Heritability Estimates for Reaction Resistance to Sweetpotato Chlorotic Leaf Distortion Caused by *Fusarium lateritium*

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Abstract. Narrow-sense heritabilities for reaction to chlorotic leaf distortion (CLD), incited by *Fusarium lateritium* Nees: Fr., were estimated in sweetpotato [*Ipomoea batatas* (L.) Lam] by variance component analysis and parent–offspring regression. Visually rated severity reactions to CLD varied greatly among the 20 parents used to generate half-sib progeny from open-pollinated nurseries in 1990 and 1991. Progeny from each nursery were evaluated along with parents in a completely randomized design in two consecutive years. Narrow-sense heritability (h^2) estimates based on variance components were moderate on an entry mean basis at 0.61 in 1990, 0.38 in 1991, and 0.33 for the two years combined. Slightly higher, but still moderate, estimates were obtained on an individual plant basis. Narrow-sense heritability estimates using parent–offspring regression were 0.35 in 1990, 0.33 in 1991, and 0.33 for the two years combined. Predicted next-generation response was highest using a half-sib family recurrent selection among three schemes compared at a 10% selection intensity. Our data indicate –0.63 improvement in the half-sib family CLD severity rating in one breeding cycle.

Chlorotic leaf distortion (CLD) is a widely distributed disorder of sweetpotato incited by *Fusarium lateritium* (Clark et al., 1990). This exopathogen is unique among *Fusarium* species in that it grows on and within a mucilage-like material, possibly excreted by pearl glands located on the apical meristem, leaf primordia, and young leaves of sweetpotatoes (Clark, 1992). Generally, *Fusarium* spp. cause cortical rots, root rots, and vascular wilts on sweetpotato (Clark and Moyer, 1988).

Fusarium lateritium appears as a white epiphytic material consisting of fungal hyphae and macroconidia on newly formed leaves. Under periods of bright sunlight and vigorous growth, infected young leaf tissue becomes chlorotic and, less frequently, distorted and twisted. Under cloudy weather, all leaves on plants recover from chlorosis. Expanded, mature leaves recover from chlorosis even under bright sunlight.

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The objective of this study was to obtain narrow-sense heritability estimates to determine the effectiveness of breeding for reaction to *F. lateritium* on sweetpotato. This study was a part of a larger one to identify the effects this disease has on the growth, development, and economic impact on sweetpotato.

Materials and Methods

Plant material and experimental design. In 1990 and 1991, 20 genetically varied sweetpotato selections obtained from the U.S. Dept. of Agriculture–Agricultural Research Service, U.S. Vegetable Laboratory, Charleston, S.C., were replicated once in each row of a 12-row, open-pollinated, crossing nursery (Table 1). In 1991 and 1992 field tests, the parents and progeny from the previous-year's nursery were evaluated for their reaction to *F. lateritium*. A randomized complete-block design with three replications was used. Each parent was represented in each block by a five-plant plot of the parental clone and five half-sib progenies.

Inoculation and disease assessment. All transplants were inoculated with a suspension of 1.0×10^6 macroconidia and microconidia from a single-spore-derived colony of *F. lateritium* isolate 91-27-2 from Puerto Rico, identified and described by Clark et al. (1995). The inoculum was prepared by washing the surface of a 5- to 7-day-old PDA petri dish culture (90 mm in diameter) with 100 ml of sterile distilled water.

Plants were evaluated for reaction to *F. lateritium* 114 and 68 days after planting in 1991 and 1992, respectively, after >4 days of sunny weather that resulted in severe symptom expression. The following CLD severity

index was used: 0 = no symptoms; 1 = slight epiphytic white growth of fungus on youngest leaf; 2 = extensive epiphytic growth on youngest leaves, no chlorosis or other symptoms; 3 = same as 2 plus mild chlorosis on youngest expanded leaf; 4 = same as 3 except chlorosis on two to three leaves, severe on youngest leaf; 5 = same as 4 with leaf distortion and marginal necrosis on any of the youngest leaves.

