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ABSTRACT

The genetic nature of resistance to early (*Cercospora arachidicola* Hori) and late [*Cercosporidium personatum* (Berk. & Curt.) Deighton] leafspot of peanut (*Arachis hypogaea* L.) is quantitative, making selection for resistance difficult in segregating populations. In many areas of peanut production, without fungicide application one or both diseases may significantly reduce yields. A study was conducted to obtain heritability estimates, responses to selection, and relationship of resistance of two peanut populations for early and late leafspot resistance. Selection based on F_2 family means in the F_3 generation via defoliation, infection, and sporulation was performed for early and late leafspot in North Carolina and Georgia, respectively, within populations of PI 314817/[TG3/EC 76446 (292)] and (PI 314817/ICGS 4). Divergent selections for each disease were evaluated in the F_4 generation at the same locations the following year for resistance by visual rating of infection and defoliation. Broad-sense heritability estimates ranged from low to high (0.12–0.88) for components of resistance to each leaf-spot disease. Narrow-sense heritability estimates from parent–offspring regression (0.18–0.74) and realized heritability (0.60–1.41) were significant for late leafspot resistance and early leafspot resistance in the PI 314817/[TG3/EC 76446 (292)] population. Results indicated that selection based on family means would be successful. Selection of individual plants within families did not significantly improve genetic progress. Moderate to high correlations (0.41–0.86) existed between early and late leafspot disease components indicating possible genetic linkage or host-plant physiology that conferred resistance to both diseases in one population.

AMONG foliar fungal disease of peanut, early and late leafspot are the most widespread and destructive. Leafspots, if not controlled, can cause extensive defoliation and necrosis that significantly reduce yields (8,13[p. 7–15]). Chemical controls can increase production costs by 10% (7). The development of resistant breeding lines with high yield would increase net income for peanut farmers and reduce dependence on chemical control.

Effective selection in early generations of segregating material can be achieved only when additive genetic effects are substantial and heritability is high. Additive gene action has been reported to be significant for both early (9,10) and late (14,16,21) leafspot resistance. Green and Wynne (9) determined that nonadditive effects are also important for early leafspot resistance. Dominance was significant for the resistance components lesion size, latent period, and sporulation from a generation means analysis on late leafspot by Jogloy (14). Nevill (16) concluded from F_2 populations skewed toward the susceptible parents that resistance to both leafspot diseases is polygenic and recessive. Estimates of narrow-sense heritabilities (12,14,15) have ranged from low to high for components of resistance. Jogloy (14) found that heritability estimates were variable among crosses tested and among components of resistance within crosses. In general, broad-sense heritability estimates for components of resistance have been higher than narrow-sense estimates (2,3,15), substantiating the evidence that nonadditive gene effects add to the total genetic variance. Resistances to the two leafspot diseases on peanut is thought to be genetically independent (2). Through tandem selection in diverse populations, selection of individual families with resistance to both leafspot diseases should be possible.

Effective early generation selection for leafspot resistance would be advantageous and allow for procedures such as independent culling, tandem selection or index selection involving other traits such as yield, seed quality, and multiple pest resistance. Iroume and Knauft (12) recommended that selection among crosses be performed in early generation for late leafspot resistance, but they concluded that within-family selection would not be effective because of low heritability. Reports of response to selection or of realized heritability for resistance to leafspot are lacking in the literature.

The objectives of this study were to (i) evaluate the response of peanut genotypes to selection within and among F_2-derived families; (ii) determine realized heritabilities from family selections for early and late leafspot; (iii) compare broad-sense, narrow-sense, and realized heritability estimates in the populations; and (iv) determine the relationship of resistance to early and late leafspot through correlated response to selection.

MATERIALS AND METHODS

Two biparental populations from a 10-parent diallel cross were chosen for this study based on general and specific combining abilities for components of resistance to early leafspot and late leafspot tested in the hybrid (F_1) generation (1). Two of the parents {PI 314817 and [TG3/EC 76446(292)]} were identified as being highly resistant to late leafspot and moderately resistant to early leafspot by the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) (20). The other parent (ICGS 4) is a high-yielding, small-seeded Virginia peanut from ICRISAT. The F_2 seed from the two crosses {PI 314817/[TG3/EC 76446(292)] and PI 314817/ICGS 4} and parents were grown in the greenhouse during the winter of 1986–1987. Plants were harvested and F_3 seed from the 50 and 40 highest yielding F_2 plants in Cross 1 {PI 314817/[TG3/EC 76446(292)]} and Cross 2 [PI 314817/ICGS 4], respectively, were used for leafspot assessment during the summer of 1987.

