



Physiological responses, yield, and latex-related traits of promising *Hevea brasiliensis* genotypes across two Amazonian climate zones with seasonal water deficits: implications for germplasm selection

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Abstract

This study aimed to assess changes in physiological responses, early rubber yield and latex biochemical quality in nine promising rubber tree (*Hevea brasiliensis*) genotypes and the clone IAN 873 (control) during first year tapping in large-scale clonal trials under seasonal water deficits in two climate zones in the Colombian Amazon. Our results showed that, with a larger water deficit (i.e., dry season and semi-humid warm location), all genotypes had a lower photosynthetic rate, lower extrinsic water use efficiency, and lower leaf water potential. On the contrary, a higher yield and a greater metabolic activity related to latex production were evidenced in the semi-humid warm location than in the humid warm location. Thus, the highest yield values and traits related to latex quality were observed in the rainy season and in the semi-humid warm location, where the FX 3899 P1 and FDR 4575 genotypes had a significantly higher productive yield, an intermediate DRC, a higher sucrose consumption, a more active metabolism and a greater capacity to prevent stress with an increase in the content of thiols in the latex. Greater physiological and productive adaptability, with and without the water deficit, were observed in the genotypes FX 3899 P1, FDR 4575 and GU 198 in both climate zones. This better adapted germplasm to water limitations has a high selection potential for *H. brasiliensis* breeding programmes in the northwestern Colombian Amazon.

Keywords *Hevea brasiliensis* · Promising genotypes · Leaf gas exchange · Early yield · Latex quality · Clone selection · Water deficit · Abiotic stress

Introduction

Hevea brasiliensis (Willd. ex A. Juss.) Müll.Arg. is the principal commercial source of natural rubber. Native to the Amazon basin, this tropical tree is now widely cultivated across Southeast Asia [1]. Properties such as

superior abrasion resistance, elongation, and low internal heat buildup, which are not replicated by synthetic rubber, make natural rubber an essential raw material in the manufacture of tyres, pharmaceuticals, balloons, gloves, and other products [2]. In 2020, the global average yield reached 1.2 t ha⁻¹ and production exceeded 14.8 million t [3], of which Asia produced the largest amount with 91.2%, followed by Africa with 6.8% and Latin America with 2% [4]. Plant breeding programmes have focused on obtaining genotypes with high early yield potential and adaptability to diverse edaphoclimatic conditions (i.e. contrasting environments), aimed at increasing yield and overall production. To achieve this, genotypes are evaluated on different agronomic parameters that relate to biomass production, physiological responses and yield [5]. Desirable genotypes show greater growth, superior yield and are stable during the extraction phase [6]. The physiology and productivity of crops are considered part of their phenotype, which refers to

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the observable characteristics of an organism, including its physical and physiological traits influenced by both genetic factors and environmental conditions. In this context, the productivity of the rubber tree is shaped by genetic, ecological, and physiological factors. Therefore, understanding the performance of *H. brasiliensis* under different climatic conditions is essential, as the adaptation of trees to diverse environments is a key determinant of successful rubber cultivation [7].

Although the Amazon is a humid biome with high levels of precipitation [8], recent research indicates that tropical forests in the Amazon may be more susceptible to future droughts compared to tropical forests in other regions [9], some ecoregions have experienced droughts becoming increasingly frequent, intense and widespread [10]. Leite-Filho et al. [11] confirmed that in areas with higher levels of deforestation the start of the rainy season is delayed, along with a greater probability of dry periods at the beginning and end of said season. Espinoza et al. [12] showed a considerable increase in the frequency of dry days, especially between September and November.

Fassoni-Andrade et al. [13] identified that rainfall in the north of the Amazon is higher, while in the south drought is more present. This can be intensified in the southern Amazon (the area where our study is located), where the agricultural frontier advances faster than in any other region of the world [11]. Given this scenario, there are climatic variations between periods and locations; therefore, research should be conducted to understand the interactions of different genotypes with the environment and evaluate the resistance of water stress to the conditions of a changing climate, providing greater security when recommending clones.

In *H. brasiliensis*, studies on photosynthesis and water relations have mainly been conducted under controlled environments, whereas evaluations under field conditions are scarce due to the simultaneous variation of environmental factors, which makes such studies more complex. Understanding the adaptation processes of agricultural species is therefore essential [7]. Under field conditions, plants face periods with water deficits in the soil and in the atmosphere throughout their life cycle, affecting many metabolic pathways and physiological processes [14]. Physiological variables such as transpiration rate, net photosynthesis rate and stomatal conductance, among others, are widely studied because of their relationship with the adaptation of the rubber tree to environmental conditions and dry natural rubber production [15].

In addition to productive yield and physiological variables, parameters associated with early yield are significant to rubber tree breeding programmes. Vigour based on trunk circumference is a selection criterion because it is associated with the start of exploitation and early yield [16], where

good trunk growth guarantees constant production throughout the useful life of a plantation [17]. Likewise, the biochemical parameters of latex are highly relevant to genetic improvement programmes, where high productive yield of natural rubber depends on a good metabolic development of laticiferous cells. For this reason, latex diagnosis represents the dynamics of latex flow and regeneration [18]. The interpretation of latex biochemical parameters helps to significantly reduce the selection time in breeding programmes [19] thus increasing the efficiency of early selection of genotypes. Genotypes selection during the first year of production can diminish evaluation period in rubber tree breeding programmes [6].

Although the physiological yield of different promising *H. brasiliensis* genotypes has been widely assessed in the growth phase [20], and growth and productive precocity have been analysed in a conventional breeding programme [6, 21], the influence of abiotic factors on physiological and productive yield and latex quality during the early tapping phase has been little explored. We hypothesised that seasonal water deficits significantly affect the physiological and productive performance, as well as latex quality, during the initial tapping phase in rubber trees. However, genotypes exhibiting greater vigour and enhanced physiological responses such as higher water use efficiency, stomatal conductance, improved leaf water potential, and superior photosynthetic performance can sustain early yield and latex quality despite seasonal variations. These findings suggest that physiological traits may serve as effective predictors of adaptation to the climatic conditions of the Colombian Amazon region. To validate this hypothesis, the present study aimed to evaluate the physiological performance, early rubber yield, and latex biochemical properties of different clones in two contrasting climate zones during the first year of tapping, based on large-scale clonal trials conducted in the Colombian Amazon. This research is part of the breeding and selection process for developing new rubber tree clones with improved yield and adaptability for future cultivation in the region. The next step will evaluate traits related to physiological yield, vigour, anatomical bark-related traits, yield stability, and latex biochemical and physical quality in the post-tapping phase before making a final recommendation to farmers.

Materials and methods

Study location

This research was conducted in two locations with hilly landscapes (flat to slightly undulating surface with slopes between 2 and 4%) in the northwestern Colombian Amazon

in the Department of Caquetá: (i) Location A: Belén de los Andaquíes, rural area of Agua Dulce (1°25'28" N and 75°52'11" W, at 300 m above sea level), and (ii) Location B: San Vicente del Caguán, rural area of Buenos Aires (2°2'40.8" N and 74°55'11.7" W at 344 m.a.s.l.) [22].

Climate

Belén de los Andaquíes has a warm-humid climate, with an annual rainfall of 3471 mm, a mean temperature of 25 °C, 1462.2 h of sunshine per year, 85.7% relative humidity (*RH*), and a Lang index of 138.7. San Vicente del Caguán presents a warm semi-humid climate, with an annual rainfall of 2503 mm, a mean temperature of 25.4 °C, 1552.3 h of sunshine per year, 79.1% *RH*, and a Lang index of 98.6 [23]. In both areas, precipitation follows a monomodal distribution with two distinct seasons: a rainy season from March to June and a dry season from November to February. The period from July to November is considered a transition to the dry season [23]. For this study, microclimatic data were collected, including relative humidity (*RH*, %), air temperature (*AT*, °C), photosynthetically active radiation (*PAR*, $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$), and vapor pressure deficit (*VPD*, kPa). These data were recorded monthly with a portable weather station (Decagon Devices Inc., Pullman, WA, USA) from March 2019 to February 2020. Data were analysed for both the rainy (March–June 2019) and dry (November 2019–February 2020) seasons.

Soils

In Caquetá, the soils exhibit high compaction, low fertility, low infiltration capacity, and low base saturation, while aluminium saturation is high and the levels of calcium

(Ca), phosphorus (P), magnesium (Mg), potassium (K), and sodium (Na) are low [24]. In Belén de los Andaquíes, the soils present a pH of 4.80, an organic matter content (OMC) of 1.07%, 0.62 organic carbon (OC) an average saturation of 27.7%, and stand out for their clayey texture. In contrast, the soils of San Vicente have an average pH of 5.05, 1.21% of OMC, 0.71 of OC, saturation of 28.7% and the texture is classified as clayey-loam-sandy [21].

