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Hayman's diallel analysis of traits related to the production and quality of papaya fruit

Deisy Lúcia Cardoso ([1]); Marcelo Vivas ([2]); Antonio Teixeira do Amaral Junior ([2]);
Messias Gonzaga Pereira ([1*])

([1]) Universidade Anhanguera (UNIDERP), Unidade Agrárias, Avenida Alexandre Herculano, 1400, 79037280 Campo Grande (MS), Brazil.

([2]) Universidade Estadual do Norte Fluminense Darcy Ribeiro (UENF), Centro de Ciências e Tecnologias Agropecuárias (CCTA), Laboratório de Melhoramento Genético Vegetal (LMGV), Av. Alberto Lamego, 2000, 28013-602 Campos dos Goytacazes (RJ), Brazil.

(*) Corresponding author: messiasgpereira@gmail.com

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Abstract

In papaya, information on the genetic control of traits related to the production and fruit quality are still scarce. In this sense, this study estimated genetic parameters and analyzed the inheritance of traits related to the production and quality of papaya fruit through complete diallel cross (F1's, reciprocal and parents). The number of commercial fruit, fruit weight, fruit yield, thickness of the pulp, firmness of the fruit and the soluble solids content were quantified. Number of commercial fruit, firmness of the fruit and the total soluble solids content had no significant effect in the three sufficiency tests of the additive-dominant model. The estimate of the average degree of dominance indicated partial dominance between alleles that act in the genetic control of the three traits. There was predominance of effects associated with additive components compared to the components associated with dominance effects for the three traits. For the number of marketable fruits and fruit firmness, predominant, but not exclusive recessive alleles, work to increase the mean value of this variable. In turn, for soluble solids content, predominant, but not exclusive dominant alleles, work to increase the mean value of this variable.

Key words: *Carica papaya,* genetic control, hybridization, plant breeding.

1. INTRODUCTION

Papaya (*Carica papaya* L.), a typically tropical plant, has significant importance in the national and global production of fruit plants; the Brazilian Southeast and Northeast are the regions with the highest production. Despite its importance in the national scenario, there are few institutions working with the breeding of this crop. As a result, there is still little information about the inheritance of the main traits for the culture.

Knowledge of the genetic control of a trait is of paramount importance to the efficient conduction of a breeding program, allowing the breeder to choose the best procedure to be used as well as the most efficient breeding methods to conduct the segregating populations (Cruz et al., 2012). To meet this need, several genetic designs are available, highlighting the diallel crosses. Diallel consists of crossing the parents in pairs, and its analysis allows to infer about heterosis (Gardner & Eberhart, 1966), to estimate the general and specific combining ability (Griffing, 1956) and to study the genetic control of traits (Hayman, 1954a, b). According to Cruz et al. (2012), this last analysis provides information on the genetic control, genetic values of parents and the limits of selection of traits under study. The Hayman's methodology (Hayman, 1954a, b) has some restrictions for genetic-statistical model, namely: i) absence of epistasis; ii) absence of maternal effect; iii) absence of multiple allelism; iv) genes distributed independent among the parents; v) diploid segregation; and vi) homozygous parents. These restrictions, according to Cruz et al. (2012), are drawbacks to the use of this methodology.

Although it provides important results for the breeder, diallel crosses are seldom used in papaya, with few reports of their use in the estimation of combining ability (Marin et al., 2006b; Vivas et al., 2012b, c, 2013b, 2014a), and effects of heterosis (Marin et al., 2006a; Vivas et al., 2012c, 2014b). With regard to the use of the methodology proposed by Hayman (1954a, b), in papaya, studies are even more scarce, only the one developed by

Vivas et al. (2013a). In the aforementioned, the authors estimated parameters related to genetic resistance of papaya to early blight and powdery mildew. They verified at least four genes or gene blocks with dominance for powdery mildew severity and at least one for severity of early blight in leaf and fruit. They also found partial dominance for powdery mildew severity and complete dominance for severity of early blight in leaf and fruit.

