# Genetic analysis of sweet pepper tolerance to low phosphorus availability in the soil

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## ABSTRACT

The objective of this study was to evaluate the mode of inheritance for sweet pepper (*Capsicum annuum* L.) tolerance to low P availability in soil, defined here as the ability of plants to produce relatively more biomass (total dry weight) under low P conditions. A complete diallel cross was used involving six previously selected genotypes, three tolerant and three intolerant to low P availability in soil. At 75 days after sowing, total dry weight, shoot and root dry weight, ratio root:shoot dry weight, and total P content in the plant were evaluated. There were no significant reciprocal differences in any of the assessed traits. The results showed that genes controlling tolerance to low P were predominantly but not exclusively dominant. Out of the three tolerant parents, two concentrated dominant genes, and the other, recessive genes for tolerance to low P. The analysis of the genetic components of variation showed that both the additive and the dominant gene effects were involved in the control of all the characteristics, with a greater contribution from the dominance to the genetic variability among parents and $F_1$ hybrids. The estimates of the broad-sense heritabilities were high, while the narrow-sense were in general comparatively low. Their magnitudes, however, were at a level that allowed successful selection.

**KEY WORDS**: *Capsicum annuum* L., breeding, diallel, inheritance.

## INTRODUCTION

The genus *Capsicum*, a member of the *solanaceae* family, includes several important crop species. Sweet pepper (*Capsicum annuum* L.) is one the most important vegetable in Brazil, which also is used for processing. The specie is found distributed from Mexico to North of South America (Andrews, 1984). The sweet pepper flower is normally self-pollinated, although outcrossing up to 91% has been reported in *Capsicum* (Tanksley, 1984). It is normally grown as annuals, although may be maintained as perennial.

In recent decades, considerable efforts have been spent towards the understanding of the genetic control of the efficient use of phosphorus (P) by annual crops, especially in tropical America. Low P availability has been considered one of the most limiting factors in plant growth in highly weathered tropical soils (Sánchez and Salinas, 1981). Besides the natural deficiency, P fertilizers are not always available or affordable to farmers and may be only marginally effective since the P fixation by Fe and Al oxides make applied and natural P unavailable to plants (Fageria et al., 1988). Genetic improvement of P efficiency in sweet pepper may be a viable alternative or a complement to intensive fertilization of considerable interest to breeders, farmers and consumers. It can help to extend the life of the natural phosphate reserves and to reduce the production costs and environment pollution, which are targeted in sustainable management practices.

The occurrence of genotypic variability related to low P tolerance is crucial to breeding programs aiming at developing more efficient sweet pepper varieties. Regarding this aspect, the presence of substantial genotypic variability in sweet pepper germoplasm in the vegetative responses to low P availability in soil is reported by Oliveira et al. (1999).

Selection in segregating generations following hybridization is a current practice in sweet pepper breeding. However, the efficacy of selection depends on the nature of the genetic systems which determine the traits of interest and the degree to which the environmental effects influence their expression (Cruz and Regazzi, 1994). Knowledge of the type and relative importance of the gene effects which act in the determination of the traits will help sweet pepper breeders design effective breeding programs for developing improved low P tolerant varieties. With this information, greater and faster genetic gains are expected than those obtained through empirical breeding which are based only on the observational ability of the breeder.

Among the biometrics methods for genetic analysis are the diallel analysis methods, which allow an assessment of the genetic system that controls the trait under study and supply useful information to parent choice for hybridization, breeding methods and selection procedures. Due to the amount of information they give on the inheritance of quantitative traits, the diallel cross procedures proposed by Jinks and Hayman (1953) and Hayman (1954a, b) have been widely used in the understanding of the genetic control of the traits of a set of homozigous parents (Hayman, 1954b). Examples of analysis of inheritance of tolerance to limited P availability using this diallel analysis have been reported in the literature (rice - Chaubey et al., 1994; soybean - Spehar, 1995). However, the inheritance of traits related to low P tolerance in sweet peeper has not been elucidated yet.

