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Evaluation of the sexual expression in a segregating BC_1 papaya population

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ABSTRACT - *In Brazil mainly hermaphrodite plants are exploited for papaya cultivation. Variations of the elongate (normal) hermaphrodite flowers to carpelloid, pentandric and sterile female forms occur in these plants, influenced by genetic as much as by environmental factors. The objective of this study was to estimate these variations of elongate hermaphrodite flowers to deformed and sterile female forms as well as fruit deformations. The results permitted the identification of BC_1 plants that were more stable to temperature fluctuations in the winter 2003 and summer 2003/04 in Linhares-ES. For instance, the normal number of hermaphrodite flowers (NHF) varied from 1 to 46 and 0 to 25 in the BC_1 generation, in winter and summer, respectively, while for the 'Golden' genotype these values varied from 7 to 36 in the winter and were zero in the summer as a result of 100% of flower sterility.*

Key words: *Carica papaya*, high temperatures, carpelloid, sexual reversion.

INTRODUCTION

Cultivated papaya (*Carica papaya* L.) presents three basic flower types: female, male and hermaphrodite. The selection of hermaphrodite papaya trees for commercial production raises a particular problem, since the sexual expression of these plants is very variable and influenced by genetic as well as environmental factors (Awada 1958, Arkle Junior and Nakasone 1984).

Variations of (normal) elongate hermaphrodite flowers to carpelloid, pentandric and sterile female forms occur in hermaphrodite plants. In the winter, when night temperatures are low, stamens are transformed to carpel-like structures, termed carpelloid stamens. Other factors that induce carpelloid stamens are high soil moisture, high relative air humidity and high nitrogen levels (Awada 1953, Arkle Junior and Nakasone 1984).

In the hermaphrodite flowers of the hot summer months the ovary is aborted (Awada 1958, Storey 1941). Low nitrogen levels and water stress also favor female sterility (Awada 1953, 1958).

Carpelloid fruits occur when the stamens of hermaphrodite flowers are transformed into carpel-like structures. This phenomenon sets in at the beginning flower development, resulting in defective fruits without commercial value, popularly known as cat-face. Pentandric fruits occur due to the insertion of the stamens

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in the ovary wall of a pentandric hermaphrodite flower, where they form deep furrows in the ovary wall. Pentandric fruits are very similar to those produced by female plants, rounded, with a large internal hollow and externally visible furrows, which depreciate the commercial value.

The range of determinant factors of the sexual phenotype in plants includes from the sexual chromosomes in *Marchantia polymorpha* and *Silene latifolia* to hormonal regulation in *Zea mays* and *Cucumis sativa* (Tanurdzic and Banks 2004). For papaya however there are still many questions open. Among the hypotheses proposed to explain the sex determination in this species, the most widely accepted is the one proposed by Hofmeyr (1938) and Storey (1938) according to which the sex inheritance is monogenic, with three alleles designated m, M^1 and M^2. Storey (1953) established that the dominant combinations, M^1M^1, M^2M^2 and M^1M^2 are probably zygotic lethal. According to Storey (1941) the individual carriers of the genotypes are mm, M^1m and M^2m, are denominated ginoic (female), androic (male) and andromonoic (hermaphrodite), respectively.

Based on RAPD markers (Random Amplified Polymorphic DNA), Sondur et al. (1996) mapped a locus (*SEX 1*) linked to sex determination in *Carica papaya* and cited the alleles proposed by Storey (1938) and Hofmeyr (1938) such as allele (*SEX1-M*) that determines masculinity and (*SEX1-H*) that determines hermaphroditism, both dominant over allele (*sex1-f*), which in the homozygous form determines femininity.

This study aimed to evaluate the sex expression of papaya in the winter of 2003 and summer of 2003/04, in segregating BC_1 generation, in the county of Linhares, state of Espírito Santo, estimating the variations of the elongated hermaphrodite flowers to deformed and sterile female forms as well as fruit aberrations in carpelloid and pentandric forms.

