



Research article

Estimation of genetic parameters for rubber yield and girth growth in a synthetic population

Sophiya Suwanchana^a, Chalermopol Phumichai^{a,*}, Sujin Jenweerawat^a, Skorn Koonawootrittriron^b, Thitaporn Phumichai^c, Kannikar Teerawatnasuk^d

^a Department of Agronomy, Faculty of Agriculture, Kasetsart University, Bangkok 10900, Thailand

^b Department of Animal Science, Faculty of Agriculture, Kasetsart University, Bangkok 10900, Thailand

^c Rubber Research Institute, Rubber Authority of Thailand, Bangkok 10900, Thailand

^d Chachoengsao Rubber Research Center, Rubber Authority of Thailand, Chachoengsao 24160, Thailand

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Abstract

Rubber tree (*Hevea brasiliensis*) breeding programs take a long time and it is costly to create, evaluate and select superior progenies of cross breeds. Consequently, this study assessed a synthetic population of 288 rubber tree clones selected from a seedling orchard and derived from five female parent trees (varieties AVROS 2037, BPM 1, IAN 873, PB 260 and RRII 118) that were useful for systematically enhancing cross-pollination among several clones and for breeding superior rubber genotypes. The genetic parameters were estimated of rubber yield and tree girth growth within each synthetic population. Variance components and genetic parameters were estimated using average information restricted maximum likelihood procedures. The estimated additive genetic variances of rubber yield and tree girth growth were greater than the permanent environmental variances and residual variances of the studied population. The results indicated a narrow-sense heritability estimate based on individual values of 0.608 ± 0.029 and repeatability of 0.633 ± 0.027 for rubber yield; and 0.913 ± 0.007 – 0.927 ± 0.006 for girth growth (repeatability ranged 0.965 ± 0.003 – 0.982 ± 0.002). Genetic correlations between rubber yield and tree girth growth traits were positive ($r_g = 0.63$ – 0.64). There was also a positive phenotypic correlation ($r_p = 0.48$ – 0.49) between the rubber yield and girth growth traits. These results indicated that this synthetic population is a superior progeny with the potential for improving both rubber yield and tree girth growth.

Introduction

The rubber tree *Hevea brasiliensis* (Willd. ex A.Juss.) Muell.Arg., the major source of natural rubber, is an outbreeding monoecious species (Simmonds, 1986) that is pollinated by midges and thrips (Rao, 1961). *Hevea* rootstocks have been used pervasively since

the earliest years of commercial rubber in Thailand, even though the *Hevea* clones now exhibit high heterozygosity due to the natural cross-pollination process most often used (Kinnarat and Rattanawong, 2002). The clone RRIM 600 is the most cultivated variety of rubber tree in Thailand (Sangsing et al., 2004), accounting for 60% (approximately 3.584 million ha) of the area in Thailand planted in rubber trees (Rubber Authority of Thailand, 2018). Commonly, rubber tree seeds in Thailand are gathered exclusively from the farmer's

* Corresponding author.

E-mail address: chalermopol.ph@ku.th (C. Phumichai)

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own rubber plantation; consequently, most of the rubber tree plants in Thailand are clones of RRIM 600.

Rao et al. (2008) noted that inbreeding depression often occurs in seedlings grown in open-pollinated seed lots due to the self-pollination of the parents. Indeed, inbreeding depression is a concern for farmers who use seeds exclusively collected from RRIM 600 in their seed orchards. In contrast, open pollination in seed orchards of elite trees allows the production of seeds with higher genetic quality and diversity (Pakkanen et al., 2000). Furthermore, interplanting several good parents in a synthetic seed orchard minimizes inbreeding depression and these good parents then produce a roughly random array of outbred hybrids (Simmonds, 1986). Pawsoi et al. (2013) studied the first generation of synthetic *H. brasiliensis* clones derived from a polycross of multiple parents that were created to establish a seed orchard useful for systematically enhancing cross-pollination among several clones.

