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DIRECT AND INDIRECT GENETIC GAINS FOR GROWTH AND REPRODUCTIVE TRAITS IN *Inga edulis*[1]

GANHOS GENÉTICOS DIRETOS E INDIRETOS PARA CARACTERES DE CRESCIMENTO E REPRODUTIVOS EM *Inga edulis*[1]

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ABSTRACT - In this study parameters, correlations, and expected direct ($DG_g\%$) e indiretos ($IG_g\%$) genetic gains from mass selection and selection among progenies were estimated for growth, crown architecture, and reproductive traits in 105 open-pollinated *Inga edulis* progenies, 18 months old, established at three sites in the Peruvian Amazon, aiming at the simultaneous selection of multiple traits. Significant differences were detected among progenies for most traits within sites and joint sites. The estimation of narrow-sense heritabilities, mean-progeny heritability, and additive within progeny heritability showed that the traits are under genetic control and can be improved by mass selection or selection among progenies. The genotype-environment interaction was low for all traits, showing that selection can be carried out in only one of the site. The estimated genetic parameters were generally higher at site 1, indicating this site as more suitable for selection. The estimated genetic parameters were higher for diameter at breast height (D) in the joint site analysis, suggesting this trait as more suitable for direct selection. Genetic correlations were significantly greater than zero between D and the traits height, crown diameter, and fruit length, demonstrating that simultaneous genetic improvement of multiple traits is possible through direct selection for D. The greatest direct ($DG_g\%$) e indirect ($IG_g\%$) genetic gains were obtained through among and within progeny selection. The results show that crown architecture and reproductive traits can respond well to indirect selection based on direct selection for D.

Keywords: Genetic variability, Heritability, Forest breeding, Agroforestry, Aguaytia basin.

RESUMO - Nesse estudo foram estimados parâmetros, correlações e ganhos genéticos diretos ($DG_g\%$) e indiretos ($IG_g\%$) esperados pela seleção massal e seleção entre progênies para caracteres de crescimento, arquitetura da copa e reprodutivos em 105 progênies de polinização aberta de *Inga edulis*, com 18 meses de idade, estabelecidas em três sites da Amazônia peruana, visando a seleção simultânea de múltiplos caracteres. Diferenças significativas foram detectadas entre as progênies para a maioria dos caracteres dentro dos sites e conjunto de sites. As estimativas das herdabilidades no sentido restrito, herdabilidade média entre progênies e aditiva dentro de progênies mostraram que os caracteres estão sob controle genético e podem ser melhoradas por seleção massal ou seleção entre progênies. A interação genótipo-ambiente foi baixa, mostrando que a seleção pode ser realizada em apenas um dos sites. Os parâmetros genéticos estimados foram geralmente maiores no site 1, indicando este site como mais adequado para seleção. Os parâmetros foram maiores para o diametro a altura do peito (D) na análise conjunta de sites, sugerindo este caractere como mais adequada para seleção direta. As correlações genéticas foram significativamente positivas entre D e os caracteres altura, diametro da copa e comprimento dos frutos, demonstrado que o melhoramento genético simultâneo de múltiplos caracteres é possível por meio da seleção direta para D. Os maiores ganhos $DG_g\%$ e $IG_g\%$ foram obtidos pela seleção entre e dentro de progênies. Os resultados mostram que a arquitetura da copa e caracteres reprodutivos podem responder bem à seleção indireta baseada na seleção direta para o D.

Palavras-chave: Variação genética, Herdabilidade, Melhoramento florestal, Agrofloresta, Bacia de Aguaytia.

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1 INTRODUCTION

In recent years, *Inga edulis* Mart. (Fabaceae) has gained greater relevance not only for its ecological function in tropical forest ecosystems but also for its economic and social role in Amazonian communities. Its potential as a component of agroforestry systems has been reinforced by various studies showing its effectiveness in improving soil fertility and promoting food security (Takahashi et al. 2019; Lojka et al. 2020). Moreover, participatory domestication strategies have been adopted to conserve its genetic diversity and promote local adaptation, particularly in regions where this species plays a pivotal role in sustaining rural livelihoods (Simons and Leakey 2016; Lojka et al. 2023). Furthermore, the species is on the red list of endangered species (Marrugo 2019).

Recent genetic analyses confirm the high intraspecific diversity of *I. edulis* and its suitability for selection programs aimed at fruit productivity and adaptability (Rollo et al. 2020). Investigations into its role in ecosystem services, including carbon sequestration and erosion control, further highlight its value in climate-smart agriculture and restoration (Ocaña Zuñiga et al. 2023; Java Iberico 2024). The integration of *I. edulis* in degraded landscapes has also been encouraged due to its fast growth and capacity for nitrogen fixation, which accelerates soil rehabilitation processes (Pérez Peña 2022). However, despite its potential, *I. edulis* has not been widely included in structured breeding programs, and quantitative genetic studies remain scarce. Thus, exploring its genetic parameters through field trials is essential to support evidence-based improvement and conservation strategies.

Inga edulis is a tree native to South America, widely cultivated in agroforestry systems as a shade tree for coffee and cocoa crops (Ribeiro et al. 1999), food, timber, and medicine (Carvalho 2014). Its geographic distribution is from northwestern Argentina, Colombia, Ecuador, Peru, and Venezuela (Carvalho 2014). *Inga edulis* is a pioneer species and an early secondary species (Garcia et al. 2011) with a life cycle of less than 20 years (Prance and Silva 1975). It has rapid growth and adult trees can reach up to 28 m in tree height and 90 cm in D (diameter at breast height), although the tree generally varies from 5–10 m in height (Carvalho 2014). The stem is generally short, the crown is dense, flat and spread out (Carvalho 2014). The flowers are hermaphrodite, probably pollinated by insects, especially bees and wasps (Carvalho 2014). The fruit is follicle-shaped, measuring 30–200 cm length by 2–5 cm wide and the seeds are ellipsoid, smooth and glabrous, measuring 2–3 cm length and 1–1.5 cm wide (Carvalho 2014). The number of ovoid seeds can vary from 10–20. Fruiting is asynchronous in each population, allowing fruit production almost all year round, and in plantations, fruit production can begin at less than 2 years of age (Prance and Silva 1975). Despite its rapid growth and diverse uses, the species has not been the subject of any genetic improvement program (Lojka et al. 2023). Furthermore, the species has shown strong introgression with *Inga ingoides*, allowing the selection of hybrids through interspecific hybridization to further increase the yield and tolerance to flooding of the crop (Rollo et al. 2016; Rollo et al. 2020).

