

COMBINING HIGH YIELDS OF CANE AND SUCROSE IN SUGARCANE THROUGH RECURRENT SELECTION

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ABSTRACT

Breeding efforts continue to be the primary means of increasing sugarcane yields. Fifty sugarcane parents were used to initiate an intrapopulation recurrent selection program, aiming at increasing the cane yield in an initially high sucrose content population. Based on tons of Brix per hectare, the best 20 % of the families were selected and recombined. Five plants originating from half-sib remnant seed of the selected families were used to form the recombined population. After five, 2-year recurrent cycles, the selection improved Brix by 0.7 % per year, cane yield (Mg cane ha⁻¹) by 2.4 % per year, and Brix production (Mg Brix ha⁻¹) by 2.5 % per year. The application of recurrent selection in a population with high sugar content and early maturity was effective for increasing its cane yield potential, without reducing the sugar content. Although the base population was comprised of clones of high sugar content, it was possible to obtain positive gains through recurrent cycles for sugar content.

Keywords: sugarcane; within population recurrent selection; sugar content; half sibs

INTRODUCTION

The selection within a given family aims at increasing the frequency of desirable genes for certain population traits. This is the basis for the recurrent selection process, since the gene frequency is gradually changed following a recurrent process. The intrapopulation recurrent selection is based on a progeny test where the genotypes are assessed via the mean performance of their progenies. The prediction of genetic gain of a given selection scheme has been one of the most important contributions to breeding of quantitatively inherited traits. Ideally, the gains obtained with recurrent selection are continuous and progressive.

Different types of recurrent selection methods may be applied for population breeding. In each method, the observed rate of improvement will be a function of the selection intensity, the selection and recombination units, the magnitude of additive genetic variance, the phenotypic standard deviation of the selection unit, and the depression due to endogamy, pondered by the effective population size. The number of years necessary to complete one selection cycle also is very important.

Following the methodology described by Hull (1945), Breaux (1984) utilized the following scheme in the Louisiana breeding program for variety development: (a) selection of high sugar varieties, (b) intercrossing of the selected varieties, (c) planting large populations of individuals,

(d) stringent selection for sucrose content, and (e) intercrossing of selected clones to establish the following cycle. The first crosses between 1930 and 1940 involved the Co and POJ varieties, with Pol % cane of 9.7 %. Since inception, four recurrent cycles were completed by 1980, with individuals having, on average, 14.1 Pol % cane. This strategy was based on the mass selection of superior individuals, resulting in very long intervals between-cycles, since successive multiplications were necessary for an efficient selection of the best individuals. This resulted in small gains per year.

Legendre (1992, 1995) analyzing the continuity of the recurrent process described by Breaux (1984) for one more cycle, obtained a reduction in the magnitude of sugar increase from the fourth to the fifth cycle (from 14.1 to 13.0 Pol % cane). This author concluded that future progress in sugar content may be more difficult to obtain, and the varieties used for crossing may have reached a plateau. In Argentina, Cuenya and Mariotti (1991) obtained negative results for the increase in sugar content, in two cycles of recurrent selection.

In Indonesia, Sukarso and Sastrowijono (1995) used recurrent selection procedures similar to those used by Breaux (1984), but reduced the recombination time. These authors managed to conduct three selection cycles in three consecutive years, with the sole purpose of increasing the stalk diameter, and promising results were obtained.

Cox et al. (1994) tested a recurrent scheme for sugar content with 20 families, selecting the best clones as early as in Stage 1, with immediate recombination. Estimates of narrow-sense heritability obtained in such study were higher than 0.6.

This study used an intrapopulation recurrent selection scheme with half-sib families with the aim of pyramiding desirable traits, particularly cane yield, in short selection cycles. The original population consisted of early-maturing and high sucrose content genotypes.

MATERIALS AND METHODS

Population of cycle 0, A_0 , was formed by a set of 50 elite early-maturing, high sugar genotypes from the Copersucar germplasm bank. These parents were recombined in a poly-cross in 1992, in Camamu, Bahia, Brasil, giving origin to 47 half-sib families. After a germination test, these families were divided into two seed sets, one for planting the selection unit and the other for planting the recombination unit (Fig. 1).

