

Genetic control of quantitative and qualitative traits of *Calycophyllum spruceanum* in the Peruvian Amazon

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Abstract: Abstract - Families of 38 month-old *Calycophyllum spruceanum* planted at three locations in the Peruvian Amazon were analyzed for breeding purpose. Significant differences were detected among families, sites and combined sites for the traits trunk diameter (D), height (H), number of nodes (NN), number of branches (NB) and survival rate (SUR), except for NN at site 2 and SUR at site 3 and combined sites. The correlation of the genotype-environment interaction was simple for D, H, NN, and SUR (0.77-0.89). Heritability was generally highest for D, H, NN, and NB (0.12-0.7), and the genotypic coefficient of variation ranged from 8.6-27.4%. Genetic correlations between these traits within and among sites ranged from 0.35-1.0. The selection of 75 trees from different families, within blocks and locations, suggested the possibility of genetic gains (6.1-29.8%) for D, H, NN, and NB, and that the remaining effective population size can be exploited in future selection cycles.

Keywords: Genetic correlations, genetic variation, heritability, progeny test, tree breeding

INTRODUCTION

Calycophyllum spruceanum (Benth.) (Rubiaceae) is a heliophytic pioneer tree found in alluvial forests in Brazil, Bolivia, Colombia, Ecuador and Peru, up to 1000 m above sea level (Reynel et al. 2003, Sears et al. 2014, Ramírez 2016, Saldaña et al. 2021). The tree has multiple uses; its timber is exported to various parts of the world in view of the beautiful creamy brown color and high density of the wood, which makes it durable and suitable for construction (Taylor 2005). The very straight, cylindrical bole of adult trees can reach diameters of 50-120 cm and a height of 20-35 m, with a crown in the upper third. A study on this species with seeds from different origins in the Peruvian Amazon reported growth to a height of 1.4-1.6 m within 6 months and to 3.5-4.7 m within one year (Sotelo Montes et al. 2003). In Peru, the response potential of the species in plantations for industrial purposes is considered highly efficient and promising (Orrego and Bustamante 2017). At the national and international level, the demand for *C. spruceanum* is on the rise, due to the wood properties and low production costs. In recent years, the species has been counted among the first 10 commercial species for saw wood production, with very diverse applications, e.g., as structural timber for construction, furniture and sporting goods (Orrego and Bustamante 2017, Saldaña et al. 2021).



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Due to the economic and social relevance of *C. spruceanum* wood production by small farmers, the genetic variability of wild populations of the species has been the focus of some research based on genetic markers (Russel et al. 1999, Dávila-Lara et al. 2017, Saldaña et al. 2021) and quantitative traits (Sotelo Montes et al. 2003, Sotelo Montes et al. 2006, Sotelo Montes et al. 2007a, Sotelo Montes et al. 2007b, Sotelo Montes et al. 2007c, Sotelo Montes et al. 2008, Boivin-Chabot et al. 2004, Weber and Sotelo Montes 2005, Dawson et al. 2009, Weber et al. 2009, Thauchen et al. 2011). However, information about the genetic variation and control of growth and quality traits of the species is currently limited, since these studies addressed only a minor part of the species distribution.

Due to the increase in deforestation, forest fires and intense selective cutting in the environments of *C. spruceanum*, as well as the increased demand for its seeds for reforestation (Carmo et al. 2017), strategies of conservation and breeding of the species are urgently needed. Provenance and progeny tests, underlying the determination of genetic variation within and among populations, genetic inheritance (heritability) and phenotypic and genetic correlations between quantitative and qualitative traits have been used for both *ex situ* conservation and breeding of populations (Sebbenn et al. 2005). These data are fundamental to evaluate whether a germplasm collection strategy efficiently represents and conserves the genetic variation of populations of a species *ex situ* and for successful selection in breeding programs (Sebbenn et al. 2009a). Provenance and progeny tests can therefore be used for both purposes simultaneously, *ex situ* conservation and production of somewhat improved seeds, for both commercial and environmental reforestation (Sebbenn et al. 2005, Sebbenn et al. 2009a). To this end, the best trees with desirable traits are selected (Sebbenn et al. 2009a, Canuto et al. 2016). Likewise, testing families from different origins allows a better understanding of the genetic variability in populations of a species and detects the most adaptable genotypes to the environmental conditions of a reforestation site (Menegatti et al. 2016, Revilla-Chávez et al. 2022).

