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Studies on the inheritance of flowering in sugarcane*

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Summary. Inheritance of first, maximum and average flowering date and percent flowering was investigated in sugarcane crosses involving early, mid, and late flowering parents in all possible combinations. Parental and F_1 progeny data were taken on plant crops in 1983 and 1984 and a ratoon crop in 1985. Individuals in 1984 and 1985 were clones of the genotypes used in 1983. Heritabilities within years ranged between 0 and 0.3, indicating only moderate additive genetic variance. Approximately 30% to 50% of the observed variation could be attributed to genetic sources as measured by repeatability estimates. Contribution of female parents was more important than male parents, indicating an important role for cytoplasmic effects in flowering response. Heritabilities based on females were substantially larger than corresponding male estimates. Progeny flowered less frequently and later than parents, suggesting that early, frequent flowering depended on specific gene combinations which were lost during crossing.

Key words: Heritability – Repeatability – Cytoplasmic effects

Introduction

Flowering is essential for the production of improved varieties of sugarcane through crossing, but is detrimental in commercial varieties as yield reductions result. Within *Saccharum,* a broad range in flowering dates can be found. With photoperiod manipulation, however, it is possible to induce flowering in virtually all varieties, and much use is made of this technique to synchronize flowering and achieve desirable crosses. Breeders thus could select against natural flowering in the field, but still make desired crosses through induced flowering.

While there are studies that address inheritance of flowering in sugarcane, there is some disagreement. Heritabilities reported for percent flowering on a replicated plot mean basis were 0.94 (Hogarth 1971) and 0.92 (Lyrene 1977). But Hogarth (1971) in a companion experiment estimated heritability to be 0.24 and Lyrene (1977) reported male parent offspring regression heritability estimates of 0.45 and 0.46. Regression on female parent gave estimates of 0.63 and 0.81, perhaps indicating cytoplasmic effects. Heritability for flowering date estimated by parent offspring regression was greater than 1.0 (Roach 1968). These reports were all based on one year of plant cane data. Lyrene (1977) pointed out this weakness and suggested the need for studies of repeatability of flowering.

Concerning the behavior of crosses, Loh (1956) reported that flowering parents crossed with non-flowering parents generally resulted in non-flowering offspring. But Stevenson (1965) stated that flowering was a dominant character in sugarcane. Roach (1968) also found flowering percentages in offspring which exceeded mid-parent values. The results of Loh were based on commercial hybrids while the latter two reports used species crosses. This may explain the differing results. Roach (1968) also presented data showing flowering dates of crosses were similar to mid-parent values, supporting additive inheritance.

Flowering, as measured by date and frequency, is obviously genetically controlled, but further work

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seems warranted. This paper reports the results of a three year study on the inheritance of flowering in sugarcane.

Materials and methods

From previous histories of flowering behavior, parents with early (E), mid (M) and late (L) flowering were identified from the breeding population at the Sugarcane Field Station, Canal Point, Florida. Crosses involving all possible biparental combinations of E, M, and L parents were used for this study. Cross type and number of F_1 progeny in each cross are reported in Table 1. The progenies of the crosses had been selected for agronomic type only. No direct selection pressure had been exerted for flowering, brix, or pith.

In September 1982, all progeny of each cross were planted in plots 1.6 m long and 1.6 m apart within rows which were separated by 1.6 m. Field notes on flowering were taken three times at 10-day intervals in December 1983. Total stalks in each clonal plot and the number of stalks that flowered in each 10-day period were recorded. During the last round of observations on flowering, all stalks in early or late boot-stage were considered as flowering.

The above experiment was repeated in December 1983 using clones of twenty progeny selected at random from each cross and planted in a randomized block design with three replications. For cross numbers 80-452 and 79-385 twenty progeny were not available, so all 17 and 7 clones, respectively, were planted. Each replication included parental clones. In each replication, two stalks from the selected progeny were cut into three-bud sets and planted in rows 1.6 m apart with a 1 m plot length and 1.6 m between plots within a row. The experimental area was bordered with a commercial sugarcane variety. Data were collected as described above in December 1984 on this plant cane, and again in December 1985 on the stubble crop (a vegetative clone) from this planting.

