

METHODOLOGY

Selection and genetic gain in rubber tree (*Hevea*) populations using a mixed mating system

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Abstract

The components of genetic variation and genetic gain obtained with three selection methods - individual, combined and multi-effect index selection - were compared in rubber tree [*Hevea brasiliensis* (Willd. ex ADR. de Juss.) Muell. Arg.] progenies. The rubber tree is a cross pollinating species with a mixed reproductive system in which the self pollination rate is 22%. Twenty-two half sib progenies were planted at experimental stations at Pindorama, Votuporanga and Jaú, in São Paulo State, using a randomized and complete block design, with five replications and ten plants per plot. Dry rubber production was assessed when the plants were three years old. Based on the genetic variability of the populations, Pindorama was the best environment for the expression of variability. At the individual level, heritability was seriously affected when random progenies from an open pollinating population were considered as half sib progenies. Considerable overestimation of genetic gains occurred during individual, combined and multi-effect index selection when the rubber tree reproductive system was not considered as mixed. Selection based on the multi-effect index maximizes genetic progress and should be used more in rubber tree breeding programs.

INTRODUCTION

The rubber tree [*Hevea brasiliensis* (Willd ex ADR. de Juss.) Muell. Arg.] is considered a preferentially cross pollinating, perennial species, with a long breeding cycle. Usually, three selection stages are involved and 25 to 30 years are required until the final choice of clones for large scale planting can be made (Gonçalves *et al.*, 1988). This long breeding process has led to considerable investment in studies of genetic parameters to maximize the selection progress. Of particular interest to breeders are the genetic variance, heritability and gains provided by different selection methods.

Studies on genetic variation have been carried out in Malaysia (Nga and Subramanian, 1974; Tan *et al.*, 1975; Tan and Subramanian, 1976; Tan, 1977, 1978a,b) and Nigeria (Alika and Onokpise, 1982; Alika, 1985). In Brazil, studies on the heritability of various traits have been done by Siqueira (1978), Valois *et al.* (1978), Paiva *et al.* (1982, 1983), Gonçalves *et al.* (1990, 1992, 1996), Moreti *et al.* (1994) and Boock *et al.* (1995).

These studies have considered the rubber tree as an open pollinating species. Simmonds (1989), however, reported an average self pollination rate of 22% with an esti-

ated amplitude of 16-28%. More recently, Paiva (1992) obtained a mean inbreeding rate above 20% in natural populations. These findings identify the rubber tree as a species with a mixed reproductive system.

The assumption that the covariance among individuals within the progeny (COV_p) of an open pollination population in a forest ambient corresponds to 25% of the additive genetic variance (σ^2_A) usually leads to an overestimation of this variance. Consequently, the heritability coefficient and genetic gains from selection are equally overestimated (Squilace, 1974; Namkoong, 1981). This occurs because some species allow a certain rate of self pollination, which normally increases the covariance among individuals in the progeny. In addition, use of the relationship $\sigma^2_A = 4 COV_p$ results in the overestimation of additive variance (Resende *et al.*, 1995b).

This situation is typical of *Eucalyptus* species, which have rates of self pollination ranging from 8 to 40%. Moran and Bell (1983) and Griffin *et al.* (1987) considered *Eucalyptus* species to have a mixed reproductive system.

Adoption of the model presented by Cockerham and Weir (1984) for species with a mixed reproductive system allows better characterization of the genetic structure of such populations. This practice provides a more suitable

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definition of the components of genetic variation and, consequently, of the effects of self pollination in estimating genetic parameters (Resende *et al.*, 1995b, 1996). In addition, the considerations presented by Namkoong (1966) and Squilace (1974) were based only on additive genetic variance, and did not consider the other components of genetic variation which occur where there is inbreeding.

Thus, any recommendations on how to choose the genetic material for large scale planting should take into consideration the variability associated with a mixed reproductive system, which, in the case of the rubber tree, includes the self pollination rate.

In the present study, the genetic variation and genetic gain associated with individual, combined and multi-effect index selection in rubber tree progenies were compared, assuming an open pollinating species with a mixed reproductive system.

MATERIAL AND METHODS

The genetic material used consisted of 22 progenies of half sibs from open pollinated seeds, obtained from 22 parent clones selected phenotypically from an *H. brasiliensis* population composed of material of Asian origin introduced to Instituto Agrônomo de Campinas (IAC) in 1952.