Evaluation of Original Populations, 1987

The F_3 seed from individual F_2 plants was randomly divided to perform field experiments at the Georgia Coastal

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Plain Experiment Station, Tifton, GA, for assessment of resistance to late leafspot and at the Peanut Belt Research Station, Lewiston, NC, for assessment of resistance to early leafspot. Each experiment consisted of a randomized complete-block design with two replicates. Five plots of each parent and susceptible check per replicate were included at each location; however, no infector rows were included. 'Florigiant' and NC Ac 3033 were used as susceptible checks for the Lewiston and Tifton locations, respectively. Seeds were planted on 12 May 1987 at Lewiston and on 20 May 1987 at Tifton. Each plot consisted of a single five-seed row. Seeds were spaced 25 cm within rows and 90 cm between rows.

Field screening was performed at Lewiston for early leafspot resistance and at Tifton for late leafspot resistance. During multiple years of observation, the predominant diseases were early leafspot at Lewiston and late leafspot at Tifton. Disease assessment was based on reactions of genotypes to natural occurrence of the disease. The third fully expanded leaf from the terminal of the mainstem of each plant was tagged ≈65 d after planting. Lesion number, lesion size, and sporulation ratings were recorded from tagged leaves on 21 and 26 Aug. 1987 (101 and 98 d after planting) at Lewiston and Tifton, respectively. A visual rating of disease using an evaluation method for percent defoliation (defoliation rating 1–10) and percent of diseased canopy (infection rating 1–10) based on individual plants was performed 26 Aug. 1987 (98 d after planting) at Tifton and 1 Sept. 1987 (112 d after planting) at Lewiston. Percent defoliation was visually assessed again 24 Sept. 1987 (117 d after planting) at Tifton and 10 and 22 Sept. 1987 (120 and 132 d after planting) at Lewiston. Family means and rankings were calculated for each trait in each experiment. Rank correlations were performed among all traits using entry means (18).

The rankings among family means within each cross of the following traits were combined and used as a basis of selection of the five most and the five least resistant families within each cross and for each leafspot disease.

For late leafspot resistance the traits were (i) lesion number from tagged leaf in field (98 d after planting); (ii) sporulation rating from tagged leaf in field (98 d after planting); and (iii) visual defoliation rating 98 d after planting).

For leafspot resistance the traits were (i) lesion number from tagged leaf in field (101 d after planting); (ii) visual infection rating (112 d after planting); and (iii) visual defoliation rating (120 d after planting). Other traits lacked variation and were not used as selection criteria.

Pods from individual plants within selected families were harvested on 9 and 10 Oct. 1987 at Lewiston and Tifton, respectively. Once pods had dried to ≈6% moisture, the peanuts were shelled and equal amounts of seed from individual plants within F_2 families across locations and replicates were bulked and prepared for planting at the two locations in 1988. Remnant seeds from individual $F_{2,3}$ plants harvested at Lewiston in 1987 were used in a separate leafspot experiment at Lewiston in 1988. The two most and the two least resistant F_3 plants within each previously selected most and least early leafspot-resistant F_2-derived family were selected based on the same criteria as for family selection. Individual plants harvested via mass selection of remaining plants on visually assessed resistance to early leafspot were also included in the test.

Evaluation of F_2 Family Selections, 1988

The Bulked F_2 and F_4 seed was used to prepare evaluations of resistance at Lewiston and Tifton. At each location seed of the most and least leafspot selections for each disease, parents, and checks were planted in a RCBD with four replicates. Plots consisted of two 28-seed rows with plants spaced 25 cm within rows and 90 cm between rows. Experiments were planted on 9 and 10 May 1988 at Tifton and Lewiston, respectively.

Late leafspot was evaluated by rating plots for percent defoliation and percent canopy diseased (infection) at Tifton on 18 Aug., 1 Sept., and 16 Sept. 1988 (101, 115, 130 d after planting). One leaf from midcanopy of 10 randomly selected plants was sampled within each plot on the first two dates. Lesions were counted and recorded as average number per leaf.