A rating scale of 1 to 4 was used to designate the date of flowering for each stalk in the study. Stalks which flowered during the first 10 days of December were assigned $v_1 = 1$; those which flowered during the next 10 days, i.e. from December 11 to 20, were assigned $v_2 = 2$; those which flowered during the last 10 days of December were rated $v_3 = 3$; and those which did not flower by the end of December were rated $v_4 = 4$. For each individual (clonal plot), consisting of a total of N stalks, average flowering date was calculated using $\Sigma s_i v_i / N$, where s_i is the number of stalks flowering on the i^{th} date. First flowering date was the value of the first stalk to flower and maximum flowering date was the value when the largest number of stalks flowered. Percent flowering was simply $100 * \Sigma s_i / N$.

The plant crop data (1983 and 1984) were combined for analysis of variance to measure genotype-year interactions. Block variation was preadjusted out of the 1984 data before combining with the 1983 data. The ratoon crop of 1985 was analyzed as a randomized complete block design.

For the genetic analysis standard assumptions were made, diploid inheritance (sugarcane is actually an irregular polyploid though bivalent segregation may predominate, Hogarth 1971), parents are a representative sample from a random mating population, and no epistasis. Estimates of variance components due to females (σ_f^2) and males nested within females ($\sigma_{m(f)}^2$) were derived from the analysis of variance by equating mean squares with their expectations (Becker 1984).

Table 1. Description of material used in the experiment

Cross no.	Type of cross[a]	Maternal parent	Paternal parent	No. of clones[b]
80-410	E×E	CP68-1067	× CP77-403	43
80-58	E×M	CP68-1067	× CP76-1053	42
78-143	E×L	CP68-1067	× CP71-1240	163
80-452	M×E	CP72-1210	× CP75-1632	21
78-815	M×M	CP72-1210	× CP70-1133	20
78-583	M×L	CP72-1210	× CP74-2005	66
79-385	L×E	CP75-1553	× CP75-1082	8
79-483	L×M	CP75-1553	× CP70-1133	42
79-351	L×L	CP75-1553	× CP72-1370	33

[a] E = early, M = mid, and L = late flowering type
[b] Number used in 1983. For 1984 and 1985, a maximum of 20 clones were used

Assuming additive (V_A), dominance (V_D), and maternal (V_M) genetic variances, these variance components have expectations

$4\sigma_{m(f)}^2 = V_A + V_D$ and $4\sigma_f^2 = V_A + 4V_M$.

The total genetic variance (V_G) was obtained by adding female and male variance components as shown, with expectation

$4\sigma_{m(f)}^2 + \sigma_f^2 = 1.25\,V_A + V_M + V_D$.

Total phenotypic variance (V_P) was calculated as the sum of all variance components, including interactions with years or reps but excluding the major environmental differences due to the main effects of years and reps.

Estimates of narrow-sense heritability ($h^2 = V_A/V_P$) were obtained from female and male variance components, biased as indicated by the expectations above, and broad-sense heritability (g^2) was estimated by V_G/V_P (Falconer 1981). Since parental information was available, h^2 was also estimated from regression of mean offspring on male and female parental means. Regression estimates based on the male parent are not biased by V_D, but the female estimates are still biased by V_M. Broadsense heritability was also estimated from a repeatability analysis in which the variation due to years and reps was removed, and then the variance between individuals (crosses and clones) was compared to the variance within.

Results

Means for two representative traits are given in Table 2, along with the dominance ratio. Parental values show that the average flowering date for E parents was between 1.1 and 2.2, M parents ranged between 1.3 and 2.6, and L parents averaged 2.4 to 4.0. Progeny means did not show such a clear cut pattern, but using the dominance ratio helped clarify progeny response. Dominance ratios greater than 100 indicate that the offspring value lies outside of the parental range. This happened frequently. Also since most of the dominance ratios were positive, the progeny flowered later than the midparent mean.

