Parent-Offspring Relationships in Apomictic Guayule

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The genetic base of guayule (*Parthenium argentatum* Gray) germ plasm that is available is narrow; yet, significant variability has been described within this germ plasm. This variability is surprising because guayule reproduces by facultative apomixis (asexual reproduction by seed), but evidence suggests that progress through selection is feasible. It has been hypothesized that this variation has arisen through periodic sexual reproduction; however, this has not been quantified. This study was designed to describe and compare eight components of yield and the expression of two isozyme systems in twenty parent plants and half-sib, open-pollinated families from each parent. Extensive variation for all characters was found among both the parents and the progeny, with fresh and dry weights being highly correlated to rubber yield. Parent–offspring regressions were not significantly different from zero. This implies low heritabilities for the major components of yield in guayule, and we believe that family selection, rather than single-plant selection, may generate higher-yielding and more genetically uniform lines at an escalated rate than single-plant selection. Periodic sexuality resulting in genetic variation was estimated by differences in isozyme expression within the half-sib families. Fifteen of the twenty progeny families were polymorphic for either esterase or peroxidase or both isozymes. This amount of sexuality is significant, and guayule must be considered an open-pollinated crop. We conclude from this study that we should rethink our breeding procedures to include controlled pollination and family selection.

KEY WORDS: Components of yield, esterase, facultative apomixis, family selection, genetic variation, heritability, isozyme polymorphisms, parent-offspring regressions, *Parthenium argentatum*, peroxidase.

Guayule (*Parthenium argentatum* Gray, Asteraceae) is a rubber-producing, small woody perennial shrub native to the Chihuahuan desert region of north-central Mexico and southwest Texas. The United States is totally dependent upon imports of natural rubber at an annual cost of nearly one billion dollars (1). Guayule also produces significant amounts of resins, bagasse and waxes that may generate the additional revenues necessary to make guayule commercialization successful (1,2).

Successful commercialization of guayule depends upon the development of higher-yielding lines. Early breeding efforts were relatively ineffective due in part to the small number of individuals involved in guayule breeding, but mainly due to the lack of knowledge about guayule's rather complicated reproductive biology.

Guayule contains a natural polyploid series with chromosome numbers ranging from $2n = 36$ (diploid) to $8n = 144$ (octaploid). In addition, guayule populations contain many aneuploid plants, and plants with up to five B-, or accessory, chromosomes. Diploid plants reproduce sexually, but are self-incompatible, forcing outcrossing. Polyploid plants reproduce predominantly by apomixis (asexual reproduction by seed); however, fertilization and meiotic reduction do occur. Apomixis in guayule is environmentally influenced and has been shown to be of genetic origin and not a product of ploidy level (1).

A great deal of variability for rubber and plant growth characteristics that are major components of yield have been described in guayule (3,4). This is the result of the facultative nature of apomixis, with various levels of sexuality and apomixis being expressed both within and between plants (5). The facultative nature of apomixis in guayule allows for the periodic release of variability that can be exploited by breeders. Variability is the basis upon which breeding programs are built, and the high amount of variability existing among and within guayule lines indicates that significant yield progress through selection is feasible (3,4).

Selection in guayule has been significantly aided by the description of the major components of yield and their relationship to rubber production (3,6). In general, rubber content (%) was not found to be highly correlated with rubber yield, and in fact there was often a negative correlation. Fresh and dry plant weights, as well as other characters related to biomass production, were highly and consistently correlated to rubber yield (3,6). The characters shown to be the best predictors of rubber content were plant fresh and dry weights, percent dry weight and plant volume. The best predictive model for rubber yield includes plant height and width, volume and dry weight (6).

With a better understanding of guayule's reproductive biology and the relationships among its major components of yield, significant increases in yield have been realized through single-plant selection (1,2,7,8). However, progress has not been as dramatic as expected. We hypothesize that this is due to our inability to control the variability generated during seed production because of the facultative nature of apomixis.

The purpose of this study was to test the relatedness of parents and their open-pollinated, half-sib progeny families for eight major components of yield and two isozyme systems. By measuring the components of yield in both the parents and their progeny, heritability estimates may be made. Isozymes are well described genetically and are not influenced by environmental factors (2). Thus, variation in either isozyme banding patterns or intensity of bands allows us to estimate the amount of outcrossing and meiotic reduction that occurs in seed production.

