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Trends in Variances and Heritabilities with Age for Growth Traits in Eucalyptus Spacing Experiments

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Abstract

Three experimental designs were carried out in the Congo to analyse the impact of spacing on trends in variance and heritability with age and to assess the genotype by spacing interaction in a eucalyptus breeding programme. Three populations of eucalyptus hybrids encompassing respectively 12 clones, 12 and 16 full sib families were established in square or rectangular plots of 30, 36 and 36 trees respectively, at spacings of 625, 1111 and 2500 trees/ha. Height and circumference were measured at different ages, from the juvenile stage up to the adult size of the trees.

Results showed that genetic effect was significant from the juvenile stage for the three experiments. Family by spacing interaction was not significant throughout the growth period but, for the clonal population, the interaction was highly significant after age 3, with changes in clone ranking. Trends in between or within family or clone coefficient of variation with age exhibited two main phases. During the first phase the coefficient of variation decreased and during the second phases it was constant for the genetic effect and strongly increases in the case of within clone and within family effect. This two phases could correspond to a juvenile and a mature phase. In the case of these three experiments some results showed that the juvenile phase could be reduced with closer spacing, as suggested by the Franklin's model.

Heritabilities based on the clone and family mean were very high for the three experiments due to the sample size and the high control of the environment in the design. Heritabilities based on individual trees were smaller because of the high within plot variance. These two parameters rapidly reached a plateau and the two phases mentioned for variances were not observed. Although heritability at close spacing decreased with age for the family experiments, due to the strong increase of the within clone and family variance, the impact of spacing was not statistically significant. The high heritability on the family means basis and the absence of family by spacing interaction permits the family selection at close spacing with a good efficiency specially during the juvenile phase.

Key words: Spacing by genotype interaction, phase of growth, coefficient of variation, family, clone.

Introduction

Forest trees are long-lived organisms and the expression of genes in relation to age and competitive environment is likely one of the most important features to consider in tree genetics and tree breeding.

Numerous studies have been conducted in an attempt to understand the variation in genetic and environmental variances with tree age in the most widely planted species like pines (WHITE and HODGE, 1992; KUSNANDER *et al.,* 1998) and eucalyptus (BORRALHO *et al.,* 1992; BOUVET and VIGNERON, 1995; WEI and BORRALHO, 1998). These studies have especially facilitated the development of methods to predict the optimal age of selection (SATO, 1994; BOUVET and VIGNERON, 1995; JOHNSON *et al.,* 1997). Several studies have also been implemented to test some models of stand development (NAMKOONG and CONKLE, 1972; NAMKOONG *et al.,* 1976) and specially the FRANKLIN's model (LAMBETH, 1983; FOSTER, 1986; BALOCCHI *et al.,* 1993). In his model, FRANKLIN (1979) compares the magnitude of genetic versus environmental variances at different stages of the stand development for two pine species. In the model, stand development was divided into three phases: the juvenile-genotypic, the mature genotypic and the suppression co-dominance phase. FRANKLIN suggested that by hastening the onset of the mature-genotypic phase by inducing fast growth at close spacing and ”perhaps by manipulating other environmental factors“ one could improve the prediction of ranking at mature age.

Very few studies, crossing genetic entries and spacing, have been carried out to test these hypotheses. This is mainly due to the large effort needed to carry out such experiments in the field. Some have tried to analyse the effect of competition at the nursery stage (ADAMS *et al.,* 1973; TAUER, 1975; TUSKAN and VAN BUIJTENEN, 1986) or through retrospective tests with seedlings tested in the nursery at different spacings and adult trees in the field (JANSSON *et al.,* 1998). The conclusions remain

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conflicting and not applicable to field conditions (Jonsson *et al.,* 2000). Experiments on genotype by spacing interaction in the field are particularly rare. An analysis of Douglas fir *Pseudotsuga menziesii var. menziesii* families show that variance structure was not affected by close spacing as predicted by Franklin (Campbell *et al.,* 1986). In a study on *Eucalyptus saligna*, Patino-Valera and Kageyama (1995) did not show a clear impact of spacing on variance structure due to the limited period of measurement, only growth up to 32 months was measured. Similarly, Brouard and John (2000) did not have a detailed analysis with a Marynen design to test the trend of genetic variation with age with spacings varying from 2500 to 1111 trees/ha.

In order to address this important issue and also to test the efficiency of family and clone selection using close spacing, three experimental designs have been implemented in the framework of the eucalyptus breeding programme in the Republic of the Congo. These field experiments are designed to analyse the effect of spacing on genetic parameters for height and circumference in clonal and full sib family populations. The analysis of these two kinds of genotypes, clones and families, allows us to assess the impact of competition according to different structures of within-genotype competition. Height and circumference will be analysed separately as these traits do not have the same behaviour in a competitive environment (Delwaulle, 1983).

The objectives of this paper are (i) to quantify the impact of spacing on between and within families (clones) variation, (ii) to assess the genotype by competition interaction in a eucalyptus clonal or family population, (iii) and to test the hypothesis of distinct phases in variance trends with age and that competition shortens the length of the juvenile phase.

Materials and Methods

Genetic material

Data were obtained from three field trials established in the Republic of the Congo in the experimental area of the research centre "Unité de Recherche sur les plantations Industrielles du Congo" (04°45'S, 12°00'E, alt 50 m). The climate is tropical humid with a mean annual temperature of 24 °C, a mean annual rainfall of 1200 mm and a dry season from May to October. The first experiment, R90-13, used a set of 6 hybrid families of *Eucalyptus urophylla* x *Eucalyptus grandis* and 6 families of *Eucalyptus urophylla* x *Eucalyptus pellita* planted in 1991 at two spacings 2 m x 2 m (2500 trees/ha) and 4 m x 4 m (625 trees/ha). Within each hybrid, the six families were created by controlled pollination of 6 different unrelated parents trees of each species in a single pair mating design. Within each density, the experiment was a complete block design with a 36-tree square plot in three replicates. To minimise the impact of competition between plots, only the 16 inner trees were measured. The second experiment, R91-1, used a set of 12 hybrid clones of *Eucalyptus tereticornis* x *Eucalyptus grandis* planted in 1992 at three spacings 2 m x 2 m (2500 trees/ha), 3 m x 3 m (1111 trees/ha) and 4 m x 4 m (625 trees/ha). The clones have been selected within natural hybrid population. The genetic base of the hybrid population was very narrow, *E tereticornis* parent trees belonging to the progeny of one single tree introduced in the Congo in the sixties. Clones were probably related but it was not possible to define the kinship coefficient among them. Within each density, the experiment was a complete block design with a 30-tree rectangular plot in three replicates. To minimise the impact of competition between plots, only the 12 inner trees were measured. The third experiment, R95-10, used a set of 16 hybrid families of *Eucalyptus urophylla* x *Eucalyptus grandis.* The hybrid families were created by controlled pollination in a single pair mating design of 16 unrelated parents for each species. The latter were chosen in order to represent a broad genetic base of each parent population. The trial was planted in 1995 at the same three spacings 2 m x 2 m (2500 trees/ha), 3 m x 3 m (1111 trees/ha) and 4 m x 4 m (625 trees/ha). The experiment was a split plot design with 3 replicates, with a 36-tree square plot, spacing being the main effect and family the secondary effect. To minimise the impact of competition between plots, only the 16 inner trees were measured.

Measurements

Circumference at breast height (C) and total height (H) were measured at different ages. Generally, measurements were done monthly during the youngest ages, half-yearly during the juvenile phase, and yearly during the mature phase. Results presented here concern the juvenile and the mature phases in eucalyptus plantations, i.e. from two months up to 80 months.

