Heritabilities and Correlations for Pod Yield and Leafspot Resistance in Peanut (*Arachis hypogaea* L.): Implications for Early Generation Selection[1]

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ABSTRACT

The purpose of this study was to investigate early generation selection methods for the identification of peanut (*Arachis hypogaea* L.) crosses with combined high yield and disease resistance. Eleven crosses were chosen in the S_1 on the basis of yield and disease reaction. The S_2 was evaluated under natural disease infection for pod yield and leafspot resistance, causal organisms *Cercospora arachidicola* Hori and *Cercosporidium personatum* (Berk. and Curt.) Deighton. Resistance was measured by leaf necrotic area and defoliation. Narrow sense heritabilities for all the traits were estimated by sib analysis and regression of S_2 plant performance on S_1 plant performance. Genetic correlations among traits and the relative efficiency of indirect selection for all the traits were also computed. The results suggest that selection among crosses for all the traits would be advantageous in the S_1 (h^2_f=67 to 79%) as compared to individual plant selection (h^2_2=16 to 26%) or within family selection (h^2_w=3 to 5%). Selection of genotypes within crosses would be the poorest strategy in early generations. Negative genetic correlations were noted between yield and leafspot severity. The expected progress in increasing resistance of peanut genotypes through selection for yield (30 to 40% of the response from direct selection for resistance) indicated that selection for yield under disease pressure may be advantageous for developing high yielding, leafspot tolerant genotypes.

Key Words: Leafspot resistance, yield, early generation selection, breeding.

Early and late leafspot, caused by *Cercospora arachidicola* Hori and *Cercosporidium personatum* (Berk. and Curt.) Deighton, respectively, are important diseases in peanut (23). Smith (23) recently reviewed the symptoms, disease cycle, epidemiology, and current control measures for these diseases. Since fungicides to control leafspot increase production costs by 10% (6), developing genotypes that combine high yielding ability with sufficient amount of resistance to these diseases would be desirable.

Current evidence indicates that resistance to both these diseases is quantitatively inherited with a large additive effect (15, 18, 22, and 26). Recent work by Coffelt and Porter (6) indicates cytoplasmic factors may also be involved . The usefulness of heritability estimates and correlations between metric characters in designing breeding schemes and evaluating breeding programs has been reported (1, 7, 8, and 14).

Based on literature reviews of the quantitative genetics of peanut (11, 27, and 28), narrow and broad sense heritabilities for pod yield have ranged from 16 to 79% and 28 to 82%, respectively. High correlations between pod weight and number of pods, number of seeds, seed weights, and maturity traits have also been reported. Chiou and Wynne (5) obtained narrow sense heritability estimates of 24, 24, and 22% for yield, protein, and meat content, respectively. Broad sense heritabilities for the same traits were 62, 54, and 75%, respectively. Positive genetic correlations were found between fruit length, seed weight per 20 fruit, protein content, and yield; and between oil and protein content. They concluded that yield improvement through selection for correlated traits would not be as efficient as direct selection for yield itself. Nigam *et al.* (20) reported that weight per mature seed showed significant positive correlation with most of the vegetative traits, as well as mature pods per plant, mature pod weight, and mature seed per plant.

Although Higgins (13) stated in 1956 that "apparently susceptibility to leafspot is positively correlated with quantity and maturity of the nut-crop", there have been few investigations of the quantitative relationship between leafspot resistance and yield in peanuts.

The purpose of this study was to determine selection potential for leafspot resistance and yield by estimating narrow sense heritabilities and correlations for pod yield and disease severity in the segregating first selfed generation (S_1) of crosses between high yielding and leafspot-resistant peanut genotypes.

Materials and Methods

Design and Methods

The material used in this study came from a series of crosses initiated in the peanut breeding program at the University of Florida. The disease reactions of parental lines were reported by Monasterios (17). Five of these lines also showed high yielding ability and will be referred to as "high yielding". Sixty-nine crosses, including 49 single crosses and 20 double crosses, were made between leafspot resistant and high yielding peanut genotypes and were advanced to the S_1.

