Age Trends in Variances and Heritabilities in *Eucalyptus* Factorial Mating Designs

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Summary

This article presents the analyses of the first mating designs established in the 2 reciprocal recurrent selection schemes of *Eucalyptus* in Congo. Height, circumference and volume were measured until 3 or 4 years (half of the rotation age). The objective was to observe trends in variances and heritabilities with age in order to find growth phases which could indicate an optimal age for early selection.

Results showed that variances and heritabilities were strongly influenced by the experimental process (nursery, planting, environmental effects).

No marked changes between the juvenile stage and the mature stage could be seen through the trend in variance components with age.

Narrow-sense heritability on the male or female progeny mean basis, used for parent selection, could drastically change during the first two years of growth. In several cases it increased and then reached an apparently stable value until plantation rotation. These result indicate that early selection of the parents before 2 years may not be beneficial.

Broad-sense heritability on the individual basis, used for clone selection, became constant after the first year. It was higher for height than for circumference and volume and therefore gave a better predictive value for the former trait when selected early.

The trends in genetic parameters with age were analysed in relation to FRANKLIN's model, in order to better understand the results. Narrow-sense heritabilities on the male or female progeny means basis and genetic variances suggest that measurements were made during the second phase of the FRANKLIN's model. Broad-sense heritability on the individual basis did not conform to the FRANKLIN's model.

Key words: mating design, variance components, heritability, early selection, *Eucalyptus* hybrids.

FDC: 232.11; 165.41; 165.72; 176.1 *Eucalyptus.*

Introduction

In order to improve the productivity of the clonal plantations of *Eucalyptus* in Congo, a reciprocal recurrent selection scheme based on full-sib families was implemented for 2 hybrids, *E. urophylla* • *E. grandis* and *E. urophylla* • *E. pellita* (VIGNERON, 1991). The theoretical attractiveness of such a strategy when 2 species are complementary, when they are not much improved and when the varieties produced are clones or full-sib hybrid families, has been widely discussed (GALLAIS, 1990). Research must now be oriented towards selection techniques that improve assessment of genotypic value and shorten the generation interval.

Several studies have shown that a better knowledge of the genetic parameter trend with age influences the selection efficiency. These studies have particularly attempted to find the optimal age of early selection (LAMBETH *et al.,* 1983; FOSTER, 1986; GILL, 1987; BASTIEN and ROMAN-AMAT, 1990; VAN WYK, 1990; GREENE and LOWE, 1992; KING and BURDON, 1991; WU *et al.,* 1992). In the case of *Eucalyptus,* few reports were published about change in genetic parameters over the plantation rotation (BORRALHO *et al.,* 1992a and b). Results in this field are needed because of the numerous programmes being established in many parts of the world.

Within the framework of the 2 reciprocal recurrent selection schemes, the first factorial mating designs enable the analysis of trends in genetics parameters with age.

The objective of this study is to eventually find, by analysing trends in variance components and in heritabilities with age, an optimal early selection age for:

- the parents which will be involved in the intra-species recombination phase,
- the ortets selected for clone production.

Materials and Methods

Location

The factorial mating designs were established by the Centre Technique Forestier Tropical du Congo (CTFT-CONGO) at the experimental research station of Kissoko located in the commercial plantation of UAIC (Unité d'Afforestation Industrielle du Congo), 15 km east of Pointe Noire (lat. 4°45'S, long. 11°54'E, alt. 50 m). The soils are psammitic, ferralilitic, 90% sand and 5% clay. The climate is tropical, mean annual rainfall is 1200 mm and mean annual temperature is 24 °C, with a dry season from May to October.

Vegetation before planting was a savanna with *Imperata diplandra* and *Anona arenaria.*

Mating design

The mating designs used are factorial. Two designs were established in the field in 1989, the R89-20 and the R89-21 and 2 in 1990, the R90-11 and the R90-10. Parameters are shown in *table 1.* The crossings were made by controlled pollination but, owing to technical problems, the mating designs are not correctly balanced. The ratio of full cells to total cells is weak, less than 50%.

The factorial designs of 1990 concerned a wider sample of the parental populations but are more unbalanced than those of 1989.

In *E. urophylla* • *E. grandis* mating designs, 1 female and 6 males were common to R89-20 and R90-11. In *E. urophylla* • *E. pellita* mating designs, 3 females and 7 males were commun to R89-21 and R90-10.

In 1989, 11 *E. urophylla* females were common to *E. urophylla* • *E. grandis* and *E. urophylla* • *E. pellita* mating designs. In 1990, 16 *E. urophylla* females were common to *E. urophylla* • *E. grandis* and *E. urophylla* • *E. pellita.*

The main characteristics of the parents were as follows (BURGER, 1990):

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Table 1. – Mating design parameters (excluding dwarfs, broken trees and disconnected families).

	*E. urophylla*E.grandis*		*E. urophylla*E.pellita* (1)	
parameter	R89-20	R90-11	R89-21	R90-10
No males	9	14	11	22
No females	15	16	14	19
No families	51	94	42	133
No trees	1612	3906	1328	6284
TR1 (2)	37%	42%	27%	32%

[1]) *E. urophylla* is the female species, *E. grandis* et *E. pellita* are the male species.

[2]) TR1: ratio of the number of crossings made to the number of possible crossings.

Males:

– *E. grandis*

The provenance origins are tropical. Most of the individual trees were selected on their mature-age phenotypes for growth, morphological and adaptative traits.

– *E. pellita*

Trees came from 5 provenances with a high proportion from the provenance of Helenvale (Australia). They were also selected on their mature-age phenotype for growth, morphological and adaptative traits.

Females:

– Individuals of *E. urophylla* came from 4 provenances and some trees are of unknown origin. Some females belonged to the same half-sib family.

A feature which characterizes females comparitively to males, is the quality of selection. As already stated, male trees were selected on their mature-age phenotype. On the contrary, the females were selected either for their abundance of flowers (in many cases they were border trees which benefited from more light), or for their early growth at 1 or 2 years after establishment before being grafted in a clonal seed orchard. In fact none of the *E. urophylla* females were selected on their mature-age phenotype.

Field design

Mating designs R89-20 and R89-21

These 2 mating designs were established according to a completely randomized field design with variable number of replicates (1 to 4) among crosses. The experimental unit was a square plot of 4 • 4=16 trees. The trial was surrounded by 2 border rows. Spacing was 3 m by 5 m. A starter fertilizer was applied after planting; 150 g of N-P-K 13-13-21 at the base of each tree.

Mating designs R90-10 and R90-11

These 2 designs were established in 32 incomplete blocks which could be grouped into 4 large incomplete blocks. As the analyses using the 2 alternative designs gave the same results and as there was a very high edaphic homogenity within each large block, it was decided to retain the analysis from the 4-block design.