In the present study the diallel analysis was used to investigate the mode of inheritance for sweet pepper tolerance to low P availability in the soil, in order to provide information for future sweet pepper P efficiency breeding programs.

## MATERIAL AND METHODS

Six sweet pepper (*Capsicum annuum* L.) homozigous lines from the Universidade Federal of Viçosa Germplasm Bank were previously chosen based on their ability to produce relatively more biomass in low P soils (Oliveira et al., 1999) and intercrossed in a diallel system to obtain all possible hybrid combinations, including reciprocals. Three low P tolerant genotypes (P-141-152-F14, P-142-215-F15 and P-142-403-F11) and three low P intolerant (P-141-150-F10, P-141-190-F16 and P-142-270-F12) were used as parents in the crosses.

The populations (parents, $F_1$ and $F_1$ reciprocals), totalling 36 treatments were organized in a randomized complete block design with four replications. Each experimental unit consisted of one pot with 2.45 $dm^3$ soil containing one plant per pot. The soil used in the experiment was a red yellow podzolic (oxisol), according to the Brazilian soil classification, and had the following chemical properties before the P treatment applications: pH 5.1 (1:2.5 soil-water ratio), extractable phosphorus (P) 2.0 mg $kg^{-1}$, extractable potassium (K) 40 mg $kg^{-1}$, extractable calcium (Ca) 1.7 $cmol_c$ $kg^{-1}$, extractable magnesium (Mg) 0.6 $cmol_c$ $kg^{-1}$, extractable aluminum (Al) 0.1 $cmol_c$ $kg^{-1}$ of soil.

The soil was air dried, sieved and homogenized before receiving a base fertilization with macro and micro nutrients as follows: 200 mg P $dm^{-3}$ soil (triple superphosphate), 100 mg N $dm^{-3}$ soil ($NH_4NO_3$), 160 mg K $dm^{-3}$ soil ($K_2SO_4$), 80 mg S $dm^{-3}$ soil ($K_2SO_4$, $MgSO_4.7H_2O$, $ZnSO_4.7H_2O$, $CuSO_4$), 0.81 mg B $dm^{-3}$ soil ($H_3BO_3$), 1.33 mg Cu $dm^{-3}$ soil ($CuSO_4$), 3.66 mg Mn $dm^{-3}$ soil ($MnCl_2.4H_2O$), 0.15 mg Mo $dm^{-3}$ soil ($(NH_4)_6.Mo_7.O_{24}.4H_2O$) and 4 mg Zn $dm^{-3}$ soil ($ZnSO_4.7H_2O$). An 2:1 equivalent amount of Ca:Mg was supplied and $CaCl_2.2H_2O$ was used as a source of Ca in addition to the triple superphosphate. The compounds $MgSO_4.7H_2O$ and $MgCl_2.6H_2O$ were used as Mg sources. All nutrients were thoroughly mixed with the soil in each individual pot before planting. Nitrogen was supplied in its totality after germination at 10 days intervals. The dose of 200 mg P $dm^{-3}$ soil was considered low P availability in a previous experiment used to select the genotypes of this experiment (Oliveira et al., 1999).

The experiment was conducted in a greenhouse over a 11 week period, from February to May 1996. Each pot was frequently watered to maintain soil moisture

at approximately 85% of field capacity throughout the experiment and monitored by weighing pots at four day intervals. Seventy five days after sowing, the plants were harvested, separated into the leaves, stems and roots components, which were dried to constant weight in a forced-draft oven at about 70 ºC, weighed, milled, digested with a mixture of nitric and perchloric acids (2:1) and colorimetrically analyzed for P (Braga and Defelipo, 1974).

The diallel analysis proposed by Jinks and Hayman (1953) and Hayman (1954a, b) was used to investigate the genetic control of the total dry weight – TDW (roots, stem and leaves), the shoot dry weight – SDW (stem plus leaves), the root dry weight (RDW), the ratio between the root and shoot dry weights (RRS), and the total P content in the plant (TPP). The diallel analysis was carried out after checking for adequacy of the genetic model, which implied homozygosity of the parents, diploid segregation, absence of multiple allelism, independent gene distribution among the parents, no reciprocal differences and absence of non-allelic interactions.