The selection unit was planted in blocks in October 1992. The number of replications and of plants per replications varied from cycle to cycle. In April of the following year, the trial was harvested and the plots cultivated to be evaluated 12 months later. Brix was based on a 10-stalk sample from each half-sib family. Single stalks from 10 different plants from each family were assembled for each 10-stalk sample. We selected the highest yielding 10 families ($Mg \text{ Brix ha}^{-1}$) based on the harvested and weighed plot of the half-sib families. The recombination unit was planted one year after the selection unit. Here, 50 seedlings were planted from each of 50 families. On May of the following year, during the hybridization campaign, and based on the best families from the selection unit, we selected five seedlings within each family, to produce the 50 plant-population for the next cycle. As selection criteria for these seedlings, we looked for

Bressiani et al., Combining High Yields of Cane and Sucrose in Sugarcane Through Recurrent Selection

plants induced to flowering and with Brix and vigor higher or equal the average of the selected family.

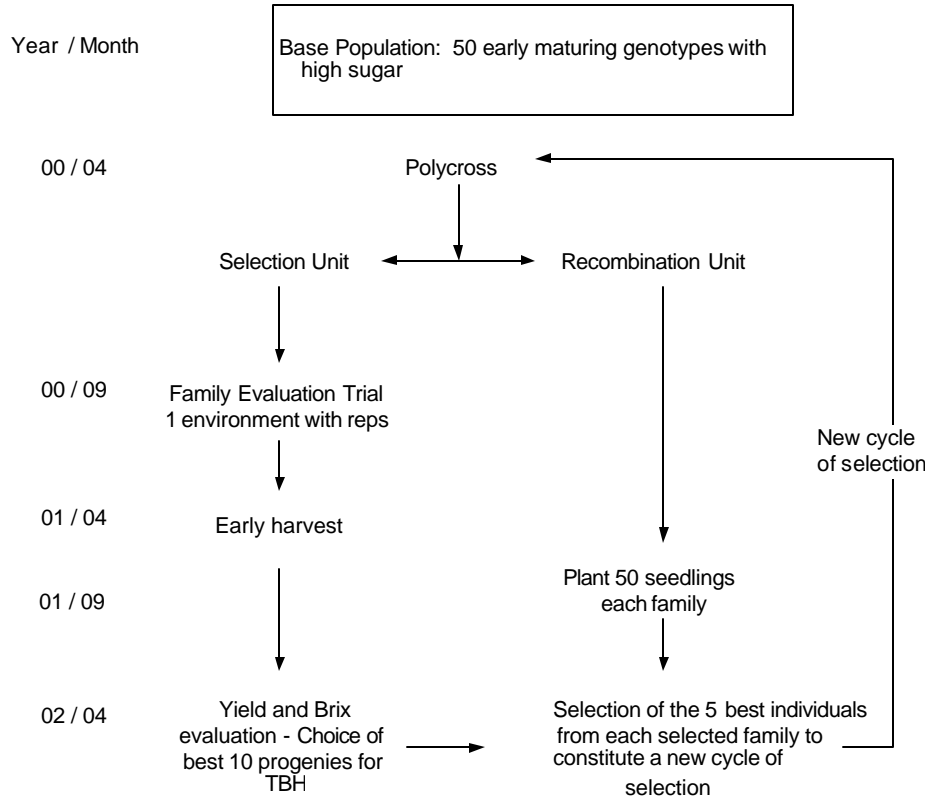
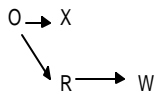


Figure 1. Flow diagram of activities for the intrapopulation recurrent selection program during its most recent cycle (from 2000 to 2002).

The general scheme for the family selection is:



Where 0 represents the parents on the reference population; X is the selection unit; R is the recombination unit, and W represents one individual in the improved population which is genetically related to X through R and 0 (Nyquist, 1991).

The selection among families is based on the family mean, which is compared with the population mean or the average of all other families. The selection unit is $x = \bar{Y}_L - \bar{Y}_\cdot$, where Y_{ijk} is the phenotype of the k^{th} plant from the i^{th} family in the j^{th} replication. There is a parent-progeny relationship among X , W and R , that also is correlated, as a half-sib, with each one of the nr plants from the i^{th} family. This happens in such a way that W is correlated with each plant in X , as a half uncle-nephew. So, $COV(X, W) = (1/8)s_A^2$, where $COV(X, W)$ measures half of the genetic variance between half sibs, for the between-family selection only by the female parent side. The selection gain (ΔG) between families will be (Hallauer & Miranda Filho, 1988):

$\Delta G = i(1/8)\mathbf{s}_A^2/\mathbf{s}_p$, where i represents the standardized selection differential; \mathbf{s}_A^2 corresponds to the additive genetic variance which, in the case of half-sib progenies, equals $4\mathbf{s}_f^2$. \mathbf{s}_p corresponds to the phenotypic standard deviation at the half-sib means level.

