Genetic gains for obtaining improved progenies of oil palm in Colombia

**Andrés Tupaz-Vera · Iván Ayala-Diaz ·
Carlos Felipe Barrera ·
Hernán Mauricio Romero**

Abstract The success of breeding programs depends on the available genetic variability and the adequate selection of parents to produce seeds that generate added value to the developed cultivars that solve limiting problems of the crops. The determination of genetic gain is a powerful tool to advance the selection of outstanding progenitors that are subsequently used to obtain improved cultivars for traits of interest. With the main objective of calculating the genetic gain in different cycles, this research evaluated the yield, vegetative parameters, and oil production components in two oil palm populations identified as C0-Monterrey and C1-Vizcaina. The analysis was carried out using the analysis of variance. Genetic variation and heritability coefficients for all the evaluated traits were also calculated to obtain the components of phenotypic, genotypic, and environmental variation. Genetic gains (Δg) were more representative in the yield traits of fresh fruit bunches, with 19%, for the number of bunches per plant, with a Δg of 18.7%, and for the oil to bunch with a Δg of 6%. Low environmental influences were observed in the phenotypic variation for the different traits evaluated. Finally, high heritability values were observed for genetic traits such as height increase, with 93%, and average bunch weight, with 85%. The development of new progenies using elite *dura*-type female parents derived from these evaluated populations, with excellent yields of fresh fruit, bunch components, and slow growth, will be the future of oil palm cultivation. In the meantime, progeny trials must focus on improving the ability to select outstanding parents for the best DxP progenies.

Keywords Genetic traits · Heritability · Genetic variance · Response to selection

A. Tupaz-Vera · I. Ayala-Diaz · H. M. Romero (✉)
Oil Palm Biology and Breeding Research Program,
Colombian Oil Palm Research Center - Cenipalma,
Bogotá, Colombia
e-mail: hromero@cenipalma.org

C. F. Barrera
Department of Agronomy, Universidad Nacional de
Colombia, Medellín, Colombia

H. M. Romero
Department of Biology, Universidad Nacional de
Colombia, Bogotá, Colombia

Introduction

The oil palm (*Elaeis guineensis* Jacq.) is the crop with the highest production in metric tons of oil among all oilseed crops, representing more than 36% of the total production of edible oils (USDA 2020). It is the species with the highest oil extraction per unit area, producing up to 10 t ha^{-1} under optimal agronomic management conditions and highly productive improved cultivars (Romero et al. 2021). However, oil palm is the second largest oilseed cropland in the world after soy, with more than

23 million hectares cultivated worldwide (Annual 2021). Colombia ranks fourth worldwide, behind Indonesia, Malaysia, and Thailand, and first in Latin America in palm oil production. In Colombia, oil palm is one of the most developed agricultural sectors in national agriculture; currently, 595,722 hectares are planted (Sispa 2021).

The oil palm is a diploid, monoecious, and cross-pollinated species. Although oil palm has high variability and allelic diversity in the available genetic resource, most commercial cultivars have a narrow genetic base. Furthermore, their origin is limited to a small number of palms. Thus, the female progenitor Deli *dura* comes from the four palms of the Bogor Botanical Garden planted in 1848. The pollen source of a male *pisifera* parent descends from a limited number of plants (Al-Khayri et al. 2019). In the breeding of oil palm, there are three types of palms by their fruit form, *dura*, *pisifera,* and *tenera,* which differ by the thickness of the endocarp (Beirnaert and Vanderweyen 1941; Reyes et al. 2015; Singh et al. 2013).

For the commercial production of seeds, *dura* palms or A group population, which are always used as a female parent, are crossed with a *pisifera* palm as a male parent or B group population, resulting in *tenera* or DxP-type seeds, which have higher oil contents due to the reduced thickness of their mesocarp (Rajanaidu 2016). In palm breeding, the *dura* and *pisifera* populations are worked independently (Al-Khayri et al. 2019). Recurrent reciprocal selection (RRS) allows the breeding of the two populations, A and B, to occur independently and in each trait of interest. Later, the two populations are combined, where progeny tests are established to evaluate the breeding value of the parents in combination with the other heterotic group; based on those results, the evaluation and selection in a new breeding cycle are made. Thus, a high degree of genetic variation is maintained within the populations.

On the other hand, the strategy of making family and individual selections using the family and individual palm selection (FIPS) method in oil palm allows the identification of *dura* palms as female parents to produce commercial *tenera* (*dura* × *pisifera*) cultivars. Here the selection of candidate parents can be based on the behavior of the progenies or at the level of individual palms. Individual selection emphasizes the evaluation of traits with high heritability.

Meanwhile, traits with lower heritability are evaluated through the behavior of family or progeny tests (Ngando-Ebongue et al. 2012).

The success of breeding programs depends on genetic variability; in practice, the utility of genetic gain through selection allows for better breeding criteria for selecting genetically superior individuals (Gomes Junior et al. 2021). In evaluating, selecting, and developing individuals who show genetic superiority in agronomic traits, estimating genetic gains becomes essential for the industry's success for different crops (Pavlotzky and Murillo 2014; Rocha et al. 2021).

Genetic gain is a universal concept applied in quantitative genetics in plant breeding, which is used to evaluate the progress over time of a breeding program (Batte et al. 2021). According to Rutkoski (2019), genetic gain or response to selection refers to the change made or expected in the genetic value of a population between breeding cycles. In this sense, when a change is made between generations through natural or artificial selection, a selection differential is established that integrates the association of traits and biological efficacy (fitness) (Falconer and Mackay 1996). Genetic gain is also known as the *breeder equation* that predicts the evolutionary change of a trait. When performing an artificial selection for a given trait, populations diverge over time according to the number of generations of selection (Kelly 2011).

In a perennial species such as oil palm, the estimation of genetic gain per unit of time (productive life cycle or the time to carry out a breeding cycle) can identify the efficiency of the methods used in a breeding program (Lustri et al. 2021). The available reports of the values of genetic gains (Δg) for oil palm are scarce.