Early leafspot was assessed using the same procedure. Plot ratings were performed at Lewiston on 11 Aug., 26 Aug., 11 Sept., and 23 Sept. 1988 (93, 108, 124, and 136 d after planting). Average lesion number, defoliation, and infection ratings were recorded on a plot basis in 1988, due to the increased number of plants per plot.

Evaluation of Individual F_3 Plant Selections, 1988

A randomized complete-block experiment with four replicates was prepared and planted at Lewiston on 10 May from individual F_3 plant selections for early leafspot resistance, as previously described. A plot consisted of a single 28-seed row with the spacing as in the previously described experiments. Each plot was a progeny row and randomization was based on plants selected within four classes for each biparental population: Class 1 was the most resistant plant and Class 2 the least resistant plant within the most resistant family; similarly, Class 3 and Class 4 were the single most and least resistant plants within the least resistant family.

Plots were evaluated by rating percent defoliation and percent diseased canopy on 14 and 26 Aug. and 11 and 23 Sept. 1988 (97, 108, 124, 136 d after planting). Lesion counts from 10 randomly selected leaves within plots were recorded on 11 and 26 Aug. 1988 (93 and 108 d after planting). An analysis of variance, means, and contrasts were calculated for all traits.

Broad-Sense Heritability

The VARCOMP procedure of SAS (19) was used to calculate the maximum likelihood estimates of broad-sense heritability ($\hat{H}$) for resistance traits on F_2-derived lines in 1987. Environmental variance was estimated as the mean square for the replicate × F_2 family interaction. The standard error of the heritability estimate was calculated from the equation

$$\mathrm{SE}(\hat{H}) = \frac{\dfrac{2}{(rd)^2}\left[\dfrac{(\text{mean squares among families})^2}{n+1}\right]}{\dfrac{1}{rd}(\hat{\sigma}_e^2) + \dfrac{1}{r}(\hat{\sigma}_{GR}^2) + \hat{\sigma}_G^2}$$

with r = number of replicates, d = number of plant samples per plot, n = number of F_2 families, $\hat{\sigma}_e^2$ = variance due to error, $\hat{\sigma}_{GR}^2$ = variance due to the interaction between replicate and family means and σ_G^2 = variance due to differences among family means.

Narrow-Sense Heritability

Narrow-sense heritability ($\hat{h}^2$) was estimated by parent offspring regression of selected lines in the F_3 and F_4 generations using the model

$$Y_i = a + bX_i + e_i$$

with Y_i = mean measurement of offspring (F_4) from the ith family, X_i = mean measurement of parents (F_3) from the ith family, and e_i = error. The regression coefficient (b) is thus

$$b = \frac{\sum_i (X_i - \overline{X})(Y_i - \overline{Y})}{\sum_i (x_i - \overline{X})^2} = \frac{\sigma_{xy}}{\sigma_x^2}$$

with σ_{xy} = covariance of parent–offspring and σ_x^2 = total variance of parental measurements (σ_{ph}^2). With inbred parents.

$$\hat{h}^2 = b/2\theta_{xy}$$

where θ_{xy} = coefficient of relatedness between X and Y or parent and offspring. The θ_{xy} is 7/8 between the F_3 and F_4 generation of self-pollinated species. The standard error of estimates was calculated as

$$\mathrm{SE}(\hat{h}^2) = \frac{\mathrm{SE}(\hat{b})}{2\theta_{xy}}$$

Realized Heritability

Realized heritability (H_R) was estimated by the general equation $H_R = R/S$ where R is response measured as differences of the means of most and least resistant selections in the F_4 (1988) and S is the selection differential measured from differences in the means of most and least resistant selections in the original F_3 population (1987). Means were adjusted to standard deviation units due to heterogeneous variances across years. Standard errors were calculated from the equation (17):

$$\text{Variance } (H_R) = \frac{1/n[H_R(1 - H_R)^2\sigma_p^2] + \sigma_0^2}{S^2}$$

with n = number of selected families, σ_p^2 = phenotypic variance of population from which parents were drawn (F_3), and σ_0^2 = phenotypic variance of the offspring population (F_4).