As in 1989, the experimental unit was a square plot of 4 • 4=16 trees. The trial was surrounded by 2 border rows. Spacing was 3 m by 5 m. A starter fertilizer was applied after planting; 150 g of N-P-K 13-13-21 at the base of each tree.

Measurements

The growth traits measured and calculated at different ages were the following:

H(n) : total height at n months,

C(n) : circumference at breast height at n months,

VI(n) : individual volume at n months calculated using the cone formula.

In R89-20 and R89-21 the last measurements were taken at 48 months and in R90-10 and R90-11 at 38 months. This is approximately half of the harvesting age in Congolese commercial plantations.

Data analyses

The analyses were performed excluding dwarfs which were not considered representative of the reference population. These dwarfs were characterised by very short internodes, small shrivelled leaves and a very different growth pattern; 2.5 m at 3 years in comparison to an average of 13 m for the normal population. The percentage of dwarfs may be not negligible, being approximately 10% for *E. urophylla* • *E. grandis.*

For the mating designs of 1989, the following random model was used (model [1]).

$$y_{ijk} = \mu + m_i + f_j + m^*f_{ij} + r_{ijk} \qquad [1]$$

- μ is the overall mean;
- y_{ijk} is the phenotypic mean value of plot "k" of the crossing between male "i" and female "j", with variance σ^2_t and expectation μ;
- m_i is the random effect of male "i", with variance σ^2_m and null expectation;
- f_j is the random effect of female "j", with variance σ^2_f and null expectation;
- $m \bullet f_{ij}$ is the random interaction effect between male "i" and female "j", with variance $\sigma^2_{m \bullet f}$ and null expectation;
- r_{ijk} is a residual, random effect with variance σ^2_r and null expectation.

For the mating designs of 1990, the block effect was incorporated in the following mixed model (model [2]).

$$y_{ijk} = \mu + b_k + m_i + f_j + m \bullet f_{ij} + r_{ijk} \qquad [2]$$

where y_{ijk}, m_i, f_j, $m \bullet f_{ij}$ and r_{ijk} are the effects described above and b_k is the fixed effect of block k, $1<k<4$.

The analysis of variance was performed with SAS Proc GLM SS3 (Azais, 1994) and the variance components were estimated with S.A.S Proc Varcomp method ml (maximum of likelihood) (SAS Institute, 1988).

The factorial mating design allowed estimation of some genetic variance components: additive and dominance variances. We assumed that epistatic variance was negligible and that the inbreeding coefficient of the parents was zero.

The formulas for estimation of additive variances, in the case where 2 parental populations belong to 2 different species, are the following:

– additive variance within the female population:

$$\sigma^2_{Af} = 4\,\sigma^2_f \qquad [3]$$

– additive variance within the male population:

$$\sigma^2_{Am} = 4\,\sigma^2_m \qquad [4]$$

– additive variance estimated for the hybrid population is the average of these 2 estimates:

$$\sigma^2_A = 2\,(\sigma^2_f + \sigma^2_m) \qquad [5]$$

Variance of dominance effects will be defined as:

$$\sigma^2_D = 4\,\sigma^2_{m \bullet f} \qquad [6]$$

And the estimate of total genetic variance $\sigma^2_{G,}$ of the hybrid population is:

$$\sigma^2_G = \sigma^2_A + \sigma^2_D \qquad [7]$$

Heritabilities

The broad-sense heritability on an individual basis is given by the following formula:

$$H^2_{sl} = \frac{2\,(\sigma^2_m + \sigma^2_f) + 4\sigma^2_{m \bullet f}}{\sigma^2_m + \sigma^2_f + \sigma^2_{m \bullet f} + \sigma^2_e} \qquad [8]$$

This parameter defines the reliability of the phenotypic value of an individual to predict its clonal value.

σ^2_e was estimated by a separate analysis using models on individual observations.

The narrow-sense heritability on the male progeny mean basis:

$$h^2_{Am} = \frac{1/4\,\sigma^2_{Am}}{\sigma^2_m + \sigma^2_{m \bullet f}/f' + \sigma^2_r/f'b'} \qquad [9]$$

f' : harmonic mean of number of females crossed with one male, b' : harmonic mean of number of repetitions.

This parameter defines the reliability of the mean values of a male progeny for predicting its crossbreeding value (with females of another species).

The narrow-sense heritability on the female progeny mean basis:

$$h^2_{Af} = \frac{1/4\,\sigma^2_{Af}}{\sigma^2_f + \sigma^2_{m \bullet f}/m' + \sigma^2_r/m'b'} \qquad [10]$$

m' : harmonic mean of number of males crossed with one female, b' : harmonic mean of number of repetitions.

This parameter defines the reliability of the mean value of the female progeny for predicting its crossbreeding value (with males of another species).

Standard error of heritability will be given by the ratio of standard deviation of the numerator to the denominator (BECKER, 1985).

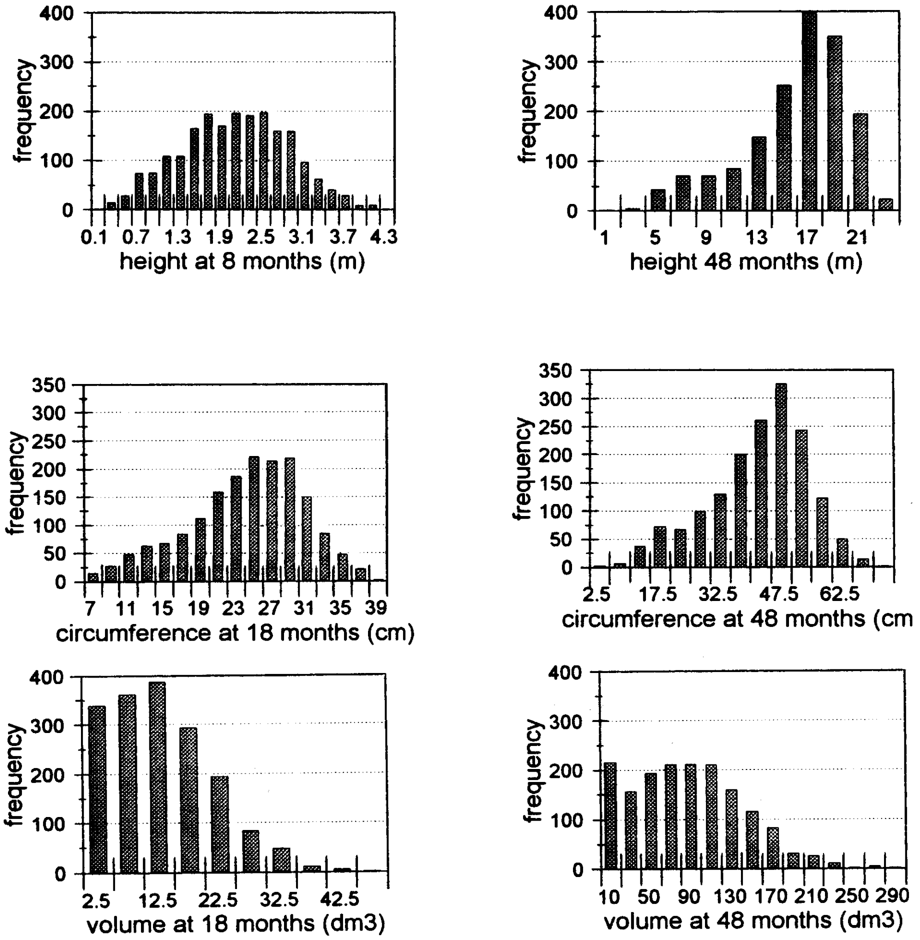

Figure 1. – Trends in frequency distribution with age for the individual growth traits, example of the factorial design *E. urophylla* • *E. grandis* R89-20.

