*e*-ISSN 1983-4063 - *www.agro.ufg.br/pat* - Pesq. Agropec. Trop., Goiânia, v. 46, n. 4, p. 401-406, Oct./Dec. 2016

# Inbreeding depression in crambe[1]

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## ABSTRACT

Inbreeding depression in plants, caused by selfing or crossing among plants with a high degree of relatedness, is a genetic phenomenon that affects quantitative traits. This study aimed at verifying the occurrence of inbreeding depression in crambe progenies originated from selfing, in comparison with open pollination progenies. A randomized blocks design, with three replications, in a 32 x 2 factorial arrangement, with 32 crambe progenies and two reproduction systems (artificial selfing and open pollination), was used. Grain yield, 1,000-grain weight, plant height and final stand were evaluated. A significant interaction was observed between progenies and reproduction systems in all traits evaluated. A reduction in grain yield, 1,000-grain weight and plant height occurred in the majority of the selfing progenies, when compared to open pollination progenies. Inbreeding depression was observed in all traits, especially for grain yield. The heritability coefficients of selfed progenies were higher than the open pollinated ones, except for 1,000-grain weight.

KEYWORDS: *Crambe abyssinica* Hochst; selfing; open pollination; heritability.

## RESUMO

### Depressão por endogamia em crambe

A depressão por endogamia em plantas, causada por autofecundação ou cruzamento entre plantas com alto grau de parentesco, é um fenômeno genético que afeta os caracteres quantitativos. Objetivou-se verificar a ocorrência de depressão por endogamia em progênies de crambe originadas de autofecundação, em comparação com progênies de polinização livre. O delineamento experimental foi em blocos casualizados, com três repetições, em esquema fatorial 32 x 2, em que foram avaliadas 32 progênies de crambe sob dois sistemas de reprodução (autofecundação artificial e polinização livre). Foram avaliados a produtividade de grãos, massa de 1.000 grãos, altura de planta e estande final. Observou-se interação significativa entre progênies e sistemas de reprodução para todas as características avaliadas. Para a maioria das progênies, houve redução na produtividade de grãos, massa de 1.000 grãos e altura de plantas oriundas de autofecundação, em comparação com as progênies de polinização livre. Houve depressão por endogamia para todas as características avaliadas, especialmente para a produtividade de grãos. Os coeficientes de herdabilidade para as progênies oriundas de autofecundação foram maiores do que para as de polinização livre, exceto para massa de 1.000 grãos.

PALAVRAS-CHAVE: *Crambe abyssinica* Hochst; autofecundação; polinização aberta; herdabilidade.

## INTRODUCTION

Crambe (*Crambe abyssinica* Hochst), a species of the *Brassicaceae* family (Desai et al. 1997), has attracted the interest of producers due to its short cycle and possibility of completely mechanized cultivation. This winter crop, a low-cost off-season alternative in Brazil, is planted after the soybean harvest (Pitol 2010). The seeds are its main raw material, containing approximately 37 % of oil (Glaser 1996) with 55-60 % of erucid acid (Lessman & Berry 1967), which may be used as an industrial lubricant, corrosion inhibitor or as an ingredient in synthetic rubber manufacturing. One of the products that may be obtained from the crambe oil is erucamide, an organic amide and erucic acid derivative that may be employed in cosmetics and other industrial uses (Falasca et al. 2010).

The University of North Dakota (USA) has the most consistent crambe breeding program, where existing germplasm is evaluated and selection is made among and within populations developed through

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[1] Manuscript received in Jun./2016 and accepted for publication in Nov./2016 (http://dx.doi.org/10.1590/1983-40632016v4641811).

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hybridization and subsequent selfing (Knights 2002). This breeding program makes assessments in all crop seasons by comparing newly selected lines with cultivars. In 2011, the North Dakota State University - Carrington Research Extension Center published the grain yield results (1,501.8-1,637.5 kg ha$^{-1}$) for the BelAnn, Meyer and Westhope cultivars (NDSU 2011). In Brazil, the only existing crambe genotype is the FMS Brilhante cultivar, obtained by the Fundação MS, with grain yield of 1,400 kg ha$^{-1}$ (Pitol 2010).

