

The role of pith, tube, and stalk density in determining sugarcane sucrose content and stalk weight *

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Summary. Selection against pith and tube is one of the major criteria used to eliminate inferior sugarcane (Saccharum spp.) cultivars in early stages of new cultivar evaluation. Understanding the genetic relationships for these traits would facilitate crossing and selection decisions. This study was conducted to determine heritability, genetic coefficient of variation, and the potential for genetic advance by selection for pith, tube, and stalk density. Correlation and path-coefficient analysis studies were conducted to determine the effects of Brix, pith, and stalk density on sucrose content and the effects of stalk volume, tube, and pith on stalk weight. Eighty randomly selected cultivars (four progeny from each of 20 crosses), representing a first clonal stage of a Louisiana sugarcane breeding population, and their parents were planted at St. Gabriel/LA, and yield data were collected in 1986, 1987, and 1988. Pith and tube exhibited large genotype and genotype-by-year variation, whereas variation in stalk density was nonsignificant. Broad-sense and narrow-sense heritabilities were high, moderately high, and low for pith, tube, and stalk density, respectively. Pathcoefficient analysis revealed that stalk volume was the major factor determining stalk weight. Tube and pith were factors that decreased stalk weight. As expected, Brix was the single most important factor determining sucrose content, however, high stalk density and low pith were also associated with high sucrose content. Sugarcane breeders should practice stringent selection for low pith across years to increase stalk weight and sucrose content. Since stalk density was effectively increased by high sucrose content and low pith, the use of stalk density in breeding and selection should be avoided. The minimal

effect of tube on stalk weight suggests that its use as selection criteria be minimized or dropped.

Key words: Saccharum spp. – Genetic variance – Heritability – Path-coefficient analysis – Genetic correlation

Introduction

Sugarcane (Saccharum spp.) cultivars typically originate from large seedling populations derived by crossing elite parents. In Louisiana, selected individuals from the seedling populations are clonally propagated in first clonal (single-row 1.8-m) plots. Selections from first clonal plots are subsequently established in second clonal (single-row 4.9-m) plots (Breaux 1972). Selection against pith and tube is practiced extensively in each of these three stages. Pith is composed of white, cottony, dead parenchyma cells found in the stalk and is usually associated with low sucrose production and milling problems. Tube is a hollow core running through the center of the stalk internodes. Genetic studies to assess the effects of pith, tube, and stalk density on sucrose content and stalk weight are lacking and would be useful in establishing more effective crossing and selection criteria.

Sugarcane breeders agree that the incidence of pith and tube has both a genetic and an environmental basis. Dutt and Rao (1950) reported that pithy × pithy crosses always yielded a higher percentage of pithy seedlings, whereas the use of even one non-pithy parent decreased the percentage of pithy seedlings. Imran (1986) reported narrow-sense heritability values for pith ranging from $0.360 (\pm 0.275)$ to $0.006 (\pm 0.052)$. Broad-sense heritability estimates for pith were less than 9%. Water stress has commonly accounted for pith and tube development in

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sugarcane (Dillewijn 1952). In Nigeria, irrigation is continued until harvest for cultivars that have a tendency to develop pith (Evans 1966). Increasing nitrogen fertilization causes increased pith development, whereas increasing phosphorous tends to decrease with development (Verma 1948). Flowering tends to increase pith development in sugarcane (Lakshmikantnam 1946; Evans 1966). Imran (1986) reported a positive correlation between pith and percent flowering, indicating a tendency for earlier flowering cultivars to have higher levels of pith. Lakshmikantnam (1946) also reported that ratoon crops have a higher incidence of pith than plant cane crops. Evans (1966) provides a comprehensive review of the genetic and environmental effects of pith and tube on sugarcane yield and quality.

The objectives of this study were: (1) to obtain heritabilities, genetic coefficients of variation, and genetic advance estimates for pith, tube, and stalk density in order to assess selection and breeding potential, and (2) to determine the relationships of pith, tube, and stalk density to sugarcane stalk weight and sucrose content through correlation and path-coefficient analysis.

