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Indirect Selection for Seed Yield in Sacha-Inchi (*Plukenetia volubilis*) in Brazil

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Abstract: Breeding programs for improvement of sacha-inchi, *Plukenetia volubilis* L., generally aim to select individuals with greater seed yield since there is a strong correlation between seed yield and oil production. However, the manual removal of seed husks for evaluating this trait is laborious and costly, thereby discouraging breeding efforts. Accordingly, the objective of the present study was to estimate gains from indirect selection of seed production in sacha-inchi progenies, focusing on maximizing efficiency in improvement programs. Genetic parameters along with direct and indirect selection gains were estimated for seed yield traits in 12 open-pollinated progenies. Strong genetic correlations were observed between total number of fruits (TNF), total weight of fruits (TWF), and total weight of seeds (TWS) per plant ($r > 0.96$). Notably, all three traits demonstrated high heritability ($h^2 > 0.81$). Therefore, plants with high TNF and TWF (Cuzco, Dos de Mayo, Shanao, Aucaloma, and AM-7) can be used to indirectly select the genetic traits of higher seed yields (GS% = 23%). Genetic gain for dry seed production with a selection index of 42% was estimated at 23%, which corresponds to 118 kg.ha^{-1}. Future sacha-inchi improvement programs can select progenies with high TNF and TWF to facilitate the selection of progenies with high TWS.

Keywords: genetic correlation; phenotypic correlation; heritability; genetic parameter; nutraceutical species

1. Introduction

Sacha-inchi (*Plukenetia volubilis* L., Euphorbiaceae) is a twining vine plant that grows naturally at the edges of secondary forests. Natural populations of sacha-inchi are found in the Lesser Antilles, Suriname, and the northwest portion of the Amazon basin, which includes parts of Venezuela, Colombia, Ecuador, Peru, Bolivia, and Brazil [1]. Today, the species is typically grown by small producers, usually at altitudes of ≤900 m [2–4]. Environmental differences between the species' natural range and the areas where the plant is cultivated indicate the species can adapt to different pedoclimatic conditions, including those found in southeast Brazil (e.g., São Paulo; [5]) and southeast Yunnan, China (e.g., Xishuagbanna; [6]).

The plant species is cultivated for having nutraceutical properties. Its seeds contain high levels of unsaturated fatty acids, such as linoleic acid (35–41%) and linolenic acid (37–44%), tocopherols (0.786–0.137 mg.g^{-1}), and proteins (27%) [7,8], thereby attracting scientific and commercial interest [9]. The oil content in the dried seeds of *P. volubilis* ranges from 33–58% [9]. In Manaus, Amazonas, Brazil, 37 genotypes of *P. volubilis* were included having average dry seeds of 10.2% with ranges of 10.2–58.0% [2–4].

There are no sacha-inchi cultivars improved by public institutions or by private enterprise. Even though genetic variation is present, crops are being developed without considering the optimum genetic features to facilitate an increase in yields among different producing regions. Farmers acquire seeds through exchanges or from local markets [4]. The dynamics of self-supplying seeds possibly have contributed to the reduced diversity of crops grown by communities of small producers in large geographic areas [3]. Contrastingly, populations that are more isolated from main trading centers are likely more divergent.

The results of AFLP-based genetic diversity studies indicate that there is a significant difference between the sacha-inchi population from the community of Dos de Mayo (San Martin, Peru) and populations from communities located within a 70 km radius [2,3], further suggesting that the crop could be improved using mass selection. Producers chiefly use larger seeds to establish their crops, with the aim of increasing yield. However, because the species is allogamous [10] and selection is performed after fruit production, such efforts only apply to female genitors. Thus, the genetic gains are lower than those obtained from controlled crossings.

Studies of the genetic basis of sacha-inchi seed yield components and the correlations between them may advance the development of selection strategies that promote greater genetic gains and allow farmers to develop cultivars more rapidly with higher yields.

Even though the species has been the focus of botanical, morphological, genetic, agronomic, and food technology studies [9], there are still many gaps in the species' production system. One of the most prominent of these gaps is the absence of cultivars, and even though sacha-inchi has been used and cultivated for millennia, the species is still considered incompletely domesticated. In fact, the species' germplasm was only recently characterized.

As the oil extracted from sacha-inchi seeds is the most commercially relevant product from the species, seed yield is an important variable in cultivar selection [6]. However, to evaluate seed yield, seeds must be manually removed from the fruits after collection. This process can be expensive when assessing a large number of samples. Valente et al. [11] demonstrated that the simultaneous selection of several sacha-inchi yield traits (i.e., number of fruits, weight of fruits, and number of seeds per plant) yielded similar genetic gains. Nonetheless, comparisons of these traits with significant seed yield have yet to be reported.