Rubber tree breeding cycles involve 20–30 yr between pollination and yield (Priyadrasan, 2011). Therefore, early yield tests are generally used to reduce the time it takes to complete a testing cycle. Tests are often performed during a single era, which can be useful for evaluating and predicting the yield stability of young rubber tree progenies (Gonçalves et al., 2009). The current research study used the HMMm (Hamaker Morris-Mann modified) method of testing, which was conducted during the early selection era (3-year-old progenies). Each test was done repeatedly, and the various characteristics were evaluated over time to produce data leading to a more effective selection method.

Variance components and genetic parameters may be used to identify and select optimal traits (Gonçalves et al., 2006, Verardi et al., 2012, Liu et al., 2013, Zhao et al., 2013). The REML/BLUP (restricted maximum likelihood/best linear unbiased prediction) method (Gouvêa et al., 2013) is effective for developing a selection index of traits that identify specific genetic parameters in superior progenies. The current study took into account the reality that variations in trait values of a population may vary due to genetic factors; therefore, the parameter estimates of traits obtained from one population are not accurate parameters of the same traits in another population. The current aimed to identify a superior elite progeny of RRIM 600. Limited research has been done previously that examined variance components and genetic parameters in a synthetic population of rubber tree clones to predict rubber yield and tree girth growth traits. Thus, the objectives of the current study were to estimate the variance components and genetic parameters in a synthetic population of rubber tree clones, testing heritability, repeatability, and genetic and phenotypic correlations that affect rubber yield and girth growth.

Materials and Methods

Plant materials

The study involved five female *Hevea* rubber tree varieties and their 288 half-sib seedlings progenies, which had been open-pollinated: AVROS 2037 (57 seedlings), BPM 1 (53 seedlings), PB 260 (59 seedlings), IAN 873 (58 seedlings) and RRII 118 (61 seedlings) as shown in Table 1. Molecular markers were used to identify the pollen of the male parent for each of the half-siblings, consistent with an identification process developed by Pawsoi et al. (2013). Progeny tests were set up using a randomized complete block design with five treatments for each of the cross-pollinated progenies and RRIM 600 (which was the checked variety), with eight replications and eight plants in each 4 m × 4 m plot (Fig. 1A). The research took place in the Chachoengsao Rubber Research Center at the Rubber Research Institute of Thailand (13°41' N, 101°04' E; 69 m above mean sea level).

The dry rubber yield (measured in grams per tapping per plant) of each three-year-old rubber tree seedling was determined from 30 tapping samples taken from each tree over time, using the Hamaker Morris-Mann (HHM) test modified for three-year-old seedlings (Tan and Subramaniam, 1976). The first five tapping samples taken while the trees were still adapting to the panels were unreliable and were discarded. The tapping panels were opened 40 cm above the ground (Fig. 1B), using a S/2 (half-spiral) cut (Fig. 1C) and a d/3 (one tapping every 3 d) system for a total of 35 tappings. Girth growth (measured in centimeters per plant) was measured every month for 4 mth using a tape measure. The girth growth of each seedling was measured above the ground at 50 cm (Girth 1), 100 cm (Girth 2), 150 cm (Girth 3) and 170 cm (Girth 4), as shown in Fig. 1D.

Statistical analysis

An average information-restricted maximum likelihood (AI-REML) repeatability model was used to estimate the variance components for this synthetic population of rubber tree clones (Gilmour et al., 2000). The fixed effects factors used in the model consisted of treatments and the block and year-month-group, the random effects consisted of the additive genetic effect, the permanent environment effects consisted of management, common environment and the residual. The model is described as:

y = Xb + Za + Wpe + e

Table 1 Numbers of open-pollinated progenies from five half-sib families

Female parent	Number of rubber clones assayed	Number of open-pollinated offspring per male parent
AVROS 2037	57	BPM 1 (2), IAN 873 (30), PB 260 (9), RRII 118 (7), AVROS 2037 (9)
BPM 1	53	AVROS 2037 (5), IAN 873 (23), PB 260 (16), RRII 118 (3), BPM 1 (6)
IAN 873	59	AVROS 2037 (8), BPM 1 (3), PB 260 (20), RRII 118 (7), IAN 873 (21)
PB 260	58	AVROS 2037 (1), BPM 1 (6), IAN 873 (27), PB 260 (24)
RRII 118	61	AVROS 2037 (6), BPM 1 (3), IAN 873 (37), PB 260 (14), RRII 118 (1)
Overall	288	

Numbers in parentheses indicate progeny numbers for each female and male parent (Pawsoi et al., 2013).