Lara-Fioreze et al. (2016) carried out a selection process with the FMS Brilhante cultivar, obtaining a genetic gain of two-fold higher grain yields. It is, therefore, important that crambe breeding maintains the progress and development of new genetic materials. For that, knowledge on this crop, especially for traits related to the reproductive system, is crucial.

Although few studies have described crambe as a preferentially autogamous plant (Beck et al. 1975), intercrossing rates ranging 9-14 % have been previously reported (Vollmann & Ruckenbauer 1991).

The inbreeding phenomenon influences many quantitative traits and is related to increases in homozygosity at *loci* with some degree of dominance (Charlesworth & Charlesworth 1999). There are two genetically distinct ways in which increased homozygosity can lower fitness: increased homozygosity for partially recessive detrimental mutations and increased homozygosity for alleles at *loci* with heterozygote advantage (‘overdominance’). Deleterious alleles will generally be present in populations at low frequencies (mutation-selection balance), whereas overdominant alleles at a *locus* are maintained at intermediate frequencies by balancing selection (Charlesworth & Willis 2009). Darwin (1876 and 1877) was the first to point out that the evident adaptations of many plants to ensure outcrossing could be understood in terms of the selective advantage of avoiding inbreeding depression.

In autogamous plants, inbreeding only results in loss of vigor in early generations (Allard 1999). This is not a disadvantage, since it causes the formation of different genotypic classes (dominant and recessive), increasing the possibility of selecting against recessive detrimental alleles.

Knowledge on inbreeding depression in crambe is important, since breeding occurs through selection among and within populations previously improved via hybridization and subsequent selfing. The method used to obtain pure lines in crambe is a combination of the “bulk” or population method and the “genealogic” or “pedigree” method (Knights 2002). These methods were implemented for autogamous plants, with outcrossing rates of less than 5 %. Moreover, studying the effects of inbreeding in crambe is important for the exploitation of heterosis and its possible use by the production of crambe hybrids.

Accordingly, this study aimed at verifying the occurrence of inbreeding depression in selfed crambe progenies, when compared to the respective open pollinated progenies.

## MATERIAL AND METHODS

The experiment was performed with selected genotypes from the FMS Brilhante cultivar, which has shown to be a genetically heterogeneous cultivar (Lara-Fioreze et al. 2016). In 2010, progenies of 32 superior genotypes of the FMS Brilhante were cultivated in 15-L pots filled with fertilized soil, under greenhouse conditions, in Botucatu, São Paulo State, Brazil. Each progeny was cultivated in five pots, with two plants per pot. At flowering, the inflorescences of five plants from each progeny were protected with a waterproof paper bag and the other five plants were open pollinated. The bags were maintained on the inflorescences until the fruit formation. At harvest, seeds from selfed and open pollinated progenies were collected separately.

In March 2011 (off-season), an experiment was conducted under field conditions, in Botucatu, in which a randomized blocks design, in a 32 x 2 factorial scheme, with three replications, was used. The factors consisted of 32 progenies and two means of reproduction (selfing and open pollination), obtained in the previous step. Sowing was carried out manually, and the experimental plot consisted of three 1-m rows with ten plants per row and spacing of 0.25 m between rows. The center row was the only one harvested. Planting and management, such as thinning, weed removal and harvest, were performed manually.

During the crop cycle, the following traits were evaluated in the crambe progenies: a) plant height: the height of ten plants in the center row, from the soil to the apical inflorescence, was measured using a ruler; b) final stand: the number of plants in the harvest row was counted before harvest; c) grain yield (kg ha$^{-1}$): estimated as a function of the grain yield of each experimental plot (harvest row), corrected for a moisture content of 13 %; d) 1,000-grain weight: weight of eight replications of 100 seeds from each plot, taking the average of one hundred measurements, and converting the values to one thousand, using an analytical scale with accuracy of 0.001 g.

Because of the variability in the plant stand of the plots, grain yield data were corrected by covariance for the ideal stand (Cruz 1971). Based on the data obtained, variance analysis was performed using the F-test ($p < 0.05$), and the means were compared by the Scott-Knott test ($p < 0.05$) for all traits evaluated.

The inbreeding depression (ID) rates were obtained by comparing the average values of the open pollination and selfing progenies for the 32 genotypes, for all traits evaluated, according to the formula ID (%) = 100 - ((selfed * 100)/open pollination).

