Multi-year progeny test identifies superior progenies and a biennial yield pattern in macaw palm (Acrocomia aculeata)

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Multi-year progeny test identifies superior progenies and a biennial yield pattern in macaw palm (*Acrocomia aculeata*)

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Afiliação

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Abstract

The macaw palm (*Acrocomia aculeata*) is a native Neotropical palm with potential for vegetable oil production, particularly for biofuel generation. However, its domestication remains incipient, and information on long-term progeny performance is still limited. This study evaluated fruit yield and biennial bearing in a macaw palm progeny test to identify superior families for genetic improvement. Thirty-six half-sib progenies from two regions of Minas Gerais, Brazil, were assessed for fruit production from 2019 to 2024 at the Federal University of Viçosa, Minas Gerais. The experiment followed a randomized complete block design with three blocks and three plots per block. Genetic variances, parameters, and progeny performance were estimated using mixed linear models (REML/BLUP) implemented in the ASReml package in R. Biennial bearing was identified based on multi-year yield patterns and phenotypic correlations among consecutive and alternating production cycles. Mean fruit production ranged from 1.34 kg plant^{-1} in 2019 to 26.32 kg plant^{-1} in 2022. Most of the genetic variability for yield was concentrated within progenies, with a broad-sense heritability of 0.36, indicating high intrafamilial heterogeneity. Four of the evaluated progenies stood out for their superior performance, year-to-year stability, and, in some cases, early flowering. Intrafamilial selection within these progenies, totaling eight individuals, increased the population mean yield by 30.12%. A pattern of negative biennial bearing was observed, reinforcing the importance of multi-year evaluations for accurate selection, with no association with accumulated annual precipitation. The selected progenies are promising candidates for directed crosses and may contribute to advances in macaw palm breeding programs.

Keywords Earliness · Genetic variability · Macauba · Mixed models · REML/BLUP · Yield stability

Introduction

The macaw palm (*Acrocomia aculeata* (Jacq.) Lodd. ex Mart), a cross-pollinated species belonging to the Arecaceae family, is native to the Neotropical region and widely distributed across Brazil, especially within the Cerrado and Atlantic Forest biomes (Lorenzi et al. 2010; Plath et al. 2016). The state of Minas Gerais stands out as one of the main centers of diversity for the species, harboring populations with broad genetic variability and adaptation to diverse edaphoclimatic conditions (Lanes et al. 2015; Kantar et al. 2017; Vargas et al. 2021). This diversity represents a strategic resource for breeding programs, enabling the selection of genotypes with high yield potential and wide adaptability (Rosado et al. 2019). Over the past decades, more than six thousand publications on macaw palm have been indexed on Google Scholar (https://scholar.google.com), highlighting the growing scientific interest and relevance of this emerging oilseed species; however, only seven studies address plant breeding, indicating that genetic improvement remains largely unexplored (Vargas et al. 2021).

With estimated yields ranging from 16.000 to 25.000 kg ha^{-1} of fruits and up to 5.000 L ha^{-1} of oil, the macaw palm would surpass several traditional oilseed crops, such as oil palm and soybean, in productivity per hectare (Teixeira 2005; Motoike and Kuki 2009; Conceição et al. 2015). This high productive potential, combined with the versatility of its fruits and solid residues, positions the species as a promising alternative source of vegetable oil and value-added products (Machado et al. 2015; Duque et al. 2025; da Silva et al. 2026). Moreover, macaw palm cultivation offers environmental advantages, such as adaptation to marginal soils and the capacity to contribute to the restoration of degraded areas (Ciconini et al. 2013; Evaristo et al. 2016). These attributes reinforce its role in the development of more sustainable and economically viable cropping systems.

However, the absence of structured commercial plantations limits the economic exploitation of the species and increases pressure on its natural habitats (Evaristo et al. 2016; Coser et al. 2016; Colombo et al. 2018). Native populations, which are the main sources of fruit harvesting, are characterized by high phenotypic heterogeneity, with variations in population density, plant age, and fruit quality, which hinders the development of more productive and homogeneous cultivation systems (Manfio et al. 2011; Ciconini et al. 2013; da Silva et al. 2026).

Given this scenario, the establishment of breeding programs is essential to promote the domestication and rational use of macaw palm. Progeny testing is a key stage in these programs, as it allows the evaluation of offspring performance and the inference of parental genetic merit for traits of interest (Cruz

et al. 2014). Through such trials, it is possible to estimate genetic parameters, quantify variability, and accurately select superior genotypes (Viana and Resende 2014; Resende 2016; Borém et al. 2021). Nevertheless, most studies on the species remain limited to the assessment of morphoagronomic and productive traits within a single reproductive cycle, hindering the identification of materials with stable performance across years. Even this recent study has largely adopted this one-time evaluation approach (Oliveira et al. 2025).

The scarcity of multi-year assessments hampers the understanding of reproductive stability and earliness among macaw palm genotypes. This limitation is further exacerbated by the species' long juvenile phase, which extends the selection and cultivar recommendation process, increasing both time and costs. Moreover, many studies are still conducted in natural populations under uncontrolled conditions, reducing the accuracy of genetic estimates and compromising selection efficiency (Viana and Resende 2014; Resende 2016). Therefore, it is hypothesized that integrating phenotypic information collected over several consecutive years, under a controlled experimental design and using progenies derived from selected mother trees, would yield more consistent estimates of genetic parameters.

With the progress of the macaw palm breeding program developed at the Federal University of Viçosa, a progeny test was established in 2012 using genetic material selected from native populations with high fruit processing mass index (Oliveira et al. 2025). To the best of our knowledge, this is the first multi-year evaluation of production in a macaw palm progeny test. Incorporating criteria such as yield stability and reproductive precocity in the selection of parental lines enhances accuracy and efficiency in cultivar development, strengthening the integration of the macaw palm into Brazil's oilseed crop sector.

We believed that progeny testing provides a more precise understanding of the reproductive pattern of the macaw palm. Therefore, the objective of this study was to evaluate fruit production and biennial bearing in macaw palm trees established in a progeny test. The findings of this study advance the evaluation and selection of superior progenies for genetic improvement purposes and provide valuable insights for the domestication of native perennial species with high agro-industrial potential.

Materials and Methods

Macaw palm progeny test - genetic material and location

The macaw palm progeny test was established on June 2, 2012, comprising 36 half-sib progenies derived from natural populations located in two municipalities in the state of Minas Gerais, Brazil. Eighteen

progenies originated from Luz (progenies 1–18) and eighteen from Santa Luzia (progenies 19–36), totaling 324 plants, with 162 individuals from each provenance (Fig. 1). The progenies were preliminarily selected from 105 progenies of natural populations from the same regions, based on the processable mass index (IMP), as described by Manfio et al. (2011), where IMP = fruit equatorial diameter – 2 × endocarp thickness. Mature fruits with higher IMP values had their seeds subjected to pre-germination protocol (Motoike et al. 2007). After approximately 12 months of nursery development, the seedlings were transplanted to the field to establish the progeny test. Crop management and maintenance practices followed the technical recommendations proposed for the species (Pimentel et al. 2011).

