

Adaptive genetic variation for climate-resilient breeding in cacao (Theobroma cacao L.)

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Abstract

Breeding abiotic stress tolerance in tropical perennial crops is essential as weather conditions are becoming more erratic due to climate change. Cacao is a very valuable global commodity cultivated in West Africa, Asia, and Latin America but its production is vulnerable due to persistent diseases and reduced water availability for farming. Cacao wild populations as a result of continued exposition to different soil and climate conditions in Amazonia offer valuable adaptive genetic variation for breeding abiotic stress tolerance. We conducted a genetic-environmental association (GEA) analysis using 157 georeferenced cacao genotypes representing different geographic locations and forest habitats. We also used local environmental information, including 20 climatic and 15 soil variables associated with germplasm collection sites in Amazonia, as well as genotypic data from 42 single-nucleotide polymorphism (SNP) markers. The GEA analysis identified genotype associations with environmental variables suggesting adaptation to seasonal droughts and high temperatures, and to low-fertility soils in Southwestern and Eastern Amazon. This study represents progress in characterizing cacao germplasm and improves our understanding of the adaptive genetic variation available in diverse cacao populations and its optimal utilization for breeding climate resilient and abiotic stress tolerant cacao varieties.

Introduction

Broadening the genetic base and breeding for climate adaptation in tropical perennial crops is necessary to meet increasing demands in new varieties with improved adaptive traits, especially in the face of current climate variability and future climate change scenarios (Challinor et al., 2014; Kole et al., 2015; Sultan & Gaetani, 2016). Accordingly, climate adaptation and genetic improvement of agronomic traits are important for crop species that are under various stresses such as drought, heat, salinity, pests and diseases (Kole et al., 2015; Pixley et al., 2023). Cacao, cultivated by smallholder farmers in tropical regions to produce seeds for the global chocolate industry, is susceptible to abiotic stress, which reduces its yield potential (Gateau-Rey et al., 2018; Ruf et al., 2015).

Cacao in plantations can tolerate minor dry seasons (Alvim, 1977; Wood & Lass, 1985), but models predict that cacao yield is reduced up to 50% by limited water availability (Zuidema et al., 2005). Continued droughts and lack of climate adaptation in cultivated cacao likely will reduce global productivity, especially in West Africa, which is a climate change hot spot and the world's first cacao producer (Ariza-Salamanca et al., 2023; Schroth et al., 2016; Sultan & Gaetani, 2016). In fact, the surge in international cacao prices at the beginning of 2024 (not seen since the 1970s) is attributed to reduced production in West Africa due to diseases and low rainfall (JPMorgan, 2024; Moreno, 2024). Lack of climate resilience to more frequent droughts in cultivated cacao was also observed in Brazil during the El Niño Southern Oscillation (Enso) 2015–2016 event, which resulted in decreasing yield (Gateau-Rey et al., 2018). This severe drought reduced yields by 89% (at 277 kg ha⁻¹, the lowest value recorded since 1990), resulted in cacao tree mortality of 15%, and increased incidence of witches' broom disease (WBD) caused by *Moniliophthora perniciosa* (Gateau-Rey et al., 2018). Accordingly, in addition to traditional agronomic traits such as yield and disease resistance, mainly to WBD, Black Pod Rot or BPR (caused by *Phytophthora* spp.) and Frosty Pod Rot or FPR (caused by *Moniliophthora roreri*), cacao breeders should consider adaptation to limited water availability and other climatic stresses for next-generation varieties (Bekele & Phillips-Mora, 2019; Lahive et al., 2019; Santos et al., 2014).

To increase the cacao climate resilience not only cultivars with drought tolerance should be planted, but associated forest cover should be also considered (Blaser et al., 2018; Lahive et al., 2019). For example, there is a complementary water use between cultivated cacao (with shallow roots) that uses water from the top soil and shade trees such as *Gliricidia* spp. (with deeper roots) that use water from deeper soil layers (Schwendenmann et al., 2010). In addition, when comparing cacao monocultures to agroforests, *Cabruca*s (native forest with scattered cacao trees) provided better resilience to dry and warm conditions that originated from the Enso event in Brazil (Heming et al., 2022). An ideal shade cover for cacao agroforests should not exceed 30%, as estimated for West African cacao cultivation (Blaser et al., 2018). This tree cover provides climate resilience, does not reduce water availability for cacao trees, and does not reduce yield (Blaser et al., 2018).

The rich cacao genetic diversity in Amazonia likely can offer valuable alleles for breeding cultivars for climate adaptation. Based on the wide geographic distribution of cacao in Amazonia, populations grow naturally in areas with current mean precipitation under 1000 mm yr⁻¹ (Nieves-Orduña et al., 2023). In addition, during the Last Glacial Maximum (LGM), the eastern Amazon forest – where Guiana cacao is native (Lachenaud et al., 2007) – persisted even when rainfall was only 60% of today's levels (Wang et al., 2017). Areas in Amazonia that receive less than 2000 mm yr⁻¹, likely supported dry-forest habitats (Bush, 2017). Accordingly, during these past periods of reduced precipitation in Amazonia, tree species underwent evolutionary adaptation to drought as a strategy for long-term survival (Oliveira et al., 2019). In fact, ecological adaptation to drought drives the natural distribution of tree species in Amazonia (Esquivel-Muelbert et al., 2016; Oliveira et al., 2019). However, existing tree populations in Amazonia, including cacao's primary gene pool, are under threat due to more drastic climate change and increased deforestation (Gomes et al., 2019), which underscores the need for future cacao germplasm collections targeting drought tolerance traits. In addition, from the existing germplasm collections, the natural genetic variance to cope with abiotic stress such as water deficit and heat needs to be investigated to enhance yield and abiotic stress adaptation (Bekele & Phillips-Mora, 2019; Lahive et al., 2019).

Cacao breeding programs can benefit from using modern standard phenotyping protocols for screening drought tolerance in genotypes. For example, in valuable tropical crops such as *Musa* spp. (bananas and plantains), standard protocols for screening vegetative, floral and fruit traits are combined to select genotypes and cultivars that can withstand drought while maintaining high yield (Carpentier et al., 2021). Experimental approaches, such as yield evaluation in irrigated and non-irrigated farm conditions, help to select genotypes and cultivars with drought tolerance traits in tropical crops (Carpentier et al., 2021; Uwimana et al., 2020). In addition, evaluation of cacao yield should consider at least seven years of data collection, which is the optimal time in cacao breeding to reach conclusions about clones' agronomic performance (Da Chaves et al., 2022; Dessauw et al., 2024). Early experiments that

simulated drought conditions in the greenhouse, helped to pre-select cacao genotypes and cultivars with drought tolerance traits (Araújo et al., 2024; Carvalho et al., 2022; Dos Santos et al., 2016; Santos et al., 2014; Santos et al., 2023). Further experiments identified that cacao drought tolerant clones in greenhouse experiments were also tolerant under field conditions (farmer fields) (Carvalho et al., 2024). This confirms that pre-screening helps to identify candidate cacao clones for improving breeding populations aiming to include climate resilience traits (Carvalho et al., 2024). In addition, mass selection in cultivated cacao (farmers' fields) that experienced continuous seasonal drought events in Brazil allowed for the identification of 108 drought tolerant clones, which can be used as superior rootstock or for breeding (Silva et al., 2023). Ancestry analyses of these drought tolerant candidate genotypes revealed different admixed individuals of Contamana, Iquitos, and Amelonado clusters as well as Iquitos and Amelonado genotypes (Silva et al., 2023).