Plant material

The plant material consisted of 9-year-old trees in the adult stage (growth stage 3 and code 35, BBCH scale) [25] from nine promising genotypes from Central and South America, along with the clone IAN 873 (control) (Table 1). These materials were chosen because of their resistance to the disease South American Leaf Blight (SALB), vigour, and outstanding production traits, with good results in experiments in Brazil [26, 27] and Ecuador [28, 29]. The clone IAN 873 was selected as the control due to its traditional status and widespread commercial use in Colombia, with extensive studies available on its yield and growth performance. However, over the past two decades, it has shown a decline in both productive potential and resistance to SALB [30].

Experiment design and plot maintenance

In July 2009, two large-scale clonal assays (LSCTs) [31] were established in the Department of Caquetá, one at each study location, as described in previous research [22, 32]. Each of these LSCTs consisted of an experiment that had four repeats distributed randomly in Fisher blocks, in each repetition 10 treatments or genotypes were included, with a total of 60 trees per genotype per repeat, which is equivalent

Table 1 Plant material origin and description: 10 rubber tree genotypes tested in Caquetá, Colombia, 2019–2020. Source: [28–30]

Genotype	Parents (Female x Male)	Entity of origin	Year of introduction into Caquetá	Country of origin
CDC 312	AVROS 308 x MDX 40	CIRAD	2002	Guatemala
CDC 56	MDX 91 x RRIM 614	CIRAD	2002	Guatemala
FDR 4575	FDR 18 x F x 3032	CIRAD	2002	Brazil
FDR 5597	HAR 68 x TU 42–525	CIRAD	2002	Brazil
FDR 5788	HAR 8 x MDF 180	CIRAD	2002	Brazil
FX 3899 P1 (polyploid)	F4542 x AVROS 363	EMBRAPA	1996	Brazil
FX 4098	PB 86 x B 110	CIRAD	2000	Brazil
GU 198	GT 711 x F x 16	CIRAD	2000	Guatemala
IAN 873 (control)	PB 86 x FA 1717	IAN	1964	Brazil
MDF 180	Primary clone	CIRAD	2002	Perú

AVROS: Algemene Vereniging Rubberplanters Oostkust Sumatra; B: Belterra, Brazil; CDC: Clavellinas Dothidella Cross; FB: Ford Belem; FDR: Firestone Dothidella Resistant; FX: Ford Cross; MDF: Madre de Dios Firestone; MDX: Madre de Dios Cross; HAR: Harbel Estate (Firestone), Liberia; TU: Turrialba, Costa Rica; PB: Prang Besar, Malaysia; GT: Gondang Tapen, Indonesia; FA: Ford Acre; F: Ford, Brasil; GU: Guatemala; IAN: Instituto Agronómico do Norte; RRIM: Rubber Research Institute of Malaysia. CIRAD: Agricultural Research Center for International Development; EMBRAPA: Brazilian Agricultural Research Corporation; INCORA: Colombian Agrarian Reform Institute

to 60 trees per elementary plot. The spatial arrangement of trees in each LSCT was $7.0 \text{ m} \times 3.0 \text{ m}$, resulting in a planting density of 476 trees per hectare. The total extension distributed to each experiment covered 5.04 hectares. A fertilisation programme was implemented, consisting of semi-annual applications of $1000 \text{ kg ha}^{-1} \text{ year}^{-1}$ of organic matter derived from chicken manure compost. This compost, consisting of poultry litter composed of broiler chicken excreta mixed with bedding materials such as sawdust, rice husks, and other substrates commonly used in poultry houses, had a moisture content of 71.8%, a pH of 7.44, and contained 0.516% total nitrogen (TN), 0.323% P, and 0.330% K. In addition, an NPK fertiliser with minor elements was applied at a rate of $270 \text{ kg ha}^{-1} \text{ year}^{-1}$, following the methodology reported in previous studies [30]. Weed control was carried out quarterly, while no specific management strategies for diseases and pests were implemented.

Field and laboratory data collection

The field and laboratory evaluations (physiological, early yield and latex biochemical quality) were carried out during the first year tapping (early tapping) from March 2019 to February 2020, and the data were recorded according to genotype, season and location.

Vigour

The tree vigour of all genotypes at each location was decided as a function of trunk girth growth [6, 33, 34]. Thus, two parameters were evaluated: (i) girth at opening (*Go*) (cm), defined as the girth at commencement of tapping, i.e., this trait was only measured on those trees that reached a girth circumference greater than 45 cm at a height of 1 m above the ground; and (ii) Girth increment rate (*GIR*) (cm year^{-1}), computed between the opening phase and end of the first year tapping.

Gas exchange and foliar micro-environmental parameters

Gas exchange and foliar micro-environmental parameters were measured during the first year of tapping using a portable photosynthesis system (CIRAS-3, PP Systems, Amesbury, MA, USA), following standard conditions reported in previous studies [20, 22]. Measurements were taken from mature healthy leaves of four replicated trees per genotype during peak photosynthetic activity (09:00–12:00 h) in both rainy (April–May) and dry (December–January) seasons at both locations. The variables analysed included net CO_2

assimilation rate (*A*) ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), stomatal conductance (*gs*) ($\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$), transpiration rate (*E*) ($\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) and extrinsic efficiency in water use ($WUE_e = A/E$) ($\mu\text{mol CO}_2 \text{ mmol H}_2\text{O}^{-1}$), along with foliar micro-environmental parameters such as *PAR* ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$), *HR* (%), *VPD* (kPa) and *AT* ($^{\circ}\text{C}$) [20, 22, 32].

Water relations parameters

Leaf water potential was measured at predawn (Ψ_L PD, 3:00 h) and midday (Ψ_L MD, 12:00 h) using a Schöllander pressure chamber (PMS 1515D, USA). Measurements were taken on mature leaves from four replicated trees per genotype, and averages were calculated for each replication [20, 32]. Soil water potential was measured at 3:00 h (Ψ_s PD) and 12:00 h (Ψ_s MD) using MPS-6 sensors (Decagon Devices Inc, Pullman, WA, USA), volumetric water content (VWC) (%) and soil temperature ($^{\circ}\text{C}$) were measured implementing EC-5 sensors (Decagon Devices Inc, USA) at 3:00 h (ST_{PD} and VWC_{PD}) and 12:00 h (ST_{MD} and VWC_{MD}), respectively. The three soil parameters were measured at a depth of 40 cm, as reported in previous studies [20, 32].

Early yield-related traits

Trees of each genotype with a circumference greater than 45 cm (at 1 m height) were tapped following a standard half-spiral system with periodic stimulation using ethephon: 1/2S↓ d/4 6d/7 10 m/y ET 2.5% 1 (2) Ba 4/y (i.e., a downward half-spiral, with a cycle of four days followed by a weekly day of rest, over 10 months of the year, and application of 1 g Ethephon stimulant at 2.5% every three months, 2 cm on the virgin upper bark) [21, 26, 35, 36]. One hour after the procedure, 1.0 mL of 5.3% formic acid was applied with plastic cups to each tree to coagulate the latex and avoid production losses [37]. Latex was coagulated with formic acid, collected, dried, and weighed every 15 days. Early dry rubber yield (*EDRY*, $\text{g tree}^{-1} \text{ tap}^{-1}$) was calculated by dividing the coagulum by the number of tapped trees and tapping days [6, 21, 38]. In addition, dry rubber content (*DRC*, %) was calculated using 10 g of latex preserved in 0.5 mL of 5% ammonia, which was coagulated using formic acid and dried at 55°C for 48 h in an oven [39]. The *TSC* was determined from an aliquot of 2.5 mL of latex that dried at 65°C for 4 h [39, 40]. The *EDRY*, *DRC* and *TSC* traits were assessed for each genotype across seasons and locations.