This study aimed to determine the genetic control of the traits related to fruit production and quality in a diallel with eight papaya lines (parents), with the main goal of obtaining statistical genetic inferences for the implementation of future papaya breeding programs.

2. MATERIAL AND METHODS

Fifty-six hybrids (F1's, reciprocals and parents) were obtained for composition of a complete diallel including eight parents: 'Maradol', 'JS 12-N', 'JS 12-4' and 'Sekati' - 'Formosa' group; and, 'Waimanalo', 'Golden', 'Sunrise Solo 72-12' and 'São Mateus' - 'Solo' group. The experiment was established at the Farm Romana of the Company Caliman Agrícola S/A, in Linhares, Espírito Santo State. The parents were chosen on the basis of prior information obtained in topcross studies (Ide et al., 2009; Vivas et al., 2011, 2012a), partial diallel (Marin et al., 2006a, b) and genetic diversity (Quintal et al., 2012). We sought to use in the diallel crosses, parents that demonstrated to have good qualitative and quantitative agronomic traits, not only in terms per se, but also in terms of breeding values.

The 56 combinations (F1's and reciprocals) and their parents were evaluated in a randomized block experimental design with four replications; each plot consisted of 10 plants (double rows with five plants each row). We used the spacing of 2.0×1.4×3.6 m. The cultivation performed according to the company's routine were: correction of pH and soil base saturation (V = 85%); fertilizer in the furrow based on 150 kg ha^{-1} P_2O_5, and 10 liter.m^{-1} chicken manure: cattle manure compost at 1: 1; topdressing of 300 kg N, 650 kg K20, 80 kg P_2O_5, 90 kg Ca and 30 kg Mg via fertirrigation, which is located and applied by spraying. The planting scheme was three seedlings per hole and after sexing, it was kept the hermaphroditic plant, when existent.

We evaluated: i) Total number of commercial fruits (NCF): by counting all fruits with commercial characteristics, respectively at 170, 225 and 320 days after transplanting, being used for analysis the sum of fruit numbers; ii) average fruit weight (AFW): in grams, by weighing on an analytical balance five fruits of each plot; iii) fruit yield (FY): in t ha^{-1}, by multiplying the number of fruits per plant by the average fruit weight per plant, respectively, at 170, 225 and 320 days after transplanting and transformed into t ha^{-1}; iv) fruit firmness (FF): in Newton (N), measures were taken in the equatorial region of the fruit, in three equidistant points on the inside of the fruit; v) content of total soluble solids (TSS): in Brix, by using a digital refractometer, in five fruit of each plot; and vi) pulp average thickness (PAT): in mm, by measuring the mesocarp, after the cross section of the fruit, by measuring the thickness of the pulp at two points with the aid of a graduated ruler, using the average of five fruits of each plot.

For each evaluated trait, an analysis of variance was run. And the traits that met the assumptions, assessed by sufficient tests of the additive-dominant model (Cruz et al., 2012), were analyzed by Hayman's analysis (Hayman, 1954a, b). The analyses were conducted using the software GENES (Cruz, 2013).

3. RESULTS AND DISCUSSION

For all traits, there was a significant effect of genotypes (parents and their hybrids) by F-test. The experimental coefficient of variation (%) ranged from 5.81 (pulp thickness) to 23.47 (fruit yield). These results indicate an experimental accuracy, thus validating the conclusions to be inferred. The average fruit weight, although assessed, was not included in the analysis, due to the maternal effect for this trait. Generally, the restrictions on use of the Hayman's method (Hayman, 1954a, b) were evaluated by sufficiency tests of the additive-dominant model, based on heterogeneity of $\hat{W}_i - \hat{V}_i$. The traits NCF, FY and SST revealed no significance in the three tests, showing the adaptation to restrictions imposed and the feasibility of use of the additive-dominant model (Table 1). For the other traits, there was significance in at least one of the tests, culminating with the inadequacy of the model. As a result, these characteristics were excluded from subsequent analysis.