Considering the narrow genetic base of cultivated cacao (Cornejo et al., 2018; Nieves-Orduña et al., 2024) and the fact that germplasm collections and breeding programs have prioritized disease resistance and yield (Bartley, 2005; Bennett, 2003; Boza et al., 2014; Goenaga et al., 2009; Gutiérrez et al., 2016; Phillips-Mora et al., 2013; Toxopeus, 1969), it could be challenging to identify adaptive divergence within improved populations to address climate variations that limit cacao cultivation. Here, we aim to identify cacao climate-related single-nucleotide polymorphism (SNP) markers from widely distributed wild cacao samples in Amazonia using a genetic-environmental association (GEA) approach, and to investigate the association of SNP genotypes linked to agronomic traits with climate and soil variables. Thus, wild and underutilized genotypes conserved in *ex situ* collections with adaptive potential can be used for developing (via breeding) climate resilient cacao varieties. In addition, breeders can exploit positively correlated traits such as agronomic performance and climate adaptation.

Methods

Cacao germplasm and agronomic SNPs

The 157 wild cacao accessions studied represent a broad geographic distribution from west to east in Amazonia and cover divergent climatic conditions (Fig. 1). The accessions analyzed here were obtained from the *ex situ* collection at CATIE, Costa Rica, and the International Cocoa Quarantine Centre, UK, which facilitate access and validation of results by any cacao breeding program. These accessions included groups coded as IMC, MO, NA, PA, POUND, and SCA, collected in the 1930s by Frederick J. Pound in the Peruvian Amazon while searching for genotypes resistant to WBD (Bartley, 2005; Bekele & Phillips-Mora, 2019). In addition, wild cacao accessions coded as LCT EEN from the Ecuadorian Amazon and EBC from the Colombian Amazon (Allen, 1988), RB and CSUL from Western Brazil (Turnbull & Hadley, 2025), and GU accessions from French Guiana (Lachenaud, 2015) were included.

Considering past human interventions in Amazonia by pre-Columbian societies and their impact on plant domestication (Barlow et al., 2012; Clement et al., 2015; Levis et al., 2017; Levis et al., 2018), the wild cacao accessions here studied, although collected as seeds or budwood, likely experienced cultivation or past human dispersal. This germplasm also represents different cacao genetic clusters previously identified by (Motamayor et al., 2008): Amelonado (2), Nacional (2), Curaray (6), Contamana (7), Guiana (12), Iquitos (26), Marañon (29), Nanay (10), and Purus (4). The studied wild accessions are listed in Supplementary Table S1. Detailed ecological, geographic, collection details and agronomic information can be obtained from the International Cocoa Germplasm Database (ICGD) (Turnbull & Hadley, 2025).

For the GEA analysis, we used the data set of genotypes generated for the 157 cacao accessions in our previous study (Nieves-Orduña et al., 2024). In this study, new genetic resources for cacao breeding were identified based on SNP analysis. This was achieved by genotyping wild accessions, breeding populations, and cultivars with a new and customized 51 SNP array containing markers associated with agronomic traits: 40 SNPs associated with disease resistance and 11 SNPs with yield components (Nieves-Orduña et al., 2024). By using a final set of 42 SNPs—retained for having at least 75% call rate to ensure data quality—associated with agronomic trait variation in our GEA analysis, we aim to identify genes that are associated not only with agronomic performance but also with climate and soil variables.

Climate and soil variables

The global climate database WorldClim 2.1 was used to obtain 19 bioclimatic variables associated with each georeferenced wild accession (Fick & Hijmans, 2017). The average for the years 1970–2000 were extracted from GeoTIFF files at spatial resolution of 30 seconds (Fick & Hijmans, 2017). Aridity index averaged for 1970–2000 was obtained from the Global Aridity Index and Potential Evapotranspiration Database Version 3 (Zomer et al., 2022). In addition, 14 soil properties were obtained from SoilGrids 2.0 at a resolution of 250 m and a depth of 0–5 cm (Poggio et al., 2021; Turek et al., 2023) and available soil phosphorus based on reference maps for the Amazon region (Darela-Filho et al., 2024). GeoTIFF and netCDF files were loaded and visualized using QGIS 3.40.4 (Team, 2025), and the *Point sampling tool* was used to obtain climate and soil variables for each geographic location. In addition, climate diagrams showing divergent climatic conditions where cacao grows in natural habitats were obtained using the software Climate Charts (Zepner et al., 2021). The full set of climate and soil variables used for GEA analysis is presented in Supplementary Table S2.

Genetic-environment associations

To detect SNP markers associated with climate and soil variables, we used latent factor mixed model (LFMM) analyses, which test the association between genotypes and environmental variables (Frichot et al., 2015). Two methods, *lfmm* and *lfmm2*, were implemented for each environmental variable using the R package *LEA* (version 3.18) (Frichot et al., 2015). Missing genotypes in the input file (*lfmm*) were imputed using the *impute* function. Based on previous population structure analysis, the number of latent factors *K* was set to four (Nieves-Orduña et al., 2024). The *lfmm.pvalues* function identified SNPs associated with environmental variables and implemented the genomic control method for adjusted *p*-values (Frichot & Francois, 2024).

The *p.adjust* function implemented in R (R-CoreTeam, 2023) was used to adjust *p*-values based on the false discovery rate (FDR) method. Associations with SNPs were considered significant at the adjusted *p*-values < 0.05. Effect of environmental gradients on genotypes were tested using ANOVA and Tukey's HSD. Mean heterozygosity for each individual was calculated based on all 42 SNPs, and its correlation with climate and soil variables was tested using Spearman's *rho*.

Geographic and environmental distances

To test whether geographic distances are correlated with environmental distances, we performed a Mantel test using the R package *Ecodist* (Goslee & Urban, 2007). The georeferenced collection sites (Supplementary Table S1) were used to calculate the geographic distance matrix using the QGIS tool *Distance Matrix* (Team, 2025). Environmental distances were calculated using the *dist* function in R (R-CoreTeam, 2023) for relevant climate and soil variables.

Results

Associations with climatic variables

The *lfrmm2* method identified significant associations between six SNPs and seven climatic variables, with two variables related to temperature (BIO5, representing maximum temperature of warmest month, and BIO7, representing temperature annual range) and five related to precipitation (BIO12 - annual precipitation, BIO14 - precipitation of driest month, BIO17 - precipitation of driest quarter, BIO18 - precipitation of warmest quarter, and BIO19 - precipitation of coldest quarter) (Table 1, Supplementary Tables S2 and S3). Through the *lfrmm* method, we identified significant associations between two temperature variables (BIO5 - maximum temperature of warmest month and BIO6 - min temperature of coldest month) and three SNPs (Table 1, Supplementary Table S3). The SNP Tcm009s02031341, which was identified by both *lfrmm2* and *lfrmm*, was associated with multiple climatic variables, including precipitation variables BIO12, BIO14, and BIO17 (Table 1), variables that are strongly correlated with each other (Supplementary Fig. S1).

The geographic distribution of Tcm009s02031341 alleles across Amazonia shows a pattern where the G allele is found outside of northwestern Amazonia, which experiences less precipitation (for example, see the allele distribution according to BIO14 in Fig. 2a). This pattern is confirmed by association of the GG genotype with significantly lower precipitation in the driest month (BIO14, about 110mm) compared to the AA and AG genotypes (about 170–180 mm), with similar association observed with variables BIO12 and BIO17 (Fig. 2b).