Latex biochemical quality-related traits

Latex biochemical quality parameters including sucrose (*SC*) (mM), inorganic phosphorus (*IPC*) (mM) and thiol (*TC*) (mM) contents were assessed using standard

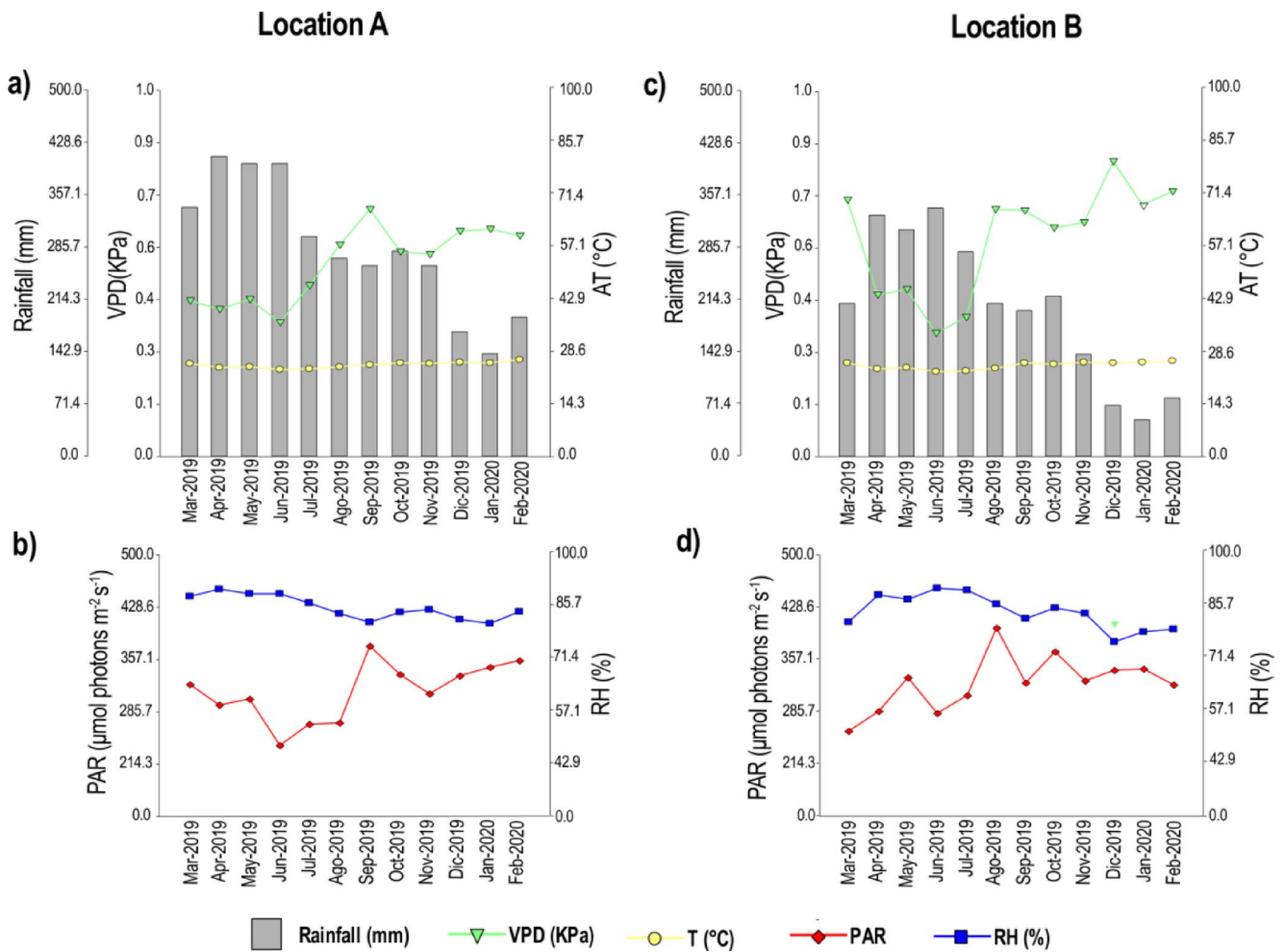


Fig. 1 Monthly microclimatic parameters for two localities with different climates: **a, b** humid warm (Belén de los Andaquíes “Location A”) and **c, d** semi-humid warm (San Vicente del Caguán “Location B”), with two contrasting seasons: rainy (March to June 2019) and

dry (December 2019 to February 2020). Rainfall, air temperature (*AT*), relative humidity (*RH*), photosynthetically active radiation (*PAR*), and vapor pressure deficit (*VPD*)

spectrophotometric methods [26, 36]. The *SC* was figured out by the Anthrone method, adapting the method of Purwaningrum et al. [36]. The *IPC* was carried out with the Molybdenic Vanado method according to She et al. [41]. The *TC* was performed with the Ellman method according to Purwaningrum et al. [36]. These traits were evaluated for each genotype across seasons and locations.

Statistical analysis

The linear mixed-effects (LME) models were adjusted for all variables. For gas exchange, water relations, yield-related traits and latex biochemical quality, the factors genotype, season, location and their interactions were included as fixed effects. For the vigour-related traits (*Go* and *GIR*), only the factors genotype and location were analysed. The blocks nested at the locations and the plots associated with the genotypes within the blocks were analysed as random

effects [20–22]. The assumptions of the LME models (normality and homoscedasticity) were evaluated with a Q-Q plot and a residuals vs. predicted plot, respectively. Differences between means were determined with Fisher’s LSD test ($\alpha=0.05$). A Pearson correlation analysis was performed to measure the degree of correlation between the variables. A principal component analysis (PCA) was performed with a Monte Carlo test (999 permutations) to assess the significance ($\alpha=0.05$) of the relationships between all variables and fixed effects. The vigour-related variables were included in the PCA as supplementary variables [42]. The LME models were fitted with the function *lme* (package nlme) [43] in R 4.0.3 [44] using the interface in InfoStat v.2020 [45]. Visualisation of the Pearson correlation matrix was performed with the functions *corrplot* (package corrplot) [62] and *chordDiagram* (package circize) [47] in

Table 2 Analysis of variance of the fixed effects. Location (L), Genotype (G), season (S) and their interactions, on the Girth opening (G_o) (cm), Girth increment rate (GIR) (cm year^{-1}), CO_2 assimilation rate (A) ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), transpiration rate (E) ($\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$), stomatal conductance (g_s) ($\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$), extrinsic water use efficiency (WUE_e) ($\mu\text{mol CO}_2 \text{ mmol H}_2\text{O}^{-1}$), leaf water potential predawn (Ψ_{LPD}) (MPa), leaf water potential midday (Ψ_{LMD}) (MPa), early dry rubber yield ($EDRY$) ($\text{g tree}^{-1} \text{ tap}^{-1}$), dry rubber content (DRC) (%), total solids content (TSC) (%), sucrose content (SC) (mM), inorganic phosphorus content (IPC) (mM) and thiols content (TC) (mM)

Variable	F based P values	Go	GIR	A	E	g_s	WUE_e	Ψ_{LPD}	Ψ_{LMD}	EDRY	DRC	TSC	SC	IPC	TC
L	0.488	0.0001	0.0421	0.0001	0.0016	0.0016	<0.0001	0.0161	0.2653	0.371	0.0842	0.0674	0.0064	0.4476	<0.0001
G	0.0082	0.0002	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.0007	<0.0001	<0.0001
S	–	–	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.6226	<0.0001
L x G	0.8049	0.0027	<0.0001	<0.0001	<0.0001	<0.0001	0.0051	0.0019	<0.0001	0.124	0.2867	0.1427	0.3033	0.2859	0.0022
S x P	–	–	0.1635	<0.0001	0.6483	0.0006	0.0006	0.025	0.4520	0.7928	0.5508	0.1464	0.0814	<0.0001	<0.0001
G x P	–	–	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.0550	0.0054	0.01	<0.0001	<0.0001	0.235	<0.0001
L x G x P	–	–	<0.0001	<0.0001	<0.0001	<0.0001	0.0205	0.0152	0.0014	0.0039	0.9235	0.7541	0.3511	0.0488	<0.0001

– Does not apply

the R language. The PCA and Monte-Carlo tests were performed in the ade4 [48] and factoextra [49] packages from R.

Results

Microclimatic conditions

Figure 1 shows the variation of the main microclimatic factors in the study area between March 2019 and February 2020. A monomodal rainfall distribution with two distinct seasons was observed in both locations: rainy (March to June 2019) and dry (November 2019 to February 2020).

In location A, the highest precipitation ($>400 \text{ mm month}^{-1}$) and RH ($>88\%$) occurred in the rainy season, along with higher values of AT ($>25^\circ\text{C}$), PAR ($>345 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$) and VPD ($>0.6 \text{ kPa}$) in the dry season. On the other hand, in location B, the lowest values of precipitation ($<90 \text{ mm month}^{-1}$) and RH ($<80\%$) were recorded in the dry season, along with lower values of AT ($<24^\circ\text{C}$) and PAR ($<340 \text{ mm month}^{-1}$) in the rainy season. In general, lower values of precipitation and RH were recorded in location B, along with higher values of VPD (0.34 to 0.81 kPa) throughout the cycle of microclimatic evaluations.

