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ARTICLE

Genetic control of leaf spinescence in BRS Imperial, Pérola, and Pico de Rosa pineapple cultivars

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Abstract: *Leaf spinescence in pineapple plants was evaluated in a total of 2.014 F1 individuals as follows: 1.125 plants of the progeny of the Imperial BRS cv. × Pérola cv. cross, and 889 plants of the progeny of the Pico de Rosa cv. × BRS Imperial cv. cross. The genetic hypothesis with two loci and epistatic interaction of the piping (P) over spiny (S) trait was tested. The chi-square test was performed on deviations between the observed and expected numbers based on the genetic hypotheses formulated. The "BRS Imperial" × "Pérola" and "Pico de Rosa" × "BRS Imperial" progenies segregated into 1:0:1 (spineless:spiny tip:spiny), expressing phenotypes of their respective parents. The spineless leaf ("BRS Imperial") is determined by the "Ppss" genotype, with the locus "P" in heterozygosity and the locus "S" in recessive homozygosity. The spiny leaf margin ("Pérola" and "Pico de Rosa") is controlled by the "ppss" genotype.*

Keywords: *Ananas comosus var. comosus, spineless leaf, spiny, genotype.*

INTRODUCTION

The presence of spines/thorns on the pineapple leaf margin creates difficulties in seedling handling operations during planting, crop management practices, and fruit harvesting as it requires complete protection against scratches/cuts on hands, arms, and legs, which hinders workers' movement among plants. Leaves without spines along the entire leaf margin facilitates these crop operations and also provides consumers with greater convenience in handling the pineapple and holding it by the crown at farmer's markets and supermarkets, as well as during cleaning operations, storage, and manual peeling.

The main pineapple cultivar planted in Brazil (Reinhardt et al. 2018), known as "Pérola" or "Branco de Pernambuco", has spiny leaf margins and vigorous growth, with long leaves and dark green color. Its fruit has a conical shape, mainly directed to the domestic fresh fruit market. Average fruit weight is 1.6 kg; the pulp has a cream-white color with abundant juice and intense aroma, and total soluble solids are between 13-16 °Brix. The Jupi cv. is similar to the Pérola cv., but differs in cylindrical fruit shape and yellowish pulp color. Both cultivars are highly susceptible to fusariosis, a fungal disease (*Fusarium guttiforme*) that severely affects Brazilian production.

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In Brazil, the development of new pineapple (*Ananas comosus* var. *comosus*) cultivars aims to combine genes that control resistance to fusariosis and leaf margins without spines in a single plant, as well as genes of dozens of other traits related to improvement of fruit quality and greater yield stability (Cabral et al. 2009, Ventura et al. 2019, Reinhardt et al. 2012).

The Brazilian Agricultural Research Corporation - Embrapa (Empresa Brasileira de Pesquisa Agropecuária) has developed three smooth-leaf and fusarium-resistant cultivars: "BRS Imperial" ("Perolera" × "Smooth Cayenne-56"), released in 2003, with yellow peel and pulp; "BRS Vitória" ("Primavera" × "Smooth Cayenne-08"), released in 2006, with white flesh and yellow peel; and "BRS Ajubá" ("Perolera" × "Smooth Cayenne-14"), released in 2009, and recommended especially for growing in the northwest region of the state of Rio Grande do Sul and the Uruguay River valley. The Agronomic Institute of Campinas - IAC (Instituto Agronômico de Campinas) released the IAC Fantástico cv. in 2010 (from open pollination of a "Tapiracanga" × "Smooth Cayenne"), which has fusariosis resistance, yellow flesh, and spines only at the leaf tip.

The phenotype with piping leaf (spineless leaf) facilitates handling of plant materials during the selection and classification processes by size, accelerates pineapple mealybug (*Dysmicoccus brevipes*) treatment by immersion, and contributes to better movement of workers among rows, speeding planting, weeding, spraying, fertilizing, and harvesting operations.