RESULTS AND DISCUSSION

Disease traits of the base population measured in the field for early leafspot resistance were all moderately to highly correlated, with the exception of sporulation rating (Table 1). Rank correlation coefficients of traits involving late leafspot were generally low to moderate (Table 1). There was a significant negative correlation between lesion size and lesion number. Chiteka et al. (4) found that variability was greatest for sporulation ratings, plant appearance scores, and lesion diameters when comparing a large number of homogeneous lines. They found that sporulation was also highly correlated with other disease components and was associated with disease assessment scores (5). The genetic material of this study does not show such a high correlation, and this may be due to breaking of associations among the traits through crossing and selfing of progeny.

Families generally showed no correlation or low correlations between early and late leafspot lesion number, lesion size, sporulation, and infection ratings (Table 1); however, defoliation Ratings 1 and 2 for early leafspot and defoliation rating for late leafspot were moderately correlated (0.44–0.57).

Broad-sense heritability estimates for early leafspot parameters were generally high for Cross 1 (Table 2). Estimates were consistent for early leafspot across defoliation ratings, indicating sufficient expression of genetic variability and adequate disease pressure throughout the season. Heritability of early leafspot parameters for Cross 2 were moderate to low, except for the third defoliation rating. In this case, the heritability estimate for defoliation increased across time, indicating that genetic variability is insufficient for selection during early stages of the disease for Cross 2.

Broad-sense heritability estimates for late leafspot were consistent over crosses and were generally moderate to high for all parameters (Table 2). Selection based on defoliation would probably be most appropriate due to its high heritability. Reductions in yield are attributed in large part to premature defoliation in diseased fields (6).

Narrow-sense heritability estimates were calculated from parent–offspring regression (Table 2). Linear regression generally accounted for a high percentage of the variation in Cross 1 (R^2 = 0.55–0.81); however, the linear component of the variation was small for Cross 2 (R^2 = 0.06–0.39), except for defoliation rating of late leafspot (R^2 = 0.79). Infection rating of both crosses, defoliation Rating 3 of Cross 1 for early leafspot, and lesion number of both crosses for late leafspot had narrow-sense heritability estimates as high or higher than broad-sense estimates. All other components had smaller estimates. Low heritability was observed for all traits of early leafspot resistance in Cross 2 except for infection rating.

If both methods of heritability estimation are accurate, the lower narrow-sense estimates indicate non-

Table 1. Rank correlation coefficients among traits for F_2 peanut families evaluated for early and late leafspot resistance at Lewiston, NC, and Tifton, GA, during 1987.

	Late leafspot				Early leafspot				
							Defol. rating†		
	Lesion no.	Lesion size	Sporulation	Defoliation	Lesion no.	Infec. rating	1	2	3
Early leafspot									
Lesion no.	0.22*	0.09	0.24*	0.01					
Infection rating	0.18	0.15	0.25*	0.00	0.67**				
Defoliation rating 1	0.32*	0.23*	0.01	0.57**	0.42**	0.41**			
Defoliation rating 2	0.17	0.28**	−0.01	0.44**	0.53**	0.53**	0.81**		
Defoliation rating 3	0.14	0.23*	0.08	0.20	0.56**	0.62**	0.57**	0.70**	
Sporulation	0.01	−0.02	0.24*	−0.06	0.12	0.02	−0.22*	−0.12	−0.16
Late leafspot									
Defoliation rating	0.46**	0.22**	0.21*						
Sporulation	0.36**	0.03							
Lesion size	−0.24*								

*,** Significantly different from zero at the 0.05 and 0.01 probability levels, respectively.

† Defoliation ratings 1, 2, 3 were taken at three dates and are on a scale of 1 to 10, low to high.

