

Association and heritability of sugarcane smut resistance to races A and B in Hawaii*

K. K. Wu¹, D. J Heinz¹ and D. M. Hogarth²

¹ Department of Genetics and Pathology, Hawaiian Sugar Planters' Association, P.O. Box 1057, Aiea, HI 96701, USA

² Bureau of Sugar Experiment Stations, Queensland, Australia

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Summary. This study was conducted to estimate the degree of association of smut (Ustilago scitaminea Syd.) resistance in sugarcane (Saccharum spp.) between races A and B in Hawaii and to estimate the heritability of resistance to both races. The estimated degree of association was 0.18. Although statistically significant, the degree of association of resistance between races A and B was near zero and therefore of no practical importance. Selection for resistance to one race would have little effect on the frequency of resistance to the other race in the following sexual generation. Heritabilities in the broad sense estimated from the parent population on a plot mean basis were 0.96 and 0.91 for races A and B, respectively. Selection for smut resistance should be very effective between populations of asexual generations. Heritabilities in the narrow sense estimated from parent-progeny regression analysis on a family mean basis were 0.51 and 0.47 for races A and B, respectively. Selecting and breeding for resistance should result in a fairly rapid increase in the frequency of resistance in the progeny population.

Key words: Saccharum spp. – Ustilago scitaminea Syd.

Introduction

Culmicolous smut (Ustilago scitaminea Syd.) of sugarcane (Saccharum spp.) is airborne and exists in nearly all the sugar cane-producing countries of the world. Different races of the organism have been reported in four countries: two races each in Brazil (daSilva and Sanguino 1978), the United States of America (Hawaii) (Comstock et al. 1977), and the Republic of China (Taiwan) (Hsieh and Lee 1978; Lee-Lovick 1978; Leu and Teng 1972), and four races in Pakistan (Muhammed and Kauser 1962). Of the two smut races reported in Hawaii, race A was identified in 1971 and race B in 1976.

Quantitative genetic studies by Walker (1980) reported low heritability of smut resistance and suggested that parents should not be selected for smut resistance alone, if improvement was expected in agronomic and quality characters. Wu et al. (1983) reported moderate individual heritability of resistance to smut race A and found no correlation between race A smut resistance and yield components. They suggested that selection for smut resistance in the early stages of selection for yield characteristics would not adversely affect the chances of selecting smut-resistant, highyielding clones.

Identification of two races of smut in Hawaii provided the opportunity to determine (1) if selection in a progeny population for smut resistance to one race significantly changes the percentage of individuals resistant to another race; (2) the differences in resistance to the two smut races in a large progeny population in terms of genetic and population parameters; and (3) if one could predict a range in the percentage of smut resistant individuals in a progeny population based on the parents' reactions to the two races.

The objectives of the study were to determine the degree of association and distribution of sugarcane reaction to both races A and B; to compare environmental and genetic variances and heritabilities of sug-

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arcane to races A and B; and to establish linear regressions to be used in predicting the range in percentage of smut infection in the progeny population.

Materials and methods

Seven sets of factorial crosses (one 5×5 , two 5×4 , two 4×4 , and two 3×3) were made in 1974 (Hogarth et al. 1981). The parents used in each set of the factorials were chosen from a reference population on the basis of availability of tassels on the days when crosses were being made. The fifty parental clones included in this study were considered a random sample of the reference population in which all breeding clones were vegetatively maintained.

Forty-eight seedlings per cross and cuttings of the parental clones were planted in a field in May 1975. After eight months of growth, four three-bud stem cuttings from each parent and each progeny clone were cut, of which two were hot-water treated and planted in a propagation field as a seed source; two were immersed for 10 min in a smut (race A) spore suspension (5×10⁻⁶ spores/ml H₂O) (Byther and Steiner 1974) and planted in a subplot in a field where only race A spores were present. A randomized block design with four replicates for each cross and one replicate for each parent was used in these studies. Each experimental plot contained 12 subplots distributed within three adjacent rows with 1.5 m between rows and 0.9 m between subplots within rows. The fields of both parent and progeny populations were ratooned in July 1976. Each clone of the ration crop was rated according to the percentage of stalks infected with smut race A in January 1977.