The objective of this paper was to determine the genotypic combinations associated with control of pineapple leaf margin spinescence in "BRS Imperial", "Pérola" and "Pico de Rosa" based on the phenotypic evaluation of segregating progenies developed by the plant breeding program of the Agronomic Institute of Pernambuco State - IPA (Instituto Agronômico de Pernambuco).

MATERIAL AND METHODS

The experiment was carried out at the Itambé Experimental Station (lat 7° 24' 16.80" S, long 35° 10' 54.00" W, alt 190 m asl) belonging to IPA. The municipality of Itambé is located in the North region of the *Zona da Mata* of Pernambuco. The climate in the region is hot and humid As (Köppen), with mean annual temperature of 25 °C, and mean annual rainfall of 1.200 mm year^{-1}.

A total of 2.014 F1 individuals were evaluated: 1.125 plants of the progeny of the BRS Imperial cv. × Pérola cv. cross, and 889 plants of the progeny of the Pico de Rosa cv. × BRS Imperial cv. cross. These progenies were developed by the plant breeding program of IPA through controlled pollinations, according to the technical recommendations of Cabral et al. (2009). "BRS Imperial", "Pérola", and "Pico de Rosa" were chosen as parents due to contrasts in the leaf margin spinescence trait (Figure 1). These cultivars were planted side by side to obtain hybrid seeds. Twenty plants of each cultivar were grown from peduncle slips, with one plant per 10 L capacity plastic buckets that were kept in a greenhouse under micro-sprinkler irrigation. Soil (2/3) and cattle manure (1/3) was used as substrate, and 10 g of single superphosphate was added per 10 L of the substrate mixture. Flowering was induced by treatment with calcium carbide in liquid form. Seeds were extracted from ripe fruit, washed under running water, and dried at 37 °C for 48 hours. The seeds were then distributed in polyethylene trays with blotter paper as substrate, which

Figure 1. Pineapple parent leaf margin: Spineless or smooth of the BRS Imperial cv. (A); totally spiny of the Pérola cv. (B) and Pico de Rosa cv. (C)

was moistened with distilled water. Trays were sealed with PVC film and kept in a seed germination chamber at 25 °C under continuous light for up to 75 days after sowing.

Seedlings were transplanted from expanded polystyrene trays containing Plantmax HT commercial substrate and kept under 50% shading and mist irrigation. At 90 days after transplanting, seedlings were placed in individual black polyethylene bags (15 x 10 cm) containing soil (2/3) + cured manure (1/3) and kept under full sun and micro-sprinkler irrigation. After acclimatization, seedlings were planted in the experimental field at a spacing of 1.2 m between rows and 0.6 m between plants in each row under a rainfed growing system. Rainfall data for the growing period are shown in Table 1. Fertilization was performed considering the following results of soil fertility: P = 5 mg dm^{-3}, pH = 5.7 (H2O), Ca = 3.7 cmolc dm^{-3}, Mg = 1.00 cmolc dm^{-3}, Na = 0.03 cmolc dm^{-3}, K = 0.27 cmolc dm^{-3}, Al = 0.00 cmolc dm^{-3}, H = 5.36 cmolc dm^{-3}, S = 5.00 cmolc dm^{-3}, CEC = 10.40 $cmolcdm^{-3}$. At 12 months after planting, adult plants were evaluated for the presence or absence of spines along the leaf margin by viewing with the naked eye or by touch.

Table 1. Monthly rainfall distribution during the field growth period. Instituto Agronômico de Pernambuco (IPA), Itambé Experimental Station, state of Pernambuco, Brazil

Year/month	**Rain** (mm)	**Year/month**	**Rain** (mm)
2017-May	147.0	2018-Mar	105.0
2017-Jun	191.0	2018-Apr	235.0
2017-Jul	380.0	2018-May	175.0
2017-Aug	83.0	2018-Jun	136.8
2017-Sep	63.0	2018-Jul	124.0
2017-Oct	40.0	2018-Aug	2.0
2017-Nov	5.0	2018-Sep	4.5
2/017-Dec	8.0	2018-Oct	3.0
2018-Jan	201.9	2018-Nov	4.7
2018-Feb	217.0	2018-Dec	48.0

Source: Agência Pernambucana de Águas e Clima - APAC (http://www.apac.pe.gov.br/).