EXPERIMENTAL PROCEDURES

All parents and progeny in this study are descendants from single-plant selections from Dr. D.D. Rubis. Open-pollinated seeds of selection 1388 (Generation 1) were planted at Marana, Arizona, in 1982. These progeny rows were evaluated in 1986 by Drs. D.A. Dierig, A.E. Thompson and D.T. Ray, and open-pollinated seed from six selections (N6-2, N6-3, N6-4, N6-5, N7-2 and N7-3; Generation

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2) were planted in progeny rows in 1988 at Maricopa, Arizona. Open-pollinated seed was collected from individual plants in each progeny row, and these are the twenty parents (Generation 3) in the present study: N6-2-2, N6-2-4, N6-2-16; N6-3-3, N6-3-4, N6-3-5, N6-3-7; N6-4-1, N6-4-3, N6-4-5, N6-4-6; N6-5-9, N6-5-11; N7-2-5, N7-2-7, N7-2-11, N7-2-16; N7-3-3, N7-3-7, N7-3-12. These seeds were planted in progeny rows in 1989 at Maricopa, Arizona, and each progeny row was considered a family of progeny (Generation 4).

The twenty parent plants (3-year-old), and six plants from each family of progeny (2-year-old) were evaluated for rubber content (%), resin content (%), rubber yield (g/plant), fresh weight (kg/plant), dry weight (kg/plant), dry weight percent, height (cm) and width (cm) in 1991, as previously described (3,4,6). Analysis of variance and linear regression were performed with Statistical Analysis System (SAS) software for analysis. Isozyme analyses for esterase and peroxidase were performed by standard procedures (2).

RESULTS

The means of the twenty parent plants and the 120 progeny plants of the combined families are presented in Table 1. For six of the eight characters the means of the progeny are lower than the means of the parent plants. Four of the eight parent-progeny regressions are negative, although none were significantly different from zero.

A large range of phenotypic expression was observed for the eight components of yield in both the parents and the progeny (Table 1). However, for all characters, the range and SD of phenotypic expression were greater among the parents than among the progeny. This was probably due to the difference in age between the parents (3-year-old stand) and the progeny families (2-year-old stand), and not a difference in genetic variability.

Linear correlation was performed to study the relationship between rubber yield and the 7 other characters (Table 2). In both the parents and progeny, fresh and dry weights were highly and positively correlated with rubber yield. Rubber content in the progeny and plant width and height in the parents were also correlated with rubber yield.

Isozyme polymorphisms were observed among the six progeny in fifteen of the twenty families (Table 3). Five families expressed polymorphism for esterase, another five families were polymorphic only in their expression of peroxidase and five additional families were polymorphic for both esterase and peroxidase. Thus, only five families of progeny did not express variation in their isozyme banding patterns for these two isozymes. Seven of the twenty parent plants have been characterized for expression of these two isozymes (data not presented). In four of the seven parent plants, there were differences in the isozyme banding patterns between the parent and some of their six progeny in the expression of either esterase or peroxidase. This is an indication that either meiotic reduction or fertilization took place in the seed production.

DISCUSSION

Variation for characters that are major components of yield in guayule has been reported previously (1–6). Thus, the variation we observed for these characters was not surprising. Also, the relationships among the yield components are similar to those previously reported (3,6). These data indicate that there is a significant amount of variation in guayule, and we believe it is derived from the facultative nature of apomixis (5).

We surmise that the high amount of variability observed in these populations suggests that significant progress through selection is feasible (1–7). Selection in guayule to date is almost exclusively by single-plant selection (1,2). In single-plant selection, individuals are measured for the desired character, and the best plants are chosen as parents. Since guayule was reported to reproduce by apomixis, in almost all cases open-pollinated seed from selected plants was used to produce the next generation. Selection of individual plants is usually the simplest and most rapid method when heritabilities for desired characters are high. That progress has been made through single-plant selections in guayule has been shown in both the Arizona and California breeding programs (2,8,9).

Parent–progeny regressions were not significant, suggesting that heritability for these characters is low. Heritabilities have not been previously reported in guayule, and our data help explain why progress has not always been as rapid as expected. In cases of low heritabilities, single-plant selection is significantly less effective than family selection. In family selection, whole families of progeny, either full-sibs or half-sibs, are used to evaluate the parents. Parents are not selected on their own merits, but on those of their progeny.