Studies on the correlations between plant traits in selection populations are pertinent to plant improvement, especially due to the possibility of obtaining selection gains indirectly. Indirect selection is justified when a trait of interest is prohibitively costly or too complex to evaluate but is closely associated with another trait that is less costly or less complex to assess [12,13]. The decision to utilize indirect selection should be taken into consideration when estimating the gains of the process, which depend on the magnitude of the connection between the traits and their heritability, and the gap between such gains and those obtainable using direct selection.

To achieve continuous genetic gains with successive selection cycles, it is also important to maintain genetic diversity within the breeding population. In this regard, it is important to employ an appropriate selection intensity [14]. Mass selection allows the selection of individuals that will produce the subsequent generation. Even though this selection strategy can result in lower genetic gains, it allows the rapid generation of new cultivars with higher yields and is recommended for species in the initial stages of improvement [15,16].

The objectives of this study were 1) to estimate the genetic parameters and direct and indirect selection gains for seed production in open-pollinated sacha-inchi progenies and 2) to select superior individuals to produce improved seeds.

2. Materials and Methods

2.1. Study Area

The experiment was performed in the experimental field of the Embrapa headquarters in the western Amazon region (Manaus, Amazonas (AM), Brazil; 2°53′37.2″ S, 59°58′23.0″ W). The soil in the area is classified as dystrophic yellow ferrosol with a clayey texture according to the Brazilian System of Soil Classification [17]. The region has a humid equatorial climate, with a short dry season (July–September with a monthly rainfall of 50–100 mm), dry–humid transitional month (October), and a long humid season (November–June with a monthly rainfall of 200–300 mm). The mean annual temperature is 27 °C [18].

2.2. Experimental Design

The experiment was conducted using a randomized block design with 12 half-sib progenies, three repetitions, and ten plants per plot. The progenies were obtained from open-pollinated fruits, eight from open markets of the Benjamin Constant, Amazonas, Brazil (Dos de Mayo, Shanao, São Pedro, Cuzco, Aucaloma, Ponto Renato, João Guerra, and Novo Horizonte) from the merchant’s farm and four progenies from Embrapa’s active sacha-inchi germplasm bank (AM-7, AM-13, AM-17, and AM-21) of the Careiro, Amazonas, Brazil (Table 1). The sacha-inchi progenies samples are registered in the Manuel de Arruda Câmara herbarium of the Universidade Estadual da Paraíba (UEPB)—Campina Grande-Brazil, indexed under: SP:513555 (Novo Horizonte), UFACPZ:4868 (Cuzco), EAFM:2916 (Aucaloma), EVB:3271 (São Pedro), RB:RB00890091 (Shanao), RB:RB00088211 (Ponto Renato), HPL:2975 (Dos de Mayo), Botany:V0216784F (João Guerra), Botany:U.1268467 (AM7), Botany:U.1268462 (AM13), CGMS:75389 (AM17), and CGMS:65891 (AM21).

Table 1. Description of the *Plukenetia volubilis* progenies’ names in the study, source location, and geographic coordinates.

Progenies	Source Location	Geographic Coordinates
Novo Horizonte	Benjamin Constant, AM, Brazil	4° 22′ 45.5″ S, 70° 00′ 28.6″ W
Cuzco	Benjamin Constant, AM, Brazil	4° 23′ 03.6″ S, 70° 00′ 38.4″ W
Aucaloma	Benjamin Constant, AM, Brazil	4° 22′ 45.5″ S, 70° 00′ 28.6″ W
São Pedro	Benjamin Constant, AM, Brazil	4° 24′ 03.3″ S, 70° 01′ 06.8″ W
Shanao	Benjamin Constant, AM, Brazil	4° 22′ 45.5″ S, 70° 00′ 28.6″ W
Ponto Renato	Benjamin Constant, AM, Brazil	4° 23′ 15.3″ S, 70° 01′ 00.3″ W
Dos de Mayo	Benjamin Constant, AM, Brazil	4° 30′ 03.7″ S, 69° 56′ 04.9″ W
João Guerra	Benjamin Constant, AM, Brazil	4° 24′ 46.4″ S, 70° 03′ 14.0″ W
AM7	Careiro, AM, Brazil	3° 31′ 45.0″ S 59° 49′ 07.9″ W
AM13	Careiro, AM, Brazil	3° 50′ 16.9″ S, 60° 22′ 35.3″ W
AM17	Careiro, AM, Brazil	3° 50′ 16.9″ S, 60° 22′ 35.3″ W
AM21	Careiro, AM, Brazil	3° 50′ 16.9″ S, 60° 22′ 35.3″ W

