Research Article

Growth parameters of backcross-derived *Elaeis oleifera* (Kunth) Cortés from Taisha - Ecuador and their potential for plant breeding in oil palm[1]

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ABSTRACT

The palm *Elaeis oleifera* from Taisha was first described in 1986, but remains a valuable genetic resource to be evaluated, as it may be important for obtaining high-yielding hybrid genotypes and good-quality oil. This research aimed to determine the attributes of *Elaeis oleifera* (O) Taisha, *E. guineensis* Jacq. (G), their hybrids (O × G) and backcrosses [(O × G) × G = Bc], regarding leaf, stipe and pollen parameters, to expand the potential knowledge toward the obtention of interspecific hybrids that improve the crop competitiveness and sustainability. Contrasts were shown between both genotypes. *E. oleifera* showed a foliar emission of 1.67 leaves per month, when compared to a mean value of 2.37 leaves per month for O × G, Bc and *E. guineensis*. The leaf area of the leaf number 17 was 5.55 m² for *E. oleifera* and 8.50 m² in the other materials. Additionally, *E. oleifera* reached a shorter height and lower number of leaflets for the leaf 17 and stipe growth, in comparison to the other genotypes that showed vegetative hybrid vigor. Regarding pollen germination, *E. oleifera* and *E. guineensis* showed high percentages, whereas the hybrids obtained 14.26 % and Bc 62.47 %. Therefore, the introgression of genes from *E. oleifera* to *E. guineensis* for slow growth and smaller foliar area and from backcrosses for high pollen germination can be useful for selecting and obtaining high-yield improved hybrids and short and compact palms.

KEYWORDS: *Elaeis* spp., interspecific hybrid, pollen germination.

RESUMO

Parâmetros de crescimento de retrocruzamentos derivados de *Elaeis oleifera* (Kunth) Cortés de Taisha - Equador e seu potencial para melhoramento genético em dendê

A palmeira *Elaeis oleifera* de Taisha foi descrita pela primeira vez em 1986, mas continua sendo um valioso recurso genético a ser avaliado, pois pode ser importante para a obtenção de genótipos híbridos de alto rendimento e óleo de boa qualidade. Objetivou-se determinar os atributos de *Elaeis oleifera* (O) Taisha, *E. guineensis* Jacq. (G), seus híbridos (O × G) e retrocruzamentos [(O × G) × G = Bc], quanto aos parâmetros de folha, estipe e pólen, para ampliar o conhecimento potencial na obtenção de híbridos interespecíficos que melhorem a competitividade e sustentabilidade da cultura. Contrastes foram evidenciados entre os dois genótipos. *E. oleifera* apresentou emissão foliar de 1,67 folhas por mês, em comparação a um valor médio de 2,37 folhas por mês para O × G, Bc e *E. guineensis*. A área foliar da folha número 17 foi de 5,55 m² em *E. oleifera* e 8,50 m² nos demais materiais. Adicionalmente, *E. oleifera* atingiu menor altura e menor número de folíolos na folha 17 e crescimento do estipe, em relação aos demais genótipos que apresentaram vigor híbrido vegetativo. Quanto à germinação de pólen, *E. oleifera* e *E. guineensis* apresentaram altas porcentagens, enquanto os híbridos obtiveram 14,26 % e Bc 62,47 %. Portanto, a introgressão de genes de *E. oleifera* para *E. guineensis* para crescimento lento e menor área foliar e de retrocruzamentos para alta germinação de pólen podem ser úteis para selecionar e obter híbridos melhorados de alto rendimento e palmeiras curtas e compactas.

PALAVRAS-CHAVE: *Elaeis* spp., híbrido interespecífico, germinação de pólen.

INTRODUCTION

The African palm *Elaeis guineensis* Jacq. was introduced to Ecuador in 1940, and was established in the tropical experimental station of the National Agricultural Research Institute of Pichilingue, Los Ríos province (Montúfar et al. 2018). In 1986, the botanists Henrik Balslev from the University of Aarhus, Denmark, and Andrew Henderson from the New York Botanical Garden reported the first native population of 10 individuals of the American oil palm *Elaeis oleifera* (Kunth) Cortés in the municipality of Taisha, in the Morona Santiago province of the Ecuadorian Amazon (Montúfar et al. 2018).

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Elaeis guineensis is grown worldwide in tropical areas, and its oil yield is 10 times the average in a year, when compared to other oil crops such as soybean and sunflower, exceeding 4 t ha^{-1} $year^{-1}$ (Kwong et al. 2016). On the other hand, *E. oleifera* shows a low yield, with an oil-to-bunch ratio of 5 %, but the quality and composition of its oil are better than that of *E. guineensis* (Rajanaidu et al. 2000, Barcelos et al. 2015). *Elaeis oleifera* constitutes a strategic genetic resource for the global development of oil palm, as a source of remarkable morphological and physiological traits (Barcelos et al. 2015). It exhibits a slow height growth of 10-15 cm per year, as well as resistance to pests, such as *Rhynchophorus palmarum* and *Strategus aloeus*, and diseases common to *E. guineensis* like bud rot and red ring disease. It also has unique qualitative traits, such as cone-shaped bunches and olive-green immature fruits (Forero-Hernández & Romero-Angulo 2012).