In January 1977, two three-bud uninoculated stem cuttings excised from each of the clones in the propagation field were hot-water treated and planted again in a nearby field. After nine months of growth, two three-bud stem cuttings were excised from each parent and each progeny clone, immersed for 10 min in a smut (race B) spore suspension $(5 \times 10^{-6}$ spore/ml H₂O), and randomly planted in subplots $(1.5 \times 0.9 \text{ m})$ within a plot in an isolated area where only race B spores were present. The field was ratooned in June 1978. The clones of the ratoon crop were rated for smut race B infection in March 1979. Smut rating in the ratoon was based on the scale presented in Table 1 (Wu et al. 1983). On a practical basis, individuals with a grade of 5 were also considered susceptible.

Frequency distributions of smut resistance (smut grade) were used to show the phenotypic differences between sugarcane populations in reaction to each race, while simple linear correlations were used to estimate the degree of association of smut reaction of clones between the two races.

Progeny analysis

For genetic analysis, the seven sets of factorials used in this study were analyzed individually using plot means and then pooled into one analysis of variance. Smut ratings of individual clones in subplots within each plot were used to calculate the within-plot variance. The sources of variation, degrees of freedom, and expected mean squares of the pooled analysis of variance using plot means are represented in Table 2.

Estimates of variance components were obtained by using the following equations or estimators:

$$\sigma_{m}^{2} = (M-I)/A, \ \sigma_{f}^{2} = (F-I)/B, \ \sigma_{mf}^{2} = (I-E)/C, \ \text{and} \ \sigma_{e}^{2} = E.$$

| Grade | % of infected stalks | Description |
|-------|----------------------|--------------------|
| 1 | 0 | Highly resistant |
| 3 | 1-15 | Resistant |
| 5 | 16-20 | Intermediate |
| 7 | 21-50 | Susceptible |
| 9 | 51-100 | Highly susceptible |

Table 2. Sources of variation, degrees of freedom (df), and expected mean squares of the pooled analysis of variance using plot means

| Source of variation | df | Mean squares | Expected mean squares |
|---------------------|-----|-----------------|---|
| Sets | | | |
| Replicates/sets | 21 | | |
| Males/sets | 20 | Μ | $\sigma_e^2 + C\sigma_{mf}^2 + A\sigma_m^2$ |
| Females/sets | 22 | F | $\sigma_{e}^{2} + C\sigma_{mf}^{2} + B\sigma_{f}^{2}$ |
| Male × females/sets | 66 | Ι | $\sigma_e^2 + C \sigma_{mf}^2$ |
| Whole-plot error | 324 | E | $\sigma_{\rm e}^2$ |

Where A, B and C are the coefficients of variance components; C=(the weighted average number of replications per set); A=(the weighted average number of female parents replications per set); B=(the weighted average number of male parents replications per set); and the weights are the degrees of freedom per set

The within-plot variance component (σ_w^2) (Table 3) was determined by pooling within-plot variances from the 450 progeny plots in this study. Values of variance components were used to calculate the estimates of environmental and genetic parameters.

Environmental parameters in this study were plot-to-plot variance (σ^2_{plot}) and within-plot plant-to-plant variance $(\sigma^2_{\text{plant}})$. Their estimates were obtained by

$$\sigma_{e}^{2} - (1/n) \sigma_{w}^{2} (= \sigma_{plot}^{2})$$

and

a

$$\sigma_{\rm w}^2 - \sigma_{\rm m}^2 - \sigma_{\rm f}^2 - 3 \sigma_{\rm mf}^2 (= \sigma_{\rm plant}^2);$$

where n is the harmonic mean of the number of surviving individuals in each plot.

Genetic parameters in the progeny population were additive genetic variance (σ^2_A) and non-additive genetic variance (σ^2_{NA}) , neglecting the components of epistatic variance. Their estimates were obtained through the following equations:

$$\sigma^2_{\rm A} = 2 \left(\sigma^2_{\rm m} + \sigma^2_{\rm f} \right)$$

and

$$\sigma^2_{\rm NA} = 4 \sigma^2_{\rm mf}.$$

The estimate of total genetic variance (σ^2_G) in the progeny population was the sum of σ^2_A and σ^2_{NA} or $2(\sigma^2_m + \sigma^2_f) + 4\sigma^2_{mf}$.