2.3. Seedling Production and Planting

The sacha-inchi progenies were sown on August 1, 2018, in styrofoam trays containing Plantmax® commercial substrate with the following chemical composition: N = 5.81 $g.kg^{-1}$; P = 0.95 $g.kg^{-1}$; K = 4.35 $g.kg^{-1}$; Ca = 14.14 $g.kg^{-1}$; Mg = 1.68 $g.kg^{-1}$; S = 0.31

$g.kg^{-1}$; B = 27.80 $mg.kg^{-1}$; Fe = 19,826.0 $mg.kg^{-1}$; Cu = 0.01 $mg.kg^{-1}$; Mn = 225.0 $mg.kg^{-1}$; Zn = 76.40 $mg.kg^{-1}$. The resulting seedlings were transplanted into plastic bags, with dimensions of 20 cm × 30 cm, 14 days after sowing. The bags contained 2 kg of substrate, dystrophic yellow ferrosol with laying hen manure, in a ratio of 3:1. The chemical composition of the final substrate was: pH (water) 7.18; N = 6.42 $g.kg^{-1}$; P = 1.06 $g.kg^{-1}$; K = 5.05 $g.kg^{-1}$; Ca = 18.01 $g.kg^{-1}$; Mg = 1.92 $g.kg^{-1}$; S = 0.29 $g.kg^{-1}$; B = 29.04 $mg.kg^{-1}$; Fe = 17,405.0 $mg.kg^{-1}$; Cu = 0.09 $mg.kg^{-1}$; Mn = 282.0 $mg.kg^{-1}$; Zn = 66.20 $mg.kg^{-1}$. When seedlings had two pairs of leaves and were ~20 cm high in bags, 15 days after the seedlings developed, the definitive planting was carried out. In fields, the soil acidity was corrected to pH 6.0 and based on the results of soil chemical analyses, 2 $t.ha^{-1}$ dolomitic limestone (relative efficiency 80%) were applied 56 days before planting. In the planting pits, in dystrophic yellow ferrosol, 15.0 g urea, 35.0 g triple superphosphate, 23.0 g potassium chloride, and 1 kg laying hen manure were applied for foundation fertilization. On December 3, 2018, March 1, 2019, and June 3, 2019 (approximately every three months), a top-dressing was performed using 35 g urea, 35 g triple superphosphate, 23 g potassium chloride, and 1 L laying hen manure per plant.

The plants were cultivated using an espalier support system, with 3 m between rows and 2 m between plants. In each row, concrete posts were placed every 6 m and wires were fixed horizontally at 1.0 and 1.5 m from the soil. The plants were trained by tying the stems to the wires using cotton ties, and the crop received drip irrigation (1 L water per plant per day (d)) every 2 days during the rainy season (November–May) if it did not rain during that interval, and daily during the dry season (July–September).

2.4. Data Collection

Fruit collection was initiated in March 2019, ~212 days after planting, and was performed every week until August 2019 (i.e., for a total of six consecutive months). The fruits were collected by hand when they were dark brown (at the stage of maximum maturity before fruit dehiscence) dried in the shade at ambient temperature for 7 d, and dried further indoors at 18 °C for 30 d. After processing, the fruits of each progeny were evaluated for total number of fruits per plant (TNF), total weight (g) of fruits per plant (TWF), total number of seeds per plant (TNS), total weight (g) of seeds per plant (TWS), mean weight (g) of fruits (MWF), number of seeds per fruit (NSF), mean weight (g) of seeds (MWS), and TWS:TWF ratio.

2.5. Data Analysis

The components of variance and genetic parameters of each trait were estimated according to Cruz et al. (2012) and using the Genes software [19].

Analysis of variance (ANOVA) was performed according to the following statistical model:

$$Y\text{ij} = \mu + G\text{i} + B\text{j} + e\text{ij}, \quad (1)$$

Where Yij represents observation of the nth progeny (i) of the nth block (j); μ represents overall mean; Gi represents random effect of the nth progeny; Bj represents random effect of the nth block; and $e$ij represents random effect of the experimental error.

Broad-sense heritability was estimated as $h2 = \sigma 2g/\sigma 2f$, with the estimated $\sigma 2f$ calculated based on the mean of families. The coefficient of genetic variation between the progenies (CVg), the coefficient of environmental variation (CVe), and the coefficient of relative variation (CVr) were calculated using $CVg = 100(\sigma 2g)1/2/\overline{x}$, $CVe = 100(\sigma 2e)1/2/\overline{x}$, and $CVr = CVg/CVe$, respectively, where $\overline{x}$ is the overall mean.