S_1 seed derived from single F_1 plants from each of the 69 crosses were evaluated in a field test planted May 17, 1983 at the main agronomy farm, University of Florida, Gainesville, where the soil type is an Arredondo fine sand (loamy, siliceous, hyperthermic Grossarenic Paleudult, pH 5.8). The experimental design was a randomized complete block (RCB) design, replicated four times. Standard University of Florida Cooperative Extension Service recommendations were followed for production, with the exception of fungicides, which were omitted. Entries were grown on 6.6 m single row plots spaced 0.91 m apart with 0.25 m between plants within the row. Spreader rows of the susceptible cultivar Florunner were planted every seventh row as a source of inoculum for leafspot disease. Four plants/cross/replication were selected randomly for evaluation. Information was recorded from each selected plant for disease reaction and dry pod yield per plant. Because distinguishing the differences between early and late leafspot is difficult in rapid field assessments, the leafspot readings were combinations of the two diseases. Laboratory verifications of leafspot disease on Florunner indicated approximately 90% of the necrotic area was caused by late leafspot. Three disease assessments were made on each plant. Two measurements of leaf necrotic area were made, each on the fifth fully expanded leaf from the top of the mainstem, using modified Horsfall-Barratt diagrams developed by Nevill and Littrell (19). The first necrotic area measurement was made

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120 days after planting (DAP) and will be referred to as LSA. The second reading was made 140 DAP and will be referred to as LSB. In addition, percent total defoliation was recorded on the mainstem at harvest (referred to as DEF). Entries were harvested 142 DAP.

In 1985, S_2 seed from 39 of these crosses were available. Eleven of these were selected on the basis of their S_1 average performance of the 12 best yielding plants from the 16 previously selected. The selection criteria were i) average S_1 yield, ii) highest ranking in terms of average S_1 yield and low average LSA, iii) highest ranking in terms of average S_1 yield and low average LSB, and iv) highest ranking in terms of average S_1yield and low average defoliation.

The 11 crosses were assigned at random to plots in a randomized complete block design replicated four times. The experiment was planted at the Green Acres agronomy farm of the University of Florida near Gainesville, on May 23, 1985. Soil type at this farm is the same as at the main agronomy farm. Conventional production practices were observed except for fungicide sprays, which were omitted. Border rows on either side of the field planted with the cultivar Altika were the source of inoculum for natural leafspot infection. Plots consisted of 11 rows, 2.4 m in length spaced 0.91 m apart, each randomly planted with one of the 12 S_1 selections from a given cross. Therefore, 528 rows (11 crosses x 12 plants x 4 replications) constituted the experiment, with 9 plants per row spaced 0.3 m apart, making a total of 4752 plants. Two competitive plants per row were selected, giving a total of 1056 plants evaluated. Data similar to that of the 1983 experiment were collected. Plants were also dug 142 DAP.

Statistical Analysis

A least squares mixed model with nested and cross classified effects was used to describe the performance of the S_2 lines as follows

$$y_{ijkl} = \mu + \alpha_i + \beta_{ij} + \gamma_k + \alpha\gamma_{ik} + (\beta\gamma)_{(ij)k} + \varepsilon_{ijkl}$$

y_{ijkl} = performance in the k^{th} rep of the l^{th} S_2 line from the j^{th} S_1 line from the i^{th} cross
μ = overall mean
α_i = fixed effect due to the i^{th} cross
β_{ij} = random effect due to the j^{th} S_1line in the i^{th} cross
γ_k = fixed effect arising from the k^{th} rep
$(\alpha\gamma)_{ik}$ = cross by rep interaction
$(\beta\gamma)_{(ij)k}$ = interaction of the j^{th} S_1 line in the i^{th} cross with the k^{th} rep
ε_{ijkl} = residual.

The relation of the S_1 lines to their S_1 parents was described by a linear regression model as follows.

$$y_i = B_o + B_1 x_i + E_i$$

where

y_i = continuous dependent variable representing the performance of the i^{th} S_2 line
B_o = intercept
B_1 = total regression coefficient
x_i = continuous independent variable representing the i^{th} S_1 parent performance
E_i = random error.

Heritability and Correlations Estimates

Heritabilities were estimated by two procedures:

1. By sib analysis

The analysis of variance was preformed using a mixed model least squares and maximum likelihood computer program (LSML76 [12]).

The sources of variation pertaining to the model and the expectations of mean squares are presented in Table 1.