Taking into account the importance of oil palm for agribusiness, the description of genetic advancement within its improved populations, and the scarcity of specific reports of the Δg between breeding cycles in traits not only of production but also of variables related to bunch components, oil production and vegetative traits, this research aimed to report the Δg and genetic parameters related to the traits of interest in oil palm using a *dura*-type population for two breeding cycles. This population was created to generate *dwarf* progenies due to its slow stem growth in combination with the high production of bunches and oil content. The population is derived from Deli

dura palm genotypes (Bastidas 2003) that were introgressed with germplasm from Africa (Tupaz-Vera et al. 2021).

Materials and methods

Plant material

This study was conducted on two oil palm populations. Although the populations evaluated correspond to successive cycles of selection that began in Southeast Asia and passed through Central America and Colombia, there was no phenotypic information on previous cycles of recurrent selection. Therefore, the initial population of this study corresponds to C0-Monterrey, a *dura*-IFA type population planted in the municipality of Puerto Wilches (Santander-Colombia) in the Monterrey plantation located at 65 m.a.s.l., with an average temperature of 28 °C and average annual accumulated rainfall of 2869 mm. The palms were planted in the '60 s.

The second population, C1-Vizcaina derived from C0-Monterrey, is a trial composed of dwarf *dura* progeny planted in 2005 in the Palmar de La Vizcaina Experimental Field (CEPV) of the Colombian Oil Palm Research Center (CENIPALMA), located in the municipality of Barrancabermeja (Santander-Colombia), at an elevation of 102 m.a.s.l., an average temperature of 29.3 °C and an average annual rainfall of 3472 mm. For C0-Monterrey, measurements were made between 1996 and 2002, and for C1-Vizcaina, measurements were taken between 2008 and 2020. For the C1-Vizcaina population, the management and agronomic practices were performed under the management standards of the CEPV, which included balanced fertilization in kilograms per plant of N (1.23), P (0.50), K (2.51), Mg (0.34), S (0.21) and B (0.05) according to the foliar and soils analyses.

For the C0-Monterrey population, 127 plants were evaluated and selected for presenting a promising phenotype. The palms had good bunch crowns, totally green palms without deficiencies or pest attacks, and, in particular, they were dwarf palms. The selected palms came from three commercial plots of *dura*-IFA cultivars, which occupied 63 ha (approximately 9000 palms). Out of the 127 palms, 13 were chosen for different genetic traits. From this selection, seven crosses were made that gave rise to the second improved

population C1-Vizcaina *dura* palms. This population was developed to introgress yield traits (fresh fruit bunches and oil contents) with traits of dwarf palms (reduced stem growth). The C1-Vizcaina population was evaluated for 12 years in the CEPV under a randomized complete block design (RCBD), with three blocks and 12 plants for each experimental unit.

Phenotyping of yield and vegetative traits and bunch components

For the two populations C0-Monterrey and C1-Vizcaina, yield phenotyping measurements such as FFB: fresh fruit bunches (kg palm^{-1}), BNO: number of bunches (palm bunches^{-1}), ABW: average bunch weight (kg) were made. In C1-Vizcaina, yield records were taken in each palm of the experimental unit during two or three production cycles every given month:

The values of these traits were obtained as follows (Corley and Tinker 2016):

$$FFB \text{ (kg palm}^{-1} \text{ year}^{-1}) = \sum_{i-1}^{n} BWTi$$

$$BNO \text{ (bunches palm}^{-1} \text{ year}^{-1}) = \sum_{i-1}^{n} BNOi$$

$$ABW \text{ (kg)} = \frac{FFB}{BNO}$$

where n represents the number of cycles of production expressed in kg.

In the case of the C1-Vizcaina population, five growth measurements were performed on the vegetative traits between 2009 and 2020. Using the methodology proposed by Corley and Breure (1981), the traits of rachis length (RL), leaflet width (LW), and the number of leaflets (LN) were calculated. Palm height (HT) was measured from the ground level to the base of the leaf 41 according to the phyllotaxis. HT was calculated using the formula:

$$HT \text{ per year (Height increase/year)} = (height \text{ in year } t)/(t-2),$$

where t is the age of the palm expressed in years, from the date of planting to the moment of a given measurement (Corley and Tinker 2016).

The bunch components and oil content were estimated according to Corley and Tinker (2016) and modified by Prada and Romero (2012). Two to three bunches of each palm were sampled between 2008 and 2020, with a general average of 24 bunches per progeny for each evaluation period. The bunch components that were calculated were mean fruit weight (MFW), oil to bunch (OB), normal fruits to bunch (NFB), mesocarp to fruit (MF), kernel to fruit (KF), and shell to fruit (SF).

Statistical analysis

The genetic parameters were calculated in the C1-Vizcaina population. The data collected were subjected to an analysis of variance (ANOVA) under a generalized linear model, which is presented below:

$$Y_{ik} = \mu + G_i + B_k + \varepsilon_{ik}$$

where Y_{ik}: is the phenotype of the ith palm in the progeny and the kth block; μ: is the general average; G_i: is the effect of the ith progeny; B_k: is the effect of the kth block; ε_{ik}: is the effect of the experimental error.

The variance components were calculated, and broad sense heritability and coefficient of genetic variation for each trait were estimated (Falconer and Mackay 1996).

Heritability in the broad sense

$$H_B^2 = \frac{\sigma^2 g}{\sigma^2 f}$$

where $\sigma^2 g$: genotypic variance; $\sigma^2 f$: phenotypic variance.

Coefficient of genetic variation

$$CV_g = \frac{\sqrt{\sigma^2 g}}{\mu} \times 100$$

where $\sigma^2 g$: square root of the genotypic variance; μ: general mean of the population.

Genetic gains (Δg) were calculated according to the formula by Cruz and Carneiro (2003) for the yield, vegetative measures, and oil production components traits.

$$\Delta g = H_B^2 DS = H_B^2 (X_S - X_0)$$

where DS: selection differential between X_s and X_0; X_S: mean of the selected palms; X_0: mean of the palms of the original population; H_B^2: broad sense heritability.

For the case of this research, the percentage of selected palms (Xs) corresponded to 10% of the total population.

