Genetic variation for early flowering, survival and growth in sugar gum (*Eucalyptus cladocalyx* F. Muell) in southern Atacama Desert

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Abstract The aim of this study was to examine the genetic control of time-to-flowering (precocity) in 39 open-pollinated families of *Eucalyptus cladocalyx* in southern Atacama Desert, Chile, with the view to the selection of trees that flower earlier but with minimal impact on survival and growth. A Bayesian approach, implemented using Gibbs sampling algorithm, was used in data analyses. Precocity was assessed as a binary response at age three and was found to be highly heritable. The estimates of posterior mean and of the 95% posterior interval of the heritability were 0.51 and [0.46–0.56], respectively. Estimated genetic gain ranged from 36.15 to 41.22% (selection intensities of 14.29 and 7.48%, respectively). Total height, basal diameter and survival (measured at age 5) had a positive and relatively moderate genetic correlation with early flowering ($r = 0.23$, 0.29 and 0.11, respectively) indicating that selection for early flowering alone would have a moderate impact on growth and survival. Early flowering of *Eucalyptus cladocalyx* was found to be highly heritable in southern Atacama Desert populations, which could be used to improve the honey production in situations where flowers from native species are not available in sufficient quantities.

Keywords Arid environmental conditions · Breeding value · Genetic gain · Gibbs sampling · Heritability

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Abbreviations

D	Diameter
EF	Early flowering
GD	Genetic diversity
GG%	Predicted genetic advance
H	Height
MCMC	Monte-Carlo Markov Chain
N_{SF}	Number of selected families
S	Survival

Introduction

Eucalyptus tree species are grown commercially all around the world for many reasons including timber, essential oil production, pulpwood and honey (He

and Barr 2004; YueMing et al. 2004; Hajari et al. 2006). Many *Eucalyptus* species are particularly well adapted to dry climatic conditions (Cohen et al. 1997; Wildy et al. 2004; Akhter et al. 2005) while others can tolerate other environmental extremes such as saline soils (Rawat and Banerjee 1998; Akilan et al. 1997; Marcar et al. 2002). Given that almost 50% of the world's land area can be classified as drylands, (Williams 2000) it is clear that there is potential for more extensive use of such species.

In Chile, for example, arid and semiarid zones comprise about 30 million ha, or 40%, of the country's area (Ormazábal 1991). Large areas of other countries in South America, such as Argentina, Brazil and Peru are similarly dry. Agroforestry practices that integrate tree and shrub plantings with crops and/or livestock are recognized alternatives to conventional agriculture in these drylands. In northern Chile, for example, the Coquimbo district has little agriculturally productive land (Ormazábal 1991) and dryland salinity is perceived as a severe environmental, economic and social threat (Mora et al. 2007, 2008). Given the constraints on the local environment, it is highly desirable for trees to be used for many applications which contribute to sustainable land use, rather than just a single product.

One reason that *Eucalyptus cladocalyx* F. Muell (sugar gum) is currently grown in Chile is because it can be used for honey as well as timber production (Manikis and Thrasivoulou 2001; Mora 2006). It is preferred over other species because of its moderate tolerance to salinity (Marcar et al. 1995), its ability to grow in arid environment (Gleadow and Woodrow 2002; Woodrow et al. 2002; McDonald et al. 2003) and relative resistance to *Phoracantha semipunctata* (Hanks et al. 1994). Harvesting of plantations for fuel and posting poles generally starts at about 10–12 years after planting. Honey production has the potential to be an important additional source of income for local farmers and needs to be included in long term forest management plan.

Eucalyptus cladocalyx flowers provide a reliable source for the production of honey, complementing the less prolific endemic and native species in Chile (Montenegro et al. 2003). The problem is that the trees do not produce flowers until they are 3–6 years old. Early flowering has been identified as an important trait in other eucalypt breeding programs (Chambers et al. 1997; Wiltshire et al. 1998). The purpose of previous research on flowering has been primarily to

accelerate progeny testing and the production of genetically improved seed (Meilan 1997). The inclusion of genes for precocious flowering into a breeding population of eucalypts that are primarily used for timber or pulp production could be undesirable in the long term, if the continuing expression of this trait in successive generations led to significant reductions in wood yield due to the energy loss involved in wasteful flower and fruit production (Chambers et al. 1997).