MATERIAL AND METHODS

Experimental site

The experiment was installed on the commercial area of the company CALIMAN AGRÍCOLA S/A, county of Linhares (lat 19° 06'-19° 18' long 39° 45'-40° 19' W), state of Espírito Santo, Brazil (Rolim et al. 1999). The soils of the company are classified as red yellow podzolic for the most part, of clayey-sandy texture, semi-evergreen forest phase with a plain to slightly undulated (coastal plateaus). The regional climate is of the type Awi of Köppen (wet tropical), with rainy summers and dry winters. In the period from 1975 to 1995 the mean annual precipitation was estimated at 1224.3 mm, the mean temperature at 23 °C and relative air humidity at 83.5% (Rolim et al. 1999).

Plant material

In this study, hermaphrodite plants of a BC_1 generation were used derived from a first cross between the dioecious variety 'Cariflora' (recurrent parent) and the elite variety 'Sunrise Soil 783' (SS 783). Fifteen hermaphrodite plants of the elite genotype 'Golden' were included for comparison. The genotype 'Cariflora', in its dioecious form, presented a high degree of loci in heterozygosis, raising an expectation of expressive genetic variability in the BC_1 generation, auspicious for the selection of superior plants.

The genotype 'Cariflora' is a dioecious genotype with fruits of yellow and moderately firm pulp and a mean weight of around 1.67 kg, with appealing taste and smell (Conover et al. 1986). On the other hand, genotype 'SS 783' is an elite variety with pear-shaped fruits weighing in the mean 0.52 kg, of red pulp and good quality.

'Golden' is derived from mass selection performed on the production fields of 'Sunrise Soil' of the Caliman Agrícola S/A company, in the state of Espírito Santo. It has pear-shaped fruits, red-orange pulp and weighs on average 0.45 kg.

Installation and evaluation of the experiment

The experiment was installed on March 25, 2003. The seedlings were transplanted to two rows with a final spacing of 1.5 x 3.6 m. Fertilization, management, pest and disease control and further crop treatments were applied as customary on the commercial plantations of the company Caliman Agrícola S/A.

One hundred and eighty days after transplanting (DAT), which was at the end of the winter of 2003 (September) and 330 DAT summer of 2003/04 (February), 137 and 108 hermaphrodite BC_1 plants were evaluated, respectively. Fifteen plants of the elite genotype 'Golden' were included for comparison in both periods.

The following traits were evaluated: total number of flowers (TNF), number of deformed flowers (NDF), number of sterile flowers (NSF), number of normal flowers (NNF), number of total fruits (NTFr), number of carpelloid fruits

(NCFr), number of pentandric fruits (NPFr), and number of commercial fruits (NComFr). Due to the practical constraint of separating carpelloid from pentandric flowers by the external phenotype, these were grouped together in one category of deformed flowers.

Climate Data

The main climatological data of the county of Linhares-ES of the months that preceded the flower evaluations in each period are presented in the Tables 1 and 2. Table 3 shows the data of the period between the years of 1974 and 2004, in both evaluation periods of the experiment.

Statistical analysis

The means were compared by the *t* test at the level of 5 % probability using software Genes, version 0.1.

RESULTS AND DISCUSSION

The climate characterization of the winter of 2003 and summer of 2003/04 in Linhares showed a considerable variation in the air temperature between the two periods, with means of 21.8 °C and 25.8 °C, respectively (Table 1). Besides, greater thermal amplitudes were verified in the winter months, although there was also a considerable variation between the maximum and minimum temperatures in the summer months. The mean temperature values in the two evaluation periods were very close to the data of the years 1974 to 2004 (Table 3).

The difference of mean precipitation between the two periods was discrepant, with a four-fold increment in the summer (214.5 mm) compared to the winter (48.5 mm) (Table 2). The mean precipitation values in the two evaluation periods were very discrepant to the data of the years of 1974 to 2004 (Table 3) in the summer months.