Materials and methods

A plant cane, first ratoon, and second ratoon sugarcane crop representing a first clonal stage of a Louisiana sugarcane breeding population was studied. The population consisted of 80 randomly selected genotypes representing four progeny from each of 20 crosses. The genotypes represented had undergone some selection as detailed by Breaux (1972), with the exception that seedlings were not screened for mosaic.

Parents and progeny were planted on November 6, 1985 in a randomized complete block design with three replicates. The test was conducted on a Commerce silt loam soil at the St. Gabriel Research Station of the Louisiana Agricultural Experiment Station. Single-row plots (1.83 m long and 1.83 m wide with 0.61 m alleys) were planted with four stalks each. Recommended cultural practices as described by Breaux et al. (1972) were used.

Data were collected on: sucrose yield (Mg/ha), cane yield (Mg/ha), sucrose content (g of sucrose/kg cane), stalk number (stalks/m²), stalk length (m), stalk diameter (cm), stalk weight (kg), stalk volume (cm³), stalk density (g/cm³), pith and tube rating, and juice Brix (%). Millable stalks per plot were counted in August each year. An eight-stalk sample was hand harvested from each plot on November 9-12, 1986 for the plant cane crop, on November 1-4, 1987 for the first ratoon crop, and on October 11–13, 1988 for the second ratoon crop. Samples were cut at ground level, topped through the apex, stripped of leaf material, bundled, and tagged. Volume of the eight-stalk bundle was estimated by water displacement in a calibrated 30-cm diameter water-filled cylinder. Bundle weight and length were recorded. The diameter of five stalks was measured at the midstalk internode. Before milling, two stalks were cut and rated for pith and tube. The amount of pith was rated on a one to five scale: 1 = no pith and 5 = maximum pith. Tube was rated binominally for either a solid stalk or the presence of a tube. Ratings for tube were made only in 1987 and 1988, so all parameter estimates for tube are based on 2-year rather than 3-year data. A three-roller mill (500 kg/cm² pressure) extracted juice from each sample. A subsample of the juice was taken for quality analysis. Brix (percent soluble solids in the juice w/w) was measured by refractometer, and sucrose content was calculated as described by Legendre and Henderson (1972). Stalk density was calculated as stalk weight divided by stalk volume. Cane yield was estimated as the product of stalk number and mean stalk weight for each plot. Sucrose yield was calculated as the product of cane yield and sucrose content divided by 1,000.

The statistical model used to calculate the phenotypic variances and covariances was

$$T_{ij} = \mu + R_i + Y_j + E_{ij}$$

where T_{ij} was observation *i* in year *j*, μ was the overall mean, and R_i was the replication effect. Since each crop was grown in a particular year, year and crop were confounded, which was represented by Y_j . E_{ij} was the residual which included all genetic effects and error.

Sugarcane is asexually propagated; therefore, all genetic variation is exploitable between stages of selection (Falconer 1981). All genetic variances and covariances calculated were broad-sense estimates, and the statistical model used was

$$T_{ijk} = \mu + R_i + Y_j + G_k + GR_{jk} + GY_{jk} + E_{ijk}$$

where T_{ijk} was the observation in replication *i*, year *j*, and genotype *k*. μ was the overall mean, R_i was the replication effect, Y_j was the year effect, G_k was the genotype effect, GR_{ik} was the interaction of the genotype with replication, GY_{jk} was the interaction of genotype with year, and E_{ijk} was the residual. Variances and covariances were estimated by equating mean squares and cross-products with their expectations (Becker 1984).

Broad-sense heritability was calculated as:

$$H_i = \sigma_g^2 / (\sigma_g^2 + \sigma_{gr}^2 / r + \sigma_{gy}^2 / y + \sigma_e^2 / y r)$$

where σ_g^2 was the genetic variance, σ_{gr}^2 was the genotype by replication variance, σ_{gy}^2 was the genotype by year variance, σ_e^2 was the error variance, r was the number of replications, and ywas the number of years. Three heritabilities were estimated. H_1 was estimated on an individual plot basis (r=1, y=1) and was used to simulate the actual selection scenario at first clonal selection stage in 1 year. H_2 (r=3, y=3) and H_3 (r=1, y=3) were calculated to examine the effect of years (or crops) on the heritability.

Narrow-sense heritability was estimated by regressing the full-sib progeny mean on mid-parent means after adjusting for replication and year effects $(h^2 = b_{op})$.