About the microclimatic variables at the leaf level (PAR , AT , RH and VPD), significant statistical differences were found in 89.3% of the cases (Table S1; Supplementary Materials). Parameters related to the foliar microenvironment (Table S2; Supplementary Materials) had a similar behaviour to those reported by the microclimatic stations (Fig. 1). Higher values of PAR , AT and VPD were reported in the dry season, and a higher relative humidity was recorded in the rainy season. Between locations, higher values of PAR , AT and VPD were evidenced in location B, and a higher relative humidity was observed in location A. Between genotypes, the PAR ranged between 325.75 and 1067.66 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ in the CDC 56 and FDR 4575 genotypes, respectively. The AT varied between 35.97 $^\circ\text{C}$ in the FX 4098 genotype and 37.29 $^\circ\text{C}$ in IAN 873. The RH had a maximum of 67.54% in CDC 312 and a minimum of 62.36% in FX 3899 P1. The maximum VPD was registered in the genotype FX 3899 P1 (2.19 kPa), and the minimum value was observed in CDC 56 (1.78 kPa).

Vigour

Statistically significant differences were found between the genotypes for Go and, in the genotype x location interaction for GIR (Table 2). On average, only the GU 198 and FDR 5597 genotypes had a mean $Go > 51 \text{ cm}$ higher than that observed in IAN 873 (control) (Table 3).

Table 3 Mean values for the girth opening (*Go*) and girth increment rate (*GIR*) in 10 rubber tree genotypes

Genotype	<i>G_o</i> (cm)			<i>GIR</i> (cm year ⁻¹)		
	Humid warm	Semi-humid warm	Average	Humid warm	Semi-humid warm	Average
CDC 56	45.00±3.07	48.25±1.95	46.62 bc	1.76±0.86	5.19±0.52 b	3.47 bcd
CDC 312	48.00±2.72	48.30±1.33	48.15 bc	1.82±0.76	3.68±0.33 cd	2.75 cd
GU 198	50.50±1.24	54.05±1.16	52.28 a	2.01±0.30	5.59±0.29 b	3.80 b
IAN 873	47.94±1.90	46.50±3.60	47.22 bc	1.78±0.49	2.70±1.03 cd	2.24 d
FX 4098	49.37±1.29	48.41±1.25	48.89 abc	2.44±0.31	7.21±0.32 a	4.82 a
FX 3899 P1	48.60±3.60	49.09±2.17	48.84 abc	1.70±1.03	4.86±0.58 bc	3.28 bcd
MDF 180	48.40±1.86	46.09±3.07	47.24 bc	1.73±0.49	2.70±1.03 cd	2.88 bcd
FDR 4575	45.39±2.40	47.08±2.10	46.23 c	1.94±0.67	3.30±0.53 cd	2.62 cd
FDR 5597	52.12±2.49	53.46±1.28	52.79 a	3.01±0.67	4.33±0.32 bc	3.67 bc
FDR 5788	49.87±1.08	51.19±1.08	50.53 ab	2.15±0.26	4.79±0.26 bc	3.47 bcd
Mean	48.52	49.24	-	2.03 b	4.57 a	-

– Does not apply

Values in the columns corresponded to mean and standard error. Values followed by different letters are significantly different (Fisher's LSD test, $p < 0.05$); means without letters do not differ significantly.

The genotypes of location B presented the highest *GIR* (4.57 cm), compared to location A (Table 3). In location A, there were no significant differences in the mean *GIR*, while a higher vigour was seen in genotypes FX 4098, GU 198, CDC 56, FX 3899 P1, FDR 5788 and FDR 5597 (> 4 cm year⁻¹) in location B.

Leaf gas exchange

Statistically significant differences were found in all gas exchange traits in the highest order interaction (Table 2). There were statistically significant differences for *A* between genotypes and seasons (Table 2). In the dry season at location A, there was an average reduction of 59.97% in the mean *A* with respect to that observed in the rainy season (Fig. 2a), while at location B, this reduction was greater, 88.87% (Fig. 2b).

In general, there was a higher photosynthetic yield during the rainy season at the two localities, and five genotypes (CDC 312, CDC 56, FX 3899 P1, IAN 873 and MDF 180) showed statistically significant differences in the mean *A* between both localities (Fig. 2a, b). The genotypes that had a higher photosynthetic rate in the rainy season showed a greater reduction of this trait in the dry season *AT* in the location A, the genotypes that had the highest mean *A* in both seasons were CDC 312, GU 198 and FDR 5788, while at the location B, they were CDC 56, FDR 4575 and FDR 5788.

Greater differences in the transpiration rate (*E*) between seasons were evidenced in the genotypes evaluated at location B (Fig. 2d). In this location, the highest mean *E* was observed in the rainy season. In addition, regardless of the season, seven of the ten genotypes had lower transpiration rates in location A compared to location B (Fig. 2c, d). The highest mean *E* was reported in the genotypes CDC 56,

FDR 4575, IAN 873, FDR 5597, and GU 198 during the rainy season at location B. A higher stomatal conductance (*g_s*) was evidenced during the rainy season in the CDC 312 and CDC 56 genotypes in the location A follow of location B (Fig. 2e, f). The highest extrinsic water use efficiency (*WUE_e*) was evidenced in the genotypes established in the location A during the rainy season (Fig. 2g, h).

On average, there was an efficiency greater than 55% at the location A. In addition, the location B had a lower water use efficiency that was strongly associated with a higher transpiration rate. In general, the FDR 5597 and FX 3899 P1 genotypes expressed the highest means of *WUE_e* during the rainy season at the location A.

Water relations

Significant differences in the mean values of predawn ($\Psi_{L PD}$) and midday leaf water potential ($\Psi_{L MD}$) were found for the higher order interaction (Table 2). At both sites, the $\Psi_{L PD}$ and $\Psi_{L MD}$ were lower in the dry period (Fig. 3). In general, at both sites and in both periods, the means of Ψ_L at midday ($\Psi_{L MD}$) (Fig. 3a, b) were lower than those observed at predawn ($\Psi_{L PD}$) (Fig. 3c, d). At location A, clone FX 3899 P1 had the lowest $\Psi_{L PD}$ value during the dry period, with a smaller effect on the $\Psi_{L MD}$ mean in genotypes FX 3899 P1, FX 4098, and MDF 180. At location B, clones FX 3899 P1 and FX 4098 had the lowest mean $\Psi_{L PD}$ in the dry period, while clone IAN 873 reached the lowest mean $\Psi_{L MD}$ in the same period.

The water relations at the soil level exhibited expected behaviour, as seen at the foliar level (Online Resources 1 and 2). The largest differences in the means of predawn ($\Psi_{s PD}$) and midday soil water potential ($\Psi_{s MD}$), predawn (ST_{PD}) and midday soil temperature (ST_{MD}), and predawn (VWC_{PD}) and midday volumetric water content (VWC_{MD}) were