Table 1. Sources of variation and expected mean squares for parameters of leafspot resistance in S_1 and S_2 field evaluations.

Sources of variation	d.f.	Expected mean square
Cross (c)	a-1	$\sigma^2_R + k_4\sigma^2_S + k_5\theta^2_C$
S_1 line	a(b-1)	$\sigma^2_R + k_4\sigma^2_S$
Rep	c-1	$\sigma^2_R + k_1\sigma^2_{Sr} + k_3\theta^2_r$
Cross x Rep	(a-1)(c-1)	$\sigma^2_R + k_1\sigma^2_{Sr} + k_2\theta^2_{Cr}$
S_1 line x Rep	a(b-1)(c-1)	$\sigma^2_R + k_1\sigma^2_{Sr}$
S_2 line (S_1 line x Rep)	abc (d-1)	σ^2_R

a = cross no. (11); b = no. of S_1 lines (12); c= replication no. (4)
d = S_2 line (S_1 line x replication) (2)

The following variance components were estimated:

σ^2_S = component arising from differences among the S_1 lines
σ^2_{Sr} = component arising from the interaction of S_1 lines with the different replications
σ^2_R = the component arising from differences within S_1 lines.

The total phenotypic variance for the individual S_1 lines performance was calculated as:

$$\sigma^2_{P_{S_1}} = \sigma^2_{S_1} + \sigma^2_{S_1 r} + \sigma^2_R$$

The intraclass correlation in the S_1 generation was estimated as

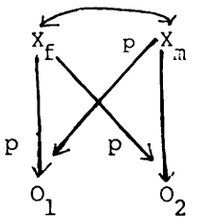
$$t = \frac{\sigma^2_{S_1}}{\sigma^2_{P_{S_1}}}$$

The narrow sense heritability of an individual measurement was computed by weighting it intraclass correlation by the inverse of the coefficient of relationship r_{oo}between two S_2 self-full-sibs as follows:

$$h^2 = \frac{t}{r_{oo}}$$

The coefficient of relationship was derived by adapting the method of Squillace (25) as follows:

Each S_1 parent was considered to be two individuals, X_f (female) and X_m (male), with coefficient of relationship $r_{X_f X_m} = 1$



S_1 generation $F_p = 0.5$

S_2 generation $F_O = 0.75$

The path coefficient from parents to their offsprings in each path were computed as:

$$p = \sqrt{\frac{0.5\ (1 + F_p)}{1 + F_O}} = 0.4629$$

Four paths connecting the two offspring were identified, the product of the path coefficients and correlations involved in each connecting path was computed, and the product for all paths were summed to give r_{oo} as follows:

$$O_1 X_f X_m O_2 = p \times r_{X X} \times p = 0.21427$$

$$O_1 X_f O_2 = p \times p = 0.21427$$

$$O_1 X_m O_2 = p \times p = 0.21427$$

$$O_1 X_m X_f O_2 = p \times r_{X X} \times p = 0.21427$$

$$r_{oo} = 0.857$$

The heritability of an individual measurement was further partitioned into the between family and the within family heritability as:

$$h_f^2 = \frac{1 + (n-1)\, r_{oo}}{1 + (n-1)\, t} h^2 \qquad h_w^2 = \frac{1 - r_{oo}}{1 - t} h^2$$

2. By parent-offspring regression

Narrow sense heritabilities between and within family were estimated by correcting the relevant regression coefficient for the relationship r_{op} between the S_2 and S_1 generations, $r_{op} = 0.75$ (24).

$$h^2 = \frac{b_{S_2S_1}}{2r_{op}}$$

$b_{S_2S_1}$ = regression coefficient of S_2 on S_1 generation

r_{op} = parent offspring coefficient of relationship

Components of covariance between pod yield and the various ratings of leafspot severity and among the leafspot severity readings were estimated using expected covariances as in Table 2. Phenotypic (r_p, genetic (r_A), and enviromental (r_E) correlations between pairs of traits x and y were computed from the relevant covariance and variance estimates as the ratio of their covariance ($Cov_{(xy)}$) over the product of the square roots of their respective variance estimates, $\hat{\sigma}^2_{(x)}$ and $\hat{\sigma}^2_{(y)}$ as follows:

$$r_{(x,y)} = \frac{Cov_{(xy)}}{\sqrt{\hat{\sigma}^2_{(x)} \times \hat{\sigma}^2_{(y)}}}$$

The total phenotypic covariance ($Cov_{P_{S_1}}$) was estimated in a manner analogous to the total phenotypic variance.