This study was designed to evaluate the genetic variability of *I. edulis* individuals based on selection criteria related to adaptability, growth, canopy structure, and fruit productivity to different ecological conditions. This study aimed to estimate the variations, parameters, and genetic correlations for growth, crown architecture, and reproductive traits in 105 open-pollinated *I. edulis* progenies at 18-months old, and to evaluate the possibility of simultaneous selection for multiple traits for applications in environmental restoration plantations. Our specific objectives were: i) To determine the narrow-sense heritability, mean-progeny heritability, and additive within progeny heritability for growth, architecture, and reproductive traits; ii) To determine the additive genetic correlation coefficient between pairs of growth, architecture, and reproductive traits; iii) To estimate the predicted direct genetic gains for mass selection and among and within progeny selection for D, and the predicted indirect genetic gains for other growth, architecture, and reproductive traits.

2 MATERIAL AND METHODS

2.1 Study Area and Trial Establishment

The trial was established in 1998 in the Peruvian Amazon, in the province of Coronel Portillo and Padre Abad in the department of Ucayali, eastern Peru. The study area extends approximately from 8° 18′ S to 8° 36′ S latitude and from 75° 06′ W to 74° 30′ W longitude, encompassing a mosaic of landscapes in Amazonian forests with lowland and mid-terraced agroforestry zones (Figure 1). To establish the progeny test, open-pollinated seeds were collected from 105 trees (referred to here as progenies) in the Aguaytia River basin. For collect seed, we selected the mother trees on base in the three criterions defined on base in the main objective of the famer for planting the trees in your lands. The selection was made by consulting the farmers, asking them why they had *I. edulis* trees on their properties: a) for fruit production (F), for shade (S), or for no specific reason, referred to as random (R). For each criterion, 35 mother trees were selected for seed collection. The progeny test was established using a split-plot design, with the plots representing the three seed collection treatments (F, S, R), and the 35 progenies of each treatment established within the subplots, each progeny represented by one plant, totaling 105 progenies (Table 1). The subplots were planted using a spacing of 2.5 × 2.5 m. The progeny test was set up using ten blocks (B1–B10) distributed under varying environmental, topographic, and management conditions, and in heterogeneous soils, classified into three sectors (called sites). Within each sector, the experiment was repeated three to four times (blocks): blocks B1, B2, B6, and B7 were planted in the Federico Basadre and Nueva Requena Highway (CFB, Site 1) sector, blocks B3, B4, and B5 in the Tournavista Highway (TOUR, Site 2), and blocks B8, B9, and B10 in the Curimaná Highway (CURI, Site 3) sector (Figure 1).

Figure 1. Location map of *Inga edulis* seed collection and blocks establishment from the Aguaytia River basin; blocks B1, B2, B6, and B7 were planted in the Federico Basadre Highway (CFB, Site 1) sector, blocks B3, B4, and B5 in the Tournavista Highway (TOUR, Site 2) sector, and blocks B8, B9, and B10 in the Curimaná Highway (CURI, Site 3) sector.

Figura 1. Mapa de localização da coleta de sementes e blocos estabelecida de *Inga edulis* coletadas em 1997 na bacia do rio Aguaytia; os blocos B1, B2, B6 e B7 foram plantadas no trecho da Rodovia Federico Basadre (CFB, Sítio 1), os blocos 3, B4 e B5 no trecho da Rodovia Tournavista (TOUR, Sítio 2) e os blocos B8, B9 e B10 no trecho da Rodovia Curimaná (CURI, Sítio 3).

