

# Inheritance of leaf spininess and segregation of leaf color in pineapple (*Ananas comosus* L. Merrill)

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## ABSTRACT

Progenies from 13 artificial and six open-pollinated intervarietal pineapple crosses were analyzed for leaf spininess and leaf color. A new hypothesis for the inheritance of the leaf spininess trait based on the observed segregations is put forward. It clearly explains the segregation of 11 out of the 13 artificial crosses, whereas the current accepted hypothesis (Collins and Kernes, *J. Heredity* 37: 123-128, 1946) explains only eight of the 13 crosses.

Three crosses were crucial for the acceptance or rejection of both hypotheses. The crosses Boituva x Smooth Cayenne and Pérola x Smooth Cayenne, which involve "non-piping" and heterozygous for the S locus (Ss) parents, gave rise to spineless individuals in the offspring, at the expected frequency of three spiny to one spineless. This fact cannot be explained by Collins and Kernes' (1946) hypothesis. The cross Roxo-de-Tefé x Rondon resulted in nearly 100% spiny descendants, different from the frequency expected by the Collins and Kernes' hypothesis (50% spiny: 50% spineless).

The new hypothesis allows the identification of two new clones as "piping" types (Manauara Inerme and Pina Negra) and confirms that the genotypic constitution of the Rondon clone is probably ppss (spineless "non-piping"). When the genotype is pp, the S locus produces the completely spiny phenotypes (ppSS and ppSs), which are dominant over the spineless one (ppss). The partial leaf spininess of the cultivar Smooth Cayenne, described as heterozygous for the S locus (ppSs), must be caused by genotype x environment interactions, genetic background effects, modifying genes and/or other unknown facts. Green leaf color has incomplete dominance over purple leaf color, but green predominates.

The edible pineapple (*Ananas comosus* L. Merrill) is a self incompatible species, parthenocarpic, and vegetative propagation is traditionally used (Brewbaker and Gorrez, 1967; Pickersgill, 1976). The presence of seeds in the fruits in commercial plantations is unlikely since a single cultivar is normally used. However, it is relatively easy to obtain seeds by artificial

biparental crossings or by open pollinations when various genotypes are present in the same area (as in a germplasm bank). The species is therefore allogamous and heterozygous, with hermaphroditic flowers which are usually pollinated by insects (Cabot, 1987; Loison-Cabot, 1990). The level of seed production in artificial and open-pollinated crosses depends on the compatibilities between the participating genotypes (Spironello *et al.*, 1994).

In spite of the possibility of obtaining seeds, few studies have been carried out on the inheritance of morphological and fruit quality traits using analysis of individuals of segregating progenies. Most studies have

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only emphasized aspects related to the selection of individuals, carriers of desirable characteristics, in plant breeding programs (Aguilar, 1981; Couto, 1981; Giacomelli and Sobrinho, 1983; Cabot, 1987, 1989).

Leaf spines make planting, crop management and fruit harvesting difficult. Thus, according to Loison-Cabot (1988) and Loison-Cabot and Lacoëuilhe (1990), priority has been given to obtaining new spineless cultivars with other useful traits, such as resistance to *Fusarium*, high vitamin C content, cylindrically shaped fruit, resistance to lodging, etc.

The spiny leaf trait was studied by Collins and Kernes (1946), who concluded that it is caused by two independent and epistatic loci (P and S). The P allele codes for spineless leaves (totally without spines on the edges), independent of the S locus. The P allele, called "piping", causes morphological alterations of the leaf edges. The lower epiderm folds over and covers the upper epiderm of the leaf, forming a narrow, slightly whitened strip, due to the greater wax content of its tissue. In the presence of the pp genotype, the trait becomes controlled by the S locus. The SS and Ss genotypes have an intermediate number of spines on the edges of their leaves and ss has completely spiny leaf edges. These authors infer that intermediate or partial spininess (SS and Ss) is dominant over completely spiny leaves (ss). According to this hypothesis, all the spineless individuals, without exception, must have the P allele in their genotypic constitution.

## MATERIAL AND METHODS

The following genetic materials were used in this study: a) spineless leaf varieties (Perolera cultivar and the clones Rondon, Manauara Inerme and Pina Negra); b) varying degrees of leaf spininess (Smooth Cayenne cultivar) and, c) completely spiny leaf edges (Pérola cultivar and the clones Roxo-de-Tefé, Turi-Verde, Guiana, Rioja and Boituva). The leaves varied in color from pale green (Turi-Verde) to deep purple (Roxo-de-Tefé).