The additive variance ($\hat{\sigma}^2_{A_{S_1}}$) and covariance ($Cov_{A_{S_1}}$) components were obtained by multiplying the corresponding phenotypic value by r_{oo}.

The remaining enviromental components were derived from the above by subtraction as:

$$Cov_E = Cov_{P_{S_1}} - Cov_{A_{S_1}}$$

$$\hat{\sigma}^2_{E_{S_1}} = \hat{\sigma}^2_{P_{S_1}} - \hat{\sigma}^2_{A_{S_1}}$$

Table 2. Expected covariances for the relevant sources of variation for pairs of parameters of leafspot resistance in S_1 and S_2 field evaluations.

Sources of variation	d.f.	Expectation of mean products
S_1 line	a(b-1)	$Cov_R + k_4\, Cov_S$
S_1 line x Rep: (S_1r)	a(b-1)(c-1)	$Cov_R + k_1$ CovSr
Remainder	abc(d-1)	Cov_R

a = cross no. (11); b = no. of S_1 lines (12); c = replication no. (4)
d = S_2 line (S_1 line x replication) (2)

The efficiency of indirect selection relative to direct selection was calculated according to the method presented by Falconer (8) assuming equal selection intensity for all the traits but opposite in sign when addressing pod yield and leafspot severity ratings.

Results and Discussion

Least square means for pod yield per plant, LSA, LSB, average percentage leaf necrotic area (LSAB), and DEF were significantly different among selected crosses and replications ($p = 0.005$) (Table 3). Likewise, S_1 progeny lines differed for all traits studied. Average LSA for the S_1 progeny lines ranged from 1 to 7%, and for LSB from 2 to 10%. Average defoliation ranged from 70.5% to a high of 92.6%. Yield, in grams of dry pods/plants, extended from 26 to 242. For all traits except DEF, replications were a significant source of variation.

Variance components for the relevant sources of variation and heritability estimates from sib analysis are presented in Table 4. Narrow sense heritability estimates of all traits were 16 to 20%, 67 to 78%, and 3 to 5% for individual S_1 lines performance, family mean, and within family deviation, respectively. The estimate of narrow sense heritability of family mean for pod yield (73%) was comparable to the one reported for the same trait by Gibori *et al.* (10) in the F_2 of a 9 x 9 diallel among peanut genotypes.

Narrow sense heritability estimates obtained by parent-offspring regression procedure (Table 5) were generally lower than those estimated by variance components. Increased or decreased heritability estimates by this method may occur when parents and offspring are evaluated in separate environments (2,9). Scaling effects may have occurred in the two generations of this study. In 1983 there were 28 cm of rain in September, while in 1985 only 7.5 were recorded. This excess rainfall the first year of the study may have contributed to the more severe leafspot infestation recorded. The standard cultivar Florunner had a 35% increase in necrotic area and 20% more defoliation in 1983 than in 1985. The differences in the amount of the disease in the two enviroments used in this study, as well as the differences in pod yield due to mechanical and hand-harvesting in the S_1 and S_2 generations, respectively, may explain the overall downward bias on heritability estimates associated with the high standard error of estimation. An estimation of heritability in standard units (simple linear parent-offspring correlation coefficient corrected for previous inbreeding) has been suggested (2) to free the estimates from the differential environmental effect on parents and offspring. Fernandez and Miller (9) consi-

Table 3. Summary of the results of analysis of variance for parameters of leafspot resistance in S_1 and S_2 field evaluations

Sources	d.f.	Traits: Necrotic area (1st reading) LSA	Necrotic area (2nd reading) LSB	Necrotic area (average of the two:LSAB)	Defoliation	Pod Yield
Cross	10	45.47***	21.66***	32.13***	104.74***	17777.84***
S_1 line	121	3.72***	2.51***	2.51***	30.79***	2470.77***
Rep	3	64.30***	26.74***	42.47***	17.56***	8544.63***
Cross x Rep	30	4.05***	3.14***	2.47***	28.95***	2081.31**
S_1 line x Rep	363	2.15***	1.35***	0.96***	11.28ns	1196.71***
Remainder	*506-527*	*1.40*	*0.96*	*0.73*	*12.73*	*795.49*

*** significant at p=0.005

** significant at p=0.01

ns=nonsignificant

Table 4. Variance components, heritabilities (percent) for individual measurement (h^2) with standard error, family mean (h^2_f), and within family deviation (h^2_w) for parameters of leafspot resistance in field evaluations.