Table 2. – Overall means and coefficients of variation (CV) for absolute height, circumference and volume in different mating designs of the 2 hybrids.

E. urophylla*E.grandis

design R89-20							design R90-11						
	height (m)		circumference (cm)		volume (dm3)			height (m)		circumference (cm)		volume (dm3)	
age	mean	CV	mean	CV	mean	CV	age	mean	CV	mean	CV	mean	CV
8	2.14	33					4	0.78	20				
18	7.26	27	23.6	27	12.9	64	16	5.59	18	17.8	20	5.2	52
29	10.26	26	32.5	28	34.2	62	27	10.29	18	28.7	21	25.2	49
36	13.40	25	36.3	29	55.8	61	38	13.35	17	34.6	22	46.9	51
42	14.46	25	39.0	29	70.0	62							
48	15.77	26	41.4	30	86.6	63							

E. urophylla*E.pellita

design R89-21							design R90-10						
	height (m)		circumference (cm)		volume (dm3)			height (m)		circumference (cm)		volume (dm3)	
age	mean	CV	mean	CV	mean	CV	age	mean	CV	mean	CV	mean	CV
8	2.01	31					5	1.35	19				
18	6.51	26	23.9	23	11.4	58	17	7.45	17	23.3	18	11.6	42
29	9.89	21	32.7	23	31.5	54	28	11.25	15	31.3	18	32.2	42
36	12.62	20	36.6	24	50.5	53	39	14.56	15	38.3	19	61.0	43
42	13.95	19	39.6	23	64.9	52							
48	15.12	19	41.8	24	78.9	53							

CV: coefficient of variation calculated on the individual basis.

The standard deviation of variance will be calculated by the standard deviation of a linear combination with the estimation of maximum likelihood given by S.A.S software (S.A.S Institute, 1988).

Results

Trends in growth

Height

This trait presents a marked trend in distribution with age. The distribution is close to normal at 8 months and then develops a pronounced negative skewness. This is demonstrated by the example of R89-20 population (*Figure 1*). This change is common with *Eucalyptus* stands in Congo and reflects increase of competition between individuals.

For *E. urophylla* • *E. grandis,* height growth is similar for the 2 mating designs after 2 years (*Table 2*).

The coefficient of variation diminishes with age for the 2 designs (*Table 2*), which can be explained by the death of weak individuals. Indeed, the mortality rate sharply increases until 3 years and reaches 16% in R89-20 and 10% in R90-11. The coefficient of variation is weaker for the R90-11. This could be due essentially to sampling or different environmental effects.

For *E. urophylla* • *E. pellita* height growth differed at 36 months between the 2 designs and the sampling effects or the soil can explain this difference. The fact that the trials are separated in the experimental research station of Kissoko reinforces this last hypothesis. As for *E. urophylla* • *E. grandis,* the coefficient of variation diminishes with age (*Table 2*) and this trend can be due to the mortality which increases with age and reaches 14% at 36 months in R89-21 and 6% at 39 months for R90-10.

Circumference

This trait showed a more pronounced negative skewness with increasing age (*Figure 1*), reflecting strong competition effects.

Within each hybrid, we observe differences in growth between the trials which can be attributed to sampling and soil effects (*Table 2*).

As for height, the coefficients of variation are weaker for the trials of 1990 (*Table 2*), which can be explained in the same way. On the other hand, coefficients of variation have a tendancy to increase with age. This pattern is probably due to measurement of very small individuals that were not measured at the previous ages because of their insufficient height (below 1.3 m) but may also be due to an increase of competition which affects circumference more than height.

Volume

On the contrary to height and circumference, volume is characterized by positive skewness (*Figure 1*). This asymmetry is usual for the biomass traits and can be attributed to the effects of competition between individuals (BENJAMIN and HARWICK, 1986).

The differences of growth between the designs are marked for this trait (*Table 2*).

The coefficients of variation are higher than those of height and circumference (*Table 2*), but their trend with age is less clear; they diminish with age for the 1989 trial and are stable for the 1990 trial.

Results of analysis of variance and variance component estimation

The estimates of variance components, standard error and FISHER's test are presented in appendix (*Tables 1* and *2*).

These tables emphasize the differences of variance structure between the mating designs for the same hybrid. This is demonstrated for *E. urophylla* • *E. pellita* where σ^2_{m}, σ^2_{f} and $\sigma^2_{m \bullet f}$ are not significantly different from zero in R89-21 for circumference and volume, whereas they are significantly different from zero at the $P<0.0001$ level in R90-10 for all traits at all ages. Standard errors, especially for male and female variances are high and emphasize the effect of small size of parental populations. We also note lower standard errors for the trials of 1990 which is expected because of the larger population of males, females and crossings. The ratio of variance of the genotypic effects to the phenotypic variance is generally weak and shows the importance of non-genetic effects in the total variability.

Trends in variance components with age

Figures 2 and *3* present trends with age of male additive variance, σ^2_{Am}, female additive variance σ^2_{Af}, dominance variance, σ^2_{D} and residual variance σ^2_{r} for the 1989 and 1990 designs for each hybrid. Several points can be underlined.

We note for each hybrid a stronger residual variance, σ^2_{r}, in the 1989 trial in comparison to the 1990 trial. This result can be explained by a lesser control of soil effects in 1989 (no blocking), by better weed control in 1990 and maybe also by the selection of seedlings at the nursery stage in 1990. This selection possibly resulted to eliminate the less ideal seedlings and possibly reduced environmental effects by decreasing mortality and stand heterogeneity.

The female additive variance, σ^2_{Af}, exceeded the male additive variance, σ^2_{Am}, for all traits and for both designs of each hybrid. The difference between these two variance estimates tends to increase with age, in particular after 2 to 3 years.