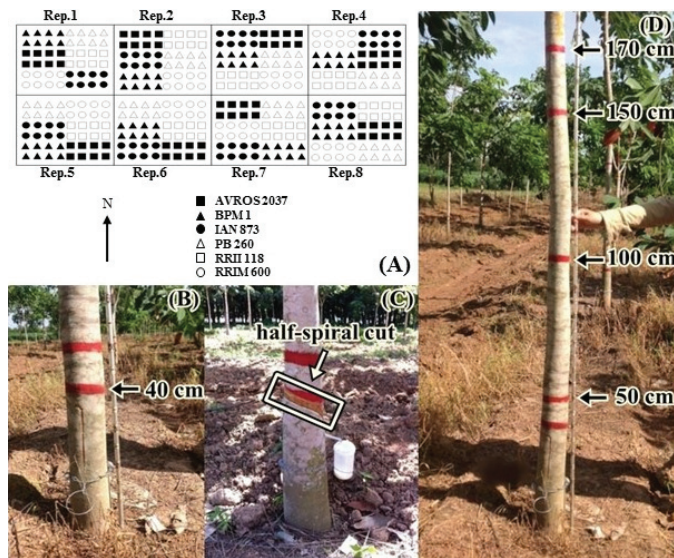


Fig. 1 (A) Map of synthetic population of rubber tree clones in seedling orchard (filled square = AVROS 2037, filled triangle = BPM 1, filled circle = IAN 873, open triangle = PB 260, open square = RR11 118, and open circle = RRIM 600); (B) position of tapping panel; (C) tapping system (S/2 d/3); (D) position of girth growth measurement at 50 cm (Girth 1), 100 cm (Girth 2), 150 cm (Girth 3) and 170 cm (Girth 4)

where y is the vector of observations of the studied traits, b is the vector of fixed effects (contemporary groups, known environmental effects and non-genetic effects), a is the vector of random additive genetic effect of individuals, pe is the vector of random permanent environmental effects of individuals, e is the vector of residuals, X is the incidence matrix records related to fixed effects, Z is the incidence matrix records related to random additive genetic effect of individuals, and W is the incidence matrix records related to permanent environmental effects. The variance and covariance matrices of random effects in a , pe and e are described as:

$$\text{var} \begin{bmatrix} a \\ pe \\ e \end{bmatrix} = \begin{bmatrix} G \otimes A & 0 & 0 \\ 0 & P \otimes A & 0 \\ 0 & 0 & R \otimes I \end{bmatrix}$$

where A is the additive genetic relationship matrix among individuals, I is the identity matrix, G , P and R are the additive genetic, permanent environmental variance and covariance matrices, respectively, for the three traits. Variance components—additive genetic variance (σ_a^2), permanent environmental variance (σ_{pe}^2), phenotypic variance (σ_p^2) and residual variance (σ_e^2)—were estimated

for all traits using an AI-REML procedure (Gilmour et al., 2000). The phenotypic variance was defined as $\sigma_p^2 = \sigma_a^2 + \sigma_{pe}^2 + \sigma_e^2$. The variance component estimates were used to calculate genetic parameters (narrow-sense heritability, h^2 ; genetic correlations, r_g ; and repeatability, t). Heritability was computed as $h^2 = \sigma_a^2 / \sigma_p^2$, repeatability was computed as $t = (\sigma_a^2 + \sigma_{pe}^2) / \sigma_p^2$ and the correlation between genotypic and phenotypic was computed as $r_{agy} = \sigma_{agy} / (\sigma_{ag} \cdot \sigma_{ay})$, where r_{agy} is the additive genetic covariance between girth and yield, σ_{ag} is the estimated additive genetic variance for girth and σ_{ay} is the estimated additive genetic variance for yield.