The genetic ($\sigma_g^2$) and environmental ($\sigma_e^2$) variances were estimated based on the mathematical expectations of the mean squares. The heritability coefficient was obtained according to the formula $h^2 = \sigma_g^2/(\sigma_g^2 + \sigma_e^2)$.

All data were analyzed using the Genes software (Cruz 2001).

## RESULTS AND DISCUSSION

Significant differences were observed for the sources of variation in all traits evaluated (Table 1). The mean square significance for means of reproduction shows differences between selfed and open pollinated progenies for all traits. The significant interaction between progenies and means of reproduction indicates that the crambe progenies did not respond similarly with respect to means of reproduction. This is interesting, because the progenies were all selected from the same heterogeneous cultivar (Lara-Fioreze et al. 2016). In autogamous species, a homogeneous phenotype between progenies is expected as an effect of the homozygous *loci*. However, that was not observed in this study.

For plant height, the progenies 10, 11, 13, 18, 23, 24, 26, 28, 29, 30, 31 and 32 obtained the highest values in open pollination (Table 2). The decrease in plant height in selfed plants was first described by East & Hayes (1912), when studying corn.

In crambe, as well as in other crops, plant height is a very important trait, particularly for mechanical harvesting. Moreover, for being an herbaceous plant, whose branches form near the base (Desai et al. 1997), plant height is positively correlated with grain yield (Cargnelutti Filho et al. 2010).

The selfed progenies 1, 3, 7, 12, 16, 22, 24, 26, 27, 28 and 29 showed a significant reduction in the final stand, when compared with their open pollinated counterparts. However, the selfed progenies 6 and 30 exhibited an opposite response, showing a higher final stand (Table 2).

A higher final stand may be related to two causes: higher germination or higher plant survival. Nevertheless, according to Baskin & Baskin (2015), it did not seem to be a strong relationship between a decrease in germination and an increase in the coefficient of inbreeding (F), in 743 species studied.

For grain yield, only the progenies 2, 8, 14 and 17 showed no significant differences between selfed and open pollinated plants. The progenies 13, 16, 20 and 30 showed a statistically lower 1,000-grain weight in selfed progenies. Only the selfed progeny 4

Table 1. Mean squares for plant height, final stand, grain yield and 1,000-grain weight, in crambe progenies obtained using two means of reproduction (selfing and open pollination).

| Source of variation | DF | Plant height | Final stand | Grain yield | 1,000-grain weight |
|---|---|---|---|---|---|
| | | cm | | kg ha$^{-1}$ | g |
| Block | 2 | 124.23 | 27.29 | 11,780.58 | 2.94 |
| Parental genotype (Pr) | 31 | 424.15* | 14.35* | 271,669.30* | 2.04* |
| Mean of reproduction (Wr) | 1 | 11,696.41* | 206.25* | 14,022,083.40* | 2.86* |
| Pr x Wr | 31 | 496.52* | 20.94* | 208,810.93* | 1.31* |
| Error | 126 | 207.12 | 6.48 | 26,911.31 | 0.69 |
| CV (%) | | 23.68 | 41.73 | 36.72 | 10.35 |

* Significant by the F-test ($p < 0.05$).

exhibited a statistically higher 1,000-grain weight than that of the open pollinated progeny. In general, the average grain yield values were lower in selfed progenies (Table 2).

There are two hypothesis for inbreeding depression: first that favorable alleles tend to be dominant or partially dominant, and second that heterozygotes have a higher phenotypic value than homozygotes (Crow & Kimura 1970). According to Allard (1960) and Falconer (1987), the theory of partial dominance states that dominance in alleles causes a difference between the phenotypic values of homozygotes and heterozygotes, emphasizing that the depression caused by inbreeding is proportional to the degree of dominance. Inbreeding depression is also higher for *loci* with uniform allele frequencies. Thus, since the quantitative traits are controlled by many *loci*, a decline in the phenotypic value of this characteristic will also depend on the average degree of dominance that controls it.