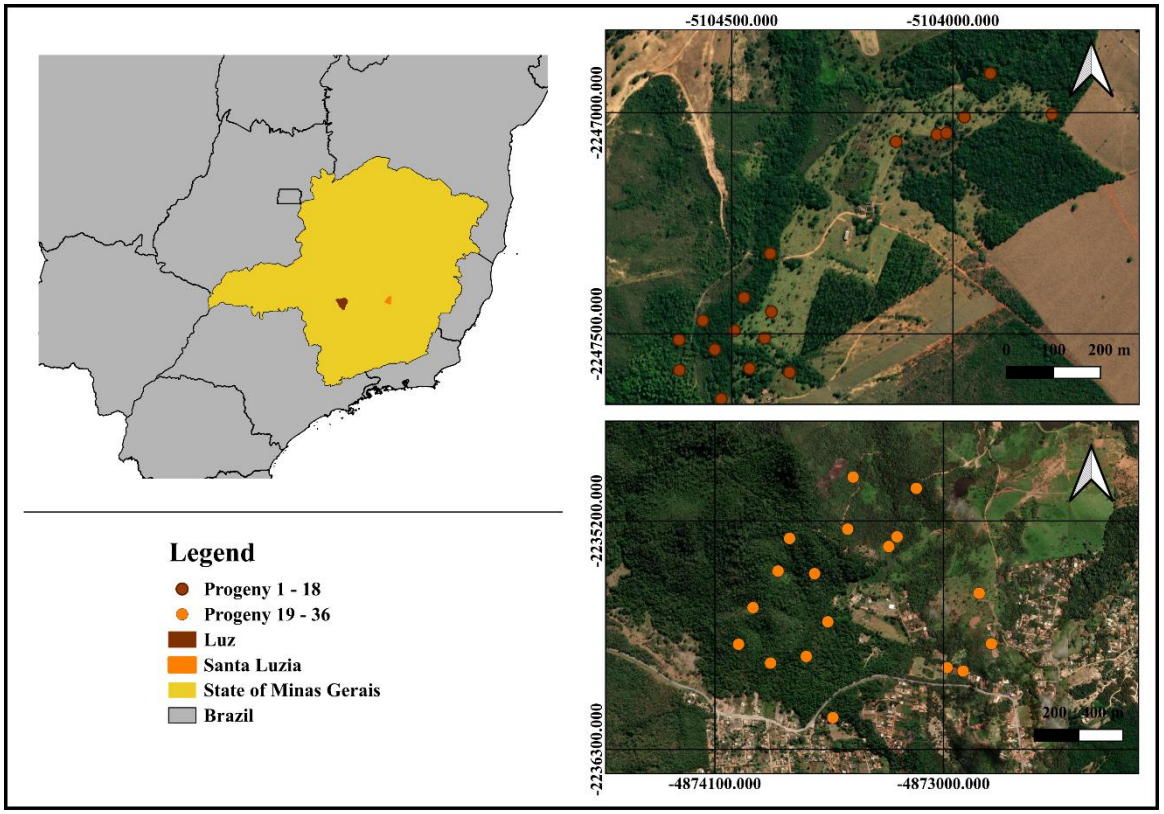

Fig. 1 Provenances of the evaluated macaw palm progenies, originating from the municipalities of Luz, MG (1-18, in brown) and Santa Luzia, MG (19-36, in orange)

The experiment was conducted at the Teaching, Research, and Extension Unit of the Federal University of Viçosa, located in Araponga, Minas Gerais, Brazil (20°39′07.01″ S; 42°31′43.52″ W; 810 m a.s.l.). According to the Köppen–Geiger classification, the regional climate is Cwb, characterized by mild temperatures, rainy summers, and a mean annual temperature of approximately 18 °C, with an average annual precipitation of 1.357 mm.

Phenotypic evaluation

The variable evaluated was fruit yield (kg plant^{-1}), measured annually over six consecutive years (2019-2024). Based on this variable, yield stability and flowering earliness among progenies were also analyzed.

Flowering occurred between October and January, and harvesting took place from December to April, coinciding with the period of physiological maturity of fruit bunches, which was identified by the natural abscission of the first fruits (Montoya et al. 2016). At this stage, the bunches were cut close to the stem using a sickle, and the fruits were manually detached. Mature fruits that had naturally fallen to the ground were also collected to ensure a more accurate estimate of the total fruit yield per plant. Weighing was performed using a portable digital scale.

Yield stability was assessed based on the regularity of production throughout the six years, considering both the occurrence of production in consecutive years and the consistency of annual means. Progenies showing continuous production with higher mean yields were classified as more stable, whereas those with interruptions or irregular means were considered less stable.

Flowering earliness was assessed based on production observed in 2019, the first evaluation year, by calculating the proportion of plants that produced fruits. Progenies were classified into three categories: early, when all nine individuals produced fruits in 2019 (100%); intermediate, when at least one individual produced fruits in the first year (11.1%); and late, when no individuals produced fruits in 2019 (0%).

Experimental design and statistical analyses

The experiment followed a randomized complete block design (RCBD) with three replications. Each plot consisted of three plants spaced 5 × 5 m apart. The statistical model used for the analyses was:

$$Y_{ijklm} = \mu + Y_i + O_j + B_k + P_l + (P{:}Plot)_{lm} + (P{:}Year)_{li} + \varepsilon_{ijklm} \quad \text{(A)}$$

where: Y_{ijklm} - fruit yield of plot m, progeny l, in block k, from origin j, in year i; μ - overall mean; Y_i – fixed effect of year i (i = 2019, ..., 2024); O_j - fixed effect of origin j (Luz or Santa Luzia); B_k - fixed effect of block k (k = 1, 2, 3); P_l - random effect of progeny l $(l = 1, \ldots, 36)$; $(P{:}Plot)_{lm}$ - random interaction between progeny l and plot m; $(P{:}Year)_{li}$ - random interaction between progeny l and year i; ε_{ijklm} - random residual error, where $\varepsilon_{ijklm} \sim$ NID (0; σ^2).

After fitting the general model including all years, separate analyses were also performed for each year, in order to obtain specific estimates for each evaluation cycle, as follows:

$$Y_{kl} = \mu + B_k + P_l + \varepsilon_{kl} \quad \text{(B)}$$

where: Y_{kl} - observed fruit yield of progeny l, in block k; μ - overall mean; B_k - fixed effect of block k; P_l - random effect of progeny l; and ε_{kl} - random residual error, assumed as $\sim$ NID (0; σ^2).

The estimation of variances and genetic parameters was performed using mixed linear models through the *Restricted Maximum Likelihood/Best Linear Unbiased Prediction* (REML/BLUP) procedure, implemented in the *ASReml* package in R software (Butler et al. 2017; R Core Team, 2024). To test the significance of the progeny effect, a *Likelihood Ratio Test* (LRT) was applied.

Genetic gain from selection was estimated at two hierarchical levels: among superior progenies and within progenies (selected individuals). The estimates were obtained based on predicted means generated by mixed models. Genetic gain was calculated according to the following expression:

$$\mathrm{Gs} = \mathrm{H}^2 \mathrm{x}\ \mathrm{Ds} \text{ or } \mathrm{Gs}\ (\%) = \frac{\mathrm{Gs}}{\mathrm{X_0}} * 100, \text{ where, } \mathrm{Ds} = \mathrm{X_s} - \mathrm{X_0}$$

where: Gs – genetic gain from selection; H^2 – broad-sense heritability; Ds – selection differential; $\mathrm{X_s}$ – predicted mean of the selected progenies; $\mathrm{X_0}$ – predicted mean of the original population.

Broad-sense heritability was estimated separately for the Progeny and Progeny:Plot effects, based on the variance components obtained from the adjusted model, according to the following expression:

$$\mathrm{H}^2 = \frac{\hat{\sigma}_g^2}{\hat{\sigma}^2_{g} + \frac{\hat{\sigma}_e^2}{r}}$$

where: $\hat{\sigma}_g^2$ – genetic variance of the evaluated component (Progeny or Progeny:Plot); $\hat{\sigma}_e^2$ – residual variance; r – number of replications.

The mean of the new population after selection ($\mathrm{X_n}$) was estimated as:

$$\mathrm{X_n} = \mathrm{X_0} + \mathrm{Gs}$$

Biennial bearing analysis

To identify patterns of biennial bearing, phenotypic correlations were performed using the annual *Best Linear Unbiased Estimators* (eBLUEs) (from 2019 to 2024), successive biennial periods (2019_2020, 2021_2022, 2023_2024), and alternating biennial periods (2019_2021, 2020_2022, 2021_2023, 2022_2024), following the methodology adapted from Fanelli Carvalho et al. (2020). The estimates were obtained from linear models fitted by year (model B), with progeny and block considered as fixed effects. The correlations were calculated using the pairs.panels function from the *psych* package (Revelle 2015).