The common allele of the Tcm009s02031341 SNP was also associated with BIO5 representing the maximum temperature of the warmest month (Table 1). The geographic distribution of Tcm009s02031341 alleles according to BIO5 shows that the GG genotype occurs mostly outside of northwestern Amazonia in southern and eastern regions, which experience higher temperatures (Fig. 3a). This pattern is confirmed by the distribution of genotypes: the homozygous (GG) genotype occurs mostly in the area with higher temperatures (32°C) compared to AA and AG genotypes (30–31°C) (Fig. 3b). Among the accessions studied, these homozygotes GG at the SNP Tcm009s02031341 were observed in the Eastern Amazon (GU-Guiana cluster) and Southwestern Amazon accessions, C SUL 3, and RB 37, 39, 41 (Purus cluster). In its natural habitat, these cacao accessions can tolerate maximum temperatures of 32°C during the warmest month (BIO5) and precipitation < 60 mm during the driest month (BIO14) (Fig. 4).

Climate gradients and geographic distance

The partially isolated as well continuous spatial structure of environmental variables likely promotes adaptation to both continuous selection gradient and patchy habitats. The Mantel test ($r = 0.47, p = 0.001$) revealed a high correlation between geographic distance and differences in precipitation of the driest month (BIO14), indicating a pronounced spatial clinal precipitation pattern due to annual dry season in southwestern and eastern Amazonia. This pattern suggests a reduced precipitation gradient that may drive continuous selection (Fig. 2a). A weaker but significant correlation (Mantel's $r = 0.14, p = 0.001$) was observed between geographic distance and mean annual precipitation (BIO12) differences, suggesting adaptation to a broader precipitation gradient extending from the wetter northwestern Amazon to the less humid southwestern and eastern Amazon (Figs. 1 and 2b). In contrast, the non-significant correlation (Mantel's $r = 0.01, p = 0.387$) between geographic distance and precipitation of the warmest month (BIO18) suggests that local genetic adaptation is likely driven by patchy habitats rather than broad continuous spatial gradients (Fig. 6). Another climatic variable that showed no correlation with geographic distance is temperature of the warmest month (BIO5; Mantel's $r = 0.02, p = 0.306$), suggesting that cacao local adaptation to higher temperatures (31–32°C) may be driven by environmental heterogeneity at smaller spatial scales (Fig. 3).

Table 1
Cacaocandidate SNPs associated with climatic variables and related genes.

Significant SNP	Climatic variable	Method	Chromosome	Gene identifier ¹	Description	Putative Gene function / Biological process	Type of SNP (Ref AA/Alt AA)
Tcm009s02031341*	BIO5, BIO7, BIO12, BIO14, BIO17, BIO19	<i>lfmm2</i>	IX	Thecc.09G040300	RNA recognition motif (RRM)-containing protein	Cross-tolerance to multiple stresses (e.g., drought, salt, heat) (Shim et al., 2021; Yan et al., 2022)	Non-Syn (Asn/Ser)
Tcm006s13222057**	BIO18	<i>lfmm2</i>	VI	Thecc.06G070400	Peptide deformylase 1A	Regulate plant responses to abiotic stress, promotes root growth and drought tolerance (Kim et al., 2021)	Non-Syn (Arg/Leu)
Tcm008s05909121	BIO19	<i>lfmm2</i>	VIII	Thecc.08G115600	Serine hydroxymethyltransferase 6	Growth, development, and stress responses (Singh et al., 2024).	Non-Syn (Pro/Leu)
Tcm004s00289192	BIO19	<i>lfmm2</i>	IV	Thecc.04G002700	Protein of unknown function DUF716	n/a	Non-Syn (Asn/Ser)
Tcm009s02031341*	BIO5	<i>lfmm</i>	IX	Thecc.09G040300	RNA recognition motif-containing protein	Described above	Non-Syn (Asn/Ser)
Tcm002s08269115	BIO6	<i>lfmm</i>	II	Thecc.02G153900	Oxoprolinase 1	Enhancing abiotic stress resistance to heavy metals and heat (Lei et al., 2024; Singh et al., 2025)	Non-Syn (Ser/Leu)
Tcm006s13371871	BIO6	<i>lfmm</i>	VI	Thecc.06G071000	Galactose oxidase/kelch repeat superfamily protein	KFBs are involved in abiotic stress responses (e.g., drought, salinity) (Tang et al., 2022). Circadian rhythm regulation, flowering time, and light signaling (UniProt, 2025).	Non-Syn (Thr/Tle)

¹SNP location, Gene ID, and description are based on the Matina reference cacao genome (*Theobroma cacao* v2.1; (Motamayor et al., 2013) available at https://phytozome-next.jgi.doe.gov/info/Tcacao_v2_1. * SNPs identified by both *lfmm2* and *lfmm* methods.

** Associated also with soil variables (Table 2). BIO5 - Max Temperature of Warmest Month; BIO6 - Min Temperature of Coldest Month; BIO7 - Temperature Annual Range (BIO5-BIO6). BIO12 - Annual Precipitation; BIO14 - Precipitation of Driest Month; BIO17 - Precipitation of Driest Quarter; BIO18 - Precipitation of Warmest Quarter; BIO19 - Precipitation of Coldest Quarter. Non-Syn – nonsynonymous nucleotide substitution. Ref AA– amino acid in the reference genome, Alt AA - alternative amino acid observed in some samples.

Correlation of cacao individual heterozygosity with climatic variables in Amazonia

Cacao individual heterozygosity correlated with increased wetter conditions and stable precipitation. Annual precipitation (BIO12; $p = 0.49$, $p < 0.001$), precipitation of the driest month (BIO14; $p = 0.57$, $p < 0.001$), precipitation of the driest quarter (BIO17; $p = 0.57$, $p < 0.001$), and precipitation of the warmest quarter (BIO18; $p = 0.59$, $p < 0.001$) showed positive correlations with individual heterozygosity (Supplementary Table S4 and Fig. S2). This is confirmed by the positive correlation with the Aridity Index ($p = 0.55$, $p < 0.001$) which increases with more humid conditions. A significant negative correlation was observed between heterozygosity and precipitation seasonality, measured as the coefficient of variation (BIO15; $p = -0.51$, $p < 0.001$), indicating that areas with more stable precipitation—such as the northwestern Amazon—tend to have higher heterozygosity (Supplementary Fig. S2 and S3). Additionally, the max temperature of the warmest month (BIO5) showed a weak negative correlation with heterozygosity ($p = -0.24$, $p < 0.01$) suggesting that higher temperatures could be associated with lower heterozygosity (Supplementary Fig. S2 and S3). Taken together, these results indicate that in its natural habitat, cacao populations exposed to drier conditions, greater precipitation variability, and warmer temperatures tend to exhibit lower heterozygosity (Supplementary Fig. S2 and S3). Overall, the geographic distribution of heterozygosity persists in the more humid and climatically stable northwestern Amazon, the putative center of origin of cacao—while homozygosity shows higher levels in the less humid and hotter southwestern and eastern Amazon—the native habitat of the Guiana cluster (Supplementary Fig. S2 and S3).

Association with soil variables

The *lfrmm2* method detected significant associations between four SNPs and eight soil variables, six relating to soil fertility and two to physical properties (Table 2, Supplementary Table S5). Both SNPs Tcm004s00615809 and Tcm006s13222057 were associated with multiple chemical properties such as nitrogen, cation exchange capacity (CEC), organic carbon stock and available phosphorus. In addition, the SNP Tcm006s13222057 was associated with seven soil variables and the climatic variable BIO18 (Precipitation of Warmest Quarter) (Tables 1 and 2). The geographic distribution of Tcm006s13222057 alleles across Amazonia shows a pattern where the homozygous genotype (GG) is associated with low nutrient requirements for important soil chemical properties such as CEC and phosphorus (Fig. 7). The *lfrmm* method identified two SNPs (Tcm009s08066239 and Tcm004s00615809) associated with two physical properties, sand content and volumetric water content (Table 2, Supplementary Table S5). SNP Tcm004s00615809 was identified by both methods with volumetric water retention at 15 000 cm suction. The homozygous GG genotype (Tcm004s00615809) is more frequent under soil conditions characterized by lower sand content (~ 33%), higher clay content (~ 34%), and higher water holding capacity (~ 18 kPa) compared to AA and AG genotypes (Fig. 5). Suggesting the GG genotype preference for clay-rich soils that provide higher water availability, while alternative genotypes are better adapted to soils with less water availability.