The progeny tests were set up at three experimental stations belonging to IAC in São Paulo State. The characteristics of these localities are described below.

a) Jaú experimental station: latitude 22°17'S, longitude 48°34'W and altitude of 580 m. The soil is clay textured dark red latosol deep and flat with a well-drained topography. An Aw (Köppen) climate predominates in this region, with a defined dry season, annual mean temperature of 21.6°C, average humidity of 70% with extremes of 77% in February and 59% in August. The mean annual rainfall is 1,344 mm.

b) Pindorama experimental station: latitude 21°13'S, longitude 48°56'W and altitude of 560 m, with red-yellow podzolic soil of medium texture which was TB eutrophic, deep, abrupt and well drained (Lepsch and Valadares, 1976). The climate is tropical continental, with a wet summer and a dry winter period with reduced temperatures and rainfall. The mean annual temperature is 22.2°C, with a maximum of 28.9°C and a minimum of 16.6°C. The mean annual rainfall is 1,390 mm. The period from October to April usually has a favorable precipitation for growth and production. Low precipitation and temperatures occur from May to September.

c) Votuporanga experimental station: latitude 20°25'S, longitude 49°50'W and altitude of 450 m. The soil is podzolic sandy phase type and the climate tropical continental, with a hot, wet summer and a cool, dry winter period with low temperatures and rainfall. The mean annual temperature is 22.3°C and the mean annual rainfall is 1,420 mm.

The seeds were collected at the IAC experimental center, then germinated in polyethylene bags, at the three ex-

perimental stations and taken to their definitive locations when they showed two leaf umbrellas. The seedlings were set out in a randomized complete block design with 22 treatments, five replications and ten plants per plot (1.5 m x 1.5 m) in single rows. The progenies were assessed for rubber production when they were three years old.

Dry rubber production (RP) was determined by the Hamaker-Morris-Mann (HMM) test modified for three-year-old seedlings (Tan and Subramanian, 1976) using the mean dry rubber production from three cuts per plant. The tapping panel was opened 20 cm from the soil, using the 1/2S d/3 system, with a total of 35 cuts. The first five samples, which corresponded to the "breaking in of the panel" stage, were discarded. The term 1/2S corresponded to the half spiral cut and the term d/3 expressed the interval between tappings, i.e., tapping three days.

The analysis using the statistical model below considered all variables (except the mean) as random effects.

$$Y_{ijk} = \mu + p_i + b_j + e_{ij} + d_{ijk}$$

where Y_{ijk} = observed value of the k th plant in the j th replication within the i th progeny, μ = general mean, p_i = effect of the i th progeny ($i = 1, 2, \dots, 22$), b_j = effect of the j th replication ($j = 1, 2, \dots, 3$), e_{ij} = experimental error associated with the ij th plot and d_{ijk} = effect of the k th plant within the ij th plot.

Estimates of the genetic and phenotypic parameters were obtained using the SELEGEN genetic statistical software developed by Resende *et al.* (1994).

Heritability coefficients at the individual within plot level (h^2_d), progeny mean (h^2_f), plot mean (h^2_p), individual within blocks (h^2_{ib}) and individual plants (h^2_{ie}) associated with the different effects of the linear model, were estimated by the following expressions (Resende and Higa, 1994).

$$h^2_d = \frac{3 / 4\sigma_A^2}{\sigma_d^2}$$

$$h^2_f = \frac{[(3 + nb) / (4nb)]\sigma_A^2}{\sigma_p^2 + \frac{\sigma_e^2}{b} + \frac{\sigma_d^2}{nb}}$$

$$h^2_p = \frac{[(3 / (4n))\sigma_A^2]}{\sigma_e^2 + \frac{\sigma_d^2}{n}}$$

$$h^2_{ib} = \frac{\sigma_A^2}{\sigma_p^2 + \sigma_e^2 + \sigma_d^2}$$

$$h^2_{ie} = \frac{\sigma_A^2}{\sigma_p^2 + \sigma_e^2 + \sigma_d^2 + \sigma_b^2}$$

where $\sigma_A^2 = 4\sigma_p^2$, σ_A^2 = additive genetic variance, σ_e^2 = among plots environmental variance, σ_d^2 = among plants within plots phenotypic variance, σ_p^2 = among progenies genetic variance, n = number of plants/plot and b = number of blocks.