Within-spacing genetic analysis

Statistical analyses were conducted within each spacing with the following mixed models.

Experiment R90-13 (family)

$$y_{hijk} = \mu + h_h + b_i + f(h)_{jh} + b{*}f(h)_{ijh} + r_{hijk} \qquad \text{model [1]}$$

where y_{hijk} is the kth tree in the jth family in the ith block in the hth hybrid

μ is the overall mean,

h_h is the fixed effect of the hth hybrid,

b_i is the fixed effect of the ith bloc,

$f(h)_{jh}$ is the random effect of the jth family in the hth hybrid, with variance of σ^2_f and mean 0.

$b{*}f(h)_{ijh}$ is the random effect of the interaction between jth family and the ith bloc in the hth hybrid with variance of σ^2_{b*f} and mean 0,

r_{hijk} is the residual random effect including within-plot environmental and genetic variance, with variance of σ^2_w and mean 0,

Experiment R91-1 (clonal) and R95-10 (family)

$$y_{ijk} = \mu + b_i + f_j + b{*}f_{ij} + r_{ijk} \qquad \text{model [2]}$$

where y_{ijk} is the kth tree in the jth family (or clone) in the ith block,

μ is the population mean,

b_i is the fixed effect of the ith bloc,

f_j is the random effect of the jth family (or clone), with variance of σ^2_f and mean 0,

$b{*}f_{ij}$ is the random effect of the interaction between jth family (or clone) and the ith bloc, with variance of σ^2_{b*f} and mean 0,

r_{hijk} is the residual random effect including environmental and genetic variance if any, with variance of σ^2_w and mean 0,

Spacing by genotype interaction analyses

Analyses of clone or family by spacing interaction were performed at the mean plot level, using the following mixed models varying according to the structure of the experimental design:

Experiment R90-13

$$y_{dhij} = \mu + d_d + h_h + d{*}h_{dh} + b(d)_{id} + f(h)_{jh} + f(h){*}d_{jhd} + r_{dhij} \qquad \text{model [3]}$$

d_d is the fixed effect of the dth density

h_h is the fixed effect of the hth hybrid,

$d{*}h_{hd}$ is a random effect of the interaction between the dth density and the hth hybrid,

$b(d)_{id}$ is the fixed effect of the i^{th} bloc in the d^{th} density,

$f(h)_{jh}$ f is the random effect of the j^{th} family in the h^{th} hybrid, with variance of σ^2_f and mean 0,

$f(h){*}d_{jhd}$ is the random effect of the interaction between j^{th} family in the h^{th} hybrid and the d^{th} density, with variance of $\sigma^2_{f(h)*d}$, and mean 0,

r_{dhij} is the residual random effect including environmental and genetic variance, with variance of σ^2_w and mean 0,

Experiment R91-1

$y_{dij} = \mu + d_d + b(d)_{id} + c{*}d_{jd} + r_{dij}$ model [4]

$c{*}d_{jd}$ is the random effect of the interaction between j^{th} clone and the d^{th} density, with variance of σ^2_{c*d} and mean 0,

All the other effects are described in model [3]

Experiment R90-15

$y_{dij} = \mu + d_d + f_j + b_i + b{*}d_{id} + f{*}d_{jd} + r_{dij}$ model [5]

$f{*}d_{jd}$ is the random effect of the interaction between j^{th} family and the d^{th} density, with variance of σ^2_{f*d}, and mean 0,

All the other effects are described in model [3]

In order to homogenise residual variances, height and circumference at the different ages were transformed by logarithmic transformation. In models [3], [4] and [5], residual variances are assumed to be identical for all spacings, BARTLETT's test was used to verify variance homogeneity (SNEDECOR and COCHRAN, 1989)

Genetic parameters

Genetic and environmental variance components were calculated using the SAS VARCOMP procedure and the REML method (SAS INSTITUTE INC., 1988).

To compare the trends in variance components with age, the coefficient of variation relative to the three main effects was calculated (with y... as overall mean) as follows

$CV_{family} = (\sigma^2_f / y...)$ for family and $CV_{clone} = (\sigma^2_c / y...)$ for clone

$CV_{block*family} = (\sigma^2_{b*f} / y...)$ for family or $CV_{block*clone} = (\sigma^2_{b*c} / y...)$ for clone

$CV_{within} = (\sigma^2_w / y...)$ for family and clone

Broad sense heritability based on the family or clone means can be defined by the following formula:

$H^2_{family\ means} = \sigma^2_f / (\sigma^2_f + \sigma^2_{b*f} / b + \sigma^2_w / bn)$ and $H^2_{clone\ means} = \sigma^2_c / (\sigma^2_c + \sigma^2_{b*c} / b + \sigma^2_w / bn)$

Where b is the number of replications and n is the number of individual trees per plot.

Broad sense heritability on the individual tree basis, reflecting more strongly the effect of competition on individual tree, was also calculated and can be defined by the following formula: $H^2_{family\ ind} = 2{*}\sigma^2_f / (\sigma^2_f + \sigma^2_{b*f} + \sigma^2_w)$ and $H^2_{clone\ ind} = \sigma^2_c / (\sigma^2_c + \sigma^2_{b*c} + \sigma^2_w)$. For $H^2_{family\ ind}$ we assumed that the total genetic variance equal twice the family variance which is a good approximation in the frame of these eucalyptus hybrid populations (BOUVET and VIGNERON, 1996).

Standard error of heritability was calculated according to the Dickerson method (DICKERSON, 1969 in BECKER, 1984).

Results

Effect of spacing on mortality and growth

The trials were differently affected by mortality (*table 1*). Experiments R90-13 and R91-1 showed a low percentage of dead trees with a slightly higher value for 2500 trees/ha (3.3% at 625 tees/ha compare to 5% at 2500 trees/ha at 86 months in R 90-13 and 2.1% at 625 trees/ha compare to 3.9% at 2500 trees/ha at 74 months in R91-1). This higher value can be explained by the stronger competition in close spacing which generally accelerates the death of the trees affected by disease and pest. The impact of spacing has been observed in other species (XIE *et al.,* 1995). In contrast, experiment R95-10 showed a high percentage of mortality, especially at 625 trees/ha (12% at 59 months) and 2500 trees/ha (11.3 at 59 months) compared to 1111 trees/ha (6.2 at 59 months), probably due to termite-generated damage during the young stage.

Table 1. – Trends in mortality (%) with age (months) in the different trials according to the density – 625, 1111 and 2500 trees/ha.

Family trial R 90-13			Clonal trial R91-1				Family trial R 95-10			
age	625	2500	age	625	111	2500	age	625	1111	2500
12	0.7	1.0	12	1.6	2.3	3.4	11	5.4	3.4	7.5
26	1.7	3.6	24	1.6	2.3	3.5	20	9.7	4.6	9.4
48	1.7	3.6	48	2.1	2.5	3.9	39	11.0	5.1	10.4
86	3.3	5.0	74	2.1	2.5	3.9	59	12.0	6.2	11.3

Although the age of observation in these experiments is relatively young for forest trees, 86 months for the oldest, the period of measurement concerned by this study gives a good idea of the tree response to spacing because adult size was reached in the three trials. Tropical eucalyptus species generally show growth that is rapid during the first three years and then progressively declines. This observation is confirmed here and illustrated in *figures 1a* to *1f.* This rapid growth leads to a strong competition which significantly affects circumference but also height (*figures 1b, 1d* and *1f*). It is generally considered in forest trees that spacing affects circumference more than height, especially when dominant height is considered (PARDE and BOUCHON, 1988; DHOTE, 1997). However in tropical eucalyptus, several trials have also demonstrated the strong impact of spacing competition on height growth (DELWAULLE, 1988; BOUVET, 1997; BROUARD and JOHN, 2000). The impact of spacing on total biomass exhibited a different pattern. The volume per hectare increased with the density as demonstrated by the values calculated with the cone formula: 108.3 m^3 / ha and 148.1 m^3 / ha for respectively 625 and 2500 trees/ha in R90-13, 75.9 m^3 / ha, 79.2 9 m^3 / ha and 83.4 m^3 / ha for respectively 625, 1111 and 2500 trees/ha in R91-1, 82.2 m^3 / ha, 98.2 9 m^3 / ha and 100.4 m^3 / ha for respectively 625, 1111 and 2500 trees/ha in R95-10. Even with an approximate formula for volume, which does not take into account the form of the tree, these estimations confirm the well known result that close spacing increase the biomass production by unit area.