Soil gradients and geographic distance

Soil phosphorous differences between locations showed a strong association with geographic distance (Mantel's $r = 0.5$, $p = 0.001$), indicating a clear spatial structure. This pattern suggests a continuous selection gradient, with high P availability in the northwestern to lower levels in southwestern and eastern Amazon. Under this spatial structure, the homozygous genotype GG of the Tcm006s13222057 SNP may be better adapted to lower phosphorus availability (Fig. 7). In the case of volumetric soil water retention at 15 000 cm suction (Mantel's $r = 0.01$, $p = 0.398$), no correlation with geographic distance was found, reflecting its heterogenous distribution, where local adaptation is likely driven by patchy environmental conditions. Under this spatial structure, the homozygous genotype GG (Tcm004s00615809) is associated with low sand, high clay proportions and increased water holding capacity (Fig. 5).

Correlation of cacao individual heterozygosity with soil variables in Amazonia

Individual heterozygosity correlated with higher sand but lower clay soil content, which resulted in a negative correlation with soil water holding capacity (Supplementary Fig. S4). In other words, homozygous genotypes occur more frequently on soils with higher clay content, and soil clay contents showed a positive correlation with soil water holding capacity (Supplementary Figs S5 and S6). In addition, higher levels of heterozygosity are associated with better chemical soil conditions. Soil pH, cation exchange capacity, organic carbon, and available phosphorous show a positive correlation with heterozygosity (Supplementary Table S4). As expected, CEC correlates positively with key soil nutrients such carbon content, nitrogen and phosphorus (Supplementary Table S4), suggesting better soil nutrient availability at northwestern Amazon, where heterozygosity is higher (Supplementary Fig. S7).

Table 2
Cacao candidate SNPs associated with soil variables and related genes.

Significant SNP ¹	Soil variables	Method	Chromosome	Gene identifier	Description	Putative gene function / Biological process	Type of SNP (Ref AA/Alt AA)
Tcm006s13222057**	cec, nitrogen, ocd, ocs, soc, phosphorous, cvfo	<i>lfmm2</i>	VI	Thecc.06G070400	Peptide deformylase 1A	Regulate plant responses to abiotic stress, promote root growth, drought tolerance, and responses to nitrogen and phosphate deficiency (Kim et al., 2021; Wu et al., 2022)	Non-Syn (Arg/Leu)
Tcm004s00615809*	cec, nitrogen, ocs, water_at_1500cm, phosphorous	<i>lfmm2</i>	IV	Thecc.04G008900	Prenyltransferase family protein	Enhancing drought tolerance through ABA signaling, promoting stomatal closure (Tian & Wang, 2025)	Premature stop codon
Tcm010s00936105	cec, nitrogen	<i>lfmm2</i>	X	Thecc.10G018400	Malectin/receptor protein kinase family protein	Regulating plant growth and development, signal transduction and stress response (drought, salt, plant immunity) (Ortiz-Moreno et al., 2022; Zhu et al., 2023).	Non-Syn (Lys /Arg)
TcSNP1870	nitrogen	<i>lfmm2</i>	IV	n/a	n/a	n/a	n/a
Tcm004s00615809*	sand, water_at_1500cm	<i>lfmm</i>	IV	Thecc.04G008900	Prenyltransferase family protein	Described above	Premature stop codon
Tcm009s08066239	sand, water_at_330cm	<i>lfmm</i>	IX	Thecc.09G141300	RING/U-box superfamily protein	Responses to drought, salinity, temperature extremes, and oxidative stress (Han et al., 2022; Yu et al., 2025).	Non-Syn Gln/Arg
¹ SNP location, Gene ID, and description are based on Matina reference cacao genome (<i>Theobroma cacao</i> v2.1) (Motamayor et al., 2013) available at https://phytozome-next.jgi.doe.gov/info/Tcacao_v2_1 . * SNPs identified by both <i>lfmm2</i> and <i>lfmm</i> methods							

** Associated also with climatic variables (Table 1). cec - cation exchange capacity; ocd - organic carbon density; ocs - organic carbon stocks; soc - soil organic content; cvfo - volumetric fraction of coarse fragments. Non-Syn – nonsynonymous nucleotide substitution. Ref AA– amino acid in the reference genome, Alt AA – alternative amino acid observed in some samples.

Discussion

Based on the GEA analysis of cacao accessions collected across the Amazon forest, the most ecologically complex tropical biome (ter Steege et al., 2006), potential adaptive genetic variation was found in southwestern and eastern Amazon that may have economic value for breeding tolerance to abiotic stress.

Climate adaptation in Amazonia

Climate differences within the natural habitat of cacao are primarily due to higher mean annual precipitation (BIO12) in the western Amazon, rather than related to annual temperature differences (BIO1) (Fig. 1). The cacao accessions analyzed in western Amazon experience an annual precipitation of 2719 mm and a mean annual temperature of 25°C. In southwestern Amazon, the annual precipitation is 1895 mm, and the mean annual temperature is 26°C.

In eastern Amazon, the annual precipitation is 2313 mm, and the mean annual temperature is 25°C (Fig. 1). In addition, southwestern and eastern accessions experience the driest conditions, receiving less than 60 mm during the driest month but with maximum temperatures around 32°C (Fig. 4).

These contrasting patterns are evident in climate diagrams showing absence of dry seasons in western Amazon — the center of the cacao genetic diversity (Motamayor et al., 2008; Nieves-Orduña et al., 2021) — versus the occurrence of pronounced dry seasons in southwestern and eastern Amazon (Fig. 1). In addition, cacao genotypes with higher heterozygosity are more prevalent in the humid western Amazon (Supplementary Fig. S3). Lower heterozygosity is more prevalent in the driest southwestern and eastern Amazon, where seasonal droughts and warmer temperatures are persistent (Supplementary Fig. S3).

This geographic genetic variation in cacao aligns with large-scale tree ecological studies in Amazonia, where tree species-richness distribution is influenced mainly by precipitation patterns, tree diversity being higher in the more humid and fertile western Amazon (linked to Andean geology) compared to less humid southwestern and eastern Amazon (Esquivel-Muelbert et al., 2016; Hoorn et al., 2010; Luizé et al., 2024; ter Steege et al., 2023). While tree species concentrated in northwestern Amazon are sensitive to seasonal drought which limited species distribution (Luizé et al., 2024), Amazonian tree species with higher drought tolerance are expanding their abundance and range due to trends in water deficit in southwestern and eastern Amazon (e.g., dry-affiliated genera *Bertholletia*, *Brosimum*, and *Pseudolmedia*) (Esquivel-Muelbert et al., 2019).