Initially, the analysis of variance of the diallel table was carried out using the statistical model $Y_{rs} = m + J_r + J_s + J_{rs} + K_r - K_s + K_{rs}$, where $J_{rs} = L + L_r + L_s + L_{rs}$ ($r^1s$), in order to test the significance of the components "a", "$b_1$", "$b_2$", "$b_3$", "c" and "d" defined by Hayman (1954a). The significance of the various sources of variation were assessed by the F test. However, since we would not expect that such variation sources would be influenced to the same extent by the environment, the sums of the squares of the specific errors were obtained for "a", "b", "$b_1$", "$b_2$", "$b_3$", "c" and "d", which are the interactions with the environment of the corresponding main effects (Hayman, 1954a; Mather and Jinks, 1982). The heterogeneity among the mean squares from the "a", "b", "c", and "d" and "$b_1$", "$b_2$", and "$b_3$" were assessed by Bartlett's test (Steel and Torrie, 1980).

Since no reciprocal differences were detected, the entries in the diallel table were substituted by their reciprocals means, and the following statistics were estimated: $V_{0L0}$ (variance among parents), $V_r$ (variance of the r-th array or column); $V_{1L1}$ (mean of the variances of the arrays); $W_r$ (variance of the means of the arrays); $W_{0L01}$ (covariance between the parents and their offspring in the r-th array); (covariance between the parents and the means of their offspring); and $(M_{L1} - M_{L0})^2$ (square of the difference between the general mean ($M_{L1}$) and the mean of the parents ($M_{L0}$)). Fitting of the data to the additive-dominance model was checked using the values of $W_r$ and $V_r$ to assess the homogeneity of the $W_r - V_r$ differences, by two tests: 1) a linear regression of Wr on Vr and a test of the significance of the angular coefficient of the straight line ($H_0$: b = 1 vs $H_a$: b ≠ 1); and, 2) weighing $W_r$ and $V_r$ by a 45º rotation on the axles represented by these statistics, and testing the angular coefficient of the straight line ($H_0$: b' = 0 vs $H_a$: b' ≠ 0).

As the additive-dominance model was sufficient to explain the segregation pattern observed for the assessed traits, the analysis of variance was interpreted and the statistics obtained from the diallel table were used to estimate the genetic variation components $D$, $H_1$, $H_2$, $h^2$, and $F$. The significance of the various components of variation was assessed by the t test. When t > 1.96, the component was considered significant at the 0.05 probability level (Singh and Chaudhary, 1979).

The relationships among the genetic variation components were also used to estimate specific parameters and to assist in the interpretation of the results. Additionally, the regression of $W_r$ on $V_r$ was used to obtain two further results, the average degree of dominance and the relative genetic constitution of the homozygous parents. The correlation (r) between $\overline{Y}$ (mean of the parental values) and $W_r + V_r$, an indicator of the relationship among favorable alleles and dominance, was also calculated. Data were analyzed using the Genes computer program (Cruz, 1997).

## RESULTS AND DISCUSSION

Nutritional efficiency has been defined in many ways in diverse contexts (Föhse et al., 1988; Clark, 1990; Bailian et al., 1991). In the present study, the P efficiency is defined as the ability of plants to produce relatively more biomass (total dry weight) under low P availability in soil. However, the inheritances of traits other

than just total dry weight - relevant and related to tolerance - were also analyzed.

The validity of the a simple additive-dominance genetic model was confirmed by the two sufficiency tests for all the assessed traits (Table 1), although TDW, SDW, RDW, and TPP required data transformation to a logarithmic scale. According to Hayman (1954b) and Mather and Jinks (1982) the interactions among non-allelic genes may frequently be eliminated by adjusting the measuring scale of the data, being the logarithmic transformation suitable when the limits of the scale require grouping.