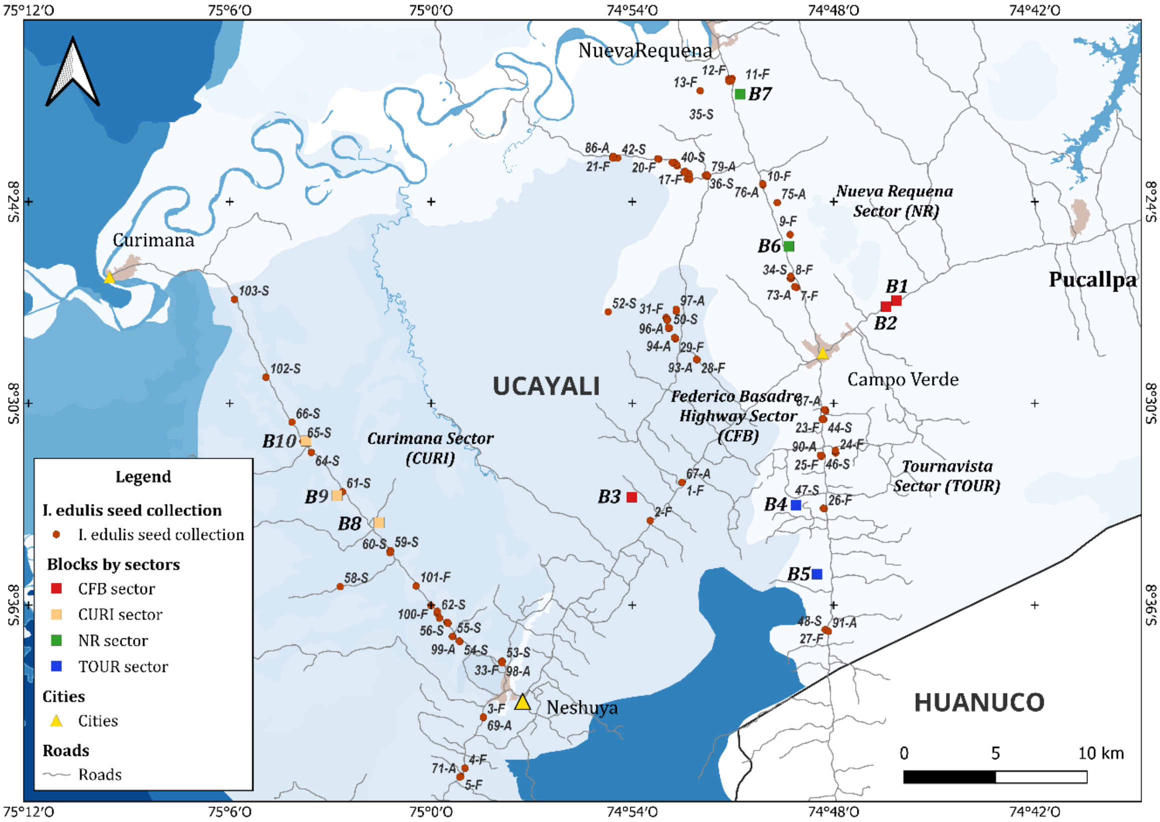

Table 1. Characteristics of experimental design, showing the number of sites, blocks (Bl), plots (treatments: Fruit (S), Shade (S), and Random (R)), subplots per plot, number of progenies per treatments (Np), total number of progenies per block (Npt), and number of trees per subplot (Nsp).

Tabela 1. Características do delineamento experimental, mostrando o número de sites, blocos (Bl), parcelas (tratamentos: Fruto (S), Sombra (S) e Aleatório (R)), subparcelas por parcela, número de progênies por tratamento (Np), número total de progênies por bloco (Npt) e número de árvores por subparcela (Nsp).

				Treatments (Np)				
Sites	Bl	Plots (treatments)	Subplots/plot	Fruit (F)	Shade (S)	Random (R)	Npt	Nsp
Site 1								
	B1	3	35	35	35	35	105	1
	B2	3	35	35	35	35	105	1
	B6	3	35	35	35	35	105	1
	B7	3	35	35	35	35	105	1
Site 2								
	B3	3	35	35	35	35	105	1
	B4	3	35	35	35	35	105	1
	B5	3	35	35	35	35	105	1
Site 3								
	B8	3	35	35	35	35	105	1
	B9	3	35	35	35	35	105	1
	B10	3	35	35	35	35	105	1

2.2 Evaluated Traits

The following phenotypic traits were measured in the trees at 18 months-old: D (diameter at breast height, cm), measured with a dendrometric ruler; total tree height (H, in m), measured with a clinometer; crown diameter in the North-South (DN, in m) and East-West (CE, m) directions, respectively, and average crown diameter (CD, m) calculated by $CD = (CN + CE)/2$; number of fruits per trees (NF); average fruit length (FL, in cm), calculated by the average fruit length per tree.

2.3 Data Analysis

To determine if there were significant differences between treatments (F, S, R), Tukey's test was used, assuming that the treatments had a fixed effect. The analysis was performed manually using an Excel spreadsheet.

The data were analyzed using linear mixed models under the REML/BLUP (restricted maximum likelihood/best linear unbiased prediction) approach, based on model 15 for each site and model 10 for the joint sites, considering open-pollinated progenies, replications (blocks), and one plant per subplot, using the SELEGEN-REML/BLUP software (Resende 2016). Components of variance and genetic parameters were estimated for each site by,

$$y = X_r + Z_a + W_b + \text{e}, \qquad \text{Eq. 1}$$

where y is the data vector, r is the vector of replication effects (assumed to be fixed) added to the overall mean, a is the vector of individual additive genetic effects (assumed to be random), b is the vector of block effects (assumed to be fixed), and e is the vector of errors (random). Uppercase letters represent the incidence matrices for the aforementioned effects. The following variance components were estimated: σ_a^2= additive genetic variance; σ_f^2= genetic variance among progenies; σ_e^2= environmental variance; σ_p^2= total phenotypic variance. The narrow-sense heritability (h_i^2), mean-progeny heritability (h_f^2), and additive within progeny heritability (h_w^2) for each trait were estimated by:

$$h_i^2 = \frac{\sigma_a^2}{\sigma_a^2+\sigma_e^2} \qquad \text{Eq. 2}$$

$$h_f^2 = \frac{(1/4)\sigma_a^2}{\sigma_f^2+\frac{\sigma_e^2}{J}}, \qquad \text{Eq. 3}$$

$$\text{and } h_w^2 = \frac{0.75\sigma_a^2}{0.75\sigma_a^2+\sigma_e^2} \qquad \text{Eq. 4}$$

where J is the number of blocks. Components of variance and genetic parameters were estimated for joint sites as:

$$y = X_r + Z_a + W_b + T_i + \text{e}, \qquad \text{Eq. 5}$$

where y is the data vector, r is the vector of repetition effect (assumed to be fixed) added to the overall mean, a is the genotypic effects (assumed to be random), b is the vector of blocks effect (assumed to be fixed), i is the vector of genotype x environment interaction effects (assume to be random), and e is the vector of errors (assumed to be random). Uppercase letters represent the incidence matrices for the aforementioned effects. The following components of interest were estimated: σ_a^2= additive genetic variance; σ_f^2= genetic variance among progenies; σ_{ge}^2= variance of the genotype-environment interaction; σ_e^2= environmental variance. The narrow-sense heritability (h_i^2) and mean-progeny heritability (h_f^2) for each trait were estimated by:

$$h_i^2 = \frac{\sigma_a^2}{\sigma_a^2+\sigma_{ge}^2+\sigma_e^2} \qquad \text{Eq. 6}$$

$$h_f^2 = \frac{(1/4)\sigma_a^2}{\sigma_f^2+\frac{\sigma_{ge}^2}{S}+\frac{\sigma_e^2}{SJ}}, \qquad \text{Eq. 7}$$