Broad-sense genetic variation was measured by the genetic coefficient of variation (GCV) as

 $GCV(\%) = 100 \times (\sigma_q^2/\text{progeny mean})$

Genetic advance (GA) was estimated as

 $GA(\%) = 100 i \sigma_p H_1/\text{progeny mean}$

where i = 1.76 (standardized selection differential for a selection intensity of 10%), and σ_p was the phenotypic standard deviation for the progeny (Allard 1960).

Phenotypic and broad-sense genetic correlations were calculated from the variances and covariances and subjected to path-coefficient analysis as described by Dewey and Lu (1959). Path-coefficient analysis requires an additive cause and effect relationship among variables. Therefore, the data were logarithmically transformed to satisfy the assumption of additivity for the path system.

Variance and heritability standard errors were calculated as described by Dickerson (1969). Standard errors of the pheno-typic and genetic correlations were calculated as described by Becker (1984).

Results and discussion

Analysis of variance showed that genotypes differed in pith and tube (Table 1). Year and genotype by year (GY)variation were significant for pith and tube. The significant GY interaction suggests that pith and tube differed in magnitude or rank among genotypes over years. No source of variation was significant for stalk density. Testing over years would be required to effectively screen cultivars against pith and tube.

Genetic variance was the predominant variance component for pith (Table 2). Genetic variances for all three traits were probably low due to selection in the singlestool testing stage (Breaux 1972). Error variance (an estimate of $G \times E$ variation) was the largest variance component for tube and stalk density. Kang et al. (1983) reported genotype by replication variances (GR) as large as GY variation for sugarcane traits such as plant height, stalk number, cane yield, and sucrose yield. GR was negative for all traits. Negative estimates may be due to inadequate modeling, sampling, or experimental technique (Hallauer and Miranda 1981). Increasing sample size or numbers of locations would yield more reliable data during cultivar testing.

Screening cultivars against pith and tube in Louisiana is normally performed over years with one replication per year. Broad-sense heritability (H_3) for tube suggested moderate repeatability, with 33% of the observed variation explained by genetic causes (Table 2). H_3 for pith was high, 0.850, and larger than values reported by Imran (1986). These data suggest that pith is a repeatable trait under standard Louisiana selection practices. Stalk density was not repeatable in this selection scheme. On a phenotypic mean basis (H_2) , 94% and 53% of the variation observed in pith and tube, respectively, was accounted for by genetic variation (Table 2). These values are probably biased upward due to evaluation at a single location (Dudley and Moll 1969). The repeatability of stalk density was low. The use of additional replications and locations in sugarcane cultivar testing would be advantageous when screening for pith and tube; however, the value obtained from additional replications and/or locations in the current selection scheme may not offset the additional effort and cost.

Crossing elite parents is the vital first link in producing improved sugarcane cultivars. Narrow-sense heritability (h^2) for pith was high, while values for tube and stalk density were lower. More stringent screening of the parent population against high levels of pith should facilitate the production of progeny populations low in pith. Selection against tube and low stalk density in the parent population would be ineffective due to low h^2 values.

The genetic coefficient of variation (GCV) and genetic advance (GA) were high for pith, indicating the potential to produce progeny populations with lower levels of pith.

Table 1. Mean squares for the progeny population for the traits. (3-year analysis for pith and stalk density and 2-year analysis for tube)

Source	df	Pith	Stalk density	df	Tube
Replication (Rep)	2	0.018	0.010	2	0.225
Year	2	0.481 **	0.004	1	1.766*
Genotype	79	1.649 **	0.011	79	1.751 **
Genotype × Rep	158	0.082	0.008	158	0.380
Genotype × Year	158	0.105*	0.009	79	0.926**
Error	320	0.083	0.009	160	0.396

**** Significance at the alpha levels 0.05 and 0.01, respectively

 Table 2. Variance components, heritabilities, means, genetic coefficients of variation, and genetic advance for pith, tube, and stalk density for the progeny population