Mixed model Equation

A mixed model equation was used to solve BLUP for the least squares means of each fixed effect, the estimated breeding value (EBV) of the random additive genetic effect and the permanent environmental effects of each individual, as described as (Henderson, 1984):

$$\begin{bmatrix} X'X & X'Z \\ Z'X & Z'Z + A^{-1}\lambda \end{bmatrix} \begin{bmatrix} b \\ u \end{bmatrix} = \begin{bmatrix} X'y \\ Z'y \end{bmatrix}$$

Results and Discussion

Estimated variance components

The variance components (additive genetic variance, phenotypic variance, permanent environmental variance and residual variance) were estimated for this synthetic population of rubber clones (Table 2). The estimated additive genetic variances of rubber yield ($77.76 \pm 8.01 \text{ g}^2$) and tree girth growth (12.99 ± 1.08 – $24.54 \pm 2.03 \text{ cm}^2$) were greater than the permanent environmental variances (0.76 – 3.03 site^2) and residual variances (0.27 ± 0.01 – $46.94 \pm 2.63 \text{ unit}^2$) for the studied population. These results showed the greatest additive genetic variability in the rubber production trait and tree girth growth and indicated that this characteristic could be used reliably to identify the candidate plant for elite selection. The additive genetic variance estimates were greater than the residual variance, suggesting a high genetic variability resulting in a high heritability value.

Similar variance components were also reported in different studies by Verardi et al. (2012), who focused on additive genetic variances (7.81), environment variance between plots (0.74), residual variance (1.93) and phenotypic variance (10.48) of rubber yield in Sao Paulo, Brazil. However, the small values for permanent environmental variance (0.76 – 3.03 site^2) indicated that the clones in this population were subjected to similar management and could be considered as having grown in a single environment (Xu, 2016).

Table 2 Variance components (mean $\pm$ SE) of rubber yield and girth growth

Parameter	Additive genetic variances (σ_a^2)	Phenotypic variances (σ_p^2)	Permanent environmental variances (σ_{pe}^2)	Residual variances (σ_e^2)
Rubber Yield (g^2)	77.76 ± 8.01	127.73 ± 8.18	3.03	46.94 ± 2.63
Girth 1 (cm^2)	24.54 ± 2.03	26.65 ± 2.03	1.16	0.95 ± 0.04
Girth 2 (cm^2)	15.85 ± 1.31	17.10 ± 1.31	0.78	0.47 ± 0.02
Girth 3 (cm^2)	13.78 ± 1.14	14.81 ± 1.14	0.76	0.27 ± 0.01
Girth 4 (cm^2)	12.99 ± 1.08	14.22 ± 1.09	0.77	0.46 ± 0.02

Girth 1, Girth 2, Girth 3 and Girth 4 refer to tree girth measured at 50 cm, 100 cm, 150 cm and 170 cm, respectively, above ground.

High repeatability estimates showed that relying on these traits would be effective and less impacted by environmental effects.

Genetic parameters

The heritability of all traits in this population was estimated (Table 3). The narrow sense heritability estimates were 0.608 ± 0.029 for rubber yield, the most important commercial trait, and those of a girth growth ranged between 0.913 ± 0.007 and 0.927 ± 0.006 . Notably, the heritability estimates in this study were higher than in other studies, such as on populations of rubber tree seedlings planted in the State of Sao Paulo, Brazil (Gonçalves et al., 2006, Verardi et al., 2012). These earlier studies only measured the girth growth at 50 cm above the soil. The open pollinated progenies used in these studies were selected from rubber tree (*Hevea brasiliensis*) populations which had been introduced from Asian clones to Brazil. However, heritability is specific to a population (Van Der Werf and De Boer, 1989).

The study by Gouvêa et al. (2013) analyzed the heritability traits of rubber tree seedlings at two different sites (Jau and Votuporanga) and found a narrow sense heritability rubber yield for each of the two sites of 0.115 ± 0.063 and 0.208 ± 0.068 , respectively, and a mean girth growth of 0.438 ± 0.09 and 0.464 ± 0.09 , respectively. Souza et al. (2017) reported data analysis collected from three sites in Sao Paulo, Brazil (Jau, Votuporanga and Pindorama) with the narrow sense heritability of rubber yield being 0.17 ± 0.01 , 0.29 ± 0.11 and 0.57 ± 0.15 , respectively, and the girth growth being 0.67 ± 0.16 , 0.58 ± 0.14 and 0.67 ± 0.1 , respectively.