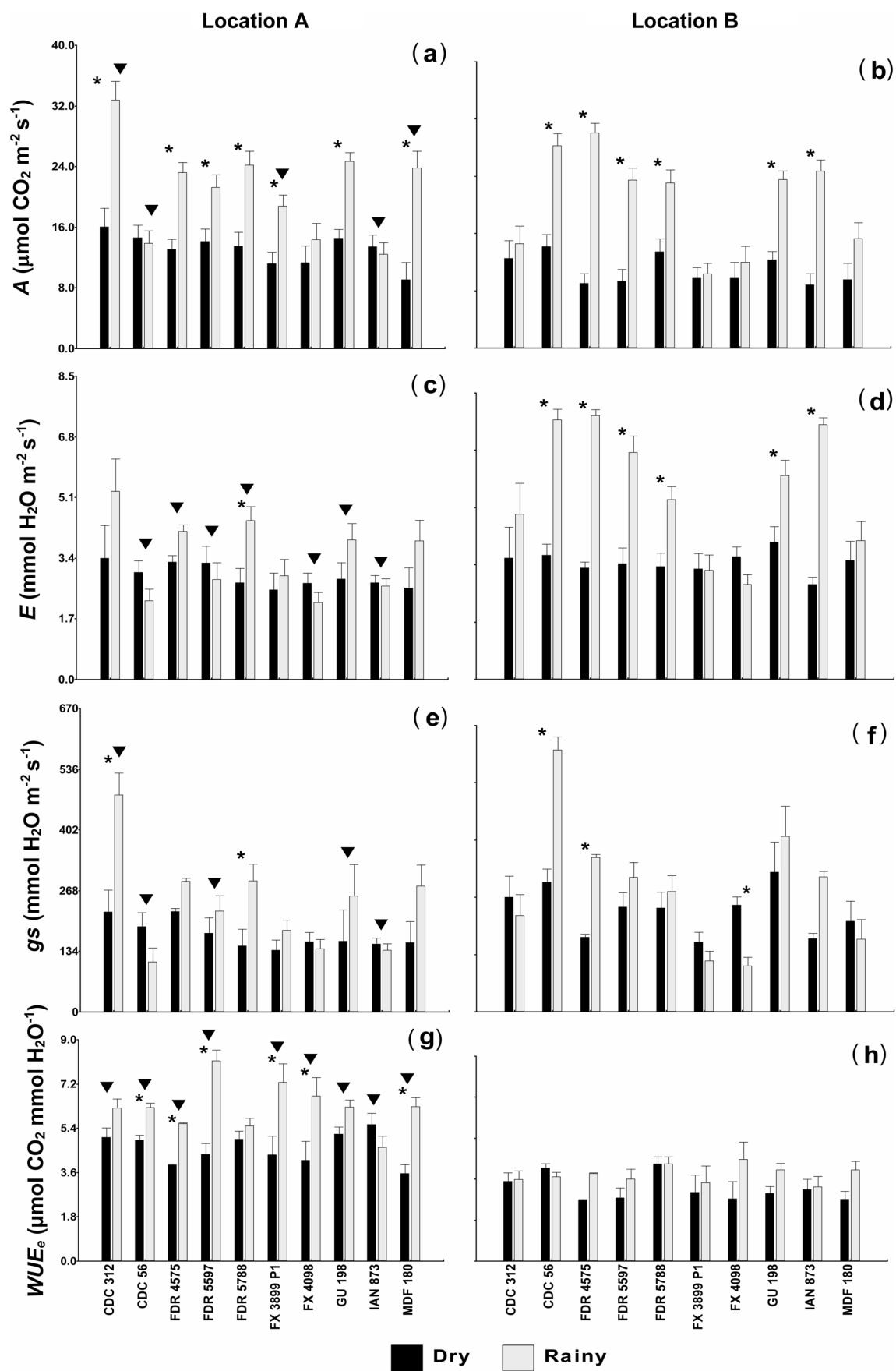


Fig. 2 Leaf gas exchange traits in 10 rubber tree genotypes in two seasons at two locations with different climates in Caquetá (Colombia). **a** and **b**, CO_2 assimilation rate (A); **c** and **d**, transpiration rate (E); **e** and **f**, stomatal conductance (g_s); **g** and **h**, extrinsic water use efficiency (WUE_e); **a**, **c**, **e** and **g**, humid warm location (Location A); **b**, **d**, **f** and **h**, semi-humid warm (Location B). An asterisk indicates significant differences between the mean values of the humid warm and semi-humid warm localities. An inverted triangle indicates significant differences between the mean values of the dry and rainy seasons. These mean differences were statistically significant according to Fisher's LSD test ($p < 0.05$). The values reflect the mean $\pm$ SE of four repetitions ($n = 4$)

observed between the seasons (Online Resource 1). Thus, the means of these parameters were significantly lower in the dry season. Between localities, only the mean VWC_{PD} was lower in the dry season ($p < 0.05$) (Online Resource 2). The soils associated with genotypes FDR 5788, FX 3899 P1 and GU 198 had a higher water status at predawn ($\Psi_{s_{PD}}$), while at midday ($\Psi_{s_{MD}}$) the soils associated with genotypes CDC 312, MDF 180 and FDR 5788 had higher $\Psi_{s_{MD}}$ values. The lowest ST_{PD} and ST_{MD} values were recorded in soils associated with clones FX 3899 P1 and FX 4098, respectively (Online Resource 2). The soils with the highest means for VWC_{PD} and VWC_{MD} were associated with genotypes FDR 5597 and MDF 180, respectively (Online Resource 2).

Early rubber yield-related traits

Significant differences in mean early dry rubber yield ($EDRY$) were observed in the highest-order interaction. In contrast, mean values for dry rubber content (DRC) and total solid content (TSC) were significantly affected by the genotype $\times$ season interaction (Table 2). The highest $EDRY$ values, ranging from 21.79 to 41.22 g tree $^{-1}$ tap $^{-1}$, were recorded at location B during both the rainy and dry seasons in genotypes FX 3899 P1 and FDR 4575 (Fig. 4b). Conversely, genotype MDF 180 exhibited the lowest yield. In location A these genotypes exhibited slightly higher latex yields (ranging from 22.40 to 30.94 g tree $^{-1}$ tap $^{-1}$) compared to the other genotypes (Fig. 4a). Except for FX 3899 P1, latex yields decreased during the dry season at both sites. Conversely, all genotypes exhibited higher DRC and TSC values during the rainy season, with no significant differences observed between localities (Fig. 4c–f). The highest mean DRC values were recorded in genotype FDR 5788 during the rainy season at both location B (49.37%) and location A (48.84%) sites (Fig. 4c, d). Similarly, the highest mean TSC values were observed in genotype CDC 312 at the location A (51.71%) and location B (51.69%) localities (Fig. 4e, f). Overall, genotypes with higher latex yields, such as FX 3899 P1 and FDR 4575, also exhibited slightly higher mean DRC and TSC values.

Latex quality

Significant statistical differences were evidenced in the means of the contents of sucrose (SC), inorganic phosphorus (IPC) and thiols (TC) in the higher order interaction (Table 2). Overall, SC content was higher during the dry season at both localities, except in genotypes IAN 873 and MDF 180, which exhibited greater SC concentrations during the rainy season at location B (Fig. 5a, b). At location A, only genotypes CDC 312 and CDC 56 showed significantly higher mean SC values in the dry season (1.47 and 1.39 mM, respectively) (Fig. 5a). Furthermore, genotypes FX 4098 and GU 198 recorded significantly lower SC levels at the location A compared to the location B (Fig. 5a, b).

For IPC , higher mean values were recorded during the dry season at location A (Fig. 5c), in contrast to the trend observed at location B (Fig. 5d). A significant increase in mean IPC during the dry season at location A was observed only in genotype FDR 5788 (Fig. 5c). No significant differences in IPC means were evidenced between the two localities. At location A, the highest IPC values were found in genotypes FDR 5597 and FX 4098 (both > 5.2 mM) during the dry season (Fig. 5c), whereas at location B, genotypes FDR 4575 and FX 3899 P1 exhibited higher values (both > 5.3 mM) during the rainy season (Fig. 5d).

In 60% of the genotypes at location A (Fig. 5e), the TC means were significantly lower than those observed at location B (Fig. 5f). In general, higher levels of thiol were observed at both localities during the rainy season. The largest variations in TC values were observed at location B. At this location, significantly higher TC means during the rainy season were evident in 70% of the genotypes. Under these conditions, the FDR 4575 genotype had the highest thiol content (0.6 mM) (Fig. 5f).

Multivariate analysis of physiological, early yield and latex-related traits

Most of the bivariate relationships were positive, especially the relationships between gas exchange parameters and water relationships, while sucrose content, in general, was negatively correlated with these physiological traits (Fig. 6a). 53.84% of the correlations were statistically significant. Of these, 79.59% were positive correlations, and the remaining 20.41% were negative (Fig. 6b). High correlations were observed between DRC vs. TSC , Ψ_L vs. DRC and TSC , and between A and the latex-related traits: TC , DRC , and TSC . The $EDRY$ was positively correlated with TC , $\Psi_{L_{PD}}$ and $\Psi_{L_{MD}}$. The SC and TC , were positively correlated with growth rate (GIR). Among the negative correlations, the most relevant