The accumulated annual precipitation data for Araponga, Minas Gerais, were obtained using the DataClimaBR application, developed on the Google Earth Engine platform. To evaluate the potential influence of water availability on fruit production, precipitation data from 2018 to 2023 were associated with fruit production data from 2019 to 2024, relating precipitation in a given year to production observed in the subsequent year. This approach is justified because floral induction and part of the reproductive development occur in the cycle preceding harvest.

Results

Estimates of variances and genetic parameters

The statistical analysis revealed significant effects of Year and Block on fruit yield, demonstrating the influence of environmental conditions and spatial variation on the performance of the progenies. In contrast, the Origin factor (Luz and Santa Luzia) showed no significant effect, indicating that differences between provenances did not affect the mean fruit yield of the progenies (Table 1).

Table 1 Analysis of the fixed effects of origin, year, and block on fruit yield of macaw palm, based on the Wald test (F-statistic)

SV	Df	Wald F-statistic
Origin	1	2.00^{ns}
Year	5	398.74***
Block	2	32.43***

*** ($p < 0.001$); ^{ns} not significant

Genetic variability was detected among the progenies, with a genetic variance ($\hat{\sigma}_g^2$) of 3.10 and broad-sense heritability (H_a^2) of 0.04, confirming the presence of exploitable genotypic differences for fruit

yield (Table 2). The phenotypic variance ($\widehat{\sigma}_f^2$) was 247.23, with an overall observed mean ($\bar{x}$) of 14.06 kg of fruits per plant and a high coefficient of experimental variation (CVe) of 99.34%, reflecting the strong heterogeneity of the evaluated genetic material and the marked influence of environmental factors. The Progeny:Plot interaction showed a genetic variance $\widehat{\sigma}_g^2$ of 37.09, and a broad-sense heritability H_a^2 of 0.36, also indicating substantial genetic variability within the 36 progenies. In contrast, the Progeny:Year interaction revealed a genetic variance $\widehat{\sigma}_g^2$ of 11.69 and H_a^2 of 0.15, suggesting that progeny performance varied across the productive cycles.

Fruit yield varied substantially among years, with the highest mean values observed in 2022 ($\bar{x} =$ 26.32 kg.plant^{-1}) and 2024 ($\bar{x} = 22.58$ kg.plant^{-1}), and the lowest in 2019 ($\bar{x} = 1.34$ kg.plant^{-1}), when part of the plants had not yet begun fruiting (Table 2). The highest genetic variance $\widehat{\sigma}_g^2$ was recorded in 2023 (30.46), accompanied by the highest broad-sense heritability H_a^2 (0.31), indicating a stronger expression of genetic control in that year. Conversely, the lowest heritability H_a^2 values were found in 2024 (0.06) and 2019 (0.11), reflecting a greater environmental influence on the trait under study. The coefficient of experimental variation CVe also varied notably, being highest in 2019 (358.90%) and lowest in 2022 (71.87%), highlighting differences in experimental uniformity across production cycles.

Table 2 Variance components and genetic parameters for fruit yield (kg.plant^{-1}) of 36 half-sib progenies of macaw palm evaluated in a progeny test over six years (2019-2024) in the municipality of Araponga, Minas Gerais, Brazil

	SV	Variance components and genetic parameters					
		$\hat{\sigma}_g^2$	$\hat{\sigma}_f^2$	$\hat{\sigma}_e^2$	H_a^2	CVe(%)	$\bar{x}$ (kg.plant^{-1})
General analysis	Progeny	3.10***	247.24	195.35	0.04	99.34	14.06 (0-122.15)
	Progeny:Plot	37.09***			0.36		
	Progeny:Year	11.69***			0.15		
Annual analysis	2019	1.00^{ns}	24.13	23.13	0.11	358.90	1.34 (0-36.90)
	2020	22.06 .	384.38	362.32	0.15	156.66	12.15 (0-100.80)
	2021	14.33*	167.18	152.85	0.21	134.52	9.19 (0-62.38)
	2022	19.49 .	377.37	357.88	0.14	71.87	26.32 (0-85.86)
	2023	30.46***	228.47	198.01	0.31	109.84	12.81 (0-88.45)
	2024	6.84^{ns}	298.82	291.98	0.06	75.67	22.58 (0-72.15)

$\hat{\sigma}_g^2$: genetic variance; $\hat{\sigma}_f^2$: phenotypic variance; $\hat{\sigma}_e^2$: residual variance; H_a^2*:* broad-sense heritability; **CVe***:* coefficient of experimental variation, $\bar{x}$: overall observed mean

*** ($p < 0.001$), ** ($p < 0.01$), * ($p < 0.05$), . ($p < 0.10$), ^{ns} not significant

Evaluation of fruit yield and selection of the most productive progenies

The annual mean fruit yield varied substantially over the six-year period, with minimum values in 2019 (1.34 kg.plant^{-1}), 2021 (9.19 kg.plant^{-1}) and 2023 (12.81 kg.plant^{-1}), and maximum values in 2020 (12.15 kg.plant^{-1}), 2022 (26.32 kg.plant^{-1}) and 2024 (22.58 kg.planta^{-1}) (Fig. 2A). This oscillation highlights the importance of multi-year evaluations to capture production patterns in macaw palm and demonstrates that such temporal variability must not be overlooked when selecting superior plants. Among the 36 progenies, those showing the highest productive performance were 7 (17.98 kg.plant^{-1}), 29 (17.35 kg.plant^{-1}), 30 (16.75 kg.plant^{-1}) and 18 (16.06 kg.plant^{-1}), which combined high yield, earliness, and/or production stability across years. These four progenies reached their yield peak in 2022, showed a decline in 2023, and then recovered high yields in 2024 (Fig. 2B).