The current study revealed the high heritability of rubber yield and girth growth. These results indicated that genotype was highly associated with phenotype for all traits. The estimated repeatability

was high in all traits (Table 3) and this could be used as an initial model for the implementation of a genetic improvement program in this population. However, more genetic progress to improve girth growth could be possible. The results from the current study suggested that rubber yield and girth growth measurements are repeatable and that the first data recorded from an individual clone in this synthetic population could be used for selection decisions.

Estimates for the genetic correlations and phenotypic between rubber yield and girth growth in this population are shown in Table 4. The positive genetic correlations between rubber yield and girth growth ranged from 0.636 ± 0.045 between rubber yield and Girth 4 to 0.647 ± 0.043 between rubber yield and Girth 2. Strong positive genetic correlations were found between pairs of girth growth means, ranging from 0.970 ± 0.005 (Girth 2 and Girth 4) to 0.990 ± 0.002 (Girth 1 and Girth 2). The positive phenotypic correlations between rubber yield and girth growth ranged from 0.481 ± 0.037 (Girth 1), to 0.499 ± 0.037 (Girth 2). Strong positive phenotypic correlations were found between girth growth means, ranging from 0.921 ± 0.008 (Girth 1 and Girth 4) to 0.968 ± 0.003 (Girth 1 and Girth 2). High genetic correlation was found between rubber yield and girth growth suggesting that the selection based on girth growth would lead to gains in rubber yield as well.

Genetic correlations were generally higher than phenotypic correlations. This suggested the possibility of indirect selection of a trait from direct selection of another trait. Genetic correlations of rubber yield and the four heights of measured girth growth showed that each level of girth growth can be used as direct measurement to indicate rubber yield and girth growth. The study showed that the physiological seedling tree is cone-shaped, so the third and fourth levels are optimum for girth measurement. However, three-year-old rubber trees are too young for making significant adjustments of the progenies studied.

The very high phenotypic and genetic correlations between girth growth and rubber yield that the current study identified have been reported in other studies (Gonçalves et al., 2006). Silva et al. (2014) found the highest genetic correlation was between rubber yield and latex vessel ring size (0.920 ± 0.067), would be of practical importance for indirect selection for rubber yield by selecting for latex vessel number. However, the data showed that the genetic correlations for rubber yield and tree girth growth were higher than the corresponding phenotypic correlations, indicating that the use of phenotypic correlations to evaluate traits will result in underestimation of the potential gains from indirect selection, rather than genetic ones. The high value of heritability obtained indicated that the studied traits are not significantly influenced by environmental factors. Similar correlations have been reported (Lepoittevin et al., 2011; Souza et al., 2017).

Table 3 Heritability and repeatability estimates for rubber yield and girth growth

Parameter	Mean estimate $\pm$ SE
Heritability	
Rubber yield	0.608 ± 0.029
Girth 1	0.921 ± 0.006
Girth 2	0.927 ± 0.006
Girth 3	0.931 ± 0.005
Girth 4	0.913 ± 0.007
Repeatability	
Rubber yield (g)	0.633 ± 0.027
Girth 1 (cm)	0.965 ± 0.003
Girth 2 (cm)	0.972 ± 0.002
Girth 3 (cm)	0.982 ± 0.002
Girth 4 (cm)	0.968 ± 0.003

Girth 1, Girth 2, Girth 3 and Girth 4 refer to tree girth measured at 50 cm, 100 cm, 150 cm, and 170 cm, respectively, above ground

Table 4 Genetic correlation (above diagonal) and phenotypic correlation (below diagonal) estimates for rubber yield and girth growth

Trait	Yield (g)	Girth 1 (cm)	Girth 2 (cm)	Girth 3 (cm)	Girth 4 (cm)
Rubber yield (g)		0.639 ± 0.044	0.647 ± 0.043	0.643 ± 0.045	0.636 ± 0.045
Girth 1 (cm)	0.481 ± 0.037		0.990 ± 0.002	0.977 ± 0.004	0.975 ± 0.006
Girth 2 (cm)	0.499 ± 0.037	0.968 ± 0.003		0.979 ± 0.004	0.970 ± 0.005
Girth 3 (cm)	0.491 ± 0.038	0.944 ± 0.006	0.954 ± 0.005		0.981 ± 0.003
Girth 4 (cm)	0.489 ± 0.038	0.921 ± 0.008	0.932 ± 0.007	0.965 ± 0.003	