GENES software and *ggplot2*, *Agricolae*, and *Performance* packages of the statistical software R Studio version 4.1.0 were used to perform the analysis of variance (ANOVA), the calculation of the genetic parameters, and the genetic gains.

Results

Estimation of genetic parameters

The slow-growing *dura* population or dwarf progeny of Cenipalma was generated from a drastic selection focused on palms with a low stem growth rate. The initial population was developed from 9000 *dura* IFA palms. 1.4% of the palms were considered dwarf and selected for a total of 127 plants. The palms were healthy, with a good number of bunches at the time of selection. This population of palms was considered the C0 population of Monterrey, and from the evaluation of different morpho-agronomic traits of the C0 population, the 13 best palms gave rise to the C1-Vizcaina population. Figure 1 compares the traits of interest that presented the highest coefficient of genetic variation (CVg), comparing the original population (X_0) and the mean of the selected palms (Xs). In most of the traits of interest, the values of the palms that were selected (Xs) were higher than the original population (X_0). For the FFB trait, the selected individuals (Xs) had an average of 177 kg palm^{-1} year^{-1} compared to the population mean X_0 with 135 kg palm^{-1} year^{-1}. For the trait of BNO, the selected individuals had an average value of 7.6; for the original population, the average value was 6.1 BNO. For the KF trait, the average value of population X_0 was 11.0, and for X_S, the average value was 9.1.

In contrast, for the height (HT) increase trait, there was no significant variation between the populations X_0 and X_S. However, the values for the height increase in the stem were significantly reduced in the two populations, facilitating the
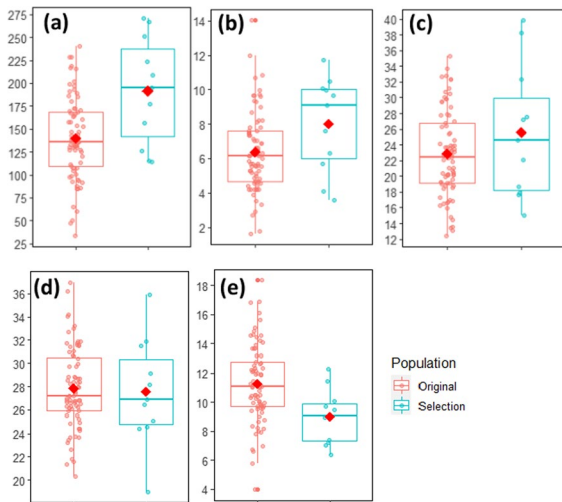
Fig. 1 Box plot for the main morpho-agronomic traits comparing the original population evaluated (127 palms), C0-Monterrey (red), and the 13 palms selected from C0 (blue) to generate RRS cycle 1 in the C1-Vizcaina population. **a** FFB: fresh fruit bunches (kg palm^{-1}), **b** BNO: number of bunches (bunches palm^{-1}), **c** ABW: average bunch weight (kg), **d** HT: height increase (m year^{-1}), and **e** KF: kernel to fruit (%). The red diamond represents the general average in the box plots, and the horizontal line represents the median

selection and the expected response to selection. The selection pressure on this trait had been previously performed to create the original population X$_0$.

From the phenotypic data collected between 2009 and 2020, the genetic parameters of 13 morpho-agronomic traits of interest were estimated (Table 1). The variance decomposition for the C1 population showed a strong influence of the genetic component and a low influence of the environmental component. HT was the trait least influenced by the environment, with a σ^{2}g of 94%, followed by the KF, with a σ^{2}g of 87.1%, and OB, with a σ^{2}g of 80%. On the other hand, lower values were presented for MFW, with a σ^{2}g of 53.8%, for SF, with a σ^{2}g of 58.8%, and 62.3% for FFB. The broad sense heritabilities ranged between 0.53 and 0.93, the latter value for the genetic trait of HT. HT showed the highest coefficient of genetic variation with a value of 15.61%, followed by the KF with 10.19%. BNO, ABW, and FFB showed 8.94%, 7.10%, and 7.10%, respectively.

Table 1 Estimation of genetic parameters for 13 traits, yield, vegetative measures, and oil production components for the C1 population improved in oil palm

Symbol	FFB	BNO	ABW	RL	LW	LN	HT	MFW	OB	NFB	MF	KF	SF
σ^{2}f	257.96	1.59	1.67	0.04	0.20	27.38	0.0040	0.64	1.11	8.78	6.36	2.63	1.81
σ^{2}g	160.69 (62.3)	1.21 (76.4)	1.43 (85.5)	0.03 (82.6)	0.17 (86.8)	21.81 (79.7)	0.0030 (94.0)	0.34 (53.8)	0.89 (80.0)	6.96 (79.3)	4.75 (74.8)	2.29 (87.1)	1.06 (58.8)
σ^{2}e	97.26 (37.7)	0.37 (23.6)	0.24 (14.5)	0.01 (17.4)	0.02 (13.2)	5.56 (20.3)	0.0002 (6.0)	0.29 (46.2)	0.22 (20.0)	1.81 (20.7)	1.60 (25.2)	0.34 (12.9)	0.74 (41.2)
H^2_B	0.62	0.76	0.85	0.82	0.86	0.79	0.93	0.53	0.79	0.79	0.74	0.87	0.58
CVg (%)	7.10	8.94	7.10	4.13	5.22	3.03	15.61	5.95	5.18	4.05	3.95	10.19	3.44
CVg/CVe	0.74	0.87	0.92	1.25	1.47	1.14	2.26	0.62	1.15	1.12	0.99	1.50	0.68
MS	773.89 ns	4.78*	5.02**	0.12**	0.61**	82.14**	0.01**	1.93 ns	3.35**	26.34**	19.08*	7.91**	5.45 ns