The phenotypic variance, \mathbf{s}_p^2 , among half-sib means will be $\hat{\mathbf{s}}_p^2 = \mathbf{s}_f^2 + \mathbf{s}_r^2$. The analysis of variance of the selection unit for Brix, cane yield (Mg cane ha⁻¹, TCH) and Brix yield (Mg cane ha⁻¹, TBH) was performed according to Vencovsky and Barriga (1992).

We included in all plantings of the selection unit cross checks and progenies representing the previous cycle. These progenies were chosen by random among those with remnant seed. This was done to allow data adjustment between cycles and to obtain the gain observed with the recurrent selection in each cycle. The adjustment was based on relative value among checks plus the representative progenies from previous cycle and the average of all populations.

RESULTS AND DISCUSSION

The number of families used in each generation varied from 44 to 57 due to differences in seed germination. Only those families that were represented in the selection unit were included in the analysis. The variation in number of plants per plot and replication suffered the same adjustments applied to the trials from the Copersucar breeding program in the period of evaluation. Selection intensities varied from 0.21 to 0.26 because of poor flowering (Table 1).

Poor flowering restricted the number of possible selections among the 50 plants per family that simultaneously met the selection criteria of good vigor, greater than average Brix, and flowering (Table 2). This number would have been easily reached if the selection applied within families had been done solely as a function of flowering. Given the great segregation present in the progenies, we determined that the seedlings to be used for recombination would have to have vigor and Brix equal to or above the progeny mean, so that the seedlings would reflect, in the worst case scenario, the family mean.

Table 1. Number of families, replicates, plants per plot and selection intensity between selection cycles.

Item	Selection cycles				
	0	1	2	3	4
Families evaluated	47	44	47	57	48
Replicates	6	3	3	2	2
Plants per plot	24	48	48	70	80
Families selected	12	10	11	12	-
Selection intensity	0.26	0.23	0.23	0.21	

Table 2. Number of plants selected from each family per selection cycle, starting with the first selection.

Family*	Recombination cycle			
	1	2	3	4
1	6	3	4	6
2	2	4	6	2
3	2	5	7	4
4	8	5	5	5
5	4	6	4	3
6	2	6	5	5
7	3	5	9	4
8	1	5	3	2
9	5	6	5	3
10	7	5	5	6
11	3	-	5	5
12	3	-	-	4
Total	46	50	58	49

* Numbers represent the position of each family within the selection unit.

The analysis of variance for tons of cane per hectare (TCH) shows significant differences ($P < 0.01$) among families during the five selection cycles (Table 3). The coefficients of variation for the experimental error were low, as compared to other studies involving sugar cane progenies (Bressiani et al., 2002; Jackson et al., 1995 a, b; Kimbeng et al., 2000). The heritability estimates at the family means level were intermediate for cycle 1 and high for the remaining cycles. The mean values for families and the selection differentials, in each selection cycle, represent the real parameters for the trial. The highest selection differentials were observed in cycles 0, 2, and 3. In these cases, the selection was made for the best families in tons of Brix per hectare (TBH), a measure that associates TCH and Brix. If the selection had been based only on TCH, the mean expected gain in each cycle would have been in the magnitude of 5 %, going from 3.6 % in cycle 1, to 7.1 %, in cycle 3, but the observed gain was very different from expected gains. In the first two selection cycles, the gain was negative, reaching high values on the last two cycles, but the average selection gain from the cycle 0 to 4 was 4.8 %. Large differences between the expected and observed gain in selections can be affected by the selection within families in the recombination unit. The low flowering rate in some families may have led to the selection of individuals below the family average. This can explain part of the negative gain in the first two cycles. However, good flowering rates may have inflated the average of selected individuals and may explain the high observed gain in the last two cycles.

Differences between expected and observed gains are common in intrapopulation breeding, even in diploid species, such as maize (Burton et al., 1971; Penny and Eberhart, 1971; Crossa and Gardner, 1989; Arriél et al., 1993). One possible explanation for such discrepancies is the

fact that the expected response to selection was derived from populations in linkage equilibrium and with infinitive effective size (Kempthorne, 1957; Falconer, 1989).

Table 3. Mean square values from the analysis of variance plus genetic and phenotypic estimates for tons of cane per hectare (TCH) over five recurrent selection cycles.