Early flowering, or precocity, is usually measured as the presence or absence of reproductive structures such as capsules or flower buds (Chambers et al. 1997). Statistically, this trait has a Bernoulli distribution, in which only two distinct non-continuous phenotypes are recorded: presence or absence of flowering events. An alternative is to use Bayesian methods, which are considered to be able to predict the breeding value of such threshold traits more precisely (Van-Tassell et al. 1998). The Bayesian approach has been used to genetically evaluate a range of different forest trees species (e.g. Sorya et al. 1998; Cappa and Cantet 2006; Waldmann and Ericsson 2006). Variations of the Monte-Carlo Markov Chain (MCMC) such as Gibbs sampling algorithm have been shown to be appropriate for the analysis of ordered categorical data in breeding programs. Moreover, such algorithms allow for the efficient exploration of very complex likelihood surfaces and calculation of Bayesian posterior distributions (Melchinger et al. 2004; Bink et al. 2008).

The timing of inflorescence developmental events and overall architecture can be influenced to a great extent by environmental cues such as nutrient availability, drought stress, light quality, photoperiod and vernalization (Ungerer et al. 2003; Van-Dijk and Hautekèete 2007). From the genetics viewpoint, the number of loci involved in regulating flowering time has been shown to depend upon both the ecotype and the environment in which the plants are grown (Clarke et al. 1995). Indeed, genetic and environmental factors are inextricably linked and phenotypic expression is determined by their joint effects (Ungerer et al. 2003). Moreover, in the case of eucalyptus species, early flowering has shown to be a highly heritable trait (Chambers et al. 1997). The aim of this study was, therefore, to determine the genetic control of time to flowering in *E. cladocalyx* with the view to the selection of trees that flower earlier, but with minimal impact on survival and growth. In order to do this a Bayesian approach was used to analyze genetic

parameters and to predict the breeding values for flowering, survival and growth traits from 39 different half-sib families growing under arid conditions in the Atacama region of Northern Chile. The results from this experiment are of particular importance as there little is known about the molecular control of these traits.

Materials and methods

Study location

The experiment was conducted in a dryland area within Choapa Province, in the rural community of Tunga Norte localized at the south of the Atacama Desert, in the Coquimbo Region, Chile (31°38′ S Latitude; 71°19′ W Longitude; and altitude of 297 m). Shrub-land vegetation dominates this arid zone and approximately 75% of the Coquimbo region is considered lowland (0–1,000 ma.s.l.) and midland (1,000–2,000 ma.s.l.) shrub-land, while agricultural areas represent less than 3% (Squeo et al. 2006).

The region has an arid Mediterranean climate (Montenegro et al. 2003) in which there are large fluctuations in water availability between La Niña (dry) and El Niño (rainy) years (Squeo et al. 2006). During El Niño episodes there is a typically above-average precipitation between 30° and 35° S Latitude in winter (June to August), while below-average precipitation is characteristic of La Niña periods (Montecinos and Aceituno 2003). Average annual precipitation is 180 mm (1973–2004, measured at the meteorological station Illapel capital of Choapa Province), ranging from 513 to 15.8 mm. Rainfall records over the experimental period (2001–2006) were: means of 226 mm y^{-1}, ranging from 103 mm y^{-1} (2003) to 394 mm y^{-1} (an El Niño year; 2002).