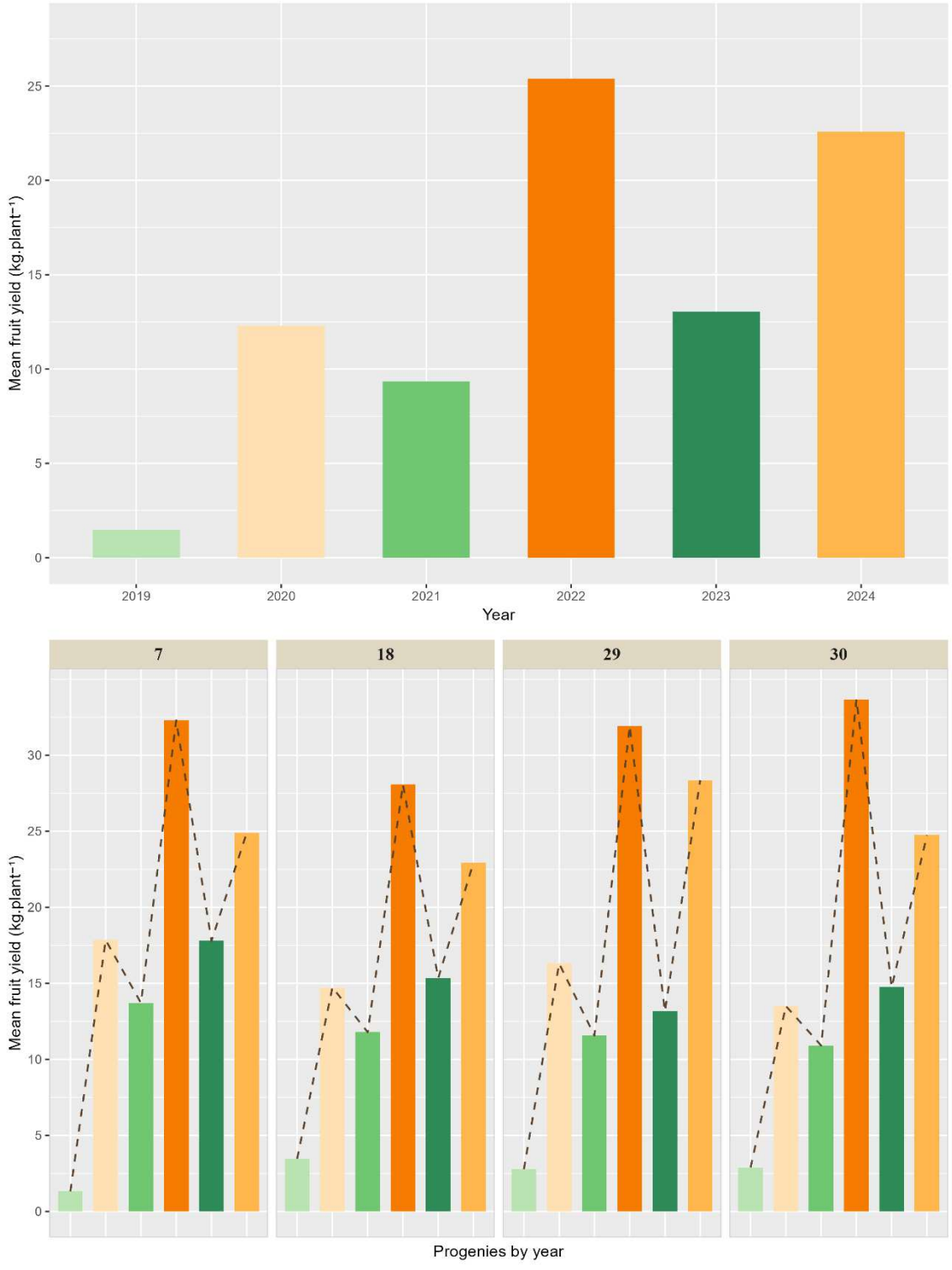

Fig. 2 (A) Mean fruit yield (kg.plant^{-1}) of 36 half-sib progenies of macaw palm evaluated from 2019 to 2024 (represented by distinct colors) in Araponga, Minas Gerais, Brazil. (B) Annual mean fruit yield of the four most productive progenies (7, 18, 29 and 30)

Among the 36 progenies analyzed, none were classified as early-maturing. Twenty-one progenies

(58.3%) were classified as intermediate, with at least one productive individual already in 2019. This group included the selected progenies 18, 29, and 30, as well as progenies 1, 2, 3, 4, 5, 6, 8, 10, 11, 12, 13, 16, 17, 23, 25, 26, 27, and 31. The remaining 15 progenies (41.7%) were classified as late, showing no production in the first year, including the selected progeny 7, together with 9, 14, 15, 19, 20, 21, 22, 24, 28, 32, 33, 34, 35, and 36. Although classified as late, progeny 7 began producing consistently from 2020 onwards, achieving the highest overall mean yield. Moreover, wide variability was observed within progenies, emphasizing the importance of intrapopulation selection. For this reason, we chose to identify two individuals per progeny that showed superior performance throughout the evaluation period (Supplementary Table 1). When analyzing the frequency of fruit production (including non-productive and dead plants), substantial variation was observed in the proportion of non-productive plants across the evaluated years (Fig. 3). In 2019, about 70% of the plants did not produce fruits, whereas in 2022 this proportion dropped to 11%, demonstrating the impact of both production cycle and environmental conditions on macaw palm fruiting. In total, 68 plants did not produce fruits in any of the six evaluation years. Some of these plants were replanted after field establishment but remained unproductive, while others may have been affected by factors such as inbreeding, resulting in low vigor or sterility. On the other hand, no progeny exhibited complete lack of production among all its individuals, indicating that even within the lowest-yielding families there was at least one productive plant, confirming the presence of intraprogeny variability with potential for selection.

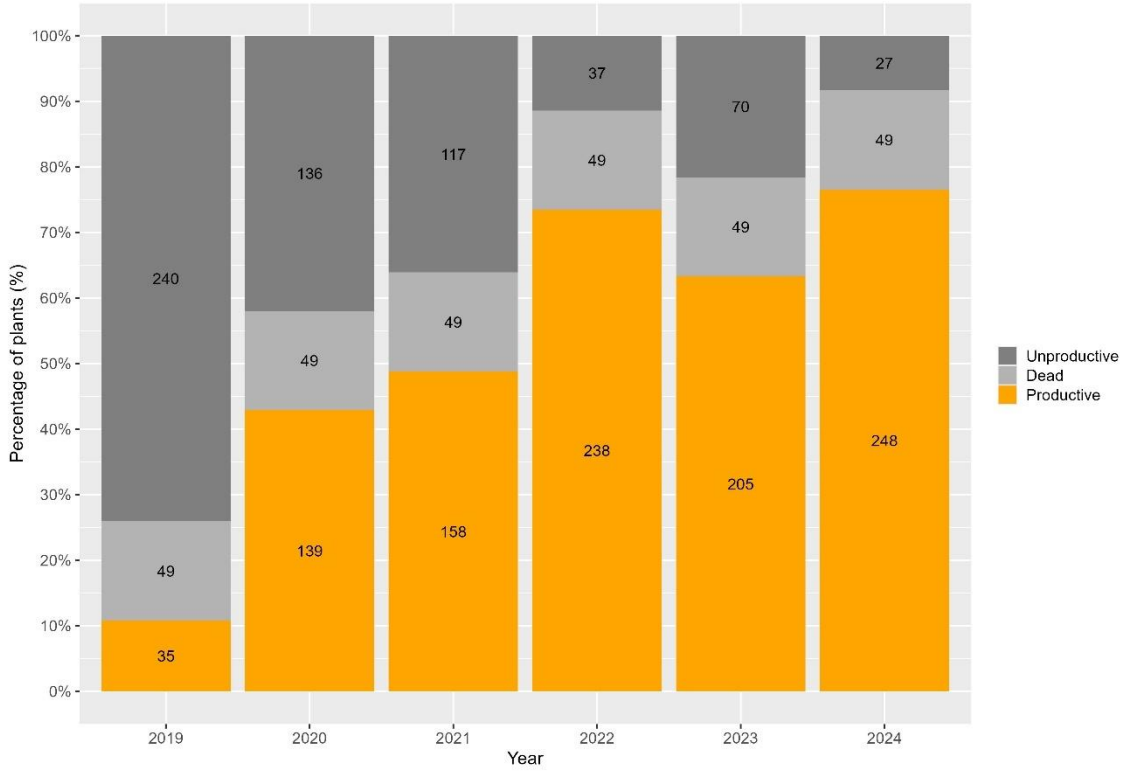

Fig. 3 Observed proportion of non-productive, dead, and productive plants over six years (2019–2024) of evaluation in a macaw palm progeny test

To quantify the benefits of this selection, genetic gains were estimated both among and within progenies (Table 3). Selection among the four superior progenies resulted in a genetic gain of 0.11 kg.plant^{-1}, corresponding to a percentage increase of 0.79%. In turn, selection within these progenies, based on the eight superior individuals, yielded a substantial genetic gain of 4.29 kg. plant^{-1}, equivalent to a 30.12% increase relative to the population mean. These results demonstrate substantial differences in the response potential to selection at different population levels, highlighting the importance of considering both progeny means and individual performance in the selection process.

Table 3 Estimates of genetic gains in fruit yield (kg.plant^{-1}) obtained from selection criteria applied among and within the most productive progenies

Selection criterion	n	X_0	Xs	Gs (Gs%)	Xn
Among progenies	4	14.23	17.03	0.11 (0.79%)	14.34
Within progenies	8	14.23	26.13	4.29 (30.12%)	18.51

n - number of selected individuals; X_0 - predicted mean of the initial population; Xs - predicted mean of the selected individuals; Gs- genetic gain from selection; Xn- predicted mean of the new population after selection

Figure 4 presents the annual mean fruit yield (kg.plant^{-1}) for the 36 evaluated progenies, as well as the multi-year mean. A wide variability was observed among the genetic materials over the years, particularly in the even years (2020, 2022, and 2024), during which most progenies exhibited higher yields, indicating a biennial bearing pattern.

Progenies 7, 18, 29, and 30 showed superior mean yields across years, with consistent performance throughout the evaluation period. For instance, progeny 7 did not show high production in 2019, being initially classified as late, but achieved the highest values in the following years, while progenies 18, 29, and 30 performed well since the first evaluation year, suggesting earliness. The multi-year analysis confirmed the pattern observed in the individual years, demonstrating the consistency of selection of these four progenies as superior genotypes.