Genotype by spacing interaction

The analyses of variance, conducted after transformation of the variable by the logarithm, showed that the family and/or clone effects were pronounced throughout the growth period for the two traits, leading to genetic variances significantly different from zero (*table 2*).

The variance of interaction was very low and considered as not statistically different from zero for the family experiments R90-13 and R95-10, but for the clonal experiment R91-1 the effect was significant after age three (*table 2*). These significant value was not due to a scale effect because changes in ranking occurred in the clonal population at age 74 months, especially for circumference, as illustrated by correlations in *table 3.*

Trends in variance and coefficient of variation

For the three experiments and for each spacing, the family or clone variance component was significantly different from zero for height and circumference, from 2 or 3 months after planting, illustrating strong genetic differences (*table 4*). The family and clone variances increased with age in the three experiments and were higher for wide spacing in the two family trials for height and circumference. In contrast, in the clonal trial R91-1, the clone variance was smaller at wide spacings for height. The variance of block by family interaction decreased progressively with age and reached the value zero at 30 or 40

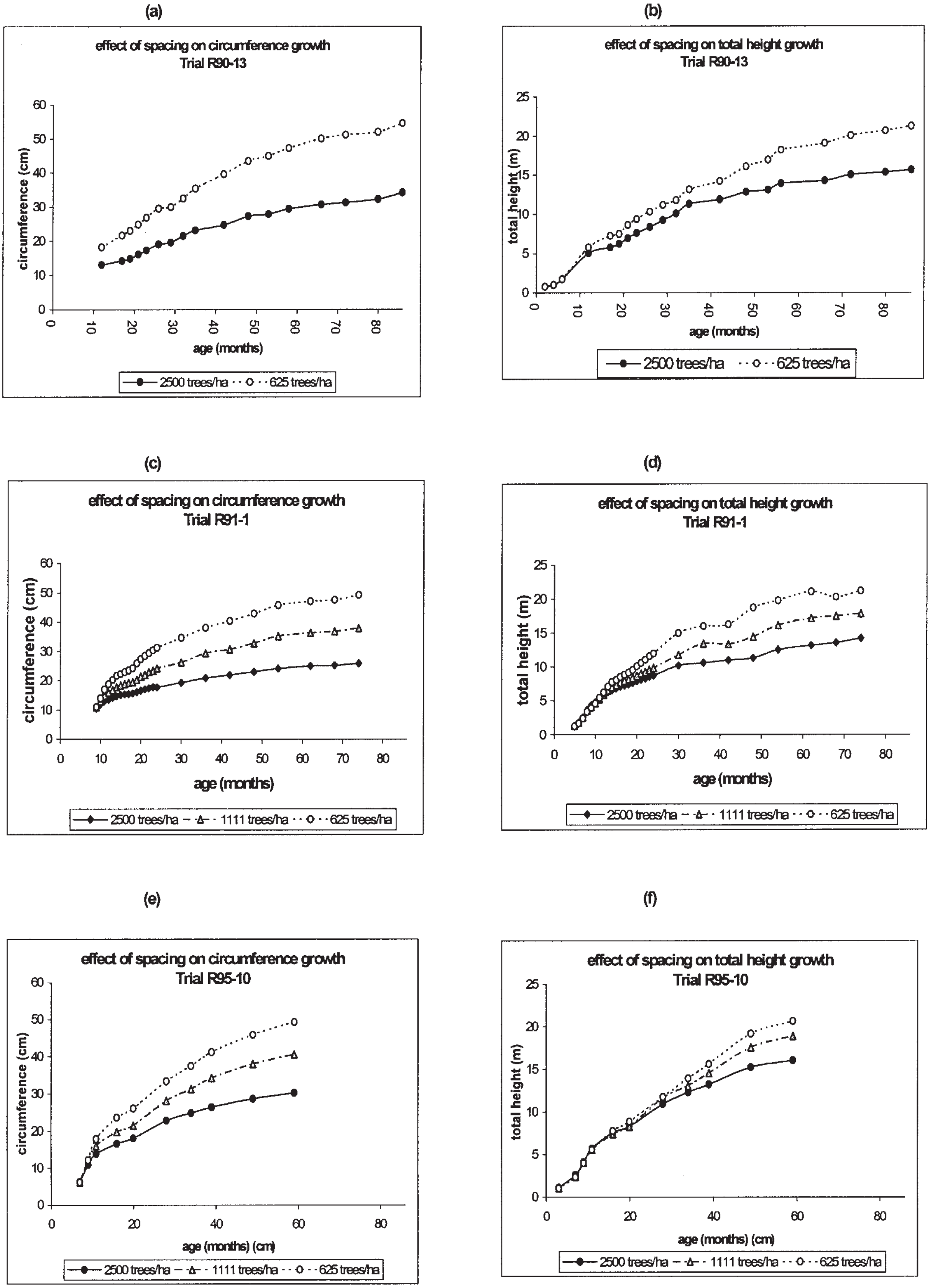


Figure 1a to 1f. – Growth in circumference (cm) and total height (m) of families and clones in the different trials by density – 625, 1111, and 2500 trees/ha at various ages (months).

Table 2. – Results of analyses of variances to test the family or clone (fam or clone) and the family(clone) by spacing interaction effect (int), for circumference and height at different ages (months): variance estimates of the random effect and probability associated with the Fisher test (ns : probability higher than 5%, ns not mentioned : probability smaller than 5%).

Family trial R 90-13			Clonal trial R91-1			Family trial R 95-10		
Trait/age	fam	int	trait/age	clone	int	trait/age	fam	int
C12	0.0041	0.0000ns	C12	0.0069	0.0000ns	C11	0.0098	0.0000ns
C26	0.0050	0.0000ns	C24	0.0053	0.0001ns	C28	0.0037	0.0000ns
C35	0.0050	0.0000ns	C36	0.0067	0.0006ns	C39	0.0040	0.0000ns
C48	0.0041	0.0000ns	C48	0.0084	0.0014	C48	0.0042	0.0000ns
C58	0.0042	0.0000ns	C62	0.0086	0.0017	C59	0.0044	0.0000ns
C72	0.0049	0.0000ns	C74	0.0088	0.0019			
C86	0.0049	0.0000ns						
H12	0.0141	0.0000ns	H12	0.0062	0.0009ns	H11	0.0098	0.0000ns
H26	0.0109	0.0017ns	H24	0.0060	0.0002ns	H28	0.0069	0.0000ns
H35	0.0112	0.0006ns	H36	0.0073	0.0005ns	H39	0.0075	0.0000ns
H48	0.0081	0.0003ns	H48	0.0076	0.0010	H48	0.0081	0.0000ns
H58	0.0077	0.0000ns	H62	0.0090	0.0031	H59	0.0079	0.0000ns
H72	0.0072	0.0000ns	H74	0.0077	0.0026			
H86	0.0073	0.0000ns						

Fam (clone): family or clone effect
Dens: spacing effect
Int: family(clone) by spacing interaction effect

months. For the clonal experiment the trend was more complex and did not show a clear pattern. The within family or clone variance increased strongly with age. This trend was more pronounced with close spacings.