Open-pollination and artificial crosses among these genetic materials were carried out in the field. The inflorescences of the female plants used for the artificial crosses were protected with waterproof paper bags when anthesis of the basal flowers started. The pollen donor flowers were also protected to prevent contamination. One inflorescence of each female plant was used for artificial pollination and the corresponding bract was marked with paint. For open pollination,

individuals of each cultivar or clone were pre-selected and then allowed to cross freely (Spironello *et al.*, 1994).

The hybrid seeds were harvested from ripe fruits, after making cross cuts 0.5 cm deep. Aseptic *in vitro* germination was used to determine the highest level of seed germination, since each hybrid seed obtained was considered of high potential value. Pineapple seeds express a significant level of dormancy due to an impermeable seed coat. Previous experimentation showed that immersing the seeds in concentrated sulfuric acid for 60 seconds to reduce dormancy is effective. After chemical scarification, the seeds were washed three times in sterile distilled water. They were then sterilized by immersion in 2.5% sodium hypochlorite for 30 seconds and washed repeatedly in sterile distilled water.

The culture medium for germination and seedling development *in vitro* was developed from previous experimental trials. It contains half the inorganic salts and vitamins of the culture medium of Murashige and Skoog (1962) plus 0.5% bacto-agar and 3% sucrose. The seeds, placed in flasks with this culture medium, were kept in a room under controlled photoperiod and temperature (16 hours of light and temperature of  $25 \pm 2^{\circ}\text{C}$ ).

After 90 days the plants were transferred to plastic trays containing a suitable mineral-organic substrate. The plants were scored for the presence or absence of leaf spines and leaf coloring 45 days after transplanting.

Individuals were separated into two distinct classes for the spiny leaf trait: a) phenotypes with spines all along the leaf edges, together with those with an irregular spine distribution and, b) spineless phenotypes. The phenotypes in the first class were grouped together, because irregular or intermediate spininess is highly subject to evaluation errors, due to interactions with the environment and the growth conditions of the plant.

The following phenotypic classification was used for the leaf color trait: UG, uniformly green; UP, uniformly purple; GPM, green with purple marks and GYM, green with yellow marks. The genotypes were distributed in the above classes as percentages.

The phenotypic frequencies observed in the biparental crosses were used to clarify the genotypic constitution of the cultivars and clones for the spiny leaf trait. The  $X^2$  test was used to test the significance of the deviations between expected and observed numbers in the proposed hypothesis. Yates' correction (Little and Hills, 1972) was used in cases with only one degree of freedom. The observed frequencies of the different phenotypes in open-pollinated crosses were

analyzed to check possible agreement with those obtained in artificial crosses.

## RESULTS AND DISCUSSION

Table I shows the leaf spininess results obtained from progenies of several artificial crosses between pineapple cultivars and clones. The possible genotypic constitutions of the parental types based on the segregation observed, according to the hypothesis of Collins and Kernes (1946) and the one put forward in this study, are also suggested.

Large differences in the parental genotypic constitutions were observed under each hypothesis. According to the hypothesis of Collins and Kernes (1946), the completely spiny types would have the ppss genotypes whereas those with partial or intermediate spininess would have ppSS or ppSs genotypes. Under the new hypothesis, the ppSS, ppSs and ppss genotypes

would express complete spininess, intermediate spininess and spineless types, respectively. In both hypotheses, the presence of the P allele conditions the spineless phenotype. However, the hypothesis of Collins and Kernes does not allow for spineless types without the presence of the P allele.

The intermediary phenotypes (SS, Ss) were not observed either in the original spiny genetic materials used in this study (Roxo-de-Tefé, Pérola, Turi-Verde, Boituva, Guiana and Rioja) or in their progenies, suggesting that dominance is complete in these cases. Indeed, in the Boituva (spiny) x Rondon (spineless) crossing, the observed segregation can be explained by both hypotheses, if the Boituva clone is heterozygous for the S locus. Similarly, in the Pérola (spiny) x Smooth Cayenne (partial spininess) crossing, the observed segregation suggests that Pérola is heterozygous (Ss). The cultivar Smooth Cayenne is the only obvious case of a Ss genotype with intermediate phenotypic expression. In this case, the presence of an interaction

**Table I** - Leaf spininess evaluation results obtained in progenies derived from artificial crosses among pineapple (*Ananas comosus* L. Merrill) cultivars and clones.