Values shown as mean $\pm$ SE

Using enhanced prediction techniques like BLUP offers greater selection precision and allows the recording period to be substantially reduced. It is also desirable and critical to choose suitable parents for crossing and such choices have traditionally been made using general and specific combining ability (GCA and SCA, respectively) phenotypic estimates (Omokhafe et al., 2007). Gilbert et al. (1973) were the first to assess the impacts of GCA in rubber trees using an incomplete diallel model. The BLUP method is an even better method because it provides each parent's expected genetic values which is reliable data for accurately selecting parents to cross and this method has been implemented for rubber breeding in Brazil (Costa et al., 2000; 2002). The BLUP method allowed identification for

the selection of potential parental and cross combinations within the current research.

The top-ranked 20 clones, based on estimated breeding values for rubber yield and girth growth compared with RRIM 600, are shown in Tables 5 and 6, respectively. The highest estimated breeding values were 35.41 ± 3.97 g rubber yield (Clone No. 1040) and 8.51 ± 1.07 cm girth growth (Clone No. 1005). The data analyzed indicated that PB260×IAN873 pair of parents had the highest GCA and SCA compared to any of the other parent pairs in the current study and that their combined character traits predicted the best rubber yield and girth growth in their progeny.

Table 5 Ranking of the top 20 clones and RRIM 600 (checked variety) based on their estimated breeding values (EBV $\pm$ SE) for rubber yield

Rank	Clone number	Cross Female $\times$ Male	Ranking based on EBV rubber yield (g)
1	1040	PB260 $\times$ IAN873	35.41 ± 3.97
2	1306	BPM1 $\times$ IAN873	32.31 ± 3.99
3	1005	PB260 $\times$ IAN873	24.63 ± 3.97
4	1176	RRII118 $\times$ IAN873	23.22 ± 4.01
5	1170	RRII118 $\times$ IAN873	23.05 ± 4.01
6	1010	PB260 $\times$ IAN873	18.91 ± 3.96
7	1039	PB260 $\times$ PB260	17.39 ± 3.97
8	1253	IAN873 $\times$ RRII118	17.38 ± 3.98
9	1014	PB260 $\times$ IAN873	17.05 ± 3.96
10	1148	RRII118 $\times$ IAN873	16.96 ± 3.96
11	1303	BPM1 $\times$ IAN873	15.58 ± 4.03
12	1046	PB260 $\times$ IAN873	15.33 ± 4.00
13	1255	IAN873 $\times$ PB260	15.25 ± 3.98
14	1266	BPM1 $\times$ IAN873	14.95 ± 3.99
15	1287	BPM1 $\times$ IAN873	14.78 ± 3.99
16	1167	RRII118 $\times$ PB260	14.59 ± 3.97
17	1336	AVROS2037 $\times$ IAN873	13.78 ± 3.97
18	1250	IAN873 $\times$ PB260	13.67 ± 3.98
19	1188	RRII118 $\times$ PB260	13.34 ± 3.97
20	1246	IAN873 $\times$ PB260	13.25 ± 3.97
RRIM 600			9.70 ± 4.00

Table 6 Ranking of the top 20 clones and RRIM 600 (checked variety) based on their estimated breeding values (EBV $\pm$ SE) for girth growth