The estimate of the average degree of dominance ($\sqrt{\hat{H}_1 / \hat{D}}$) was 0.47; 0.65 and 0.70 for number of marketable fruits, fruit firmness and total soluble solids, respectively, indicating the existence of partial dominance (Table 2). The same can be observed by the fact that the regression line of $\hat{W}_r$ on $\hat{V}_r$ intercepts the ordinate above the origin (Figures 1a-c). According to Cruz et al. (2012), the parameter $\hat{H}_2 / 4\hat{H}_1$ allows to evaluate the proportion of parents in dominant or recessive homozygosity. According to the authors, the alleles have symmetrical distribution between the parents when the $\hat{H}_2 / 4\hat{H}_1$ ratio presents values close to 0.25. In this way, it is observed that only for total soluble solids there is symmetrical distribution of alleles favorable and unfavorable for the increase in this trait (Table 2). For NCF and FF, there was no symmetry in the distribution of favorable and unfavorable alleles for the increase of these traits. For these traits, estimates of $\hat{K}_D / \hat{K}_R$ allow to infer the prevalence of dominant homozygous forms between the parents that make up the diallel, especially for NCF (Table 2). From the estimates of the parameter $\hat{h}^2 / \hat{H}_2$, we observed that there is a gene or gene block with dominance for NCF and FF and at least two for TSS (Table 2).

For the three variables, there was predominance of the effects associated with additive components ($\hat{D}$) compared to the components associated with dominance effects ($\hat{H}_1$, $\hat{H}_2$ and $\hat{h}^2$); it was also observed that the estimates obtained for $\hat{D}-\hat{H}_1$ were positive, thus confirming the inferences above (Table 3). Nevertheless, considering the estimates of the components and their respective standard deviation for total soluble solids, it is concluded that there is a possibility of additive and non-additive genetic effects in the control of this trait (Table 3). In general, it might be speculated the possibility of gains by obtaining better segregating genotypes. The opportunity of obtaining such superior segregating genotypes becomes more concrete because of the value of the coefficient of determination in the strict sense exceeds 50% for TSS and FF and greater than 70% for NCF (Table 2). Such magnitude allows affirming that the desirable alleles will be transmitted to future generations with higher reliability.

Accordingly, it is known that the allele that provides increase in the genotypic average of a certain trait may be dominant or recessive. According to Cruz et al. (2012), a measure of this association is obtained by the concentration between the average value of the parent

Table 1. Sufficiency test of the additive-dominant model based on the analysis of variance of values of $\hat{W}_r - \hat{V}_r$ and on linear regression analysis of $\hat{W}_r$, as a function of $\hat{V}_r$, according to Hayman's method (Hayman, 1954a, b)

Trait	Anova $\left(\hat{W}_i-\hat{V}_i\right)$	Regression W_i=¼(D-H_1)+bV_i		
	MS (Lines)	$\hat{b}$ ± Variance	t(H_0:b=1)	t(H_0:b'=0)
Number of fruit	683.8213^{NS}	1.030±0.006	0.381^{NS}	–1.569^{NS}
Fruit yield	101361.4735**	0.358±0.015	–5.296**	1.779^{NS}
Fruit firmness	43.5694^{NS}	1.004±0.010	0.036^{NS}	–1.556^{NS}
Total soluble solids	0.0750^{NS}	0.842±0.033	–0.869^{NS}	–1.924^{NS}
Pulp thickness	2.1147^{NS}	0.951±0.032	–0.275^{NS}	–2.413*

^{NS} non-significant. * and ** significant at 5 and 1% significant level, respectively (Tests F and/or t).