Based on the result of the ANOVA, the genetic and phenotypic correlations were estimated as $rg = \sigma g(x,y)/(\sigma gx\ \sigma gy)$ and $rp = \sigma p(x,y)/(\sigma fx\ \sigma fy)$, respectively, where $\sigma g(x,y) = (\sigma p(x,y) - \sigma e(x,y))/r$ (blocks), $\sigma gx = (\sigma p(x) - \sigma e(x))/r$, and $\sigma gy = (\sigma p(y) - \sigma e(y))/r$. In addition, path analysis [20] was performed to determine the direct and indirect effects of traits that were correlated with TWS.

The gain expected from direct selection for trait X was estimated as follows: $GSx = (Xs - Xo)\ h2x = DS \cdot h2x$, where Xs is the mean of the progenies selected for trait X, Xo is the mean of the original population. DS is the selection differential in the population and $h2x$ is the heritability of trait X. Meanwhile, the gain expected from indirect selection for trait X, through selection for trait Y, was estimated as follows: $GS = DSx(y) \cdot h2$, where $DSx(y)$ is the indirect selection differential obtained for X from the mean of the progenies selected for superiority in Y.

Relative estimated selection gain ($GS\%$) was calculated as follows: $GS\% = GS \cdot 100/Xo$, where Xo is the mean of the initial population. Intensities of 25, 33, and 42% were used for selection.

3. Results and Discussion

3.1. Genetic Parameters and Correlations

Considering the classification of the environmental variation coefficients (CVe) proposed by Pimental-Gomes [21] for the variables evaluated in the field, most values were low or intermediate, which indicated high and good experimental precision, respectively. However, TNF, TWF, and TWS yielded high CVe values and, thus, low experimental precision (Table 2). Even though there is no specific CVe classification for the variables analyzed in the present study, the TNF and TWF values reported for sacha-inchi by Valente et al. [11] were 58 and 63%, respectively, which were higher than those calculated in the present study.

Table 2. Summary of analysis of variance (ANOVA) and genetic parameters for the fruit production and quality traits of 12 sacha-inchi progenies.

SV	DF	TNF	TWF	TNS	TWS	MWF	NSF	MWS	TWS:TWF	SH (day)
					Mean square					
Blocks	2	64,650	2,878,281	957,099	978,517	0.360	0.001	0.002	0.003	1220
Progenies	11	5592 *	163,740 *	78,157 *	67,321 *	1.246 *	0.035 *	0.014 *	0.004 *	1105 ns
Error	22	820	29,220	11,380	11,984	0.177	0.011	0.002	0.00	520
Mean		132	905	509	510	7.13	3.87	1.01	0.55	212
CVe (%)		22	19	21	22	6	3	5	4	11
					Genetic parameters					
$\sigma^2 g$		1591	44,840	22,259	18,443	0.357	0.008	0.004	0.001	198
$\sigma^2 f$		1864	54,580	26,052	22,440	0.415	0.012	0.005	0.001	371
h^2 (%)		85	82	85	82	86	67	83	90	53
CVg (%)		30	23	29	27	8	2	6	6	7
CVg/CVe		1.39	1.24	1.4	1.24	1.42	0.85	1.27	1.71	0.62

SV—sources of variation; DF—degree of freedom; CVe (%)—environmental variation coefficients; σ2 g—genetic variance; σ2 f—phenotypic variance; h2—broad-sense heritability; CVg (%)—coefficient of genetic variation; * significant at $p \leq 0.05$, F test; ns not significant at $p \leq 0.05$, F test; TNF—total number of fruits per plant; TWF—total weight (g) of fruits per plant; TNS—total number of seeds per plant; TWS—total weight (g) of seeds per plant; MWF—mean weight (g) of fruits; NST—number of seeds per fruit; MWS—mean weight (g) of seeds; TWS:TWF—TWS:TWF ratio; and SH—start of harvest.

ANOVA indicated that progeny effect was significant for all variables, except for start of fruit collection, which indicates genetic variation among the progenies, further suggesting that selection gains are possible (Table 2). Additionally, variability in fruit and seed size was observed in the studied accessions (Figure 1). Biogeographical analyses showed that natural selection on a combination of traits contributed to seed size variation, while movement between forest edge/light gap and canopy niches likely contributed to the seed size extremes in *Plukenetia* in the evolutive process [22]. The success of selection depends on variability in genetic resources and their responses to changing environments [23].