Cultivar/ clone	No. of individuals		Probable parental genotypic constitution		Frequency of individuals in the progeny				X <sup>2</sup> (b)
	spiny	spineless	New hypothesis	Collins and Kernes' hypothesis	Expected spiny / spineless	Observed spiny / spineless			
(a)									
RT x PL	281	355	ppSS x PpSs	ppss x Pp--	50%	50%	44.2%	55.8%	8.28**1
RT x RD	81	3	ppSS x ppss	ppss x Ps--(c)	100%	0%	96.4%	3.6%	0.07ns <sup>4</sup>
RT x PR	17	0	ppSS x ppSs	ppss x ppss	100%	0%	100%	0%	0.00ns <sup>1</sup>
TV x RT	64	0	ppSS x ppSS	ppss x ppss	100%	0%	100%	0%	0.00ns <sup>1</sup>
TV x MI	91	108	ppSS x Pp--	ppss x Pp--	50%	50%	45.7%	54.3%	1.29ns <sup>5</sup>
TV x PN	49	16	ppSS x Pp--	ppss x Pp--	50%	50%	75.3%	24.7%	15.75**2
BT x RD	7	5	ppSs x ppss	ppss x Pp--	50%	50%	58.3%	41.7%	0.08ns <sup>4</sup>
GN x PL	38	34	ppSS x PpSs	ppss x Pp--	50%	50%	52.8%	47.2%	0.12ns <sup>4</sup>
RJ x RT	63	1	ppSS x ppSS	ppss x ppss	100%	0%	98.4%	1.6%	0.004ns <sup>3</sup>
PR x RJ	147	1	ppSs x ppSS	ppss x ppss	100%	0%	99.3%	0.7%	0.002ns <sup>2</sup>
RJ x PN	7	8	ppSS x Pp--	ppss x Pp--	50%	50%	46.7%	53.3%	0.07ns <sup>4</sup>
BT x SC	6	2	ppSs x ppSs	(d)	75%	25%	75.0%	25.0%	0.00ns <sup>1</sup>
PR x SC	90	35	ppSs x ppSs	(d)	75%	25%	72.0%	28.0%	0.45ns <sup>4</sup>

Notes: a) RT = Roxo-de-Tefé clone; PL = Perolera cultivar; RD = Rondon clone; PR = Pérola cultivar; TV = Turi-Verde clone; MI = Manuara Inerme clone; PN = Pina Negra clone; BT = Boituva clone; GN = Guiana clone; RJ = Rioja clone; SC = Smooth Cayenne cultivar.

b) X<sup>2</sup> - ns<sup>1</sup> = not significant at the probability level of 0.99; ns<sup>2</sup> = not significant at the probability level of 0.99-0.95; ns<sup>3</sup> = not significant at the probability level of 0.95-0.90; ns<sup>4</sup> = not significant at the probability level of 0.90-0.50; ns<sup>5</sup> = not significant at the probability level of 0.50-0.10; \*\*1 = significant at the probability level of 0.01-0.001; \*\*2 = significant at the probability level of 0.01.

c) Collins and Kernes (1946) consider the Rondon clone as "piping"; thus the segregation in this cross would be 1:1 (spiny:spineless); this fact was not confirmed by the observed segregation (100% spiny individuals).

d) The hypothesis does not allow for spineless individuals in these cases.

of the S locus with the cultivar genetic background (modifying genes) or with the environment is likely.

The results confirm the presence of the P allele in the Perolera (PpSs) cultivar and in the Manauara Inerme and Pina Negra clones (Pp--). The segregations of the two crossings involving the Rondon clone strongly suggest that its genotype is the "non-piping" double recessive (ppss).

The two hypotheses satisfactorily explained the segregations of the crosses RTxPR, TVxRT, TVxMI, BTxRD, GNxPL, RJxRT, PRxRJ and RJxPN, as indicated by the non-significant  $X^2$  results. Both hypotheses, however, failed to explain the segregation results from crosses RTxPL and TVxPN (significant  $X^2$  values were found). Possible explanations for the discrepancies observed in these segregations include genotype x environment interactions, self pollination, and uni or bidirectional incompatibility.

The segregations described in Collins and Kernes' (1946) work can also be explained by the new hypothesis if suitable genotypic modifications are made. There is only one case (PpSs x PpSs) where the hypothesis of Collins and Kernes (1946) has a better fit to the results (segregation 12:3:1). According to the new hypothesis, the segregation should be 13:2:1.