Plant material

Trees were planted in a complete block design, with 39 families, with 30 complete blocks each, using single-tree plots during June 2001. Trees were planted every 2 m with 3 m between rows, giving a density of approximately 1,667 trees ha^{-1}. Thirty-seven half sib families were established seed from the CSIRO Australian Tree Seed Centre base population collection and two from seed collected from trees previously established in the neighbouring Choapa Province (seed source from Chile; 31°40′ S Latitude; 71°14′ W Longitude). The Australian seed came from four localities (provenances) in its centre of origin in South Australia (Ruthrof et al. 2003): Flinders Chase National Park (Kangaroo Island) (35°57′ S Latitude; 136°42′ W Longitude; 637.9 mm y^{-1}); Marble Range (Eyre Peninsula) (34°30′ S Latitude; 135°30′ W Longitude; 485.1 mm y^{-1}), and Mt. Remarkable (32°43′ S Latitude; 138°06′ W Longitude; 242.8 mm y^{-1} and Wirrabara State Forest (33°06′ S Latitude; 138°14′ W Longitude; 256.6 mm y^{-1}) both in the Flinders Ranges. In this paper, the provenances will be referred to the sources. The original Australian source of the seed from Chile is unknown, but it is likely to be of mixed origin.

Trait measurements

Early flowering was determined by assessing 3 year old trees for presence (1) or absence (0) of capsules and/or flower buds in June 2004. Other studies of precocity in eucalypts have similarly been treated as a binary response (Chambers et al. 1997). Tree height and basal diameter of 5 year old trees were measured in June 2006. Basal diameter was recorded at 10 cm above ground level to avoid error associated with stump swell. Tree survival was also recorded as a binary response in 2006.

Statistical analysis

Probability distributions were generated for each genetic parameter using Bayesian methods. Such distributions can then be characterized by the mean, median and mode, all of which differ in their bias when viewed as potential point estimators (Ruzzante et al. 2004; Gonçalves-Vidigal et al. 2008). Wright et al. (2000) recommended using the mode for describing the posterior distribution of the parameters. This is the region of high density, the value that maximizes the function $f(h^2|y)$, or the most probable value of h^2 (Blasco 2001).

A Bayesian variance component estimation model was assumed using the Gibbs sampling algorithm. Threshold models were fitted to flowering and survival data according to Van-Tassell et al. (1998) which were considered discrete variables with binary outcomes. Linear models were fitted to growth traits.

MTGSAM program (Van-Tassell and Van-Vleck 1996; Van-Tassell et al. 1998) was used in the Bayesian analyses. Here, block and sub-race effects followed the flat prior distribution (uniform), the random effects were assumed to be normally distributed (additive genetic and residual effects), and the variance components were assumed to be distributed as an Inverted Chi-Square (Van-Tassell and Van-Vleck 1996). For more details about the joint posterior density see Van-Tassell et al. (1998). The convergence of the Gibbs chains was checked using the Heidelberger and Welch's (1983) test which was performed into the R program with CODA routine (Convergence Diagnosis and Output Analysis).

Significance of Population effects (i.e. provenance or seed source) were tested using the MIXED procedure for growth traits, and %GLIMMIX macro (logit model; canonical link function) for flowering time and survival rates (SAS-Institute 1996). Results were corroborated using credible intervals (95%) from posterior distributions of the mean population differences, estimated using WINBUGS (Bayesian inference Using Gibbs Sampling) (Spiegelhalter et al. 2003).

Genetic parameter estimates

The narrow-sense individual tree heritability $\left(h_a^2\right)$ or degree of additive genetic control was calculated for each trait using:

$$h_a^2 = \frac{\sigma_a^2}{\left(\sigma_a^2 + \sigma_e^2\right)}$$

where σ_a^2 and σ_e^2 are the additive genetic variance and residual variance, respectively. $\left(\sigma_a^2 + \sigma_e^2\right)$, is the phenotypic variance $\left(\sigma_p^2\right)$. The genetic advance, or additive genetic gain, was further estimated for each trait using the breeding values of individual trees (Furlani et al. 2005).

The genetic diversity was estimated for each trait according to Wei and Lindgren (1996):

$$GD = \frac{\left[\left(\sum k_f\right)^2 \big/ \sum k_f^2\right]}{\mathbf{N}_p}$$

where GD is the genetic diversity maintained after selection; the numerator $\left[\left(\sum k_f\right)^2 \big/ \sum k_f^2\right]$ is the effective number of selected progenies; k_f is the

number of individuals selected per progeny; $\mathbf{N}_p$ is the original number of progenies (39).