Table 2. Mean performance of genotypes in the three years of the study. Average flowering date is used to illustrate the flowering time variables which all had similar patterns

Cross[a]	Average flowering date				Percent flowering			
	Female	Male	Progeny	DR[b]	Female	Male	Progeny	DR
1983								
E×E	1.5	1.4	2.6	4,580	69	85	29	−600
E×M	1.5	2.4	3.0	224	69	23	16	−130
E×L	1.5	4.0	2.7	−3	69	0	21	−39
M×E	2.3	1.4	2.9	234	37	72	32	−129
M×M	2.3	2.2	2.6	1,900	37	33	18	−850
M×L	2.3	4.0	3.4	25	37	0	12	−35
L×E	4.0	1.9	2.6	−41	0	83	35	−16
L×M	4.0	2.2	3.2	14	0	33	11	−33
L×L	4.0	4.0	3.2	–	0	0	12	–
1984								
E×E	2.3	1.1	2.0	49	87	97	58	−680
E×M	2.3	2.6	2.6	84	87	30	43	−54
E×L	2.3	4.0	2.1	−118	87	0	57	31
M×E	2.5	1.6	2.9	170	40	86	29	−148
M×M	2.5	1.6	2.9	185	40	78	24	−184
M×L	2.5	4.0	3.1	−17	40	0	23	15
L×E	3.7	2.2	3.8	124	8	78	3	−114
L×M	3.7	1.6	3.4	70	8	78	14	−83
L×L	3.7	4.0	3.3	−330	8	0	16	300
1985								
E×E	1.1	1.1	2.2	4,140	96	100	52	−2,300
E×M	1.1	1.8	2.3	258	96	72	40	−367
E×L	1.1	3.0	2.2	13	96	24	46	−39
M×E	2.2	1.2	2.5	150	48	89	44	−120
M×M	2.2	1.3	3.1	311	48	80	27	−231
M×L	2.2	3.0	3.2	138	48	37	21	−391
L×E	2.4	1.5	2.7	158	45	93	34	−146
L×M	2.4	1.3	3.4	291	45	80	14	−277
L×L	2.4	3.0	3.3	193	45	37	19	−550

[a] E = early, M = mid and L = late

[b] Dominance ratio percent = $\frac{100\,(\text{Progeny}-(\text{female}+\text{male})/2)}{|\,\text{female}-\text{male}\,|/2}$

Percent flowering gives a similar picture if it is realized that later average flowering dates result in decreased percent flowering. Since the offspring flowered later, their percent flowering was less than parental values. The large negative dominance ratios show that offspring percent flowering was generally less than the smallest parental mean.

In the combined plant crop analysis, female line was the predominant source of variation, and interactions with year were also significant (Table 3). Progeny means in Table 2 suggest that the interaction is due to the E female line's progeny flowering earlier and more frequently in 1984, while the progeny with L mothers flowered later and less frequently as compared to 1983. This divergence in response results in an

Table 3. Analysis of variance for the 1983 and 1984 plant crops

Source	df	Mean squares			
		Flowering date			Percent flowering
		First	Maximum	Average	
Years	1	43.25	17.43	8.65	5.278
Female	2	78.23**	67.68**	56.11**	4.924**
Male (female)	6	5.62	5.17	4.18	0.283
Year * female	2	22.70*	17.02*	11.55*	2.093**
Year * male (female)	6	3.95*	2.12	1.78	0.171*
Error	912	1.459	1.358	1.162	0.072

* $P<0.05$; ** $P<0.01$

interaction. Male parents explained little of the variation, though there was some suggestion of interaction with years.

In the ratoon crop of 1985 (Table 4), females were again the major source of variation as indicated by the magnitude of mean squares, but males were a significant source of variation as well. In Table 2, comparing the progeny means for the three male lines within a female line, a trend is clear for offspring of E males to flower earlier and more frequently than L male offspring in 1985. No such trend is seen for 1983 and 1984.

These analyses of variance were used to estimate variance components needed for heritabilities (Table 5). Since females were the most important source of variation, it is not surprising that heritability estimates based on the female variance component were larger than those based on male within female. Female estimates are biased by maternal or cytoplasmic effects, which the results clearly suggest are important. Thus most emphasis should be placed on estimates based on male variance, though these are biased by dominance variance if present. The results show small heritability in 1983, but moderate heritabilities from 1984 and 1985 results.