The coefficients of genetic (CV_g %) and experimental (CV_e %) variation were estimated using the following formulas presented by Vencovsky (1987):

$$CV_g (\%) = \frac{\sqrt{\sigma_p^2}}{\bar{X}} \cdot 100$$

$$CV_e (\%) = \frac{\sqrt{\sigma_e^2 + \sigma_d^2}}{\bar{X}} \cdot 100$$

Estimates of the genetic values and the genetic progress were obtained by individual (I_i), combined (I_c) or multi-effect (I_{me}) index selection in a univariate situation, using the expressions described by Resende and Higa (1994):

$$I_i = h_{ie}^2 (X_{ijk} - \bar{X})$$

$$I_c = h_d^2 \cdot X_{ijk} - h_d^2 \cdot \bar{X}_{ij} + h_f^2 \cdot \bar{X}_{i..} - h_f^2 \cdot \bar{X}_{...}$$

$$I_{me} = h_d^2 (Y_{ijk}) + (h_p^2 - h_d^2) \bar{X}_{ij} - h_p^2 \bar{X}_{j.} + (h_f^2 - h_p^2) \bar{X}_{i..} + (h_p^2 - h_f^2) \bar{X}_{...}$$

where h_{ie}^2 is the heritability coefficient in the restricted sense at the individual level in the experiment, X_{ijk} is the value of the k th of the individual in the ij th plot, \bar{X} is the general experimental mean, $\bar{X}_{i..}$ is the progeny mean, $\bar{X}_{ij.}$ is the plot mean, X_{ijk} is the deviation of the individual value (plot) and $\bar{X}_{j.}$ is the block mean.

The progress with combined selection was equivalent to the mean of the genetic values (index) of the selected individuals. Selection by the multi-effect index was based on the product of the individual phenotypic value, plot mean, progeny mean, block mean and the general mean of the experiment using the index weighting coefficients. The method reduced the weight attributed to the general family means thus allowing a better distribution of selected individuals in the various families.

The index weighting coefficients were determined to maximize the correlation between the index and the genetic value. This maximization was obtained by regressing the genetic value on the phenotypic values, which lead to a matrix system (Henderson, 1963).

The following accuracy estimators derived by Resende *et al.* (1995a) for the different selection methods were used:

a) Individual: $\left(\frac{\sigma_A^2}{\sigma_{F_{ie}}^2} \right)^{1/2}$

b) Combined selection:

$$\left[\frac{n-1}{n} (1-r)^2 \frac{\sigma_A^2}{\sigma_d^2} + \frac{p-1}{p} \left(\frac{1+(nb-1)r}{nb} \right)^2 \frac{\sigma_A^2}{\sigma_F^2} \right]^{1/2}$$

c) Multi-effect index:

$$\left[\frac{n-1}{n} (1-r)^2 \frac{\sigma_A^2}{\sigma_d^2} + \frac{p-1}{p} \left(\frac{1+(nb-1)r}{nb} \right)^2 \frac{\sigma_A^2}{\sigma_F^2} + \left(\frac{b-1}{b} \right) \left(\frac{p-1}{p} \right) \left(\frac{1-r}{n} \right)^2 \frac{\sigma_A^2}{\sigma^2} \right]^{1/2}$$

where σ_F^2 = genotypic variance at the mean progeny level, $\sigma_{F_{ie}}^2$ = phenotypic variance at the individual level, σ^2 = residual variance at the plot level, r = genetic correlation coefficient among individuals of a single progeny (1/4 for half sibs) and n, b, p = number of plants per plot, block and progeny, respectively (see appendix).

The accuracy parameter is a very useful measurement of the precision of the genetic values predicted and it corresponds to the correlation between the true and the predicted genetic values.

The genetic parameters obtained were also estimated using the SELEGEN software (Resende *et al.*, 1994) for the dry rubber production trait by adopting a model for a species with a mixed reproduction system, and a self pollination rate of 22%. The models were considered complete (0.155 kinship coefficient) and additive (0.18 kinship coefficient) as defined by Resende *et al.* (1995b).

The complete model considered the additive genetic merit of the individuals and the dominance deviations. The additive model only considered the additive genetic merit of the individuals, i.e., the variation in genetic values was attributed to an additive effect of the genes.

The genetic model adopted corresponded to that presented by Cockerham and Weir (1984):

$$VG = (1 + F) \sigma_A^2 + (1 - F) \sigma_D^2 + 4FD_1 + FD_2 + F(1 - F)H' + (F_c - F^2)(H^2 - H')$$

where F = the endogamy coefficient; F_c = two loci joint endogamy coefficient, equivalent to

$$F_c = \frac{F(1 + 2F)}{2F}$$

σ_A^2 = additive genetic variance, σ_D^2 = dominant genetic variance, D_1 = covariance among the additive effects of the alleles and the dominance effects of homozygotes, D_2 = genetic variance of the homozygote dominance effects, H' = sum of the squares of depression caused by endogamy and

H^2 = square of the sum of the effects of endogamy depression at each locus.