The associations between gene loci and climatic variables help to develop genetic resources for breeding climate resilience as year-to-year climate fluctuations affect crop performance (Yeaman, 2025). Among the analyzed accessions, Guiana and Parinari cacao showed genotype association (e.g., GG for SNP Tcm009s02031341) with climatic stressors such as higher mean temperatures and lower precipitations (Figs. 2 and 3). In addition, the G allele (Tcm009s02031341) is associated with WBD resistance, observed in cultivated cacao under 1200 mm annual precipitation in Bahia, Brazil (Royaert et al., 2016). Notably, Guiana and Parinari cacao are used for breeding yield and disease resistance to black pod disease (*Phytophthora* spp.) in Ghana, where there is a pronounced dry season under cacao farm conditions (Ofori et al., 2020). Parinari-Guiana hybrids show an increased yield (up to 100%) compared to regular clones (Ofori et al., 2020). In addition, Parinari seedlings when evaluated for drought tolerance in Ghana, exhibited better adaptation compared to Iquitos, Nanay, Curaray, and ICS accessions (Ofori et al., 2014). Furthermore, greenhouse experiments with seedlings evaluating diverse cacao germplasms for drought tolerance identified the Parinari accession PA 13 tolerant to water deficit (Santos et al., 2014). In a growth chamber experiment that simulated different climate scenarios, the Parinari accession PA 107 showed tolerance to elevated temperatures (Mateus-Rodriguez et al., 2023). Overall, these germplasm evaluations suggest a potential agronomic and adaptive value of Parinari and Guiana cacao.

Soil adaptation in Amazonia

The natural habitat of the analyzed cacao accessions is associated with higher fertility in the northwestern (higher phosphorus and CEC) but lower fertility in the eastern Amazon (Fig. 7 and Supplementary Fig. S7). Northwestern Amazon has better soils due to Cenozoic/Andean-derived sediments in combination with higher precipitation created richer edaphic properties which facilitated continued forest evolution and higher tree diversity concentration in this area (Hoorn et al., 2010; ter Steege, 2009). Additionally, clay proportions make a difference in the general soil texture. The northwestern accessions have loamy soils (28.3% clay), while the eastern accessions have soils with higher clay content (36.7% clay) and a higher water-holding capacity (Supplementary Figs S5 and S6).

The SNP Tcm004s00615809 (Chromosome_4:621,380) introduces a premature stop codon located at the end of the gene Thecc.04G008900 encoding prenyltransferase family protein (Table 2), resulting in a shorter protein (by three amino acids shorter). Prenylate proteins play a key role in plant development and environmental stress adaptation, including enhance drought tolerance through ABA signaling, promoting stomatal closure (Tian & Wang, 2025). The homozygous GG genotype (Tcm004s00615809) correlates with clay-dominated soils with low sand content (Fig. 5). Soils with higher clay content have higher water-holding capacity, potentially conferring drought tolerance during dry periods (Supplementary Fig. S5). For example, long term monitoring of cacao farming in Bahia, Brazil demonstrated that clay soils increased cacao survival during decades of persistent low precipitation (de Souza Júnior et al., 2023). In addition, the allele G (Tcm004s00615809) has high agronomic value as it is associated with high yield in cacao (Fernandes et al., 2020).

Low soil phosphorus (P) is a limiting factor for tree growth and influences floristic composition and species geographic distribution in tropical forests (Turner et al., 2018). In Amazonia, soil phosphorous limitation occurs across ~ 60% of the basin area, reducing forest primary productivity and controlling geographical variation in tree traits, such as fine root productivity (Cunha et al., 2022). In cacao cultivation, P deficiencies delay vegetative growth and plant maturity which reduces the transition to productive plants (Weinstein et al., 2025).

The non-synonymous SNP Tcm006s13222057 is located on chromosome VI corresponds to the candidate gene Thecc.06G070400 (Peptide deformylase 1A) (Table 1). Peptidine genes in plants contribute to stress response by modulating root development and drought stress tolerance, and also play a role in adaptation responses to nutrient deficiency stress in nitrogen and phosphate (Kim et al., 2021). The homozygous genotype GG (Tcm006s13222057) associated with low available phosphorus and low CEC (Fig. 7), was detected in accessions such as SCA6 widely used for disease resistance breeding (Royaert et al., 2016), IMC67 used as a common rootstock in cacao cultivation for its vegetative vigor and conducive roots that enhance water use efficiency (Jaimez et al., 2023; Osorio Montoya et al., 2022), and eastern Amazon accessions (Guiana) (Fig. 7). These accessions have an agronomic value because low P specialists can maintain growth on infertile soils while responding positively to P fertilization (Turner et al., 2018). In addition, the G allele (Tcm006s13222057) was associated with disease resistance to *Ceratocystis* wilt (caused by *Ceratocystis cacaofunesta*), a lethal phytopathogenic fungus (Cabrera et al., 2016; Fernandes et al., 2018). Cacao genotypes associated with low levels of available soil phosphorus (P) represent a valuable genetic resource for adaptation to chemically limited soils — conditions commonly found in cacao-growing regions such as Bahia, Brazil (Tosto et al., 2024). In addition to their soil adaptability, these genotypes also offer enhanced resistance to diseases.

Overall, both climate and soil gradients influence the distribution patterns of tree species and their functional responses to environmental pressures in Amazonia (Luize et al., 2024; Quesada et al., 2012). For example, the association of the SNP Tcm006s13222057 with the variables BIO18, CEC and P, suggests a genomic region under selection affected by both climatic and edaphic factors (Tables 1 and 2). Moreover, the homozygous genotype GG was observed in response to seasonal water stress (Fig. 6) and soil nutrient limitations such as low CEC and low available P (Fig. 7).

Human influence on the expansion and adaptation of cacao to Amazonian environments

As cacao is a hyperdominant species in Amazonia (Steege et al., 2013), its current geographic distribution is likely influenced not only by climate and soil gradients (Fyllas et al., 2009; Luize et al., 2024; Quesada et al., 2012) but also by past Amazonian societies during both pre-Columbian and post-Columbian periods (Chambouleyron & Arenz, 2021; Levis et al., 2017; Nascimento et al., 2024; Peripato et al., 2023). This complex evolutionary history makes it difficult to distinguish between patterns of local adaptation or the effects of historical expansion of the species. For example, the fertile soils in western Amazon may have facilitated the establishment and domestication of fruit species influencing the current diversity of Amazonian tree communities (Steege et al., 2025). In addition, western Amazon cacao groups – identified through ancient DNA analysis – were found in archeological sites of Colombia Andes and Pacific Coast of Ecuador, dating to 5,300 years ago (Lanaud et al., 2024). This evidence implies that cacao historical expansion was facilitated by contacts among pre-Columbian communities, allowing extensive dispersal and introduction of useful plants, including cacao, from northwestern Amazon to continental America (Lanaud et al., 2024).

Cacao was observed at higher frequencies in modern forest plots located near archaeological sites in southwestern Amazonia and Guiana (eastern Amazon), suggesting that past societies favored tree cultivation and domestication (Levis et al., 2017; Levis et al., 2018). In addition, the higher frequency of cacao associated with the occurrence of pre-Columbian earthworks of wide distribution in southwestern Amazonia and Guiana, suggest expansion of this valuable tree species and past forest management practices (Peripato et al., 2023). During the post-Columbian era, Jesuit missions (1549–1767 CE) exploited and enriched successional forests with cacao trees in southwestern Amazon and from west to east along the Amazon River (Chambouleyron & Arenz, 2021; Nascimento et al., 2024). These studies reflect historical selection and expansion of cacao by humans from the northwestern Amazon to diverse habitats, as observed in modern forests in southwestern and eastern Amazon, resulting in genetic bottlenecks but also facilitating cacao adaptation to different Amazonian habitats.

Conclusions

The geographic genetic distribution of cacao populations across Amazonia has been shaped by environmental pressures associated with climate and soil variations, as well as early human-mediated selection and expansion. Specifically, associations with climatic variables, such as precipitation of the driest month (BIO14) and maximum temperatures of the warmest month (BIO5), suggest cacao adaptation to drier and hotter conditions in southwestern and eastern Amazon. These forest areas represent a target for collecting new alleles for climate adaptation from diverse wild accessions. However, cacao populations in southwestern Amazon are affected by continued deforestation (Nieves-Orduña et al., 2023), which may result in the loss of adaptive genetic variation.