and $$h_w^2 = \frac{0.75\sigma_a^2}{0.75\sigma_a^2+\sigma_e^2} \qquad \text{Eq. 8}$$

where S and J are the number of sites and blocks, respectively. The selective accuracy (AC) was estimated by,

$$AC = \sqrt{h_f^2}. \qquad \text{Eq. 9}$$

We also calculated for each and joint sites the coefficients of additive genetic variation,

$$CV_{gi}\% = 100(\sqrt{\sigma_A^2}/x), \qquad \text{Eq. 10}$$

genetic variance among progenies,

$$CV_g\% = 100(\sqrt{\sigma_f^2}/x), \qquad \text{Eq. 11}$$

and environmental variance,

$$CV_e\% = 100(\sqrt{\sigma_e^2}/x), \qquad \text{Eq. 12}$$

where x is the mean of the trait under study. The relative correlation coefficient was estimated by,

$$CV_r = CV_g\%/CV_e\%. \qquad \text{Eq. 13}$$

The genotypic correlation among performance in various sites (r_{gloc}) for each trait was estimated by,

$$r_{gloc} = \sigma_f^2/(\sigma_f^2+\sigma_{ge}^2), \qquad \text{Eq. 14}$$

while the additive genetic correlations (r_a) between pairs of traits were computed for joint sites by:

$$r_a = \frac{COVa(x,y)}{\sqrt{\sigma_{a(x)}^2\sigma_{a(y)}^2}}, \qquad \text{Eq. 15}$$

where $COVa(x,y)$ is the additive genetic covariance between trait x and y, and $\sigma_{a(x)}^2$ and $\sigma_{a(y)}^2$ are the additive genetic variance for the trait x and y, respectively. Student t-test,

$$\mathrm{t} = r_a/\sqrt{(1-\mathrm{r}_\mathrm{a}^2)/(n-2)}\,, \qquad \text{Eq. 16}$$

where n is the number of progenies was used to determine the statistical significance of the r_g values (Cruz and Regazzi 1997).

Direct and indirect predict genetic gains and for each trait and the standardized selection index (i) were calculated on base in the mass selection of 30 individuals, while among and within progeny selection of were estimated on base in the selection of 30 progenies and one individual within progeny in each site and 3 individuals within progenies in joint sites, according method proposed by Falconer and Makay (1996). The predict direct genetic gain in selection (*DGg%*) was calculated by,

$$DGg\,\% = 100(ih\sigma_a/x_p) \qquad \text{Eq. 17}$$

while h and σ_a are the standard deviation of the heritability and additive genetic variance, respectively, and x_p is the mean population of the trait on analysis. The indirect predicted genetic gain in the selection ($IG_g\%$) for trait y, with direct selection for trait x was estimated by,

$$IGg\,\% = 100(ih_{(x)}r_a\sigma_{a(y)}/x_{p(y)}) \qquad \text{Eq. 18}$$

while $h_{(x)}$ and are the standard deviations of the heritability of direct selected trait x, r_a is the additive genetic correlation between trait x and trait y, $\sigma_{a(y)}$ is the standard deviation of the additive genetic variance for trait y, and $x_{p(y)}$ is the population mean for trait y.

3 RESULTS AND DISCUSSION

3.1 Survival, Variation, and Development of Traits

The present study included the establishment of ten experimental block (B1-B10) distributed across heterogeneous soils and under diverse environmental, topographic, and management conditions. The blocks were grouped into three sectors: Federico Basadre Highway (CFB: B1, B2, B6, and B7), Tournavista Highway (TOUR: B3, B4, and B5), and Curimaná Highway (CURI: B8, B7, and B10) (Figure 1). The study area is characterized by low, middle, and high terraces with contrasting drainage conditions. The soils are predominantly acidic, with low fertility on the high terraces, while the lower terraces have sandy and highly clayey textures. Annual rainfall ranges from 1,400 mm in the lower watershed to 2,500 mm in the upper watershed (Revilla-Chávez et al. 2023).

Table 2. Mean traits for treatments of selection by fruit (F), shade/biomass (S) and random selection (R) in each and joint sites (Joint).

Tabela 2. Média dos caracteres para os tratamentos de seleção por fruto (F), sombreamento/biomassa (S) e seleção aleatória (R) em cada site e em conjunto de sites (Joint).

Site	D (cm)	MMI (cm)	H (m)	MMI (m)	CD (m)	NF	FL (cm)	SUR (%)
Site 1								
Fruit	8.71a	0.48	5.09a	0.28	4.08a	28.3a	74.7a	100a
Shade	9.31a	0.52	5.30b	0.29	4.15a	26.7a	59.2b	82.6b
Randomly	8.86a	0.49	4.83ac	0.27	3.87b	32.5a	67.5c	98.6a
Total	8.94A**	0.50	5.12A**	0.28	4.03A	29.3A	67.7A**	93.8A**
Site 2								
Fruit	7.1a	0.39	3.9a	0.22	2.9a	19.3a	63.1a	93.3a
Shade	6.8a	0.38	3.9a	0.22	3.0a	22.2a	57.6a	97.1a
Randomly	7.2a	0.40	4.0a	0.22	3.16a	18.04a	59.6a	99.0a
Total	7.0B	0.39	3.9B	0.22	3.1B	20.1B	59.9B	96.5AB
Site 3								
Fruit	8.3a	0.46	5.2a	0.29	3.6a	12.0a	53.7a	98.1a
Shade	8.1a	0.45	5.1a	0.29	3.3ab	11.9a	65.6b	97.1a
Randomly	9.0b	0.50	5.8b	0.32	3.9ac	19.4b	57.9b	97.1a
Total	8.5A**	0.47	5.4AC**	0.30	3.6C**	14.4C	57.9B**	97.5B
Joint								
Fruit	8.11a	0.45	4.79a	0.27	3.62a	21.9a	66.5a	97.4a
Shade	8.14a	0.45	4.89a	0.27	3.61a	21.5a	59.5b	91.4b
Randomly	8.39a	0.47	4.86a	0.27	3.63a	25.6a	63.1ab	98.3a
Total	8.22	0.46	4.85	0.27	3.62	23.0	63.1**	95.7**

**P< 0.01; *P< 0.05; D = diameter at breast height; H = total height of the trees; CD = crown diameter; NF = number of fruits; FL = fruit length; MMI = mean month increment; Different lowercase letters indicate significant differences between the means of the traits for the treatments (F, S, R), while different uppercase letters indicate significant differences between the means of the traits between the sites based on Tukey's test, with a 95% confidence level.