Estimated dominance variance, σ^2_{D}, was lower than additive variances for mating designs R89-20 and R89-21 and is more or less constant with age. On the other hand, for the mating designs R90-10 and R90-11, estimated dominance variance is close to female and male additive variances and sometimes greater. This difference between designs could be due to sampling effects from the parental populations. As shown in *table 1*, the sample sizes were small and the estimation of genetic parameters may change greatly from one sample to another.

The similarity of results between two hybrids established in the same year, ie, designs R89-20 and R89-21 or/and designs

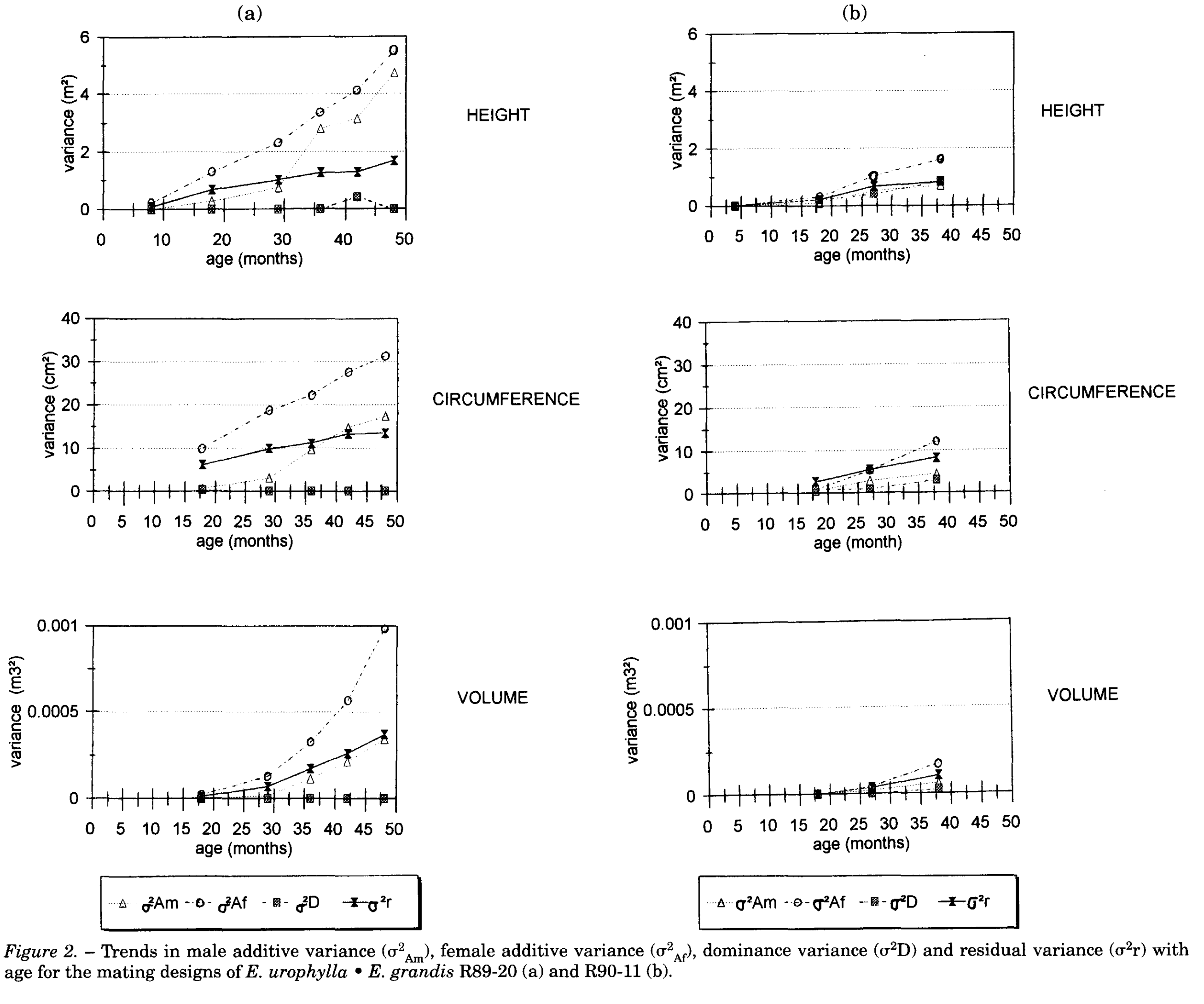

Figure 2. – Trends in male additive variance (σ^2_{Am}), female additive variance (σ^2_{Af}), dominance variance (σ^2D) and residual variance (σ^2r) with age for the mating designs of *E. urophylla* • *E. grandis* R89-20 (a) and R90-11 (b).

