges of sustainable forest management. Selection criteria enhancing the efficiency of water use for biomass production are therefore required to develop genotypes better adapted to water-limited areas making it possible to use less water for the same biomass production. These critical questions related to selection for wood products and water resource use efficiency have promoted research in ecophysiology and genetics, with some efforts to combine them. Research is still needed to gain insight into the genetic and environmental effects in phenotype variation and plasticity. The relationships between WUE (water use efficiency), growth and wood traits have been little documented, and the results are still partial and sometimes inconsistent. Depending on experiments, biomass production and WUE can be positively correlated (Le Roux et al. 1996), negatively correlated (Monclus et al. 2005) or not correlated (Cumbie et al. 2011). It is difficult to determine whether these divergent results are due to sampling or to species or environmental effects. A meta-analysis showed a positive global intra-specific correlation between $\delta 13C$ and height (Gr = 0.28, $P < 0.0001$), a stronger correlation for biomass than for height (Gr = 0.68, $P < 0.0001$), and a non-significant correlation for diameter (Gr = 0.04, $P < 0.64$) (Fardusi et al., 2016). However, the authors did not study the influence of genetic and environmental effects on these correlations. Better knowledge of genetic and environmental correlations is a key issue in guiding tree breeding programs. Several questions must be addressed, especially for Eucalyptus species planted in marginal zones where water availability may become a critical issue. What is the contribution of additive and non-additive gene effects in the expression of wood properties, WUE and biomass production? What is the magnitude of the genetic and environmental correlations between wood properties and other traits?

The objectives of our study were: (i) to gain insights into the genetic and environmental components controlling wood chemical traits, $\delta 13C$ and stem volume, and (ii) to assess the genetic and environmental correlations between those traits.

Material and methods

Field experimental data

The study was conducted using a Eucalyptus progeny trial located east of Pointe-Noire (11°59′21″E, 4°45′51″S) in Republic of Congo. Rainfall averaged 1200 mm/year. The soils were deep Ferralic Arenosols characterized by low water retention, a very low level of organic matter and poor cationic exchange capacity. The plant material resulted from controlled pollination crosses of thirteen *Eucalyptus urophylla* females and nine *Eucalyptus grandis* males according to a factorial mating design. These crosses generated 69 full-sib families and 1415 progenies. Each of the 1415 progenies was replicated three times using cuttings and a clonally replicated progeny test was planted at a stocking density of 833 trees ha^{-1}. The field experiment was a complete block design with three replications. Twenty-five trees replicated in three blocks represented each full-sib family.

Measured traits

Total tree height (HT) and circumference at breast height (C) were measured 55 months after planting and used to calculate a proxy of the total tree volume (V55) using the cylinder formula with a stem form factor of 0.3. NIRS models were used to estimate Klason lignin (KL) and holo-cellulose content (HCEL). We used existing NIRS models of multiple Eucalyptus species that included samples from this study (Chaix et al. 2015). Stable carbon isotope composition (δ13C) of wood was measured on the same samples as those used for NIRS after grinding them to a fine powder (< 0.1 mm). One mg of the powder was enclosed in a tin capsule and analyzed with an elemental analyzer coupled to an isotope-ratio mass spectrometer.

Statistical model

We used the following linear mixed model combining genetic and environmental effects to analyze the data: $y = X\text{ß} + Z_{col}{}^{col} + Z_{r:b}{}^{r:b} + Z_c a_f + Z_c a_m + Z_c d + \varepsilon$

where y was the vector of the phenotypic variable, β was the vector of fixed effects due to the general mean and blocks, col was the vector of random spatial environmental effects due to the field design column, r:b was the vector of random spatial environmental effects due to field design row by block interaction, ε was the vector of random spatial environmental effects due to microenvironmental effect. The genetic effects were defined by: a*f* (female additive), a*m* (male additive) and d (dominance). *X*, *Z*col, *Z*r:b, and *Z*c were the incidence matrices connecting the fixed and random effects to the data. The variance component estimation based on the REML method and the BLUP calculations were done using the ASReml version 3 package implemented in R software (R Development Core Team, 2011). The correlation estimates were obtained using model shown above in the multivariate formulation.

Results and discussion

Variance components

Phenotypic variabilities were highly variable depending on the traits (Table 1). The log-transformed volume stood out with a coefficient of variation (CV) of 18.9%, whereas the wood property traits showed CVs around 5.0%. The $\delta^{13}C$ values converted to intrinsic WUE (Wi), showed a CV of 9.0%. The female and male variance (σ^2_{af} and σ^2_{am}, respectively) showed close estimates for V55 and $\delta^{13}C$ (and Wi), whereas σ^2af was much higher than σ^2_{am} for HCEL and KL. This result suggested a higher variability of the *E. urophylla* parent set than the *E. grandis* parent set for these latter traits and showed a marked dominance variance for volume and stressed a preponderance of the additive variance for chemical wood traits (Makouanzi et al. 2018).