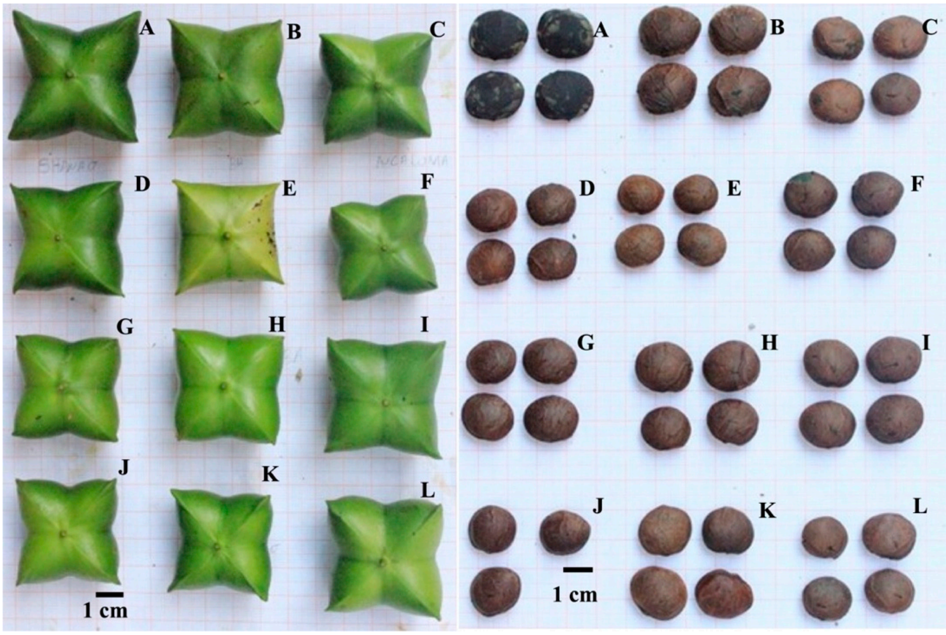

Figure 1. Size of fruits and seeds in 12 sacha-inchi accessions. A—Shanao, B—Novo Horizonte, C—Aucaloma, D—Ponto Renato, E—Cuzco, F—Dos de Mayo, G—João Guerra, H—São Pedro, I—AM13, J—AM7, K—AM17, L—AM21.

Fruit collection generally started at 212 days (~7 months) after plants were transferred to the field (Table 2). This differed from the start time reported by Valente et al. [11] for sacha-inchi fruit production in the Brazilian Amazonia (i.e., 6 months after planting).

Heritability varied from 82 to 85% for TNF, TWF, TNS, and TWS (Table 2). These results also differed from those of Valente et al. [11], who reported heritabilities of 34–36%, but this could be the result of using populations with different genetic backgrounds [12,24]. These findings may be explained by the genetic variability in progenies [25].

High estimated heritability and CVg/CVe values indicate that the conditions favored genetic gains through progeny selection (Table 2) and progeny-level mass selection [12,26,27].

High, positive, and statistically significant values (r ≥ 0.97) were obtained for the estimated genetic correlations between TWS and TNF, TNS and TWF (Table 3). Valente et al. [11] also reported a strong, positive, and significant correlation between TNF and TWF in sacha-inchi and in *Jatropha curcas* L., which belongs to the same family. A strong correlation was observed between seed weight and the remaining traits (r = 0.99) [28].

Table 3. Genotypic (upper diagonal) and phenotypic (lower diagonal) correlations between fruit production and quality traits in 12 sacha-inchi progenies.

	TNF	**TWF**	**TNS**	**TWS**	**MWF**	**NSF**	**MWS**	**TWS:TWF**	**SH (day)**
TNF		0.97 **	0.99 **	0.97 **	−0.75 **	−0.22	−0.24	0.73 **	−0.19
TWF	0.96 **		0.97 **	0.99 **	−0.54	−0.22	−0.02	0.68 *	−0.33
TNS	0.99 **	0.96 **		0.97 **	−0.73 **	−0.16	−0.25	0.73 **	−0.18
TWS	0.97 **	0.98 **	0.97 **		−0.64 *	−0.28	0.00	0.81 **	−0.32
MWF	−0.70 *	−0.49	−0.68 *	−0.57 *		0.25	0.54	−0.73 **	−0.11
NSF	−0.19	−0.16	−0.12	−0.19	0.26		−0.37	−0.30	0.08
MWS	−0.23	0.03	−0.24	0.00	0.59 *	−0.22		0.10	−0.44
TWS:TWF	0.67 *	0.61 *	0.67 *	0.73 **	−0.68 *	−0.14	−0.11		−0.22
SH (day)	−0.12	−0.2	−0.12	−0.19	−0.01	0.01	−0.21	−0.21	