A general pattern of the coefficient of variation of the three main effects of models [1] and [2] can be seen (*figures 2, 3* and *4*).

The coefficient of genetic variation CV family(clone) varies weakly for most of the growth period with values between 5 and 15% (*figures 2, a* to *f*). This pattern is the same for height and circumference. The trends of CV family(clone) show two main phases but the first one is slightly pronounced. During the first phase, which starts just after planting, the coefficient of variation decreases in some cases (*figures 2c, 2d, 2e, 2f*). This period of decrease seems to vary with the spacing in the clonal test (*figure 2c* and *2d*), the closer the spacing the shorter the period is, but this trend was not observed with the family trials. During the second phase, CV family(clone) is more or less constant. The impact of spacing is slightly more marked for the clonal experiment where a higher value of the coefficient of variation at higher density is observed (*figures 2c* and *2d*). The pattern of variation of CVfamily(clone) for the trial R90-13 appears slightly different, especially the phase of decrease a few months after planting. This may be explained by the lack of measurement between 7 and 14 months.

Table 3. – Rank coefficient of correlation and probability of null value (in parentheses) among the twelve clones between the three densities (625, 1111 and 2500 trees/ha) in experiment R91–1.

	Height at 74 months		Circumference at 74 months	
Density	625	1111	625	1111
1111	0.85(0.00)		0.85(0.00)	
2500	0.75(0.00)	0.88(0.00)	0.48(0.11)	0.73(0.01)

The coefficient of block*family(clone) interaction decreases progressively with age from 5 or 10% to zero for both traits in all three trials (*figure 3*). This may be explained by the homogenisation of the stand with age.

For CV_{within}, the spacing effect is highly expressed showing a strong increase in the coefficient with age for 2500 trees/ha and a constant value for 1111 and 625 trees/ha (*figure 4*). As for $CV_{family(clone)}$, the trends of CV_{within} with age show two marked phases (*figure 4*).

Trends in heritability

Heritabilities calculated on family (clone) mean basis showed similar patterns between the three experiments and for the two traits (*figures 5a* to *5 f*). After some initial variation, generally during the first year of growth, heritability reached a more or less constant value throughout the period of measurement. The impact of spacing can be observed in some cases. The heritability was generally smaller with close spacing specially in the family experiments with a difference of 0.25 at the end of the rotation (*figures 5a, 5b, 5e* and *5f*). However, standard errors presented in *table 5* for some ages show that these differences were not significant. No clear differences were noted between height and circumference response.

Table 4. – Trends in variance with age for family (clone), bloc by family (clone) interaction and within family (clone) effect for circumference and height at different ages (months) in the different trials according to the density – 625, 1111 and 2500 trees/ha : probability associated with the Fisher test (ns : probability higher than 5%, ns not mentioned : probability smaller than 5%).

	σ^2_f or σ^2_c			σ^2_{b*f} or σ^2_{b*c}			σ^2_w		
				trial R90-13					
Trait/age	2500	625		2500	625		2500	625	
C12	0.82	0.29		0.64	3.02		4.98	9.33	
C23	1.96	1.12		0.46	2.52		11.04	17.93	
C35	2.65	3.27		0.00ns	2.36		32.46	32.37	
C48	2.33	6.44		0.00ns	1.19		58.48	51.94	
C58	2.70	7.96		0.00ns	0.36		80.63	68.45	
C72	3.81	9.75		0.00ns	0.00		106.76	88.72	
C86	4.69	11.42		0.00ns	0.00		129.98	103.66	
H12	0.39	0.33		0.06	0.27		0.55	0.80	
H23	1.00	0.74		0.24	0.33		1.63	1.91	
H26	1.08	0.77		0.15	0.42		2.39	2.27	
H35	1.47	1.64		0.20	0.13		5.23	3.35	
H48	1.01	2.33		0.06ns	0.13		8.60	5.11	
H58	1.10	2.61		0.00ns	0.15		12.21	7.24	
H72	1.15	2.90		0.00ns	0.00		18.15	9.06	
H86	1.36	3.20		0.00ns	0.00		21.20	10.11	
				trial R91-1					
	2500	1111	625	2500	1111	625	2500	1111	625
c12	1.02	0.70	3.90	0.57	1.58	0.00	4.36	5.08	5.23
c24	2.18	1.57	5.38	0.40	3.29	0.00	10.35	11.43	8.70
c36	4.28	3.71	8.08	0.00	4.02	0.23	21.65	20.81	12.77
c48	6.49	7.43	13.83	0.00	3.23	0.13	36.92	31.88	17.95
c62	7.61	10.30	18.07	0.00	3.24	0.00	50.81	48.05	24.67
c74	8.28	12.01	19.61	0.00	3.92	0.00	57.32	56.82	29.29
h12	0.16	0.17	0.27	0.11	0.13	0.02	0.36	0.31	0.22
h24	0.46	0.42	0.59	0.22	0.51	0.08	0.98	0.70	0.43
h36	1.05	0.67	1.17	0.26	0.77	0.21	2.76	2.06	0.79
h48	1.44	0.95	1.38	0.30	0.67	0.14	4.40	2.62	1.18
h62	3.09	1.96	1.43	0.04	0.51	0.07	8.91	4.86	1.60
h74	3.09	2.07	1.03	0.01	0.45	0.04	9.78	5.15	1.40
				trial R90-15					
	2500	1111	625	2500	1111	625	2500	1111	625
c11	0.70	0.72	1.38	0.66	0.92	0.82	9.72	11.32	12.39
c28	1.63	1.79	4.09	0.31	0.00ns	0.00ns	32.09	34.15	39.26
c34	2.41	2.51	4.83	0.00ns	0.00ns	0.00ns	43.79	44.46	53.29
c49	2.84	3.79	8.19	0.00ns	0.00ns	0.00ns	78.44	87.84	95.81
c59	2.33	5.03	10.15	0.00ns	0.00ns	0.00ns	97.60	109.00	119.8
h11	0.26	0.21	0.30	0.17	0.12	0.03	0.96	0.99	0.94
h28	0.75	0.72	1.05	0.32	0.18	0.00ns	4.28	3.43	2.85
h34	1.12	0.88	1.66	0.15	0.29	0.00ns	6.38	4.82	4.10
h49	1.62	1.53	3.29	0.00ns	0.01ns	0.00ns	16.13	14.18	10.25
h59	1.58	1.89	4.11	0.00ns	0.00ns	0.00ns	19.25	17.38	11.96

Heritabilities on individual tree basis were smaller specially for circumference (*figures 5a, 5c* and *5e*). The relative difference between spacings was marked for total height, although the value was smaller than two standard errors (*table 5*). This pattern was not systematic, in clonal designs, the heritability of circumference at 625 trees / ha was higher than heritability at close spacings (*figure 5 c*).