A significant amount of variation was also reported for the tested isozymes. This indicates that much of the

TABLE 1

Comparison of Twenty Parents and the Resulting Half-Sib Families of Progeny for the Major Yield Components in Guayule

Yield component	Parents		Progeny		Parent–Progeny Regression (P)[b]
	Mean ± SD[a]	Range	Mean ± SD	Range	
Rubber yield (g/plant)	34.5 ± 28.3	1.0–112.0	32.7 ± 8.8	20.8–52.7	−0.336 (0.15)
Rubber content (%)	7.4 ± 1.0	4.8–9.1	7.5 ± 0.6	6.4–8.3	−0.423 (0.22)
Resin content (%)	8.4 ± 0.8	7.0–9.8	8.2 ± 0.4	7.3–8.6	0.047 (0.84)
Fresh weight (g/plant)	667.0 ± 541.0	20.0–2260.0	646.0 ± 143.0	475.0–995.0	0.293 (0.22)
Dry weight (g/plant)	421.0 ± 281.0	10.0–850.0	429.0 ± 99.0	308.0–665.0	−0.192 (0.42
Dry weight (%)	69.6 ± 2.9	65.0–74.0	67.0 ± 1.3	64.2–69.2	0.065 (0.79)
Height (cm)	57.0 ± 17.0	26.0–80.0	52.0 ± 8.0	40.0–74.0	−0.084 (0.73)
Width (cm)	58.0 ± 23.0	15.0–95.0	50.0 ± 7.0	39.0–70.0	0.144 (0.54)

[a]SD = standard deviation. [b]P = probability, or level of significance.

observed variation for the eight components of yield is genetic. This variation can arise either from fertilization or meiotic reduction (5). Although not reported in this paper, this variability in the isozyme banding patterns approaches 20%. This high rate suggests that guayule must be considered a partially cross-pollinated crop, and if we want to produce more uniform lines, pollination must be controlled.

From this study we have shown significant variation for yield components in guayule, but without significant correlation between parents and progeny. This suggests that another breeding scheme would be more efficient than single-plant selections. The best breeding scheme for characters with low heritabilities is family selection. The disadvantage of this method is the much-lengthened generation interval. However, because guayule is a perennial plant, we can obtain many generations of progeny from a single parent.

TABLE 2

Linear Correlation of Yield Components[a]

Yield components	Correlation (r) with rubber yield for the parents (P)[b]	Correlation (r) with rubber yield for the progeny families (P)
Rubber content	0.287 (0.219)	0.676 (0.001)
Resin content	−0.133 (0.577)	−0.136 (0.567)
Fresh weight	0.988 (0.0001)	0.960 (0.0001)
Dry weight	0.895 (0.0001)	0.966 (0.0001)
Dry weight percent	0.111 (0.642)	0.264 (0.261)
Height	0.640 (0.0024)	0.274 (0.243)
Width	0.863 (0.0001)	0.081 (0.733)

[a] In twenty parent plants to rubber yield in the parents and in the twenty half-sib progeny families to the rubber yield of the progeny families.

[b] P = probability.

TABLE 3

Variation for Isozymes, Esterase and Peroxidase, Within Six Plant Families of Progeny from Twenty Closely Related Parents[a]

Progeny family[b]	Esterase	Peroxidase	Progeny family[b]	Esterase	Peroxidase
N6-2-2	+[c]	+	N6-4-6	−	+
N6-2-4	−[d]	+	N6-5-9	−	−
N6-2-16	−	+	N6-5-11	−	−
N6-3-3	+	−	N7-2-5	+	+
N6-3-4	+	+	N7-2-7	−	+
N6-3-5	+	+	N7-2-11	−	−
N6-3-7	−	+	N7-2-16	+	−
N6-4-1	+	−	N7-3-3	+	+
N6-4-3	−	−	N7-3-7	+	[e]
N6-4-5	−	−	N7-3-20	+	[e]

[a] Each family is derived from open-pollinated seed, and six individual plants were chosen at random for isozyme analyses.

[b] Parent number from which progeny were derived.

[c] + = Variation for isozyme expression within the six-plant half-sib family. At least one of the six progeny has a different isozymic banding pattern.

[d] − = No variation for isozyme expression within the six-plant half-sib family.

[e] Data not complete.

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