Heritability and genotypic gain from selection in rubber (Hevea brasiliensis)

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Abstract

Yield improvement of rubber in Nigeria started in the early sixties with the aim of replacing existing low yielding planting materials. Heritability estimates (h^2) for rubber yield, bark thickness, girth size, crown density and stem form were examined from ten bi-parental families. Yield was found to have a moderately low h^2 (0.15) while h^2 for bark thickness was 0.17. Heritabilities for girth and crown density were negligible ($h^2 = -0.103$ and -0.014). A high h^2 estimate (0.608) was obtained for stem form. Selection based on yield superiority was applied using a truncation point of 60g/tree/tapping.

Genotypic progress of 10.87% was realised over the mean of the population in one generation cycle.

Key words: Heritability, Selection differential, genotypic gain, yield (g/tree/tapping).

Zusammenfassung

In den frühen sechziger Jahren wurde in Nigeria ein Projekt begonnen, mit dem Ziel, den Ertrag von *Hevea brasiliensis* durch Züchtung zu verbessern und das vorhandene Pflanzenmaterial mit nur geringem Ertrag zu ersetzen. Hierzu wurden Heritabilitätsschätzungen (h^2) für die Latex-Produktion, die Rindenstärke, den Umfang, die Kronendichte und die Stammform von 10 bi-parentalen Familien durchgeführt.

Für den Ertrag wurde eine mäßige Heritabilität ($h^2 =$ 0,15) gefunden, während h^2 für die Rindendicke 0,17 betrug. Die Heritabilitäten für Umfang und Kronendichte waren unbedeutend ($h^2 = -0{,}103$ und $-0{,}014$). Ein hoher h^2-Schätzwert mit 0,608 wurde für die Stammform erzielt. Die Selektion, die auf der Überlegenheit im Latex-Ertrag basierte, wurde angewendet, indem von einem Minimum von 60g Latex je Baum je Schnittstelle ausgegangen wurde.

Ein Züchtungsfortschritt von 10,87% wurde, bezogen auf das Populationsmittel, in einem Generationszyklus erreicht.

Introduction

Rubber *(Hevea brasiliensis)* is grown in Nigeria primarily as an export crop. Recently about 40% of the total rubber produced in the country was consumed locally. Introduction of genetically improved planting materials was done in the early sixties. The major sources of introductions were Malaysia and Srilanka. The plant introductions were made to be used directly to replace the existing low yielding planting materials and secondly to be used as new breeding stock.

Yield (latex production) is the most economical characteristic of *Hevea* tree. Characters such as bark thickness, girth, canopy density and stem form are of secondary interests. The genetic correlations between yield and the secondary characteristics are very low and make it impossible to select for high yields through the use of the secondary characters. Heritability estimates ($h^2 = 0.11$ to 0.50) have been obtained for yield (Tan *et al.*, 1975; Alika and Onokpise, 1982; Nga and Subramanlam, 1974). In *Hevea* breeding populations the precision in the estimation of h^2 had generally been affected by restricted number of parents, small family sizes and relative absence of genotype × environment interaction effects in the estimates. These inadequacies result in some degree of bias in the h^2 estimate for yield.

Genotypic advance made from a single generation cycle in a breeding programme is important in the measure of success achieved through breeding. Rubber is a forest tree crop and takes above 15 years to complete a breeding cycle. In *Hevea* breeding there is usually a lapse of 2 years from pollination to field planting, a wait of 6—7 years until tapping is started, then a 5—6 year period of tapping and clonal evaluations (Alika, 1980). An enhanced genotypic gain from selection would be profitable in a crop with such longevity cycle. The magnitude of genotypic progress from selection for any trait is however dependent on the amount of h^2 and the selection differential. Tan *et al.* (1975) reported a genetic advance of 2.4 per cycle for yield when 20% selection pressure was applied. Since h^2 for yield is generally low and number of parents and family sizes are considerably limited in most *Hevea* breeding populations family selections and high selection differentials may be an advantage. Goggans and Meir (1973) favoured family selections rather than mass selection where heritabilities are low.

We report here heritability estimates for rubber yield in 5,6 and 7th years of tapping, girth size, bark thickness, stem form and canopy density. Prediction for genotypic gain was examined, for yield, bark thickness and stem form while phenotypic correlations between the secondary characters were presented.