Therefore, this study analyzed the genetic variation and control of quantitative and qualitative traits of 38-month-old *C. spruceanum* trees in progeny trials in the Peruvian Amazon, to obtain information for the implementation of second-generation seed orchards with high seed quality for forest restoration.

MATERIAL AND METHODS

Study sites and progeny tests

The progeny tests were established at three locations in the Aguaytía river basin, on the eastern slope of the Cordillera, in the department of Ucayali, Peru (between lat 9° 24' 25.87" S, long 75° 54' 38.91" W and lat 7° 57' 36.47" S, long 74° 5' 33.64" W, in an area 100 km E-W and 60 km N-S). The vegetation of the area is mainly tropical premontane forest, with a mean annual temperature of 26 °C (Holdridge 1978). Rainfall increases with increasing elevation: at sites 1, 2 and 3, at average elevations of 150, 200, and 260 m asl, respectively, mean annual precipitation is 1656.3, 1926.45, and 2501.0 mm ha⁻¹ year⁻¹, respectively (Hijmans et al. 2005). However, water stress of 1, 4 and 5 months was observed at sites 3, 2 and 1, respectively (Ugarte-Guerra and Domínguez-Torrejón 2010). Data of the progeny tests and characteristics of the three experimental sites are listed in Table 1.

The progeny tests were arranged in a randomized complete block design, with five blocks, 200 open-pollinated families and two plants per plots. The families were derived from seeds collected from 200 seed trees in June 1998, at 13 sites in the Aguaytía river basin: 39 families from the district of Nueva Requena; 5 families from the Neshuya river, at km 49.5 of the countryside highway Carretera Federico Basadre (CFB); 5 families from the Tahuayo river basin, at km 72 CFB; 10 from the Curimaná river basin; 6 from the Aguaytía river basin; 7 from the Yurac-Aguaytía river basin; 21 from Puerto Inca; 6 from Von Humboldt; 43 from Macuya; 50 from

Table 1. Location, progeny test and edaphoclimatic characteristics of evaluation plots of *Callycophyllum spruceanum* at three sites in the Aguaytía river basin, Ucayali, Perú

Description of the trials	Site 1	Site 2	Site 3
Number of families	200	200	200
Number of blocks	5	5	5
Number of plants per plot	2	2	2
Elevation (m) ^ε	150	200	260
Rainfall (mm/ha/year) ^ε	1656	1926	2501
Number of months under water stress ^ε	5	4	1
Terrace ^ε	low	medium	high
Soil ^ε	very sandy	sandy loam	clayey
Phosphorus availability (P)	low	low	high
Levels of K, Ca and MG ^ε	medium	medium	high

^ε Hijmans et al. (2005); ^ε Ugarte-Guerra and Domínguez-Torrejón (2010); K= Potassium; Ca= Calcium; Mg= Magnesium

San Alejandro; 7 families from along the CFB up to km 72; 6 from along the Curimaná road; and 3 families from the Aguaytía river basin along the CFB to the district of Tournavista (Table 2). Each block comprised a total of 400 plants, 200 plots and 2 plants per plot, at a spacing of 2.5 x 2.5 m, on an area of 2,500 m² per block. Two plant rows around the blocks were considered border rows that were not evaluated and they were separated by a 5-m wide fire strip. At the time of planting, 1600 kg of earthworm humus ha⁻¹ and 320 kg of rock phosphate ha⁻¹ (1 kg and 200 g per plant, respectively) were applied to the experimental area. In the second and third years, fertilization was repeated, with 112 kg ha⁻¹ urea, 316 kg ha⁻¹ rock phosphate and 160 kg ha⁻¹ potassium chloride (i.e., 70, 185, and 100 g of each product per plant, respectively). During the first 12 months, plants stunted by weeds, insects and rodents were eliminated.