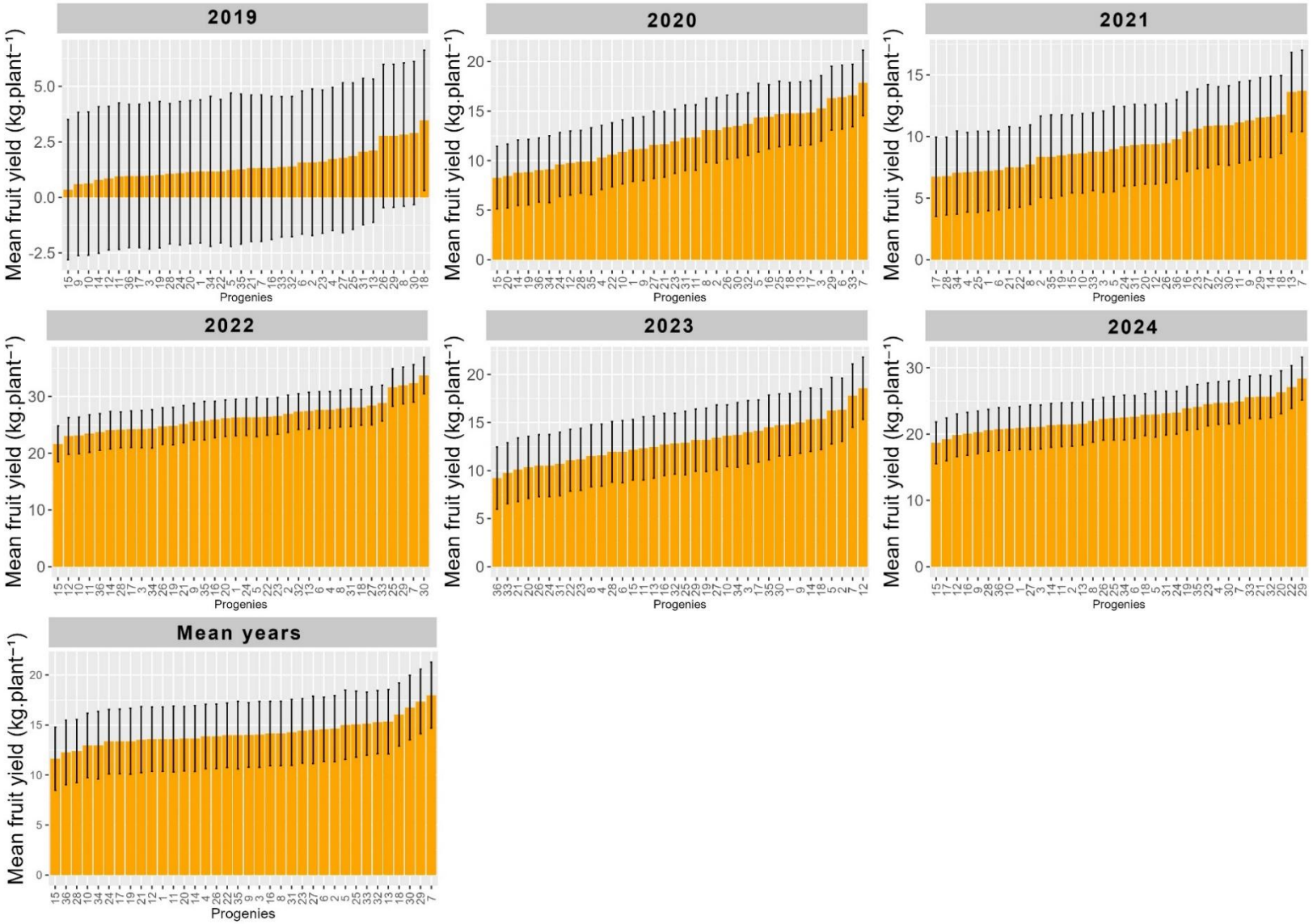

Fig. 4 Mean fruit yield (kg.plant^{-1}) of 36 macaw palm progenies evaluated from 2019 to 2024, including the multi-year mean. Vertical bars indicate the standard error of the mean for each progeny in each year

Identification of biennial bearing pattern

The correlation analysis between consecutive and biennial years revealed a consistent pattern of alternating fruit yield over the six years evaluated. Even years (2020, 2022, and 2024) exhibited higher mean yields than odd years (2019, 2021, and 2023), characterizing a negative biennial bearing pattern (Fig. 5). Correlations between consecutive years (Fig. 5A) were predominantly weak and non-significant, such as 2019-2020 ($r = 0.19^{ns}$), 2020-2021 ($r = 0.30^{ns}$), 2021-2022 ($r = 0.25^{ns}$), 2022-2023 ($r = 0.07^{ns}$), 2023-2024 ($r = -0.30^{ns}$). These results indicate low predictability in productive performance across successive years, suggesting temporal instability in progeny behavior, that is, the absence of a consistent pattern allowing the prediction of one year's performance based on the previous one.

In contrast, alternating year pairs such as 2020-2022 (r = 0.58***) and 2022-2024 (r = 0.43**) was significantly positive, revealing regular production cycles in which progenies maintain performance in alternating years. In the lower panels of Fig. 5A, the wide dispersion and large ellipses reflect the low consistency of eBLUEs between adjacent years.

Correlations between consecutive and alternating biennia (Fig. 5B) were mostly moderate to strong and highly significant, particularly for 2019_2020 - 2020_2022 (r = 0.87***), 2021_2022 - 2020_2022 (r = 0.81***), 2021_2022 - 2022_2024 (r = 0.72***) and 2020_2022 - 2022_2024 (r = 0.73***), These results demonstrate high concordance in performance when comparing cycles of the same phase, whether high–high or low–low yield periods.

On the other hand, weak correlations between biennia of opposite phases, such as 2019_2021 - 2022_2024 ($r = 0.16^{ns}$), 2020_2022 - 2021_2023 ($r = 0.28^{ns}$) and 2021_2023 - 2022_2024 ($r = -0.00^{ns}$), were expected, since progenies with high performance in high-yield years tend to show low performance in low-yield years. For mixed-phase pairs, such as 2019_2020 - 2023_2024 ($r = 0.24^{ns}$) and 2023_2024 - 2019_2021 ($r = 0.20^{ns}$), the simultaneous presence of high- and low-yield years attenuates the correlation, combined with possible shifts in the mean level between periods. Visually, the narrower ellipses in Fig. 5B, compared with those in Fig. 5A, indicates greater concordance of eBLUEs when years are aggregated into biennia, further supporting the occurrence of negative biennial bearing.