Table 2. Estimates of genetic and non-genetic parameters for the number of commercial fruit (NCF), fruit firmness (FF) and total soluble solids (TSS), according to Hayman's method (Hayman, 1954a, b)

Parameters[1]	Parameter values		
	NCF	FF	TSS
$\sqrt{\hat{H}_1 / \hat{D}}$	0.4740	0.6573	0.7045
$\hat{H}_2 / 4\hat{H}_1$	0.1161	0.1340	0.2657
$\hat{K}_D / \hat{K}_R$	3.6931	1.6617	1.0807
$\hat{h}^2 / \hat{H}_2$	–0.0226	0.9216	2.2430
$\hat{h}^2_R$	0.7461	0.5892	0.5184
$\hat{h}^2_A$	0.8135	0.6673	0.6679

[1] $\sqrt{\hat{H}_1 / \hat{D}}$: average degree of dominance; $\hat{H}_2 / 4\hat{H}_1$: proportion of parents in dominant or recessive homozygosity (symmetry); $\hat{K}_D / \hat{K}_R$: dominant/recessive relationship; $\hat{h}^2 / \hat{H}_2$: number of genes with dominance; $\hat{h}^2_R$: coefficient of determination in the strict sense; $\hat{h}^2_A$: coefficient of determination in the broad sense.

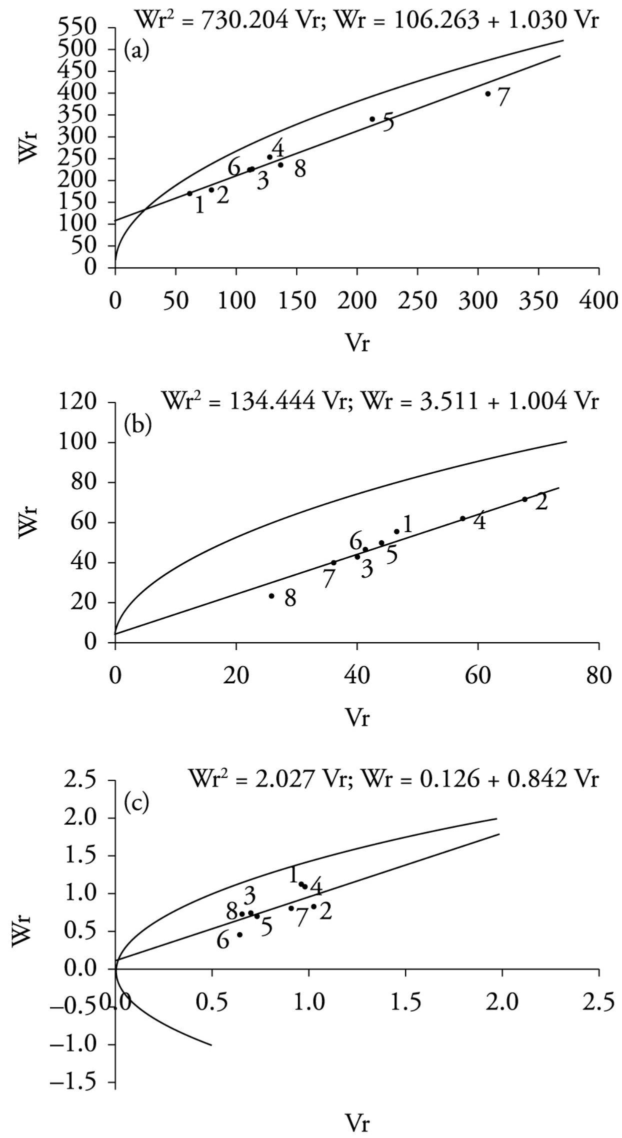

Figure 1. Regressions of $\hat{W}_r$ on $\hat{V}_r$, for the number of marketable fruit (a), fruit firmness (b) and total soluble solids (c); parents: 1 = 'Maradol'; 2 = 'JS12-N'; 3 = 'JS12-4'; 4 = 'Sekati'; 5 = 'Waimanalo'; 6 = 'Golden'; 7 = SS72-12'; and, 8 = São Mateus'.