Discussion

Competition within and between families

In these experiments, the nature and the effects of competition between and within families or clones are different. With a square or rectangular plot design, a significant number of trees per plot (16 trees per plot in R90-13, 12 in R91-1 and 16 in R95-10) and a buffer line around the plot, the competition increases markedly with spacing within each plot and then within the family(clone) but weakly between each plot and then between each family or clone. This result is demonstrated by the increase in variance and CV_{within}, the decrease in $CV_{block*family(clone)}$ and the somewhat constant value for the $CV_{family(clone)}$ with age. The small increment in $CV_{family(clone)}$ with age is due to the low competition between contiguous plots of the same density. In the three experiments presented here, the situation differs from designs where the competition between and within families is of the same nature, from row plot or single tree plot design where the different genotypes are mixed. In the latter, the few results show that increasing competition among the genotypes increases genetic variance and genetic coefficient of variation (STONECYPHER and MCCULLOUGH, 1981; WILLIAMS *et al.,* 1983; HART, 1986 as cited by FOSTER, 1989; SAINT CLAIR and ADAMS, 1991).

These three experiments are not really appropriate to study the impact of spacing on gene expression because competition is not acting in the same way between and within genotypes. As mentioned above they were established to test the efficiency of family and clone selection at close spacing in the frame of monoclonal and monofamily plantation. This experimental approach is based on the theoretical demonstration that the

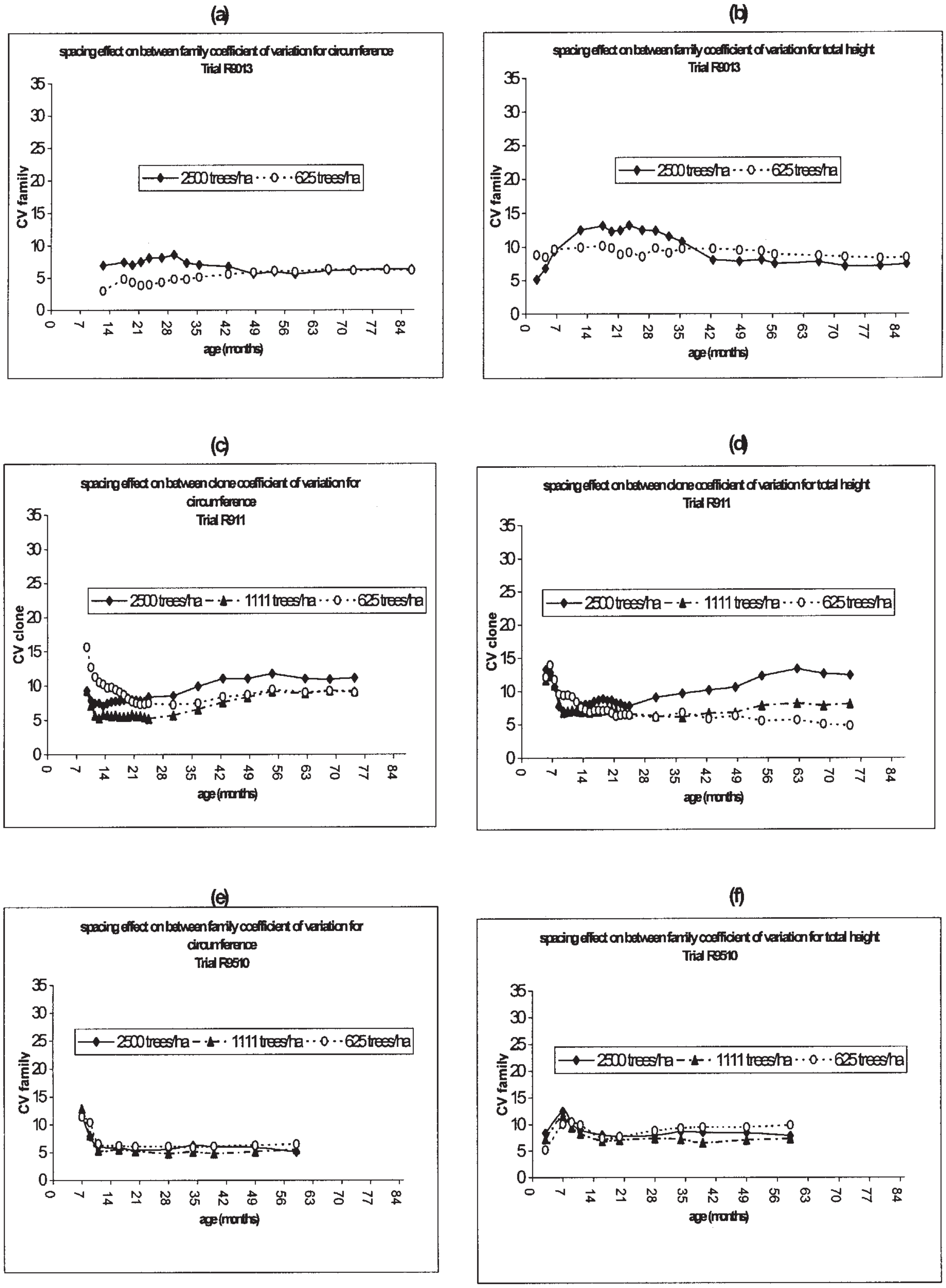


Figure 2a to 2f. – Trends in family or clone coefficient of variation with age for circumference and height for the two spacings in the three experiments.

genetic gain is maximised when the genotype test system is closed to the mode of plantation (mixed or pure) (GALLAIS, 1991). These experiments however allow the comparison of gene expression in the situation of progressive degree of competition within family or clone and in the quasi-absence of competition between family or clone.

Stability of eucalyptus genotypes

Interaction between spacing and genotype was not significant in the two experiments with full sibs. The absence of interaction stresses the low interactivity of a full-sib family when the local environment is changing, especially when light and soil resources vary. This result tallies with analyses on