RESULTS AND DISCUSSION

Table I shows the analysis of variance for RP. Significant among-family differences were detected by the F test. This variability was an essential condition for establishing a genetic breeding program and it could be effectively exploited to increase rubber production.

The experimental coefficients of variation ($CV_e\%$) obtained for RP at Pindorama (37.7%), Votuporanga (33.5%) and Jaú (43.1%) indicated that this trait is subject to great experimental errors. However, these values agree with similar estimates by Paiva *et al.* (1982) and Alves *et al.* (1987) who obtained $CV_e\%$ of 38.3% and 50.4%. The levels were similar to those reported by Moreti *et al.* (1994).

The genetic variation coefficient, which expresses the amount of existing genetic variation as a percentage of the general mean, was higher at Pindorama (40.9%) than at Votuporanga (26.0%) and Jaú (15.6%). This result confirmed the F test results for progeny differences and characterized Pindorama as a more suitable environment for expression of the genetic variability in this population. These results also agreed with those reported by Moreti *et al.* (1994) for the same trait.

The RP heritability coefficients associated with the different genetic effects used in the selection methods are shown in Table II. The heritability estimates obtained by the different models varied within and among locations according to the selection method used. Higher heritability values were observed for effects where the rubber tree was considered as a cross pollinating species, with greater values for Pindorama, followed by Votuporanga and Jaú.

The estimates obtained for the species, when considered as cross pollinating, compared to those found in models used for a mixed reproductive system, showed that heri-

tability at the progeny level was practically unaffected at the three locations studied, even after allowing for the presumable inbreeding rate for the population. On the other hand, heritability at the individual level was considerably affected when progenies from open pollination were considered as half sibs.

When the rate of self pollination was not considered, the overestimation of heritability between the cross pollination and mixed models was 2% for Jaú, 4.6% for Votuporanga and 11.8% for Pindorama for the complete model. With the additive model, this variation was even more expressive: Pindorama, 18.7%, Votuporanga 7.4% and Jaú 3.2%.

These results agree with those reported by Resende *et al.* (1995b) for various *Eucalyptus* populations, for which the genetic gain (directly proportional to heritability) was overestimated during mass selection. More specifically for heritability, Hodge *et al.* (1996) pointed out that estimates for *E. globulus* and *E. nitens* progenies were overestimated mainly because of the effects of inbreeding depression which were disregarded when open pollination progenies were considered as half sibs.

For among-progeny selection, using open pollination and half sibs, the covariance ($COV_{us,pm}$) between a selection unit and the breeding population was exactly the same as the genetic variance among progenies (Resende *et al.*, 1995a). Consequently, there was no error in among-progeny selection and the heritability obtained could be used in expressing the genetic gain when working with legitimate half sibs. On the other hand, for mass selection among-half sib progeny, the among-progeny variance component was multiplied by four, increasing the covariance among the individuals in the progeny. Thus, use of the relationship $\sigma_A^2 = 4 COV_p$ caused overestimation of σ_A^2 (Resende *et al.*, 1995b). This overestimation will be bigger the greater the self pollination rate.

Table III shows the accuracy and direct genetic gains associated with the different effects used in the selection methods for RP, assuming the species was cross pollinating with a mixed reproductive system.

The accuracy and genetic gain estimates for RP varied within and among locations in the different selection methods. When the accuracy values associated to the genetic gain are greater, the expected progress with selection was also greater, i.e., the greater the precision in selection the greater the gain. The genetic gain was much more expressive at Pindorama than at Votuporanga or Jaú. These results agree with those obtained by Moreti *et al.* (1994) for mass selection and can be explained by the high heritability values at the individual level at Pindorama compared to those at Votuporanga and Jaú. They also indicate that Pindorama was a more favorable environment for the expression of genetic variability, as shown by the RP coefficients of genetic variation ($CV_g\%$).

The multi-effect index approach was more advantageous than individual or combined selection because the gain estimates were always superior. This tendency was simi-

Table I - Mean squares from ANOVA of the experimental coefficient of variation (CV_e) and genetic coefficient of variation (CV_g) for rubber production (RP) in 22 three-year-old open pollinated progenies of *Hevea*, at three locations.