Interspecific hybrids between *E. oleifera* and *E. guineensis*, called O × G, inherit some desirable traits from their parents. The leaves of the O × G hybrids are considerably larger than those of any of their parents, but maintain the arrangement of leaflets in a single plane of *E. oleifera* (Corley & Tinker 2003). The number of leaflets in the O × G hybrid is intermediate between its parent species; however, its leaflets are larger than *E. guineensis*, and its leaf area is greater than that of its parents (Rivera et al. 2013). The characteristics of slow increase in height, separation of leaf bases and parthenocarpy, as well as fruit shape and color, are also conserved in the O × G hybrid. This hybrid has a great potential to improve the crop competitiveness and sustainability, if compared to *E. guineensis*, mainly due to its resistance to bud rot, which is perhaps the greatest threat to the oil palm industry in America (Torres et al. 2004). However, the O × G hybrid requires assisted pollination during the useful life of the crop, what increases production costs (Castiblanco et al. 2013).

The success of natural or assisted pollination in oil palm is essential for oil production, since it determines the number of well-formed fruits. In this process, pollen quality, expressed as viability and germination, is of utmost importance (Criollo & Domínguez 2018). The germination rate in the O × G hybrid (Coarí × La Mé) was 11 %, when compared to *E. guineensis* (La Mé) and *E. oleifera* (Coarí), which showed germination rates of 62 and 82 %, respectively (Camayo-Mosquera et al. 2021).

The *E. oleifera* Taisha palms have been little studied, in relation to other American palms such as Coarí and Sinú, and are an important resource of genetic breeding for hybrid formation with *E. guineensis*, since they present a slow longitudinal growth, long peduncles, flowers free of spathes (Arias et al. 2015), high numbers of fertile fruits in the bunch and a shorter leaf length, which are characteristics that allow optimization of some agricultural practices. They also have a higher content of unsaturated fatty acids than other palms of African origin (Mendoza et al. 2022) and present resistance to pests (*Rhynchophorus palmarum*) and diseases such as the bud rot complex, factors that, together, are of great importance for the selection and obtention of high-yielding genotypes and good oil quality.

This research aimed to determine attributes of *E. oleifera* Taisha (O), *E. guineensis* (G) and their O × G hybrid and backcross [(O × G) × G = Bc], regarding leaf, stipe and pollen parameters, in order to expand the potential knowledge to obtain hybrids with tree architecture that allow improving the crop competitiveness and sustainability.

MATERIAL AND METHODS

The field study was carried out during 2018, in Palmar del Río, located in San José de Guayusa, Francisco de Orellana province, Ecuadorian Amazon (between 0º19'S and 77º06'W, at an altitude of 280 m above the sea level). The conditions at the study site are: average monthly rainfall in the last decade of 266 mm, solar radiation of 11.95 MJ m^{-2} day^{-1}, minimum temperature of 18.6 ºC and maximum of 32.8 ºC, relative humidity of 78 %, and Inceptisol soil of relatively flat topography (Barba & Baquero 2013).

The experiment was structured in already established plantations of native *E. oleifera* palms from the locality of Taisha and the commercial genotypes of *E. guineensis* Yangambi, La Mé and Avros, and their hybrid descendants O × G and Bc, which had differences in the age of the genotypes. The planting densities were commercial ones. Thus, for *E. guineensis*, it was 143 plants ha^{-1} (9 × 9 m), and, in the hybrids, backcrosses and for *E. oleifera* Taisha, 128 plants ha^{-1} (9.5 × 9.5 m). The crop agronomic management practices were commercial ones, without affecting the sensitivity to the effects of the treatments.

The treatments were classified according to their genetic composition of the percentage of

E. guineensis from Taisha, as it follows: *E. oleifera* with 0 %; O × G hybrids with 50 %; backcross (Bc) to *E. guineensis* [(O × G) x G] with 75 %; and *E. guineensis* La Mé and Avros with 100 %. The treatments consisted of the following genotypes: T1: *Elaeis oleifera*, 21 years old, and *virescens* fruits, from the municipality of Taisha, Morona Santiago, located in the Ecuadorian Amazon; T2: *Elaeis guineensis* Avros (Algemene Vereniging van Rubberplanters ter Oostkust van Sumatra), 9 years old, with vigorous growth, high oil yield, *nigrescens* and large fruits, and thick mesocarp; T3: *Elaeis guineensis* La Mé, 7 years old, from the experimental station La Mé - Ivory Coast - L'Institut de Recherches pour les Huiles et Oléagineux, with short height, production of a high number of bunches of smaller size and small *nigrescens* fruits; T4: interspecific hybrid between *E. oleifera* × *E. guineensis* Yangambi (H1), 13 years old; T5: *E. oleifera* × *E. guineensis* La Mé (H2), 13 years old; T6: *E. oleifera* x *E. guineensis* Avros (H3), 14 years old, with *E. oleifera* from Taisha always as the female parent; T7: backcross (Bc) to *E. guineensis* [(O × G) × G], 8 years old, from the cross between an O × G hybrid (*E. oleifera* × *E. guineensis* Avros) as the female parent and *E. guineensis* Avros as the male parent.

The number of evaluated palms was determined according to the number of crosses between different Taisha *oleifera* and the same *guineensis* male parent (O × G hybrids), considering five palms per cross. For the H1 hybrid with three crosses, 15 palms were taken; for the H2 and H3 with six crosses, 30 palms of each hybrid were taken; and from the Bc with two crosses, ten palms were taken, for 85 evaluated palms.