Traits	σ^2_S	σ^2_{Sr}	σ^2_R	σ^2_p	$h^2 \pm$ s.e. (%)	h^2_f	h^2_w (%)
Necrotic area (1st reading: LSA)	0.291	0.374	1.398	2.068	16.45 ± 9.95	67.23	2.74
Necrotic area (2nd reading: LSB)	0.223	0.197	0.962	1.382	18.82 ± 10.57	70.81	3.20
Necrotic area (average of the two: LSAB)	0.246	0.115	0.726	1.087	26.40 ± 12.26	78.96	4.87
Defoliation (DEF)	2.323	-0.483*	12.251	14.574	18.59 ± 10.51	70.51	3.16
Pod yield	211.953	202.533	795.495	1209.981	20.43 ± 10.96	72.83	3.54

* negative estimate has been set to zero in the calculations.

dered such estimates questionable because they might over-estimate heritability. When expressed in standardized units (Table 5), within family heritability, except for pod yield, showed a trend similar to that observed from sib analysis. For the between family heritabilities, the tendency was diverse and inconsistent except for pod yield. Enviromental changes apparently had more effect in modifying the disease reaction among than within families.

Biases in heritability estimates from intraclass correlation have also been studied. Allard (1) presented results showing that heritability estimates derived by this procedure would be biased upward by the G X E interaction if the test was conducted in a single environment. In the present study, that type of bias was partially compensated for by the variance component derived from S_1 lines by replication interaction. Ponzoni and James (21) reported that there was an inherent, but usually negligible, bias in the estimation of intraclass correlation. Some proportion of dominance and epistatic genetic variance generally causes an upward bias of the heritability estimated by any method. Cahaner and Hillel (4) showed that the degree of bias was greater for the parent-offspring procedure as compared to the family analysis method in the F_2 and F_3 generations of self-fertilizing species.

Our results support the finding of other workers that genetic studies involving disease resistance, especially when measured on a scale sensitive to enviromental changes, should be carried out at a single location with

Table 5. Regression coefficients and heritabilities for parameters of leafspot resistance for S_1 family mean and within S_1 family deviation estimated by parent-offspring regression.

Traits	Between family: $b_S \pm$ s.e.	Between family: $h^2_f \pm$ s.e.	Within family: $b_{WS} \pm$ s.e.	Within family: $h^2_w \pm$ s.e.
Pod yield	0.69 ± 0.48	0.46 ± 0.32 (0.29)	-0.04 ± 0.028	-0.026 ± 0.02 (0.032)
Necrotic area (1st reading: LSA)	-0.19 ± 0.09	-0.13 ± 0.06 (-0.37)	0.03 ± 0.014	0.02 ± 0.009 (0.043)
Necrotic area (2nd reading: LSB)	0.11 ± 0.03	0.073 ± 0.02 (0.53)	0.01 ± 0.005	0.006 ± 0.003 (0.057)
Necrotic area (average of the two: LSAB)	0.09 ± 0.057	0.06 ± 0.057 (0.23)	0.02 ± 0.007	0.013 ± 0.004 (0.056)
Defoliation (DEF)	-0.06 ± 0.087	-0.04 ± 0.057 (-0.16)	0.02 ± 0.024	0.013 ± 0.010 (0.027)

( ) heritabilities in standarized units = correlation between S_2 and S_1 adjusted for the degree of previous inbreeding.

enough replications to compensate partially for the genotype by enviroment intraction.

Narrow sense heritabilities of family means for all the traits were higher than those of individual measurement and within family deviation. This suggests that more progress would be expected in early generations by selecting for crosses in the S_1 than by selecting S_1 lines on the basis of their phenotypic value or their value within families. A similiar conclusion has been reached by Allard (1) from an extensive review of the literature on early generation selection for yield. He suggested that families should be selected that would associate a high mean with genetic variance. The importance of joint consideration of high heritability estimates and the magnitude of the genetic variance in making prediction on selection advances has also been pointed out by Burton (3). He reported that a genetic coefficient of variation calculated by the formula (genetic variance) /x x 100, together with a heritability estimate, would give the best picture of the amount of progress to be expected.