Source of variation	Mean squares		
	Pindorama	Votuporanga	Jaú
Replicates	0.0384	0.0424	0.0387
Progenies	0.6665**	0.1162**	0.0972*
Residual	0.0966	0.0281	0.0474
Within plot	0.5943	0.2718	0.3522
Mean	0.8250	0.5013	0.6381
CV_e (%)	37.6708	33.4483	34.1135
CV_g (%)	40.9229	26.0248	15.6401

¹The degrees of freedom for repetition, progenies and residual were 4, 21 and 84, respectively. * $P < 0.05$, ** $P < 0.01$.

Table II - Heritability coefficients (species considered allogamous with a mixed reproductive system) associated with different effects in the selection methods for rubber production (RP) in three-year-old *Hevea* at three locations.

Locations	Heritabilities	Reproductive system		
		Allogamous	Mixed (P.C. 0.155)*	Mixed (P.C. 0.18)**
Pindorama	Individual within plot level (h_d^2)	0.575	0.427	0.341
	Progeny mean (h_p^2)	0.906	0.893	0.885
	Progeny mean (h_p^2)	0.354	0.263	0.210
	Individual with blocks (h_{ib}^2)	0.611	0.493	0.425
	Individual plants (h_{ie}^2)	0.613	0.495	0.426
Votuporanga	Individual within plot level (h_d^2)	0.194	0.144	0.115
	Progeny mean (h_p^2)	0.803	0.792	0.785
	Progeny mean (h_p^2)	0.188	0.139	0.111
	Individual with blocks (h_{ib}^2)	0.243	0.186	0.168
	Individual plants (h_{ie}^2)	0.242	0.196	0.168
Jaú	Individual within plot level (h_d^2)	0.085	0.063	0.050
	Progeny mean (h_p^2)	0.543	0.535	0.531
	Progeny mean (h_p^2)	0.063	0.047	0.037
	Individual with blocks (h_{ib}^2)	0.106	0.086	0.074
	Individual plants (h_{ie}^2)	0.106	0.086	0.074

*22% self-fertilization rate; complete model with 0.155 parental coefficient (P.C.). **22% self-fertilization rate; additive with 0.18 P.C.

Table III - Accuracy and direct genetic gain (%) associated with different univariate selection units for rubber production, considering the species allogamous with a mixed reproductive system for three-year-old *Hevea* at three locations.

Locations	Selection*	Allogamy		Mixed (P.C. 0.155)**		Mixed (P.C. 0.18)***	
		Accuracy	Gain (%)	Accuracy	Gain %	Accuracy	Gain (%)
Pindorama	Individual	0.783	218.7	0.703	176.3	0.653	151.9
	Combined	0.786	211.2	0.735	174.1	0.715	154.1
	Multi-effects	0.789	218.6	0.745	178.8	0.722	157.5
Votuporanga	Individual	0.492	94.7	0.442	76.3	0.410	65.8
	Combined	0.578	91.2	0.578	76.6	0.588	68.6
	Multi-effects	0.587	95.9	0.584	80.0	0.592	71.1
Jaú	Individual	0.326	31.7	0.293	25.5	0.272	22.2
	Combined	0.441	34.9	0.452	30.6	0.467	28.4
	Multi-effects	0.445	36.0	0.455	31.3	0.469	28.7

*Selection in the trial = clonal seed orchard. **22% of ratio; full model with parental coefficient (P.C.) = 0.155. ***Additive model with P.C. = 0.18.

lar to that reported by Sturion *et al.* (1994), Resende *et al.* (1995a, 1996), and Sampaio (1996).

Resende and Higa (1994) discussed the tendency for higher gains in selection using the multi-effect index and explained that selection among and within progenies and combined selection used two sources of information for selection: the deviation of the individual value relative to the progeny mean in the block and the progeny mean rela-

tive to the general mean of the progeny test. These authors noted that in breeding schemes where the remaining seeds were not used, the additive genetic variance fraction was not considered, but was retained in the plot effects. The multi-effect index, in addition to using these two sources of information, further considers the plot effect and adds to the estimated gain those fractions of additive genetic variance retained in the plots.

RESUMO

Combined selection tends to select many individuals from certain families because of the greater weight given to the progeny information. In breeding populations, this does not present major problems, since in the next generation there will be selection against inbred individuals with undesirable traits, as long as the effective population size is adequate for obtaining the selective limit. Special care should be taken in production populations to prevent crossing among related individuals, which can lead to inbreeding depression. These precautions include careful orchard installation with a good distance among relations (Resende and Higa, 1994).