There were no reciprocal differences for any of the traits assessed, as showed by the non-significance of the "c" and "d" sources of variation in the analysis of variance (Table 2). The lack of reciprocal effects indicated that it makes little difference whether a plant is used as a seed or pollen parent. Maternal effects in traits related to tolerance to low P and, or to other mineral elements have also not been detected in other species (Witeaker et al., 1976; Giordano et al., 1982; Spehar, 1995). The absence of reciprocal effects and fit to the simple genetic model indicate that further estimations of various genetic components of tolerance to low P are justified when using this diallel analysis procedure.

**Table 1 -** Sufficiency tests of the additive-dominant model based on the analysis of regression of $W_r$ on $V_r$ for total dry weight, shoot dry weight, root dry weight, ratio root:shoot dry weight and total P content in the plants.

| Characteristic | Regression $\left[W_r = \frac{1}{4}(D - H_1) + bV_r\right]$ | | |
|---|---|---|---|
| | b | t ($H_o$: b = 1)[b] | F = $t^2$ ($H_o$: b' = 0)[c] |
| Total dry weight[1] | 0.85±0.40 | -0.38[ns] | -0.44[ns] |
| Shoot dry weight[1] | 0.84±0.38 | -0.42[ns] | -0.37[ns] |
| Root dry weight[1] | 0.65±0.41 | -0.87[ns] | -0.10[ns] |
| Root:shoot dry weight ratio | 1.06±0.18 | 0.31[ns] | -0.68[ns] |
| Plant total P content[1] | 0.99±0.43 | -0.03[ns] | -0.83[ns] |

[ns] not significant at the 0.05 probability level ([b]by t - test; [c]by F - test).
[1] means transformed to a logarithmic scale.

The analysis of variance and the estimates of the genetic and non-genetic components of variation of total dry weight, shoot dry weight, root dry weight, ratio root:shoot dry weight, and total P content in the plant are presented in Tables 2 and 3, respectively. Significant "a" effects were detected in the analysis of variance, indicating the presence of genetic variability among the parental lines. Significant "b" indicated that dominance is present, and is predominantly unidirectional for all traits, according to the significance of the "$b_1$" source of variation (Table 2). The positive signal of the estimates of the contrast between the means of $n^2$ elements of the diallel table ($M_{L1}$) and of the n parents ($M_{L0}$) (Table 4) indicate that the dominance deviations occurred in the direction of the greater mean for all traits. Besides dominance, additive variation also contributed to

**Table 2 -** Analysis of variance for total dry weight (TDW), shoot dry weight (SDW), root dry weight (RDW), ratio root:shoot dry weight (RRS) and total P content in the plant (TPP).

| Sources of variation[1/] | Degrees of freedom | Mean squares | | | | |
|---|---|---|---|---|---|---|
| | | TDW | SDW | RDW | RRS | TPP |
| Replications (B) | 3 | 92.12 | 88.77 | 108.23 | 80.25 | 108.39 |
| Treatments | 35 | 20.68** | 19.00** | 25.34** | 89.08** | 21.40** |
| a | 5 | 78.51** | 70.12** | 96.79** | 318.97** | 82.81** |
| b | 15 | 21.83** | 20.60** | 26.33** | 86.67** | 21.98** |
| $b_1$ | 1 | 53.13** | 46.48** | 81.99** | 314.91** | 62.93** |
| $b_2$ | 5 | 6.81** | 5.62** | 10.90** | 64.15** | 7.41** |
| $b_3$ | 9 | 26.69** | 26.05** | 28.71** | 73.83** | 25.53** |
| c | 5 | $0.23^{ns}$ | $0.41^{ns}$ | $0.53^{ns}$ | $3.32^{ns}$ | $0.41^{ns}$ |
| d | 10 | $0.28^{ns}$ | $0.32^{ns}$ | $0.52^{ns}$ | $20.62^{ns}$ | $0.32^{ns}$ |
| Error pooled | 105 | 0.59 | 0.64 | 0.67 | 14.14 | 1.06 |
| Ba | 15 | 0.69 | 0.84 | 0.88 | 11.59 | 1.95 |
| Bb | 45 | 0.63 | 0.62 | 0.70 | 13.69 | 1.19 |
| $Bb_1$ | 3 | 0.10 | 0.08 | 0.12 | 9.29 | 1.30 |
| $Bb_2$ | 15 | 0.93 | 0.99 | 0.86 | 10.78 | 1.67 |
| $Bb_3$ | 27 | 0.52 | 0.48 | 0.68 | 15.79 | 0.91 |
| Bc | 15 | 0.43 | 0.50 | 0.43 | 9.71 | 0.48 |
| Bd | 30 | 0.57 | 0.64 | 0.63 | 18.32 | 0.73 |
| CV (%) | | 3.31 | 3.65 | 4.74 | 10.76 | 4.10 |