Elaeis oleifera from Taisha has *virescens*-colored fruits in the immature stage and orange color in the ripening stage, while *Elaeis guineensis* has *nigrescens* fruit color in the immature stage and are dark red in the mature stage. According to the classification descriptors of Forero-Hernández & Romero-Angulo (2012) for the coloration of the fruit exocarp, the color of the fruits in immature and mature stages in O × G hybrids and backcrosses was determined.

The visual descriptor suggested by Moreno & Bastidas (2017) was used to determine the arrangement of leaflets in the rachis. The foliar emission rate in the oil palms was measured as the number of leaves emitted per year (Rivera et al. 2013). For its calculation, leaf one, which is the one that has not completely opened yet, was marked. After six months, the new leaves produced from the marked leaf were counted (Corley & Tinker 2003).

The leaf that occupies the position 17 was taken in each palm (Corley & Tinker 2003). This leaf is used as a model for different measurements and comparisons in oil palms due to its nutrient stability and average location within the total number of leaves in a palm tree. The leaf was measured once in each palm to indicate the dimensions of its petiole and rachis. The number of leaflets on the leaf 17 is the total number of leaflets distributed on both sides of the rachis of a leaf. It was determined in each palm by cutting this leaf at the level of the first rudimentary leaflet to count the leaflets on one side and multiplying this value by two (Rivera et al. 2013).

The leaf area of the leaf 17 (LA17) was calculated according to the specific model for palms adapted to the American tropics proposed by Contreras et al. (1999), in line with the equation $Ci = (L * W) * n$, where L and W are the average lengths and widths of the largest 'i' leaflets, respectively, and n is the number of leaflets on the leaf. To estimate the LA17, the adequate number of leaflets to use 'i' depends on the material to be evaluated; therefore, in *E. guineensis* and Bc, six leaflets were evaluated, as opposed to eight in the hybrids and three in the American palms (Contreras et al. 1999). The mathematical model to measure the LA17 was: *E. guineensis* and Bc: LA17 = 0.944 * (C6); *E. oleifera*: LA17 = 0.54 * (C3); O × G hybrids: LA17 = 0.639 * (C8).

The annual growth rate of the stipe was quantified as the ratio between the palm height and its age, in years, in the field (Rivera et al. 2013). The palm height is the distance measured from the ground to the petiolar base of the leaf number 33, calculated as: Growth rate (cm) = stem height/palm age.

For pollen germination, a male inflorescence was identified from each studied palm, isolating it in a permeable paper bag at 7 to 10 days before anthesis. The inflorescences were harvested when they reached the phenological stage 607 or anthesis (Forero-Hernández & Romero-Angulo 2012). They were left to dry in a climate-controlled room at 22 ºC, for 3 hours. Then, the inflorescence was shaken, and the pollen was sifted and dried in filter paper envelopes in an oven at 38 ºC, for 12 hours, until a humidity of 8 % was obtained. At the end of the process, samples were identified and stored at -10 ºC for evaluations over the next 5 days (Chia et al. 2009). The germination test was carried out by seeding approximately 1 mg of pollen on glass slides with agar-agar, which were placed in Petri dishes (Chia et al. 2009). The dishes were incubated in an oven at 37 ºC, for 2 hours. Then, they were removed and three fields per sample were observed using a 40x magnification light microscope. Germinated grains were those that showed a pollen tube length greater than or equal to the diameter of the pollen grain. The germination percentage was calculated using the following formula: Pollen germination (%) = [(number of germinated pollen grains)/(total number of pollen grains)] x 100, where the number of total grains = germinated grains + non-germinated grains.

A completely randomized design was used, with seven palm genotypes (treatments) consisting of five experimental units. The proportion of each trait was determined as percentage for qualitative data. An analysis of variance was performed on quantitative data after the Shapiro-Wilk test to verify the normality of variances and the Levene test for homoscedasticity. The comparison of means was carried out by orthogonal contrasts between the treatment groups, taking the percentage of *E. guineensis* in each group as a comparison criterion. Positive coefficients were given to the highest percentage of *E. guineensis* (0, 50, 75 or 100 %) in all contrasts, since this palm is a benchmark in agribusiness worldwide. Data processing was carried out using the Statistical Analysis Systems software (SAS® 9.2).

RESULTS AND DISCUSSION

One hundred percent of the O × G (T4, T5 and T6) hybrid palms showed a linear arrangement of leaflets or in a single plane, while Bc [(O × G) × G)] (T7) palms showed 100 % intercalated leaflets. The O × G hybrids conserved the arrangement of *E. oleifera* leaflets, which are regularly distributed along the rachis and inserted on a single plane (Arias et al. 2015). However, the Bc showed leaflets in an alternate arrangement like *E. guineensis*, due to its genetic constitution, with an average contribution of 75 % of *E. guineensis* as a recurrent parent. It is also possible that the number of studied palms was not enough to determine segregation.