Table 1. Seasonal temperature variations in the air in the winter of 2003 and summer of 2003/04, in the county of Linhares-ES

Month/year	Air temperature (°C)				
	Maximum mean	Minimum mean	Mean	Absolute maximum	Absolute minimum
July/2003	27.9	16.9	21.5	32.2	13.0
August/2003	27.1	17.1	21.3	31.8	12.4
September/2003	28.1	18.5	22.5	34.4	13.4
Mean (winter)	27.7	17.5	21.8	32.8	12.9
December/2003	31.3	22.6	26.2	34.6	19.6
January/2004	29.7	22.5	25.4	33.4	19.2
February/2004	30.8	22.4	25.8	35.6	19.6
Mean (summer)	30.6	22.5	25.8	34.5	19.5

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Table 2. Seasonal precipitation variations in the winter of 2003 and summer of 2003/04, in the county of Linhares-ES

Month/year	Precipitation (mm) and Relative air humidity (%)			
	Total height	Maximum in 24h	Data	Relative air humidity
July/2003	76.7	28.6	14	82
August/2003	36.9	13.6	03	79
September/2003	31.8	18.8	30	79
Mean (winter)	48.5	20.3	-	80
December/2003	234.9	58.9	07	80
January/2004	282.3	63.3	31	85
February/2004	126.2	22.4	27	83
Mean (summer)	214.5	48.2	-	82.7

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Table 3. Data of temperature and precipitation means of the summer and winter months in the county of Linhares-ES, in the period from 1974 to 2004

Month/year	**Air temperature** (°C)	**Precipitation** (mm)
July	21.0	52.7
August	21.4	45.8
September	22.2	68.4
Mean (winter)	21.5	55.6
December	25.4	206.5
January	26.0	170.0
February	26.2	86.2
Mean (summer)	25.9	154.2

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The extreme (maximum and minimum) values and means of the flower traits and their respective amplitudes and standard deviations are shown in Table 4. The total number of flowers (TNF) was significantly larger in the winter, in both the treatments, reduced by 46.34 and 81.83% in the summer in the BC_1 generation and in the genotype 'Golden', respectively. Comparing the two treatments in each period, the difference between the BC_1 mean and the 'Golden' mean was only 3.37 units in the winter while in the summer the difference was 14.23 units.

The number of deformed flowers (carpelloid + pentandric) (NDF) was significantly larger in the winter for both treatments, with values from 0 to 43 in the BC1 and 0 to 4 in the 'Golden' genotype. In the summer, these flower variations were little expressive in BC_1 and nil in 'Golden'. The period of occurrence of most flower deformations was therefore the winter, above all in BC_1 with a broad variability for this trait, indicated by the amplitude of 43 units and by the standard deviation seven times higher than that of 'Golden'.

Opposite to the flower deformation, female sterility in hermaphrodite flowers (suppression of the ovary) was significantly more frequent in the summer, where all plants, independent of the treatment, presented at least two sterile flowers. The results indicate a broad genetic variability between the BC_1 plants, with an amplitude of 84 units and 14 times higher standard deviation than the deviations of genotype 'Golden' in the summer. Comparing the two treatments in both periods, the responses of genotype 'Golden' differed from BC_1 in amplitude and standard deviation values. In the latter there was a considerable increment in the summer, while the values were lower in 'Golden'. In the BC_1 generation there were evidently genotypic variations between the trees, whereas in 'Golden' the variations between trees can be considered essentially environmental, thus justifying the abrupt differences of genetic variability, in favor of the BC_1 population.

Table 4. Minimum, maximum and mean values of amplitude and standard deviation of the flower traits in hermaphrodite plants of a BC_1 generation and of the elite genotype 'Golden', 180 DAT and 330 DAT, in the winter of 2003 and summer of 2003/04, respectively

Treatment	**Winter**					**Summer**				
	Minimum	**Maximum**	**Mean**	**Amplitude**	**Standard deviation**	**Minimum**	**Maximum**	**Mean**	**Amplitude**	**Standard deviation**
	Number of total flowers									
BC_1	18	80	38.37Aa	62	10.75	2	86	20.59 Ab	84	16.32
Golden	27	40	35.00 Ba	13	3.60	4	8	6.36 Bb	4	1.28
	Number of deformed flowers									
BC_1	0	43	9.96 Aa	43	8.84	0	2	0.05 Ab	2	0.25
Golden	0	4	1.20 Ba	4	1.21	0	0	0 Bb	0	0
	Number of sterile flowers									
BC_1	0	33	8.26 Ab	33	7.09	2	86	15.88 Aa	84	15.05
Golden	0	8	3.81 Bb	8	2.10	4	8	6.36 Ba	4	1.28
	Number of normal flowers									
BC_1	1	46	20.15 Ba	45	9.37	0	25	4.67 Ab	25	5.81
Golden	7	36	28.94 Aa	29	6.87	0	0	0 Bb	0	0