σ^{2}f: phenotypic variance, σ^{2}g: genotypic variance, σ^{2}e: environmental variance, H^2_B: heritability in the broad sense, CVg (%): coefficient of genetic variation, CVg/CVe: ratio between coefficient of genetic variation and coefficient of variation of experimental error, MS: mean squares, FFB: Fresh fruit bunches (kg palm^{-1}), BNO: Number of bunches (palm bunches^{-1}), ABW: Average bunch weight (kg), RL: Rachis length (cm), LW: Leaflet width (cm), LN: Number of leaflets, HT: Height increase (m year^{-1}), MFW: Mean fruit weight (gr), OB: Oil to bunch (%), NFB: Normal fruits to bunch (%), MF: Mesocarp to bunch (%), KF: Kernel to fruit (%), and SF: Shell to fruit (%). *p < 0.05; **p < 0.01; not significant (ns) p > 0.05, the percentage of genotypic and environmental variance is shown in parentheses

Genetic gain

The calculated Δg was determined considering the H^2_B and the selection differential of the two breeding cycles studied. However, we expected that H^2 in C0 population is similar to C1, despite the de absence of statistical design and different agronomic management in C0; thus Δg presented in this document is approximate. The calculations were performed for 13 morpho-agronomic traits of greater relevance in oil palm cultivation. Between the two evaluated populations, X_0 (C0-Monterrey) and X_1 (C1-Vizcaina), the Δg for FFB was 18.87%, equivalent to an annual increase of 1.26% in yield increase. For the BNO trait, Δg was 18.69%, corresponding to a 1.25% gain per year, and finally, for the ABW trait, Δg was 5.94%, equivalent to an annual gain of 0.40% (Table 2).

For the bunch components, MF had a Δg of 1.11%; KF had a Δg −15.03% and 5.61% for OB from C0 to C1 cycles. The Δg for SF presented a negative value of −3.84%, which is explained by the fact that the shell to fruit was reduced in the improved C1-Vizcaina progeny compared to the C0-Monterrey population. For the vegetative traits of the crop, the genetic gain (Δg) in the increase in height (HT), rachis length (RL), and the number of leaflets (LN) showed negative values of −3.44%, −3.35%, and −1.16%, respectively.

Performance of the best individuals within each progeny

The family and individual palm selection (FIPS) methodology was used in selecting the best individuals who will be part of the female parents for the commercial production of DxP seeds and which will be crossed for a new cycle of *dura* parent breeding. However, the selection of the outstanding palms is not enough because have to be evaluated in progeny tests (DxP or DxT), where combining ability (general or specific) between group A and B is tested, and best combination addressed the parent selection for commercial production.

As a truncation point or threshold of selection for FFB, a minimum value of 200 kg palm^{-1} was set. The P3 progeny presented the highest average at the family level, with a value of 209 kg palm^{-1} of FFB. This family had individual palms with values higher than the selection value, with yields between 258 kg palm^{-1} and 341 kg palm^{-1} (Fig. 2a). However, in oil palm, breeders are more focused in bunch number (BNO) and average bunch weight (ABW) to achieve the minimum FFB selection threshold (>200 kg palm per year), the progenies evaluated in C1 presented two features; progenies with a high number of bunches, but with low ABW, such as P5 and P3, had averages of 16.2 and 15.7 bunches palm^{-1}, respectively. In these progenies, there were individuals with more than 18 and up to 24 bunches palm^{-1}. In contrast, the progenies P1 and P6 had the highest averages of

Table 2 Genetic gain for different genetic traits in two oil palm breeding cycles

Symbol	FFB	BNO	ABW	RL	LW	LN	HT	MFW	OB	NFB	MF	KF	SF
X_0	135.70	6.10	22.90	4.90	8.30	170.00	0.27	8.60	18.30	68.50	53.20	11.00	31.70
X_s	177.00	7.60	24.50	4.70	8.40	167.50	0.26	8.50	19.60	69.00	54.00	9.10	33.80
X_1	181.10	13.80	15.30	4.46	8.28	153.12	0.38	9.50	19.25	65.13	55.63	14.87	29.50
DS	41.30	1.50	1.60	-0.20	0.10	-2.50	-0.01	-0.10	1.30	0,50	0.80	-1.90	2.10
Δg	25.61	1.14	1.36	-0.16	0.09	-1.98	-0.01	-0.05	1.03	0.40	0.59	-1.65	1.22
Δg year $^{-1}$	1.26	1.25	0.40	-0.22	0.07	-0.08	-0.23	-0.04	0.37	0.04	0.07	-1.00	0.26
Δg (%)	18.87	18.69	5.94	-3.35	1.04	-1.16	-3.44	-0.62	5.61	0.58	1.11	-15.03	-3.84
Δg year^{-1} (%)	1.71	0.08	0.09	-0.01	0.01	-0.13	0.001	0.003	0.07	0.03	0.04	-0.11	0.08