Pearson correlation coefficients were calculated among traits using the estimated breeding values, as a measurement of the genetic association between two traits. Bootstrap confidence intervals with 95% probability were estimated for Pearson correlations using the SURVEYSELECT procedure (SAS-Institute 1996) with 1,000 random samples.

Results

Flowering and growth

Early flowering, growth and survival differed significantly among provenances ($P < 0.05$; see Table 1). The magnitude of the difference between the best and worst provenance was 9% for survival, 19% for diameter, 43% for height and 82% for early flowering. Mean tree survival over the 5-year period was high (92.65%) and ranged from 88% in provenances from Flinders Chase to 96% in those from Wirrabara. Early flowering varied from 5% in Flinders Chase to 30% in Illapel-Chile, with an overall average of 21% for the trial. After five growing seasons, tree height ranged from 1.98 m in Marble Range to 3.47 m in Wirrabara. Similarly, Marble Range also had the lowest growth in diameter (55 mm) and Wirrabara the highest (68 mm).

Heritability

Estimates of variance components and narrow-sense heritability from the Bayesian posterior distributions are given in Table 2. The Markov chains (Gibbs samples) achieved convergence for all parameters (variance components and heritability) using a total of 230,000 Gibbs sampling rounds for each replicate. The first 30,000 rounds were discarded as the burn-in or initialization period (Van-Tassell et al. 1998). Marginal posterior distributions for heritability are given in Fig. 1. Mean posterior estimate of narrow-sense heritability (h^2) was similar to mode posterior estimate for the threshold model in early flowering. For growth traits (linear model) and survival the difference between mean and modal estimates reflects some lack of symmetry in posterior distribution estimates (Van-Tassell et al. 1998; see Fig. 1).

Table 1 Population means for growth (height and basal diameter measured at age 5), early flowering (recorded at age 3) and survival (recorded after 5 growing seasons) evaluated at southern Atacama Desert for 39 half-sib families of *Eucalyptus cladocalyx*

Population	Trees evaluated (number)	Families evaluated (number)	Early flowering (%)	Height (m)	Diameter (mm)	Survival (%)
MT Remarkable[a]	480	16	25 a	3.15 b	62.22 b	94 ab
Marble Range[a]	120	4	23 a	1.98 c	55.01 c	90 ab
Wirrabara[a]	270	9	25 a	3.47 a	67.95 a	96 a
Flinders Chase[a]	240	8	05 b	3.27 ab	62.11 b	88 b
Illapel-Chile	60	2	30 a	3.03 b	58.87 bc	90 ab

[a] Seeds from the CSIRO Australian Tree Seed Centre base population collection

Columns with the same letter indicates that provenances are not significantly different at $\alpha = 0.05$ for that trait (credible intervals from posterior distribution of mean differences)

Precocity was highly heritable and had the highest value of heritability of all the traits measured: $h^2 = 0.52$ (range = 0.48-0.57). Tree height, basal diameter and tree survival were moderately heritable with posterior means and credible intervals of $h^2 = 0.28$ (0.21-0.37), $h^2 = 0.14$ (0.04-0.28) and $h^2 = 0.22$ (0.09-0.38), respectively. The 95% credible set from the threshold model for early flowering did not include the point posterior estimates of heritability for growth and survival traits.

The predictions of additive genetic effects were calculated for individual trees for all combinations of traits. Correlative analysis detected a moderate, positive relationship between early flowering and the growth traits. This moderate association was confirmed by the estimated Pearson correlation (see Table 3) with mean and Bootstrap intervals of 0.23 (0.18; 0.27) and 0.29 (0.25; 0.34). The correlations between early flowering and growth breeding values were also significantly different from zero ($P < 0.05$). The genetic association between early flowering and survival was lower, with mean and Bootstrap intervals of 0.11 (0.06; 0.15).