Estimates of genetic parameters

The data were arranged in a randomized block design and processed as described below. The REML/BLUP procedure (restricted maximum likelihood/best unbiased linear prediction) by the linear mixed model was used in individual analyses to estimate the variance components and genetic parameters of each trait evaluated at each site, using the SELEGEN software, based on the statistical Model 1 (Resende 2016), $y = Xr + Za + Wp + e$, where y , r , a , p and e are the data, effects of repetition (fixed) added to the overall mean, individual additive genetic effects (random), effects of portion and the error or residual vector (random), respectively. Capital letters represent the incidence matrices for the

Table 2. Score used to measure stem shape (SSH) in 38-month-old *Calycophyllum spruceanum* trees

Class	Terminal but presence	Terminal but dominance	Branch orientation	Branch position	Stem	Score
Stem shape	yes	yes	vertical	different	straight	100
	yes	yes	horizontal	different	straight	98
	yes	yes	vertical	different	crooked	96
	yes	yes	horizontal	different	crooked	94
Branched stem	yes	yes	vertical	different	-	92
	yes	yes	horizontal	different	-	90
	yes	yes	vertical	single plane	-	88
	yes	yes	horizontal	single plane	-	86
	no	yes	vertical	different	-	84
	no	yes	horizontal	different	-	82
	no	yes	vertical	single plane	-	80
	no	yes	horizontal	single plane	-	78
	yes	no	vertical	different	-	76
	yes	no	horizontal	different	-	74
	yes	no	vertical	single plane	-	72
	yes	no	horizontal	single plane	-	70
	no	no	vertical	different	-	68
	no	no	horizontal	different	-	66
no	no	horizontal	single plane	-	64	
no	no	vertical	single plane	-	62	
Inclined stem shape	yes	yes	vertical	different	-	60
	yes	yes	horizontal	different	-	58
	yes	yes	vertical	single plane	-	56
	yes	yes	horizontal	single plane	-	54
	no	yes	vertical	different	-	52
	no	yes	horizontal	different	-	50
	no	no	vertical	single plane	-	48
	no	no	horizontal	single plane	-	46
	yes	no	vertical	different	-	44
	yes	no	horizontal	different	-	42
	yes	no	vertical	single plane	-	40
yes	no	horizontal	single plane	-	38	

said effects. For combined site analysis, Model 4 (Resende 2016) was used: $y = Xr + Za + Wp + Ti + e$, where y is the data vector; r the vector of repetition effects (fixed) added to the overall mean; a the vector of individual additive genetic effects (random); p the vector of plot effects (random); i the vector of the effects of the genotype - environment (GE) interaction (random); and e the error or residual vector (random). Capital letters represent the incidence matrices for the said effects. By analysis of variance, the following components of interest were estimated: σ_A^2 = additive genetic variance; σ_f^2 = genetic variance among families; σ_e^2 = variance due to family \times replication interaction effects; $\sigma_{e(s)}^2$ = variance due to the interaction between the families within and replications within environments; σ_{ge}^2 = variance of the GE interaction; and σ_w^2 = phenotypic variance within family. The genetic correlations between sites (r_{ge}), mean heritability among families (h_m^2) and within family (h_w^2) for each site were estimated by: $h_m^2 = \frac{\sigma_f^2}{\sigma_f^2 + \frac{\sigma_e^2}{J} + \frac{\sigma_w^2}{\bar{n}J}}$ and $h_w^2 = \frac{(1-0.25)\sigma_A^2}{\sigma_w^2}$, and for combined

analysis of sites (s) by: $h_{m(s)}^2 = \frac{\sigma_f^2}{\sigma_f^2 + \frac{\sigma_{gxe}^2}{S} + \frac{\sigma_{e(s)}^2}{SJ} + \frac{\sigma_w^2}{\bar{n}SJ}}$, and $h_{w(s)}^2 = \frac{[(1-0.25)/\bar{n}]\sigma_A^2}{\sigma_{e(s)}^2 + \frac{\sigma_w^2}{\bar{n}}}$, where S , J and \bar{n} are the number of sites,

replication and the harmonic mean of the number of plants per plot. We also calculated the coefficients of environmental

variance ($CV_e(\%) = 100(\sqrt{\sigma_e^2}/x)$), genetic variance among families ($CV_g(\%) = 100(\sqrt{\sigma_g^2}/x)$), and additive genetic variation among families ($CV_{g_i}(\%) = 100(\sqrt{\sigma_A^2}/x)$), where x is the mean of the trait under study. The relative correlation coefficient was estimated by $CV_r = CV_g(\%)/CV_e(\%)$. The genetic (r_g) and phenotypic (r_f) correlations between pairs of traits were computed as proposed by Resende (2002), taking only traits with genetic variation among families into consideration. The genetic gain by selection among and within families (G_{aw}) was estimated for each site for selection intensities of 37.5% of the best families (70:200) and 25% of the best trees within families (5:10), based on the equation, $G_{aw}(\%) = 100(d_a h_m^2 + d_w h_w^2)/x$, where d_a and d_w are the selection differentials among and within families, respectively. d_a was estimated by $d_a = x_{sa} - x$, where x_{sa} is the mean of the selected families and x the population mean for the traits under study. d_w was estimated by $d_w = x_{sw} - x$, where x_{sw} is the mean of selected trees within family for the traits under study.