($\bar{Y}_{rr}$) and average concentration of dominant and recessive genes given by $\hat{W}_r + \hat{V}_r$. For the number of marketable fruits (NCF) and fruit firmness (FF), the positive and moderate correlations (r) (0.53 and 0.64, respectively for NCF and FF) show that predominant, but not exclusive recessive alleles work to increase the mean value of this variable (Table 4). On the other hand, for total soluble solids content, the negative and moderate correlation (r) (–0.58) shows that predominant, but not exclusive dominant alleles, work to increase the mean value of this variable (Table 4).

For the number of marketable fruits (NCF), the parent 'Sunrise Solo 72/12' retained the largest concentration of recessive alleles, while the parent 'Maradol' and 'JS 12-N' showed the highest concentration of dominant alleles (Table 5, Figure 1a). The parent with maximum recessive homozygosity for NCF should present $\hat{W}_i + \hat{V}_i$=1037.47 ($= \hat{W}_R + \hat{V}_R$). Among the parents, 'Sunrise Solo 72/12', although retaining the highest concentration of recessive alleles, shows $\hat{W}_7 + \hat{V}_7$ equal to 706.22, highlighting the possibility of obtaining more productive lines from the selection in segregating populations derived from the diallel crossings (Tables 4 and 5). The increase in the number of marketable fruits can be obtained with the highest concentration of recessive genes, and the maximum expected value ($\hat{Y}_R$) is 96.49. 'Sunrise Solo 72/12' is the parent closest to this value (Tables 4 and 5).

For fruit firmness (FF), the parents 'JS 12-N' and 'Sekati' showed the highest concentration of recessive alleles, while São Mateus' retained the highest concentration of dominant alleles (Table 5, Figure 1b). The parent with maximum recessive homozygosity should present $\hat{W}_i + \hat{V}_i$=256.72 ($= \hat{W}_R + \hat{V}_R$). 'JS 12-N' was the parent with the highest concentration of recessive alleles, with $\hat{W}_2 + \hat{V}_2$ equal to 138.41, well below the maximum estimated, thus demonstrating the possibility of obtaining lines through selection of segregating populations (Tables 4 and 5).

The parents 'Maradol' and 'Sekati' showed the highest concentration of dominant alleles, while 'Goldem' retained the largest concentration of recessive alleles (Table 5). The parent with maximum dominant homozygosity for TSS should present $\hat{W}_i + \hat{V}_i$=0.13 ($= \hat{W}_D + \hat{V}_D$). 'Goldem', which showed the closest value (1.11), is still far from this value, indicating the possibility of obtaining lines with greater magnitudes of TSS in segregating populations derived from the diallel crossings. The increase in TSS may be obtained with the highest concentration of dominant genes, with the maximum expected value ($\hat{Y}_D$) of 13.34. 'Sunrise Solo 72/12' is the parent closest to this value (Tables 4 and 5).

4. CONCLUSION

Only the traits number of commercial fruit (NCF), fruit firmness (FF) and soluble solids content (TSS) are suited to restrictions on the viability of the additive-dominant model proposed by Hayman.

The variation of additive nature contributes to gene control, with partial dominance in the three traits.

Table 3. Estimates of genetic and non-genetic parameters for the number of commercial fruit (NCF), fruit firmness (FF) and total soluble solids (TSS), according to Hayman's method (Hayman, 1954a, b)

Components[1]	Values of the components ± standard deviation		
	NCF	FF	TSS
$\hat{\varepsilon}$	49.044±10.45	26.60±2.58	0.46±0.09
$\hat{D}$	681.160±31.34	107.84±7.74	1.57±0.25
$\hat{H}_1$	153.044±72.05	46.59±17.78	0.78±0.59
$\hat{H}_2$	71.066±62.69	24.96±15.47	0.83±0.51
$\hat{h}^2$	–1.608±42.04	23.00±10.38	1.85±0.34
$\hat{F}$	370.556±74.06	35.24±18.28	0.08±0.61
$\hat{D}-\hat{H}_1$	528.116±61.87	61.25±15.27	0.80±0.51

[1] $\hat{\varepsilon}$: environmental variance component; $\hat{D}$: component of variance associated with additive effects; $\hat{H}_1$ and $\hat{H}_2$: components of variance associated with dominance deviations; $\hat{h}^2$: quadratic component determined by the average difference between hybrids and parents; $\hat{F}$: component associated with the covariance between additive and non-additive effects; $\hat{D}-\hat{H}_1$: component expressing the difference between additive and dominant gene effects.