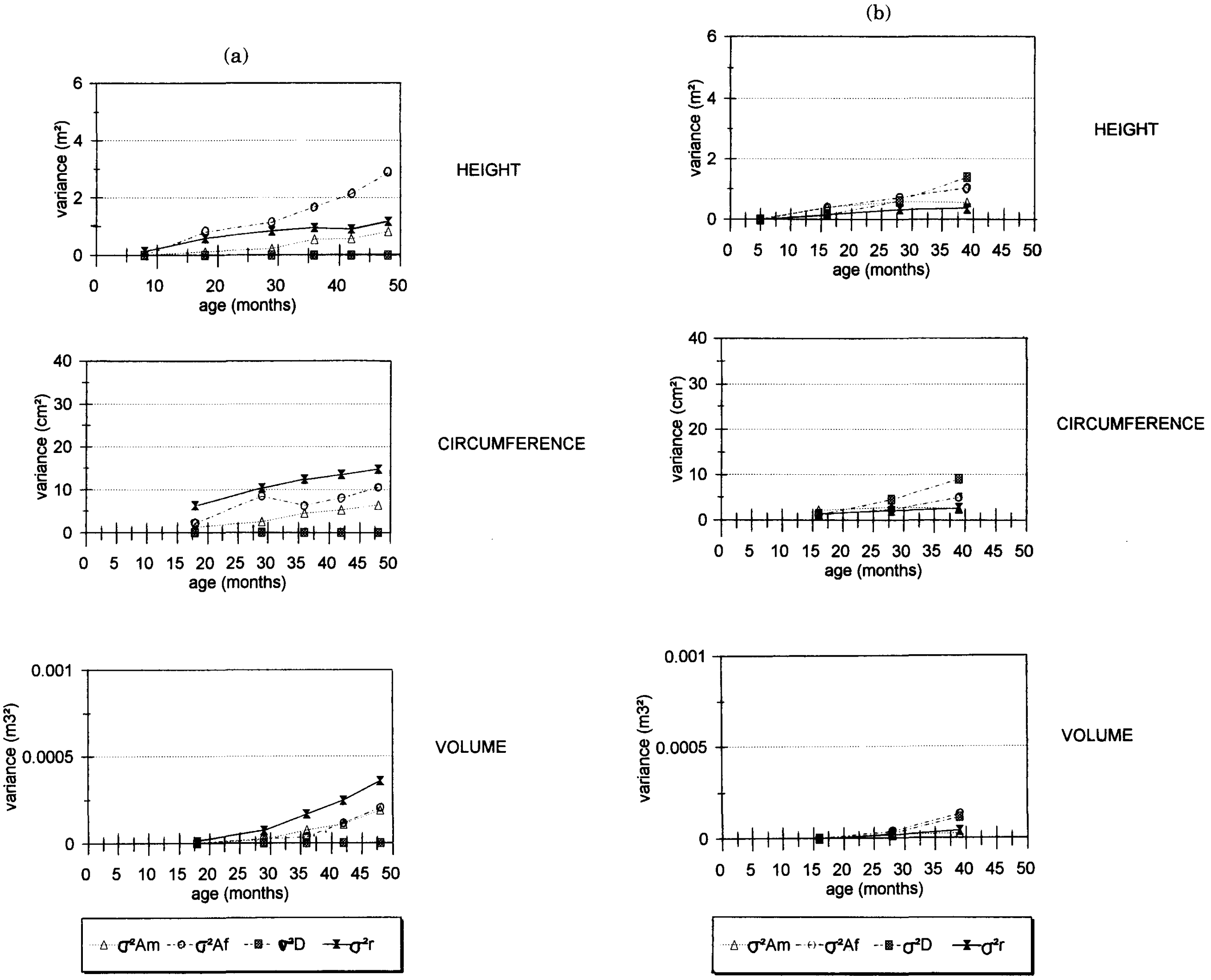

Figure 3. – Trends in male additive variance (σ^2_{Am}), female additive variance (σ^2_{Af}), dominance variance (σ^2D) and residual variance (σ^2r) with age for the mating designs of *E. urophylla* • *E. pellita* R89-21 (a) and R90-10 (b).

R90-10 and R90-11, is maybe due to them all having more or less the same parents of *E. urophylla* or maybe due to the strong effect of experimental process (nursery, planting, experimental design, environmental effects...).

Trends in variances with age do not show any systematic change of pattern which could separate two developing phases, the first related to establishment of trees, the second related to growth under strong competition. However, an increase of σ^2_{Af} and σ^2_{Am} is observed for height and volume in the design R89-20 after 2 years (*Figure 2a*), and an increase of σ^2_{Af} for height in R89-21 (*Figure 3a*).

Trends in heritability

As this parameter strongly depends on population, field design, environment, and trait (LAMBETH *et al.*, 1983; RINK and CLAUSEN, 1989), the trend in the different heritabilities H^2_{sl}, h^2_{Af} and h^2_{Am} with age is presented for each factorial design of each hybrid (*Figures 4* and *5*).

As the mating designs present specific characteristics, trends in heritabilities are not very homogeneous. It is however possible to formulate some general rules.

h^2_{Af} and h^2_{Am} are obviously higher than H^2_{sl}, a predictable result considering the high number of trees within each parental progeny.

Broad-sense heritability, H^2_{sl}, is higher for height than for circumference and volume. This is very likely due to height being less sensitive to environmental effects caused by competition or mortality (creation of empty spaces between trees). This result has been observed for other populations of *Eucalyptus* (BORRALHO *et al.*, 1992a; WHITEMAN *et al.*, 1992) and for other forest species (GIANNINI and RADDI, 1992). This difference is less clear for h^2_{Af} and h^2_{Am} because the environmental effects are strongly minimized (see formulas [9] and [10]).

Trends in heritabilities h^2_{Af} and h^2_{Am} with age are sometimes characterized by an increase followed by a plateau. This is the case for h^2_{Am} for the trials of *E. urophylla* • *E. grandis* R89-20 and R90-11 for the 3 growth traits (*Figures 4a* and *4b*) and for h^2_{Af} and h^2_{Am} for height in R89-21 (*Figure 5a*). This change could indicate (more clearly than for the variances), a trend with age in gene expression as stands develops. This tendency is not found in R90-10 where the value of h^2_{Am} decreases with age (*Figure 5b*). No obvious explanation can be put forward but as the residual effects are the same for h^2_{Af} and h^2_{Am}, the trend of h^2_{Am} could be related to the trend of additive variability of *E. pellita* crossed with *E. urophylla.*

Discussion

The objective of this study was to observe trends in variances and heritabilities with age, in order to find some growth phases which could indicate a preferential early selection age. The trend of variances does not offer very clear results. Heritability estimates shows some trends but the results differ between designs. Numerous factors must change variance components and heritabilities during the first 3 or 4 years:

- mortality, the rate of which increases until 3 years and then stabilizes, especially for *E. urophylla* • *E. grandis.* A rate of 16% is reached for R89-20 and of 10% for R90-11. This mortality may affect the relative frequencies of genotypes and therefore variances;
- change of microenvironmental effects between planting and crown closure already mentioned in other studies (Namkoong *et al.,* 1972; Kremer, 1981; Durel, 1990). In the designs studied, the microenvironmental effects at the beginning of growth could have been caused by the uncontrolled environmental conditions at the nursery stage (no randomisation of seedlings) or by environmental effects when planting (fertilization, soil, weed competition);
- competition among trees, which is, without any doubt, the most commonly used explanation of the trend in variance with age (Namkoong and Conkle, 1976; Tuskan and van Buijtenen, 1986; Cotterill and Dean, 1988; Foster, 1989; Balocchi *et al.,* 1993), can influence the expression of variability in these designs. The *Eucalyptus* species are also sensitive to competition as shown by frequency distributions shown in *figure 1* and by other experiments in Congo (Bergonzini, 1982).

In order to better understand the results, it is possible to place them within the framework of Franklin's model, (Franklin, 1979), which suggests 3 phases in the evolution of additive variance and heritability.

In the first, the juvenile genotypic phase, the additive variance remains constant or increases slightly and heritability diminishes. This phase corresponds to microenvironment capture after planting and to the progressive increase of competition until crown closure. Its duration is very short. In the second, the mature genotypic phase, inter-tree competition intensifies. Additive variance increases strongly as does the heritability which then reaches a plateau. This phase is the longest one.