Materials and Method

In the early sixties exotic genetic stock of *Hevea* were introduced and planted at the Rubber Research Institute of Nigeria Mainstation at Benin City. Some of the plantings at full maturity were selected as parents to be used to generate a breeding population. These selected parents were intermated either singly or severally amongst themselves. Mating between parents were achieved through hand pollination. In hand pollination the staminal column of the pollen parent was removed from the male flower and placed on top of the stigma of the female (seed) parent. To avoid the presence of extraneous pollen after pollination the stigma of the female parent was covered with a piece of cotton wool smeared in fresh latex. After fertilization has taken place and pod formation and maturity have been achieved the matured pod was enclosed in a perforated polyethylene bag to avoid loss of the progeny seed through pod dehiscence.

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Table 1. — Form of Analysis of variance.

Source of Variation	d.f.	Mean Squares	Expected Mean Squares
Among families	f-1	MS_f	$\sigma_w^2 + K_1\sigma_f^2$
Within family	n-f	MS_w	σ_w^2
Total	n.-1		

$n. = \sum n_i$ = Total number of individuals in the population

n_i = Number of individuals within the i^{th} family

f = Number of families

K_1 = $(n. - \sum n_i^2/n.)/(f-1)$

σ_f^2 = Genetic variance due to differences between mating pairs

σ_w^2 = Variances due to within family differences

Progeny seeds were harvested and planted in the nursery between 1965 and 1967. After eighteen months the seedlings were disbudded and planted into the field. The plantings were done in single unreplicated plots. At maturity (Seven years after planting) the trees were opened for tapping. Yield (latex production) was collected by tapping the bark of the tree on a half spiral cut and alternate daily. Dry rubber yield was collected twice monthly which gave a total tapping of 22 times in a year. Tapping was not usually done in the month of February. Yield was expressed as g/tree/tapping by dividing the total plot yield for the 22 tapping by the number of tapping in a year and the number of trees per plot. Girth was measured by the use of a steel tape at a height 150 cm from the ground. A metal gauge was used in measuring the bark thickness at the same height. Observation on the shape of tree (Stem form) was made. Generally there is need to select trees that possess very erect stems rather than trees that are leaning considerably to one side. Bent trees are more susceptible to wind breakage than erect stems. Losses of latex during tapping are experienced greatly with leaning trees. In the determination of stem form a 4 - point grading system was used with the highest grade as the most desirable: 4 = very erect, 3 = erect, 2 = bent, 1 = very bent. A similar 4 - point grading scale was used in the determination of canopy density: 4 = very heavy, 3 = heavy, 2 = light, 1 = very light. Canopy size of trees is a necessary characteristic in areas where wind speed is high. Trees with very heavy canopy are more prone to wind damage than light canopy trees. Avoidance of trees with heavy canopy during selection in favour of trees with light to fairly heavy canopies may be desirable to maintain good stands in a plantation.

Genetic and other components of variance for each trait were estimated by equating observed mean squares to their expectations and solving for the components.

In the estimation of variance components, parental crosses that fitted into the single pair mating design (bi-parental) were selected from the entire population. The population contained two genetic components which consisted of:

(a) Components due to differences between the family pairs (σ^2_f) and

(b) Components due to within family differences (σ^2_w). The genetic components and expectations are shown on *Table 1.* The genetic parameters were calculated after imposing two restrictions. The two assumptions in the model were: absence of dominance ($\sigma^2_D = 0$) and no common family environment ($\sigma^2_{Ec} = 0$).

The covariance and causal components were estimated as

$$\sigma_f^2 = \text{Cov (FS)} = \frac{1}{2}\sigma_A^2 + \frac{1}{4}\sigma_D^2 + \sigma_E^2 \text{ and } \sigma_A^2 = 2\sigma_f^2$$

While $$\sigma_w^2 = \sigma_T^2 - \text{Cov (FS)} = \frac{1}{2}\sigma_A^2 + \frac{3}{4}\sigma_D^2 + \sigma_{E_w}^2 \;;$$

$$\sigma_{E_w}^2 = \sigma_w^2 - 2\sigma_f^2 \quad \text{where}$$

σ_A^2 = additive genetic variance ;

σ_D^2 = dominance variance ;

σ_{Ec}^2 = common environmental variance ;

$\sigma_{E_w}^2$ = environmental variance within family members and

σ_T^2 = total population variance.