Means followed by the same upper case letter in the columns and by the same lower case letter in the lines did not differ from each other by the t test at the level of 5 % probability

The mean number of normal flowers (NNF), represented by the difference between the total number of flowers and the number of deformed flowers + the number of sterile flowers, was drastically reduced in both treatments in the summer, where 100% of the 'Golden' flowers were sterile. In the BC_1, in spite of the reduction in the mean value of the normal flowers in the summer, there was a wide dispersion with values from 0 to 25.

Recently, flower development has been the focus of a large number of studies, particularly with the model species *Arabidopsis thaliana* and *Anthirrinus majus*. These two plants have hermaphrodite flowers, i.e., they have functional male and female reproductive organs in the same flower (Fonseca and Dornelas 2002). In *Arabidopsis thaliana*, for instance, plants grown at 18 °C and at 23 °C presented distinct flowering periods and morphological leaf aspects (Samach and Wigge 2005). According to these authors, the low air temperature delays flowering and leads to alterations in the leaf number, appearance and morphology.

In the present study, the mean TNF was substantially reduced in the summer, particularly in the genotype 'Golden'. In this period, conversely to the winter, the TNF was represented to a great extent by the NSF, especially in the BC_1, where there was greater dispersion and higher standard deviation of TNF. Results therefore indicated that the increment in the TNF in the summer is directly related with the increment in the NSF. On the other hand, in the winter, although the mean of the NSF was approximately half of the summer for both treatments, there was a pronounced incidence of deformed flowers, principally in BC_1, where plants with values from 0 to 43 were observed, that is, with amplitude of 43 units.

The mean number of normal flowers (NNF) in the winter was 52.5 and 82.7% of the TNF in BC_1 and in 'Golden', respectively. This difference between the treatments was mainly a consequence of the greater incidence of deformations in the BC_1, which was on average eight times higher than in 'Golden'. In the summer however, the NNF was drastically reduced in both treatments, representing in the mean 22.7% of the TNF in BC_1 and nil normal flowers in 'Golden'. Despite the low mean value observed in BC_1, some plants stood out as more tolerant to climatic adversities of the summer. On the other hand, the elite genotype 'Golden', widely cultivated in the papaya producing regions of the states of Espírito Santo and Bahia, does not have the adaptation mechanisms to overcome these problems, and therefore, suppressed the ovary of 100% of its differentiated flowers in the summer. This response of the 'Golden' genotype, in the summer, reflects an irregular distribution of the fructification and of the harvest over the year and consequently causes an impact on fruit supply and market value. In the segregating BC_1 generation however, we

Table 5. Minimum, maximum and mean values of amplitude and standard deviation of the traits fructification in hermaphrodite plants of the BC_1 generation and the elite genotype 'Golden', 180 DAT and 330 DAT, in the winter of 2003 and summer of 2003/04, respectively

Treatment	Winter					Summer				
	Minimum	Maximum	Mean	Amplitude	Standard deviation	Minimum	Maximum	Mean	Amplitude	Standard deviation
	Number of total fruits									
BC_1	2	47	21.11 Ab	45	9.22	2	104	39.17 Aa	102	19.08
Golden	7	20	14.06 Bb	13	4.00	28	55	39.21 Aa	27	7.45
	Number of carpelloid fruits									
BC_1	0	9	0.67 Ab	9	1.31	0	16	4.17 Aa	16	3.18
Golden	0	0	0 Ba	0	0	0	0	0 Ba	0	0
	Number of pentandric fruits									
BC_1	0	18	0.98 Ab	18	2.63	0	22	1.91 Aa	22	3.83
Golden	0	0	0 Ba	0	0	0	0	0 Ba	0	0
	Number of commercial fruits									
BC_1	1	46	19.46 Ab	45	9.22	2	85	33.10 Ba	83	16.92
Golden	7	20	14.06 Bb	13	4.00	28	55	39.21 Aa	27	7.45

Means followed by the same upper case letters in the columns and by the same lower case letters in the lines did not differ from each other by the t test at 5 % probability observed a selection potential of superior genotypes, more stable regarding the distribution of normal flowers and accordingly, of fructification throughout the year.