Table 4. Estimates of the correlations between the mean values of the parents ($\overline{Y}_{rr}$) and the sum of the covariance between means of the parents and averages of the r-th row ($\hat{W}_r$), and the variance between the averages of the r-th row ($\hat{V}_r$), expected values of the coordinates $\hat{W}_R;\hat{V}_R$ and $\hat{W}_D;\hat{V}_D$ and value predicted for the parents with maximum concentration of dominant ($\hat{Y}_D$) and recessive ($\hat{Y}_R$)alleles obtained for number of commercial fruit (NCF), fruit firmness (FF) and total soluble solids (TSS), according to Hayman's method (Hayman, 1954a, b)

Parameter	Parameter estimates		
	NCF	FF	TSS
$r(\overline{Y}_{rr},\hat{W}_r+\hat{V}_r)$	0.5311	0.6401	–0.5848
$\hat{W}_R;\hat{V}_R$	578.7546; 458.7166	130.3461; 126.3729	2.2727; 2.5483
$\hat{W}_D;\hat{V}_D$	130.1612; 23.2016	3.6079; 0.0968	0.1339; 0.0088
$\hat{Y}_R$ Limit	96.4948	113.5169	3.4698
$\hat{Y}_D$ Limit	18.9223	48.3580	13.3359

Table 5. Values of the sum of the covariance between averages of parents and averages of the r-th row ($\hat{W}_r$), and the variance between the averages of the r-th row ($\hat{V}_r$); and averages of the number of commercial fruit (NCF), fruit firmness (FF) and total soluble solids (TSS), according to Hayman's method (1954a,b)

Genotypes	NCF		FF		STT	
	$\hat{W}_r+\hat{V}_r$	AVERAGE	$\hat{W}_r+\hat{V}_r$	AVERAGE	$\hat{W}_r+\hat{V}_r$	AVERAGE
'Maradol'	232.23	21.56	101.28	58.88	2.09	7.93
'JS 12-N'	259.06	37.83	138.41	94.71	1.86	10.63
'JS 12-4'	339.43	28.43	82.15	76.71	1.45	10.23
'Sekati'	381.51	25.66	118.97	70.41	2.08	8.83
'Waimanalo'	552.56	13.37	93.35	67.89	1.44	10.78
'Golden'	336.21	62.23	87.12	71.93	1.11	10.88
'Sunrise Solo 72/12'	706.22	93.44	75.60	69.25	1.72	12.02
'São Mateus'	373.35	40.28	48.69	61.46	1.39	10.10

REFERENCES

Cruz, C. D. (2013). GENES: a software package for analysis in experimental statistics and quantitative genetics. Acta Scientiarum. Agronomy, 35, 271-276. http://dx.doi.org/10.4025/actasciagron.v35i3.21251.

Cruz, C. D., Regazzi, A. J., & Carneiro, P. C. (2012). Modelos biométricos aplicados ao melhoramento genético. Viçosa: Editora UFV.

Gardner, C. O., & Eberhart, A. S. (1966). Analysis and interpretation of the variety cross diallel and related populations. Biometrics, 22, 439-452. http://dx.doi.org/10.2307/2528181. PMid:5970549.

Griffing, B. (1956). Concept of general and especific combining ability in relation to diallel crossing systems. Australian Journal of Biological Sciences, 9, 463-493.

Hayman, B. I. (1954a). The analysis of variance of diallel tables. Biometrics, 10, 235-244. http://dx.doi.org/10.2307/3001877.

Hayman, B. I. (1954b). The theory and analysis of diallel crosses. Genetics, 39, 789-809. PMid:17247520.