Heritability on single tree and family mean basis were estimated according to Becker (1975).

$$h^2 = 2\sigma_f^2 / (\sigma_f^2 + \sigma_w^2) \text{ ....(a)}$$

$$h_f^2 = \sigma_f^2 / (\sigma_f^2 + \frac{\sigma_w^2}{k}) \text{ ....(b)}$$

Genotypic gain from selection was calculated as :

$$G_s = i\,\sigma_p\,h^2 \text{ ....(c)}$$

where

i = selection intensity,

σ_p = population standard deviation and

h^2 = heritability

Results

Estimates of heritabilities, additive, environmental and total population variances are shown on *Table 2.*

Variances due to causal agents (σ^2_{Ew}) within family

Table 2. — Heritabilities, additive and environmental variances for dry rubber yield and other quantitative secondary characters of *Hevea.*

Variable	σ_A^2	σ_{Ew}^2	$\sigma_{Ew}^2:\sigma_A^2$	σ_p^2	h^2	h_f^2
Dry rubber yield (g/tree/tapping)						
5th year of tapping	29.020	593.610	20:1	637.140	0.045	0.219
6th year of tapping	56.080	335.920	5:1	420.040	0.133	0.463
7th year of tapping	107.840	695.350	6:1	857.110	0.125	0.447
Mean over 7 years of tapping	33.820	169.200	5:1	219.930	0.150	0.495
Girth (cm)	-21.094	225.902	11:1	204.810	-0.107	-
Renewed bark thickness (cm)						
1st tapping bark panel	0.046	0.194	4:1	0.263	0.177	0.539
2nd tapping bark panel	0.043	0.219	5:1	0.283	0.152	0.498
Stem form	0.148	0.022	0.1:1	0.244	0.608	0.840
Crown density	-0.003	0.290	97:1	0.285	-0.013	-

Table 3. — Genotypic gain from selection based on yield, bark thickness and stem form from a population of 10 bi-parental families.

	Response ($G_s = i\sigma_p h^2$)		
Proportion Selected %	Yield	Bark thickness (Panel A)	Stem form
10	3.82	0.156	0.515
20	3.03	0.122	0.410
30	2.51	0.101	0.388
40	2.07	0.084	0.288

members were found to be moderate - large for all the variables studied except for stem form. Ratios of common environmental variances within the families to additive genetic variance varied from 0.1:1 to 97:1 with the largest ratio occuring in crown density. Ratios between the two genetic parameters were moderate for yield (5:1 to 6:1) except for the 5th year of tapping (20:1) which was the year the tapping panel was changed. The least ratio was obtained for stem form where 60% of the total variation was accounted for by the additive genetic variation. Heritabilities for 5, 6 and 7th year yields were generally low (0.045, 0.133 and 0.125) while h^2 for the mean of seven years was 0.150. The h^2 for mean yield over seven years of tapping was presented in order to obtain a highly representative estimate for dry rubber yield. The low h^2 in the fifth year may be accounted for by changes in the tapping panel of the trees. The h^2 estimates due to family means were 0.219, 0.467 and 0.447 respectively for the 3 years. The h^2 estimates for canopy density and girth size of trees were negative (-0.014 and -0.103). Very high h^2 value was obtained for stem form (0.608) while h^2 for renewed bark thickness of the first and second tapping bark panels respectively were moderately low ($h^2 = 0.177$ and 0.152).

Predicted response per cycle from single trait selection using different selection intensities are presented in *Table 3.* Genotypic advance of 2.07 to 3.82 were obtained for yield over the base population where selection pressures of 40 to 10% were applied. Reasonable genotypic progress over the parental population was found to be present for bark thickness (0.084 to 0.156) and stem form (0.288 to 0.515) respectively.

Genotypic gain from selection for yield was also calculated by:

$$G_s = h^2 S$$

The selection differential (S) was obtained as the difference between the mean of selected parents and the base population, while h^2 was obtained as the ratio of additive genotypic variance to the population variance. A yield truncation point ($\bar{X}_s \geq 60$ g/tree/tapping) was used. At a truncation point of (60 g/tree/tapping), thirteen individuals which approximated 10% selection pressure were selected. The population mean was 39.43 while the mean of select parents was 68 g/tree/tapping. Heritability for yield was as shown previously

$$G_s = (0.15)\ (28.57)$$
$$= 4.3 \text{ g/tree/tapping}$$

when the genotypic gain (4.3 g/tree/tapping) was expressed as percentage over the population mean a genetic response of 10.37% was obtained. The genetic gain (4.3 g/tree/tapping) obtained through the second method $G_s = h^2 S$ was slightly higher than that obtained theoretically $G_s = i\sigma_p h^2 = 3.82$ g/tree/tapping) by the use of the proportion, of individuals selected relative to the total population.

Phenotypic correlations among selected secondary characteristics are shown on *Table 4.* Very weak and sometimes negative correlations exist amongst the secondary characters measured. The relationship between yield and the secondary characters were not calculated because of the already known non-significance between the characters.