Higher accuracy and gains were observed for selection methods where the rubber tree was considered a cross pollinating species, with more expressive values at Pindorama, followed by Votuporanga and Jaú.

The overestimation of genetic gains in individual selection was 19.4% at Pindorama and Votuporanga and 19.5% at Jaú. With combined selection it was 17.6% at Pindorama, 16.1% at Votuporanga and 12.4% at Jaú. For multi-effect index selection, the rate was 18.2% at Pindorama, 16.6% at Votuporanga and 12.9% at Jaú.

More expressive values of the overestimation of genetic gains were obtained in the cross pollinating and mixed-additive models. For individual selection the overestimation was 30.5% at Pindorama and at Votuporanga and 29.9% at Jaú. For combined selection, it was 27.0% at Pindorama, 24.8% at Votuporanga and 18.8% at Jaú. For selection by the multi-effect index, it was 27.9% at Pindorama, 25.8% at Votuporanga and 20.2% at Jaú.

These results agree with those reported by Resende *et al.* (1995b) for several *Eucalyptus* species where the genetic gain was overestimated in individual selection. Overestimation was caused mainly when inbreeding depression was not considered and the open pollination progeny was treated as half sibs. In this context, the discussion by Resende *et al.* (1995b) about heritability is fully applicable when dealing with genetic progression and selection.

Our findings are similar to these of Moran and Bell (1983) and Griffin *et al.* (1987) for *Eucalyptus* species, which led to these species being considered as having a mixed reproductive system. The model suitable for populations with a mixed reproductive system has not been applied to the rubber tree.

The specific model for species with mixed reproductive systems presented by Cockerham and Weir (1984) allows better characterization of genetic structure of such populations. This practice provides a more suitable definition of the components of genetic variation and consequently of the effects of self pollination when estimating genetic parameters (Resende *et al.*, 1995b). This approach should be useful for obtaining precise estimates of genetic parameters in rubber trees.

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O presente trabalho objetivou comparar os componentes da variação genética e ganho genético obtidos através da seleção individual, combinada e pelo índice multi-efeitos em progênes de seringueira [*Hevea brasiliensis* (Willd ex ADR. de Juss.) Müell. Arg.], considerando-a como espécie alógama e de sistema reprodutivo misto, com taxa de adefecundação de 22%. Vinte e duas progênes de meio-irmãos foram plantadas nas Estações Experimentais de Pindorama, Votuporanga e Jaú, no estado de São Paulo, no delineamento de blocos ao acaso, com cinco repetições e dez plantas por parcela. Aos três anos de idade o caráter produção de borraça seca foi avaliado. Os resultados demonstraram haver variabilidade genética nas populações, bem como caracterizaram Pindorama como um ambiente mais propício para a expressão da referida variabilidade. As herdabilidades ao nível de indivíduos são consideravelmente afetadas ao assumir progênes de polinização aberta como sendo de meio-irmãos. Superestimativas consideráveis de ganhos genéticos ocorrem na seleção individual, combinada e índice multi-efeitos, quando não se considera o sistema reprodutivo misto para a seringueira. A seleção com base no índice multi-efeitos maximiza o progresso genético e deve ser utilizada.

APPENDIX

Derivation of the multi-effect index and associated accuracy.

The linear model for an individual observation in a progeny test is: $Y_{ijk} = u + b_j + p_i + e_{ij} + d_{ijk}$, where:

u = general mean, fixed, $E(u) = u$ and $E(u^2) = u^2$

b_j = block effect, random, $E(b_j) = 0$ and $E(b_j^2) = \sigma_b^2$

p_i = progeny effect, random, $E(p_i) = 0$ and $E(p_i^2) = \sigma_p^2$

e_{ij} = plot effect ij , random, $E(e_{ij}) = 0$ and $E(e_{ij}^2) = \sigma_e^2$

d_{ijk} = within plot effect ijk , random, $E(d_{ijk}) = 0$ and $E(d_{ijk}^2) = \sigma_d^2$

In terms of deviations the model is of the form:

$$Y_{ijk} = \bar{Y} \dots + (\bar{Y}_{ijk} - \bar{Y}_{ij.}) + (\bar{Y}_{ij.} - \bar{Y}_{i..} - \bar{Y}_{.j.} + \bar{Y} \dots) + (\bar{Y}_{i..} - \bar{Y} \dots) + (\bar{Y}_{.j.} - \bar{Y} \dots),$$

