Inbreeding depression as a cause of fruit abortion in structured populations of macaw palm (*Acrocomia aculeata*): Implications for breeding programs

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**A B S T R A C T**

*Acrocomia aculeata* (Jacq.) Lodd. ex Martius is an outstanding species to produce biofuels from its fruit oil. This species occurs in small populations and, consequently, inbreeding depression limits its development and jeopardizes its traits, mainly on fruit number (fruit abortion). Thus, this study aimed to estimate inbreeding depression, genetic and population parameters, verify the direct and indirect selection for pulp oil production and model the structured population effect. The data were collected in *A. aculeata* germplasm collection, referred to 44 half-sib families, and eight out of them had at least one inbred individual. All families were clustered in populations according to their geographic coordinates. The inbreeding depression reduced the fruit number and is one of the causes of fruit abortion. It was more severe in productive traits, indicating they are likely ruled by the dominance effect. The heritabilities were high for most of traits. The genetic gain of pulp oil production was 178% for direct selection, 173% and 171% for indirect selection, considering fruit moist matter and fruit number, respectively. Productive and vegetative traits had a low and high fixation index, respectively. There is evidence of genetic drift for vegetative traits. The model with structured populations obtained high accuracy. A reciprocal recurrent selection is indicated for macaw palm’s genetic breeding. Therefore, this work helps to establish strategies to keep the genetic variability of *A. aculeata* for a sustainable breeding program and to confirm it as a source of renewable energy and a new oil crop for biofuel production.

1. Introduction

*Acrocomia aculeata* (macaw palm, macauba) belongs to the Arecaceae botany family. It is a perennial species, has a height of 20–30 m, around 20–30 cm of diameter at breast height, monopodial growth, its fruits have a diameter of 2.5–5 cm, and it has androgynous inflorescences with protogyny, which are pollinized by the wind and insects (da S. César et al., 2015; Scariot et al., 1991). Its natural habitat is Latin America (Crocomo and Melo, 1996) and southeast Brazil, the latter can be the diversity center according to the Vavilov’s theory on crop origins (Lanes et al., 2015), where one of the largest macaw palm germplasm banks is.

There is great potential on its fruit in producing cosmetics, medicines, and mainly biofuel, obtained from its pulp oil (César et al., 2015). The macaw palm’s pulp oil production (5–6.2 tons per hectare) (Motoike and Kuki, 2009; Pires et al., 2013) is similar to the production of oil palm (2–8 tons per hectare), considered the most productive oil crop in the world (FAO, 2013; MAPA, 2015; Mielke, 2013). Thus, macaw palm is a strategic species for biofuel production used as renewable energy to avoid global warming (Dincer, 2000).

Unfortunately, macaw palm is not domesticated and the investment in a breeding program to improve oil’s production and others agricultural aspects would be crucial to large scale biofuel production (CETEC, 1983; Crocomo and Melo, 1996). Thus, pre-breeding studies are required (repeatability of some traits, genetic diversity, mating system, morphological, and physiological description) (Lanes et al., 2016, 2015; Manño et al., 2012; Pires et al., 2013).

A crucial study were done by Lanes (2014) about macaw palm’s mating system and the consequences of inbreeding depression on growing and development of seedlings. The macaw palm showed a low number of progenies by selfing, which likely indicates inbreeding depression and high rates of fruit abortion due to a mutational load (Lanes et al., 2016).

The inbreeding depression arises due to the cross between relatives...
and self-pollination. Hence, the traits are drastically affected by a great number of recessive mutant alleles or homozygous alleles in loci where heterozygous alleles would be better, causing a reduction on the offspring’s fitness (Charlesworth et al., 2009).

In this context, the field observations of early high fruit abortion rates can be associated to the lack of pollinators (noticed in relation to artificial pollination) (Brito, 2013), insects attacks (Montoya et al., 2015; Oliveira and de Ávila, 2011) or inbreeding depression. Thus, inbreeding depression mainly remains unknown on macaw palm productive aspects like fruit number (fruit abortion) and other traits.

The opposite of inbreeding depression also remains unknown. The outbreeding depression occurs when the mean of self-pollinated individuals are superior to crossbreeding individuals (Frankham et al., 2011).

Inbreeding and outbreeding depression help to clarify the genetics mechanisms of traits in which were established throughout the evolutionary history of a species. This allows one to know which effects (additive and non-additive) are prevalent in traits and the mating strategies adopted to survive (self-pollination, crossing between relatives and random crossing). The mating strategies are consequences of the structure of population and help to understand how genetic variance is allocated.

The effective population size is the number of unrelated and non-inbred individuals in an ideal panmictic population, and it is directly related to diversity (Resende, 2002; Resende et al., 1997). The macaw palm occurs in small populations and can have a low effective population size. Hence, self-pollination and crosses between relatives contributes to a low effective population size throughout generations and to a low genetic diversity (Lanes et al., 2016; Resende et al., 1997). The low genetic diversity is not desirable for long-term crop improvement and increase of vulnerability in plants like insect attacks and diseases.

Thus, knowledge about population effect, inbreeding and outbreeding depression are essential to an effective genetic breeding and management of the macaw palm germplasm bank for conservation.