The phenotypic variance, defined as the sum of the genetic and environmental variance in the progeny population, could be estimated on the basis of an individual (σ^2_{P1}), a plot mean (σ^2_{P2}) , or a family mean (σ^2_{P3}) . Their estimators were

$$\sigma_{P1} = \sigma_{plant}^2 + \sigma_{plot}^2 + \sigma_G^2, \ \sigma_{P2}^2 = (1/n) \ \sigma_{plant}^2 + \sigma_{plot}^2 + \sigma_G^2,$$

and

$$\sigma^2_{P3} = (1/4 \text{ n}) \sigma^2_{plant} + (1/4) \sigma^2_{plot} + \sigma^2_G.$$

Heritability (h) in the narrow sense for smut resistance in the progeny and reference populations, represented by the 50 randomly selected parents, was estimated by the following equations:

individual plant basis $h_1 = \sigma_A^2 / \sigma_{P1}^2$ plot mean basis $h_2 = \sigma_A^2 / \sigma_{P2}^2$

and

family mean basis $h_3 = \sigma^2_A / \sigma^2_{P3}$.

Similarly, heritability (H) in the broad sense was estimated by

H 1 = $\sigma_G^2 / \sigma_{P1}^2$, H 2 = $\sigma_G^2 / \sigma_{P2}^2$, and H 3 = $\sigma_G^2 / \sigma_{P3}^2$

respectively, on the basis of an individual, a plot mean, and a family mean.

Parent analysis

Parental clones were analyzed by using a one-way analysis of variance, with among-clones and within-clones as sources of variation in each of the seven sets. Pooled mean squares were used to calculate the variance components among clones (σ_c^2) and among plants within clones (σ_p^2) . The estimate of total genetic variance (σ_G^2) in the parent population was σ_c^2 and the estimate of plant-to-plant environmental variance (σ_{plant}^2) was σ_p^2 . Heritability in the broad sense (H) in the parent population was estimated by $\sigma_G^2/(\sigma_{plant}^2 + \sigma_G^2)$.

The environmental variations estimated in this study were limited to microenvironments – that is, the within-plot and among-plot environment. Macroenvironments, such as locations and years, were not available in the study.

Parent and progeny analysis

Additional estimates of additive genetic variance (σ_A^2) and narrow sense heritability (h) on a family mean basis for the reference population were obtained, respectively, by using the covariance of the family mean and the mid-parent value and the regression coefficient of the family mean on the mid-parent value.

The linear regression of the family mean on the midparent and the linear regression of percentage of susceptible progeny (having smut grades higher than 3) on the midparents were used, respectively, to predict the average smut grades and the percent of smut susceptible individuals in the progeny of parents with known smut resistance.

Results

Degrees of association of plant reactions to smut races

The frequency distributions of smut grades for both races and for parent and progeny populations are shown in Fig. 1. The percentage of parents with smut grades ≤ 3 were 73% and 16%, respectively, for races A



Fig. 1. Frequency distribution of parents and progeny population for smut grades of *races* A and B

and B; in the progeny population, the respective values were 70% and 33%. Both parents and progeny were more resistant to smut race A than to race B.

Although smut grades appear to be discrete, they measure the degree of sugarcane's susceptibility or resistance that is continuous in nature, which precludes analysis on the basis of discrete units.

The degree of association estimated by using simple linear correlation between smut grades of race A and race B for the progeny population was 0.18 which is significantly different from zero.

Progeny analysis

The mean squares for the source of variation of male, female and male \times female interactions were highly significant (Table 3). Their variance components (Table 4) were about equal between the two smut races except for the component of male \times female interactions where the estimated values were more than doubled.

The estimates of environmental, genetic, and phenotypic variance, and heritabilities for the resistance to both races A and B are shown in Table 5. All the estimates, being larger than twice their standard errors, are quite reliable. Environmental and phenotypic variances were about equal between the two races, but genetically there was more nonadditive genetic variance for race B than for race A. Heritabilities were low at individual level but were medium to high at plot-mean and family-mean level for both races.