The covariances between the components of the model with the additive genetic value are (Resende, 1991; Resende and Higa, 1994):

$$\text{COV}(A, Y_{ijk}) = 2\text{COV}(\text{MF}) = \sigma_A^2$$

$$\text{COV}(A, \bar{Y}_{ij.}) = \frac{1}{n} 2 \text{COV}(\text{MF}) + \frac{(n-1)}{n} 2 \text{COV}(\text{MTS}) \text{ or}$$

$$\text{TS}) = \frac{1}{n} \sigma_A^2 + \frac{(n-1)r}{n} \sigma_A^2$$

$$COV(A, \bar{Y}_{i..}) = \frac{1}{nb} 2 COV(MF) + \frac{(nb - 1)}{nb} 2 COV(MTS)$$

$$\text{or TS) } = \frac{1}{nb} \sigma_A^2 + \frac{(nb - 1)r}{nb} \sigma_A^2$$

$$COV(A, \bar{Y}_{.j.}) = \frac{1}{np} 2 COV(MF) + \frac{(n - 1)}{np} 2 COV(MTS)$$

$$\text{or TS) } = \frac{1}{np} \sigma_A^2 + \frac{(n - 1)r}{np} \sigma_A^2$$

$$COV(A, \bar{Y}...) = \frac{1}{npb} 2 COV(MF) + \frac{(nb - 1)}{npb} 2 COV(MTS)$$

$$\text{or TS) } = \frac{1}{npb} \sigma_A^2 + \frac{(nb - 1)r}{npb} \sigma_A^2, \text{ where:}$$

r = additive genetic correlation between individuals within family: r = (1/4) for half-sibs and r = (1/2) for full-sibs; *COV(MF)* = parent-offspring covariance; *COV(MTS or TS)* = half-uncle-nephew (for half-sib families) or uncle-nephew (for full-sib families) covariances.

The covariances between the effects and the additive genetic effects are:

a) Within plot effect

$$COV [A, (Y_{ijk} - \bar{Y}_{ij.})] = COV (A, Y_{ijk}) - COV (A, \bar{Y}_{ij.}) = \\ = \{[(n - 1)(1 - r)]/n\} \sigma_A^2$$

b) Progeny effect

$$COV [A, (\bar{Y}_{i..} - \bar{Y}...)] = COV (A, \bar{Y}_{i..}) - COV (A, \bar{Y}...) = \\ = \frac{(p - 1)}{p} \frac{[1 + (nb - 1)r]}{nb} \sigma_A^2$$

c) Plot effect

$$COV [A, (\bar{Y}_{ij.} - \bar{Y}_{i..} - \bar{Y}_{.j.} + \bar{Y}...)] = COV(A, \bar{Y}_{ij.}) - \\ - COV (A, \bar{Y}_{i..}) - COV (A, \bar{Y}_{.j.}) + COV (A, \bar{Y}...) \\ COV [A, (\bar{Y}_{ij.} - \bar{Y}_{i..} - \bar{Y}_{.j.} + \bar{Y}...)] = \frac{(b - 1)(p - 1)}{b} \frac{1 - r}{p} \frac{1 - r}{n} \sigma_A^2$$

d) Block effect

$$COV [A, (\bar{Y}_{.j.} - \bar{Y}...)] = COV (A, \bar{Y}_{.j.}) - COV (A, \bar{Y}...) = \\ = \frac{b - 1}{b} \frac{(1 - r)}{np} \sigma_A^2$$

The block effects can be neglected as a function of its

low covariance with the genetic value. The variances of the relevant effects are:

a) Within plot effect

$$Var (Y_{ijk} - \bar{Y}_{ij.}) = E(Y_{ijk}^2) - 2E(Y_{ijk} \bar{Y}_{ij.}) + E(\bar{Y}_{ij.}^2) = \\ = [(n - 1)/n] \sigma_d^2$$

b) Progeny effect

$$Var (\bar{Y}_{i..} - \bar{Y}...) = E(Y_{i..}^2) - 2E(\bar{Y}_{i..} \bar{Y}...) + E(\bar{Y}^2...) = \\ = [(p - 1)/p] (\sigma_p^2 + \sigma_e^2/b + \sigma_d^2/nb)$$

c) Plot effect

$$Var (\bar{Y}_{ij.} - \bar{Y}_{i..} - \bar{Y}_{.j.} + \bar{Y}...) = E(Y_{ij.}^2) + E(\bar{Y}_{i..}^2) + E(\bar{Y}_{.j.}^2) + \\ + (\bar{Y}^2...) - 2E(\bar{Y}_{ij.} \bar{Y}_{i..}) - 2E(\bar{Y}_{ij.} \bar{Y}_{.j.}) + 2E(\bar{Y}_{ij.} \bar{Y}...) + \\ + 2E(\bar{Y}_{i..} \bar{Y}_{.j.}) - 2E(\bar{Y}_{i..} \bar{Y}...) - 2E(\bar{Y}_{.j.} \bar{Y}...)$$

$$Var (\bar{Y}_{ij.} - \bar{Y}_{i..} - \bar{Y}_{.j.} + \bar{Y}...) = \frac{(p - 1)(b - 1)}{p} \frac{1}{b} (\sigma_e^2 + \sigma_d^2/n)$$