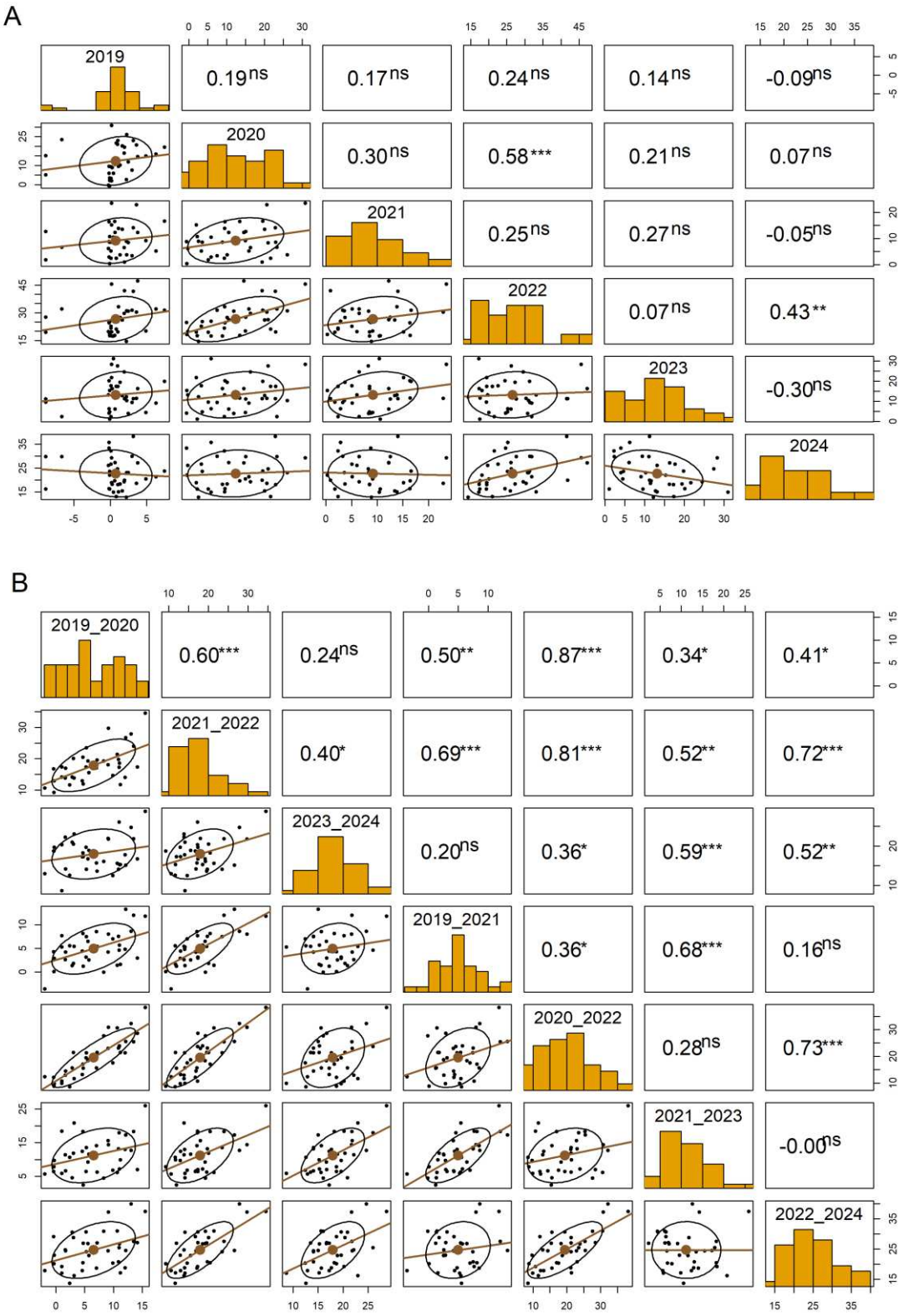

Fig. 5 Correlation between adjusted phenotypic means (eBLUEs): (A) consecutive years (2019–2024); (B) successive biennia (2019_2020, 2021_2022, 2023_2024) and alternating biennia (2019_2021, 2020_2022, 2021_2023, 2022_2024)

*** ($p < 0.001$), ** ($p < 0.01$), * ($p < 0.05$), ^{ns} not significant.

The correlation between mean annual fruit production and annual precipitation was weak and not significant (r = -0.13; p = 0.804; n = 6), indicating the absence of a linear association between these variables during the evaluated period (Fig. 6). Higher mean fruit yields were observed in the even years 2020, 2022, and 2024, which were associated with contrasting precipitation levels, ranging from approximately 1.200 to 1.500 mm, whereas lower yields occurred in 2019, 2021, and 2023, despite intermediate to high rainfall values. This pattern suggests that annual precipitation alone does not explain the observed variation in fruit production.

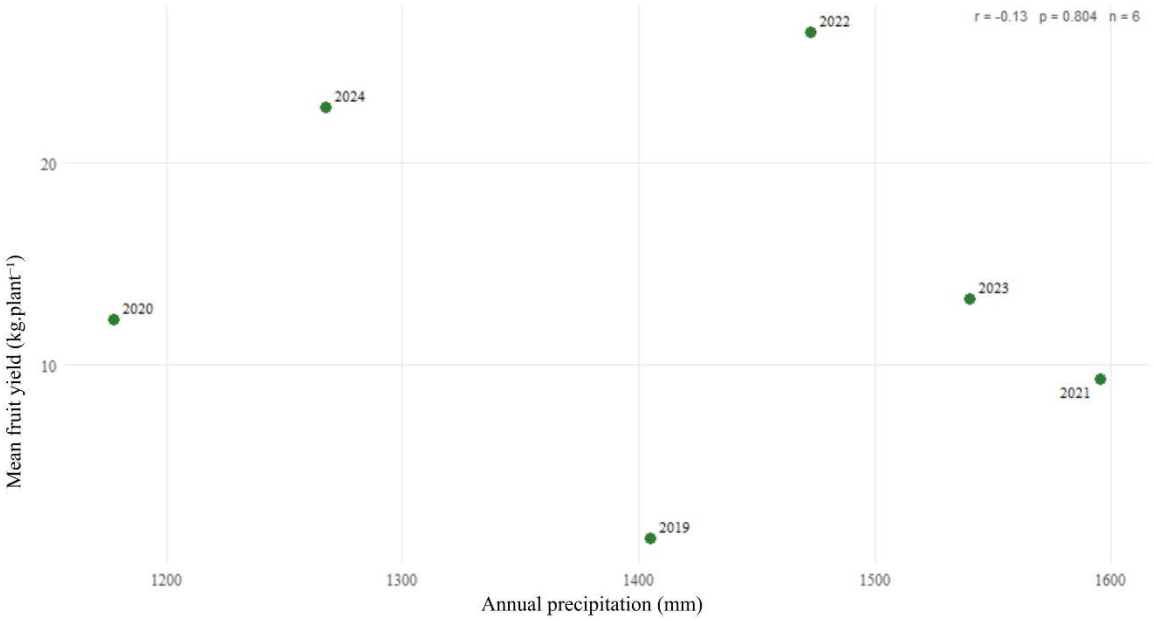

Fig. 6 Correlation between total precipitation (mm) and adjusted mean fruit production (kg plant^{-1}) of macaw palm from 2019 to 2024

Discussion

Genetic variance represents the proportion of phenotypic variation attributed to genetic differences among the evaluated individuals, forming the basis for selection response in breeding programs (Cruz et al. 2014). In the present study, although its magnitude was relatively low compared with the total variance, its presence confirms the existence of exploitable variability among the evaluated progenies. This variability is fundamental for the genetic improvement of the macaw palm, especially considering its condition as a perennial, allogamous, and still poorly domesticated species (Motoike and Hilger 2024; Lanes et al. 2016). The reduced magnitude of genetic variance may be related to the restricted sampling, which included only two regions of Minas Gerais, even though this state constitutes an important center of diversity for the species (Lanes et al. 2015). Another possible explanation is the gregarious habit of macaw palm, which tends to form local deme-type populations composed of individuals with a high degree of relatedness,

thereby reducing the detectable variability (Abreu et al. 2012; Lanes et al. 2015). Nevertheless, the wide range of mean fruit yield (Table 2) indicates the potential for selecting superior plants within the progeny test population, which is of great interest for plant breeders. In the years 2022, 2023, and 2024, some individual plants within progenies reached observed yields exceeding 80 kg, illustrating the potential for identifying outstanding genotypes.

The phenotypic variance expresses the sum of genetic and environmental variances, reflecting the total variability observed for the trait within the population (Falconer and Mackay 1996). In this study, the phenotypic variance was high, indicating the influence of local and seasonal environmental factors, in addition to the genetic variability present among progenies.

The broad-sense heritability, defined as the ratio between genetic variance and phenotypic variance, is a fundamental parameter for predicting the potential response to selection. In our study, heritability was estimated to quantify the genetic control over fruit yield, thereby guiding more effective selection strategies and directing progress in subsequent breeding cycles. This parameter is important because it represents the proportion of observed variability that is heritable, and therefore can be accumulated through selection. Heritability values below 0.15 are considered low, between 0.15 and 0.50 are moderate, and above 0.50 are high (Resende, 2002; Assis e Resende, 2011). The estimate obtained in this study was low, indicating a strong environmental influence on the evaluated trait. In addition, we observed a biennial production pattern, which causes both genetic and environmental factors to influence fruit yield and, consequently, the estimated values of genetic parameters. For this reason, several authors have recommended the use of more robust statistical approaches, such as mixed models via REML/BLUP, to improve the accuracy of genetic estimates. This condition is expected for quantitative traits under polygenic control, such as yield, in which the expression of the genetic component tends to be masked by environmental variability (Falconer and Mackay 1996; Resende 2016).