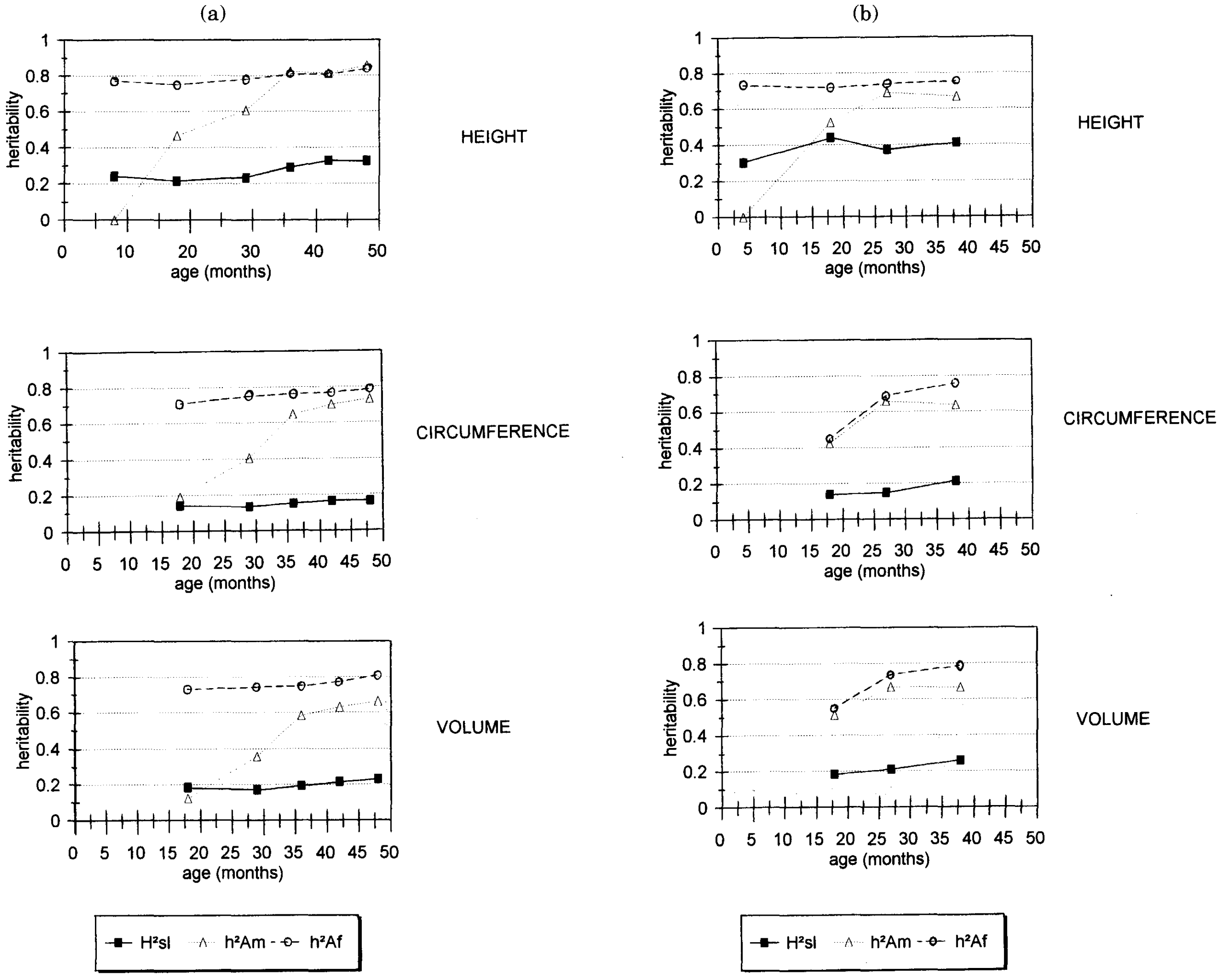

Figure 4. – Trends in individual broad sense heritability (H²sl), narrow-sense heritability on the male progeny mean basis (h^2_{Am}), narrow-sense heritability on the female progeny mean basis (h^2_{Af}) with age for the mating designs of *E. Europhylla* • *E. grandis* R89-20 (a) and R90-11 (b).