Early flowering had the highest predicted genetic gains with 41.22 and 36.15% for the selection intensities of 7.48 and 14.29%, respectively (Table 4). Early flowering and tree height showed the highest value of genetic diversity (GD), while tree survival showed the lowest value. The GD estimates vary within the interval $0 < GD \leq 1$. In this case, a value of genetic diversity close to 1 indicates that almost of the reference population variability was maintained and an estimate close to zero indicates that almost of the original population variability was extinct (Furlani et al. 2005).

Table 2 Variance components (posterior means) and narrow-sense heritability for early flowering, survival and growth traits assessed in 39 *Eucalyptus cladocalyx* families at southern Atacama Desert

Parameter	Early flowering	Height	Diameter	Survival
Additive variance	0.13	0.19	36.76	0.02
Residual variance	0.12	0.50	218.31	0.05
Phenotypic variance	0.25	0.69	255.07	0.07
Heritability				
Mean	0.52	0.28	0.14	0.22
Median	0.52	0.27	0.13	0.21
Mode	0.52	0.25	0.10	0.18
Lower cut-off	0.48	0.21	0.04	0.09
Upper cut-off	0.57	0.37	0.28	0.38

Discussion

Forest plantation programs usually aim to achieve high biomass productivities by combining tree survival and with high growth rates (Chambers et al. 1997). Tree survival in the early stages of development must, therefore, be considered in the selection programs. In the dry regions of Chile, early and prolific flowering is also desirable for honey production, in order to supplement the erratic flowering in native plants. We show here that precocious flowering in *Eucalyptus cladocalyx* is highly heritable and that does not impact negatively on tree growth. Breeding for precocity appears to be feasible as part

Fig. 1 Marginal posterior distribution of heritability (h^2) for early flowering (3 years after plantation), tree height, basal diameter and survival (at age 5) assessed in 1,170 *Eucalyptus cladocalyx* individual trees at southern Atacama Desert
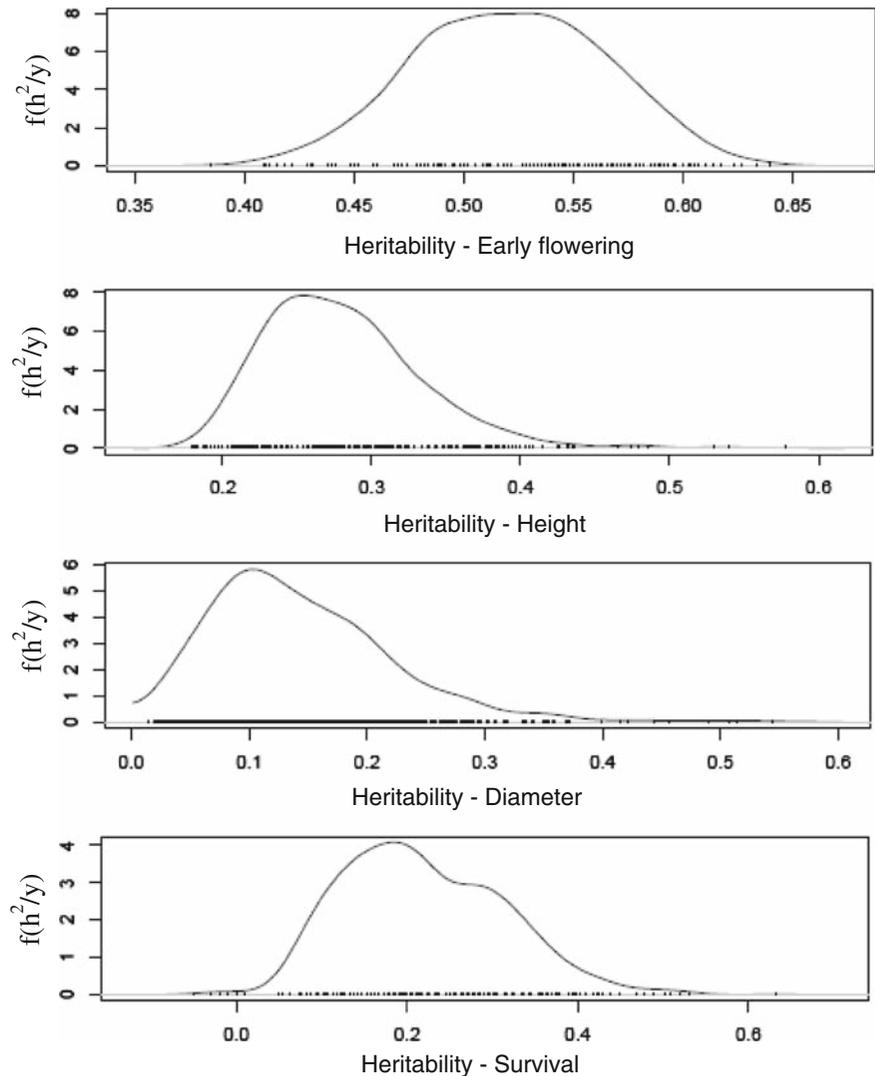