Source of variation	TCH (Mg ha ⁻¹) ²				
	Cycle 0	Cycle 1	Cycle 2	Cycle 3	Cycle 4
Families	456.28**	181.39**	431.64**	192.47**	65.97**
Blocks	385.52**	772.28**	1462.99**	175.66*	175.75**
Error	100.84	84.52	148.40	43.36	22.34
D.F. for Families	46	43	46	56	47
Mean (M)	87.40	75.76	93.11	73.53	65.69
CV _e (%)	11.49	12.14	13.08	8.96	7.19
s^2	100.84	84.52	148.40	43.36	22.34
s_f^2	59.24	32.29	94.41	74.55	21.82
CV _f (%)	8.81	7.50	10.44	11.74	7.11
s_p^2	76.05	60.46	143.88	96.23	32.99
s_A^2	236.96	129.16	377.66	298.22	87.27
\hat{H}_m^2	0.78	0.53	0.66	0.77	0.66
Selected mean (SM)	97.97	79.09	108.87	86.31	72.51
Selection differential (SD)	10.57	3.33	15.76	12.78	6.82
SG* expected %	4.9	3.6	5.6	7.1	4.0
SG observed %	-3.0	-4.6	12.9	13.7	

*SG = Selection gain (expected % = $(i(1/8)s_A^2/s_p^2)/M*100$, observed % = $(\text{mean}_{\text{adjusted } i+1} - \text{mean}_{\text{adjusted } i}) / \text{mean}_{\text{adjusted } i}$), CV_e(%) – coefficient of variation for the experimental error, s^2 – experimental error variance estimate, s_f^2 – genetic variance estimate among family means, CV_f (%) – genetic coefficient of variation among families, s_p^2 – phenotypic variance estimate among family means (Family MS / Reps), s_A^2 – additive genetic variance estimate, \hat{H}_m^2 – heritability estimate at the family means level.

The analysis of Brix showed small genetic variability (Table 4). Even though the coefficient of variation of the experimental error was small, the genetic variance among families was also small. This variance was so small in cycle 3 that there was not significant variance among families in this cycle. The mean expected gain for each selection cycle, based exclusively on Brix, was 1.4 %, which is less than a third of the one expected for TCH. This gain ranged from 0.8 % in cycle 3, to 1.8 % in cycles 0 and 1. The observed gain was different from expected gains, as was the case for TCH, but in the average of all cycles, the value was the same that is 1.4 % per cycle, which corresponds to 0.7 % per year.

Table 4. Mean square values from the analysis of variance plus genetic and phenotypic estimates for Brix over five recurrent selection cycles.

Source of variation	(Brix %) ²				
	Cycle 0	Cycle 1	Cycle 2	Cycle 3	Cycle 4
Families	2.62**	1.46**	0.90**	0.82	1.06**
Blocks	1.42*	1.13	0.44	4.13**	0.98
Error	0.46	0.38	0.50	0.57	0.43
D.F. for Families	46	43	46	56	47
Mean (M)	18.68	18.51	18.49	16.70	17.60
CV _e (%)	3.63	3.35	3.82	4.51	3.74
s^2	0.46	0.38	0.50	0.57	0.43
s_f^2	0.36	0.36	0.13	0.13	0.31
CV _f (%)	3.22	3.23	1.98	2.14	3.18
s_p^2	0.44	0.49	0.30	0.41	0.53
s_A^2	1.44	1.43	0.54	0.51	1.25
\hat{H}_m^2	0.82	0.74	0.45	0.31	0.59
Selected mean (SM)	18.66	19.21	18.49	17.03	17.82
Selection differential (SD)	-0.02	0.70	0.00	0.34	0.21
SG ¹ expected (%)	1.8	1.8	0.9	0.8	1.7
SG ¹ observed (%)	-0.4	4.3	2.6	-1.0	

*SG = Selection gain (expected % = $(i(1/8)s_A^2/s_p)/M*100$, observed % = $(\text{mean}_{\text{adjusted } i+1} - \text{mean}_{\text{adjusted } i}) / \text{mean}_{\text{adjusted } i}$), CV_e(%) – coefficient of variation for the experimental error, s^2 - experimental error variance estimate, s_f^2 - genetic variance estimate among family means, CV_f (%) – genetic coefficient of variation among families, s_p^2 - phenotypic variance estimate among family means (Family MS / Reps), s_A^2 - additive genetic variance estimate, \hat{H}_m^2 - heritability estimate at the family means level.