In the present work, spineless "non-piping" individuals were observed in the expected proportion of 3:1 (spiny:spineless) in two crosses (BTxSC and PRxSC), where the parental types are heterozygous for the S locus (ppSs genotype). Collins and Kernes' hypothesis does not support cases such as these.

In the Roxo-de-Tefé x Rondon cross, the progeny showed 96.4% spiny individuals and only 3.6% spineless types, a non-significant deviation from the expected 100% spiny type frequency. Collins and Kernes (1946), however, state that the Rondon clone is of the "piping type". In this case, the nearest expected segregation would be 50% spiny and 50% spineless types. The segregation of this cross confirms the double recessive genotypic constitution (ppss) of the Rondon clone.

Collins and Kernes (1946) also state that the "piping" phenotype has various degrees of expression because of a possible interaction with the environment (variable penetration of the P allele which allows the appearance of segregant spineless individuals without the characteristic "piping" morphology). The new hypothesis, while not contesting this possibility, would explain the "non-piping" spineless types by the presence of the double recessive ppss.

Table II presents the progeny segregation results from open pollinated crosses of some parental types. The descendants of completely spiny (Rioja,

Turi-Verde and Roxo-de-Tefé, probably all with ppSS genotype), partially spiny (Smooth Cayenne cultivar, with ppSS genotype) and spineless materials (Perolera cultivar, certainly carrier of the P allele and the Rondon clone, possibly a double recessive ppss genotype), were studied. As expected, the spiny parents of ppSS genotype produced progenies with an accentuated predominance of spiny individuals (Table II). This shows that the occurrence of spineless types is linked exclusively to the P allele frequency in the pollinating genetic pool. However, under open pollination, the ppSs Smooth Cayenne cultivar gave rise to progenies with nearly equal numbers of spiny and spineless individuals. In this case, the greater or lesser frequency of spineless individuals in the progeny is the result of a greater or lesser frequency of the P and s alleles in the pollinating population. In contrast to the spiny parents, the "piping" spineless parent Perolera (PpSs) produced a large number of spineless individuals in its progeny. The predominance of spineless types is expected since their frequency is dependent on the P allele carried by 50% of the Perolera gametes and on the frequency of the P and s alleles in the pollinating population.

**Table II** - Leaf spininess evaluation results obtained in progenies derived from open-pollinated crosses among pineapple (*Ananas comosus* L. Merrill) cultivars and clones.

Cultivar/ clone	Probable genotypes	No. of individuals in the progeny	Leaf spininess spiny / spineless (%)	
			spiny	spineless
RJ	ppSS	749	98.4	1.6
TV	ppSS	86	100.0	0.0
RT	ppSS	247	82.2	17.8
SC	ppSs	137	53.3	46.7
RD	ppss	47	53.2	46.8
PL	PpSs	110	25.5	74.5

Notes: RJ = Rioja clone; TV = Turi-Verde clone; RT = Roxo-de-Tefé clone; SC = Smooth Cayenne cultivar; RD = Rondon clone; PL = Perolera cultivar.

The Rondon clone, a "piping" type according to the literature, should produce progeny similar to the Perolera cultivar in open crossings. However, nearly equal numbers of spiny and spineless types were observed, reinforcing the new hypothesis of its double recessiveness (ppss). In this case, the Rondon clone would depend on the frequencies of the P and s alleles in the pollinating population to give rise to spineless types, a very different situation from that of the Perolera cultivar.

There are no studies in the literature regarding the inheritance of the leaf coloring trait in pineapple. The results of this work show that there is considerable variability for this trait. Four classes of phenotypes were identified: uniformly green, uniformly purple, green with purple marks and green with yellow marks.

Using the artificial crosses, and disregarding the green with yellow marks phenotype, which was relatively rare among the individuals belonging to the progenies studied, three distinct situations were defined (Table III):

a) a fairly homogeneous distribution of progeny in the uniformly green, uniformly purple and green with purple mark classes (RTxPL and RTxRD) (33% in each one);

b) concentration of the progeny in the apparently hybrid phenotypic class (green with purple marks) (TVxRT and PRxRJ);

c) concentration of progeny individuals in the uniformly green phenotypic class (TVxMI; TVxPN; GNxPL and RJxRT).

**Table III** - Leaf color evaluation results obtained in progenies derived from artificial crosses among pineapple (*Ananas comosus* L. Merrill) cultivars and clones.