The color of immature fruits varied between the O × G hybrids (T4, T5 and T6). There were fruits with *virescens* colors and with a combination of two colors changing from *virescens* to *nigrescens*. H1 (T4) (Taisha × Yangambi) did not show *virescens* color, 53 % were *nigrescens* and 47 % were combined. H2 (T5) (Taisha × La Mé) showed three color options: 7 % *virescens*, 23 % *nigrescens* and 70 % a combination of the two colors. H3 (T6) (Taisha × Avros) showed 10 % *virescens*, 13 % *nigrescens* and 77 % a combination of the two colors, while all the immature fruits of the Bc (T7) showed *nigrescens* color. On the other hand, 100 % of the ripe fruits of the three hybrids (T4, T5 and T6) exhibited a red-orange coloration, whereas those of the Bc (T7) were dark red.

As *E. oleifera* Taisha showed the *virescens* trait at the immature phase, all the O × G hybrids were expected to manifest it (Seng et al. 2007, Singh et al. 2014). However, this condition was not met, since some of the hybrids showed both colors going from *virescens* to *nigrescens*, and some others showed *virescens* or *nigrescens* fruits. This result agrees with the observations of Barcelos et al. (2015), who reported that not all F1 hybrids have the *virescens* phenotype. Although the *virescens* trait is dominant over the *nigrescens* trait (Seng et al. 2007, Singh et al. 2014), the number of *virescens* palms found in natural populations is low. In *virescens* fruits, the absence of anthocyanin does not seem to be absolute, since there is evidence of traces of a kind of anthocyanin that may be different from that normally found (Hartley 1988). Additionally, the color of *virescens* fruits is a trait that describes the change of color of immature fruits from green to bright orange upon ripening. The variation in fruit color among *E. oleifera* of different origins shows that the fruits of 90 % of the palms are orange when ripe and that color variations occur during the fruit development (Corley & Tinker 2003).

The variation in the coloration of immature fruits is explained because the changes in coloration are due to the degradation of chlorophyll by the activity of enzymes, such as chlorophyllase and chlorophyll oxidase (Azcón-Bieto & Talón 2013), as a consequence of oxidative processes, as well as by the synthesis, unmasking and predominance of other pigments such as red and yellow (carotenoids), as the fruit acquires the characteristics of maturity (Forero-Hernández & Romero-Angulo 2012). This could be the reason why the fruits of the O × G hybrids exhibit both colors. In addition, although the *virescens* trait is dominant, the number of *virescens* palms found in natural populations is small (Hartley 1988), since, in the *virescen*s fruit, the absence of anthocyanin does not seem to be absolute, there being evidence of traces of an anthocyanin that may be different from that normally found in the ordinary fruit. The *virescens* character in the immature fruit would be of great importance for the harvest of the bunch, since the harvest would not be determined by the number of naturally detached fruits, but by the color change from green to red.

When performing the normality test, the assumption of normality was accepted for all quantitative variables, and the Levene test was non-significant, with a p-value > 0.05, showing homoscedasticity of variances. According to the differences between treatments reported by the analysis of variance, mean comparisons were made with orthogonal contrasts, indicating significant differences between groups of genotypes (Table 1).

Contrasts between treatment groups showed that *E. oleifera* Taisha (T1) palms had a lower foliar emission (1.67 leaves month^{-1}), when compared to the other genotypes that had an average of 2.37 leaves month^{-1}. The hybrids and Bc did not show differences with the *E. guineensis* La Mé and Avros. However, significant differences were observed between the hybrids, with 2.20 leaves month^{-1}, and Bc, with 2.80 leaves month^{-1}. Differences were also obtained between H3, with 2.47 leaves month^{-1}, and H1 and H2, with 2.07 leaves month^{-1}. Significant differences were also found between H1 and H2, while significant differences were not observed between *E. guineensis* La Mé and Avros (Table 1; Figure 1).

Moreno & Romero (2015) observed leaf emissions of 1.4 leaves month^{-1} in *E. oleifer*a from Sinú - Colombia, whereas *E. guineensis* and the interspecific hybrids emitted approximately 2.0-2.5 leaves month^{-1}. These values are similar to those obtained in this study, allowing for elucidating

Table 1. Mean squares of pollen growth and germination per groups of genotypes Taisha (*Elaeis oleifera*), La Mé and Avros (*E. guineensis*), their O × G hybrids and backcross (Bc).

Contrasts[1/]	Foliar emission	Leaf length	Number of leaflets	Leaf 17 area	Stipe growth rate	Pollen germination
Taisha vs. {H1 + H2 + H3 + [(O × G) × G] + La Mé + Avros}	2.11**	0.25	35,152.80**	37.33**	375.39**	8,518.98**
{H1+ H2 + H3 + [(O × G) × G]} vs. [La Mé + Avros]	0.03	5.32**	944.07	42.50**	226.17*	29,440.45**
[H1 + H2 + H3] vs. [(O × G) × G]	1.32**	0.00	1,344.27*	38.82**	67.61*	8,714.80**
[H1 + H2] vs. H3	0.51*	7.04**	2,100.03*	35.82**	35.64	27.61
H1 vs. H2	0.25*	1.09*	122.50	1.82	3.70	306.69
La Mé vs. Avros	0.00	0.66	532.90	0.22	11.28	11.28

[1/] H1 = Taisha × Yangambi; H2 = Taisha × La Mé; H3 = Taisha × Avros; Bc = (O × G) × G = (Taisha × Avros) × Avros. *, ** Significant at p < 0.05 and p < 0.01, respectively.