Heritability estimates. Variance components based on half-sib family analyses, assuming a completely random model, provided estimates of narrow-sense heritability on an individual plant basis (h^2) and on a half-sib family basis (h_f^2) for each year. Respective equations for these estimates were (Nyquist, 1991):

$$h^2 \equiv \frac{\sigma_A^2}{\sigma_P^2} = \frac{4\sigma_f^2}{(\sigma_f^2 + \sigma_e^2 + \sigma_w^2)}$$

$$h_f^2 \equiv \frac{\sigma_f^2}{\sigma_P^2} = \frac{\sigma_f^2}{(\sigma_f^2 + \sigma_e^2/r + \sigma_w^2/rp)}$$

where the additive genetic variance (σ_A^2) and the phenotypic variance among individuals (σ_P^2) are estimated by the variance of the mean genotypic values of families in the population (σ_f^2), the variance of the total plot effect within replications (σ_e^2), and the variance of the phenotypic values of individual plants within a plot (σ_w^2), which includes the variance of the genotypic values of half-sib individuals within families, the variance of interaction between individual genotypes and the environment, the microenvironmental effects variance, and the error variance. Subscripts “r” and “p” represent the number of replications and the harmonic mean of the number of plants per plot, respectively. The narrow-sense heritability for half-sibs family means (h_f^2) is estimated by the genetic family variance component (σ_f^2) in the numerator and the phenotypic variance among family means (σ_P^2) in the denominator. h_f^2 is suitable for predicting genetic gain in all half-sib selection schemes, being unbiased for the parent method and biased upward by $(1/32) \cdot \sigma_{AA}^2 + \dots$ for remnant seed method (Nyquist, 1991). Narrow-sense heritability for the two years combined was estimated as follows for individual plant and family mean data, respectively:

$$h^2 \equiv \frac{\sigma_A^2}{\sigma_P^2} = \frac{4\sigma_f^2}{(\sigma_f^2 + \sigma_{fy}^2 + \sigma_e^2 + \sigma_w^2)}$$

$$h_f^2 \equiv \frac{\sigma_f^2}{\sigma_P^2} = \frac{\sigma_f^2}{(\sigma_f^2 + \sigma_{fy}^2/y + \sigma_e^2/yr + \sigma_w^2/yrp)}$$

where σ_{fy}^2 = the variance of the mean interaction effects between family genotypes and years (y). The VARCOMP = REML procedure in SAS (1987) was used to calculate the variance components for all models. The stan-

dard errors for the heritability estimates were calculated using the delta method or Taylor series approximation (Bulmer, 1980). We assumed in our models that sweetpotato behaves as a normal diploid with mostly bivalent pairing and segregation (Jones, 1965) and that epistatic interactions are insignificant.

Genetic gain estimates. Theoretical genetic gain or the predicted, next-generation response was calculated at a 10% selection intensity. Response estimates are reported for three selection schemes: 1) half-sib, remnant seed, recurrent selection (i.e., remnant half-sib plants are combined in a nursery the following year based on the half-sib progeny tested the previous year); 2) half-sib parent recurrent selection (i.e., parents producing the selected half-sibs are recombined the following year); and 3) mass selection of half-sib individuals. Theoretical gains were estimated for the combined data set (1991 + 1992) using the following equations, respectively (Nyquist, 1991):

- 1) $R = h_f^2 \cdot i \cdot \sigma_{pf}$
- 2) $R = 2h_f^2 \cdot i \cdot \sigma_{pf}$
- 3) $R = c \cdot h^2 \cdot i \cdot \sigma_p$

where the expected response to selection, R , is estimated by h_f^2 , the narrow-sense heritability for half-sib family means averaged over locations, years, and replications; h^2 is narrow-sense heritability on an individual plant basis; c is the parental control factor for mass selection ($c = 0.5$); i is the standardized selection differential; σ_{pf} is the phenotypic standard deviation among family means; and σ_p is the phenotypic standard deviation of the individual plant.

Twice the simple linear regression coefficient of individual offspring scores on their respective parent means (Falconer, 1960) provided a second estimate of narrow-sense heritability (h^2). This estimation relies heavily on the assumption that no environmental correlations (genotype $\times$ environmental interaction) exist for parents and progeny evaluated in the same environment. Since this assumption often fails (Casler, 1982), we regressed progeny means from one environment onto the parental values from a different environment to free the heritability estimates from the correlated bias (Nyquist, 1991). Hence, the heritability estimate based on the parent-offspring regression was calculated as the mean of the regression coefficients of the 1991 offspring values regressed on the 1992 parental mean and the 1992 offspring values regressed on the 1991 parental mean. The regression coefficients and the standard error of the estimates were obtained using the PROC GLM procedure (SAS, 1987).

Preliminary analysis of the data set showed homogeneous variances to exist between years and between families using Levene's test (Milliken and Johnson, 1992). We, additionally, found the data set to be normally distributed using Q-Q and stem and leaf plots; these two tests are all PROC UNIVARIATE procedures in SAS (1985).

Table 1. Mean chlorotic leaf distortion (CLD) indices of parents and their progeny in 1991, 1992, and for the two years combined.