Genetic param- eter	Pith	Tube	Stalk density
$ \frac{ \sigma_g^2 }{\sigma_g^{p_r} \sigma_g^{p_r} \sigma_g^{p_r} \sigma_e^{2} } \\ H_1 \\ H_2 \\ H_3 \\ h^2 \\ Mean \\ GCV (\%) \\ GA (\%) $	$\begin{array}{c} 0.172 \\ \pm \\ -0.0003 \\ \pm \\ 0.007 \\ \pm \\ 0.083 \\ \pm \\ 0.657 \\ \pm \\ 0.938 \\ \pm \\ 0.853 \\ \pm \\ 0.471 \\ \pm \\ 0.203 \\ 84.7 \\ 51.5 \end{array}$	$\begin{array}{cccccc} 0.003 & 0.140 \pm 0.009 \\ 0.001 & - 0.005 \pm 0.007 \\ 0.001 & 0.177 \pm 0.009 \\ 0.007 & 0.396 \pm 0.044 \\ 0.012 & 0.198 \pm 0.013 \\ 0.017 & 0.478 \pm 0.036 \\ 0.048 & 0.429 \pm 0.079 \\ 0.063 & 0.127 \pm 0.074 \\ 0.499 \\ 28.1 \\ 27.3 \end{array}$	$\begin{array}{c} 0.00023 \pm 0.00008\\ - 0.00030 \pm 0.00079\\ 0.00010 \pm 0.00079\\ 0.00900 \pm 0.00071\\ 0.025 \pm 0.009\\ 0.198 \pm 0.009\\ 0.078 \pm 0.080\\ 0.111 \pm 0.171\\ 0.101\\ 0.2\\ 3.2 \end{array}$

^a Standard error

The variation for tube was moderate. Efforts to increase stalk density through direct selection would be difficult at best due to low GA values.

In some cases, the magnitude of the phenotypic and genetic correlation estimates differed in magnitude, indicating the influence of the environment on trait relationships (Table 3). Phenotypic correlations of pith, tube, and stalk density with the other sugarcane yield components were lower than the genetic relationships.

In cause and effect situations, trait relationships may be correlated due to a common association with other traits. Path-coefficient analysis is useful in partitioning the correlation coefficient into its direct and indirect effects, thereby eliminating the correlation bias due to common association. Stalk volume, tube, and pith comprised the cause and effect relationship determining stalk weight (Fig. 1). At both the phenotypic and genetic level, direct effects showed that stalk volume was the trait of predominant influence on stalk weight, followed by negative effects for tube and pith (Table 4). Indirect effects at the





Fig. 1. Path diagram showing the cause and effect relationship between stalk weight and its components, stalk volume, tube, and pith. (P and r denote path-coefficient and correlation coefficient, respectively)

Fig. 2. Path diagram showing the cause and effect relationship between sucrose content and its components, Brix, pith, and stalk density. (P and r denote path-coefficient and correlation coefficient, respectively)

Table 3. Phenotypic and genetic correlations among traits of the progeny population (upper and lower values represent broad-sense genetic and phenotypic correlations, respectively)

Trait	Sucrose yield	Cane yield	Sucrose content	Brix	Stalk weight	Stalk no.	Stalk length	Stalk diameter	Stalk volume	Pith	Tubé
Stalk density	0.095 - 0.128**	-0.091 0.107**	0.857* 0.085**	0.842* 0.113**	-0.665* 0.300** -	0.105 -0.026	$-0.061 \\ -0.007$	-0.888* -0.126**	-0.717 ** -0.144 **	-0.711 -0.159**	-1.128* 0.131*
Pith	0.001 0.039*	0.073 0.075*	-0.222* -0.105**	-0.217* -0.115**	-0.220* -0.097**	0.182 0.036	-0.007 0.186**	0.250* 0.076*	0.237 * 0.173 **		-0.162* -0.134*
Tube	0.231 * 0.063 *	0.290* 0.094**	$-0.204* \\ -0.100**$	-0.192* -0.084**	0.287* 0.072*	0.182* 0.068*	$0.026 \\ -0.006$	0.596** 0.194**	0.416** 0.131 **		

*, ** Significance at the alpha levels 0.05 and 0.01, respectively

 Table 4. Phenotypic and genetic path-coefficient analysis of stalk weight and its components

Table 5.	Phenotypic and	genetic	path-coefficient	analysis	of su-
crose co	ontent and its cor	nponent	s		