The genetic hypothesis with two loci (P - piping and S - spiny) with epistatic interaction of “P” over “S” (Collins and Kerns 1946) was considered, controlling leaf margin spinescence with three phenotypic classes as follows: 1) spineless (P - - -); 2) “Cayenne” type or spiny tip (ppS -); and 3) spiny leaf margin (ppss). According to this inheritance model, the following genotypic combinations were analyzed: “PPSS”, “PPSs”, “PPss”, “PpSS”, “PpSs”, and “Ppss” for spineless leaf margin of “BRS Imperial”; and “ppss” for spiny leaf margin of “Pérola” and “Pico de Rosa” (Table 2).

The chi-square statistical test (χ^2) was performed on deviations between observed and expected numbers, based on the genetic hypotheses, and the effect of heterogeneity was verified among progenies. The value of χ^2 was obtained by the following expression: $\chi^2 = \sum[(oi - ei)^2/ei]$, where *oi* = observed number of plants for the class evaluated; and *ei* = expected number of plants for the class evaluated. Hypotheses with the calculated $\chi^2 \geq$ the tabulated χ^2 were rejected; and hypotheses with the calculated $\chi^2 <$ the tabulated χ^2 were not rejected. The significance level (*p* value) was estimated using the probability function of the chi-square variable. Statistical analyses were performed by the Genes software (Cruz 2006).

RESULTS AND DISCUSSION

Evaluations of the “spineless” and “spiny” leaf margins converged to the same hypothesis of segregation when their data analyzed by the chi-square test confirmed genetic control of that trait. Both progenies (BRS Imperial cv. × Pérola cv. and Pico de Rosa cv. × BRS Imperial cv.) segregated into 1:0:1 (spineless:spiny tip:spiny), expressing the phenotypes of their respective parents (Table 3). This result and its reliability were corroborated by associated error probabilities of

Table 2. Testing of genetic hypothesis with two loci (P - piping and S - spiny) with epistatic interaction of “P” over “S” for three phenotypic classes of leaf margin spinescence (Collins and Kerns 1946)

Genotypic hypothesis for leaf margin spinescence		**Expected phenotypic relation within progeny**
“Spineless” (BRS Imperial cv.)	**“Spiny” (Pérola and Pico de Rosa cvs.)**	**spineless: spiny tip: spiny**
PPSS	ppss	1: 0: 0
PPSs	ppss	1: 0: 0
PPss	ppss	1: 0: 0
PpSS	ppss	1: 1: 0
PpSs	ppss	2: 1: 1
Ppss	ppss	1: 0: 1

92.87% and 97.35%, respectively, to the both progenies, if the genotypic hypotheses are rejected. Plants with "Cayenne" type or "spiny tip" leaf were not found in any of the progenies evaluated. These results confirm the genetic theory proposed by Collins and Kerns (1946) and indicate that "BRS Imperial" has genotype "Ppss" for spineless leaf; that is, it contains the locus "P" (piping) in heterozygosity and the locus "S" (spiny) in recessive homozygosity. Also, denote that "Pérola" and "Pico de Rosa" cultivars have the same "ppss" genotype for spiny leaf margin; that is, they have double recessive homozygosity.

The other genotypic hypotheses evaluated ("PPSS", "PPSs", "PPss", "PpSS", and "PpSs") were discarded for "BRS Imperial" in crosses with the double recessive genotype "ppss" of "Pérola" and "Pico de Rosa", since the different expected phenotypic relation does not explain the observed phenotypic classes and frequencies (Table 2). For the "PPSS", "PPSs", and "PPss" genotypes crossed with the "ppss" genotype, the same probability (100%) of descendent plants with spineless leaves was obtained; that is, the dominant homozygous locus P with epistatic effect did not allow segregation of the progeny, regardless of its combination with alleles of the S locus. Regarding the hypotheses of the crosses between the "PpSS" and "PpSs" genotypes with the "ppss" genotype, the possibilities of segregation 1:1:0 (spineless:spiny tip:spiny) and 2:1:1 (spineless:spiny tip:spiny) does not explain too the observed phenotypic classes and frequencies (Table 2). Table 3 presents the results of the chi-square test (χ^2), associated with the genotypic combinations of the 1:0:1 (spineless:spiny tip:spiny) phenotypic ratio regarding the hypothesis of the cross between the "Ppss" genotype and the "ppss" genotype.