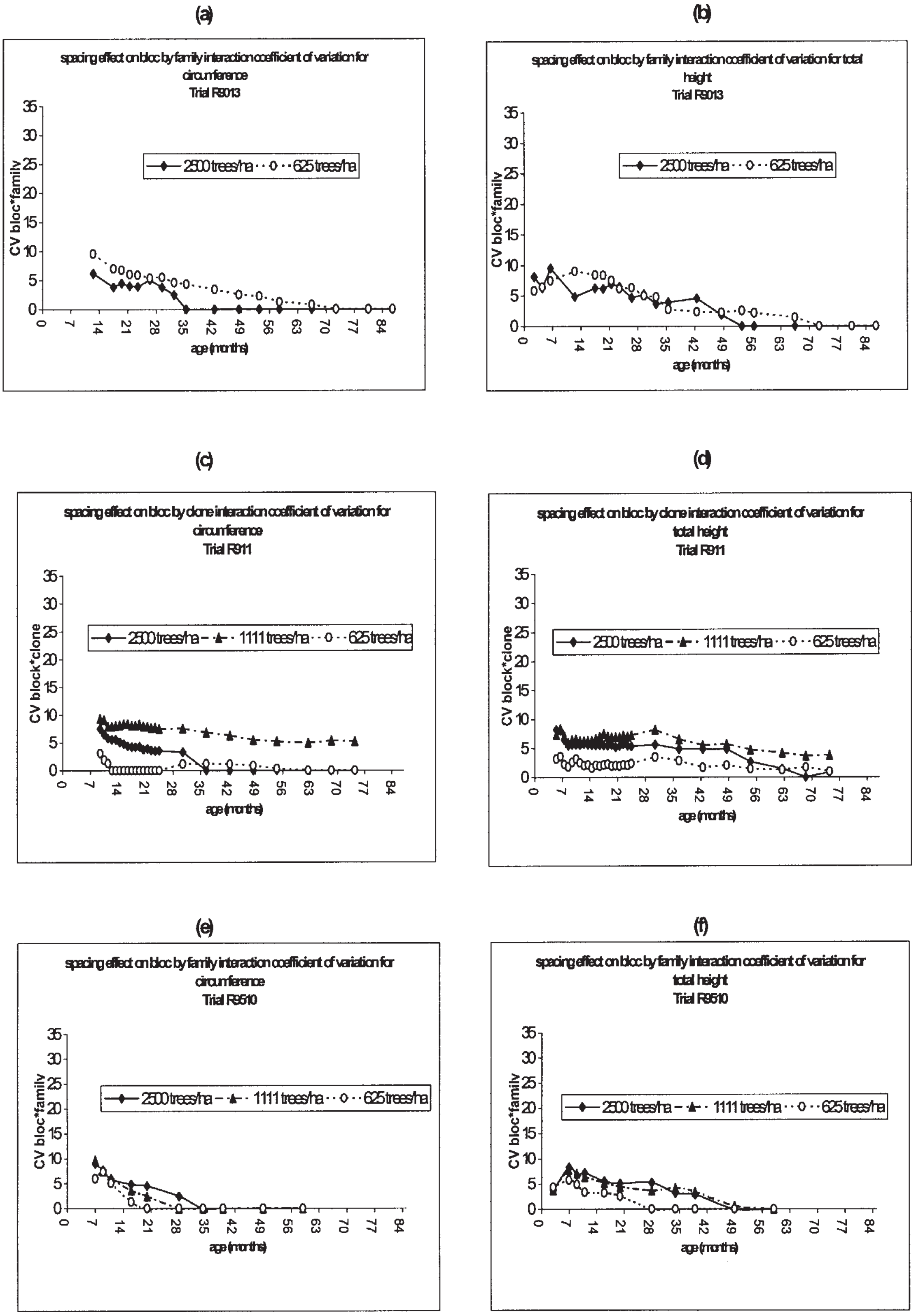
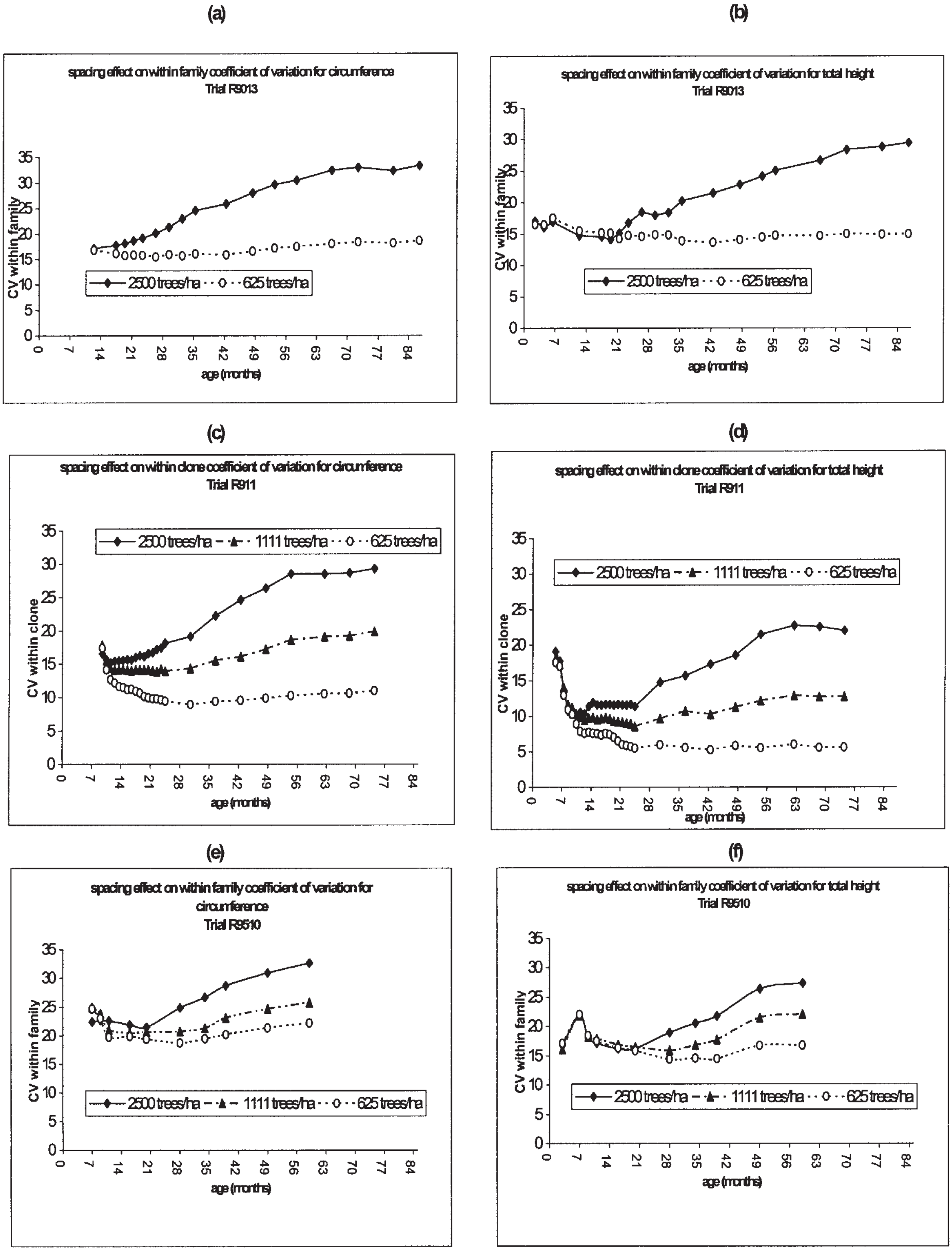


Figure 3a to 3f. – Trends in family or clone by block interaction coefficient of variation with age for circumference and height for the three spacings in the three experiments.

other forest tree species (Reighard *et al.*, 1986; Campbell *et al.*, 1986; Magnussen and Yeatman, 1987; Dreyfus, 1990; Saint Clair and Adams, 1991).

Some variances of interaction were considered as statistically different from zero in the clonal experiment R91-1 and rank changes were observed showing that interaction was not only the result of scale effects. A higher interaction was expected in this clonal population because clonal material is generally more sensitive to changing environment due to the absence of genetic variation within each clone (Gallais, 1991). Furthermore, the clones were drawn from a natural hybrid *Eucalyptus tereticornis* x *Eucalyptus grandis* characterised by a very narrow genetic base in the Congo. A single mother tree of *Eucalyptus tereticornis* produced all the trees introduced in the Congo.


(a) spacing effect on within family coefficient of variation for circumference Trial R9013

(b) spacing effect on within family coefficient of variation for total height Trial R9013

(c) spacing effect on within clone coefficient of variation for circumference Trial R911

(d) spacing effect on within clone coefficient of variation for total height Trial R911

(e) spacing effect on within family coefficient of variation for circumference Trial R9510

(f) spacing effect on within family coefficient of variation for total height Trial R9510

Figure 4a to 4f. – Trends in family or clone within coefficient of variation with age for circumference and height for the three spacings in the three experiments.