* Significant at $p \leq 0.01$, *t*-test; ** significant at $p \leq 0.05$, *t*-test; TNF—total number of fruits per plant; TWF—total weight (g) of fruits per plant; TNS—total number of seeds per plant; TWS—total weight (g) of seeds per plant; MWF—mean weight (g) of fruits; NST—number of seeds per fruit; MWS—mean weight (g) of seeds; TWS:TWF—TWS:TWF ratio; and SH—start of harvest.

Sacha-inchi producers in Peru trade seeds according to their weight [4]. The results of the present study indicate that both TNF and TWF had high heritability estimates and were strongly correlated with TWS (Tables 2 and 3).

The aforementioned sacha-inchi producers select plants for the size of the seeds they produce [9], because larger seeds are expected to yield greater mean seed weight. However, the present study found no significant correlation between mean seed weight and total seed weight per plant (Table 3). This suggests that the selection practiced by the farmers, if performed on this population, would fail to improve overall yield. The comparison of means between progenies in relation to fruit and seed characteristics is found in Table S1. In the individual analysis of the means by the Scott–Knott test, it can be observed that each characteristic has a different response.

Path analysis was performed to investigate the direct and indirect effects of traits that were significantly correlated with seed production (i.e., TNS, TWS, and MWF) (Table 4) [13,29]. The TWF had a strong, positive, and direct effect on TWS (0.725; Table 4), which indicated that indirect selection would be successful. Interestingly, Umamaheswari et al. [30] (also based on path analysis) found that the TWF of *J. curcas* was valuable for the indirect selection seed and oil yield.

Table 4. Estimated effects of fruit and seed traits on the total weight and seed weight of plants from 12 sacha-inchi progenies.

Fruit and Seed Traits	Effect and Correlation Coefficient	Standardized Coefficients
Total number of fruits per plant	Direct effect on total weight (g) of seeds per plant	0.046
	Indirect effect using total weight (g) of fruits per plant	0.711
	Indirect effect using total number of seeds per plant	0.222
	Indirect effect using mean weight (g) of fruits	0.006
	Total (correlation coefficient)	0.985
Total weight (g) of fruits per plant	Direct effect on total weight (g) of seeds per plant	0.725
	Indirect effect using total number of fruits per plant	0.045
	Indirect effect using total number of seeds per plant	0.218
	Indirect effect using total weight (g) of fruits per plant	0.005
	Total (correlation coefficient)	0.994
Total number of seeds per plant	Direct effect on total weight (g) of seeds per plant	0.222
	Indirect effect using total number of fruits per plant	0.046
	Indirect effect using total number of seeds per plant	0.714
	Indirect effect using mean weight (g) of fruits	0.006
	Total (correlation coefficient)	0.988
Mean weight (g) of fruits	Direct effect on total weight (g) of seeds per plant	−0.011
	Indirect effect using total number of fruits per plant	−0.025
	Indirect effect using total weight (g) of fruits per plant	−0.286
	Indirect effect using total number of seeds per plant	−0.116
	Total (correlation coefficient)	−0.438
Determination coefficient		0.995

3.2. Selection Gains in Sacha-Inchi Progenies

The direct selection gains for TNF (25%) and TWF (20%) were similar to the indirect gain for TWS (23%; Table 5). Therefore, the improvement program may increase the total weight (g) of seeds per plant by 23% during the first selection cycle (one year) by simply increasing TNF and TWF. This result differs from the recommendation of Valente et al. [11], who proposed that more productive progenies could be produced by simultaneously increasing TNS, TNF, and TWF. In the present study, the results indicate that the selection of progenies that produce more seeds may be achieved indirectly by evaluating TNF or TWF, as previously mentioned.

Table 5. Direct and indirect selection gains of yield traits and fruit quality in 12 sacha-inchi progenies.