Analysis found deviations between the observed and expected data within each progeny, according to the two-gene theory, and epistatic interaction of the locus "P" over the locus "S" (Collins and Kerns 1946), controlling leaf margin spinescence. Genic or non-allelic interactions consist of relationships between two or more independently distributed gene pairs that jointly control only one trait.

Table 3. Chi-square test (χ^2) for genetic hypothesis with two loci (P - piping and S - spiny) and epistatic interaction of "P" over "S" (Collins and Kerns 1946), controlling leaf margin spinescence

Items	**Progenies** (Female parent × Male parent)	
	BRS Imperial cv. × Pérola cv.	**Pico de Rosa cv. × BRS Imperial cv.**
Genotypic hypothesis	"Ppss" × "ppss"	"ppss" × "Ppss"
Phenotype	spineless × spiny	spiny × spineless
Phenotypic relation	(spineless: spiny tip: spiny)	
Expected phenotypic ratio	1: 0: 1	1: 0: 1
Observed number (*O*)	561: 0: 564	444: 0: 445
Expected number (*E*)	562.5: 0: 562.5	444.5: 0: 444.5
$O - E$	-1.5: 0: 1.5	-0.5: 0: 0.5
$(O - E)^2/E$	0.004: 0: 0.004	0.0005: 0: 0.0005
Calculated χ^2	0.008	0.001
P (%)	92.87	97.35

Table 4. Chi-square test (χ^2) for heterogeneity among the progenies, considering the genotypic combinations "Ppss" for the BRS Imperial cultivar and "ppss" for the Pérola and Pico de Rosa cultivars

Progenies	**Hypothesis (1: 0: 1)**			
	spineless: spiny tip: spiny	**df**	**χ^2**	**P** (%)
"BRS Imperial" × "Pérola"	561: 0: 564	1	0.008	92.87
"Pico de Rosa" × "BRS Imperial"	444: 0: 445	1	0.001	97.32
Total	1005: 0: 1009	2	0.009	99.54
Deviation	-	1	0.007	92.89
Heterogeneity	-	1	0.001	97.25

According to the genetic theory of Collins and Kerns (1946) with three phenotypic classes, spiny leaf margin may have the following genotypes: "PPSS", "PPSs", "PPss", "PpSS", "PpSs", or "Ppss". The presence of only one P allele is sufficient to suppress spiny leaf, regardless of its combination with the other alleles at the 2 loci. Plants with spineless leaves are preferred for growing because of ease of handling and harvesting; "Cayenne" type or "spiny tip" can be controlled by the "ppSS" or "ppSs" genotypes. The presence of spines along the entire leaf margin is controlled by the double recessive "ppss" genotype.

Generally, qualitative traits, such as the leaf color in papaya (Nascimento et al. 2019), flower color and growth habit in linseed (Yadav et al. 2017), resistance to yellow rust in wheat (Rodríguez-García et al. 2019), resistance to fusarium wilt in common bean (Batista et al. 2017), traits related to maturity in cowpea (Santos et al. 2020), and pineapple plant leaf margin spinescence are little or not at all affected by the environment, but are or 2017under simple genetic control conditioned by one or a few genes. Such traits are studied by analyzing generations, with separation of individuals into distinct phenotypic classes or proportions (Collins and Kerns 1946, Souza et al. 2011, Urasaki et al. 2015).

Quantitative traits have complex inheritance, conditioned by many genes with small individual effects, and are greatly affected by the environment. In these cases, the inheritance and variation of traits are studied on the population level through estimation of genetic parameters (Candido et al. 2017, Rohaeni and Yunani 2017, Sakulphrom et al. 2017, Coelho et al. 2019).