**P< 0,01; *P< 0,05; D = diâmetro à altura do peito; H = altura total das árvores; CD = diâmetro da copa; NF = número de frutos; FL = comprimento dos frutos; MMI = incremento médio mensal; Letras minúsculas diferentes indicam diferenças significativas entre as médias dos caracteres para os tratamentos (F, S, R), enquanto letras maiúsculas diferentes indicam diferenças significativas entre as médias dos caracteres entre os sites, com base no teste de Tukey, com um nível de confiança de 95%.

The total survival rate (SUR) of I. edulis at 18-months-old was high (95.7%), ranging among sites from 93.8–99.5% (Table 2), indicating the good adaptation of the species in the three sites. This good adaptation can be explained by the fact that the seeds for to establish the progeny test were collected within the area where the trial was planted (Figure 1). High survival rates (90%) were also reported in *I. edulis* up to 4 years old (Azevedo et al. 2015). Regarding the treatments of seed collection from selection by fruit (F), shade/biomass (S) and random selection (R), significantly differences (P< 0.05) were detected for survival (SUR) in sites 1 and joint sites (Table 2). Tukey test (treatments assumed as fixed effect) showed that survival was significantly lower for S in site 1 and joint sites, indicating that the lowest survival in site 1 is due to the low survival from seed collection for treatment S.

Significantly differences were detected among treatments for D, H, DC, and FL in site 1 and 3. Tukey test showed that D was significantly lower for F and R than S treatment in site 1 and for F and S than for R treatments in site 3. Tukey test showed that H was significantly lower for R than F and S treatment, as well as significant lower for F than S in site 1, and significant lower for F and S than for R in site 3. Tukey test showed that DC was significantly lower for R than F and S treatment in site 1, and significant lower for S than R in site 3. Tukey test showed that FL was significantly lower for S than F and R and lower for R than F in site 1, and lower for F than S and R in site 3. These results can be attributed to the fact that the shade collections were obtained mostly from zones with different agroecological conditions than the highland soils, which are soils with higher rainfall and fertility than the middle lands, where 14 of 35 progenies were collected from highland soils (Figure 1), which have a higher average of Magnesium (Mg) and cation exchange capacity (CEC) compared to the blocks located in middle land soils with less rainfall and fertility.

The development of traits varied among the sites. Tukey test detected significant differences ($P< 0.05$) among sites for all traits (Table 2). All traits were significantly lower in site 2 than in sites 1, D, DC, NF and FL were also significant lower in site 3 than site 1, while in contrast, H was significant in lower in site 1 than site 3 and CD and NF were significant lower in site 2 than in site 3. The highest values for D, CD, NF, and FL in site 1 suggest that the environmental conditions of this site (probably greater availability of nutrients, water, and light) is the most favored for the development of the species.

Although the greater MMI observed in the present study for H may be attributed to the younger age, it also indicates good height growth. Falcão and Clement (2000) also reported CD of up to 3 m at 3 years old, value lower (2.9–4.22 m) than those observed here, which reinforces the good architectural development of the trees at 18 months of age. In *I. edulis* plantations in Central Amazonia at 3 years old, a H of 4 m was reported (Falcão and Clement 2000), which corresponds to an MMI of 0.111 m. The MMI for H at 18 months of age in site 1 and 3 was higher than that reported for *I. edulis* 4-months-old plantations growing in degraded areas (MMI = 0.837 m/4 months = 0.21 m) and dry soil (MMI = 0.892 m/4 months = 0.22 m) (Azevedo et al. 2015). Sites 1 and 3 also showed the highest DC and FL values, although FL did not show significant difference between sites 2 and 3. FL at all sites and at joint was higher than that reported for *I. edulis* in wild stands (39 cm) and lower than in cultivated stands (83 cm) (Rollo et al. 2020), as well as higher than that reported for *Inga laurina* (51.71–58.14 cm) (Farias et al. 2020). Our results for FL also corroborate those observed in plantations in the Peruvian Amazon, where fruit length can exceed 2 m, but in trees in natural populations it rarely exceeds 50 cm (Pennington 1997).

3.2 Genetic Variation and Parameter

Significant differences were detected among progenies for most traits, both in the analyses within sites and in the joint analysis of sites (Table 3). Significant differences were detected among progenies for D and FL in all sites and joint site analyses, for H and CD in sites 2 and 3, and in the joint site analysis, and for NF in site 3 and in the joint site analysis. These results indicate that the population mean for most traits can be improved by selecting progenies with higher values for the traits in genetic improvement programs.

Table 3. Mean and genetic parameters for traits for each and joint sites.

Tabela 3. Médias e parâmetros genéticos para os caracteres em cada site e conjunto de sites.