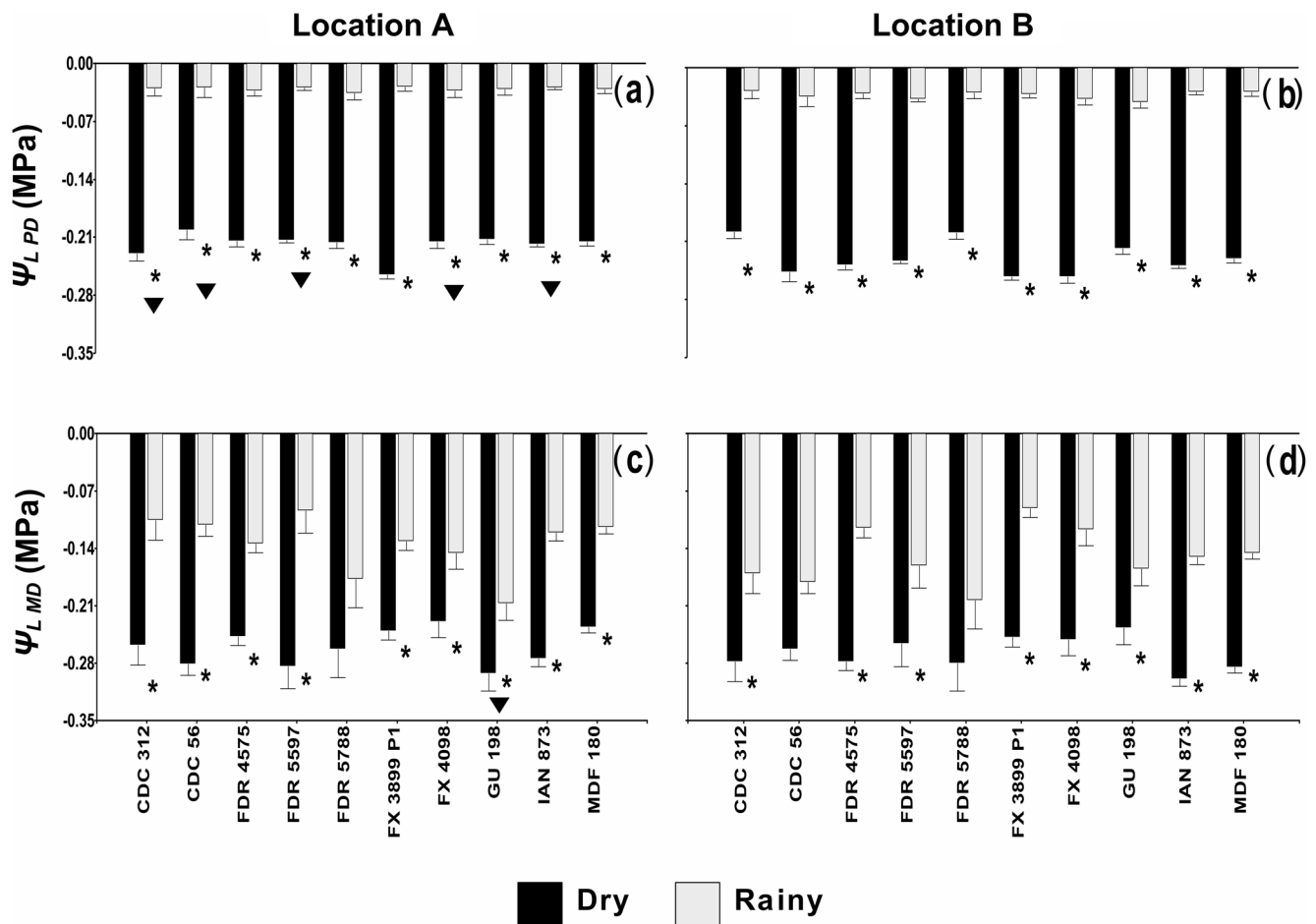


Fig. 3 Leaf water potential in 10 rubber tree *genotypes* in two seasons at two locations with different climates in Caquetá (Colombia). **a** and **b**, leaf water potential at pre-dawn ($\Psi_{L PD}$); **c** and **d**, leaf water potential at midday ($\Psi_{L MD}$); **b** and **c**, humid warm (Location A); **b** and **d**, semi-humid warm (Location B). An asterisk indicates significant dif-

ferences between the mean values of the humid warm and semi-humid warm localities. An inverted triangle indicates significant differences between the mean values of the dry and rainy seasons. These mean differences were statistically significant according to Fisher's LSD test ($p < 0.05$). The values reflect the mean $\pm$ SE of four repetitions ($n = 4$)

were between SC vs. A, $\Psi_{L PD}$, $\Psi_{L MD}$, DRC, TSC, WUE_e and EDY. GIR was also negatively correlated with WUE_e .

The relationships among variables such as location, season, and genotype were evaluated using principal component analysis (PCA) (Fig. 7a–d). The first two principal components accounted for 57.3% of the total variance. Clear clustering patterns were observed based on genotype ($p < 0.01$; 14%) (Fig. 7b), location ($p < 0.01$; 8%) (Fig. 7c), and season ($p < 0.01$; 36%). Overall, the highest trait values were significantly associated with the rainy season and the location B, except for sucrose content (SC), which was higher during the dry season regardless of location (Fig. 7c, d). In general, genotypes exhibited superior physiological and productive performance during the rainy season and at location B. However, genotypes FX 3899 P1, FX 4098, and IAN 873 demonstrated reduced performance during the dry season at location A.

Discussion

In this study, physiological and biochemical responses associated with rubber latex yield and quality were analysed as phenotypic indicators for the early selection of promising *H. brasiliensis* genotypes under seasonal water deficit conditions in two predominant climate zones of the northwestern Colombian Amazon. Among the climatic variables, precipitation stands out as the most influential factor, since excessive rainfall not only increases total water input but also the frequency of rainy days, both of which interfere with tapping and result in crop losses.

Other environmental factors such as PAR, AT and VPD play an important role in regulating the plant water status, which is directly related to latex production [50]. In this sense, it has been shown that the average AT affects latex regeneration, while the minimal AT affects latex flow [51].

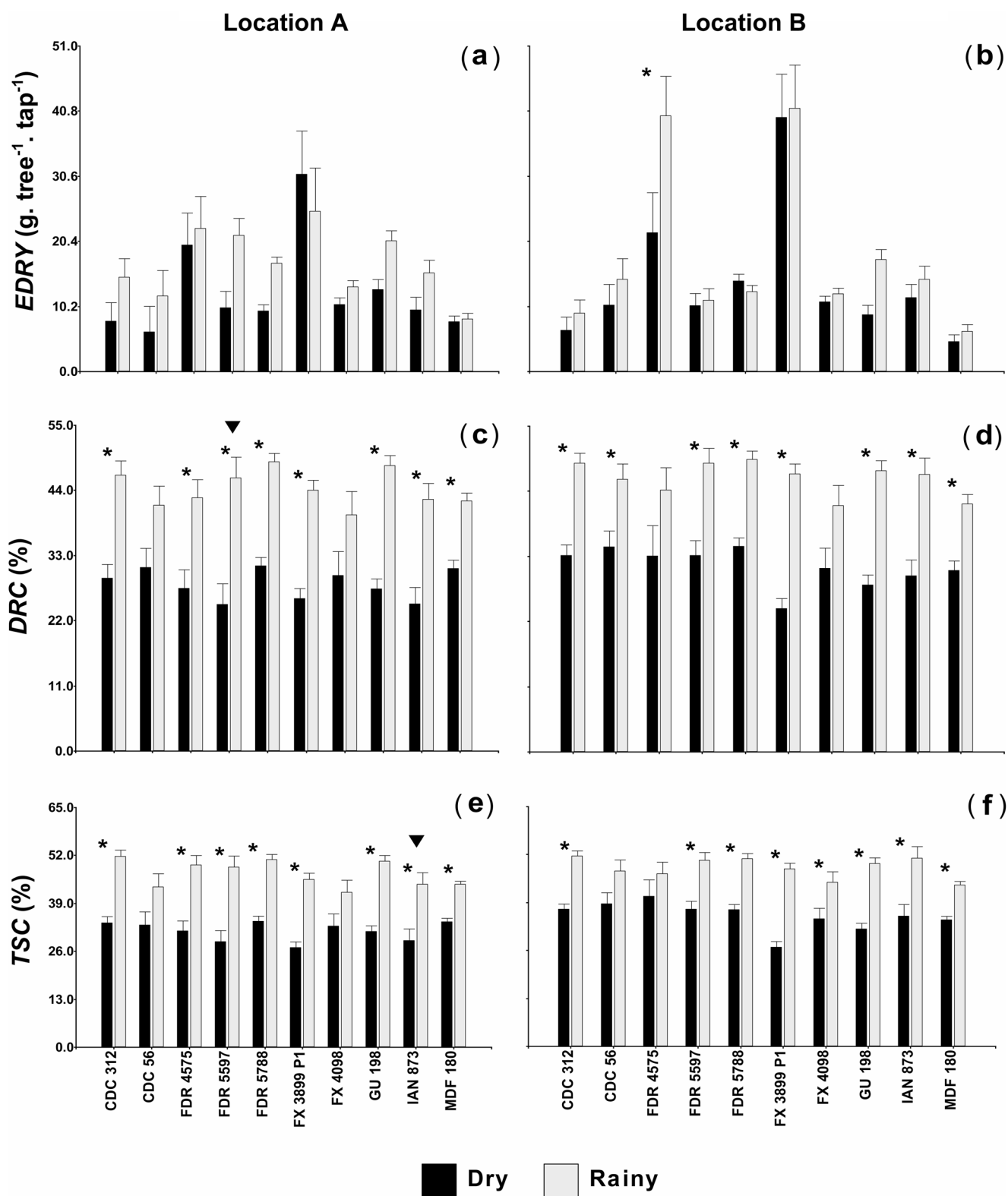


Fig. 4 Early yield-related traits in 10 rubber tree genotypes in two seasons at two locations with different climates in Caquetá (Colombia). (a) and (b), early dry rubber yield (*EDRY*); (c) and (d), dry rubber content (*DRC*); (e) and (f), total solid content (*TSC*); (a), (c) and (e), humid warm (Location A); (b), (d) and (f), semi-humid warm (Location B). An asterisk indicates significant differences between the mean values