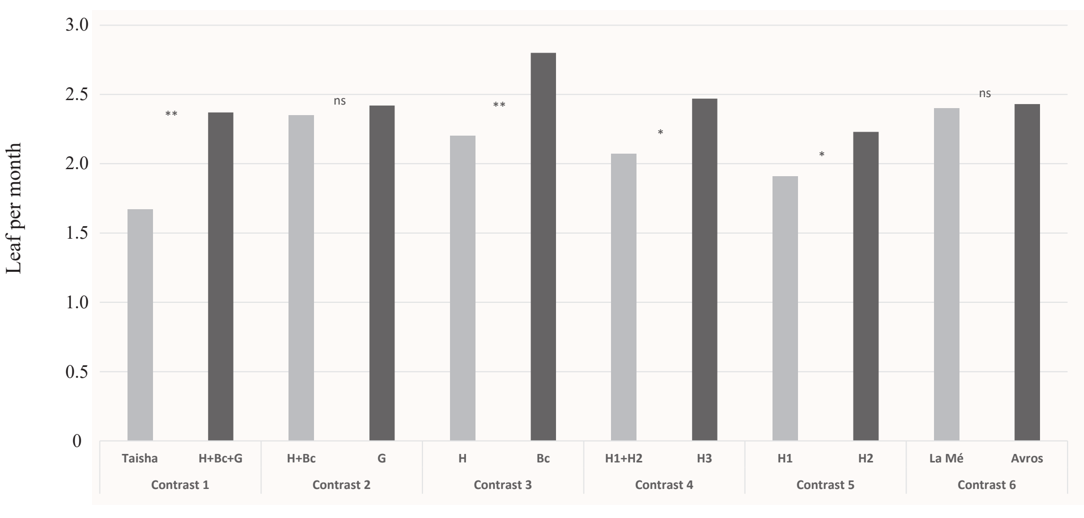

Figure 1. Comparison of means among genotype groups for the variable foliar emission. Taisha: *Elaeis oleifera*; La Mé and Avros: *E. guineenses*; G = La Mé + Avros; H1 = Taisha × Yangambi; H2 = Taisha × La Mé; H3 = Taisha × Avros; H = H1 + H2 + H3; Bc = (O × G) × G = (Taisha × Avros) × Avros. *, ** Significant at p < 0.05 and p < 0.01, respectively; ns: not significant (p > 0.05).

the behavior of each material. A high leaf production may help to determine a high bunch yield in the short term, what represents a great advantage of O × G hybrids, Bc and *E. guineensis* over *E. oleifera* Taisha, which showed a lower foliar emission. La Mé, the youngest population in the study (7 years old), showed an emission of 2.4 leaves month^{-1}, what is considered stable. However, the environment is decisive for foliar emission, since this variable has been observed to be lower for palms of the same genetic origin in regions of low rainfall. This can be explained by the fact that the growth phase requires large amounts of water and mineral elements, and that the oil palm is very sensitive to drought (Cayón 1999).

Significant differences were not observed for the length of the leaf 17 between *E. oleifera* Taisha with 5.07 m and the other groups of hybrids, Bc and *E. guineensis.* However, differences were obtained between the group of hybrids and Bc with a mean of 5.61 m and *E. guineensis* Avros and La Mé with 4.72 m. These two genotypes showed the lowest mean, if compared to the other treatments, and did not show differences between them or between the hybrids and Bc. Regarding the leaf length of the hybrids, differences were observed between H3, with 6.58 m, and H1 and H2. The leaf length was also significantly different between these two hybrids, with H2 and H1 having 5.46 m and 4.8 m, respectively (Figure 2A).

The results for the length of the leaf 17 in this study are similar to those obtained by Rivera et al. (2013), who reported values of 5.9 m for the leaf 17 in 7-year-old hybrids, and between 5.7 and 7.5 m for 10 to 31-year-old *E. oleifera* palms, without significant differences between *E. oleifera* and 7-year-old hybrids. According to Arias et al. (2015), in American palms of different origins, Taisha from Ecuador showed shorter leaves, since some phenotypic traits of *E. oleifera* accessions differ depending on the country of origin.

Regarding the number of leaflets on the leaf 17, the lowest mean value was that of the genotype *E. oleifera* Taisha, with 173.60 leaflets. In contrast, the other groups of hybrids, Bc and *E. guineensis* showed 263.17 leaflets on the leaf 17. Differences were also observed between the hybrids and Bc, with the latter showing 273.40 leaflets. Additionally, among hybrids, high statistical differences were found between H3, with 271.20 leaflets on the leaf 17, and H1 and H2, with 246.10 leaflets on the same leaf. However, no statistical differences were observed between H1 and H2 (Table 1; Figure 2B).

Regarding the O × G hybrids, the number of leaflets in H3 (Taisha × Avros) was higher than in H1 (Taisha × Yangambi) and H2 (Taisha × La Mé), indicating that the variability of the number of leaflets is provided, largely, by the morphology of the male parent used. Considering that the hybrids showed an intermediate value between the parent species, it is important to select *E. guineensis* material to be used in plant breeding. Additionally, this variable is of great importance, since leaflets are the units capable of capturing light and performing photosynthesis, determining the palm's leaf area and, therefore, its yield (Rivera et al. 2013).