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_e) effects and variance ratios for the traits measured at age 55 months: the individual tree volume (V55), the stable carbon isotope composition ($\delta^{13}C$), the intrinsic water use efficiency (Wi), the klason lignin content (KL) and the holo-cellulose content (HCEL). Standard errors of the estimations (SE) and coefficients of phenotypic variation (CV) are indicated.

					Variance components							
Trait	**Mean**	**Min**	**Max**	**CV (%)**	σ^2_{af}	**SE**	σ^2_{am}	**SE**	σ^2_d	**SE**	σ^2_e	**SE**
V55 (m^3)*	3.95	−4.00	5.89	28.83	0.302	0.139	0.236	0.138	0.742	0.283	0.882	0.048
$\delta^{13}C$ (0/00)	−29.37	−31.14	−27.24	nd	0.081	0.022	0.096	0.023	0.000	0.000	0.121	0.006
Wi (µmol 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
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
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

*The average of V55 without logarithmic transformation was 0.079 m^3 and its coefficient of variation was 74%.

Correlations

Globally, our results stressed the low to moderate genetic and environmental correlations between traits (Table 2).

Table 2: Genetic, environmental and phenotypic correlations between the different traits (the volume (V55), the intrinsic water use efficiency (Wi), the klason lignin content (KL) and the holo-cellulose content (HCEL). ρ_a, ρ_d, ρ_g, ρ_e and ρ_p are the additive, dominance, total genetic, residual (environmental) and phenotypic genetic correlations.

Traits	**V55**					**HCEL**					**KL**				
	ρ_a	ρ_d	ρ_g	ρ_e	ρ_p	ρ_a	ρ_d	ρ_g	ρ_e	ρ_p	ρ_a	ρ_d	ρ_g	ρ_e	ρ_p
HCEL	0.118 (0.126)	0.000 (0.000)	0.118 (0.126)	-0.267 (0.031)	-0125 (0.039)										
KL	0.238 (0.092)	0.000 (0.000)	0.261 (0.146)	0.344 (0.030)	0.298 (0.036)	-0.257 (0.12)	0.000 (0.000)	-0.257 (0.12)	0.023 (0.031)	-0.079 (0.035)					
Wi	-0.260 (0.088)	0.000 (0.000)	-0.260 (0.088)	0.195 (0.033)	-0.034 (0.039)	-0.101 (0.100)	0.000 (0.000)	-0.101 (0.100)	-0.045 (0.032)	-0.065 (0.036)	-0.192 (0.085)	0.000 (0.000)	-0.192 (0.08)	0.104 (0.032)	-0.038 (0.036)

We noted small positive additive genetic correlations (ρa < 0.300) between V55 and wood chemical traits and low negative additive genetic correlations between V55 and $\delta^{13}C$ (or Wi) (ρa = −0.260). Similar results were reported for *Eucalyptus robusta* (Rambolarimanana et al. 2018), but previous studies showed that wood chemical traits and volume are generally poorly correlated in Eucalyptus (Hein et al. 2012). More generally, results on other species show small to moderate correlations between $\delta^{13}C$ and growth traits in, for example, *Populus sp*. (Verlinden et al. 2015). Studies addressing the correlation between wood $\delta^{13}C$ (Wi) and growth traits are scarce, and differences between hardwood and softwood species are still poorly documented. The origin of correlation, pleiotropy or linkage disequilibrium (statistical association) remains unknown. With our data, the additive correlation between Wi ($\delta^{13}C$) and V55 was negative (−0.260) and the environmental correlation was positive (0.195). The sign inversion between additive and environmental correlations suggested a correlation due to linkage disequilibrium (Gallais 1990). However, the estimates were small with high standard error and further studies are needed to draw relevant conclusions. Correlations between wood chemical traits and $\delta^{13}C$ (or Wi) were not strong and negative estimates were observed (ρa = -0.101 and ρa = -0.192 for HCEL and KL, respectively). The correlations due to the dominance effect were null for all the combinations of $\delta^{13}C$ (or Wi), KL or HCEL because the estimates of the dominance variance were null. As a result, the total genetic correlations were equal to the additive genetic correlations. Most of the environmental correlations were small (ρe < 0.200 in absolute value), except between V55 and KL (ρe = 0.344). Similar patterns were noticed for phenotypic correlations.

Conclusion and perspectives

Our study provides the combination of traits related to biomass, wood chemical properties and water use efficiency in the multi-trait selection of Eucalyptus. We noted a preponderance of the additive variance for chemical wood traits, essentially due to the female variance. The small positive additive genetic correlations were noted between tree volume and wood chemical traits and low negative additive genetic correlations between tree volume and water use efficiency. Our findings are encouraging and show that inclusion of wood and δ13C in the selection process may lead to Eucalyptus varieties adapted to marginal zones still presenting good performance for biomass and wood chemical traits.

Aknowlegments

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