Table 3. Degrees of freedom, mean squares, and expected mean squares of the pooled analysis in the progeny population. $\sigma_e^2 = (1/n) \sigma_w^2 + \sigma^2$ plot-to-plot; where n is the harmonic mean of the number of plants per plot, which were 9.7 and 7.2 for the tests of smut races A and B, respectively. $\sigma_w^2 = \sigma^2$ plant-to-plant+some genetic variance

| Source of variation | df | Mean sq | Expected | |
|------------------------|-------|---------|----------|--|
| | | Race A | Race B | mean squares |
| Using plot means: | | | | |
| Males | 20 | 12.82** | 10.62** | $\sigma_{e}^{2} + 4\sigma_{mf}^{2}$ + 17.2 σ_{m}^{2} |
| Females | 22 | 12.76** | 12.96** | $\sigma_e^2 + 4\sigma_{mf}^2$ + 16.0 σ_f^2 |
| Males × females | 66 | 2.03** | 3.56** | $\sigma_a^2 + 4\sigma_{mf}^2$ |
| Whole-plot error | 324 | 1.12 | 1.41 | σ_{e}^{2} |
| Using plants within pl | ot: | | | |
| Within-plot | 4,339 | 8.97 | | σ_{w}^{2} |
| ± | 3,436 | _ | 8.53 | $\sigma_{\rm w}^2$ |

** Significant at 0.01 probability level

 Table 4. Estimates of variance components in the progeny population

| Statistic | Race A | Race B | |
|---------------------|-----------------|-----------------|--|
| $\sigma_{\rm m}^2$ | 0.63 ± 0.22 | 0.41 ± 0.19 | |
| $\sigma_{\rm f}^2$ | 0.67 ± 0.23 | 0.59 ± 0.24 | |
| $\sigma_{\rm mf}^2$ | 0.23 ± 0.10 | 0.54 ± 0.16 | |
| σ_{e}^{2} | 1.12 ± 0.09 | 1.14 ± 0.11 | |
| $\sigma_{\rm w}^2$ | 8.97 ± 0.19 | 8.53 ± 0.21 | |

Parent analysis

Environmental, genetic, and phenotypic variance, and heritability for resistance to both races A and B are shown in Table 6.

Plant-to-plant environmental variance in the parent population estimated by the within-plot variance component was purely environmental with no confounding genetic variance. This was because the plants in each subplot of a plot were clones of the same genotype, whereas progeny plots consisted of subplots of clones, each with different genotype.

Plant-to-plant environmental variation for race B, estimated from the parent population, was 5.54. When estimated from the progeny population it was 5.91. Both estimates are in close agreement.

Plant-to-plant environmental variation for race A, estimated from the parent population, was 2.72. When estimated from the progeny population, 6.99. The difference was highly significant.

Plot-to-plot environmental variance was confounded with the clonal variance component because there was only one replication for each parent.

Total genetic variance in the parent population was estimated by the clonal variation component, being 7.35 and 5.76, for A and B, respectively. The higher genetic variance for race A compared to race B was due to low plant-to-plant environmental variance for race A (2.72 vs. 5.54), since the total phenotypic variance for both races was about equal: 10.07 vs. 11.30.

Heritability in the broad sense on an individual basis has no practical meaning, because plants within

Table 5. Estimated environmental, genetic, and phenotypic variance, and heritabilities for the progeny population. (σ^2 plot, σ^2 plant) =(plot-to-plot, plant-to-plant environmental variance). ($\sigma^2 A$, $\sigma^2 NA$, $\sigma^2 G$)=(additive, non-additive, total genetic variance). ($\sigma^2 P1$, $\sigma^2 P2$, $\sigma^2 P3$)=(phenotypic variance on an individual, a plot mean, and a family mean basis). h=heritability in the narrow sense; H=heritability in the broad sense; 1=on an individual basis; 2=on a plot mean basis; 3=on a family mean basis