Rank	Clone number	Cross Female $\times$ Male	Ranking based on EBV girth (cm)
1	1005	PB260 $\times$ IAN873	8.51 ± 1.07
2	1196	IAN873 $\times$ PB260	7.81 ± 1.08
3	1053	PB260 $\times$ IAN873	7.27 ± 1.07
4	1336	AVROS2037 $\times$ IAN873	6.61 ± 1.08
5	1253	IAN873 $\times$ RRII118	6.57 ± 1.08
6	1040	PB260 $\times$ IAN873	6.29 ± 1.08
7	1230	IAN873 $\times$ RRII118	6.07 ± 1.10
8	1027	PB260 $\times$ IAN873	5.94 ± 1.07
9	1188	RRII118 $\times$ PB260	5.83 ± 1.08
10	1246	IAN873 $\times$ PB260	5.58 ± 1.08
11	1255	IAN873 $\times$ PB260	5.26 ± 1.08
12	1250	IAN873 $\times$ PB260	5.09 ± 1.08
13	1309	BPM1 $\times$ PB260	5.08 ± 1.09
14	1356	AVROS2037 $\times$ RRII118	5.05 ± 1.08
15	1006	PB260 $\times$ IAN873	5.03 ± 1.07
16	1194	IAN873 $\times$ PB260	4.94 ± 1.08
17	1335	AVROS2037 $\times$ IAN873	4.92 ± 1.08
18	1254	IAN873 $\times$ PB260	4.88 ± 1.08
19	1047	PB260 $\times$ IAN873	4.79 ± 1.10
20	1008	PB260 $\times$ IAN873	4.66 ± 1.07
RRIM 600			3.80 ± 1.09

Conflict of Interest

The authors declare that there are no conflicts of interest.