	Mean	h_i^2	h_m^2	h_w^2	AC	$CV_{gi}\%$	CV_r	r_{gloc}
Diameter (D, cm)								
Site 1	8.96*	0.306	0.498	0.248	0.705	13.8	0.33	
Site 2	6.9*	0.126	0.246	0.098	0.496	9.0	0.19	
Site 3	8.5**	0.110	0.218	0.086	0.467	9.9	0.18	
Joint	8.2**	0.196	0.689	0.156	0.830	11.9	0.25	0.844
Height (H, m)								
Site 1	5.1	0.106	0.211	0.082	0.459	5.8	0.17	
Site 2	3.9*	0.031	0.067	0.023	0.258	4.2	0.09	
Site 3	5.4**	0.107	0.212	0.084	0.460	5.8	0.17	
Joint	4.8*	0.095	0.485	0.074	0.696	6.1	0.16	0.681
Crown diameter (CD, m)								

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to be continueted

Table 3. continuation
Tabela 3. continuação

	Mean	h_i^2	h_m^2	h_w^2	AC	$CV_{gi}\%$	CV_r	r_{gloc}
Site 1	4.04	0.134	0.258	0.104	0.508	8.8	0.20	
Site 2	3.0*	0.111	0.220	0.086	0.469	8.8	0.18	
Site 3	3.6*	0.104	0.207	0.039	0.455	9.5	0.17	
Joint	3.6*	0.108	0.521	0.084	0.722	8.8	0.17	0.708
Number of fruits (NF)								
Site 1	28.5	0.236	0.411	0.188	0.641	40.4	0.28	
Site 2	17.8	0.114	0.225	0.088	0.475	27.8	0.15	
Site 3	11.7**	0.020	0.043	0.088	0.207	19.7	0.07	
Joint	20.7**	0.177	0.635	0.142	0.797	41.4	0.23	0.716
Fruit length (FL, cm)								
Site 1	67.1*	0.418	0.618	0.350	0.786	16.7	0.42	
Site 2	53.0*	0.086	0.176	0.066	0.419	8.4	0.15	
Site 3	57.1**	0.111	0.219	0.090	0.468	11.1	0.18	
Joint	60.3*	0.112	0.530	0.087	0.728	9.8	0.18	0.715

**P< 0.01 and *P< 0.05. with 1 and 0.5 degrees of freedom for likelihood ratio test (LRT), $\chi 2$ deviance chi-square; $CV_{gi}\%$ = coefficient of individual additive genetic variation; h_i^2 = narrow-sense heritability; h_m^2 = mean-progeny heritability; h_w^2 = within-progeny heritability; AC = selective accuracy; CV_r = coefficient of relative variation; r_{gloc} = genotypic correlation between performance in various environments.

**P< 0.01 e *P< 0.05. com 1 e 0.5 graus de liberdade para o teste da razão de verossimilhança (LRT), qui-quadrado de desvio $\chi 2$; $CV_{gi}\%$ = coeficiente de variação genética aditiva individual; h_i^2 = herdabilidade no sentido restrito; h_m^2 = herdabilidade da média de progênie; h_w^2 = herdabilidade aditiva dentro da progênie; AC = acurácia seletiva; CV_r = coeficiente de variação relativa; r_{gloc} = correlação genotípica entre o desempenho em vários ambientes.

Narrow-sense heritability (h_i^2) ranged from low to moderate among traits (0.020–0.418), and was also lower than the mean-progeny heritability (h_f^2: 0.043–0.618) for site and joint analyses (Table 3). These results indicate that all traits are under genetic control and can be improved by both mass and progeny selection. Heritabilities and selective accuracy (AC) for progeny selection for the same site and joint site analyses were higher for D (h_i^2: 0.110–0.306; h_f^2: 0.218–0.689; AC: 0.467–0.830) than for H (h_i^2: 0.031–0.107; h_f^2: 0.067–0.485; AC: 0.258–0.696), CD (h_i^2: 0.104–0.134; h_f^2: 0.207–0.521; AC: 0.455–0.722), and NF (h_i^2: 0.020–0.236; h_f^2: 0.043–0.635; AC: 0.207–0.797), as well as higher or similar to those of NF in sites 2 and 3, and for joint site analysis (h_i^2: 0.086–0.112; h_f^2: 0.176–0.530; AC: 0.419–0.728). Furthermore, the additive individual coefficient of variation ($CV_{gi}\%$) and the coefficient of relative variation (CV_r) for the analyses of the same site and joint site analysis were also higher for D ($CV_{gi}\%$: 9.0–13.8%; CV_r: 0.18–0.33) than for H ($CV_{gi}\%$: 4.2–6.1%; CV_r: 0.09–0.17) and CD ($CV_{gi}\%$: 8.8–9.5%; CV_r: 0.17–0.20), and higher than NF for CV_r (0.07–0.28), and higher FL for $CV_{gi}\%$ and in site 2 ($CV_{gi}\%$: 8.4%) and joint site analysis ($CV_{gi}\%$: 9.8%) and high or similar for CV_r in sites 2 and 3, and joint site analysis (CV_r: 0.15–0.18). The exception was NF for $CV_{gi}\%$ at each and joint site analysis (19.7–41.4%) and FL in sites 1 (16.7%) and 3 (11.1%), and for CV_r in sites 1 (0.42). We emphasize that at and joint site analysis, D presented higher values for all parameters for most traits, with expectation for NF for $CV_{gi}\%$, as already comment. The genetic parameters for most sites, as well as in the combined analysis of sites, were lower for H than those observed for other traits. The exception was observed at site 3, where the parameters h_i^2, h_f^2, AC, and CV_r were higher or similar for H than for CD and NF. Genetic parameters, both in most site and in the joint site analysis were also lower for CD than those observed for NF and FL, with the exception of site 3, where the parameters h_i^2, h_f^2, AC, and CV_r were higher or similar for CD than for NF, and higher or similar for all parameters estimated for CD than for FL at site 2. Regarding reproductive traits, all genetic parameters were higher or similar for NF than for FL at site 2 and in the joint site analysis, as well as at sites 1 and 3 for $CV_{gi}\%$. Furthermore, the genotypic correlation among performance in various sites (r_{gloc}) was higher for D (0.844) compared to the other traits (0.681–0.716), indicating that gene-environment (G×E) interaction is simple for all traits and shows that selection can be performed across all sites. In other words, selection can be performed at only one site, and the improved genetic material (seeds or propagules) can be used for planting at all sites. These results indicate that D is the most suitable trait for direct selection aimed at increasing productivity in terms of growth, architecture, and reproductive traits in the simultaneous genetic improvement of multiple traits. The results also show that traits can be genetically improved by both mass selection and progeny selection. D has generally been reported in many studies as having higher heritability than tree height. For example, higher h_i^2 for D than H and ranging from low to moderate has been reported for *Guazuma crinita* (Revilla-Chávez et al. 2022), *Pinus caribaea* var. *caribaea* (Zulian et al. 2024), *Pinus caribaea* var. *hondurensis* (Macedo et al. 2015), *Pinus elliottii* var. *elliottii* (Romanelli and Sebbenn 2004), *Pinus taeda* (Souza et al. 2022), and *Neolamarckia cadamba* (Que et al. 2021). Due to this, the D has been also considered the most suitable trait for selection (Aguiar et al. 2019; Revilla-Chávez et al. 2022, Chávez and Sebbenn 2024; Torres-Dini et al. 2024). The generally lower heritability for H than for other traits suggests high sensitivity to the environment. This pattern was also recorded in *Cedrela odorata* (Paredes-Villanueva et al. 2019) and in the hybrid *Eucalyptus grandis* × *E. urophylla* (He et al. 2023), where the growth height trait tends to be more influenced by site conditions.