| Environmental variance [*] | | Genetic variance | | Phenotypic variance* | | Heritability ^a | |
|--|-------------------------------|---|---|--|---|---|---|
| Race A | Race B | Race A | Race B | Race A | Race B | Race A | Race B |
| $\sigma^{2} \text{ plot} = 0.19$ ± 0.09 $\sigma^{2} \text{ plant} = 6.99$ ± 0.44 | $0.23 \pm 0.11 5.91 \pm 0.54$ | $ \begin{array}{rcl} \sigma^{2}A &= 2.60 \\ \pm 0.65 \\ \sigma^{2}NA &= 0.91 \\ \pm 0.36 \\ \sigma^{2}G &= 3.51 \\ \pm 0.70 \end{array} $ | $\begin{array}{c} 2.00 \\ \pm 0.62 \\ 2.15 \\ \pm 0.62 \\ 4.15 \\ \pm 0.76 \end{array}$ | $\sigma^{2}P1 = 10.69$ ± 0.37 $\sigma^{2}P2 = 4.42$ ± 0.67 $\sigma^{2}P3 = 4.28$ ± 0.66 | $10.29 \\ \pm 0.37 \\ 5.20 \\ \pm 0.69 \\ 5.03 \\ \pm 0.70$ | $h1 = 0.24 \pm 0.05 \\ h2 = 0.59 \pm 0.08 \\ h3 = 0.61 \pm 0.08 \\ H1 = 0.33 \pm 0.06 \\ H2 = 0.79 \\ H2 = 0.79 \\ H2 = 0.79$ | $\begin{array}{c} 0.19 \\ \pm 0.06 \\ 0.38 \\ \pm 0.09 \\ 0.40 \\ \pm 0.10 \\ 0.40 \\ \pm 0.07 \\ 0.80 \\ \pm 0.05 \end{array}$ |
| | | | | | | ± 0.05 H3 = 0.82 ± 0.04 | ± 0.05 0.83 ± 0.04 |

^a All the estimates in the table were larger than $2 \times SE$

| Environmental variance | | Genetic variance | | Phenotypic variance | | Heritability | | | |
|---|---------------|------------------|------------------|---------------------|---------------|----------------------|--------------------------------------|----------------------|--|
| Race A | Race B | Race | A | Race B | Race | A | Race B | Race A | Race B |
| $\sigma^2 \text{ plant} = 2.72 \\ \pm 0.17$ | 5.54 ±0.36 | σ²G | = 7.35 ± 1.53 | 5.76 ±1.3 | $\sigma^2 P1$ | =10.07 ± 1.54 | 7 11.30 H1 = (± 1.37 $\pm ($ | $H1 = 0.74 \pm 0.02$ | 0.51 ±0.07 |
| | | | | | σ² P2 | = 7.63 ± 1.53 | 6.36 ±1.31 | $H2 = 0.96 \pm 0.01$ | $\begin{array}{c} 0.91 \\ \pm 0.04 \end{array}$ |

Table 6. Estimated environmental, genetic, and phenotypic variance, and heritabilities in the parental population. H1 = Heritability in the broad sense on an individual basis; H2 = Heritability in the broad sense on a plot mean basis

Table 7. Predicted average smut grade and % susceptible individuals (with smut grade > 3) in the progeny of parents with known smut grades for smut races A and B

| Smut race | Parent average | Predicted | | | |
|--------------|----------------|---------------------------------|-----------------------------|--|--|
| | (X) | Progeny average grade (G) | Susceptible progeny % | | |
| | 1 | 2.30 ± 1.02 | 17.62 ± 13.73 | | |
| Α | 5 | 4.37 ± 1.03 | 45.10 ± 13.83 | | |
| | 9 | 6.43 ± 1.07 | 72.58 ± 13.87 | | |
| | 1 | 3.12 ± 0.99 | 38.10 ± 13.38 | | |
| В | 5 | 5.02 ± 0.97 | 61.79 ± 13.54 | | |
| | 9 | 6.92 ± 0.98 | 85.51±13.95 | | |

each plot were the same genotype. Heritabilities in the broad sense on a plot mean basis were 0.96 and 0.91 for Races A and B, respectively, indicating that grades based on plot means are highly repeatable between asexual generations.

Parent and progeny analysis

Additive genetic variance of the reference population estimated from the parent-offspring covariance were 3.00 ± 0.40 and 2.92 ± 0.42 ; heritabilities in the narrow sense on a family mean basis were 0.51 ± 0.05 and 0.47 ± 0.06 for races A and B, respectively.

Regressions

The simple linear regression for the progeny average smut grade (G) on the parent average smut grade (X) and for the percentage (%) of smut susceptible progeny (with smut grade > 3) on X is:

G = 1.779 + 0.51 X for race A G = 2.651 + 0.47 X for race B % = 10.75 + 6.87 X for race A % = 32.14 + 5.93 X for race B

The regression coefficients were all highly significant $(0.51 \pm 0.05, 0.47 \pm 0.06, 6.87 \pm 0.69, \text{ and } 5.93 \pm 0.76)$.