Low heritability for fruit yield was also reported by Oliveira et al. (2025), consistent with the still poorly domesticated nature of the macaw palm. Although reduced heritability values limit direct genetic gains, selection remains feasible when combined with multi-year evaluations and the use of appropriate statistical models, such as REML/BLUP. These methods allow for the adjustment of environmental effects and enhance the accuracy of genotypic predictions, even under high residual variability (Resende 2016; Viana and Resende 2014).

Additionally, the low fruit production or its complete absence in 68 individuals over six years (Fig. 3) negatively affected the proportion of phenotypic variance attributed to genetic effects. The presence of

these individuals inflated the residual variance, thereby reducing the heritability value and consequently lowering the accuracy of genetic predictions. This pattern also contributed to the high experimental coefficient of variation observed. The experimental coefficient of variation is a relative measure of experimental precision, with values above 30% considered high in field experiments (Pimentel-Gomes 2009). In this study, the elevated coefficient may be associated with the wide genetic variability of the progenies, which originated from native populations, and with the influence of environmental factors across the evaluation years. This condition is expected for perennial species with quantitative traits that are strongly influenced by the environment (Resende 2016).

Field operational factors also contributed to the high values of the coefficient of variation, such as harvest delays in 2022 and 2023, when fruits were collected at an advanced stage of ripening, which may have resulted in losses due to natural abscission, fermentation, or variations in moisture content, thereby compromising experimental uniformity. However, part of this variability can also be attributed to the biological behavior of the species itself, which exhibits wide phenotypic heterogeneity (Manfio et al. 2011). These limitations highlight the importance of rigorous experimental design and the adequate allocation of labor to reduce experimental error and improve the accuracy of genetic estimates.

The significant Progeny:Plot interaction indicated greater segregation within progenies than among them, characterizing high intrafamilial variability. This is consistent with the genetic structure of the evaluated progenies, composed of half-sibs derived from open pollination, which results in marked phenotypic heterogeneity among individuals within the same progeny (Lanes et al. 2016). Moreover, the fact that none of the progenies showed complete absence of production, despite the presence of non-productive individuals (Fig. 3), highlights this internal variability. This pattern represents both an opportunity, by allowing the selection of superior individuals, and a challenge, in obtaining stable and homogeneous genotypes. The absence of a significant effect for the Origin factor supports this interpretation, as it suggests that most of the genetic variability is concentrated within progenies rather than among progenies. This finding is consistent with the results of Mengistu et al. (2016), who identified greater intrapopulational genetic diversity and signs of inbreeding in natural macaw palm populations. This apparent coexistence between high variability and inbreeding can be explained by the fact that individuals resulting from inbred crosses tend to exhibit reduced vigor and are naturally eliminated in the early stages of development, leaving the more heterozygous and adapted genotypes, which helps maintain diversity within populations (Lanes et al. 2016). While those authors based their conclusions on population-level genetic analyses, the present study provides field-based evidence derived from a controlled experimental

design and multi-year evaluation, adding robustness to the inferences and emphasizing the importance of intrapopulational selection.

Given the high genetic variability observed within progenies, intrafamilial selection emerges as an efficient strategy for the macaw palm breeding program. This approach allows the identification of high-performing individuals, optimizing the use of the available genetic variability. The progressive elimination of non-productive plants also favors phenotypic homogeneity and facilitates the formation of more stable elite populations (Motoike and Hilger 2024). It is recommended that this selection be conducted based on multi-year evaluations, prioritizing the choice of promising parents. These parents, selected from intrafamilial evaluation, can be incorporated into recurrent selection cycles, for instance. This method promotes the gradual accumulation of favorable alleles through successive cycles of recombination among superior plants, while maintaining the genetic variability of the population (Borém et al. 2021). Recurrent selection accelerates genetic progress, increases the efficiency of the breeding program, and enables the development of cultivars of perennial allogamous species within a shorter time frame (Motoike and Hilger 2024).

The Progeny:Year interaction highlighted the variation in genotypic performance over time, potentially associated with interannual variation in accumulated precipitation. This cumulative water availability has been considered more determinant for macaw palm fruit production than specific environmental events occurring during particular phases of the species' life cycle (Barbosa 2021). This oscillation reinforces the need for multi-year evaluations to encompass both high- and low-yield years. Therefore, breeding programs should take this instability into account when estimating genetic values and planning crosses, in order to identify consistent genotypes. The use of mixed models (REML/BLUP) was essential to isolate environmental effects, adjust unbalanced data structures, such as differences in the number of productive plants per progeny and asymmetries in the number of observations per year, and to estimate genetic components with greater accuracy. This methodology has been validated in studies with other palm species, such as peach palm (*Bactris gasipaes*), açaí palm (*Euterpe oleracea*), and oil palm (*Elaeis guineensis*) (Farias Neto and Resende 2001; Farias Neto et al. 2008; Cedillo et al. 2018). Furthermore, this approach allowed for the adjustment of environmental effects and precise and accurate selection, consolidating itself as a fundamental tool for the genetic improvement of perennial species (Resende 2002; Viana and Resende 2014). Thus, the adoption of strategies such as intrafamilial selection, combined with multi-year evaluations and robust statistical models, is recommended to optimize genetic progress in macaw palm breeding.

The initial selection in macaw palm breeding should be based on the individual family yield, due to the wide variability observed within progenies and the high number of low-yielding individuals that reduce the population mean (Motoike and Hilger 2024). Given the presence of genetic variability (Table 2), the six-year yield assessment allowed the identification of macaw palm progenies with superior performance and desirable agronomic traits for the breeding program. Among the 36 progenies evaluated, progenies 7, 18, 29, and 30 (Fig. 2) stood out for having the highest mean fruit production based on BLUP values. These progenies were also representative in terms of earliness and/or consistent performance across years (Fig. 4). The use of BLUPs was essential to increase selection accuracy and compensate for experimental imbalances, such as the variable number of productive plants per progeny. This method allowed to isolate environmental effects and predict more reliable genotypic means, even under high residual variability. It is a widely recognized methodology, considered the most suitable for the genetic evaluation of perennial plants (Resende 2002; Viana and Resende 2014).

The earliness observed in progenies 18, 29, and 30, classified as intermediate, represents a strategic trait in macaw palm breeding, as it enables a reduction in the interval between selection cycles and anticipates the economic return (Motoike and Hilger 2024). In contrast, the absence of early production in progeny 7 did not represent a disadvantage, since this progeny exhibited high and stable yields over the years, demonstrating productive consistency, an important attribute in species with biennial alternation. In production systems, the planned combination of genotypes with different maturation times, such as early- and late-maturing types, can benefit growers by staggering the harvest, avoiding concentrated yield peaks, and optimizing the use of processing infrastructure. In addition, it contributes to a more regular supply of raw material and greater production stability throughout the cycle (Viana and Resende 2014; Motoike and Hilger 2024).

The high occurrence of unproductive and dead plants (Fig. 3) throughout the experiment indicated intense genetic segregation within progenies and highlighted the need to advance breeding cycles, as well as to consider artificial strategies, such as the clonal propagation of productive plants. This pattern supports the significance of the Progeny × Plot interaction (Table 2) and underscores the importance of intrafamilial selection as a breeding strategy. The high frequency of unproductive individuals (Fig. 3) also contributed to an increase in residual variance and in the experimental coefficient of variation, particularly during the initial years, which made it more difficult to identify superior progenies in isolated analyses. Nevertheless, our results indicate that the presence of unproductive plants, even after prior selection, tends to persist until the species reaches a more consistent domestication pattern. Therefore, it is up to plant breeders and

researchers to develop and apply statistical methodologies capable of capturing this wide variation in yield, thereby improving the accuracy of superior genotype selection.