Breeding climate resilient crop varieties provides a long-term crop adaptation strategy and sustainable production (Kole et al., 2015). In the case of cultivated cacao, plantations with genetically improved varieties (high yield under abiotic stress) are needed in climate sensitive production areas such as Bahia, Brazil (Gateau-Rey et al., 2018; Silva et al., 2023) and West Africa (Ariza-Salamanca et al., 2023; Ruf et al., 2015). Our GEA study detected adaptive genetic variation among diverse cacao germplasms, with Guiana and Parinari accessions showing potential for breeding climate-resilient varieties. These accessions have also been identified for drought tolerance and disease resistance to black pod disease under cacao farm conditions in Ghana (Ofori et al., 2020). Thus, the rich cacao genetic diversity holds potential adaptive variation in response to the worsening climate for cacao cultivation.

Outlook

Cacao germplasm with potential adaptive genetic variation should be collected. Droughts in Amazonia are becoming more frequent and intense, increasing tree mortality (da Costa et al., 2010; Feeley et al., 2012; Feldpausch et al., 2016; Malhi et al., 2009; Phillips et al., 2009). A further step in cacao genetic adaptation is to compare the allele frequencies of adaptive candidate SNPs with projected future climate conditions in the region (Duffy et al., 2015; Miles et al., 2004). This analysis will help to estimate climate vulnerable cacao populations – those with allele frequencies that do not match future climate change scenarios for key climatic variables such as precipitation of the driest month and maximum temperatures – as well as those with potential response to climate variability. In addition, long term evaluation of tree composition in Amazonia due to climate change shows a slow drift to more drought tolerant tree species impacting forest community composition (Esquivel-Muelbert et al., 2019). Thus, further questions remain, such as whether current wild cacao populations can evolve physiological adaptations fast enough to survive the warmer and drier conditions associated with deforestation in Amazonia (Franco et al., 2025).

Overall, new challenges have emerged in global cacao breeding such as adding climate adaptation while continuing increasing disease resistance and yield (Nieves-Orduña et al., 2023). Additionally, cacao yield trials (multi-year, multi-location) under abiotic stress, are needed to select germplasm that can improve yield stability. Introgression and broadening the genetic base with potential adaptive genetic variation (e.g., Guiana accessions here identified) can contribute to long term abiotic stress tolerance in cacao cultivation. In addition, updated GEA analysis expanding the sampling and geographic range by including wild cacao previously recorded from western (Imán et al., 2025; Loor et al., 2015; Vásquez-García et al., 2022) and southwestern Amazon

(Levis et al., 2017; Zhang et al., 2012), in combination with the high density Cacao SNP array (Livingstone et al., 2017), is expected to identify potential polygenic local adaptation.

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Author Contribution

HN: Conceptualization, Writing – original draft, Investigation, Methodology, Data curation, Formal Analysis, GIS-map elaboration, Writing – review & editing. MM: Methodology, Writing – review & editing. KVK: Conceptualization, Methodology, Validation, Writing – review & editing. OG: Conceptualization, Investigation, Methodology, Validation, Writing – review & editing.

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Data Availability

Data is provided within the manuscript or supplementary information files

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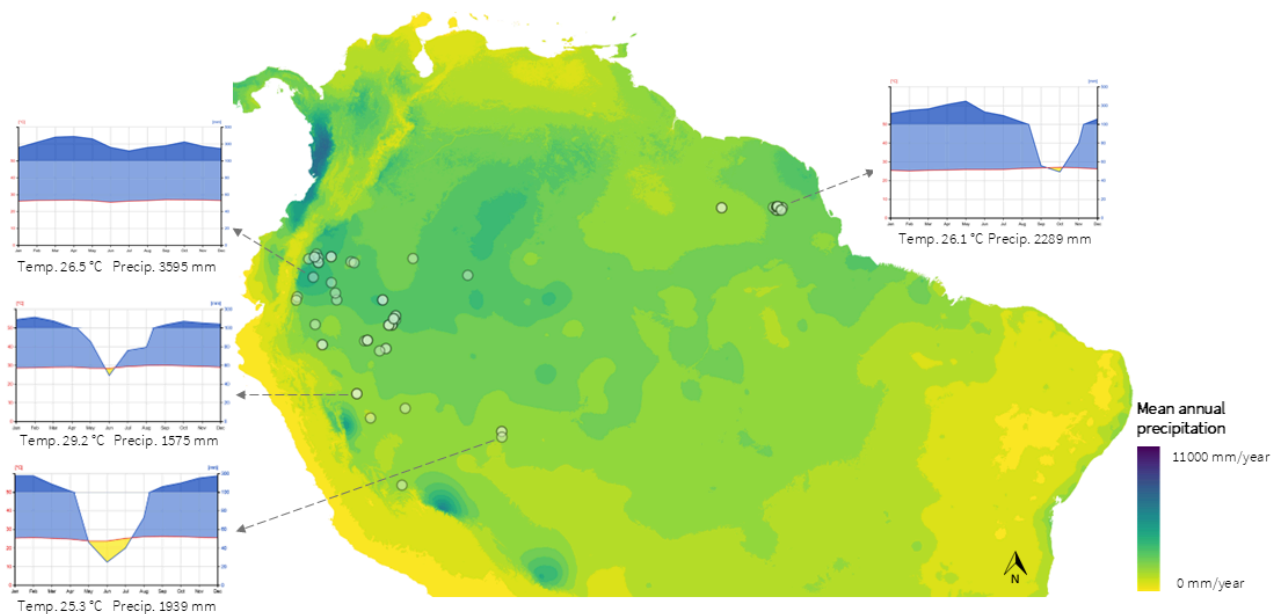


Figure 1

Geographic distribution of 157 wild cacao (*Theobroma cacao* L.) accessions analyzed for genetic environmental association including annual precipitation (for the years 1970-2000, spatial resolution 2.5 minutes) based on WorldClim version 2.1 (Fick & Hijmans, 2017). Map was using with QGIS (<http://qgis.org>). Climate diagrams for geographic locations show four divergent climatic conditions where cacao grows in wild habitats, blue colors represent humid conditions, while yellow represent drought conditions (Zepner et al., 2021).