Significant differences were observed between *E. oleifera* Taisha, with an LA17 of 5.55 m², and the group of hybrids, Bc and *E. guineensis*, with an LA17 of 8.50 m². Significant differences were also found between the group of hybrids and Bc and *E. guineensis.* Likewise, H3, with an LA17 of 10.72 m², was different from H1 and H2, which obtained a value of 7.44 m². The contrasts between H1 and H2 and *E. guineensis* La Mé and Avros did not show statistically significant differences (Table 1; Figure 2C).

The expression of the leaf area of the leaf 17 in the studied genotypes showed a lower value for the *E. oleifera* and *E. guineensis* parents, and a higher value for the O × G hybrids and Bc. These results match those reported by Bastidas et al. (2007), indicating that O × G hybrids have leaves that are considerably larger than those of any of their parents, given the expression of vegetative hybrid vigor (Barcelos et al. 2015). H3 (Taisha × Avros) showed a leaf area value of 11.04 m^2, in contrast to the mean of H1 and H2, with 7.02 m^2. Therefore, the leaf area of the leaf 17 is influenced by the male parent in O × G hybrids (Barba & Baquero 2013). The fact that the leaf area of the Bc in this study is intermediate between O × G genotypes and *E. guineensis* is due to the loss of hybrid vigor, as the Bc has 75 % of *E. guineensis*. Similar results were obtained by Bastidas et al. (2007), who reported a leaf area of 8.80 m^2 for the Bc from Nolí (*E. oleifera*) palms from the Sinú Valley, in Colombia, when compared to 6.50 m^2 for *E. guineensis*. The oil palms growth depends on the progressive development of their foliar area, which allows them to use solar energy more efficiently for photosynthesis. Consequently, in breeding programs, it is important to select materials by small frond production rate, small height increment and wide leaf area-to-weight ratio (Breure 2017).