Ide, C. D., Pereira, M. G., Viana, A. P., & Pereira, T. N. S. (2009). Use of testers for combining ability and selection of papaya hybrids. Crop Breeding and Applied Biotechnology, 9, 60-66. http://dx.doi.org/10.12702/1984-7033.v09n01a09.

Marin, S. L. D., Pereira, M. G., Amaral, A. T., Jr., Martelleto, L. A. P., & Ide, C. D. (2006a). Heterosis in papaya hybrids from partial diallel of 'Solo'and 'Formosa'parents. Crop Breending and Applied Biotechnology, 6, 24-29. http://dx.doi.org/10.12702/1984-7033.v06n01a04.

Marin, S. L. D., Pereira, M. G., Amaral, A. T., Jr., Martelleto, L. A. P., & Ide, C. D. (2006b). Partial diallel to evaluate the combining ability for economically important traits of papaya. Scientia Agrícola, 63, 540-546. http://dx.doi.org/10.1590/S0103-90162006000600005.

Quintal, S. S. R., Viana, A. P., Gonçalves, L. S. A., Pereira, M. G., & Amaral, A. T., Jr. (2012). Genetic divergence among papaya accessions by morphoagronomic traits. Semina: Ciências Agrárias, 33, 131-142. http://dx.doi.org/10.5433/1679-0359.2012v33n1p131.

Vivas, M., Silveira, S. F., Terra, C. E. P. S., & Pereira, M. G. (2011). Testers for combining ability and selection of papaya hybrids resistant to fungal diseases. Crop Breeding and Applied Biotechnology, 11, 36-42. http://dx.doi.org/10.1590/S1984-70332011000100005.

Vivas, M., Silveira, S. F., & Pereira, M. G. (2012a). Prediction of genetic gain from selection indices for disease resistance in papaya hybrids. Revista Ceres, 59, 781-786. http://dx.doi.org/10.1590/S0034-737X2012000600007.

Vivas, M., Silveira, S. F., Cardoso, D. L., Pereira, M. G., Vivas, J. M. S., & Ferreguetti, G. A. (2012b). Capacidade combinatória em mamoeiro para resistência a oídio. Bragantia, 71, 455-459. http://dx.doi.org/10.1590/S0006-87052012000400001.

Vivas, M., Silveira, S. F., Cardoso, D. L., Pereira, M. G., Santos, P. H. D., & Ferreguetti, G. A. (2012c). Capacidade Combinatória e heterose para resistência a pinta-preta em mamoeiro por meio de análise dialélica. Tropical Plant Pathology, 37, 326-332. http://dx.doi.org/10.1590/S1982-56762012000500004.

Vivas, M., Silveira, S. F., Amaral, A. T., Jr., Cardoso, D. L., & Pereira, M. G. (2013a). Herança da resistência do mamoeiro a doenças fúngicas com base em análise dialélica de Hayman. Bragantia, 72, 332-337. http://dx.doi.org/10.1590/brag.2013.047.

Vivas, M., Silveira, S. F., Pereira, M. G., Cardoso, D. L., & Ferreguetti, G. A. (2013b). Análise dialélica em mamoeiro para resistência a mancha-de-phoma. Ciência Rural, 43, 945-950. http://dx.doi.org/10.1590/S0103-84782013005000054.

Vivas, M., Silveira, S. F., Viana, A. P., Amaral, A. T., Jr, Cardoso, D. L., & Pereira, M. G. (2014a). Efficiency of circulant diallels via mixed models in the selection of papaya genotypes resistant to foliar fungal diseases. Genetics and Molecular Research : GMR, 13, 4797-4804. http://dx.doi.org/10.4238/2014.July.2.9. PMid:25062415.

Vivas, M., Silveira, S. F., Cardoso, D. L., Amaral, A. T., Jr., & Pereira, M. G. (2014b). Heterose para resistência a mancha-de-phoma em híbridos de mamoeiro obtidos a partir de cruzamentos entre e dentro de grupos heteróticos. Summa Phytopathologica, 40, 318-322. http://dx.doi.org/10.1590/0100-5405/2017.