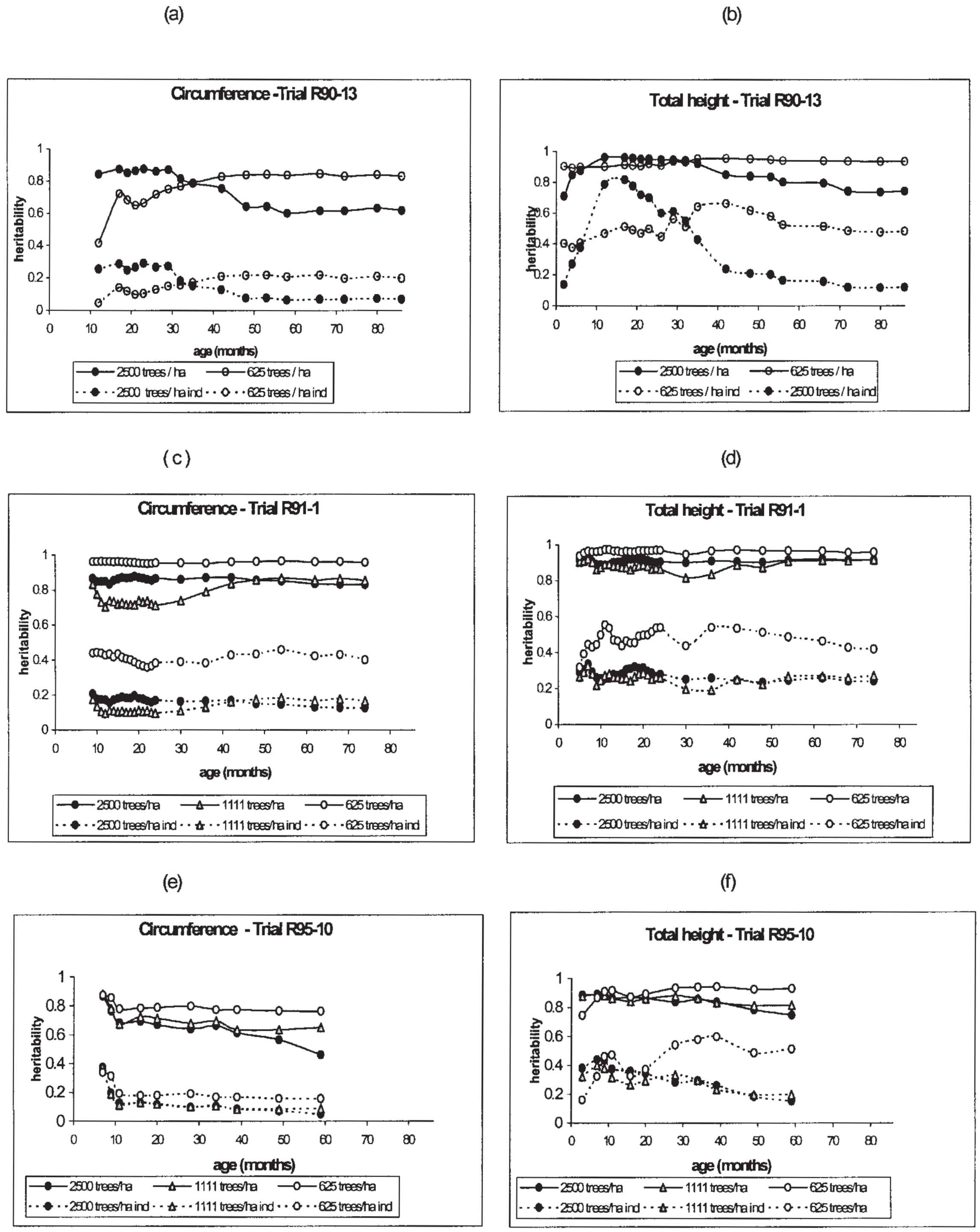


Figure 5a to 5f. – Trends in heritability on family or clone mean basis (625, 1111 and 2500 trees / ha) and on individual tree basis (625, 1111 and 2500trees / ha ind) with age for circumference and height for the three experiments.

Although very few data are available to compare this result, the conclusions concerning the trial R91-1 agrees with those observed with other clonal material of eucalyptus (BROUARD and JOHN, 2000) or other species (PANETSOS, 1980).

Competition and phase of gene expression

Two main phases are illustrated by the results. The first phase where genetic and environmental coefficients of variation decrease (*figures 2c* to *2f* and *4c* to *4f*), may be due to response of genotypes to planting stress and to the first stage of growth without competition. The end of this phase may correspond to the onset of competition. The diminution of within-genotype coefficient of variation can be explained by a strong increase of means and a small increase of variance. Actually, we observed that the variance in the first months of growth increases slowly when mean increases rapidly, the growth being accelerated by the starter fertilisation and the beginning of the rainy season two or three months after planting. This phase corresponds to the site capture and the decrease in micro-environmental effect induced by the development of the crown and of the root system. Stand closure is very rapid for eucalyptus in the Congo. It can be observed easily in the field when trees are only separated by two or three meters. When trees are separated by four meters, crown closure appears

Table 5. – Example of values of broad sense heritability based on family or clone means and on individual tree and their standard error (in parentheses) for height and circumference at different ages and for the three spacings (625 trees/ha, 1111 trees/ha and 2500 trees/ha).

Family trial R 90-13			Clonal trial R91-1				Family trial R 95-10			
Heritability on family(clone) means basis										
Trait/age	625	2500	trait/age	625	1111	2500	trait/age	625	1111	2500
C12	0.41(.90)	0.84(.42)	C12	0.96(.41)	0.70(.60)	0.85(.46)	C11	0.91(1.1)	0.78(1.1)	0.78(1.2)
C35	0.79(.46)	0.79(.37)	C36	0.95(.41)	0.79(.51)	0.87(.41)	C39	0.92(.50)	0.89(.47)	0.87(.39)
C58	0.84(.39)	0.60(.32)	C62	0.96(.41)	0.86(.44)	0.84(.41)	C59	0.87(.29)	0.89(.43)	0.93(.41)
C86	0.62(.31)	0.83(.38)								
H12	0.90(.41)	0.96(.35)	H12	0.97(.41)	0.89(.48)	0.88(.47)	H11	0.95(.98)	0.91(1.3)	0.94(.89)
H35	0.95(.37)	0.92(.37)	H36	0.97(.42)	0.84(.52)	0.91(.43)	H39	0.96(.54)	0.93(.62)	0.95(.47)
H58	0.94(.32)	0.80(.37)	H62	0.96(.41)	0.91(.43)	0.92(.41)	H59	0.96(.45)	0.93(.45)	0.95(.29)
H86	0.93(.33)	0.74(.35)								
Heritability on individual tree basis										
Trait/age	625	2500	trait/age	625	1111	2500	trait/age	625	1111	2500
C12	0.04(.10)	0.26(.12)	C12	0.42(.18)	0.10(.08)	0.17(.09)	C11	0.18(.10)	0.12(.08)	0.12(08)
C35	0.18(.10)	0.16(.08)	C36	0.38(.17)	0.13(.08)	0.17(.08)	C39	0.16(.08)	0.08(.04)	0.08(.06)
C58	0.20(.08)	0.06(.04)	C62	0.42(.18)	0.17(.09)	0.13(.06)	C59	0.16(.08)	0.08(.06)	0.04(.04)
C86	0.20(.08)	0.06(.04)								
H12	0.46(.28)	0.78(.22)	H12	0.53(.23)	0.28(.15)	0.25(.14)	H11	0.48(.20)	0.32(.16)	0.38(.20)
H35	0.64(.18)	0.42(.24)	H36	0.54(.24)	0.19(.12)	0.26(.12)	H39	0.60(.24)	0.24(.10)	0.26(.12)
H58	0.52(.08)	0.16(.20)	H62	0.46(.20)	0.27(.13)	0.26(.11)	H59	0.52(.20)	0.20(.08)	0.16(.08)
H86	0.48(.06)	0.12(.18)								

later. Concerning the root system, some experiments have demonstrated the rapidity of its development : the length of the root can reach 5 meters, 5 months after planting (BOUILLET *et al.,* 2001). The drop in between-genotype coefficient of variation may also be explained by the slow increase of variance due to a progressive homogeneity of the environmental conditions (edaphic, light, weed competition) giving the different genotypes the same site potential and diminishing the genotype by micro-environmental interaction. After this first phase, there is a somewhat stable phase with a linear trajectory which corresponds to the competitive growth of trees. These two phases could represent the juvenile-genotypic and the mature genotypic phases of FRANKLIN's model. It is too early in these trials to observe its third phase: the "suppression co-dominance phase". When looking at the old stand of eucalyptus in the Congo, the last phase could happen after 15 or 20 years at wide spacings when natural mortality appears.