Cultivar/ clone	No. of individuals in the progeny	Leaf color (% of individuals)			
		UG	UP	GPM	GYM
RT x PL	438	32.9	15.1	49.1	2.9
RT x RD	84	30.9	27.4	35.7	6.0
RT x PR	17	11.7	88.3	0.0	0.0
TV x RT	47	29.8	0.0	70.2	0.0
TV x MI	199	65.8	0.5	28.1	5.6
TV x PN	65	64.6	1.5	30.8	3.1
GN x PL	72	72.2	0.0	11.1	16.7
RJ x RT	64	53.1	0.0	35.9	11.0
PR x RJ	81	32.1	2.5	58.0	7.4

Notes: RT = Roxo-de-Tefé clone; PL = Perolera cultivar; RD = Rondon clone; PR = Pérola cultivar; TV = Turi-Verde clone; MI = Manuara Inerme clone; PN = Pina Negra clone; GN = Guiana clone; RJ = Rioja clone.

Leaf color: UG = uniformly green; UP = uniformly purple; GPM = green with purple marks; GYM = green with yellow marks.

There was a unique case of predominance of the uniformly purple class, in the RTxPR cross.

It can be concluded that green color is partially dominant over the purple, with a greater predominance of green. This fact is confirmed by the open-pollinated crosses (Table IV): when cultivars used as females have green leaves (RJ, TV and RD) the progeny individuals

are predominantly scored in the uniformly green phenotypic class. On the other hand, there is a greater frequency of individuals in the hybrid class (green with purple marks) in the progenies from the open-pollinated cross involving the uniformly purple leaf cultivar (RT). The descendants of the Perolera cultivar (purple-green leaves) are concentrated in the uniformly green and the green with purple mark classes.

**Table IV** - Leaf color evaluation results obtained in progenies derived from open-pollinated crosses among pineapple (*Ananas comosus* L. Merrill) cultivars and clones.

Cultivar/ clone	No. of individuals in the progeny	Leaf color (% of individuals)			
		UG	UP	GPM	GYM
RJ	749	73.7	0.7	19.1	6.5
TV	86	76.7	3.5	19.8	0.0
RT	247	13.4	22.7	62.7	1.2
RD	47	53.2	4.3	34.0	8.5
PL	110	45.5	10.0	34.5	10.0

Notes: RJ = Rioja clone; TV = Turi-Verde clone; RT = Roxo-de-Tefé clone; RD = Rondon clone; PL = Perolera cultivar.

Leaf color: UG = uniformly green; UP = uniformly purple; GPM = green with purple marks; GYM = green with yellow marks.

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## RESUMO

Foram analisadas as progênies de 13 cruzamentos intervarietais dirigidos assim como as de seis cruzamentos ao acaso de abacaxi, quanto às características espinhosidade e coloração de folha.

A partir das segregações observadas, é proposta uma nova hipótese da herança do caráter espinhosidade de folha, que explica, com clareza, 11 dos 13 cruzamentos dirigidos realizados. Em contraste, a hipótese vigente (Collins and Kernes, *J. Heredity* 37: 123-128, 1946) somente se ajusta a oito dos 13 cruzamentos efetuados.

Três cruzamentos foram essenciais na aceitação ou rejeição de ambas as hipóteses. Os cruzamentos Boituva x Smooth Cayenne e Pérola x Smooth Cayenne, cujos parentais são "non-piping" e heterozigotos para o locus S (Ss), deram origem a

indivíduos inermes nas descendências, dentro da frequência esperada de 3 espinhosos para 1 inermes. Este fato é inadmissível pela hipótese de Collins e Kernes. No cruzamento Roxo-de-Tefé x Rondon, a frequência observada de praticamente 100% de indivíduos com espinhos na descendência não pode ser explicada pela hipótese de Collins e Kernes, que consideram o clone Rondon como portador do alelo P ("piping").

A nossa hipótese permite a identificação de dois novos clones como sendo do tipo "piping" (Manauara Inerme e Pina Negra) e assegura que a constituição genotípica do clone Rondon é, provavelmente, ppss (inerme "non-piping").

Em resumo, na ausência do alelo P, o locus S produz os fenótipos totalmente espinhosos (ppSS e ppSs), dominantes em relação aos inermes (ppss).

A espinhosidade parcial do cultivar Smooth Cayenne, descrito como heterozigoto para o locus S (ppSs), deve ser causada por interações genótipo x ambiente, efeitos de "background" genético, atuação de genes modificadores e outras causas de natureza desconhecida.

Finalmente, a cor verde exerce dominância incompleta sobre a cor roxa, com maior predominância da cor verde.

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