of the humid warm and semi-humid warm localities. An inverted triangle indicates significant differences between the mean values of the dry and rainy seasons. These mean differences were statistically significant according to Fisher's LSD test ($p < 0.05$). The values reflect the mean $\pm$ SE of four repetitions ($n = 4$)

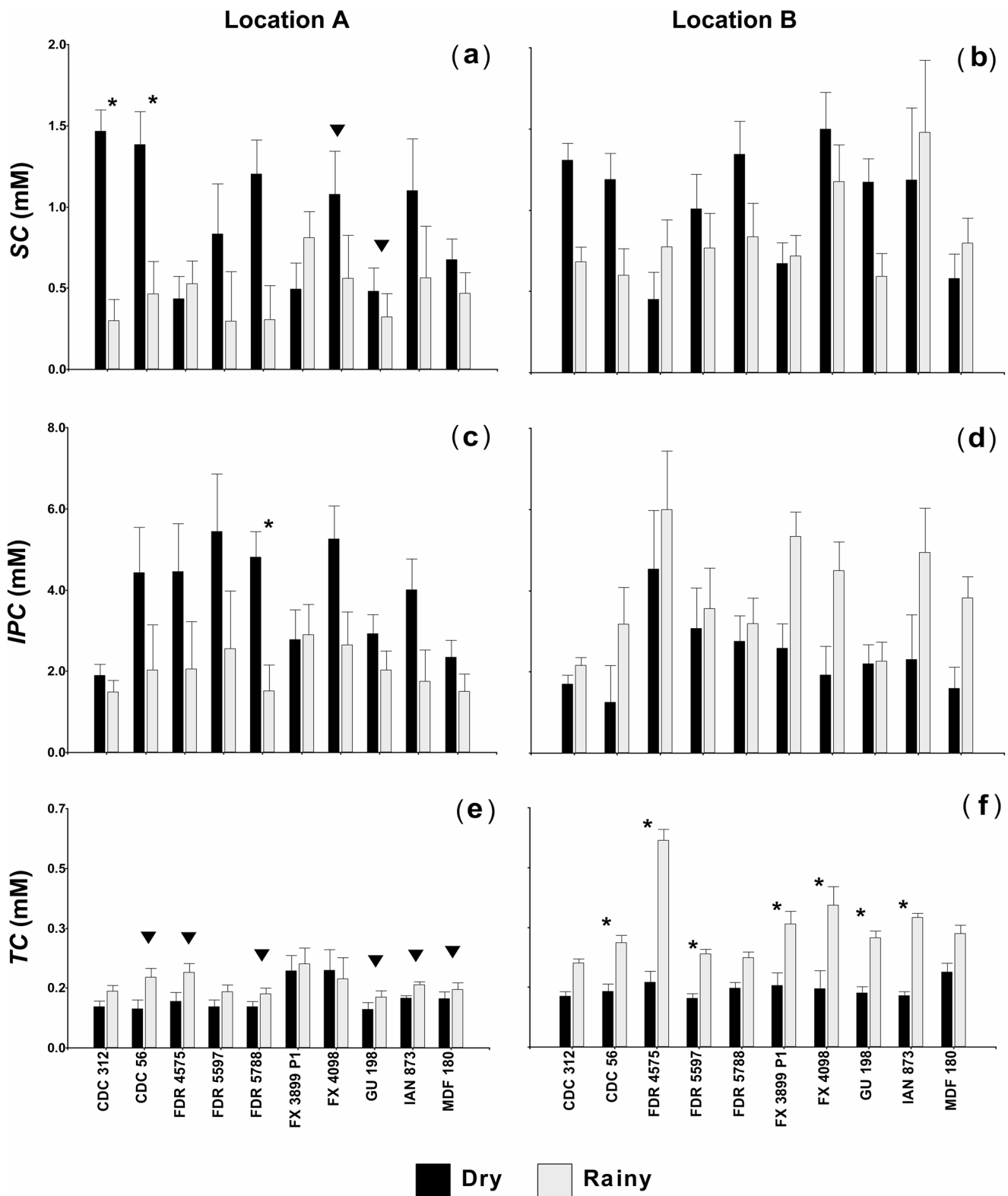


Fig. 5 Latex biochemical quality traits in 10 rubber tree (*Hevea brasiliensis*) genotypes in two seasons at two localities with different climates in Caquetá (Colombia). **a** and **b**, sucrose content (SC); **c** and **d**, inorganic phosphorus content (IPC); **e** and **f**, thiol content (TC); **a**, **c** and **e**, humid warm (Location A); **b**, **d** and **f**, semi-humid warm (Location B). An asterisk indicates significant differences between the

mean values of the humid warm and semi-humid warm localities. An inverted triangle indicates significant differences between the mean values of the dry and rainy seasons. These mean differences were statistically significant according to Fisher's LSD test ($p < 0.05$). The values reflect the mean $\pm$ SE of four repetitions ($n = 4$)

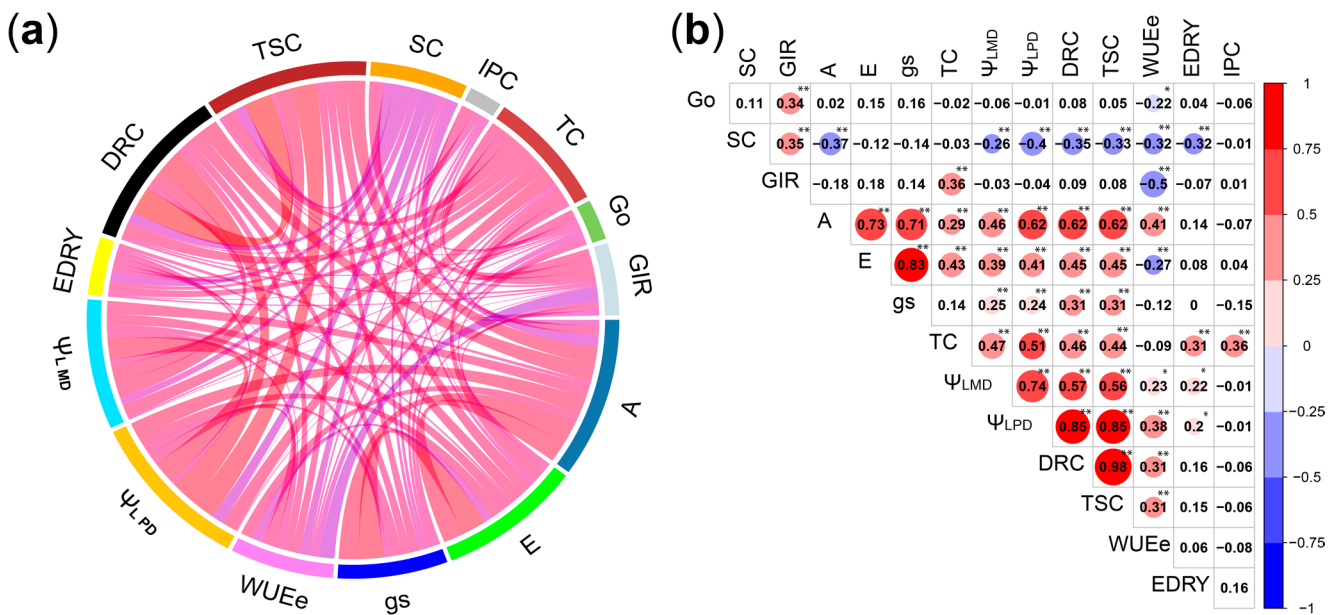


Fig. 6 Pearson's correlation coefficients between physiological, early yield and latex quality variables. **a** Chord diagram of correlation coefficients. **b** Heatmap of correlation coefficients. Colors represent direction and strength of correlation (Red colors represent positive

correlations, blue colors represent negative correlations). * Indicate significant ($p < 0.05$) and ** highly significant ($p < 0.01$) correlations, respectively

In the present study, it was observed that the highest *EDRY* values at location B were associated with lower *AT*. In contrast, at location A, higher precipitation levels (> 400 mm), combined with an *AT* of 26.3°C , resulted in reduced values of *EDRY* and *GIR*.