Legendre (1992, 1995) reported a mean gain around 0.8 % per year, during five recurrent selection cycles, from 1936 to 1988. The observed gain in our study, slightly inferior for Brix when compared to the one reported in the literature, was expected. In our study, it is important to note that the criteria used for choosing the initial population was sugar content and early maturity. Even though our main objective was to increase the TCH of the population without reducing its sugar content, the gains in the sugar content were equivalent to those obtained in the traditional breeding program, as indicated in the COPERSUCAR Annual Report 2000 (COPERSUCAR, 2001).

Cuenya and Mariotti (1991) also reported negative gains with selection for Brix, in the beginning of the recurrent process in Argentina. These authors reported a reduction of 15.3 % for the mean Brix between cycles 0 and 1 and attributed such reduction to the utilization of

genotypes with low sugar content as parents during the recombination phase. In such a study, as well as in ours, the selection of genotypes to be recombined was not based on the sugar content, but on TBH. Furthermore, only those individuals that flowered could be used for crossing.

A closer examination on the between-families coefficient of genetic variation for Brix shows a drastic reduction in the genetic variability during cycle 2, a recovery in cycle 3, with a return to the initial level, in cycle 4. Legendre (1995) reported a reduction tendency between cycles for the coefficient of variation, but the values were much higher as compared with those in our study. Results similar to those obtained by Legendre (1995) were reported by Cuenya and Mariotti (1991): 4.3 % for cycle 0 and 7.8 % for cycle 1. The low coefficient of variation between families may result from the population size and/or from the use of early-maturing and high-sugar genotypes to form the base population.

An important point on the recurrent selection scheme is that, besides increasing the frequency of favorable alleles, it also maintains sufficient genetic variability to allow genetic improvement in subsequent cycles. In the particular case of Brix, given the existing low genetic variability among families, future gains may be reduced.

Examination of the recurrent selection cycles, in terms of the productivity of Brix per hectare, shows that the genetic variance estimate among family means, the genetic coefficient of variation among families, the phenotypic variance estimate among family means, the additive genetic variance estimate and the heritability estimate at the family means level that we obtained were all similar to those obtained for TCH (Table 5). This was expected given the low genetic variability for sugar content. The expected mean gain for TBH per cycle was around 4.9 %, with the exception for cycle 3, where it reached 7.2 %. The expected mean gain was 6.1 % per cycle, ranging from -3.3 % in cycle 0, to 16.1 % in cycle 2. Again, the expected and observed gains did not correspond in each selection cycle.

The observed selection gains showed a significant ($P < 0.05$) linear improvement only for Brix. For the variables TCH and TBH, the linear regression was not significant (Figure 2). This leads to the supposition that other genetic factors, such as dominance and epistasis, influence the production potential of the segregant populations. It is worth noting that, since the Brix reading is not a measure of sugar content, but soluble solids, the selection for Brix may result in an increase of the impurity level, rather than sucrose content.

A good reference for the magnitude of the observed gains with the intrapopulation recurrent selection based on family selection is a comparison with the gains obtained in the normal genetic improvement program. Here, recombination is made among elite clones obtained from intermediate selection stages of the program. Such a procedure is also considered recurrent selection but, in this case, based on phenotypic selection of superior individuals and with a long duration cycle.

The Copersucar 1999/2000 annual report, which shows the crosses made between 1991 and 1998, demonstrates yearly gains of 0.9 %, 1.8 % and 2.9 % for Brix, TCH and TBH, respectively. Such comparisons indicate that intrapopulation recurrent selection, based on families, had an inferior gain for Brix (0.7 % per year) a slightly superior gain for TCH (2.4

%/year) and similar gains for TBH (3.0 %/year). The population used in this recurrent selection program had high values of sugar content. The data indicate high potential for genetic gain for TCH which may represent, after additional recurrent selection cycles, a population superior for TBH. Therefore, the potential exists to select more individuals for commercial planting in such a population.

Table 5. Mean square values from the analysis of variance plus genetic and phenotypic estimates for tons of Brix per hectare (TBH) over five recurrent selection cycles.