Falconer (1987) reports that the highest levels of inbreeding depression are expected in populations with high heterozygous frequencies in *loci* with gene dominance, such as in hybrids, and in populations with high genetic load, such as those that have not been improved. Based on the results obtained, it is likely that the population from which the progenies originated is only slightly improved and may also contain high genetic load.

The effect of inbreeding depression in crambe progenies may be observed in Table 2. The mean values of inbreeding depression ranged from

Table 2. Average values for plant height, final stand, grain yield and 1,000-grain weight of crambe progenies from two means of reproduction (selfing and open pollination) and their respective inbreeding depressions (ID).

| Progenie | Plant height (cm) | | ID(%) | Final stand | | ID(%) | Grain yield (kg ha$^{-1}$) | | ID(%) | 1,000-grain weight (g) | | ID(%) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Selfing | Open | | Selfing | Open | | Selfing | Open | | Selfing | Open | |
| 1 | 64.66 aA | 74.76 aA | 13.5 | 3.6 cB | 9.0 aA | 59.3 | 233.33 cB | 850.46 dA | 72.6 | 8.26 aA | 8.13 aA | -1.6 |
| 2 | 76.83 aA | 69.53 aA | -10.5 | 8.6 bA | 5.0 bA | -73.3 | 511.73 bA | 413.73 dA | -23.7 | 8.63 aA | 8.74 aA | 1.3 |
| 3 | 84.50 aA | 66.36 aA | -27.3 | 3.6 cB | 8.6 aA | 57.7 | 245.06 cB | 823.53 dA | 70.2 | 8.92 aA | 8.95 aA | 0.3 |
| 4 | 84.46 aA | 72.03 aA | -17.3 | 8.3 bA | 10.3 aA | 19.4 | 760.40 aB | 1,056.53 cA | 28.0 | 9.65 aA | 8.23 aB | -17.3 |
| 5 | 38.50 bA | 60.66 aA | 36.5 | 3.6 cA | 7.6 aA | 52.2 | 55.06 cB | 588.73 dA | 90.7 | 6.70 cA | 7.13 bA | 6.0 |
| 6 | 62.50 aA | 76.10 aA | 17.4 | 13.6 aA | 8.3 aB | -64.0 | 507.73 bB | 1,509.13 bA | 66.4 | 8.35 aA | 9.08 aA | 8.0 |
| 7 | 44.83 bA | 65.26 aA | 31.3 | 1.0c B | 6.6 bA | 85.0 | 45.60 cB | 435.73 eA | 89.5 | 8.73 aA | 8.21 aA | -6.3 |
| 8 | 49.06 bA | 65.53 aA | 25.1 | 5.0 cA | 5.3 bA | 6.3 | 145.46 cA | 337.93 eA | 57.0 | 8.09 aA | 7.44 bA | -8.8 |
| 9 | 56.70 bA | 51.83 aA | -9.4 | 4.6 cA | 8.6 aA | 46.2 | 308.66 cB | 630.93 dA | 51.1 | 8.57 aA | 7.35 bA | -16.6 |
| 10 | 35.76 aB | 73.13 aA | 51.1 | 3.3 cA | 7.0 bA | 52.4 | 80.86 cB | 979.06 cA | 91.7 | 7.63 bA | 7.36 bA | -3.7 |
| 11 | 44.33 bB | 76.16 aA | 41.8 | 4.3 cA | 6.3 bA | 31.6 | 166.13 cB | 584.06 dA | 71.6 | 8.43 aA | 7.28 bA | -15.8 |
| 12 | 60.30 aA | 69.00 aA | 12.6 | 1.6 cB | 7.0 bA | 76.2 | 59.73 cB | 799.53 dA | 92.5 | 8.82 aA | 8.39 aA | -5.2 |