additive variance is substantial for defoliation caused by late leafspot and lesion number of early leafspot for these two crosses. Heritability estimates of components of resistance to early and late leafspot have been reported to vary from zero to high. Jogloy et al. (15) reported broad-sense heritability for lesion size and sporulation to be moderate (0.49–0.68), but narrow-sense heritabilities were extremely low (<0.03) in greenhouse studies using different crosses. Estimates for lesion number and latent period were low for both narrow and broad-sense heritabilities. Anderson et al. (2), working with a different set of crosses, reported moderate to high broad-sense heritability for similar components of resistance for both early and late leafspot in the greenhouse. Thus, from previous reports, one could conclude that dominance and epistatic genetic variance are substantial. Jogloy (14), however, reported moderate to high narrow-sense heritability for components of early and late leafspot resistance in three crosses, which is in closer agreement to the present study. Iroume and Knauft (12) obtained heritabilities of 0.16 to 0.26 for necrotic area and defoliation from individual measurements of segregating material in the field. One parent of Cross 1 [TG3 × EC 76446(292)] was reported to have partial resistance to early leafspot (11). This contributed to the higher heritability estimates for Cross 1. Though both parents of Cross 1 have resistance to late leafspot, enough variability among resistance genes resulted in higher heritabilities than Cross 2, which has only one resistant parent (PI 314817).

For all parameters except late leafspot lesion number, realized heritability estimates were greater than narrow-sense heritability obtained via parent–offspring regression and in most cases were comparable or higher than broad-sense estimates (Table 2). Even after standardization, estimates for lesion number and infection rating of Cross 1 were greater than the theoretical limit. Thus, greater differences occurred between most and least resistant selections for these traits in 1988 than in 1987. In general, realized heritability was greater than expected, though trends among traits and crosses were consistent with previous estimates. Cross 2 showed less variability for resistance to early leafspot, which corresponds with parent-offspring regression results. Only lesion number, infection rating, and the third defoliation rating were significantly different from zero for Cross 2.

The different range of values between the divergent selection groups in the 2 yr of this study often occurs in peanut disease studies. The environment (including the microenvironment) may have been more conducive to disease development, which allowed greater differentiation among families during 1988. Individual plants were rated during screening of the original population, while rating was done on whole plots the following year. Also the small five-plant plots of 1987 could have reacted differently to fungal spore dispersal than in the larger 28-plant plots of 1988. The subjective rating procedure for infection and defoliation may have included a between-year experimental error that could cause a bias. A second year of evaluation may improve estimates by reducing environmental and experimental bias; however, heritability estimates from all methods were encouraging for selection of families for resistance to early and late leafspot.

Significant differences between most and least resistant selections occurred for resistance to early leafspot in Cross 1 (Table 3). This supports results of realized heritabilities. A significant decrease in lesion number, infection, and defoliation ratings occurred for early leafspot on selections for late leafspot in Cross 1, indicating a correlated response in resistance. Thus, selecting for resistance to late leafspot in Cross 1 would also improve early leafspot resistance. The high correlation coefficients between early and late leafspot components in Cross 1 support this conclusion (Table 4). Divergent selection groups for early leafspot resistance in Cross 1 were also significantly different in resistance to late leafspot (Table 3) except for lesion number.

Late leafspot resistance in Cross 2 improved through selection, as indicated by the significant differences between the most and least resistant families (Table 3). Selection for early leafspot within this cross was only moderately successful. Only lesion number and infection ratings of the two leafspots were positively correlated in Cross 2 (Table 4). Thus, correlated

Table 2. Broad-sense, narrow-sense, and realized heritability estimates for disease parameters of early and late leafspot for two peanuts crosses from field data at Tifton, GA, and Lewiston, NC, in 1987 and 1988.

	Cross 1			Cross 2		
	$\hat{H}$†	$\hat{h}^2$‡	H_R§	$\hat{H}$	$\hat{h}^2$	H_R§
			Early leafspot			
Lesion number	0.57*	0.18	1.41**	0.40**	0.04	0.67**
Sporulation	0.16	–	–	0.41**	–	–
Infection rating	0.38**	0.59**	1.29**	0.34**	0.39**	0.44**
Defoliation rating 1¶	0.65**	0.38**	0.65**	0.12*	0.09	0.21
Defoliation rating 2	0.65**	0.53**	0.74**	0.31**	0.13*	0.20
Defoliation rating 3	0.56**	0.53**	0.71**	0.56**	0.14*	0.30*
			Late leafspot			
Lesion number	0.74**	0.74**	0.60**	0.49**	0.57**	0.52
Sporulation	0.54**	–	–	0.70**	–	–
Defoliation rating	0.88**	0.26**	0.93**	0.80**	0.40**	0.93**

*,** Significantly different from zero at the 0.05 and 0.01 probability levels, respectively.