The occurrence of more flower deformations in the winter can be attributed to the lower mean air temperature (21.8 °C) and principally the greater thermal amplitudes that were on average 2.1 °C higher than in the summer. On the other hand, the higher frequency of female sterility in the summer must be directly associated to the higher mean air temperature (25.8 °C), that is, 4 °C higher than in the winter (Table 1). Still, one must take into account that the amount of rain during the summer months was atypical with a mean of 214.5 mm (Table 2), which was considerably higher than the data mean of the years from 1974 to 2004, which was 154.2 mm (Table 3). The excess of rains may have multiplied the heat stress effect on the sexual expression of both treatments. Anyway, our results demonstrate that the sexual expression of hermaphrodite papaya is highly sensitive to thermal fluctuations and excessive rains, tending to flower deformations or female sterility in response to these changes.

Based on the conditions where these results were obtained, the best period for plant selection with reduced incidence of flower deformations is the winter, mainly, in transition to spring. Plants with reduced expression of female sterility must however be selected at the end of the summer.

The extreme and mean values of the traits of fructification and their respective amplitudes and standard deviations are shown in Table 5. In the winter of 2003, in the BC_1 generation, plants with values of total number of fruits (NTFr), number of carpelloid fruits (NCFr), number of pentandric fruits (NPFr), and number of commercial fruits (NComFr.) from 2 to 47, 0 to 9, 0 to 18, and 1 to 46 were observed, respectively. In the summer of 2003/2004, these values varied from 2 to 104, 0 to 16, 0 to 22, and 2 to 85 for NTFr, NCFr, NPFr, and NComFr, respectively.

Unlike BC_1, 'Golden' presented 100% commercially valuable fruits in both periods, emphasizing that the mean yield (NComFr.) in the summer was about twice as high as in the winter (Table 5). Since the plant material was homogeneous, the variations observed in 'Golden' for NTFr and NComFr. were lower than the variations in BC_1 in both periods. With regard to the carpelloid and pentandric fruits, our results indicated a greater adaptation of 'Golden' to variations of the studied climatic factors.

Despite the lower mean commercial fruit yield in the summer, BC_1 proved promising for the selection of high-yielding plants, with low or no expression of carpelloidy or pentandry in both periods. According to the literature (Awada 1953, Arkle Junior and Nakasone 1984), the conclusion may be drawn that the greater expression of fruit deformations in the summer, particularly carpelloidy, is partly a result of the higher frequency of flower deformations observed in the winter, and also aggravated by the excess of soil moisture and the variations between maximum and minimum temperatures in the spring and summer months. It is therefore safe to say that most of the deformations in the differentiated flowers in the winter, in BC_1, were caused by the carpelloid stamens.

Hermaphrodite plants of the elite genotype 'Sunrise Soil 783', crossed initially with 'Cariflora', were sampled in the winter of 2003. The mean NDF was zero, NSF was 6% higher than in the BC_1, NPFr was zero, and NCFr around 1% lower than in BC_1. The expression of flower deformations and fructification of the BC_1 in both periods was therefore probably partly due to the genetic inheritance of the cultivar 'Cariflora', since it would never express these traits in the dioecious condition.

The variations in flower deformations and fructification observed in the genotype 'Golden' in both periods and in genotype 'SS 783' in the winter, can be associated to environmental causes. In the BC_1 generation the observed variations were however ascribed to genetic and environmental causes, and these were useful in the selection of the best plants to advance generations, raising expectations for the establishment of superior inbred lines for the set of variables under study.

According to Cronquist (1988) there is a widespread vision that all plants with flowers are originated from a common hermaphrodite ancestor, indicating that many flower development programs are common to all species. It is however believed that the hermaphroditism in papaya is recent, a product of a secondary evolution, and that this mechanism was established based on chromosome Y and modified to the new chromosome Y^2, without any alteration in chromosome X, so that the female plants were (XX), male (XY^1) and hermaphrodite (XY^2) (Horovitz and Jimenez 1967).