Table 3 Pearson's correlation coefficients (and Bootstrap confidence intervals; 95%) calculated between breeding values ($N = 1,170$) in 39 *Eucalyptus cladocalyx* half-sib families from of Australia and Chile, which are being evaluated at southern Atacama Desert. Early flowering was evaluated at 3 years-old trees, and growth traits and survival were measured after 5 growing seasons. Significant coefficients ($P < 0.05$) are in bold type

Traits	Early flowering	Height	Diameter
Height	**0.23** (0.18–0.27)	–	–
Diameter	**0.29** (0.25–0.34)	**0.49** (0.45–0.53)	–
Survival	**0.11** (0.06–0.15)	**0.09** (0.04–0.13)	**0.28** (0.23-0.32)

of a program to develop trees for multi-purpose plantations.

Tree survival is an important characteristic for agroforestry systems with hydric deficits, and the high survival rates in the current study confirms the suitability of *Eucalyptus cladocalyx* for the arid environmental conditions of southern Atacama Desert. Survival was the most consistent trait with the

Table 4 Estimates of predicted genetic advance (GG%) and genetic diversity (GD) from selection for early flowering, survival and growth traits in 39 *Eucalyptus cladocalyx* families (1,170 individual trees) evaluated at southern Atacama Desert in the growing seasons 2001–2006

Traits	Intensity of selection					
	7.48%			14.29%		
	N_{SF}	GG%	GD	N_{SF}	GG%	GD
Early flowering	22	41.22	0.314	35	36.15	0.607
Height	30	13.55	0.358	34	10.95	0.499
Diameter	17	7.52	0.200	25	6.14	0.338
Survival	11	6.38	0.169	23	5.41	0.287

N_{SF}, number of selected families

lowest magnitude of the differences between the best and worst provenance, unlike early flowering which was the most variable. Growing conditions in southern Atacama Desert in 2002 (second year of experimentation) were very good for the primary productivity (Squeo et al. 2006). The mean rainfall record in this year (394 mm), and about the midway between the areas of highest and lowest rainfall where similar *E. cladocalyx* naturally occurs in southern Australia (ca. 290–660 mm per annum, for Kangaroo Island and the Eyre Peninsula, respectively) (see Woodrow et al. 2002). The year 2002 was a rainy year associated to El Niño – Southern Oscillation (ENSO) event (Montecinos and Aceituno 2003). This effect is especially important in desert ecosystems such as the Atacama desert where water is the main limiting factor to plant productivity (Squeo et al. 2006). Vagaries in rainfall as a result of changes in the Southern Oscillation Index are also an intrinsic part of the weather systems in southern Australia, although in Australia El Niño years are associated with severe droughts.

Chambers et al. (1997) found that age-to-flowering varied markedly between species, among individuals within a species and with locality. For example, early flowering in 4 year old *Eucalyptus globulus*, for example, varied from 2 to 25%, depending on locality (Chambers et al. 1997). In the current study, the similar flowering values were found (5 or 30%, depending on population; see Table 1), with the earliest flowering detected in 3 year old trees.