The genetic correlation was always, in absolute values, higher than the phenotypic correlations (Table 6). Similiar results have been reported in other studies of peanuts (5, 16). Likewise, the environmental correlation was consistently less important than the genetic correlation among all the traits. This suggests a genetic control of the association among the traits studied that may be due to pleiotropic genes or linkage (8).

Negative phenotypic, genetic, and environmental correlations were obtained between pod yield and LSA, LSB, LSAB, and DEF. This negative association between pod yield and leafspot severity suggests that it would be possible to select genotypes combining leafspot resistance and yield by selecting under disease pressure in early generations. Very high positive correlations were observed among all the leafspot severity ratings, suggesting that LSA, LSB, and DEF measure or represent components of the same genetic event.

Results indicate that selecting for reduced LSA, LSB, LSAB, and DEF would realize 26 to 36% of the response expected by selecting for pod yield itself (Table 7). Similarly, selection for pod yield would be no better than direct selection for decreased LSA, LSB, LSAB, and DEF. However, since yield is the critical trait peanut breeders wish to improve, and because selection

Table 6. Phenotypic (r_p), genetic (r_A) and environmental (r_E) correlations among parameters of leafspot resistance in S_1 and S_2 field evaluations.

		Necrotic area (2nd reading: LSB)	Necrotic area (average: LSAB)	Defoliation (DEF)	Pod yield
Necrotic area (1st reading: LSA)	r_p	0.368^{**}_{**}	0.840^{**}_{**}	0.278^{**}_{**}	-0.244^{**}_{**}
	r_A	0.987^{**}	1.001^{**}	0.599^{**}	-0.380^{*}
	r_E	0.080^{ns}	0.807^{*}	0.211^{*}	-0.213^{*}
Necrotic area (2nd reading: LSB)	r_p		0.710^{**}_{**}	0.165^{ns}_{**}	-0.134^{ns}_{**}
	r_A		0.914^{**}	0.669^{**}	-0.272^{**}
	r_E		0.627^{*}	0.047^{ns}	-0.010^{ns}
Necrotic area (average of the two:LSAB)	r_p			0.316^{**}_{**}	-0.283^{**}_{**}
	r_A			0.715^{*}_{*}	-0.323^{**}_{**}
	r_E			0.204^{*}	-0.271^{*}
Defoliation (DEF)	r_p				-0.181^{*}_{**}
	r_A				-0.385^{**}
	r_E				-0.132^{ns}

** significantly different from zero, p = 0.01

* p = 0.05

ns = nonsignificant

Table 7. Relative efficiency of indirect selection for trait x due to selection for trait y for parameters of leafspot resistance in S_1 and S_2 field evaluations.

	Relative efficiency of selection for x (%)*				
Trait y	Necrotic area (1st reading:LSA)	Necrotic area (2nd reading:LSB)	Necrotic area (average:LSAB)	Defoliation	Yield
Necrotic area (1st reading:LSA)	-	84.8	79.0	56.3	34.1
Necrotic area (2nd reading:LSB)	97.0	-	77.2	67.3	26.1
Necrotic area (average:LSAB)	126.8	108.3	-	101.5	36.7
Defoliation (DEF)	63.7	66.5	60.0	-	36.7
Pod yield	42.4	28.3	28.4	40.4	-

* relative efficiency of indirect selection as a proportion of the progress expected when selection was for trait x itself.

for yield under leafspot pressure would also result, although at a lower rate, in improving the genetic resistance of peanut genotypes to leafspot, selection for yield under disease infection in early generations may be a start toward developing high yielding leafspot resistant genotypes.

Observation of the generation of the progenies produced by crosses selected in the S_1 generation showed that only three families in the top 10% of the high-yielding S_2 families originated from the crosses that were selected for high yielding ability. The other nine came from crosses selected on the basis of a broad sense index combining pod yield with either low LSA, low LSB or low DEF. This observation suggests that an index combing yield and disease severity traits may be useful in selecting for yield under leafspot pressure in early generations.

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