****** significant at the 0.01 probability level, by F test; [ns] not significant at the 0.05 probability level;
[1/] All mean effects were tested against the common error variances, since heterogeneity of specific errors was not detected by the Bartlett's test at 0.05 probability level.

the genetic variability among the parental lines and the $F_1$ progeny of the five traits assessed, as the dominance components, $H_1$, $H_2$, and $h^2$ and the additive component $D$ (Table 3) were significantly different from zero. For all traits, the negative and significant estimates of $(D - H_1)$ demonstrated the greater importance of the variation associated with dominance effects and indicated the presence of overdominance among the alleles of non-fixed genes. This is confirmed by a average degree of dominance above unity, estimated by the statistic $(H_1/D)^{1/2}$ (Table 4) and by the intercept of the regression of $W_r$ on $V_r$ (below the origin) (Figures 1, 2, 3, 4 and 5). In the tomato, the P-acquisition efficiency also exhibited significant dominance effects (Coltman et al., 1987). Similarly, Fawole et al. (1982) reported that in beans the P utilization efficiency was controlled by genes with a significant dominance.

**Table 3 -** Estimates of genetic and environmental components of variation with their respective standard errors for total dry weight (TDW), shoot dry weight (SDW), root dry weight (RDW), ratio root:shoot dry weight (RRS) and total P content in the plant (TPP).

| Component of variation (nature of component) | Estimate ± standard error[1] | | | | |
|---|---|---|---|---|---|
| | TDW | SDW | RDW | RRS | TPP |
| D (Additive) | 3.83±0.78* | 3.62±0.75* | 4.95±1.03* | 16.70±2.37* | 4.24±0.71* |
| $H_1$ (Dominance) | 11.65±1.99* | 10.80±1.91* | 15.49±2.61* | 44.70±6.02* | 11.52±1.81* |
| $H_2$ (Dominance) | 10.61±1.78* | 9.98±1.71* | 13.67±2.33* | 36.26±5.37* | 10.46±1.61* |
| $h^2$ (Dominance) | 7.29±1.20* | 6.37±1.15* | 11.02±1.57* | 41.77±3.62* | 8.59±1.08* |
| F (Additive-dominance) | 1.63±1.92$^{ns}$ | 1.33±1.84$^{ns}$ | 2.14±2.51$^{ns}$ | 0.37±5.79$^{ns}$ | 1.51±1.74$^{ns}$ |
| $D - H_1$ | -7.82±1.75* | -7.19±1.68* | -10.55±2.29* | -27.90±5.28* | -7.28±1.59* |
| E (Environmental) | 0.15±0.30$^{ns}$ | 0.16±0.28$^{ns}$ | 0.17±0.39$^{ns}$ | 3.54±0.89* | 0.27±0.27$^{ns}$ |

$^{ns}$ not significant (Singh and Chaudhary, 1979);
[1/] The absolute value of the component divided by the respective standard error, when > 1.96, is significant at the 0.05 probability level.