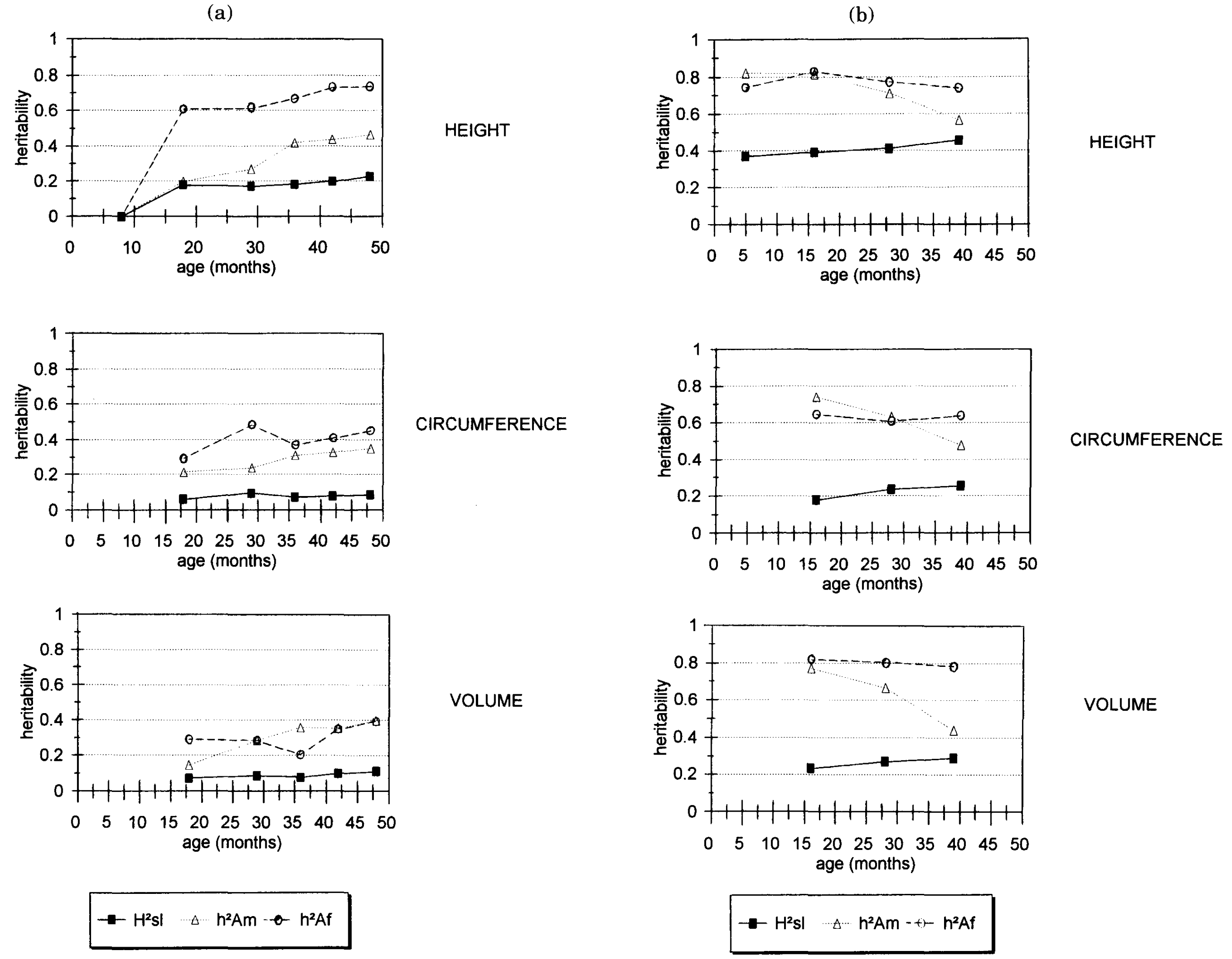

Figure 5. – Trends in individual broad sense heritability (H²sl), narrow-sense heritability on the male progeny mean basis (h^2_{Am}), narrow-sense heritability on the female progeny mean basis (h^2_{Af}) with age for the mating designs of *E. Europhylla* • *E. pellita* R89-21 (a) and R90-10 (b).

In the third phase, the codominance suppression phase, which generally occurs after the harvesting age, estimates of genetic additive variance and heritability decrease upon degeneration of the stand. This phase could occur after 15 years for *Eucalyptus* in Congo. FRANKLIN adds that the age-age correlations are higher within each phase than between phases.

If some experiments have agreed with this model (FOSTER, 1986; PORTEFAIX, 1987; BALOCCHI *et al.*, 1993), numerous forestry studies have presented different results (LAMBETH, 1980; LAMBETH *et al.*, 1983; FOSTER, 1986; GILL, 1987; COTTERILL and DEAN, 1988; GREENE and LOWE, 1992).

In the case of the experimental designs in Congo, the first phase marked by a decrease of heritability was not observed for h^2_{Af} and h^2_{Am}. The fact that h^2_{Af} and h^2_{Am} sometimes increased and reached a plateau, and that there was no abrupt systematic change in variance trends, shows that the trees may be in the second phase of the FRANKLIN's model. The first phase was not observed, perhaps due to measurements not being taken before 8 months. Other reasons could have been the large spacing which minimized competition effects and intensive silviculture which minimized microenvironmental effects, therefore allowing the additive variance to rapidly increase. After 3 years, judged by the 1989 designs, the heritability remains constant and will not significantly change. The studies made on clones show that between 3 and 7 years, the heritabilities remain constant (BOUVET, 1991).

The curve of h^2_{Am} in R90-10 which decreases sharply (*Figure 5b*) requires an explanation. The decrease of h^2_{Am} could correspond to the high homogenity at mature age of the male population of *E. pellita* used in this mating design. The fact that additive variance of *E. pellita* increased rapidly at the beginning of growth and then remained more or less constant (*Figure 3b*) could be due to the moderate growth potential for this species in the Congo.

Whatever the trend, it appears beneficial to select parents at an age where heritability reaches a stable value, provided that this trend is due to the change in additive variance and not to the change in environmental variance. In these experiments this age was found to be after 2.5 years.

The broad-sense heritability, H^2_{sl}, also showed a very different trend from those proposed by Franklin. After tending to increase, it seemed to stabilize from 2 years. As for h^2_{Af} and h^2_{Am}, H^2_{sl} should remain constant until 7 years (BOUVET, 1991). This parameter did not show a clear optimal age for clonal selection. H^2_{sl} is characterized rather by a higher value for height than for circumference, which could lead to a different strategy in early selection. As the efficiency of indirect selection depends on genetic correlation with the mature trait and on heritability of the predictor, height could then be a good predictor of mature volume if the genetic correlation is high (Gallais, 1990).

Conclusion

The analyses of the first mating designs lead to the following conclusions:

- for each hybrid, results differ greatly between mating designs, depending on the population sampling and on the trial;
- trends in variance highly depend on the genotypic effect;
- no marked change between a juvenile phase and a mature phase can be seen through trend with age of variance components;
- narrow-sense heritability on the male (female) progeny mean basis corresponding to the crossbreeding value of the parents, can markedly change during the first 2 years of growth according to the trend in variances with age, depending on the trait and on the sample. This result means that early selection of the parents prior to 2 years can not be very accurate;
- broad-sense heritability on an individual basis corresponding to the clonal value shows a less dependent trend of the trial, and remains constant after the first year. Its value is higher for height than for circumference and volume, and indicate height as a good predictor for early selection.

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Appendix

Table 1. – Estimation of variance components and results of analysis of variance for the mating designs R89-20 and R90-11; *E. urophylla* • *E. grandis.*

					mating design R89-20									
	male				female				male*female				heritability	
trait	σ^2m	prob>F	se	%	σ^2f	prob>F	se	%	σ^2m*f	prob>F	se	%	H^2sl	se
H8	0.00	0.842	0.00	0.0	0.06	0.000	0.03	34.5	0.00	0.680	0.00	0.0	0.24	0.08
H18	0.07	0.022	0.07	6.6	0.33	0.000	0.15	30.0	0.00	0.623	0.00	0.0	0.22	0.08
H29	0.19	0.005	0.14	10.5	0.58	0.000	0.26	32.2	0.00	0.691	0.00	0.0	0.23	0.08
H36	0.70	0.000	0.43	24.8	0.84	0.000	0.37	30.0	0.00	0.312	0.00	0.0	0.29	0.09
H42	0.79	0.000	0.48	24.4	1.03	0.000	0.46	31.9	0.11	0.660	0.16	3.4	0.23	0.08
H48	1.19	0.000	0.67	27.9	1.38	0.000	0.60	32.5	0.00	0.550	0.00	0.0	0.33	0.08
C18	0.18	0.110	0.35	2.0	2.50	0.000	1.18	27.7	0.11	0.279	0.68	1.2	0.14	0.08
C29	0.81	0.024	0.81	5.2	4.68	0.000	2.15	30.1	0.00	0.550	0.00	0.0	0.14	0.07
C36	2.41	0.002	1.64	12.6	5.58	0.000	2.60	29.2	0.00	0.787	0.00	0.0	0.15	0.06
C42	3.70	0.001	2.38	15.4	6.91	0.000	3.24	28.9	0.00	0.737	0.00	0.0	0.17	0.07
C48	4.37	0.001	2.68	17.0	7.83	0.000	3.65	30.5	0.00	0.719	0.00	0.0	0.17	0.06
Vi18	0.23	0.109	0.03	1.2	5.79	0.000	0.71	29.5	0.00	0.464	0.00	0.0	0.18	0.11
Vi29	4.73	0.017	5.15	4.4	32.20	0.000	4.05	29.8	0.00	0.700	0.00	0.0	0.17	0.09
Vi36	29.10	0.002	22.40	10.2	82.00	0.000	38.60	28.6	0.00	0.858	0.00	0.0	0.20	0.08
Vi42	53.90	0.002	38.20	11.7	142.00	0.000	66.10	30.7	0.00	0.767	0.00	0.0	0.22	0.08
Vi48	86.30	0.003	59.00	12.2	246.00	0.000	113.00	35.0	0.00	0.765	0.00	0.0	0.23	0.08