X_0: mean of the initial population, X_s: mean of the selected plants, X_1: improved population mean, DS: selection differential, Δg: genetic gain, Δg (%): percentage genetic gain, Δg year^{-1}: expected genetic progress, Δg year^{-1} (%): expected percentage genetic progress, FFB: fresh fruit bunches (kg palm^{-1} year^{-1}), BNO: number of bunches (palm bunches^{-1}), ABW: average bunch weight (kg), RL: length of the rachis (cm), LW: leaflet width (cm), LN: number of leaflets, HT: height increase (m year^{-1}), MFW: mean fruit weight (gr), OB: oil to bunch (%), NFB: normal fruits to bunch (%), MF: mesocarp to fruit (%), KF: kernel to fruit (%) and SF: Shell to fruit (%)
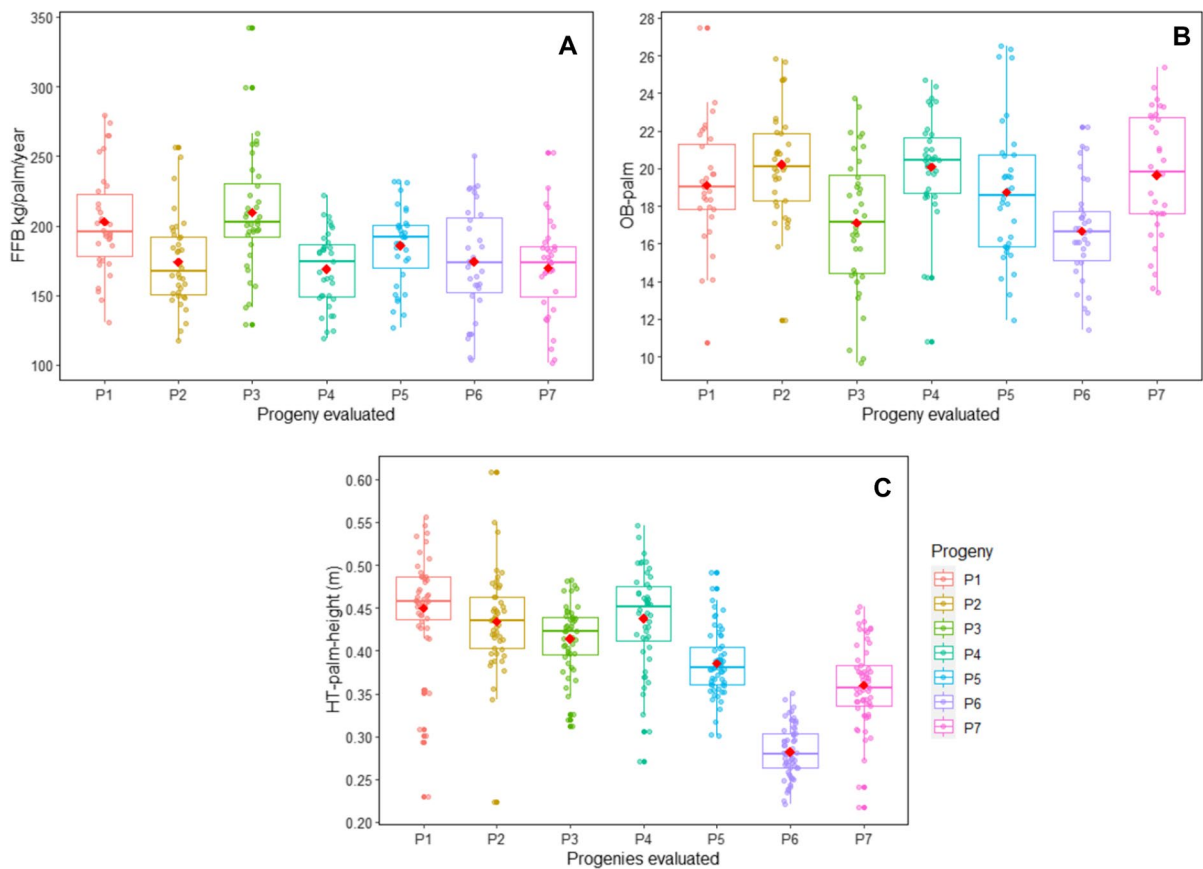
Fig. 2 Box plot for **a** production of fresh fruit bunches (FFB) in the different progenies and palms evaluated, **b** percentage of oil to bunch (OB) in the different progenies and palms evaluated, and **c** height increase trait (HT) in the different progenies and palms evaluated. The red diamond represents the general average, and the horizontal line in the boxplot represents the median of the data

ABW, but low BNO, with 17.1 and 17.0 kg, respectively. They reached the selection values with palms that produce 18 and 21 kg per bunch on average.

For oil to bunch (OB) in *dura* parents, the minimum selection threshold was 20%. On average, the P2 presented a value of 20.2%; at the individual level in this progeny, eight palms stood out for having averages above the selection value, and the values of the best individuals oscillated between 22 and 26% of OB. On the other hand, the P4 progeny presented a general average of 20.1% of OB, where six palms (36 palms in total) showed OB values between 22 and 25% (Fig. 2b).

The annual height increase (HT) presented the highest heritability in the broad sense ($H^2_B = 93\%$) and the highest coefficient of genetic variation

($CVg = 15.6\%$) in the *dura × dura* progenies evaluated in this study. The general averages ranged from 0.28 to 0.45 m year^{-1} of height increase of the plant. The best progenies were P6 and P7, with average height increments of 0.28 m year^{-1} and 0.36 m year^{-1}, respectively. Individual plants grew on average 0.22 m year^{-1} or less in both progenies. Besides the dwarfs' palms presented in progenies 6 and 7, were identified outstanding palms with FFB close to 220 kg plant^{-1}, and OB ranged from 22 to 25% (Fig. 2c).

Discussion

The artificial selection of a trait its expected change in successive breeding populations and could lead to transgressive segregation. Obtaining superior cultivars of oil palm depends on selecting parents with good traits, stability over time, and low environmental influence (Swaray et al. 2020b).

The breeding programs in oil palm emphasize the selection of high-yield progenies focusing on traits such as FFB, BNO, ABW, and OB (Swaray et al. 2020b; Myint et al. 2021). However, in our study population, the RRS cycles led to the dwarf progenies *dura* × *dura* C1-Vizcaina, which allowed the introgression not only of yield traits, but also of vegetative traits such as slow growth of the stem or *dwarf* palms that are of great interest in the cultivation of oil palm, but being aware of possible undesired effects in other key traits such as, BNO, MF, OM, etc. In the C1-Vizcaina population, outstanding families were identified for obtaining improved cultivars and genetic sources for new breeding cycles.

Using the family and individual palm selection (FIPS) strategy (Ngando-Ebongue et al. 2012) allowed the identification of the best progenies (DxD) and individual palms within dura progenies, further, outstanding *dura* must be proven in progeny test (DxP or DxT) in order to evaluate general and specific combing ability, where breeders select best parents base on their progenies performance.

The selection of female parents is expecting to increase the oil potential in future *dura* × *pisifera* progenies. Research carried out in *dura* × *dura* crosses with origins from Zambia, and Cameroon highlights the high values obtained in the MF and OB traits and how they can improve the bunch components in future progenies. Also, their importance within oil palm breeding programs as the foundation for the progress in breeding cycles is reinforced (Pedapati et al. 2021).

In oil palm, the percentage of shell to fruit (SF) in palms with *dura* fruits varies between 25 and 65%. However, to produce a greater amount of MF, which impacts higher oil contents in the fruit, genotypes with lower SF can be selected, where the desirable values of SF should ideally be below 25%. In the present study, the Δg for this trait was -4%, the initial population had a general average of 32% SF, and through selection, it was possible to reduce this value to 29.5%.