The predicted average smut grade and % susceptible individuals in a future progeny of parents with known average smut grades of 1, 5 and 9 are shown in Table 7. The prediction indicates that not all progeny from highly susceptible parents are suceptible to the disease. Where both parents were highly susceptible (grade 9) the progeny averaged 72.58% susceptible to smut race A and 85.51% to smut race B.

Discussion

The positive correlation (=0.18) for resistance to both races in the progeny population was statistically significant. However, because $r^2 < 4\%$, the correlation is considered not important on a practical basis, which may be further explained by the following:

As shown in Fig. 1, more parents (73%) were resistant to race A as a result of selection for smut resistance in the reference population in the five years prior to the introduction of race B. The clones in the reference population had not been exposed to smut race B when the crosses for this study were made; therefore, the parent clones in the study were considered as a random sample, representative of the reference population in relation to their reaction to race B. The low frequency (16%) of parent clones resistant to race B reflects little association between resistance to both races. Selection for resistance to smut race A in the reference population had little effect on the frequency of clones resistant to smut race B.

In our breeding and selection system, the reference population is vegetatively maintained. Selection in the reference population for smut resistance is routinely based on plot mean of a clone. Selection could be performed also on a progeny test based on family means. On a plot mean basis, broad sense heritability can be used on the reference population between asexual generations, while on a family mean basis, narrow sense heritability can be used between the reference population and a future progeny population. In the future progeny population, breeders are more interested in predicting the average smut grade rather than the expected genetic gains. For the future reference population, smut susceptible clones are either discarded from the current population or saved for other uses.

In a progeny population, selection for smut resistance follows a multistage process of smut testing through asexual generations. In first stage or small plot (subplot) stage, the selection is based on smut grade of an individual plant. In second and later stages, or large plot (whole plot) stages, selection is based on plot means - the average smut grade of plants of the same clone (genotype). Conducting multistage smut tests ensures that the final smut grade of a clone on a plot mean basis is repeatable. Broad sense heritability can be used in the progeny population to measure repeatability. The purpose of selection in the progeny population is to identify both smut resistant and high yielding progeny clones, which would be advanced to the future reference population as new breeding materials. The smut ratings of the new breeding materials thus selected are all recorded on plot mean basis.

Low broad sense heritability on an individual basis supports smut testing on plot-mean basis. Similarly, low narrow sense heritability on an individual basis suggests that clones should be evaluated as parents either on a plot-mean or on a family-mean basis. Since heritability on a family-mean basis is only a little higher than that on a plot mean basis in this study, it suggests that the family size could be reduced to a size similar to the plot size without seriously affecting estimates of heritabilities.

Narrow sense heritability on a family mean basis and broad sense heritability on a plot mean basis are discussed further below. To avoid confusion, the aforementioned plot mean is the mean of plants of a single genotype rather than of many genotypes.

The environmental variations estimated in this study were limited to microenvironments – that is, the within-plot and among-plot environments. Macroenvironments, such as locations and years, were not available in the study for two reasons: 1) routine smut testing is intentionally confined to one location per race to keep the smut spores from spreading, and 2) uninfected stalk cuttings of the progeny in the study were not available for smut test over years.

The within-plot microenvironmental variance estimated from the progeny population was confounded with some epistatic genetic effects; but within-plot plant-to-plant variance as estimated from the parent population was all environmental because plants within a plot were plants of the same genotype. For smut race B, variance was 5.91 vs. 5.54 as estimated from progeny vs. parent population respectively. Both estimates are in close agreement, an indication of low epistatic effects in the progeny population. For smut race A, it was 6.99 vs. 2.72. The low value of 2.72 probably occurred because more than 50% (Fig. 1) of the parent population was resistant to race A. Plants within a plot of a resistant parental clone showed almost no variation on smut grades. This is an indication that plant-to-plant environmental variation in large-plot smut testing is not independent of the distribution of smut resistance in the test population. A higher percentage of resistant individuals in a population will give a lower plant-to-

plant environmental variance estimate. The total genetic variance in the progeny population for races A and B was close, i.e., 3.51 vs. 4.15. However, the proportion of additive genetic variance was about 74% for the resistance of smut race A and 48% for smut race B. Additive genetic variance is more important for resistance to race A while additive and non-additive genetic variance both are important for the resistance to race B. It should be easier to control smut race A than race B through cross breeding.