| 13 | 38.53 bB | 73.66 aA | 47.7 | 7.6 bA | 8.6 aA | 11.5 | 58.00 cB | 843.33 dA | 93.1 | 7.80 bB | 9.53 aA | 18.1 |
| 14 | 51.36 bA | 53.26 aA | 3.6 | 7.0 bA | 3.3 bA | -52.85 | 362.40 bA | 113.60 eA | -219.0 | 7.76 bA | 7.14 bA | -8.8 |
| 15 | 46.80 bA | 60.16 aA | 22.2 | 4.0 cA | 5.3 bA | 25.0 | 60.53 cB | 469.93 eA | 87.1 | 8.40 aA | 8.11 aA | -3.7 |
| 16 | 71.06 aA | 60.03 aA | -18.4 | 1.0 cB | 8.0 aA | 87.5 | 39.53 cB | 441.73 eA | 91.1 | 6.21 cB | 8.22 aA | 24.4 |
| 17 | 47.10 bA | 67.66 aA | 30.4 | 6.0 cA | 4.0 bA | -50.0 | 211.33 cA | 257.73 eA | 18.0 | 6.13 cA | 6.98 bA | 12.1 |
| 18 | 54.43 bB | 80.50 aA | 32.4 | 8.3 bA | 7.0 bA | -19.1 | 236.00 cB | 996.66 cA | 76.3 | 7.74 bA | 8.39 aA | 7.7 |
| 19 | 74.46 aA | 55.40 aA | -34.4 | 6.0 cA | 5.0 bA | -20.0 | 104.93 cB | 534.46 dA | 80.4 | 8.60 aA | 8.32 aA | -3.3 |
| 20 | 79.53 aA | 75.96 aA | -4.7 | 6.0 cA | 7.3 aA | 18.2 | 190.40 cB | 571.46 dA | 66.7 | 7.45 bB | 8.83 aA | 15.6 |
| 21 | 65.46 aA | 62.43 aA | -4.9 | 8.6 bA | 7.0 bA | -23.8 | 210.13 cB | 580.26 dA | 63.8 | 8.05 aA | 8.25 aA | 2.4 |
| 22 | 48.70 bA | 62.03 aA | 21.5 | 3.3 cB | 9.3 aA | 64.3 | 154.06 cB | 762.86 dA | 79.8 | 7.44 bA | 8.57 aA | 13.1 |
| 23 | 53.86 bB | 84.83 aA | 36.5 | 4.3 cA | 6.6 bA | 35.0 | 100.06 cB | 605.46 dA | 83.5 | 7.53 bA | 6.84 bA | -10.1 |
| 24 | 31.10 bB | 67.06 aA | 53.6 | 3.0 cB | 7.3 aA | 59.1 | 25.60 cB | 678.13 dA | 96.2 | 6.48 cA | 8.79 aA | 26.3 |
| 25 | 44.40 bA | 60.06 aA | 26.1 | 4.3 cA | 6.0 bA | 27.8 | 87.13 cB | 1,859.46 aA | 95.3 | 7.33 bA | 8.08 aA | 9.3 |
| 26 | 42.50 bB | 79.30 aA | 46.4 | 3.6 cB | 10.0 aA | 63.3 | 59.13 cB | 698.53 dA | 91.5 | 7.38 bA | 8.14 aA | 9.3 |
| 27 | 50.83 bA | 63.66aA | 20.2 | 1.3 cB | 10.0 aA | 86.7 | 196.46 cB | 1,180.06 cA | 83.4 | 9.02 aA | 8.27 aA | -9.0 |
| 28 | 41.70 bB | 84.26aA | 50.5 | 4.6 cB | 10.3 aA | 54.8 | 123.40 cB | 1,247.53 cA | 90.1 | 7.88 bA | 8.07 aA | 2.4 |
| 29 | 33.66 bB | 67.56aA | 50.2 | 2.3 cB | 8.3 aA | 72.0 | 33.33 cB | 604.53 dA | 94.5 | 8.34 aA | 9.09 aA | 8.2 |
| 30 | 31.53 bB | 72.16aA | 56.3 | 10.0 bA | 4.3 bB | -57.0 | 77.33 cB | 352.53 eA | 78.1 | 7.31 bB | 8.66 aA | 15.6 |
| 31 | 43.86 bB | 76.76aA | 42.9 | 5.6 cA | 5.0 bA | -13.3 | 158.53 cB | 702.53 dA | 77.4 | 7.93 aA | 8.04 aA | 1.3 |
| 32 | 42.43 bB | 66.46aA | 36.2 | 3.0 cA | 5.3 bA | 43.8 | 41.33 cB | 434.80 eA | 90.5 | 7.37 bA | 8.18 aA | 9.9 |
| Average | | | 21.2 | | | 19.7 | | | 64.9 | | | 2.5 |

Averages with the same upper-case letter in the row and lower-case letter in the column are not significantly different by the Scott-Knott test ($p < 0.05$).