According to Vencovsky (1987), the most significant gain by selection occurs when the CVg/CVe ratio tends to one or values higher than one because the genetic variation is high. The present study showed this behavior in several traits, such as HT, KF, and BNO. In itself, the highest CVg and heritability values indicate the potential to make a possible selection in the genotypes analyzed (Salaya-Domínguez et al. 2012). The highest coefficient of genetic variation (CVg) with 15.9% and the highest values of heritability associated with a lower environmental influence were presented in the HT. Thus, for HT, there is the possibility of made the selection with greater precision since the phenotypic value is more reliable (Cruz and Carneiro 2003). Several studies report a high genetic weight for the expression of this trait, such as those carried out by Swaray et al. (2020a), who report an 82.5% genetic influence for this trait. The low annual growth rate of the stem in oil palm progenies is a desirable characteristic to increase crops' productive and economic life. Research in the world is focusing on breeding this characteristic. Studies by Arolu et al. (2017) highlight the high heritability of this trait, which is used to obtain compact and high-yielding progenies.

Different studies in oil palm have demonstrated the advantage of estimating the values of heritability and the coefficient of genetic variation (CVg). In the research carried out by Gomes et al. (2021), high values of heritability and coefficient of genetic variation were found to improve oil production traits in palm cultivation.

The values of heritability reported in this study (Table 3) were in some traits, congruent to those reported by several studies from Malaysia, Nigeria, Zaire, and Cameroon (Arolu et al. 2017; Noh and Rafii 2014; Swaray et al. 2020a; Nor Azwani et al. 2020). These authors reported HT values between 0.37 and 0.90; for KF, the values ranged between 0.33 and 0.65; and for the ABW trait, the recorded values were between 0.32 and 0.78.

The genetic gain (Δg) reported for yield traits is comparable with the results obtained by Swaray et al. (2020a), where they reported Δg of 27% for FFB, 29% for BNO and 24% for ABW for the entire breeding cycle. The result of obtaining high Δg in selecting a genetic trait of interest suggests the possibility

Table 3 Report of several authors for the estimation of heritability in a broad sense in different genetic traits of interest in oil palm

Symbol	FFB	BNO	ABW	RL	LW	LN	HT	MFW	OB	NFB	MF	KF	SF
$H^2_{B\_}$[a]	0.62	0.76	0.85	0.82	0.86	0.79	0.93	0.53	0.79	0.79	0.74	0.87	0.58
$H^2_{B\_}$[b]	0.67	0.74	0.78	0.74	0.35	0.63	0.82	0.42	0.51	0.43	0.55	0.50	0.53
$H^2_{B\_}$[c]	0.20	0.23	0.32	0.81	0.54	0.57	0.37	na	0.48	0.24	0.97	0.65	1.0
$H^2_{B\_}$[d]	0.17	0.37	0.47	0.72	0.64	0.52	0.90	0.56	0.36	0.19	0.56	0.55	na
$H^2_{B\_}$[e]	0.60	0.68	0.66	0.81	0.20	0.44	0.52	na	0.25	0.06	0.55	0.33	0.49

H^2_B: heritability in the broad sense, na: not applicable, FFB: Fresh fruit bunches (kg palm^{-1}), BNO: Number of bunches (palm bunches^{-1}), ABW: Average bunch weight (kg), RL: Rachis length (cm), LW: Leaflet width (cm), LN: Number of leaflets, HT: Height increase (m year^{-1}), MFW: Mean fruit weight (gr), OB: Oil to bunch (%), NFB: Normal fruits to bunch (%), MF: Mesocarp to fruit (%), KF: Kernel to fruit (%) and SF: Shell to fruit (%)

[a]This Study

[b]Swaray et al. (2020a; b)

[c]Nor Azwani et al. (2020)

[d]Arolu et al. (2017)

[e]Noh and Rafii (2014)

of identifying genotypes carrying genes of interest for good transmission (Fellahi et al. 2020). Research conducted by Gomes Junior et al. (2021) in oil palm cultivars reported a Δg of 6% for oil to bunch (OB) and the production of fresh fruit bunches (FFB). Studies carried out in Ecuador in *dura × dura* crosses recorded genetic gains for bunch number (BNO) of 5.8% and for FFB of 1.4% for the entire breeding cycle (Cedillo et al. 2008). The low Δg presented in this study for HT can be explained by how the initial population of this study was generated (C0-Monterrey). The selection of the base population had a high selection pressure toward dwarf palms (127 palms selected from 9000 initial palms); for this reason, the changes for this trait were marginal (<0.01% per year) between the C0 and C1 populations.

When we compare the Δg achieved in this study for yield (FFB), that was 1.3 kg year^{-1} or 1.7% per year is highly comparable to different crops, for instance, in soybeans the Δg was 43 kg ha^{-1}, corresponding to 1.1% of Δg per year^{-1} (Rotundo et al. 2016); for maize, Δg in grain yield was 111.4 kg ha^{-1} (0.62% year^{-1}) (Liu et al. 2021); and for wheat, Δg was 33.9 kg ha^{-1}, representing an increase of 1.28% per year (Woyann et al. 2019). In all studies, these increases result from rigorous breeding processes, and in recent years, the use of genomic tools has allowed further increased in the Δg. In other crops, such as bananas, emphasis is placed on the importance of estimating Δg for the selection of superior parents for the production and development of hybrids, taking into account that the success of breeding programs lies in the precise and correct selection of the parents (Batte et al. 2021).

Reports of oil palm genetic gains (Δg) are very scarce for the yield parameters, vegetative traits, and bunch components. The description of the specific genetic advancement for these traits is restricted. Thus, the importance and novelty reported in this research for palm cultivation include 13 traits of agroindustrial interest, which will be a tool for comparison and decision-making in oil palm breeding programs.