Based on the differences observed among individuals within families, intrapopulational selection was carried out, prioritizing the identification of plants with superior yield performance. A total 08 high-yielding individuals were selected among the 04 most productive progenies, considering their multi-year performance (Supplementary Table 1). This strategy allows for the exploitation of the existing genetic potential within progenies and guides future selection cycles. Our goal with this selection is to support ongoing macaw palm breeding programs and to enable the cloning and propagation of elite genotypes, thereby reducing the time required to obtain seedlings and new selected generations. For agronomical purposes, the next breeding cycles derived from this population represent a promising opportunity for genetic gain, aiming toward greater uniformity in fruit production.

The combined strategy of selection among and within progenies is widely recommended for allogamous species such as macaw palm. This type of selection enables the simultaneous exploitation of inter- and intrafamily genetic variability (Bhering et al. 2013). This approach has proven to be effective in tropical palm breeding programs, such as those for peach palm (*B. gasipaes*) (Borges et al. 2017), and shows great potential for application in macaw palm improvement. In the present study, the genetic gains clearly demonstrated this contrast (Table 3). The selection among progenies resulted in an increase of 0.11 kg.plant^{-1} (0.79%), while selection within progenies provided a gain of 4.29 kg.plant^{-1}, raising the mean of the new population by 30.12%. These results indicate that the largest proportion of genetic variance occurs at the intrafamilial level, highlighting the efficiency of individual selection for achieving genetic improvement in half-sib macaw palm populations.

By selecting 04 progenies with two individuals per progeny, the immediate genetic gain and consolidation of superior materials for the next breeding cycle can be maximized. To sustain this progress without loss of genetic variability, the reciprocal recurrent selection (RRS) is recommended, as it allows for intensified recombination between divergent groups while preventing the accumulation of inbreeding (Motoike and Hilger 2024). In natural populations of *A. aculeata* from the Southeastern region of Brazil, full-sib progenies (54.83%) and half-sib progenies (42.39%) predominate, indicating a high rate of biparental crosses and a greater propensity for inbreeding (Lanes et al. 2016). Deleterious effects of inbreeding, such as reduced vigor, fertility, and productivity, have also been documented in *E. guineensis*, *B. gasipaes*, and *Cocos nucifera* (Luyindula et al. 2005; Gunn et al. 2011; Picanço-Rodrigues et al. 2015). In this context, RRS helps maintain genetic variability and promotes yield improvement and greater

genotype stability (Borém et al. 2021).

The identification of a consistent pattern of negative bienniality over the six evaluated years confirms that fruit production in macaw palm follows an alternating cycle between high- and low-yield years. This phenomenon is characterized by intense cyclical oscillations, in which a high-yield year is followed by a low-yield year, and vice versa (Monselise and Goldschmidt 1982). In the present study, this behavior was evidenced by the significant correlations between alternating years (2020–2022 and 2022–2024) and by the high coefficients observed among even-year groupings. According to Shimakura (2011), correlation values above 0.40 can be considered moderate to strong, reinforcing the consistency of these productive associations.

The analysis of the proportion of productive plants over the years (Fig. 3) revealed a progressive increase until reaching greater stability in 2022 and 2024, which coincided with the high-yield years identified in the correlation analyses. This pattern suggests the onset of the population's productive maturity, reinforcing the hypothesis of alternation between high-yield (even) and low-yield (odd) years.

The weak correlations between biennial periods of opposite productive phases, such as 2019_2021–2022_2024, 2020_2022–2021_2023, and 2021_2023–2022_2024, reflect the negative biennial pattern, in which high-yield years tend to be followed by low-yield years, resulting in weaker associations. In pairs that combine high- and low-yield years within the same grouping, such as 2019_2020–2023_2024 and 2023_2024–2019_2021, this reduction is accentuated by the mixing of productive phases and by variations in the mean production level between periods, which contribute to weak or null correlations.

This pattern of alternating productivity is common in perennial species and is associated with the differential allocation of resources between vegetative and reproductive processes. In high-yield years, the greater investment in reproductive structures may reduce the formation and differentiation of inflorescences for the following year, resulting in a subsequent decline in yield (Smith and Samach 2013; Sharma et al. 2019).

Although environmental factors, such as water availability, may affect the production of perennial species, the lack of correlation between annual precipitation and fruit production in this study (Fig. 6) indicates that the observed biennial bearing was not determined by differences in rainfall among years. This finding supports the interpretation that the productive alternation is mainly associated with intrinsic physiological and reproductive mechanisms of the species, such as differential allocation of resources between vegetative growth and reproduction, as widely described for perennial crops exhibiting biennial bearing behavior (Monselise and Goldschmidt, 1982; Sharma et al. 2019).

Biennial bearing has been widely reported in perennial fruit crops such as apple (*Malus domestica*), olive (*Olea europaea*), citrus (*Citrus spp*.), and pear (*Pyrus communis*), and has also been clearly described in palm species such as date palm (*Phoenix dactylifera*), whose expression may be intensified by adverse climatic conditions (El-Mardi, 2005; Monselise and Goldschmidt 1982; Smith and Samach 2013). In the case of the macaw palm, this is, to the best of our knowledge, the first study to demonstrate bienniality based on multi-year progeny test analyses, highlighting the originality and relevance of the results. Recognizing this pattern is strategically important for breeding, as it allows the prioritization of progenies that maintain good performance over time, even under environmental fluctuations. The persistence of the biennial pattern throughout the evaluated period suggests the existence of a genetic basis for the phenomenon, making it potentially heritable and subject to selection. The use of complete production cycles as a basis for evaluation increases selection accuracy and strengthens recommendations for parent selection and management strategies. It is recommended that future studies incorporate physiological covariates and additional climatic data to deepen the understanding of the mechanisms underlying yield alternation and to improve genetic prediction models, thereby favoring the selection of more stable and better-adapted materials.

Conclusions

The productive genetic variability of macaw palm was concentrated within progenies, confirming intrafamilial selection as the main source of genetic gain. It was possible to identify superior materials, including progenies 7, 18, 29, and 30, which stood out for their yield performance, stability, and, in some cases, earliness, forming a strategic basis for future crosses. Intrafamilial selection within these four progenies (eight individuals) increased the mean fruit yield by 30.12%. The negative biennial pattern was confirmed and reinforces the need for multi-year evaluations to ensure accurate selection; moreover, no evidence of a linear association with annual precipitation was detected under the evaluated conditions. The selected progenies are strong candidates for controlled crosses and can significantly contribute to the advancement of macaw palm genetic improvement.

Statements and Declarations

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Author Contributions A.C.M.R. and S.Y.M. were responsible for the conception of the study and the definition of the experimental approach. A.C.M.R., P.A.S., M.G.C.S., and P.V.B. carried out the field activities and were responsible for data acquisition. Data analysis and interpretation were performed by A.C.M.R. and E.G.O.C. A.C.M.R. prepared all figures and tables. The manuscript was drafted by A.C.M.R., E.G.O.C., and K.N.K. K.N.K. revised the reference list, while E.G.O.C. critically evaluated the statistical analyses. Project coordination and funding acquisition were conducted by S.Y.M.

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Conflict of Interest On behalf of all authors, the corresponding author declares that there is no conflict of interest.

Ethical Approval All authors have read and approved the final version of the manuscript.

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Supplementary Material

Supplementary Table 1. Superior macaw palm progeny individuals based on predicted means for fruit yield and precocity classification

Progeny	Mean (Kg.plant $^{-1}$)	Individual	Predicted Mean (Kg.plant $^{-1}$)	Precocity
7	17.98	5	29.24	Late
29	17.35	7	29.01	Early
7	17.98	6	28.57	Late
29	17.35	4	26.73	Early
18	16.06	8	26.64	Early
30	16.75	9	23.81	Early
18	16.06	9	23.02	Late
30	16.75	1	22.01	Late

Supplementary Files

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- SupplementaryTable1.docx