Parent	CLD index					
	1991		1992		1991 + 1992	
	Parent	Progeny	Parent	Progeny	Parent	Progeny
W-125	2.0	1.9	0.7	1.0	1.3	1.4
W-151	2.0	1.9	2.6	1.9	2.3	1.9
W-152	1.9	1.7	1.7	0.9	1.8	1.3
W-201	0.3	1.9	1.9	0.8	1.1	1.4
W-231	2.5	2.0	2.5	1.8	2.5	1.9
W-233	0.4	1.0	1.5	0.3	0.9	0.6
W-235	1.4	1.9	0.9	1.2	1.1	1.5
W-240	0.4	0.9	1.3	1.3	0.8	1.1
W-240	0.1	0.6	0.4	1.0	0.2	0.8
W-255	0.7	0.6	1.1	0.5	0.9	0.6
W-265	1.6	1.9	1.5	0.5	1.6	1.2
W-268	1.5	1.4	1.1	0.4	1.3	0.9
W-270	1.6	1.6	0.6	0.4	1.1	1.0
W-271	0.4	1.4	1.1	0.9	0.7	1.1
W-272	1.9	1.3	1.7	1.8	1.8	0.5
W-273	1.5	1.5	1.4	1.0	1.4	1.2
W-274	0.1	0.2	1.0	0.7	0.5	0.4
W-275	0.5	0.5	0.3	0.5	0.4	0.5
W-276	0.0	1.3	1.0	1.2	0.5	1.2
85DW-8	1.4	0.7	1.1	1.2	1.3	0.9

Table 2. Additive genetic variances, phenotypic variances, and heritabilities for each year and for the two years combined from a half-sib family analyses and parent-offspring regression.

Procedure	1991	1992	1991 + 1992
Half-sib family analysis			
Individual plant basis			
Additive variance	0.61 $\pm$ 0.47	0.30 $\pm$ 0.28	0.30 $\pm$ 0.26
Phenotypic variance	1.00 $\pm$ 0.14	0.77 $\pm$ 0.09	0.90 $\pm$ 0.09
Narrow-sense heritability (h^2)	0.61 $\pm$ 0.18	0.38 $\pm$ 0.29	0.33 $\pm$ 0.17
Family mean basis			
Additive variance	0.15 $\pm$ 0.12	0.07 $\pm$ 0.01	0.07 $\pm$ 0.06
Phenotypic variance	0.30 $\pm$ 0.11	0.16 $\pm$ 0.06	0.16 $\pm$ 0.06
Narrow-sense heritability (h_f^2)	0.51 $\pm$ 0.24	0.45 $\pm$ 0.12	0.45 $\pm$ 0.20
Parent-offspring regression			
Narrow-sense heritability (h^2)	0.35 $\pm$ 0.13	0.33 $\pm$ 0.13	0.33 $\pm$ 0.13

Results and Discussion

Chlorotic leaf distortion severity index means for parents ranged from 0.2 to 2.5 for the two years combined (Table 1). This difference represents a broad range of susceptibility to the reaction of *F. lateritium* since mean ratings >2.5 have only been observed consistently in highly susceptible NC-845 (2.7). Progeny severity index means ranged from 0.4 to 1.9 for the two years combined.

Narrow-sense family heritability (h_f^2) was 0.45 across the two years on a family mean basis and slightly lower at 0.33 on an individual plant basis, using variance component estimates (Table 2). Individual and family mean h^2 estimates were higher in 1991 than in 1992, and this difference represents the confounding interactions of the genotype, the pathogen, and the environment.

Comparable h^2 estimates based on parent-offspring regression were similar for each of the two years and when combined (Table 2). These narrow-sense heritability estimates, ≈ 0.33 , were similar to those obtained on an individual plant basis in 1991 and for the two years combined using variance component estimates.

Jones (1986) considered narrow-sense heritability estimates in the range of 0.4 or higher

for variance component-based estimates and estimates from regression analysis at 0.3 or higher as suitable for improving a given trait in sweetpotato. Our regression estimates meet these minimal criteria; however, we would expect genetic gain to be low per breeding cycle, and only through modifying our breeding scheme can we expect to meaningfully improve reaction resistance to CLD. Genetic gain estimates differ little at a 10% selection intensity using either a mass selection of half-sib individuals or half-sib, remnant seed, recurrent selection. Calculations show -0.27 and a -0.32 respective improvement in the overall CLD severity index rating per cycle. The greatest gain is expected using a half-sib parent recurrent selection scheme at -0.63 . This greater gain is attributed to better control over the parent population, i.e., the male contribution to the progeny in the next breeding cycle does not represent unselected, bulked pollen. This scheme is also more manageable since a smaller number of parents are crossed, not groups of individuals (families), and thus represents a practical method of breeding for resistance to CLD.

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