Studies in model plants have demonstrated that the flowering process is regulated by a complex network of signalization pathways, modified by the environmental conditions (Araki 2001, Samach and Coupland 2000). In this context, the genetic control of the stamen carpelloidy and female sterility in papaya seems to be extremely complex. Storey (1953) suggested two independent sets of factors that can modify the sex expression in male and hermaphrodite plants under certain environmental conditions. One group of factors causes seasonal changes suppressing the development of the gynoecium (female sterility) in hermaphrodite plants, which are later normalized (fertile females). The other set promotes stamen carpelloidy, frequently with pistil fusion.

Despite the relevance of flower aberrations in hermaphrodite papaya, there are to date few studies into genetic papaya improvement, in Brazil as much as abroad, above all to verify the influence of climatic seasonality on these traits.

From the evolutive point of view, it seems safe to assume that the stress caused by the extreme temperatures, excessive humidity or water deficit in the soil and nutritional imbalance lead to physiological alterations in hermaphrodite papaya, peaking in the expression of flower deformations. Among these physiological alterations, one must not rule out the participation of some plant hormones that could mediate the expression of flower aberrations, since in other species such as *Cucumis sativus*, some species of *Vitis*, *Zea mays,* and *Mercurialis annua*, among others, the hormonal participation in sex reversion has already been well documented (Dallaporta and Calderon-Urrea 1993).

Maybe the manifestation of the variations of the elongate hermaphrodite (normal) flowers to deformed and sterile females represents an evolution strategy to overcome seasonal stress and warrant the plant subsistence. According to Horovitz et al. (1953), in spontaneous *Carica papaya* populations that return to the wild stage, the hermaphrodite form is eliminated in only few generations by the male making way for strictly dioecious populations. In this sense it is possible that the expression of flower deformations in the carpelloid and pentandric forms represents a tendency of the plant to return to the female sex, since the female plants seem to be more stable and more efficient in the allocation of photoassimilates for fruit yield. On the other hand, female sterility indicates a form of the plant saving energy without affecting the dispersion of its alleles in the population. This is to prioritize the reproductive in detriment of the productive aspect, since in some cases fruit production ceases completely. This evidently represents a tendency since in the field, there is a dynamic of these events in function of the fluctuations of the climatic, nutritional and genetic factors, which can occur at any period of the year to a higher or lesser degree.

These flower aberrations affect the commercial fruit yield negatively. The identification of plants that are better adapted to fluctuations of the main climate variables, above all air temperature, must therefore be considered as one of the main objectives of genetic papaya improvement. The need of conducting segregating generations is therefore evident, with a view to selection in improvement programs tailored for the chief producing regions of Brazil, estimating the effects of the genotype x environment interaction, preferentially, assisted by DNA markers.

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Avaliação da expressão sexual em população segregante RC_1 de mamoeiro

RESUMO - *O cultivo do mamoeiro no Brasil explora, principalmente, plantas hermafroditas. Nestas plantas, variações de flores hermafroditas elongatas (normais) para as formas carpelóides, pentândricas e femininas estéreis ocorrem, influenciadas tanto pelos fatores genéticos quanto pelos fatores ambientais. O objetivo deste trabalho foi estimar as variações das flores hermafroditas elongatas para as formas deformadas e femininas estéreis, bem como as deformações de frutos, no inverno de 2003 e no verão de 2003/04 em Linhares-ES. Os resultados possibilitaram a identificação de plantas* RC_1 *mais estáveis a flutuações de temperatura em ambas as épocas. Por exemplo, o número de flores hermafroditas normais (NFN) variou de 1 a 46 e de 0 a 25 na geração* RC_1*, no inverno e no verão, respectivamente, ao passo que, no genótipo 'Golden' esses valores variaram de 7 a 36 no inverno e foram nulos no verão devido à esterilidade de 100 % de suas flores.*

Palavras-chave: *Carica papaya*, altas temperaturas, carpeloidia, reversão sexual.

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