Pathway	Phenotypic	Genetic	Pa
Stalk weight vs stalk volume			Suc
Direct effect, P_{21} Indirect effect, via	0.961	1.273	Di: Inc
Tube, $r_{23}P_{31}$	-0.012	-0.139]
Pith, $r_{24}P_{41}$	-0.048	-0.137	5
Correlation, r_{21}	0.901	0.997	
Stalk weight vs tube			Su
Direct effect, P_{31} Indirect effect, via	-0.091	-0.336	Di: Inc
Stalk volume, $r_{23}P_{21}$	0.126	0.530]
Pith, $r_{34}P_{41}$	0.037	0.093	,
Correlation, r_{31}	0.072	0.287	
Stalk weight vs pith			Su
Direct effect, P_{41} Indirect effect, via	-0.275	-0.576	Di: Inc
Stalk volume, $r_{24}P_{21}$	0.166	0.302]
Tube, $r_{34}P_{31}$	0.012	0.054]
Correlation, r_{41}	-0.097	-0.220	
Residual (P_{r1})	0.338	0.000	Re
$1 - (P_{x1})^2$	0.886	1.000	1 —

Phenotypic	Genetic
0.891	12.555
0.001	1.933
-0.002	-13.512
0.890	0.976
-0.005	- 8.907
-0.103	-2.724
0.003	11.409
$-\overline{0.105}$	-0.222
-0.017	-16.047
0.101	10.571
0.001	6.333
0.085	0.857
0.456	0.722
0.792	0.479
	Phenotypic 0.891 0.001 -0.002 0.890 -0.005 -0.103 0.003 -0.105 -0.017 0.101 0.001 0.005 -0.105

phenotypic level were small. At the genetic level, the negative indirect effect of tube on stalk weight through its association with stalk volume was large, indicating that cultivars with large stalk volume tended to have a tube. Tube was more commonly associated with large-diameter stalks at the genetic level. Breeding programs that develop large-diameter cultivars may have problems with tube. However, this study indicated little association between tube and cane yield at both the phenotypic and genetic level. The indirect effects of pith on stalk weight, through associations with stalk volume, indicated that pith was also associated with a large-volume stalk.

Brix, pith, and stalk density comprised the relationship determining sucrose content (Fig. 2). Genetic pathcoefficient analysis produced direct and indirect effects much larger than 1.000 or -1.000 (Table 5). Path coefficients are not restricted to values between one and minus one as are correlation coefficients. As expected, phenotypic and genetic path-coefficient analysis revealed that Brix was the sole positive direct contributor to sucrose content. Kang et al. (1983) also found a high correlation between Brix and sucrose content, a variable of practical significance to producers. At the direct genetic level, pith decreased sucrose content. The genetic indirect effects of stalk density and pith on sucrose content through associations with Brix and stalk density, respectively, suggested that low pith and high stalk density are positively correlated with sucrose content. The amount of phenotypic and genetic variation explained by the path analysis $(1-P_{x1})^2$ was 0.792 and 0.479, respectively, indicating that factors in addition to Brix, pith, and stalk density contribute to sucrose content. We surmise that the addition of percent fiber and photosynthetic parameters may account for other variation in sucrose content.

Kang et al. (1983) suggested that genetic path coefficients would be more useful than phenotypic path coefficients in deciding upon effective selection criteria. Therefore, when selecting for stalk weight, stalk volume should be given greatest consideration followed by selection for low pith. New cultivars possessing a tube should not necessarily be eliminated, since tube had a negligible effect on stalk weight and cane yield. Because pith adversely affects both stalk weight and sucrose content, strict selection for low pith should be and is practiced in the early stages of sugarcane cultivar evaluation. Since it would be difficult to increase stalk density directly, selection for high sucrose content and low pith should effectively increase stalk density.

In summary, these data suggest that sugarcane breeders need to reconsider selection and crossing strategies concerning pith, tube, and stalk density. Rigid selection across years against pithy cultivars in the early stages of cultivar selection should be augmented by an effective screening of the parent population used for crossing. Tube had only minimal effects on stalk weight, and its use as selection criterion in both crossing and selection should be minimized or dropped. Stalk density can be indirectly increased by high sucrose content and low pith, thus, the use of stalk density in crossing and selection should also be avoided.

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