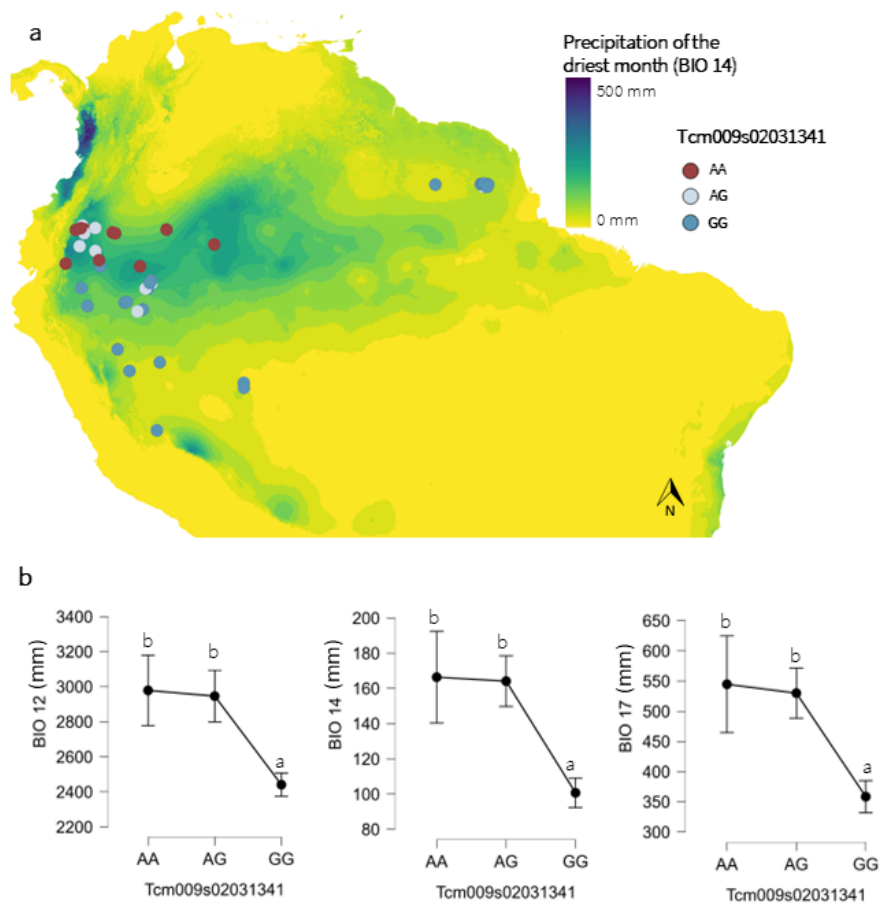


Figure 2

Genotype association of cacao (*Theobroma cacao* L.) with precipitation in Amazonia. (a) Distribution of Tcm009s02031341 genotypes across Amazonia and precipitation levels in the driest month (mm) according to the bioclimatic variable BIO14. The G allele increases in areas with less precipitation outside the northwestern Amazon.

(b) Genotypes of the candidate SNP for climate adaptation Tcm009s02031341 (different letters indicate significant differences among genotypes) according to the precipitation variables (mm) BIO12 (annual precipitation), BIO14 (precipitation of the driest month), and BIO17 (precipitation of driest quarter). The A and G allele belongs to the candidate gene Thecc.09G040300 encoding RNA recognition motif-containing protein and located in chromosome IX.

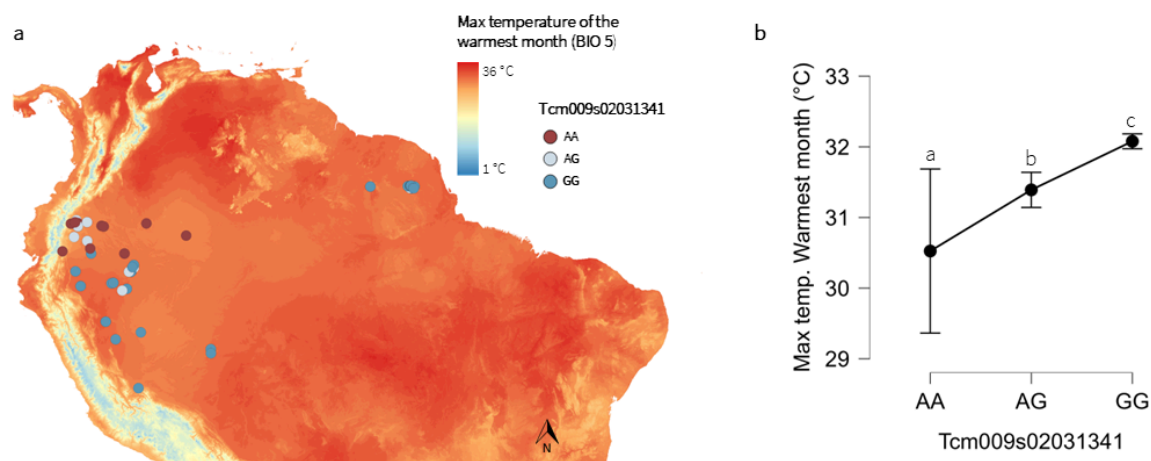


Figure 3

Genotype association of cacao (*Theobroma cacao* L.) with maximum temperatures in Amazonia. (a) Geographic distribution of Tcm009s02031341 genotypes across Amazonia and maximum temperature of the warmest month (BIO5). (b) Maximum temperature of the warmest month (°C) according to the genotypes of the candidate SNP for climate adaptation Tcm009s02031341 (different letters indicate significant differences among genotypes). The GG genotype, associated with warmer temperature, shows a distribution pattern outside northwestern Amazon. Map created with QGIS (<http://qgis.org>). The G allele on chromosome IX belongs to the candidate gene Thecc.09G040300 encoding RNA recognition motif-containing protein.

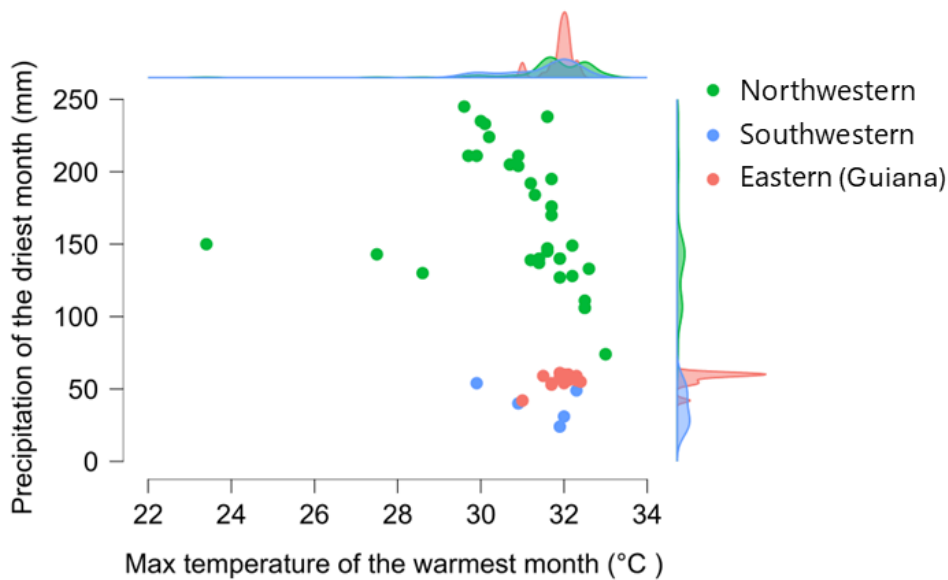


Figure 4

Maximum temperature of warmest month (BIO5) versus precipitation of driest month (BIO14) for 157 wild cacao accessions *Theobroma cacao* L. In its natural habitat, cacao originating from Guiana (eastern Amazon) can tolerate maximum temperature around 32°C and precipitation <60 mm during the driest month. In addition, accessions from the southwestern Amazon in Brazil (RB 37,39,41 [BRA]) also show climatic tolerance. These groups of accessions are homozygous (GG) for the statistically significant SNP Tcm009s02031341, which is associated with drier and warmer conditions in Amazonia.