**Table 4 -** Estimates of genetic parameters and differences between the means of the $r^2$ values of the diallel table ($M_{L1}$) and the n parental lines ($M_{L0}$) for total dry weight (TDW), shoot dry weight (SDW), root dry weight (RDW), ratio root:shoot dry weight (RRS) and total P content in the plant (TPP).

| Genetic parameter | Estimate | | | | |
|---|---|---|---|---|---|
| | TDW | SDW | RDW | RRS | TPP |
| $(H_1/D)^{1/2}$ (Dominance ratio) | 1.74 | 1.73 | 1.77 | 1.63 | 1.65 |
| $K_D/K_R$ (Ratio of dominant to recessive alleles) | 0.78 | 0.81 | 0.78 | 0.99 | 0.80 |
| $H_2/4H_1$ (Asymetry of loci) | 0.23 | 0.23 | 0.22 | 0.20 | 0.23 |
| $h^2/H_2$ (Number of effective factors with dominance) | 0.69 | 0.64 | 0.81 | 1.15 | 0.82 |
| $h^2_{BS}$ (Heritability in the broad-sense) | 0.98 | 0.97 | 0.97 | 0.86 | 0.96 |
| $h^2_{NS}$ (Heritability in the narrow-sense) | 0.54 | 0.52 | 0.55 | 0.50 | 0.54 |
| r (Mean direction of dominance) | -0.65 | -0.61 | -0.74 | -0.96 | -0.80 |
| $M_{L1} - M_{L0}$ | 0.07 | 0.05 | 0.02 | 0.03 | 0.12 |