The optimal selection procedure (the one that maximizes the correlation between predictand and predictor) is given by the multi-effect index (Resende and Higa, 1994):

$$I = b_1 d_{ijk} + b_2 p_i + b_3 e_{ij} \\ = b_1 (Y_{ijk} - \bar{Y}_{ij.}) + b_2 (\bar{Y}_{i..} - \bar{Y}...) + b_3 (\bar{Y}_{ij.} - \bar{Y}_{i..} - \bar{Y}_{.j.} + \bar{Y}...)$$

The b_i coefficients are given by:

$$\begin{bmatrix} \frac{(n - 1)}{n} \sigma_d^2 & 0 \\ 0 & 0 & \frac{(p - 1)}{p} \left(\sigma_p^2 + \frac{\sigma_e^2}{b} + \frac{\sigma_d^2}{nb} \right) \\ 0 & 0 & 0 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \\ b_3 \end{bmatrix} = \\ \frac{(p - 1)(b - 1)}{p} \frac{1}{b} \left(\sigma_e^2 + \frac{\sigma_d^2}{n} \right) \begin{bmatrix} b_1 \\ b_2 \\ b_3 \end{bmatrix} =$$

Continued on next page

Appendix - Continued

$$= \begin{bmatrix} \frac{(n-1)(1-r)}{b} \sigma_A^2 \\ \frac{(p-1)}{p} \frac{1+(nb-1)r}{nb} \sigma_A^2 \\ \frac{(1-r)}{n} \frac{(b-1)}{b} \frac{(p-1)}{p} \sigma_A^2 \end{bmatrix}$$

Resolving these equations, the multi-effect index coefficients are:

$$b_1 = \frac{(1-r) \sigma_A^2}{\sigma_d^2} =$$

= "heritability" of the within plot effect;

$$b_2 = \frac{1+(nb-1)r}{nb} \sigma_A^2 = \frac{\sigma_p^2 + \sigma_{e/b}^2 + \sigma_d^2 / nb}{\sigma_p^2 + \sigma_{e/b}^2 + \sigma_d^2 / nb}$$

= "heritability" of the progeny effect;

$$b_3 = \frac{[(1-r)/n] \sigma_A^2}{\sigma_e^2 + \sigma_d^2 / n} =$$

= "heritability" of the plot effect;

The multi-effect index can be alternatively expressed as:

$$I = b_1 Y_{ijk} + (b_2 - b_3) \bar{Y}_{i..} + (b_3 - b_1) \bar{Y}_{ij.} - b_3 \bar{Y}_{.j.} + (b_3 - b_2) \bar{Y} \dots$$

For the balanced case, the multi-effect index is equivalent to individual (animal model) BLUP, as demonstrated by Resende and Fernandes (1999).

The accuracy of the index is given by

$$\hat{r}_{IA} = [\alpha_1 \hat{b}_1 + \alpha_2 \hat{b}_2 + \alpha_3 \hat{b}_3]^{1/2}$$

$$\text{where: } \alpha_1 = (1-r) \frac{(n-1)}{n}$$

$$\alpha_2 = \frac{1+(nb-1)r}{nb} \frac{(p-1)}{p}$$

$$\alpha_3 = \frac{(1-r)}{n} \frac{p-1}{p} \frac{b-1}{b}$$

This is equivalent to:

$$\hat{r}_{IA} \left[\frac{n-1}{n} (1-r)^2 \frac{\sigma_A^2}{\sigma_d^2} + \frac{p-1}{p} \left(\frac{1+(nb-1)r}{nb} \right)^2 \frac{\sigma_A^2}{\sigma_F^2} + \left(\frac{b-1}{b} \right) \left(\frac{p-1}{p} \right) \left(\frac{1-r}{n} \right)^2 \frac{\sigma_A^2}{\sigma^2} \right]^{1/2}$$

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