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References

- Costa, R.B., Resende, M.D.V., Araújo, A.J., Gonçalves, P.S., Higa, A.R. 2000. Selection and genetic gain in rubber tree (*Hevea*) populations using a mixed mating system. *Genet. and Mol. Biol.* 23: 671–679. doi.org/10.1590/S1415-47572000000300028
- Costa, R.B., Resende, M.D.V., Gonçalves, P.S., Silva, M.A. 2002. Individual multivariate REML/BLUP in the presence of genotype $\times$ environment interaction in rubber tree (*Hevea*) breeding. *Crop. Breed. Appl. Biot.* 1: 131–140.
- Gilbert, N.E., Dodds, K.S., Subramanian, S. 1973. Progress of breeding investigation with *Hevea*. V. Analysis of data from earlier crosses. *J. Rub. Res. Inst. Mal* 23: 365–380.
- Gilmour, A.R., Cullis, B.R., Welham, S.J., Thompson, R. 2000. ASREML Reference Manual. NSW Agriculture. Sydney, NSW, Australia.
- Gonçalves, P.S., Silva, M.A., Gouvêa, L.R.L., Junior, E.J.S. 2006. Genetic variability for girth growth and rubber yield in *Hevea brasiliensis*. *Sci. Agric.* 63: 246–254. doi.org/10.1590/S0103-90162006000300006
- Gonçalves, P.S., Moraes, M.L.T., Silva, M.A., Gouvêa, L.R.L., Aguiar, A.T.E., Costa, R.B. 2009. Prediction of *Hevea* progeny performance in the presence of genotype-environment interaction. *Braz. Arch. Biol. Tech.* 52: 25–33.
- Gouvêa, L.R.L., Silva, G.A.P., Verardi, C.K., Oliveira, A.L.B., Gonçalves, P.S. 2013. Simultaneous selection of rubber yield and girth growth in young rubber trees. *Ind. Crop. Prod.* 50: 39–43. doi.org/10.1016/j.indcrop.2013.06.040
- Henderson, C.R. 1984. Applications of Linear Models in Animal Breeding. University of Guelph. Ontario, Canada.
- Kinnarat, P., Rattanawong, R. 2002. Improvement of rubber trees. In: Proceedings of the 1st Academic Matter of Rubber Tree Conference, Nongkhai, Thailand, pp. 104–123. [in Thai]
- Lepoittevin, C., Rousseau, J.P., Guillemin, A., Gauvrit, C., Besson, F., Hubert, F., Perez, D.S., Harvenget, L., Plomion, C. 2011. Genetic parameters of growth, straightness and wood chemistry traits in *Pinus pinaster*. *Ann. For. Sci.* 68: 873–884. doi.org/10.1007/s13595-011-0084-0
- Liu, Q., Zhou Z., Fan H., Liu, Y. 2013. Genetic variation and correlation among resin yield, growth, and morphologic traits of *Pinus massoniana*. *Silvae Genet.* 62: 38–44. doi.org/10.1515/sg-2013-0005
- Omokhale, K.O., Akpobome, F.A., Nasiru, I. 2007. Diallel analysis of fruit set in *Hevea brasiliensis* Muell. Arg. *Genet. Mol. Biol.* 30: 428–430. doi.org/10.1590/S1415-47572007000300021
- Pakkanen, A., Nikkanen T., Pulkkinen P. 2000. Annual variation in pollen contamination and outcrossing in a *Picea abies* seed orchard. *Scand. J. For. Res.* 15: 399–404. doi.org/10.1080/028275800750172574
- Pawsoi, N., Phumichai, T., Teerawatanasuk, K., Wongkaew, A., Phumichai, C. 2013. Microsatellite paternity analysis used for evaluation of outcrossing rate among five *Hevea* rubber clones in a systematic seed orchard. *Kasetsart J. Nat. Sci.* 47: 407–415.
- Priyadarshan, P.M. 2011. Biology of *Hevea* Rubber. CABI Publishing. Wallingford, UK.
- Rao, B.S. 1961. Pollination of *Hevea* in Malaya. *J. Rubb. Res. Inst. Malaya.* 17: 14–18.
- Rao, H.X., Patterson, B., Potts, B., Vaillancourt, R. 2008. A microsatellite study on outcrossing rates and contamination in an [*sic*] *Eucalyptus globulus* breeding arboretum. *J. For. Res.* 19: 136–140. doi.org/10.1007/s11676-008-0023-6
- Rubber Authority of Thailand. 2018. Rubber Plantation in Thailand, Rubber Authority of Thailand, Bangkok, Thailand. <http://emarket.raot.co.th/rdu/>, 16 December 2020. [in Thai]
- Sangsing, K., Kasemsap P., Thanisawanyangkura S., Sangkhasila K., Gohet E., Thaler P., Cochard H. 2004. Xylem embolism and stomatal regulation in two rubber clones (*Hevea brasiliensis* Muell. Arg.). *Trees* 18: 109–114. doi.org/10.1007/s00468-003-0286-7
- Silva, G.A.P., Gezan, S.A., Carvalho, M.P., Gouvêa, L.R.L., Verardi, C.K., Oliveira, A.L.B., Gonçalves, P.S. 2014. Genetic parameters in a rubber tree population: Heritability, genotype-by-environment interactions and multi-trait correlations. *Tree. Genet. Genomes.* 10: 1511–1518. doi.org/10.1007/s11295-014-0766-5
- Simmonds, N.W. 1986. Theoretical aspects of synthetic/polycross populations of rubber seedlings. *J. Nat. Rubber Res.* 1: 1–15.
- Souza, A.M.D., Gouvêa, L.R.L., Oliveira, A.L.B., Silva, G.A.P., Gonçalves, P.S. 2017. Estimates of genetic parameters for the rubber yield and secondary traits in rubber tree. *Ind. Crop. Prod.* 98: 19–24. doi.org/10.1016/j.indcrop.2017.01.017
- Tan, H., Subramaniam, S. 1976. A fire-parents diallel cross analysis for certain characters of young *Hevea* seedling. In: Proceedings of the International Rubber Conference RRIM. Kuala Lumpur, Malaysia, pp. 13–16.
- Van Der Werf, J.H.J., De Boer, W. 1989. Estimation of genetic parameters in a crossbred population of black and white dairy cattle. *J. Dairy Sci.* 72: 2615–2623. doi.org/10.3168/jds.S0022-0302(89)79402-9
- Verardi, C.K., Resende, M.D.V., Costa, R.B., Gonçalves, P.S. 2012. Estimation of genetic parameters in rubber progenies. *Crop. Breed. Appl. Biot.* 12: 185–190. doi.org/10.1590/S1984-70332012000300004
- Xu, Y. 2016. Envirotyping for deciphering environmental impacts on crop plants. *Theor. Appl. Genet.* 129: 653–673. doi.org/10.1007/s00122-016-2691-5
- Zhao, X., Hou, W., Zheng, H., Zhang, Z. 2013. Analyses of genotypic variation in white poplar clones at four sites in China. *Silvae Genet.* 62: 187–195. doi.org/10.1515/sg-2013-0023