In contrast to our results, higher heritabilities have been reported for reproductive traits than for growth traits, as reported by Revilla-Chávez et al. (2022) in progeny testing of *G. crinita* established in the same Peruvian Amazon region as the present study. Similarly, studies with *Elaeis guineensis* and *Theobroma cacao* have documented higher heritabilities in reproductive traits compared to growth traits (Cros et al. 2019).

3.3 Genetic Correlations

Additive genetic correlation (r_a) values ≤ 0.3 were considered low, between $0.3 < r_a < 0.5$ as moderate, between $0.5 \leq r_a < 0.7$ as moderately high, and ≥ 0.7 as high. The r_a was significantly greater than zero (P< 0.01), ranging from moderately high to high for the trait pairs D×H (0.696–0.844) and D×CD (0.524–0.934), and ranged from moderate to moderately high for H×CD (0.408–0.532), and NF×FL (0.460–0.738) at each site and in the joint site analysis (Table 4). The r_a was also significantly greater than zero, but low for the trait pairs D×FL at site 2, 3, and joint site (0.178–0.197), and CD×NF (0.181) at site 1. These results indicate a pleiotropic effect of the genes that control these traits and a favorable scenario for the simultaneous genetic improvement of multiple traits. Direct selection on one of these traits is expected to indirectly increase the others. The greater r_a value among D with H and CD indicates that D is the most suitable trait for direct selection, while H and CD can be improved indirectly. Furthermore, based on the magnitude of r_a, direct selection for D is expected to result in a moderately high to high increase in H and CD at each of the sites and for the joint sites, and a low indirect increase in NF for joint sites selection and for FL at sites 2 and 4. However, because D shows a moderately high genetic correlation with DC at site 3 and a strong genetic correlation with DC in the analysis of combined sites, and DC shows a low correlation with FL at site 3 and in joint sites, direct selection for D and the consequent indirect increase in DC will also produce a small increase in FL at site 3 and joint sites. From moderate to high genetic correlations between D×H have been reported in several studies with tree species (Sebbenn et al. 2009; Chávez and Sebbenn 2024; Torres-Dini et al. 2024; Longui et al. 2025; Oliveira Junior et al. 2025). A positive relationship between D and H with CD has also been reported other several tree species (Asigbaase et al. 2023; Ekasari and Kurnia 2023).

Table 4. Additive genetic correlation (r_a) between traits for each (1, 2, and 3) and joint sites.

Tabela 4. Correlação genética aditiva (r_a) entre caracteres para cada (1, 2 e 3) e conjunto de sites.

	Site 1	Site 2	Site 3	Joint sites
D×H	0.842**	0.844**	0.696**	0.728**
D×CD	0.934**	0.524**	0.738**	0.602**
D×NF	0.058	0.153	0.041	0.024
D×FL	0.109	0.194*	0.197*	0.178*
H×CD	0.431**	0.408**	0.532**	0.464**
H×NF	-0.051	-0.028	-0.139	-0.092
H×FL	-0.175*	-0.285**	-0.135	-0.104
CD×NF	0.181*	0.145	0.149	0.169
CD×FL	0.167*	0.038	0.075	0.090
NF×FL	0.738**	0.460**	0.617**	0.583**

**P< 0.01 and *P< 0.05 for t-test with 103 degrees of freedom.

**P< 0,01 e *P< 0,05 para o teste t com 103 graus de liberdade.

Previous studies have warned that genetic correlations can generate conflicts between traits, for example, between productivity and wood quality (Wu et al. 2013; Richards et al. 2020). In this study with *I. edulis*, significantly lower than zero and low r_a values were detected between the H×FL traits at sites 1 and 2 (from -0.285 to -0.175), indicating that direct selection for an increase in one of the traits in this pair will result in a small indirect decrease in the other trait. For example, direct selection for an increase in D in sites 1 and 2 will result in a moderately high indirect increase in H and, consequently, is expected to result in a small indirect decrease in FL. Thus, the results show that the simultaneous improvement of multiple growth (D, height) and architectural (CL) traits, prioritizing D growth, should not negatively interfere with, or at most slightly compromise, the variability of the reproductive functional traits (NF, FL) of the trees.

3.4 Direct and Indirect Genetic Gains

The greatest genetic advances were generally achieved through the strategy of selection among and within progeny (Table 5). The direct ($DG_g\%$) and indirect ($IG_g\%$) genetic gains predicted for the selection of 30 progenies and one individual within the best selected progenies at each site were greater than for the mass selection of 30 individuals in sites 2 and 3, and for the joint analysis of all traits and at all sites, as well as for direct selection for H in site 1. The exception was observed at site 1, where the selection intensity for mass selection and the strict-sense heritability for all traits were higher than at the other sites. These results coincide with estimates made in *Eucalyptus globulus* (Grattapaglia et al. 2018) and *G. crinita* (Revilla-Chávez et al. 2022). Site 1 includes 4 blocks, and the greater environmental heterogeneity may have resulted in low precision in progeny selection and genetic gains. On the other hand, the greatest genetic gains for selection among and within progeny can be attributed to the fact that the mean for a maternal progeny, calculated based on its descendants, may better represent the additive genetic value of the parents. This allows us to maximize genetic gains by selecting the best siblings from the best progeny, controlling the pedigree and maintaining genetic variability throughout the breeding program. Therefore, selection among and within progeny is the most suitable strategy for the genetic improvement of *I. edulis* populations.