					mating design R90-11									
	male				female				male*female				heritability	
trait	σ^2m	prob>F	se	%	σ^2f	prob>F	se	%	σ^2m*f	prob>F	se	%	H^2sl	se
H4	0.00	0.700	0.00	0.0	0.00	0.000	0.00	18.9	0.00	0.028	0.00	7.2	0.30	0.10
H18	0.03	0.060	0.02	6.6	0.08	0.000	0.04	20.7	0.05	0.003	0.02	13.2	0.44	0.07
H27	0.13	0.000	0.08	11.3	0.26	0.000	0.12	22.4	0.10	0.022	0.06	8.8	0.37	0.09
H38	0.18	0.010	0.11	10.9	0.41	0.000	0.19	24.6	0.22	0.001	0.09	13.7	0.41	0.09
C18	0.16	0.120	0.14	4.6	0.23	0.070	0.16	6.8	0.24	0.145	0.20	6.8	0.14	0.06
C27	0.74	0.000	0.45	9.5	1.32	0.000	0.63	17.0	0.23	0.303	0.36	2.9	0.15	0.04
C38	1.14	0.000	0.74	8.6	3.00	0.000	1.34	22.8	0.78	0.142	0.61	5.9	0.21	0.06
Vi18	0.15	0.050	0.01	6.1	0.24	0.010	0.02	9.8	0.13	0.229	0.01	5.3	0.18	0.09
Vi27	4.62	0.000	0.43	9.2	9.92	0.000	0.93	19.7	0.53	0.554	2.08	1.0	0.21	0.08
Vi38	15.10	0.000	9.37	8.9	43.10	0.000	4.07	25.5	6.09	0.326	6.96	3.6	0.26	0.09

prob > F: probability associated to FISHER F,
se: standard error of variance components and of heritability,
%: percentage of total variation,
H^2sl: individual broad sense heritability.

Table 2. – Estimation of variance components and results of analysis of variance for the mating designs R89-21 and R90-10; *E. urophylla* • *E. pellita.*

	mating design R89-21													
	male				female				male*female				heritability	
trait	σ^2m	prob>F	se	%	σ^2f	prob>F	se	%	σ^2m*f	prob>F	se	%	H^{2}sl	se
H8	0.00	0.253	0.00	0.0	0.00	0.816	0.00	0.0	0.00	0.493	0.00	0.0	0.00	0.00
H18	0.03	0.209	0.05	3.6	0.20	0.056	0.12	24.3	0.00	0.534	0.00	0.0	0.18	0.08
H29	0.06	0.057	0.08	5.3	0.29	0.009	0.17	24.1	0.00	0.902	0.00	0.0	0.17	0.08
H36	0.14	0.023	0.12	9.2	0.42	0.003	0.24	27.5	0.00	0.938	0.00	0.0	0.18	0.08
H42	0.14	0.014	0.12	9.0	0.53	0.000	0.28	33.5	0.00	0.953	0.00	0.0	0.20	0.09
H48	0.21	0.008	0.16	9.8	0.72	0.000	0.40	34.0	0.00	0.966	0.00	0.0	0.23	0.11
C18	0.34	0.274	0.49	4.8	0.56	0.485	0.67	7.9	0.00	0.246	0.00	0.0	0.06	0.04
C29	0.66	0.248	0.91	5.0	2.12	0.121	1.62	16.0	0.00	0.807	0.00	0.0	0.10	0.05
C36	1.13	0.190	1.18	7.4	1.58	0.195	1.57	10.4	0.00	0.799	0.00	0.0	0.07	0.04
C42	1.34	0.244	1.37	7.9	2.02	0.174	1.95	11.9	0.00	8.835	0.00	0.0	0.08	0.04
C48	1.61	0.136	1.52	8.4	2.64	0.080	2.32	13.8	0.00	0.877	0.00	0.0	0.09	0.05
Vi18	0.42	0.271	0.06	3.1	1.07	0.393	0.15	7.9	0.00	0.433	0.00	0.0	0.07	0.04
Vi29	5.95	0.127	6.44	6.9	6.32	0.216	7.77	7.4	0.00	0.813	0.00	0.0	0.09	0.05
Vi36	18.92	0.087	16.83	9.6	9.45	0.206	16.73	4.8	0.00	0.883	0.00	0.0	0.08	0.04
Vi42	27.57	0.081	25.12	9.1	28.86	0.100	31.46	9.5	0.00	0.926	0.00	0.0	0.10	0.05
Vi48	47.96	0.024	38.99	10.5	51.02	0.027	51.67	11.1	0.00	0.954	0.00	0.0	0.11	0.05

	mating design R90-10													
	male				female				male*female				heritability	
trait	σ^2m	prob>F	se	%	σ^2f	prob>F	se	%	σ^2m*f	prob>F	se	%	H^{2}sl	se
H5	0.00	0.000	0.00	23.3	0.00	0.000	0.00	14.8	0.00	0.113	0.00	5.1	0.35	0.08
H16	0.10	0.000	0.05	24.8	0.10	0.000	0.04	24.2	0.04	0.005	0.01	8.5	0.39	0.07
H28	0.16	0.000	0.08	19.3	0.21	0.000	0.08	24.5	0.14	0.000	0.04	16.5	0.42	0.07
H39	0.14	0.000	0.09	12.7	0.28	0.000	0.12	24.8	0.34	0.000	0.08	30.3	0.45	0.08
C16	0.49	0.000	0.22	20.0	0.28	0.000	0.43	11.3	0.30	0.001	0.12	12.2	0.18	0.04
C28	0.70	0.000	0.36	16.0	0.55	0.000	0.27	12.5	1.12	0.000	0.29	25.4	0.24	0.06
C39	0.66	0.000	0.43	9.8	1.10	0.000	0.52	16.5	2.28	0.000	0.51	33.9	0.25	0.07
Vi16	0.93	0.000	0.39	18.3	1.10	0.000	0.42	21.7	0.31	0.000	0.17	6.1	0.23	0.05
Vi28	5.39	0.000	2.61	14.0	9.66	0.000	3.77	25.0	6.09	0.000	1.81	15.8	0.27	0.05
Vi39	7.76	0.000	5.14	7.0	31.23	0.000	12.76	27.9	29.21	0.000	6.70	26.0	0.29	0.06

prob > F: probability associated to FISHER F,
se: standard error of variance components and of heritability,
%: percentage of total variation,
H^{2}sl: individual broad sense heritability.