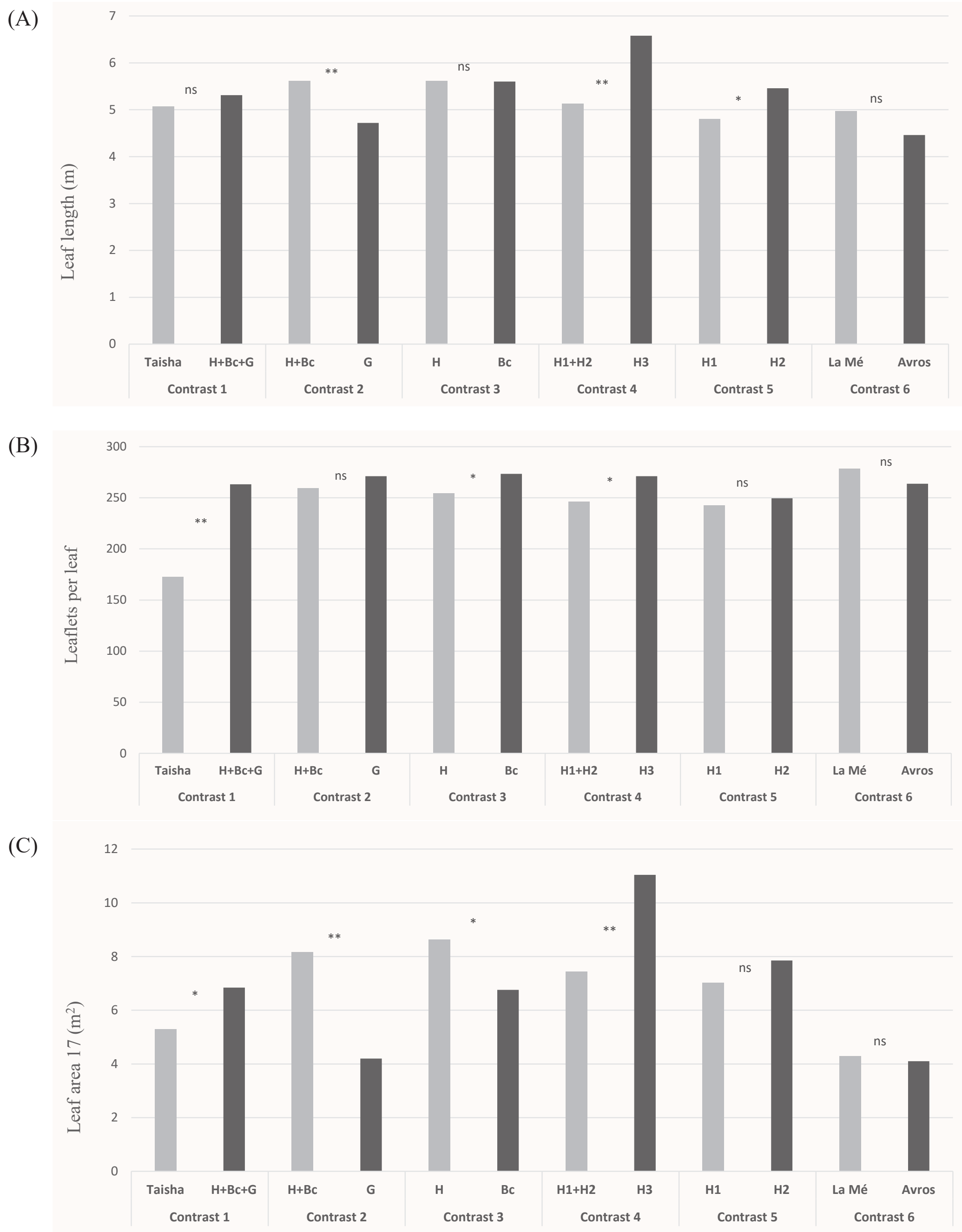

Figure 2. Comparison of means between genotype groups for the variables: A) length of the leaf 17; B) number of leaflets on the leaf 17; C) leaf area of the leaf 17. Taisha: *Elaeis oleifera*; La Mé and Avros: *E. guineenses*; G = La Mé + Avros; H1 = Taisha × Yangambi; H2 = Taisha × La Mé; H3 = Taisha × Avros; H = H1 + H2 + H3; Bc = (O × G) x G = (Taisha × Avros) × Avros. *, ** Significant at $p < 0.05$ and $p < 0.01$, respectively; ns: not significant ($p > 0.05$).

Elaeis oleifera Taisha, with a stipe growth rate of 10.25 cm $year^{-1}$, grows less than the group of hybrids, Bc and *E. guineensis*, which reported a growth of 19.61 cm $year^{-1}$. This slow-growth trait is also reported in the hybrids and Bc, in comparison to *E. guineensis*. Likewise, the hybrids, with a growth of 16.61 cm $year^{-1}$, grow less than the Bc, with 20.85 cm $year^{-1}$. There were no significant differences between the hybrids for the stipe growth rate, as well as between *E. guineensis* genotypes (Table 1; Figure 3).

The oil palm stipe requires four to six years to grow, and is formed once most of the longitudinal growth of the root system has occurred (Cayón 1999). This is one of the main phenotypic characteristics

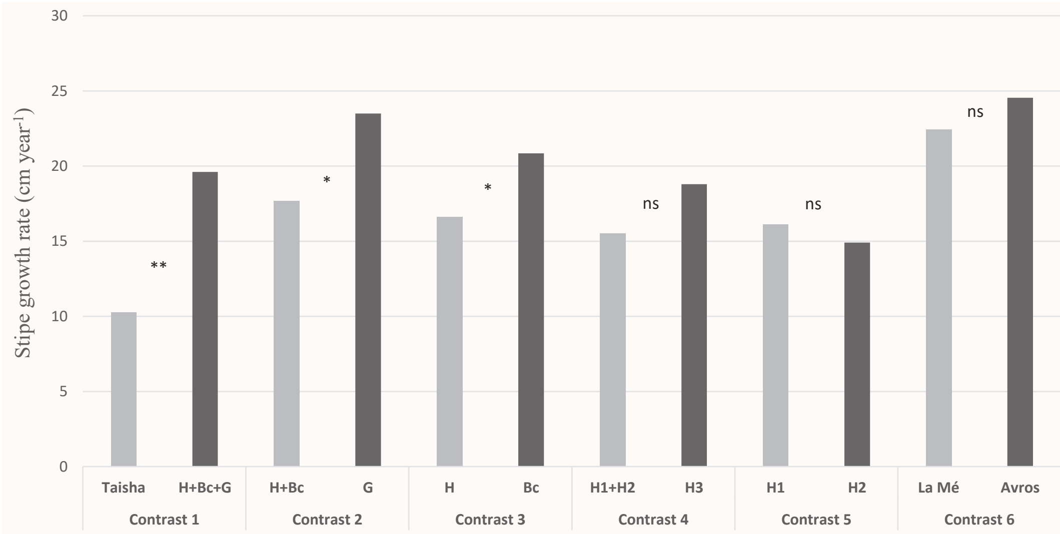

Figure 3. Contrasts of means between genotype groups for the variable stipe growth rate. Taisha: *Elaeis oleifera*; La Mé and Avros: *E. guineenses*; G = La Mé + Avros; H1 = Taisha × Yangambi; H2 = Taisha × La Mé; H3 = Taisha × Avros; H = H1 + H2 + H3; Bc = (O × G) x G = (Taisha × Avros) x Avros. *, ** Significant at $p < 0.05$ and $p < 0.01$, respectively; ns: not significant ($p > 0.05$).

that differentiate *E. oleifera* from *E. guineensis*, as the stipe of *E. oleifera* is shorter, because its annual growth is slower than that of the *E. guineensis* species.

Studies on the growth rate of *E. oleifera* palms from Colombia, Peru and Brazil report values between 9 and 13 cm year^{-1} (Rivera et al. 2013), and 8 cm year^{-1} for a species from Brazil (Peláez et al. 2010). In other words, the growth of the stipe for *E. oleifera* Taisha from Morona, Ecuador, reported in this study, is similar to other American palms. Additionally, the growth rate of other O × G hybrids from La Mé parents reported values of 12 cm year^{-1} (Rivera et al. 2013) and 11 cm year^{-1} (Peláez et al. 2010), while the hybrid H3 (Taisha × Avros) showed a higher growth rate than H1 (Taisha × Yangambi) and H2 (Taisha × La Mé). This indicates the direct influence of the male parent, since the hybrids from La Mé and Yangambi (which is a descendant of the Avros line improved to reduce growth) exhibited a lower annual growth rate in this study. Additionally, 20 % of the 30-year-old palms cannot be harvested due to the height at which bunches are located. The fast increase in height reduces the economic life of the crop, since harvest is only possible up to 15 m in height (Ho & Chiang 1999).