Discussion

The h^2 estimate for rubber yield was generally low (0.15), though our reported statistics agreed with TAN *et al.* (1975) who similarly reported a low h^2 of 0.11 for mean yield over 5 years using a N.C. design 1 of COMSTOCK and ROBINSON (1948). In contrast higher h^2 (0.50) were reported by SIMMONDS (1969) and GILBERT *et al.* (1973). The observed relatively low h^2 for yield may indicate a reduction in the genotypic variation in the base population. Though h^2 is specific to the population from which it is derived, a close similarity between our estimate (0.15) and that (0.11) reported by TAN *et al.* (1975) appear to indicate that the existing parental stock of *Hevea* presently in use may have a narrow genetic base. As stated earlier the parental stock used in this study were introduced primarily from Malaysia.

Furthermore, the magnitude of our estimates of additive genetic variance and h^2 values could have an upward bias if the assumptions in the model of absence of dominance variance and no common environment were not true. The contributions of dominance and common environmental variances if present would lead to over-estimation of these statistics. The magnitude of the observed environmental contribution to the total variation and to the mean variation within families represented by σ^2_{Ew} was found to be large and could influence the precision in the estimates of h^2 *(Table 2).* A situation of where family × micro-environment and family × macro-environment become inseparable from the estimate of σ^2_f some degree of caution has to be exercised in the interpretation of the estimates. In addition, the precision of our estimates may also have been affected by the restriction in the number of parents and their dimunitive family sizes. These restrictions in family sizes may lead to higher risks of loosing favourable

Table 4. — Phenotypic correlations between certain secondary characters in *Hevea*.

	Renewed Bark (Panel B)	Stem form	Crown size
Renewed Bark (Panel A)	0.422*	0.167	-0.01
Renewed Bark (Panel B)	-	0.272	0.147
Stem form	-	-	-0.027

D.F. = 128 * Significant at 5% probability level.

alleles and consequently result in excessive inbreeding depression or both.

Attempts at further encouraging in-breeding in *Hevea* with its already known narrow genetic base will result in further reduction of genotypic progress from selection. Efforts should be geared towards using large number of parents to generate new breeding populations. Genotypic progress may be improved further by the use of bi-parental mating design in order to generate large genotypic variation from which selection could be further practised. The differences between the h^2 on individual tree and family mean basis seriously indicate a reduction in the potential genetic gains expected from mass selection. Since family h^2 showed more potential, emphasis should be shifted to family selections rather than mass selection. Use of family selections as of now is seriously complicated by the reduced number of possible parents involved in the inter-matings. ROBERTS *et al.* (1980) emphasized that loss of a large number of families can severely limit breeding progress in future generations and most especially if the number of families in the breeding populations is small.

Efforts therefore, should be made to incorporate all useful alleles in the base population and effective population sizes should be kept large enough that they may be expected to advance.

Genotypic variations for girth size and density of canopy were found to be negligible (-0.103 and -0.014). Theoretically, negative h^2 does not exist. The presence of negative h^2 is generally due to sampling error arising from serious reductions in the total number of observations (ROBINSON *et al.*, 1955; BOGYO, 1964; GILL and JENSEN, 1968). Negative and non-significant relationship is known to exist between yield and girth (ALIKA, 1980). Continuous selection for high yielding trees could have led to a highly uniform size of trees and resulting therefore, in negligible genotypic variation for the character in a breeding population. Expected genetic progress can not be achieved for girth and canopy size where $h^2 \leqq 0$. Genotypic variation was found to be very high for stem size while very low for bark thickness. The use of clonal planting rather than seedlings must have contributed immensely in the reduction of variation for bark thickness. Effective selection progress would be made through family selection rather than mass. Conversely genotypic gains would be high through the use of mass selection for stem form character.

Predicted responses per cycle from single trait selection using 10 to 40% selection pressured were calculated *(Table 3)*. Reasonable genotypic progress could be made from one cycle of generation for the characters studied. Where future parents were selected ($\bar{X}_s \geqq 60$ g/tree/tapping) we obtained a genotypic progress of 10.87%. However, when this genotypic advance is weighed over time (15 years of a generation cycle) and expense a higher genotypic progress would be advocated. Secondly, we do know that when genotypes are tested at only one location as it is the case in our study the genotype $\times$ environment interaction remain inseparable and where this effect is large genotypic gain may be over estimated. Though, the predicted response obtained did not take account of a possible genotype $\times$ environment interaction which may result in the inflation of h^2 estimates, rubber improvement in Nigeria has some reasonable promise. The interpretation of the observed genotypic gain should however, be made with some degree of caution. Phenotypic correlations did not indicate any strong relationships between the characters studied. Selection through the use of correlated response is not possible for any of the characters. Significant correlations between bark thickness (Panel A and B) is understandable. Every character appear to have independent relationship with the other.

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