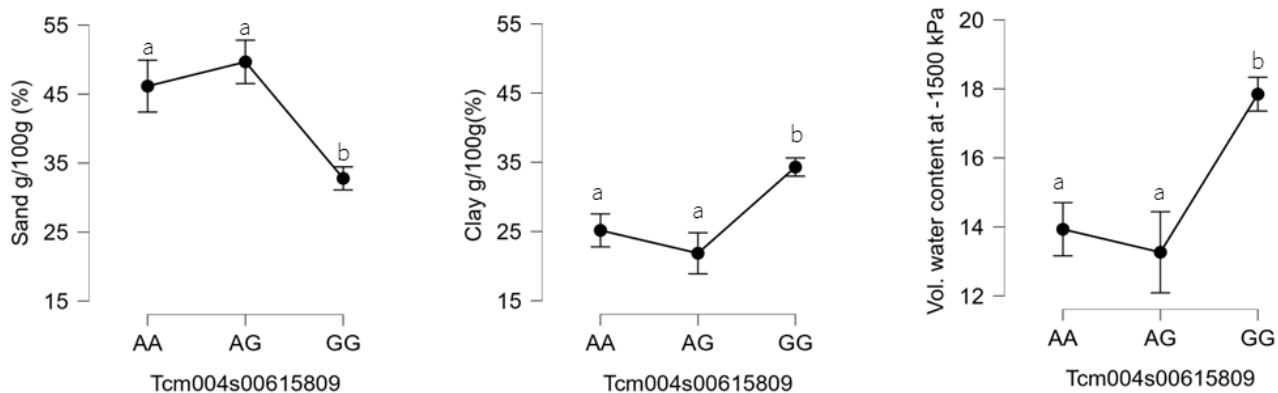


Figure 5

Associations of the Tcm004s00615809 genotypes in cacao *Theobroma cacao* L. with soil physical properties such as sand, clay, and soil volumetric water retention at 15 000 cm suction in Amazonia. Different letters indicate significant differences among genotypes. The homozygous genotype (GG) is associated with low sand and high clay adaptation pattern, which could mean its better adaptation to higher water holding capacity in drier soils.

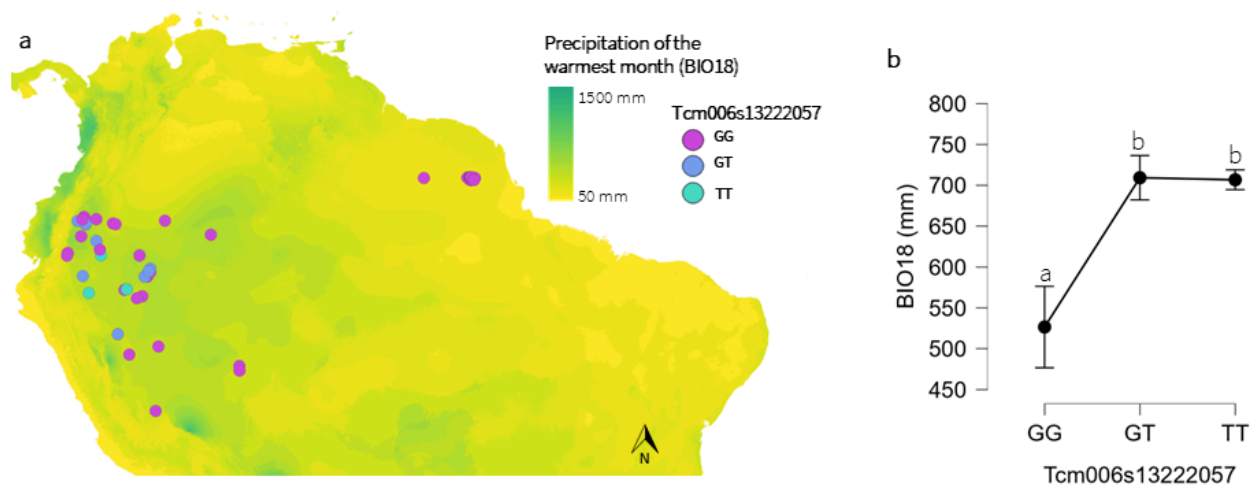


Figure 6

Genotype association of cacao (*Theobroma cacao* L.) with BIO18-precipitation of the warmest quarter (mm) in Amazonia. (a) Geographic distribution of BIO18 (Fick & Hijmans, 2017) and Tcm006s13222057 genotypes across Amazonia. (b) Relationships of the Tcm009s02031341 genotypes with BIO18. The genotype GG is associated with less precipitation (different letters indicate significant differences among genotypes). Map created with QGIS (<http://qgis.org>).

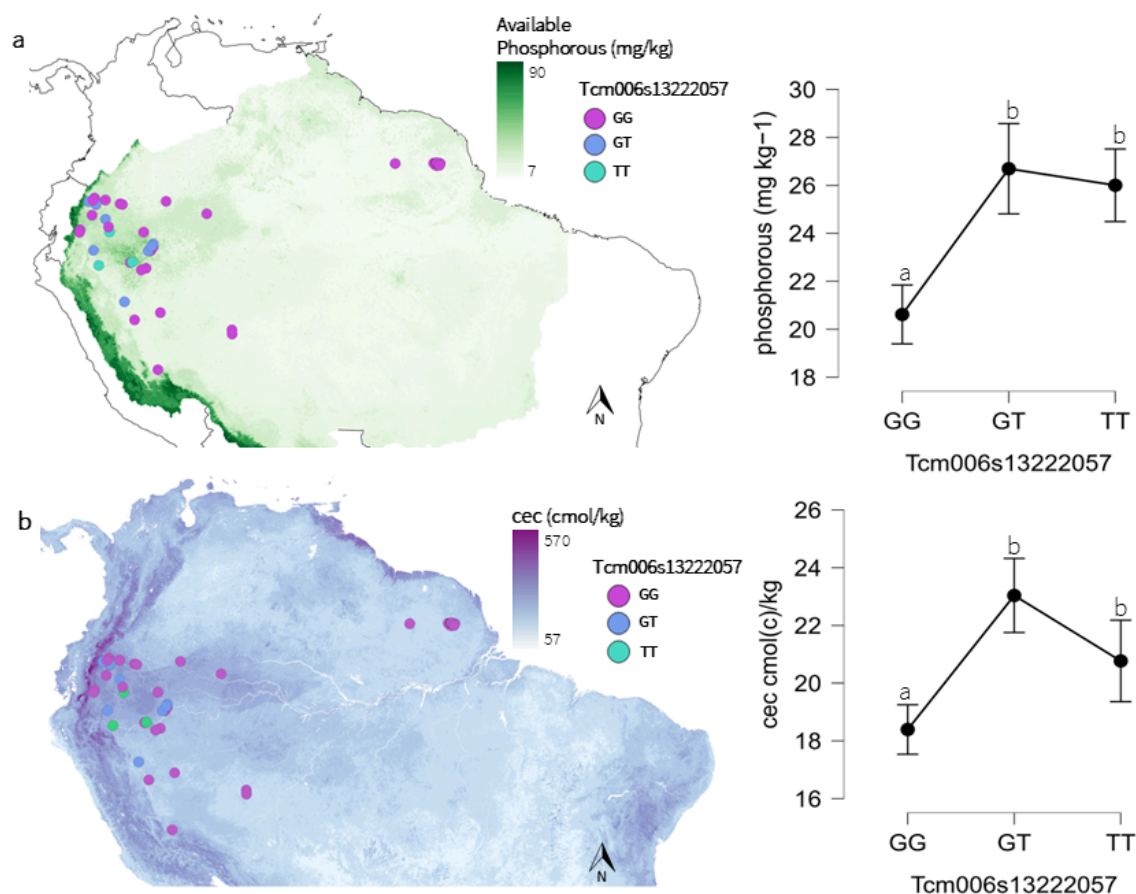


Figure 7

Genotype association of cacao (*Theobroma cacao* L.) with soil chemical properties in Amazonia.

a Geographic distribution of available phosphorous (Darela-Filho et al., 2024) and Tcm006s13222057 genotypes across Amazonia. Relation of genotypes with available phosphorous, different letters indicate significant differences among genotypes (right).

b Geographic distribution of cation exchange capacity (cec) (Poggio et al., 2021) and Tcm006s13222057 genotypes across Amazonia. Relation of genotypes with cec, different letters indicate significant differences among genotypes (right).

The homozygous genotype (GG) is associated with low nutrient requirements in both available phosphorus and cec. Map created with QGIS (<http://qgis.org>).

Supplementary Files

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