Source of variation	TBH (Mg.Brix%/100) ²				
	Cycle 0	Cycle 1	Cycle 2	Cycle 3	Cycle 4
Families	16.18**	6.80**	14.11**	6.02**	1.98**
Blocks	12.24**	23.24**	51.46**	0.58	2.59
Error	3.86	2.99	4.81	1.56	0.88
D.F. for Families	46	43	46	56	47
Mean (MO)	16.32	14.02	17.19	12.29	11.55
CV _e (%)	12.03	12.32	12.76	10.16	8.11
s^2	3.86	2.99	4.81	1.56	0.88
s_f^2	2.05	1.27	3.10	2.23	0.55
CV _f (%)	8.78	8.04	10.24	12.16	6.43
s_p^2	2.70	2.27	4.70	3.01	0.99
s_A^2	8.21	5.08	12.39	8.93	2.21
\hat{H}_m^2	0.76	0.56	0.66	0.74	0.56
Selected mean (SM)	18.27	15.17	20.14	14.69	12.90
Selection differential (SD)	1.95	1.15	2.95	2.40	1.34
SG* expected %	4.8	4.0	5.5	7.2	3.3
SG observed %	-3.3	-0.7	16.1	12.4	

*SG = Selection gain (expected % = $(i(1/8)s_A^2/s_p^2)/MO*100$, observed % = $(\text{mean}_{\text{adjusted } i+1} - \text{mean}_{\text{adjusted } i}) / \text{mean}_{\text{adjusted } i}$), CV_e(%) – coefficient of variation for the experimental error, s^2 – experimental error variance estimate, s_f^2 – genetic variance estimate among family means, CV_f (%) – genetic coefficient of variation among families, s_p^2 – phenotypic variance estimate among family means (Family MS / Repls), s_A^2 – additive genetic variance estimate, \hat{H}_m^2 – heritability estimate at the family means level.

CONCLUSIONS

The application of recurrent selection in a population with high sugar content and early maturity was effective for increasing its cane yield potential, without reducing the sugar content. Although the base population was comprised of clones of high sugar content, it was possible to obtain gains through recurrent cycles for sugar content.

The occurrence of higher progress for TCH, when compared to the conventional breeding program may offer, after a few more recurrent cycles, superior populations in TBH, increasing therefore, the possibilities of selecting more individuals for commercial planting.

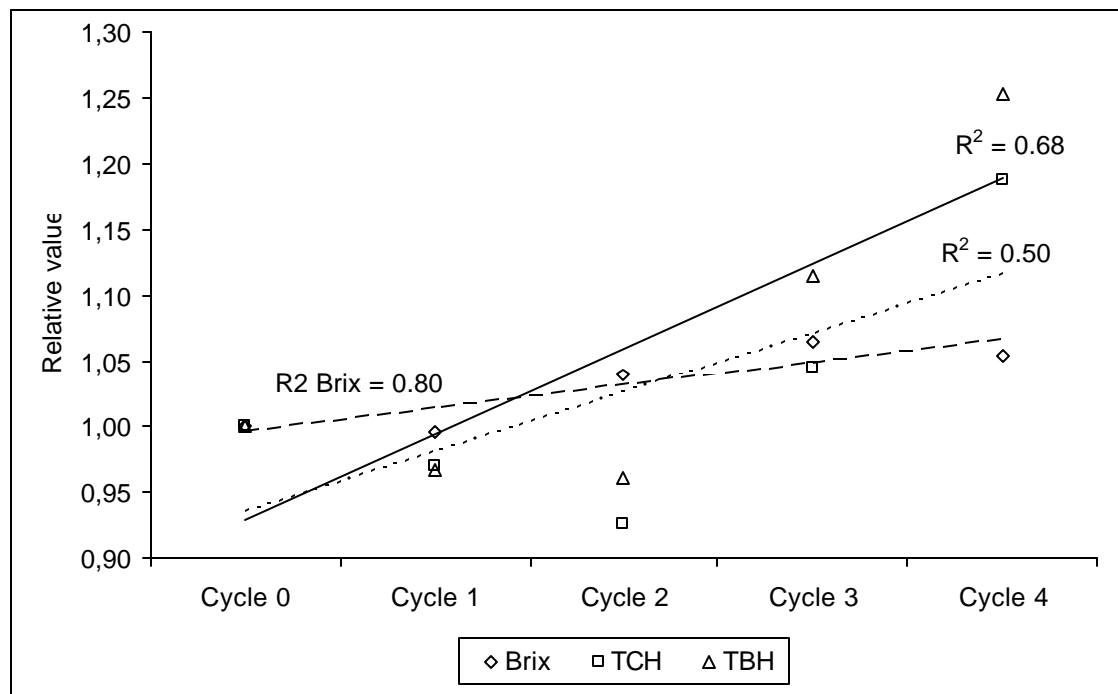


Figure 2. Gains accumulated in Brix, TCH (tons of cane per hectare) and TBH (tons of Brix per hectare) during five cycles of recurrent selection.

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