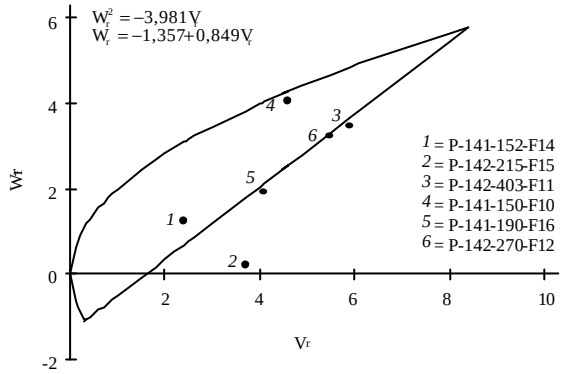


**Figure 1 -** The regression of Wr, on Vr, for total dry weight.

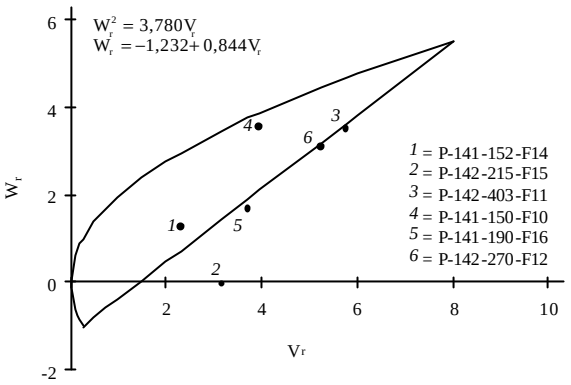


**Figure 2 -** The regression of Wr, on Vr, for shoot dry weight.

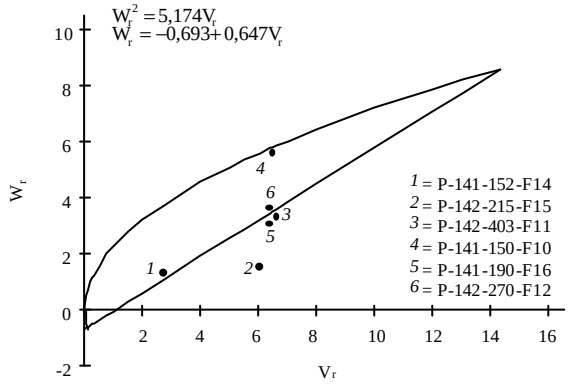


**Figure 3 -** The regression of Wr, on Vr, for root dry weight.

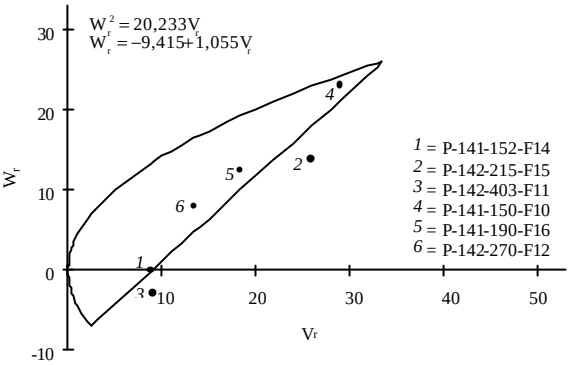


**Figure 4 -** The regression of Wr, on Vr, for ratio root:shoot dry weight.

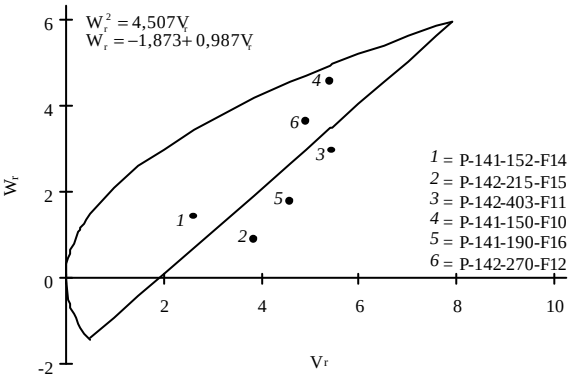


**Figure 5 -** The regression of W, on V, for total P content in the plant.

In general, the significant "$b_2$" effects in the analysis of variance (Table 2) and the ratio $H_2/4H_1 < 0.25$ (Table 4) for all traits, demonstrated that the positive and negative allelic frequencies in the group of parental lines was asymetric, indicating an unequal proportion of positive an negative genes in the parents. The statistically non-significant F estimates (Table 3) indicated that there are equal mean frequencies of dominant and recessive alleles in the loci affecting specific trait, regardless of their increasing or decreasing effects, although the values of $K_D/K_R < 1.0$ for TDW, SDW, RDW and TPP (Table 4) indicated that this equality should be interpreted with caution. The significance of the "$b_3$" source of variation in the analysis of variance (Table 2), suggested the occurrence of specific dominance deviations for certain $F_1$.

The $h^2/H_2$ ratio (Table 4) suggested that a small number of effective factors (genes or groups of genes) are controlling the expression of the various traits related with tolerance to low P in sweet pepper. Since it provides no information about effective factors exhibiting little or no dominance, an underestimation should be considered (Cruz and Regazzi, 1994). In maize, the expression of the characteristics related with tolerance to low P stress was controlled by a small number of genes (Silva et al., 1992). The negative signal and moderate magnitude of the mean

direction of dominance (r) for TDW (Table 4) indicated that the tolerance to low P availability in soil, which is expressed by the greater TDW values, was conditioned predominantly but not exclusively by dominant genes. This behavior can be confirmed by comparing the rank of the means and the parental order of dominance, given by (Table 5), where lines 1 and 2 - low P tolerants, and therefore with a greater TDW - contained a number of dominant genes, and were placed close to the origin in the $W_1$ on V regression graph (Figure 1). However, line 3 with the third greatest mean carried more recessive genes according to the means and dominance rank (Table 5) or the position on the regression graph (Figure 1). The distribution of the parental lines along the regression graph demonstrated that there were a pronounced genotypic dissimilarity among them under a low P condition, even among the tolerants.