Broad sense heritability is of interest in sugarcane since cloning is standard practice, enabling the entire genotype to be transmitted. This heritability was small in 1983, but 1984 and 1985 results suggested that genetic variation could explain 50% of the variation present. The higher heritabilities of 1984 and 1985 are presumably due to the replicated design used, though block variation was small.

Narrow sense heritabilities estimated from parent offspring regression are also given in Table 5. This method of estimation was used to provide a comparison with the variance component analysis and because the standard errors are generally smaller. Estimates based on female parental values were again much larger than male estimates, clearly indicated a substantial contribution from cytoplasmic effects. The male estimates were small for both plant crops, and only in the 1985 ratoon crop was heritability significantly different from zero.

Table 4. Analysis of variance for the 1985 ratoon crop

Source	df	Mean squares			
		Flowering date			Percent flowering
		First	Maximum	Average	
Rep	2	1.66	1.89	0.99	0.080
Female	2	67.34*	63.85*	45.74*	2.985*
Male (female)	6	7.44***	6.21***	4.22***	0.444***
Rep * male (female)	16	0.19	0.24	0.08	0.033
Error	465	1.51	1.24	0.82	0.062

* $P<0.05$; *** $P<0.001$

Table 5. Heritability (h^2) etimates from analysis of variance and parent-offspring regression and degree of genetic determination (g^2)

Trait[a]	Analysis of variance			Parent-offspring regression	
	h^2_F[b]	h^2_M[c]	g^2	h^2_F	h^2_M
1983					
DOFF	0.07 (0.11)[d]	0.08 (0.09)	0.10 (0.09)	0.28 (0.11)	0.14 (0.10)
DOMF	0.11 (0.11)	0.02 (0.06)	0.05 (0.06)	0.29 (0.11)	0.06 (0.10)
AFD	0.10 (0.12)	0.05 (0.08)	0.07 (0.08)	0.35 (0.13)	0.08 (0.12)
PTF	−0.03 (0.10)	0.22 (0.16)	0.21 (0.14)	0.24 (0.10)	0.27 (0.09)
1984					
DOFF	1.20 (0.95)	0.18 (0.15)	0.48 (0.34)	1.16 (0.10)	−0.04 (0.08)
DOMF	1.16 (0.90)	0.19 (0.15)	0.48 (0.35)	1.28 (0.16)	0.08 (0.08)
AFD	1.24 (0.95)	0.17 (0.14)	0.48 (0.43)	1.42 (0.13)	0.10 (0.08)
PTF	1.44 (1.00)	0.08 (0.24)	0.41 (0.27)	1.01 (0.07)	−0.01 (0.07)
1985					
DOFF	0.75 (0.65)	0.28 (0.16)	0.47 (0.24)	–	0.25 (0.12)
DOMF	0.86 (0.75)	0.27 (0.16)	0.49 (0.27)	1.14 (0.11)	0.15 (0.12)
AFD	0.91 (0.87)	0.28 (0.17)	0.51 (0.34)	1.52 (0.14)	0.20 (0.11)
PTF	0.73 (0.62)	0.37 (0.20)	0.55 (0.24)	0.87 (0.10)	0.27 (0.09)

[a] DOFF = date of first flowering, DOMF = date of maximum flowering, AFD = average flowering date, PTF = percent flowering
[b] Based on female parental information
[c] Based on male parental information
[d] SE

Table 6. Repeatability of flowering behavior over three years

Source	df	Mean squares			
		Flowering date			Percent flowering
		First	Maximum	Average	
Year	2	10.26	2.53	0.78	0.71
Rep (Year)	4	1.43	1.28	0.71	0.06
Clone (Cross)	163	5.15	4.52	3.33	0.27
Error	978	1.14	0.96	0.72	0.06
Repeatability		0.34	0.35	0.34	0.34
SE		0.06	0.07	0.08	0.06

Table 6 gives a repeatability analysis based on the fact that up to 20 progeny from each cross were clonally propagated in 1984 and 1985. Thus three measurements are available for these individuals. The results are consistent with Table 5 if an average is taken of the three estimates given there. Since estimates in Table 6 have smaller standard errors and are based on repeated measures of the same individual, these can be viewed with more confidence that the variance component based g^2 in Table 5.