In general, plant breeding programs have marked success in their genetic variability and in selecting progenitors that offer an excellent genetic combination for the different traits of agronomic interest (Agaba et al. 2021). In this sense, this research demonstrated the precise selection of female parents in oil palm, with good genetic combinations in their progenies and high values of genetic gain in different traits of interest for world palm cultivation. These results would lead to the creation of progenies that use elite *dura*-type female progenitors in the successive breeding cycles that meet several traits of interest for the agroindustry of the crop.

Conclusions

Through the method of recurrent reciprocal selection (RRS) and the family and individual selection

(FIPS) strategy for the cultivation of oil palm, genetic gains were achieved that allowed the advancement between generations of breeding, accompanied by high genetic variation for traits of yield, such as FFB and BNO, amount of oil and height increase (HT), all these traits of great interest for the crop. In this study, yield traits, vegetative parameters, and oil production components with less environmental influence and high values of heritability were identified, maintaining reasonable projections for future breeding cycles in the crop.

Genetic gains (Δg) were positive for yield traits, such as fresh fruit bunch production (FFB), and the number of bunches produced per plant per year (BNO) was above 18% for the entire cycle, which represents an annual increase of 1.3% for these traits. On the other hand, Δg for the bunch components, such as the total oil to bunch (OB), was 6% for the entire crop cycle, and these parameters together determine the high productivity of the crop. The genetic gains represent a good advance through the different breeding cycles in these slow-growing progenies that will be used as female parents to obtain the commercial cultivars *dura × pisifera,* in this case improving the GCA within the female population, focused on HT and oil production. However, progeny tests are mandatory to obtain the combining ability of the parents to obtain promising and outstanding progenies.

Traditional breeding techniques, based mainly on phenotypic selection, are very effective; however, the limitations for complex traits have been a current challenge. Techniques such as molecular markers, marker-assisted selection (MAS), genomic tools (genomic selection-GS, GWAS, etc.), transformation, and genetic editing are the tools of the present and the future to continue advancing in the breeding of the cultivation of oil palm. They would lead to greater Δg between breeding cycles (for example, through GS), either due to an increase in selection intensity or the decrease in the time elapsed between the cycles.

Declarations

Conflict of interest The authors have not disclosed any competing interests

References

Agaba R, Rubaihayo P, Tukamuhabwa P, Mwanga ROM, Tumwegamire S, Ndirigwe J, Heider B, Grneberg W (2021) Genetic variation and response to selection for storage root dry matter and associated traits in a population of yam bean (Pachyrhizus spp.) interspecies crosses. Euphytica 217(4):4. https://doi.org/10.1007/s10681-021-02776-1

Al-Khayri JM, Jain SM, Johnson DV (2019) Advances in plant breeding strategies: industrial and food crops, vol 6. https://doi.org/10.1007/978-3-030-23265-8

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Arolu IW, Rafii MY, Marjuni M, Hanafi MM, Sulaiman Z, Rahim HA, Abidin MIZ, Amiruddin MD, Din AK, Nookiah R (2017) Breeding of high yielding and dwarf oil palm planting materials using *Deli dura × Nigerian pisifera* population. Euphytica 213(7):1–15. https://doi.org/10.1007/s10681-017-1943-z

Bastidas S (2003) Genealogíaa del germoplasma de palma de aceite (*Elaeis guineensis* Jacq.) del proyecto de mejoramiento genético de Corpoica. Rev Palmas 24(1):21–29

Batte M, Swennen R, Uwimana B, Akech V, Brown A, Geleta M, Ortiz R (2021) Traits that define yield and genetic gain in East African highland banana breeding. Euphytica 217(10):1–10. https://doi.org/10.1007/s10681-021-02920-x

Beirnaert A, Vanderweyen R (1941) Contribution à l'étude génétique et biométrique des variétés d' *Elaeis guieneensis* Jacq. In: Publications de l' institut nacional pour l'étude agronomique du Congo Belgue, vol Serie Cien, vol 27. Institut national pour l'étude agronomique du Congo belge (INEAC), Bruxelles, p 101

Cedillo DSO, Barros WS, Ferreira FM, Dias LAdS, Rocha RB, Cruz CD (2008) Correlation and repeatability in progenies of African oil palm. Acta Sci Agron 30(2):197–201. https://doi.org/10.4025/actasciagron.v30i2.1728

Corley RHV, Breure CJ (1981) Measurements in oil palm experiments. s.ed.

Corley RHV, Tinker PB (2016) The oil palm, 5th edn. Wiley, Oxford

Cruz CD, Carneiro PS (2003) Aplicados ao Melhoramento Genetico, vol 2. UFV, British Columbia

Falconer D, Mackay T (1996) Introduction to quantitative genetics. Pearson Education Ltd Essex, Essex

Fellahi ZEA, Hannachi A, Bouzerzour H (2020) Expected genetic gains from mono trait and indexbased selection in advanced bread wheat (*Triticum aestivum* l.) populations. Revista Facultad Nacional De Agronomia Medellin 73(2):9131–9141. https://doi.org/10.15446/rfnam.v73n2.77806

Gomes DA, Alves IM, Maciel GM, Siquieroli ACS, Peixoto JVM, Pires PDS (2021) Genetic dissimilarity, selection index and correlation estimation in a melon germplasm. Hortic Bras 39(1):46–51. https://doi.org/10.1590/s0102-0536-20210107

Gomes Junior RA, de Freitas AF, da Cunha RNV, de Abreu Pina AJ, Campos HOB, Lopes R (2021) Selection gains for the palm oil production from progenies of American oil palm with oil palm. Pesqui Agropecu Bras. https://doi.org/10.1590/S1678-3921.PAB2021.V56.02321

Kelly JK (2011) The Breeder's equation. Nat Educ Knowl 5(5):1–5

Liu G, Yang H, Xie R, Yang Y, Liu W, Guo X, Xue J, Ming B, Wang K, Hou P, Li S (2021) Genetic gains in maize yield and related traits for high-yielding cultivars released during 1980s to 2010s in China. Field Crop Res 270(July):108223. https://doi.org/10.1016/j.fcr.2021.108223