This study aimed to estimate inbreeding depression effect on macaw palm’s traits, mainly, on fruit number, genetic and population parameters, genetic correlations, verify the direct and indirect selection for pulp oil production and model the structured population effect on the accuracy of genetic evaluation. To our knowledge, this is the first study which reports inbreeding depression effect on macaw palm’s traits, mainly on fruit number and as a cause of fruit abortion.

2. Material and methods

2.1. Germplasm bank and data collection

The data were collected at Araponga Experimental Farm in Araponga, State of Minas Gerais, Brazil, where the Active Germplasm Bank of Macaw Palm (BAG – Macaubá) is located. It is the official repository registered by the Brazilian Board of Management of Genetic Heritage and one of the largest A. aculeata germplasm bank in Latin America.

The BAG is located at a 1000 m height, and the climate is Cwb according to Köppen classification—the summer is rainy and winter is dry. Currently, there are 300 maternal families in this ex situ collection. They were formed through the gathering of fruits from different mother trees in their natural habitat (Brazil’s southeast) and cultivated until their productive age. The agricultural practices applied to the BAG can be found in Pires et al. (2013).

The data were collected by the Rede Macaúba de Pesquisa (REMAPE) group at Universidade Federal de Viçosa (UFV) from 2013 to 2015 and refer to 293 individuals from 44 maternal families. A part of these individuals were evaluated by Lanes (2014), who used molecular markers (SSR-Simple Sequence Repeats). The author concluded that the macaw palm is an allogamous species (98.6% of crossing) with a low level of self-pollination (1.4%), high crossing between relatives (38.3%), and found inbred individuals.

The maternal families were planted in February 2009. In this study, 8 out of 44 families have at least one inbred individual (family BGP11, BGP29, BGP31, BGP36, BGP37, BGP40, BGP47, and BGP50).

The traits analyzed were inflorescence number (T1); diameter at breast height in centimeters (T2); height of the first spathe in meters (T3); fruit number (T4); pulp oil content in grams (T5); dry matter content in grams of fruit’s components: bark (T6), pulp (T7), endocard (T8) and kernel (T9); fruit moist matter in kilograms (T10); and the total production of pulp oil in kilograms (T11).

The fruit number (T4) was considered an indicator of fruit abortion. The traits T1 to T3 were considered vegetative and T4 to T11 productive ones. The T11 trait was obtained for each plant by the multiplication of the following traits: fruit number, pulp dry matter content and pulp oil content.

After harvesting, fruits were stored for 30 days. The oil content was estimated in three fruits per individual with the Varian FT-IR 660 spectrophotometer (near-infrared spectrometry, NIR). The dry matter of the pulp, bark, endocard, and kernel were estimated by the average of five fruits per plant. The fruit’s components were dried in a kiln at 105 °C for 24 h and weighted in a precision balance.

2.2. Inbreeding depression estimation

Inbreeding depression on traits were estimated for the families with at least one inbred individual. The inbred individuals were identified according to previous analysis with molecular markers (SSR-Simple Sequence Repeats) (Lanes, 2014).

Inbreeding depression in percentage (D%) was estimated with the Eq. (1) deduced by Resende (2002).

\[
D = \frac{100}{\mu} \left( (M - S) - \frac{1}{2 - S} S - \frac{S}{2 - S} \right)
\]

Where \(\mu\) is the average of trait, \(S\) is the family self-pollination coefficient, \(M\) is the offspring phenotype mean (\(F = S/(2-S)\)), and \(S^*\) is the inbred individual phenotypic mean (\(F = 1/(2-S)\)) in populations with mix mating system. \(F\) is the inbreeding coefficient. It was considered a \(S\) of 0.22, 0.13, 0.44, 0.3, 0.1, 0.11, 0.5, and 0.3 for families BGP11, BGP29, BGP31, BGP36, BGP37, BGP40, BGP47, and BGP50, respectively (Lanes, 2014).

The linear relation between the presence/absence of inbred individuals and traits was estimated through the Analysis of Covariance (ANCOVA) in the REML (Restricted Maximum Likelihood)/BLUP (Best Linear Unbiased Prediction) method using the following statistical mixed model (Eq. (2)) (Resende, 2007):

\[
y = Xu + \beta Cov + Za + e
\]

Where \(y\) is the y data vector, \(u\) is the vector associated with the overall mean (fixed effect), \(a\) is a vector associated with random additive genetic effects, \(e\) is the residual vector (random effect), and \(X\) and \(Z\) are the incidence matrixes of respective effects. The \(\beta\) is the regression coefficient of Cov (presence/absence of inbred individuals) on \(y\). The model was fitted with the SELEGAN – REML/BLUP software (Resende, 2016).

2.3. Genetic and population parameters and genetic correlations

A multivariate k-means algorithm was used to cluster the half-sib progenies in seven populations (Hartigan and Wong, 1979). The clustering was based on the geographical coordinates (latitude and longitude) of the mother trees to check all the variation between populations due to the families’ origin. The kmeans.ddR package (Gupta et al., 2015) in the R software (R Core Team, 2015) was used, adopting a \(k = 7\).

After structuring the population, genetic components were predicted through the REML/BLUP method with the following statistical
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