Traits Selected	Answers in Traits	Xo	Xs	h2%	SG	SG %	Progenies Selected
TNF	TNF	132	171	85	34	25	1; 2; 4; 6; 7
	TWF	905	1122	82	179	20	
	TNS	509	654	85	124	24	
	TWS	510	653	82	118	23	
	MWF	7.129	6.824	86	−0.262	−4	
	NST	0.553	0.576	90	0.020	4	
TWF	TNF	132	171	85	34	25	1; 2; 4; 6; 7
	TWF	905	1122	82	179	20	
	TNS	509	654	85	124	24	
	TWS	510	653	82	118	23	
	MWF	7.129	6.824	86	−0.262	−4	
	NST	0.553	0.576	90	0.020	4	
TNF	TNF	132	171	85	34	25	1; 2; 4; 6; 7
	TWF	905	1122	82	179	20	
	TNS	509	654	85	124	24	
	TWS	510	653	82	118	23	
	MWF	7.129	6.824	86	−0.262	−4	
	NST	0.553	0.576	90	0.020	4	
TWS	TNF	132	171	85	34	25	1; 2; 4; 6; 7
	TWF	905	1122	82	179	20	
	TNS	509	654	85	124	24	
	TWS	510	653	82	118	23	
	MWF	7.129	6.824	86	−0.262	−4	
	NST	0.553	0.576	90	0.020	4	
MWF	TNF	132	102	85	−25	−19	2; 3; 8; 9;10
	TWF	905	772	82	−109	−12	
	TNS	509	401	85	−92	−18	
	TWS	510	415	82	−78	−15	
	MWF	7.129	7.695	86	0.485	7	
	NST	0.553	0.526	90	−0.025	−4	
NST	TNF	132	158	85	23	17	1; 4; 7; 11; 12
	TWF	905	1017	82	92	10	
	TNS	509	607	85	84	16	
	TWS	510	600	82	74	14	
	MWF	7.129	6.647	86	−0.414	−6	
	NST	0.553	0.585	90	0.029	5	

Xo—initial population average. Xs—average of the selected population. h2—broad-sense heritability. SG—selection gains; progenies: 1—Dos de Mayo; 2—Shanao; 3—São Pedro; 4—Cuzco; 5—AM17; 6—Aucaloma; 7—AM7; 8—AM13; 9—AM21; 10—Ponto Renato; 11—João Guerra; 12—Novo Horizonte. TNF—total number of fruits per plant; TWF—total weight (g) of fruits per plant; TNS—total number of seeds per plant; TWS—total weight (g) of seeds per plant; MWF—mean weight (g) of fruits; NST—number of seeds per fruit; and MWS—mean weight (g) of seeds.

Direct selection for increasing TWS, TNF, and TWF reduced indirect gains in MWF under different selection intensities (Table 6), which agrees with the negative correlations observed among the traits. Even though the objective of selection is to increase seed production, high selection intensity could result in an undesired reduction of genetic diversity in the improved population [9]. In contrast, the use of low selection intensity (*i*) in the first cycle of selection could increase the inclusion of genotypes that are divergent in other traits (Table 6). An *i* of 25% (three progenies) allowed the selection progenies with significantly smaller fruits (genotype: mean ± standard deviation, Aucaloma = 6.83 ± 0.38 g) and very small fruits (Cuzco = 6.02 ± 0.55 and Dos de Mayo = 6.31 ± 0.12 g), whereas an *i* of 42% (five progenies) allowed the selection of progenies with large fruits (Shanao = 8.05 ± 0.36 g), medium fruits (AM7 = 7.33 ± 0.23), small fruits (Aucaloma), and very small fruits (Cuzco; Scott–Knott test, $p < 0.05$ for each comparison). The low selection intensity used in the present study (42%) was viable because the population was small. Future studies should assess other traits, such as unsaturated fatty acid content [7,8,31–33] and disease resistance [34–36], that are relevant to the industry and farmers.

Table 6. Effect of selection intensity on the direct and indirect selection gains of yield traits and mean fruit weight in 12 sacha-inchi progenies. DSG%, direct selection gain; ISG%, indirect selection gain.