Discussion

The first question in studying flowering is how to measure the date of flowering. First, maximum and average flowering dates were calculated to see if any differences existed, which might be expected if flowering had a skewed distribution. In general, analyses of variance and heritabilities showed similar responses for these traits. Any of these variables could be used in practice as a measure of flowering date. Percent flowering is a standard measure of frequency, and along with date of flowering completely describes the flowering response.

Flowering response was found to be genetically influenced, with up to 50% of the variation observed attributable to genetic sources. It would be possible in sugarcane to make genetic progress by selecting among individuals and clonally propagating the genotypes. The influence of genotype across years can be assessed in Table 2 by the quite consistent difference among the parental values.

Breaking this genetic variance into the usual additive, dominance and maternal (cytoplasmic) components, within the limitations of the data, clearly showed the large contribution from cytoplasmic effects. Lyrene (1977) also found a difference between regressions on male and female parental means. Cytoplasmic contributions to other traits in sugarcane have been discussed by Natarajan et al. (1967) and Raghavan (1951).

Additive genetic variance had a smaller contribution to flowering response, as measured by male heritabilities. Estimates from the analysis of variance are biased by dominance, but the male parent offspring regressions are unbiased. Only the ratoon crop of 1985 showed enough additive variance to support a typical genetic selection program. Unfortunately only one year of data is available for the ratoon crop, so the greater additive variance in 1985 could be a year effect or could be due to ratooning. Other authors have reported much higher heritabilities (Roach 1968; Hogarth 1971; Lyrene 1977), but these estimates either were based on replicated plot means or on crosses between species, possibly leading to larger apparent genetic variance.

The role of dominance variance can only be inferred from the present data. Difference between analysis of variance and regression based estimates of heritability would suggest the presence of dominance variance. Only the 1984 data suggested any differences, but the large standard errors make any firm conclusions difficult. Comparing progeny means to mid-parental values with the dominance ratio produced more striking evidence for non-additivity. The progeny generally performed quite differently from the parents, showing later than expected flowering dates and reduced flowering frequency. Loh (1956) also found non-flowering to be dominant and Lyrene (1977) reported reduced flowering in F_1 progeny compared to their parents.

A plausible explanation for these results is that early and frequent flowering in the lines used in this study depends on a particular combination of genes, possibly involving the cytoplasm in some way. Upon crossing, the necessary combination is lost, decreasing flowering response. This suggests that early response lines used here have different genetic mechanisms which are not complementary upon crossing, since E × E crosses gave reduced flowering.

The results demonstrate an easy approach towards reducing flowering in commercial varieties. All that needs to be done is use a late flowering female in the crossing program. Progeny with commercially valuable characteristics in other traits which also show several years of low flowering response can be clonally propogated to form a new line, with the asssurance that the flowering response will be repeatable.

References

Becker WA (1984) Manual of quantitative genetics, 4th edn. Academic Enterprises, Pullman, Washington

Falconer DS (1981) Introduction to quantitative genetics, 2nd edn. Longman, New York

Hogarth DM (1971) Quantitative inheritance studies in sugarcane. 1. Estimation of variance components. Aust J Agric Res 22:93–103

Loh CS (1956) The advance of sugarcane breeding in Taiwan. The development of P. T. seedlings. Proc ISSCT 9 (1): 638–652

Lyrene PM (1977) Heritability of flowering in sugarcane. Crop Sci 17:462–464

Natarajan BV, Krishnamurthy TN, Thuljiram J (1967) Relative effects of parents on some economic characters in sugarcane. Euphytica 16:104–108

Raghavan TS (1951) Cytoplasmic inheritance in *Saccharum*. Curr Sci 20:138–140

Roach BT (1968) Quantitative effects of hybridization in *Saccharum officinarum* × *S. spontaneum* crosses. Proc ISSCT 13:939–954

Stevenson GC (1965) Genetics and breeding of sugar cane. Longmans, Green, London