Similar to the TDW, the moderate r estimate (and numerically negative) for SDW, RDW, and TPP (Table 4) demonstrated that dominant genes predominantly but not exclusively also controlled these traits. This behavior can be confirmed by comparing the rank of the means and the parental order of dominance (Table 5), where lines 1 and 2 ranked first and showed lower $W_r + V_r$ values and consequently were positioned nearer the origin of the regression line of Wr on Vr (Figures 2, 3 and 5). However, line 3 - which also had a high mean for these traits (Table 5) - carried predominantly recessive genes and was located far from the origin of the regression line (Figures 2, 3 and 5). For RRS, the negative estimate and the high magnitude of the mean direction of dominance (Table 4) indicated that exclusively dominant genes acted to increase RRS. The position of the parental lines along the $W_r$ on $V_r$ regression line (Figure 4) shows that lines 3, 1 and 6, with the greatest means (Table 5), were located nearer the origin of the regression line, thus exhibiting a greater proportion of dominant genes, with rare, if any, recessive genes for high RRS. Lines 2, 5 and 4, with the lowest means (Table 5), were positioned farther from the origin of the regression line (Figure 4), which indicated that they concentrate recessive genes.

The values of the broad-sense heritability ($h^2_{BS}$) were high for all traits (Table 4), probably due the genetic diversity among parental lines and $F_1$ and, also due the cultivation system used, wich allowed a good environmental control. The narrow-sense heritability ($h^2_{NS}$) was low in general compared to those of the broad-sense (Table 4), but at a level that allowed selection for low P tolerance. The sharp difference between $h^2_{BS}$ and $h^2_{NS}$ showed once again that both additive gene effects and dominance were involved in low P tolerance in sweet pepper. Similarly, estimates of heritability varying from moderate to high have also been observed for characteristics related to low-P tolerance in studies involving other plant species (Fawole et al., 1982; Chaubey et al., 1994).

The studies showed that tolerance to low P in sweet pepper, defined as the ability to grow under low P availability in soil, is genetically controlled. The presence of additive and dominant gene effects suggested that breeding programs for development of cultivars which are more tolerant to low P availability may be planned with a good chance of success. However, for further improvement of genotypes it is necessary to take into consideration the significant presence of dominance gene effects to exploit in the population. It this aspect, the results indicated that selection process in the pedigree method or its modifications should be relatively mild in the early generations or else be deferred until an advanced generation is reached with a greater degree of endogamy. On the other hand, recurrent selection with the intermating of the superior segregants should also be an alternative breeding procedure to increase the frequencies of favorable alleles. The manifestation of overdominance suggested that the exploitation of heterosis in $F_1$ hybrids may be an alternative, if there is also superiority in fruit yield and other agronomic traits.

## CONCLUSIONS

The tolerance to low P in sweet pepper, defined as the ability of plants to produce relatively more biomass, was genetically controlled by additive and mainly dominant genes effects. There were no maternal effects for any of the traits related to tolerance to low P, therefore, it makes little difference whether a plant is used as a seed or pollen parent. The parents P-141-152-F14, P-142-215-F15 and P-142-403-F11 – low P tolerants, and therefore with the greatest averages of total dry weight – when combined, may

produce segregants still more tolerants than the parents and with a pronounced genotypic variability.

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## RESUMO

### Análise genética da tolerância de pimentão ao baixo teor de fósforo no solo

O objetivo deste estudo foi avaliar o modo de herança da tolerância de pimentão (*Capsicum annuum* L.) a solo com baixo teor de fósforo (P), definida como a capacidade das plantas em produzir relativamente maior biomassa (massa seca total) em solo com baixo teor de P. Um dialelo completo envolvendo seis genótipos previamente selecionados, três tolerantes e três intolerantes ao baixo teor de P foi usado. Não houve diferenças entre cruzamentos recíprocos, em relação à massa seca total, bem como em relação à massa seca da parte aérea, massa seca de raízes, razão raiz:parte aérea e conteúdo total de P. Genes dominantes, predominantemente, mas não exclusivamente controlaram a tolerância ao baixo P. Dos três parentais tolerantes, dois concentraram genes dominantes e outro genes recessivos. A análise dos componentes de variação genéticos evidenciaram que ambos os efeitos gênicos aditivo e de dominância estiveram envolvidos no controle de todas as características, com maior contribuição da dominância para a variabilidade genética entre parentais e $F_1$. As estimativas de herdabilidade no sentido amplo foram altas, enquanto, no sentido restrito foram em geral baixas em relação às de sentido amplo.

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