Early flowering events are particularly important to tree improvement and reforestation programs

because genetically superior individuals can be identified and bred more rapidly (Meilan 1997). The generation interval is governed by the earliest age at which key traits can be reliably assessed and time to reproductive maturity (Chambers et al. 1997). In the study presented here, the heritability estimates (h^2), or degree of additive genetic control, indicate a significant genetic variation. The additive genetic control found in these populations allows tree selection for the establishment of cost-effective agroforestry systems.

Precocity of flowering has been included in others important eucalypt breeding programs (Chambers et al. 1997; Wiltshire et al. 1998) but until now little has been known about the genetic control of this in *E. caldocalyx*. We found here that early flowering was highly heritable. This is in accordance with Chambers et al. (1997) who found that the genetic control of early flowering in *Eucalyptus globulus* ssp. *globulus* was also highly heritable ($h^2 = 0.47$ or 0.59; averaged across 3 or 4 trials, respectively). Importantly, they found that flowering precocity could be considered as a single trait in their trials as there was little genotype-by-environment interaction (Chambers et al. 1997).

There have been conflicting reports on the impact that precocity might have growth traits, Chambers et al. (1997) found that early flowering was not genetically correlated with basal diameter in *Eucalyptus globulus* (average of 0.04), and concluded that selection for only this trait would have little impact on the early growth. Wiltshire et al. (1998), on the other hand, found a moderate genetic control for early flowering but only a weak genetic relationship between this trait and growth within and between populations of *Eucalyptus*. Williams et al. (2003) also found that early flowering could also affect the growth and the development of trees, although in their study early flowering was artificial promoted, rather than a genetically determined. Data presented in this paper indicate that selection for precocity may significantly enhance both growth and survival (Table 3).

Eucalyptus cladocalyx is heteroblastic, and only produces flowers when the trees are developmentally mature (Meilan 1997). It seems likely, therefore, that the flowering events detected here in 3 year old plants are a result of a shortened juvenile stage. This is important because the juvenile stage is also the

time of fastest growth. However, the growth traits were measured later, in the middle-term of the aimed harvesting time (Mora 2006). Thus, moderate relationships between early flowering and growth traits may be able to be maintained across time because the fast-growing phase occurs in the juvenile stage.

Early flowering would be advantageous in the Coquimbo region as the local farmers are extremely poor (Ormazábal 1991) and honey production from *Eucalyptus cladocalyx* trees is a potential source of extra income. For early flowering, both the genetic gain and the maintenance of high diversity levels are important for the honey production in southern Atacama Desert, in situations where native species are not available in sufficient quantities (Montenegro et al. 2003). *Eucalyptus cladocalyx* is highly variable, despite its relatively restricted distribution to three localities within Southern Australia (Ruthrof et al. 2003; Gleadow and Woodrow 2000; McDonald et al. 2003).

The results of the current study are valuable, particularly in the absence of information at the molecular level. Nevertheless, it is important to emphasize that the results are preliminary, and the next step would be to enhance the flowering sampling strategy by including a graduation scale for flowering intensity and data from two or more subsequent seasons; more intense data generation would help in more precise interpretation on flowering precocity to be used as a selection index. Anyhow, the genetic variability found in the present study may be used for breeding purposes in similar regions where environmental conditions are limiting factors to the establishment of others *Eucalyptus* species.

Conclusions

The Bayesian approach, together with Gibbs sampling technique, was found to provide practical information useful for breeding purposes and for understanding how quantitative traits are controlled genetically in *Eucalyptus cladocalyx*. We found that precocious flowering of *Eucalyptus cladocalyx* is under a high degree of genetic control. The estimated genetic correlations suggest that selecting for precocity at age three could also be allow for indirect selection of growth and survival traits in early generations. Information generated on the genetic

control of early flowering could be used by plant breeders to improve the honey production in southern Atacama Desert, in situations where native species are not available in sufficient quantities. The genetic gain was high when the selection is done directly for early flowering under water-limited conditions. Precocious trees of *Eucalyptus cladocalyx* have many practical applications in the arid zones of northern Chile and the genetic gain confirmed tremendous potential for beekeepers and farmers which are looking for precocious trees with a large distribution of flowers over the dry seasons.

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