The effective population size (N_e) after selection was estimated as $N_e = 0.5/\theta$, where θ is the group coancestry (Lindgren et al. 1996), estimated by $\theta = [mn0.5(1 + F_p) + m\theta_{xy}n(n-1)]/(nm)^2$ (Sebbenn et al. 2009b), where m and n are the number of selected families and plants within family, respectively; F_p is the inbreeding coefficient in the parental population; and θ_{xy} the coancestry between plants within family, assumed as half-sibs ($\theta_{xy} = 0.125$).

RESULTS AND DISCUSSION

Significant differences among families at sites and combined sites were detected for D, H, NN, NB and SUR, with exception for NN at site 2, and SUR at site 3 and in the combined analysis. These results indicated genetic variability among families for D, H, NN, NB and SUR and the possibility of breeding by selection of the best families (Table 3). The correlation of the GE interaction (r_{ge}) was positive and high for D, H, NN, and SUR (r_{ge} : 0.768-0.891), indicating that the GE interaction is simple. Little family rank changes for the GE interaction between sites were observed, indicating that selection for these traits can be done efficiently at a single site. In contrast, the r_{ge} for NB (0.554) and SF (0.154) indicated a complex type GE interaction, where family rank changes between sites are involved, and that selection for these traits should be performed specifically for each site.

The mean values of all traits were lowest at site 1 and highest at site 3 (Table 3). After 38 months, the mean survival rate (SUR) among sites (92.3%) indicated a high adaptation of the families to the three studied sites. The mean growth among sites for D (8.16 cm) and H (6.4 m) was greater than the mean reported for the species at other locations in Peru after 39 months (D= 5.86 cm, H= 6.21 m; Sotelo Monte et al. 2006). In contrast, the NN (35.9) and NB (12.9) were lower than the mean reported at other locations in Peru after 18 months (NN= 41.21, NB= 23.49; Sotelo Monte et al. 2003). These results showed that the families studied here have the potential to produce good quality wood (low number of knots in the wood), since the low values of NN and NB indicate wood with less defects (knots).

The traits D, H, NN, and NB generally have higher mean heritability among families (h_m^2), heritability within family (h_w^2), selective accuracy (r_a), coefficient of genotypic additive genetic variation (CV_{g_i}), and coefficient of relative variation

Table 3. Mean and estimates of genetic parameters for trait at site and combined sites in tests with 38-month-old *Calycophyllum spruceanum* progenies

	Trait	h_m^2	h_w^2	r_o	CV_{gr} (%)	CV_r	GS (%)	r_{ge}
Diameter (D, cm)								
Site 1	4.7*	0.269	0.220	0.519	11.9	0.27	18.4	
Site 2	8.6*	0.464	0.416	0.681	18.3	0.42	27.7	
Site 3	11.2*	0.512	0.383	0.715	14.5	0.46	19.5	
Combined	8.16*	0.654	0.329	0.808	15.8	0.40	26.5	0.84
Height (H, m)								
Site 1	3.2*	0.203	0.201	0.450	13.7	0.22	13.2	
Site 2	6.41*	0.555	0.520	0.745	13.5	0.44	23.9	
Site 3	8.52*	0.549	0.502	0.741	14.5	0.49	14.5	
Combined	6.4*	0.696	0.429	0.834	16.1	0.50	16.6	0.891
Stem shape (SSh)								
Site 1	94.8	0.027	0.008	0.163	1.1	0.07	0.1	
Site 2	95.3	0.030	0.012	0.172	0.9	0.08	0.1	
Site 3	95.6	0.035	0.012	0.186	0.9	0.08	0.1	
Combined	95.2	0.024	0.003	0.154	0.5	0.03	0.1	0.154
N. of nodes (NN)								
Site 1	26.9*	0.141	0.121	0.375	8.6	0.18	7.0	
Site 2	37.0	0.276	0.238	0.526	9.6	0.28	8.8	
Site 3	42.6*	0.300	0.233	0.548	8.8	0.29	6.1	
Combined	35.5*	0.473	0.263	0.687	12.0	0.35	25.5	0.85
N. of branches (NB)								
Site 1	7.9*	0.379	0.376	0.616	27.4	0.35	29.8	
Site 2	13.4*	0.321	0.288	0.567	17.9	0.32	11.7	
Site 3	17.6*	0.392	0.372	0.626	11.0	0.31	8.7	
Combined	12.9*	0.404	0.197	0.636	13.7	0.29	16.6	0.554
Survival (SUR, %)								
Site 1	86.6*	0.196	-	0.443	11.9	0.22	1.7	
Site 2	93.5*	0.039	-	0.197	3.2	0.09	0.2	
Site 3	96.9	0.023	-	0.151	1.8	0.07	0.1	
Combined	92.3	0.292	-	0.540	6.6	0.14	2.4	0.768