Significant differences were observed between *E. oleifera* Taisha with pollen germination of 93.05 % and the group of hybrids, Bc and *E. guineensis*, which showed 48.46 %. Likewise, *E. guineensis* La Mé and Avros reached 92.77 %, when compared to the hybrids and Bc, which reached only 26.31 %. The Bc, with 62.47 %, was statistically higher and different from the hybrids, which achieved 14.26 %. No significant differences were observed between the hybrids, with a value of less than 20.76 %, or between *E. guineensis* Avros and La Mé (Figure 4).

Determining pollen viability in oil palms is of great importance, with pollination being fundamental for the production of oil, since it determines the number of fruits formed in the bunches. Pollen quality, expressed as germination, allows evaluating the ability of pollen to produce a pollen tube as a measure of its viability (Davarynejad et al. 2008). Pollen viability of 98.38 % for *E. guineensis* and 35.98, 16.94 and 17.10 % for the hybrids Coari x La Mé, Amazon and Unipalma, respectively, were reported by Criollo & Dominguez (2018).

The O × G hybrid shows very low pollen viability values of less than 6 %, in contrast to the *E. oleifera* species, with values of 20-60 %, and *E. guineensis*, with viability greater than 70 % (Alvarado et al. 2000). Not all pollen grains were classified as germinated and viable: *E. oleifera* Coari showed a viability of 88 % and germination of 82 %; *E. guineensis* La Mé obtained viability of 85 % and germination of 62 %; and the O × G of these palms reached viability of 16 % and germination of 11 %

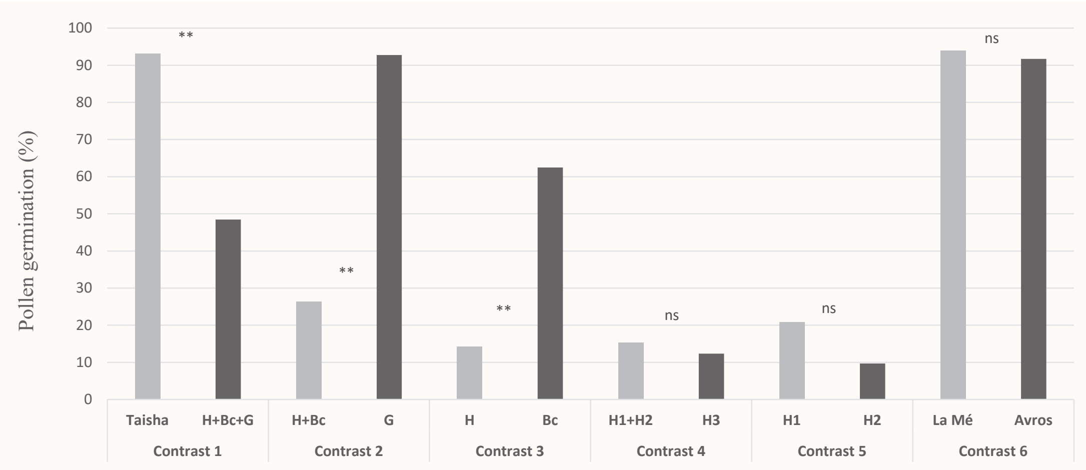

Figure 4. Mean pollen germination values for Taisha (*Elaeis oleifera*), La Mé and Avros (*E. guineensis*), O × G hybrids and backcross (Bc). G = La Mé + Avros; H1 = Taisha × Yangambi; H2 = Taisha × La Mé; H3 = Taisha × Avros; H = H1 + H2 + H3; Bc = (O × G) × G = (Taisha × Avros) × Avros. ** Significant at $p < 0.01$; ns: not significant ($p > 0.05$).

(Camayo-Mosquera et al. 2021). Although this study was not based on viability, but on germination, the obtained results are not far from those reported for the first variable. High germination values were obtained in *E. guineensis* and *E. oleifera* Taisha, whereas the O × G hybrids showed an average germination of 14.26 %, which is close to that reported by Camayo-Mosquera et al. (2021). The Bc showed a germination rate of 62.47 %, which is intermediate between O × G hybrids and *E. guineensis*. The low pollen germination may be because related species develop reproductive barriers to prevent hybridization and maintain their integrity (Xie et al. 2017). It is necessary to clarify that the viability test does not guarantee that the pollen meets the requirements for fertilization, since a pollen grain may be viable, but may also show germination problems (Camayo-Mosquera et al. 2021).

CONCLUSIONS

1. Not all clusters from Taisha O × G hybrids have *virescens* fruits, even when this character is described as dominant. Additionally, leaf morphology is a dominant trait, and the intermediate growth of the hybrid line indicates a useful source of genetic introgression for *Elaeis oleifera* Taisha. However, in Taisha's O × G hybrids, the pollen germination remains low, even though the germination is slightly increased with backcrossing, a factor that may be important to improve the crop yield;
2. *Elaeis oleifera* Taisha has a smaller leaf area and slow stipe growth, when compared to the populations of O × G hybrids, Bc and *E. guineensis*. This indicates that a good selection of the growth and development measurements of Taisha as a parent contributes to the formation of hybrids or backcrosses of compact architecture. These traits are desirable for a breeding program that may favor the agricultural work intensity and improve crop mechanization.

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