Because the experiments of the study were conducted on confined locations and over one test, estimated genetic variance is therefore defined on testing locations and confounded with the genetic (G) and year (Y) interaction variance. The GY interaction variance is considered unimportant because the rank for highly susceptible or highly resistant clones does not change dramatically over years of smut testing. Nevertheless, with this confounding, the genetic variances and the heritabilities estimated from progeny, parent, and both progeny and parent analyses were in fair agreement. The ratios of additive genetic variance between estimates from parent-progeny and progeny analysis were 3.00/2.6 (=1.15) and 2.92/2.0 (=1.46) for races A and B, respectively. The ratios of total genetic variance estimated from parent and from progeny analysis were 7.35/3.51 (=2.09) and 5.76/4.15 (=1.39) for races A and B, respectively. In both cases, the values of the ratios were greater than 1. The theoretical ratio is 1 if there is no epistatic variance and is greater than 1 if there is epistatic variance (Hogarth 1977). Epistatic variance appears to be unimportant since differences between the estimates were not great except for the total genetic variance for race A. The high ratio of 2.09 was due to a high total genetic variance of 7.35, caused by a low within plot plant-to-plant environmental variance (2.72) estimated from the parent population for race A; while the plant-to-plant environmental variance was 6.99, estimated from the progeny population. The large difference in plant-to-plant environmental variances makes the total genetic variance for race A incompatible between the two analyses.

Estimates of broad sense heritability on a plot mean basis from the parent population were 0.96 vs. 0.91 for race A vs. race B. The estimates were considered higher than expected because the total genetic variances (7.35

vs. 5.76) were confounded with plot-to-plot variances due to only one replication being used in the parent population. If 7.35 and 5.76 are adjusted by the plot-toplot variance (0.19 vs. 0.23) estimated from the progeny population, the total genetic variances would be 7.16 vs. 5.53 and the adjusted estimates of broad sense heritability would be 0.94 vs. 0.87. It indicates that smut ratings are very reliable and selection for smut resistance is very effective between asexual generations. This means that in a couple of years, smut resistance of each clone in a population can be identified easily, and susceptible clones can be discarded as desired from the population. However, in reality, selection is not only for smut-resistant clones but for both smut-resistant and high-yielding clones. In the reference population, if there are few high yielding clones with smut resistance, other clones in the reference population that are high yielding and susceptible should not be discarded (Walker 1980) but be discarded later when more clones with smut resistance and high yielding potential are selected from the progeny population and advanced to the future reference population. In the progeny population, however, susceptible progeny can be discarded early. Because a very low correlation exists between yield components and clonal resistance to races A and B (Wu et al. 1983; Wu and Heinz 1983), discarding susceptible progeny in the early stages of selection will not cause a serious bias in selecting progeny combining smut resistance and high yield potential.

Estimates of narrow sense heritability (h) on a family mean basis from progeny and from parentprogeny regression analysis were in fair agreement; 0.61 vs. 0.51 for race A and 0.40 vs. 0.47 for race B. Both estimates indicate h is close to a value of 0.5. This moderate heritability means that selecting and breeding for smut resistance should result in a fairly rapid increase in the frequency of resistance between sexual generations. In this case, selection of clones from the reference population as parents of a future progeny population is based on family means in an experimental progeny population (= the progeny population of this study), not from the smut grades of the clones themselves. Selection differential (s) is also determined in the experimental progeny population. Once s is known, genetic gain in the future progeny population can be estimated. However, selecting parents, determining s and genetic gain are not easy because an experimental progeny population has to be raised in advance. Furthermore, genetic gain in smut resistance is of no clear use to sugarcane breeders. In sugarcane, an individual, not a family of individuals, is the final goal of selection.

Based on individual performance, clones in the reference population can be selected as parents. Regressions can be used to predict the average smut grade and the percentage of smutted individuals of a family from the smut average grade of their parents. In this case selection in the reference population is on a plot mean basis. Parent selection on a plot mean basis is much easier than on a progeny family mean basis. Using regression, smut information can be obtained in advance and on each family (or cross) basis, which helps breeders in the determination of family size. For smut resistance, regression seems more useful and easier to use than narrow sense heritability between sexual generations.

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