* $P < 0.05$, with 0.5 degrees of freedom for likelihood ratio test (LRT), χ^2 deviance chi-square; r_{ge} is the genetic environmental correlation; h_m^2 and h_w^2 are the mean heritabilities among and within family, respectively; r_o is the selective accuracy; CV_{gr} and CV_r are the coefficients of additive genetic and relative variation, respectively.

(CV_r) than stem shape (SSh) and SUR, suggesting that high genetic gains by selection can be expected for D, H, NN, and NB. The coefficient h_m^2 was higher than h_w^2 for all traits (except for SUR) in the site and combined site analysis (h_m^2 : 0.024-0.696, h_w^2 : 0.003-0.52), indicating that higher genetic gains can be expected from selection among than within families. For SUR, the range of h_m^2 was 0.033 to 0.196 among sites (combined= 0.292). The selective accuracy (r_o) was 0.375 to 0.834 for D, H, NN and NB; 0.443 for SUR at site 1; and 0.54 for the combined sites, which indicated that the phenotype mean is a good predictor of the additive genetic value of families.

Our results showed that the genetic parameters were generally lower for D, H, and NN and higher for SUR at site 1 than at the other two locations. In other words, the highest genetic gains from selection can be expected at sites 2 and 3 for D, H, and NN, and at site 1 for SUR (Table 3). However, our results may have been affected by the mortality rate at site 1, resulting from inter-tree competition, which may have affected growth traits such as D and H, decreasing the estimates of genetic parameters such as h_m^2 , h_w^2 , and r_o , because D is competition-sensitive (Leonardcz-Neto et al. 2003, Pavan et al. 2011). This could explain the inverse patterns of the estimated heritability and tree mortality rate. Under this condition, an efficient genetic selection at site 1 would be difficult, because D would be affected by a major environmental effect (competition), which would also affect the selection of genotypes for the best progeny for tree growth (Pavan et al. 2011). This aspect also has a negative effect on the selection of genotypes for growth control with

regard to tree quality. For this purpose, the number of nodes (NN) is evaluated, which is related to the branching habit. The nodes are related with the wood quality for causing defects in the trunk, since most fractures in wood structures occur due to the presence of knots (Jansons et al. 2009, Corvalan-Vera 2020, Reyes-Esteves et al. 2022).

After selection, NN can be mitigated by silvicultural practices such as selective thinning and pruning. However, breeding allows a more effective long-term solution, since if sufficient genetic variation for NN is available (Vargas-Hernández et al. 2003), its expression can be controlled. Therefore, breeding programs include the control of traits associated with wood quality (Tong et al. 2013), as well as other traits related to branching, sinuosity and stem branching (Sotelo Montes et al. 2007a, Santos et al. 2010, Tung et al. 2010).

For D and H, the h_m^2 was higher than reported in a test with 36-month-old *Guazuma crinita* progenies, assessed at the same sites (Revilla-Chávez et al. 2022), where h_m^2 values were low for D (0.033-0.39, site mean = 0.369) and H (0.052-0.36, site mean = 0.34). This comparison indicated a higher potential for breeding by selection of the tested *C. spruceanum* than the *G. crinita* progenies.