Lustri EA, Siqueira WJ, Filho JAdA, Vianna SA, Colombo CA (2021) Estimates of genetic parameters for juvenile traits in macaw palm. Bragantia. https://doi.org/10.1590/1678-4499.20200463

Myint K, Amiruddin M, Rafii MY, Abd MY, Izan S (2021) Character interrelationships and path analysis for yield components in MPOB-Senegal oil palm germplasm. Sains Malays 50:699–709

Ngando-Ebongue G, Ajambang W, Koona P, Firman BL, Arondel V (2012) Oil palm. In: Technological innovations in major world oil crops, vol 1. Springer, pp 165–200

Noh A, Rafii MY (2014) Variability and performance evaluation of introgressed *Nigerian dura × Deli dura* oil palm progenies. Genet Mol Res 13(2):2426–2437. https://doi.org/10.4238/2014.April.3.15

Nor Azwani AB, Fadila AM, Mohd Din A, Rajanaidu N, Norziha A, Suzana M, Marhalil M, Zulkifli Y, Kushairi A (2020) Potential oil palm genetic materials derived from introgression of germplasm (MPOB-Nigeria, MPOB-Zaire and MPOB-Cameroon accessions) to advanced (AVROS) breeding population. J Oil Palm Res 32(4):569–581. https://doi.org/10.21894/jopr.2020.0072

Pavlotzky B, Murillo O (2014) Expected genetic gain and genotype—environment interaction in *Acacia mangium* in the northern region of Costa Rica. Agronom ía Costarricense 0(0):7–17

Pedapati A, Mathur RK, Ravichandran G, Babu BK, Bhagya HP (2021) Evaluation of bunch quality components in Dura × Dura progenies of Zambia and Cameroon sources of oil palm germplasm. J Environ Biol 42(6):1567–1577. https://doi.org/10.22438/jeb/42/6/MRN-1813

Prada F, Romero HM (2012) Muestreo y analisis de racimos en el cultivo de la palma de aceite. Tecnologías para la agroindustria de la palma de aceite, guia de facilitadores. Cenipalma

Rajanaidu N (2016) aceite en los ú ltimos cincuenta años: una aventura personal * A review of oil palm breeding for the past 50 years: Revista Palmas 37:190–202

Reyes PA, Ochoa JC, Montoya C, Daza E, Ayala IM, Romero HM (2015) Development and validation of a bi-directional allele-specific PCR tool for differentiation in nurseries of Dura, Tenera and Pisifera oil palms. Agron Colomb 33(1):5–10. https://doi.org/10.15446/agron.colomb.v33n1.47988

Rocha RB, Teixeira AL, Ramalho AR, Espindula MCa, (2021) *Coffea canephora* breeding: estimated and achieved gains from selection in the western amazon, Brazil. Cienc Rural 51(5):1–11. https://doi.org/10.1590/0103-8478cr20200713

Romero HM, Daza E, Ayala-Díaz I, Ruiz-Romero R (2021) High-oleic palm oil (HOPO) production from parthenocarpic fruits in oil palm interspecific hybrids using naphthalene acetic acid. Agronomy 11(2):290. https://doi.org/10.3390/agronomy11020290

Rotundo JL, Miller-Garvin JE, Naeve SL (2016) Regional and temporal variation in soybean seed protein and oil across the United States. Crop Sci 56(2):797–808

Rutkoski JE (2019) Estimation of realized rates of genetic gain and indicators for breeding program assessment. Crop Sci 59(3):981–993. https://doi.org/10.2135/cropsci2018.09.0537

Salaya-Domínguez JM, López-Upton J, Vargas-Hernández J (2012) Variación genética y ambiental en dos ensayos de progenies de pinus patula. Agrociencia 46(5):519–534

Singh R, Low ETL, Ooi LCL, Ong-Abdullah M, Ting NC, Nagappan J, Nookiah R, Amiruddin MD, Rosli R, Manaf MAA, Chan KL, Halim MA, Azizi N, Lakey N, Smith SW, Budiman MA, Hogan M, Bacher B, Van Brunt A, Wang CY, Ordway JM, Sambanthamurthi R, Martienssen RA (2013) The oil palm SHELL gene controls oil yield and encodes a homologue of SEEDSTICK. Nature 500 (7462):340-+. https://doi.org/10.1038/nature12356

Sispa (2021) Áreas de siembra. Sistema de Información Estadística del Sector Palmero-(2021). FEDEPALMA, Bogotá

Swaray S, Amiruddin MD, Rafii MY, Jamian S, Ismail MF, Jalloh M, Marjuni M, Mohamad MM, Yusuff O (2020a) Influence of parental dura and pisifera genetic origins on oil palm fruit set ratio and yield components in their D × P Progenies. Agronomy 10(11):1–30. https://doi.org/10.3390/agronomy10111793

Swaray S, Rafii MY, Amiruddin MD, Ismail MF, Jamian S, Marjuni M, Jalloh M, Yusuff O, Mohamad MM (2020b) Study on yield variability in oil palm progenies and their genetic origins. Biol Life Sci Forum 4(1):68. https://doi.org/10.3390/iecps2020-08760

Tupaz-Vera A, Ayala-Diaz I, Barrera CF, Romero HM (2021) Selection of elite dura-type parents to produce dwarf progenies of *Elaeis guineensis* using genetic parameters.

Agronomy 11(12):1–15. https://doi.org/10.3390/agronomy11122581

USDA (2020) United States Department of Agriculture Foreign Agricultural Service. USDA

Vencovsky R (1987) Herança quantitativa. In: Paterniani LdQ (ed) Melhoramento e Produçâo do Milho no Brasil. Ediçâo da Fundaçâo Cargill. Instituto de Genética, Esc. Sup. Agricultura Luis de Queiroz, Universidad de Säo Paulo, Piracicaba, Sao Paulo, pp 122–199

Woyann LG, Zdziarski AD, Zanella R, Rosa AC, de Castro RL, Caiero E, Toigo MDC, Storck L, Wu J, Benin G (2019) Genetic gain over 30 years of spring wheat breeding in Brazil. Crop Sci 59(5):2036–2045. https://doi.org/10.2135/cropsci2019.02.0136