Cabral et al. (1997) reported that segregations for leaf types was in accordance with the frequencies expected from the Collins and Kerns (1946) 2-gene model, with the Primavera cv. being homozygous for the spineless (piping) type. Kinjo (1993) demonstrated that F1 plants from spineless (Maipure cv.) and spiny parents segregated 1:1 with their parent phenotypes, being controlled by a single pair of alleles. Crosses between cultivars with few spines and cultivars with spiny leaf margin resulted in both phenotypes of the parents and an irregular spiny form, called "Scallop". In crosses between "Cayenne" and different types of "Cayenne", few spines, "Scallop", "spiny", and "spineless" (except for Maipure cv.) phenotypes appeared, suggesting that these traits expressed three pairs of alleles. Usberti Filho et al. (1995) evaluated the leaf margin segregation of 19 progenies that were obtained through open and artificial pollination. In contrast with the inheritance model proposed by Collins and Kernes (1946), these authors presented the following hypotheses: spineless leaf margin (not piping) of the Rondon cv. would be controlled by the recessive homozygous genotype (ppss); the completely spiny leaf margin would be controlled by the "ppSS" and "ppSs" genotypes, being dominant over "ppss"; and the partial leaf spinescence of the "Smooth Cayenne" cv. with the "ppSs" genotype would be caused by genotype × environment interactions, mutations, modifying genes, and/or unknown factors.

In general, evaluation of open-pollinated progenies may change the results. In cases of open pollination, there is no control of the pollen origin of one or more male parents and, consequently, the classes and phenotypic proportions observed in relation to the model presented by Collins and Kernes (1946) may be altered. Plant age at the time of evaluation and the interaction of the plant with growing conditions can affect the presence or absence of spines along the leaf margin, mainly in the types with spines only at the tip of the leaf and/or with irregular distribution. In these cases, for example, evaluation of spinescence in young plants before inflorescence or up until full fruit formation may also change the proportion observed in the progenies.

Unfavorable environments that cause temporary stresses on plant growth (Coppens D'Eeckenbrugge and Leal 2018) may also cause variation in the result of leaf spinescence evaluation through production of leaves with irregular leaf margins in plants that originally had spines only at the leaf tip and almost imperceptible to the naked eye. They can consequently be mistakenly classified as smooth or spineless, except plants that form a silver edge along the leaf margin, called "piping". (Coppens D'Eeckenbrugge and Sanewski 2011).

Regarding the results of the heterogeneity test (Table 4), the significance of the hypothesis, based on the total observed number of 1005:0:1009 (spineless:spiny tip:spiny), was estimated by the deviation, added within each class in both progenies. Concordance between progenies was measured by the difference between the total and deviation values, validating the null hypothesis. Therefore, there is concordance between progenies in the 1:0:1 segregation (spineless:spiny tip:spiny) with the associated error probability (p value) of 97.25%. This result supports the genetic hypothesis tested (Collins and Kerns 1946) and corroborates the genotypic combinations of "Ppss" for "BRS Imperial" and "ppss" for "Pérola" and "Pico de Rosa". It should be noted that the heterogeneity test was properly applied, since the spineless leaf (Ppss) BRS Imperial cv. was used in hybridization as both a female parent and a male parent with "Pérola" and "Pico de Rosa", respectively, both with spiny leaves (ppss).

CONCLUSIONS

The spineless leaf margin demonstrated by 'BRS Imperial' is controlled by the "Ppss" genotype, characterized by the P locus in heterozygosity and the S locus in recessive homozygosity. The spineless leaf margin phenotype is under simple genetic control and can be transferred in high proportion to first generation (F1) descendants. Spiny leaf margin, shown by "Pérola" and "Pico de Rosa" is controlled by the "ppss" genotype, represented by the P locus and the S locus, both in recessive homozygosity.

Phenotypic segregation of 1:0:1 (spineless:spiny tip:spiny) corroborates the theory of two genes with epistatic interaction of the locus "P" (piping) over the locus "S" (spiny) in control of leaf margin spinescence.

These results will be useful and applicable to pineapple breeding for selection of parents and for obtaining cultivars resistant to fusariosis and with spineless leaves.

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