Table 3. Estimates of genetic parameters in selfed and open pollinated progenies of crambe.

| Parameter | Selfed progenies | | | | Open pollinated progenies | | | |
|---|---|---|---|---|---|---|---|---|
| | Plant height | Final stand | Grain yield | 1,000-grain weight | Plant height | Final stand | Grain yield | 1,000-grain weight |
| Mean | 53.00 | 5.00 | 176.55 | 7.91 | 68.55 | 7.10 | 717.03 | 8.15 |
| $\sigma_g^2$ | 175.60 | 6.11 | 24,598.84 | 0.37 | 6.80 | 1.31 | 117,384.83 | 0.29 |
| $\sigma_e^2$ | 61.69 | 1.93 | 2,432.85 | 0.29 | 71.30 | 2.33 | 16,007.00 | 0.15 |
| $h^2$ | 0.74 | 0.76 | 0.91 | 0.56 | 0.10 | 0.36 | 0.88 | 0.67 |

2.5 % (1,000-grain weight) to 64.9 % (grain yield). Moreover, the range of variation in inbreeding depression (positive values) and the absence of inbreeding depression (negative values) demonstrate the genetic variability among the crambe progenies for the traits evaluated.

Although crambe is considered an autogamous plant, our results indicate that the allogamy rate of the population used in this study is greater than in other genotypes evaluated previously, showing a mixed reproductive system. In this regard, one hypothesis to explain the occurrence of mixed-mating populations, in which individuals produce both self and outcrossed progeny, is that they are in an evolutionary transition from outcrossing to selfing. If purging is fast, the evolutionary transition from outcrossing to selfing should occur quickly, and mixed mating populations should become rare. According to Goodwillie et al. (2005), a recent tally of mating-system estimates for 345 plant species revealed that 42 % exhibited mixed mating, defined as selfing rates between 20 % and 80 %.

It is important to underscore that the population from which the progenies were selected was not genetically improved. Our results suggest that both the large variation in inbreeding depression and high inbreeding depression values show that evolutionary processes may still be acting and that the inbreeding depression may decrease over time. Charlesworth & Charlesworth (1987) report that self-fertilization exposes these mutations to selection, thereby reducing the magnitude of inbreeding depression. Moreover, species with intermediate selfing rates maintain a substantial inbreeding depression, comparable to that of predominantly outcrossing species (Winn et al. 2011). Therefore, the population may exhibit mixed mating.

Inbreeding is not always disadvantageous, because it leads to greater genetic variance among progenies and may increase the expected genetic gain with selection (Paterniani & Miranda 1987). The genetic variance was higher in the selfed progenies, if compared with the open pollinated ones (Table 3). Consequently, the estimated heritability coefficients for plant height, final stand, grain yield and 1,000-grain weight showed differences between the selfed and open pollinated progenies. The heritability coefficients were generally higher in selfed progenies, except for 1,000-grain weight.

The heritability coefficient expresses how much of the observed phenotypic variance is due to genetics, rather than environmental. For 1,000-grain weight, although the genetic variance of the selfed progenies was higher than in open pollinated progenies, the environmental variance was higher in the later. This result indicates a greater influence of the environment on the traits of open pollinated progenies, resulting in significantly lower heritability.

Although selfing may cause a loss of initial vigor in some traits with a higher degree of dominance or in slightly improved populations with high genetic load, it is important for the genetic load to be dissipated. Therefore, inbreeding in plants may be beneficial in breeding programs. Moreover, speculation on the means of reproduction of crambe is extremely important, and since the inbreeding depression observed is related to high allogamy rates, the breeding methods used should be adapted, with effective control of cross-fertilization at certain stages of breeding. Thus, further studies should be conducted to determine the allogamy rate that occurs in crambe under different environmental conditions.

## CONCLUSIONS

1. Crambe has marked inbreeding depression, with a variable rate among the evaluated progenies;

2. The superior phenotype of open pollinated progenies, when compared to the selfed ones, indicates that crambe is not a selfing species and, probably, has a mixed mating system;
3. The highest inbreeding depression observed is for grain yield.

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