The trends of the curves of the coefficient of variation are the same for the three spacings but the length of the first phase seems to decrease with spacings. The first phase is shorten in the clonal experiment for between clone coefficient of variation (*figures 2c* and *2d*) and shorten in the three experiments for the within family or within clone coefficient of variation (*figures 4a* to *4f*). In the figures 4a to 4f, it can be observed that the coefficient of variation at 2500 trees/ha changes its trajectory at 12 months while the coefficient of variation at 625 trees/ha changes its trajectory at 24 months. This observation of changes in coefficient of variation must acknowledge that the means also differ between spacings, with the closer spacing reducing growth much earlier than with more open spacing. As proposed by FRANKLIN, the mature genotypic phase occurs then earlier when competition is increased. This hypothesis, which has been discussed several times in other studies, could be verified in these experimental results.

Trends in heritability

Heritabilities of the family or clone mean basis reach rapidly values higher than 0.7. These values are among the highest generally found for growth traits in forest trees when family or clone means are considered (OSÓRIO *et al.,* 2001). This can be explained by the strict control of weeding in the experiment, by the soil homogeneity within each block and by the high number of observations per family or clone. Heritability on an individual tree basis are smaller specially for circumference. Although difference in absolute value are marked, similar trends with age can be observed: the curves of individual tree or family (clone) mean basis are parallel. Comparisons with other results must be treated with caution, heritability for growth traits in forest trees varying greatly and depending on numerous factors such as species, experimental design, population, site, and many patterns can be observed in the literature (Lambeth *et al.,* 1983; Sato, 1994; Kusnandar *et al.,* 1998; Hannrup *et al.,* 1998). For eucalyptus, however, some results showed that heritability varies moderately during the genotypic phase for some tropical or temperate species (Borralho *et al.,* 1991; Bouvet and Vigneron, 1995; Marques *et al.,* 1996; Patino-Valera and Kageyama, 1995; Wei and Borallho, 1998). Heritability showed a similar pattern in these three experiments. It very rapidly reached a plateau and the two phases mentioned above for coefficient of variation were not obviously observed for this parameter. This rapid stationary trend can be explained by the rapid growth of these species in the tropical conditions of the Congo.

The impact of competition on heritability is not clear. Heritability is generally higher for the lower density of 625 trees/ha. This superiority can be explained by the large within family or clone variance at close spacing and a large impact of the microenvironment. The differences are, however, less than the standard error, which stresses the weak effect of spacing on this parameter under the experimental conditions of the trials and for the period of measurement concerned.

Comparison between circumference and height

Circumference is generally more sensitive to competition than height in tree species. Circumference and height were therefore analysed separately to compare their patterns when spacing decreases. These two traits responded in a similar way in these experiments when considering trends in genetics, environmental variance, heritabilities and interaction. This result confirms the assumption that these two traits are under very close genetic control.

Consequence for selection

Competition and plot size are of great importance in tree selection and are the subject of much debate (Saya *et al.,* 2001). These three experiments provide new experimental data on the effect of density when testing eucalyptus genotypes in a tree breeding programme. When eucalyptus families are tested in square or rectangular plot with a number of trees higher than or equal to 16, increasing density allows a similar efficiency of the selection at the family level compared with wider spacings during the juvenile phase. Before three years, the high value of heritability, very close to or higher than that of wider spacing, and the very low genotype by spacing interaction allows selection of genotypes at close spacing and then reduction in size and cost of experimental design. This point is important to consider in the framework of tree breeding programmes when large numbers of families are to be tested and when the experimental design is large. However, after three years, heritability becomes higher with wider spacing indicating that family selection is more efficient at wide spacing.

For clonal material, the test layout should mimic as closely as possible the characteristics of the plantation. The use of close spacings, even with large square plots, could conceivably lead to inefficient selection when the objective is to select for monoclonal plantation. When a single tree plot is used with close spacing, even greater mistakes may be made.

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Stability-related Parameters and Their Evaluation in a 17-Year Old Norway Spruce Clonal Test Series

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Abstract

Rooted cuttings of 40 different clones (genotypes) of *Picea abies* L. Karst were planted on 7 contrasting test sites (environments) in northern Germany. Various concepts on stability and genotype x environment interactions (*G*x*E*) have been discussed using height data at age 17 years. Several parametric and rank-based measures concerning *G*x*E* and stability were estimated; and the relationships among them along with the total height were determined. In addition, 5 different rank-based measures *that combine both stability and performance* of genotypes simultaneously have also been estimated. Although ANOVA tests showed significant *G*x*E*, rank-based nonparametric tests using $S^{(m)}$ statistics showed no significant differences among the clones in their interactive behavior. Overall evaluation of various stability-related parameters indicate that significant *G*x*E* interaction detected by F tests is quite small in proportion (1.92%), clones contributed 7% and sites 50% within the total variance. The observed clonal contributions to interaction sum of squares are attributable mostly to changes in environmental conditions associated with site factors. In further selection and breeding with the clonal material at hand, *G*x*E* interaction appears to be of minor importance in Norway spruce, as it is also supported by the non-significance of rank-based tests. Any one of the 5 indices that combine stability and performance appears to be a better indicator than any other single stability-related parameter in detecting genotypes with both high stability and high performance.

Key words: Genotyp x environment interaction, ecovalence, stability, environmental sensitivity, rank-based tests.

Introduction

Picea abies L. Karst. (Norway spruce) is one of the important forest tree species in central and northern Europe. The species has been subject to intensive genetic selection and breeding since the 1960s. One of the large-scale selection and clonal propagation programs on Norway spruce has been developed at the Lower Saxony Forest Research Institute (LSFRI), Dept of Forest Genetic Resources (Kleinschmit *et al.,* 1973, Kleinschmit and Schmidt, 1977, Kleinschmit, 1993). As part of this program, cuttings were taken from different provenances of outstanding performance, and rooted cuttings were serially propagated on a three-year cycle. Selection of the best clones has been carried out at each propagation cycle based on nursery and field performance of the clones. The genotypes used in this study are the outcome of such truncation selection.

Growth trends in 17-year-old Norway spruce clones at seven test sites in northern Germany were evaluated in an earlier study (Isik *et al.,* 1995). The results of this study indicated significant differences among the test sites, among the clones, and significant clone x site (*G*x*E*) interaction. However, stability-related parameters were not covered in the same study.

The objectives of this study, using the data in Isik *et al.* (1995), are to identify the most- and the least- interacting clones, to estimate various (parametric and rank-based) stability-related clonal parameters, and to make comparisons among them. Utilizing information obtained from these objectives and from the overall clonal performance, one can make inferences as to which genotypes to be selected for further breeding and plantation purposes.

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