Table 5. Direct ($DG_g\%$) and indirect ($IG_g\%$) genetic gains for mass selection and for selection among and within progenies (among-within) for each and joint sites. Indirect gains were estimated on base on direct selection for D (diameter at breast heigh).

Tabela 5. Ganhos genéticos diretos ($DG_g\%$) e indiretos ($IG_g\%$) para seleção massal e seleção entre e dentro de progênies (among-within) para cada site e conjunto de sites. Os ganhos indiretos foram estimados com base na seleção direta para D (diâmetro à altura do peito).

Site		SI%	*i*	D	H	CD	NF	FL
Mass selection								
1	$DG_g\%$	7.3	1.887	14.4	3.6	6.1	37.1	20.3
	$IG_g\%$				5.1	8.6	2.4	1.9
2	$DG_g\%$	14.4	1.554	5.0	1.2	4.6	17.4	3.8
	$IG_g\%$				2.0	2.5	2.8	0.9
3	$DG_g\%$	14.4	1.445	4.3	2.3	2.0	17.3	4.7
	$IG_g\%$				1.6	2.2	0.7	0.9
Joint	$DG_g\%$	9.0	1.808	9.5	3.4	5.2	31.4	5.9
	$IG_g\%$				3.6	4.2	0.8	1.4
Among-within		a/w	a/w					
1	$DG_g\%$	28.6/5.0	1.18/1.71	13.3	3.4	5.7	34.6	18.6
	$IG_g\%$				4.8	7.9	2.3	1.8
2	$DG_g\%$	28.6/33.3	1.8/1.097	5.3	1.3	4.9	18.6	4.1
	$IG_g\%$				2.1	2.7	3.0	1.0
3	$DG_g\%$	28.6/33.3	1.18/1.097	4.7	2.5	2.2	18.5	5.0
	$IG_g\%$				1.7	2.3	0.7	1.0
Joint	$DG_g\%$	28.6/30.0	1.18/1.159	10.5	4.2	6.3	35.1	7.1
	$IG_g\%$				4.0	4.7	0.9	1.5

SI% = intensity of selection; *i* = standardized selection indices (Falconer and Makay 1996); a/w = among and within progenies.

SI% = intensidade de seleção; *i* = índices de seleção estandartizados (Falconer e Makay 1996); a/w = entre e dentro de progênies.

The $DG_g\%$ gain was generally greater than or similar to (1.2–37.1%) the $IG_g\%$ (0.7–8.6%) at each site and for the joint sites. The exception was H and CD at site 1, H at site 2 and the joint sites, and CD at site 3. This can be attributed to the fact that the selection intensity and h_i^2 were greater for the directly selected trait D (h_i^2 = 0.306), consequently, the additive genetic variation was also greater than for H and CD, associated with the occurrence of high additive genetic correlations (r_a > 0.7) between D×H at sites 1, 2 and in joint sites, and between D×CD at sites 1 and 3.

Both the $DG_g\%$ and $IG_g\%$ were, in most cases, higher for all traits at site 1 than at the other sites. This can be attributed to the higher selection intensity adopted at site 1 (mass selection = 7.3%; within progenies = 25%), made possible by the greater number of blocks established at the site (4 blocks). Furthermore, most genetic parameters (h_i^2, $CV_{gi}\%$, and CV_r) were higher for the traits, and the r_a between D with H, CD, NF and FL was generally higher at site 1 than that observed at the other sites. These results indicated site 1 as the most suitable for selection, aiming to maximize direct and indirect genetic gains.

Our results reinforce the idea that canopy architecture and reproductive traits can respond positively to indirect selection combined with direct selection for growth traits, especially when specific phenotypic criteria are used, such as canopy type. These results also confirm that the experimental design and the differentiation between selection treatments were effective in detecting the genetic variability expressed in different types of traits and point to a concrete opportunity for breeding *I. edulis*, initially focusing on direct selection for D growth and indirect breeding of architectural and reproductive traits.

4 CONCLUSIONS

There are significant genetic differences between progenies for most traits, both within sites and joint sites. The genotype-environment interaction was of the simple type, and therefore selection can be carried out in only one site, and the improved genetic material (seeds or propagules) can be used for planting in all sites. Estimates of narrow-sense heritability (h_i^2), mean-progeny heritability (h_f^2), and additive within progeny (h_w^2) showed that all traits are under genetic control and can be improved by both mass selection and among and within progeny selection. The highest values of the genetic parameters observed for most traits at site 1 indicate that this is the most suitable site for selection. The estimated genetic parameters were higher for D in the joint site analysis, indicating that this is the most suitable trait for direct selection. The significantly greater than zero genetic correlations between D and the traits H, CD, and FL showed that simultaneous genetic improvement of multiple-traits is possible through direct selection for D. The among and within progeny selection strategy was determined to be the most suitable for obtaining greater genetic gains. Our results reinforce the idea that canopy architecture and reproductive traits can respond well to indirect selection based on direct selection for growth traits.

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6 AUTHORS' CONTRIBUTION

J.M. Revilla-Chávez: Writing – original draft, supervision. H.E. Vidaurre-Arévalo: Conceptualization, formulation or evolution of general research goals and objectives. E.E. López-Galán: Data curation, conducting tasks like data processing, cleaning, cataloging, annotating, and retention. J.J. Revila-Macedo: Investigation, searching and reviewing the literature, samples, data and other evidence. J.A. Mori-Vásquez: Methodology, development or design of methodology; Model Creation. J.A. Mego-Pérez: Investigation, searching and reviewing the literature, samples, data and other evidence. A.M. Sebbenn: Proofreading, writing, review and editing, methodology, validation, formal analysis.

7 CONFLICTS OF INTEREST

The authors declare that they have no conflict of interest related to the publication of this manuscript.

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