† $\hat{H}$ = Broad-sense heritability from variance components of 1987 $F_{2,3}$ family means using maximum likelihood estimation of PROC VARCOMP (15).

‡ $\hat{h}^2$ = Narrow-sense heritability from parent–offspring regression 1987 and 1988.

§ H_R = Realized heritability from $F_{2,3}$ and $F_{2,4}$ family means 1987 and 1988.

¶ Defoliation ratings 1, 2, 3 were taken at three dates and are on a scale of 1 to 10, low to high.

Table 3. Difference between mean values of traits of five peanut F$_{2,3}$ families from positive selection for early or late leafspot resistance and corresponding values of five F$_{2,3}$ families from negative selection.

	Leafspot selections			
	Cross 1		Cross 2	
	Early	Late	Early	Late
		Early leafspot		
Lesion number	9.5**	10.1**	2.9**	2.8**
Infection rating (1–10)				
INF2	2.0**	0.7**	0.6*	0.1
INF3	1.7**	0.5*	0.4	−0.1
INF4	0.9**	0.4	0.6**	−0.4
Defoliation rating (1–10)†				
DEF2	2.4**	1.1**	0.3	−0.3
DEF3	2.9**	0.9**	0.5	−0.4
DEF4	2.8**	1.5**	0.8**	−0.4
		Late leafspot		
Lesion number	8.0	26.0**	−1.3	11.6**
Infection rating (1–10)				
INF1	1.3**	2.0**	0.6	1.7**
INF2	1.6**	1.4**	0.6	1.1**
Defoliation rating (1–10)				
DEF1	0.9**	1.8**	0.1	1.6**
DEF2	3.4**	3.9**	0.0	2.9**

*,** Positive selections differ from negative selections according to a *t*-test at the 0.05 and 0.01 probability levels, respectively.

† Defoliation ratings 1, 2, 3 were taken at three dates and are on a scale of 1 to 10, low to high.

gains for both leafspot diseases would not be expected within this cross.

There were no significant differences between means of the most and least resistant plant selections within preselected families for all traits (data not shown). Thus, selection of individual plants within F$_2$ families was not effective, which is in agreement with Iroume and Knauft (12). Early leafspot disease traits for the most and least resistant plants within family selections were not different. We conclude that multiple plant measurements within families are necessary for effective selection for resistance to leafspot diseases.

In summary, selection based on early generation family means within two crosses was effective for improvement of both late and early leafspot resistance. Field defoliation ratings were correlated to other traits, providing ease of disease evaluation. They also were heritable, thus offering an effective method for selection. Phenotypic correlations among components of resistance between the two diseases occurred. Results were encouraging for the gain from selection of resistance to both leafspots concurrently in one of two populations. Realized heritability estimates were generally greater than narrow-sense estimates from parent-offspring regression and broad-sense estimates from expected mean squares; however, trends among traits and crosses were similar. Individual plant selections within highly resistant F$_2$ families did not improve selection response for early leafspot resistance. Lesion number, infection ratings, and defoliation ratings are the most effective traits to use in selection for resistance to both diseases. Selection for lesion size and sporulation ratings were less successful.

Table 4. Product moment correlation coefficients among leafspot traits for early peanut leafspot evaluated at Lewiston, NC, and late leafspot evaluated at Tifton, GA.

	Late leafspot			
Early leafspot	Defoliation rating, F$_3$	Lesion no., F$_4$	Infection rating, F$_4$	Defoliation rating, F$_4$
		Cross 1		
Defoliation rating, F$_3$	–	0.41	0.82**	0.79**
Lesion no., F$_4$	0.70**	0.72**	0.80**	0.86**
Infection rating, F$_4$	0.60**	0.48*	0.77**	0.76**
Defoliation rating, F$_4$	0.55*	0.44	0.83**	0.76**
		Cross 2		
Defoliation rating, F$_3$	–	−0.07	0.05	0.19
Lesion number, F$_4$	0.15	0.48*	0.45*	0.22
Infection rating, F$_4$	−0.50*	0.25	0.78**	−0.30
Defoliation rating, F$_4$	0.15	−0.07	0.11	0.20

*,** Significantly different from zero at the 0.05 and 0.01 probability levels, respectively.

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