Traits Selected	Answers in Traits	Selection Intensity												
		25% (3 Progenies)					33% (4 Progenies)				42% (5 Progenies)			
		h2%	Xo	Xs	GS	GS%	Xo	Xs	SG	SG%	Xo	Xs	SG	SG%
TNF	TNF	85	132	190	49	37	132	181	42	32	132	171	34	25
	TWF	82	905	1184	230	25	905	1153	204	23	905	1122	179	20
	TWS	82	510	685	144	28	510	678	138	27	510	653	118	23
	MWF	86	7.13	6.38	−0.64	−9	7.13	6.52	−0.53	−7	7.13	6.82	−0.26	−4
	PS	1; 4; 6					1; 4; 6; 7				1; 2; 4; 6; 7			
TWF	TNF	85	132	190	49	37	132	181	42	32	132	171	34	25
	TWF	82	905	1184	230	25	905	1153	204	23	905	1122	179	20
	TWS	82	510	685	144	28	510	678	138	27	510	653	118	23
	MWF	86	7.13	6.38	−0.64	−9	7.13	6.52	−0.53	−7	7.13	6.82	−0.26	−4
	PS	1; 4; 6					1; 4; 6; 7				1; 2; 4; 6; 7			
TWS	TNF	85	132	185	46	35	132	181	42	32	132	171	34	25
	TWF	82	905	1154	204	23	905	1153	204	23	905	1122	179	20
	TWS	82	510	690	148	29	510	678	138	27	510	653	118	23
	MWF	86	7.13	6.41	−0.61	−9	7.13	6.52	−0.53	−7	7.13	6.82	−0.26	−4
	PS	1; 4; 6					1; 4; 6; 7				1; 2; 4; 6; 7			
MWF	TNF	85	132	103	−25	−19	132	108	−20	−15	132	102	−25	−19
	TWF	82	905	796	−90	−10	905	823	−67	−7	905	772	−109	−12
	TWS	82	510	421	−73	−14	510	444	−54	−11	510	415	−78	−15
	MWF	86	7.13	7.95	0.70	10	7.13	7.79	0.57	8	7.13	7.69	0.49	7
	PS	2; 8; 10					2; 3; 8; 10				2; 3; 8; 9; 10			

Xo—initial population average. Xs—average of the selected population. h2—broad-sense heritability. SG—selection gains; PS—progenies selected: 1—Dos de Mayo; 2—Shanao; 3—São Pedro; 4—Cuzco; 5—AM17; 6—Aucaloma; 7—AM7; 8—AM13; 9—AM21; 10—Ponto Renato; 11—

João Guerra; 12—Novo Horizonte. TNF—total number of fruits per plant; TWF—total weight (g) of fruits per plant; TWS—total weight (g) of seeds per plant; MWF—mean weight (g) of fruits.

The Dos de Mayo, Shanao, Cuzco, Aucaloma, and AM7 progenies were selected based on either TNF or TWF. These progenies can be multiplied utilizing cuttings in a greenhouse with sub-irrigation [37]. After saplings (cuttings) are formed, they can be planted in isolation. The seeds produced in such a clonal garden via open pollination can then be supplied as improved seeds to producers, thus establishing an improved population [14].

After the recombination of the five selected progenies, the next generation (improved population) is expected to yield 1.122 g.plant^{-1} or 1.246 kg.ha^{-1} of dry fruits (calculation based on 1111 plants.ha^{-1}; Table 5). These predictions are greater than those of Valente et al. [11], who selected ten progenies, managed them in the same area, under the same conditions used in the present study, and reported a mean yield of 763 g.plant^{-1}, or 847 kg.ha^{-1}. Plant breeding for yield and quality traits in fruits is complex due to the polygenic nature of these traits and the existence of genetic correlations among them [38–41].

The five accessions selected in this study exhibit genetic variations that are useful for selection. Previous molecular genetic analysis of accessions from the San Martin region of Peru (Dos de Mayo, Shanao, and Aucaloma) also indicated the existence of genetic variations [3] and that the Dos de Mayo accession was distinct from the Shanao and Aucaloma accessions. Genetic variation in the Cuzco accession was also reported by Rodriguez et al. [2].

For dry seed commercialized production, the genetic gain with a selection index of 42% of the progenies was estimated at 23%. This corresponds to 118 kg ha^{-1} (population of 1111 ha^{-1}). In this present study, the oil content in the seeds was not evaluated. Therefore, it was not possible to estimate the exact productivity of the oil. Seed productivity characteristics are of interest to agriculture and agroindustry has an indirect related interest regarding buying seeds from producers but selling the oil. Yang et al. [6] verified a positive correlation between seed and oil productivity. Consequently, it can be inferred that more productive varieties are of greater interest to the farmer and agroindustry. Study of fatty acid composition will also be able to differentiate the progenies.

4. Conclusions

The selection of sacha-inchi progenies with greater total number of fruits per plant and total weight of fruits per plant provides greater indirect genetic gain in progenies, which will produce greater total weight of seeds per plant. The Dos de Mayo, Shanao, Cuzco, Aucaloma, and AM7 progenies were superior regarding the total weight of seeds. Moreover, they could be used to establish open-pollinated clonal systems to effectuate an improved population. Due to the absence of named sacha-inchi cultivars, progeny-level mass selection can be used to initiate an enhancement program and provide seeds of high genetic quality to cultivation areas.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/horticulturae8110988/s1, Table S1: Comparison of means between 12 *Plukenetia volubilis* progenies in relation to fruits and seed characteristics.

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