Genetic (r_g) and phenotypic correlations (r_p) varied between pairwise traits at the sites (Table 4). Genetic correlations (r_g) were high and positive (≥ 0.6) between pairwise traits D, H, NN, and NB at each and all sites (r_g : 0.77-1.0), except between NN and NB at site 3 ($r_g = 0.56$). The phenotypic correlation (r_p) was generally high between pairwise traits at each and all sites (r_p : 0.6-0.89), except between D and NN at site 3 (0.59), D and NB at site 2 and the combined sites (0.48-0.57) and between H and NB at site 3 and combined sites (0.42-0.56), NN and NB at sites 2 and 3, and combined sites (0.36-0.55). Our findings corroborated results of Sotelo Montes et al. (2006) for the study species, who also reported high r_g between D and H (0.89-0.91), and data of Sotelo Montes et al. (2003) and Tauchen et al. (2011), who found high r_p between D and H (0.85) and moderate r_p between NN and NB (0.45). The high r_g between D and H indicated that the two traits can be considered as one in the selection process, since the selection for trees with higher D will also induce an increase in H, and since r_g between both traits is largely influenced by the same pleiotropic genes (Vencovsky and Barriga 1992). This result is very favorable for indirect selection, since positive associations between traits indicate that selection on one trait can lead to indirect gains in another (Sotelo Montes et al. 2007a, Revilla-Chávez et al. 2022, Schoffen et al. 2023).

Table 4. Genotypic (r_g , below diagonal) and phenotypic (r_p , above diagonal) correlations for diameter (D), height (H), number of nodes (NN) and number of branches (NB) of each site and combined sites in tests with 38-month-old *Calycophyllum spruceanum* progenies

	D	H	NN	NB
Site 1				
D		0.81	0.77	0.88
H	0.89		0.79	0.96
NN	0.68	0.80		0.97
NB	0.71	0.67	0.6	
Site 2				
D		0.88	0.78	0.74
H	0.87		0.87	0.89
NN	0.67	0.74		0.85
NB	0.57	0.65	0.55	
Site 3				
D		0.85	0.82	0.71
H	0.78		0.97	0.68
NN	0.59	0.68		0.56
NB	0.65	0.42	0.49	
Combined				
D		0.89	0.91	0.95
H	0.83		0.97	0.96
NN	0.65	0.64		1.0
NB	0.48	0.56	0.36	

Table 5. Number of selected trees and families, group coancestry, and effective population size (N_e) of each site and combined sites in tests with 38-month-old *Calycophyllum spruceanum* progenies

	Site 1	Site 2	Site 3	Combined
Selected trees per block (1 tree/family)	75	75	75	75
Total number of selected trees per site	375	375	375	1125
Total number of selected families per site	172	173	175	199
Group coancestry per block: Θ_b	0.0067	0.0067	0.0067	0.0067
Group coancestry per site: Θ_s	0.0019	0.0019	0.0018	0.0011
Effective population size per block: $N_{e(b)}$	75	75	75	75
Effective population size per site: $N_{e(s)}$	265	264	270	472

The progeny test was designed to serve two purposes: the *ex situ* conservation of *Calycophyllum spruceanum* combined with the production of seeds with some level of breeding. Thus, since the installed blocks were isolated from each other within the sites, we chose the strategy of selecting 75 of the 200 families (among) and one plant within each family (selection within) per block at each site (Table 5). Therefore, each block was transformed into a seed orchard, resulting in a total of 172-175 families per site and 199 families across the three sites for selection. This established an effective population size of 75 within the blocks, varying from 264 to 270 between sites, and totaling an effective population size of 472 for the three sites. This selection strategy achieved the genetic gains expected by selection among and within families, which varied between traits and sites. As expected, the possibility of genetic gains for the traits with highest heritability (D, H, NN and NB) was between 6.1 and 29.8%.

CONCLUSIONS

Genetic variation among families was detected at each site and combined sites for the traits trunk diameter (D) and height (H) and number of branches (NB), as well as for number of nodes (NN) at sites 1 and 3 and combined sites, and for survival rate (SUR) at sites 1 and 2, which can be exploited by selection in breeding programs with 38-month-old *C. spruceanum* progenies.

The genotype - environment interaction for the traits D, H, NN, and SUR in 38-month-old trees is simple, so selection may be carried out at only one site.

The genetic control of the traits D, H, NN and NB, measured by heritability coefficients among and within families, varies from moderate to high, indicating the possibility of genetic gains by selection among and within families.

The genetic and phenotypic correlations between D, H, NN, and NB for each site and combined sites are positive and high, and selection for any of these traits will result in indirect genetic gains for the others.

The strategy of applying selection among and within families, within blocks and sites, serves two purposes: improvement by breeding and *ex situ* conservation, while the effective size of the remaining population can be exploited in other selection cycles.

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