In *H. brasiliensis*, trunk girth is the most important agro-nomic parameter for determining the maturity stage and the initiation of latex harvesting (i.e., the opening phase), as latex yield is closely associated with girth increment and production stability [36, 52]. In this study, the genotypes evaluated at location B presented the highest *Go* values (mean 49.24 cm), comparable to the findings of Sterling et al. [21] for the Colombian Amazon (mean 49.42 cm), with Krishan [53] in India (mean 49.51 cm) and with Chantuma et al. [54] in Thailand (mean 49.2 cm). These results highlight that location B exhibits climatic conditions more favourable for rubber production, tree growth and higher latex yield, in contrast to location A, where less optimal climatic conditions may negatively affect tree development and productivity.

Although high-yielding rubber trees are typically characterised by above-average girth increments during the first year of tapping [55], no significant correlation between *EDRY* and *GIR* was found in this study (Fig. 6). However, other studies have shown a negative relationship between vigour and production because photosynthates are divided into latex production and trunk growth, which results in a negative correlation [6, 56].

In the present study, *GIR* values above 4 cm year^{-1} were observed in the genotypes FX 4098, GU 198, CDC 56, FX 3899 P1, FDR 5788, and FDR 5597 at location B, although these values remain lower than those reported for high-vigour Asian clones (7.28 cm year^{-1}) [53]. Despite the higher *GIR* observed at location B, the mean *A* was below average, probably due to carbohydrate storage in parenchyma tissues, which buffers periods of low carbon assimilation [54].

From a physiological perspective, it is essential to consider the close relationship between gas exchange and photosynthesis, which is strongly associated with productivity and yield [57, 58]. In this study, higher values of *A*, *E*, *gs*, *WUEe*, *PARe*, *AT*, *RH* and *VPD* were recorded during the rainy season. This contrasts with Sterling et al. [22] who reported higher photosynthesis in the dry season due to greater extrinsic water-use efficiency. Such responses are closely regulated by *VPD*, which modulates photosynthesis and transpiration through stomatal closure [59]. Although stomatal closure provides a reserve of water in the plant, favouring photosynthesis while reducing transpiration [60], it also decreases latex flow and yield [61]. This may explain why, in the present study, location B, despite showing lower *A* and *WUEe*, recorded higher *EDRY*, coinciding with lower soil volumetric water content (*VWC*) at both predawn (*VWC_PD*) and midday (*VWC_MD*).

Regarding plant–soil water relations, a significant reduction in leaf water potential—both at midday (Ψ_{LMD}) and

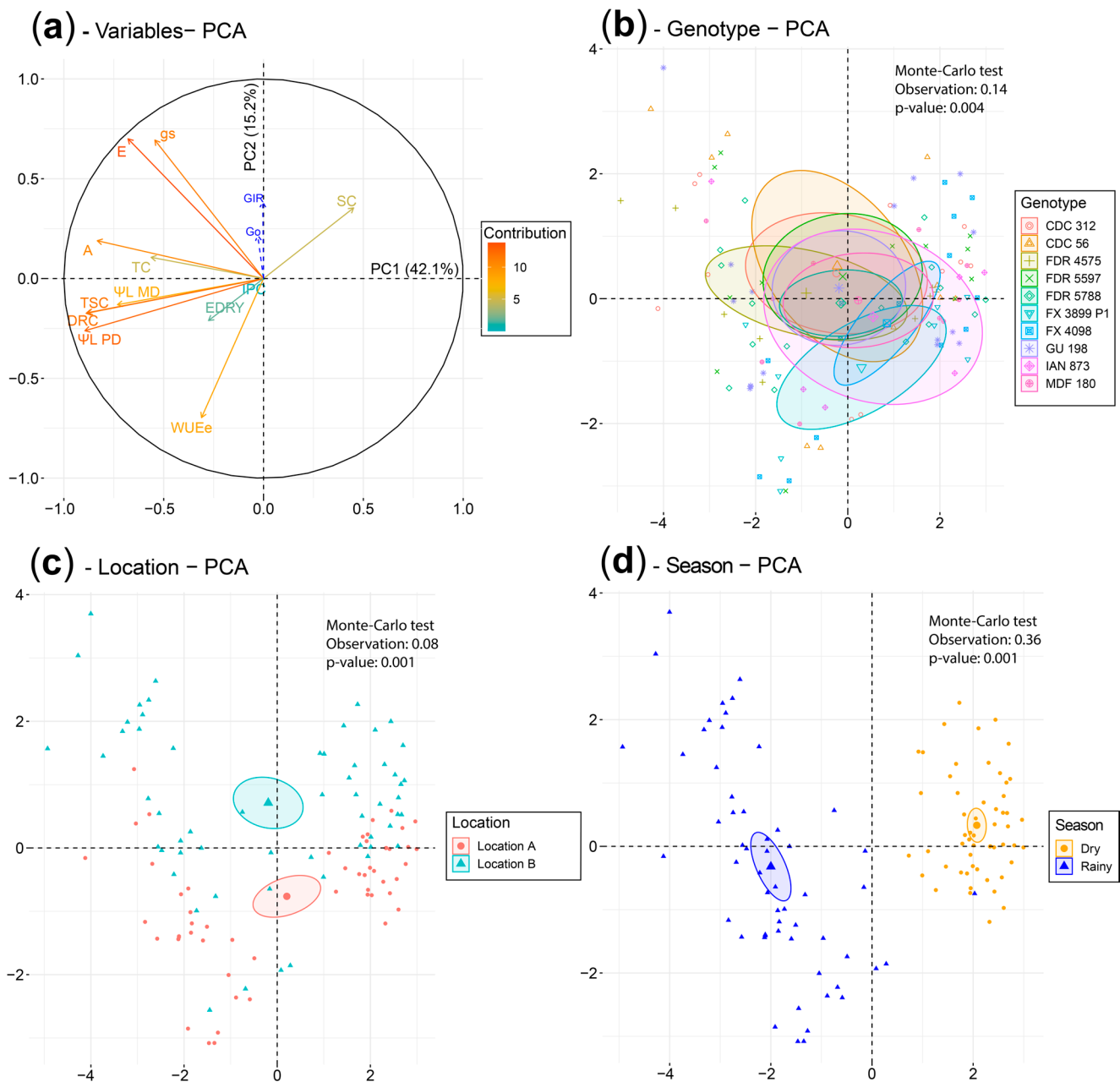


Fig. 7 Principal component analysis (PCA) with the physiological, early yield and latex quality traits, and the observations projected on the ordination plane PC1/PC2. **a** Correlation circle of physiological, early yield and latex quality variables; the color of the vectors indi-

cates the contribution of the variables to the PCs. **b**, **c** and **d**, observations grouped by genotype, location and season, respectively; 95% confidence ellipses. The dotted blue arrows represent the supplementary variables

predawn (Ψ_{PD}) was observed during the dry season (Fig. 3). However, no significant difference was detected between predawn and midday values, indicating an isohydric behaviour, consistent with findings reported in previous studies [32, 62]. Notably, genotypes FDR 5788, CDC 312, GU 198, FX 3899 P1, and FX 4098 maintained relatively higher leaf water potentials throughout the day, likely through effective stomatal regulation, suggesting their potential as drought-tolerant clones. These results are consistent with

those reported by Sterling et al. [22], who also identified these genotypes as physiologically superior and valuable for genetic improvement in the Amazon.

Microclimatic parameters such as VPD and RH are also relevant to latex flow. Rodrigo [63] indicated that VPD and RH influence latex coagulation, as a highly humid microclimate can extend latex flow duration and enhance yield. This observation contrasts with the present findings, where location A, despite its higher RH , exhibited lower latex yields

than location B (Fig. 4). This discrepancy may be explained by the combined effect of two factors. First, the humid-warm conditions in location A have previously been described as a no-escape zone for SALB, the primary disease affecting *H. brasiliensis* crops [64], under which photoassimilates are preferentially allocated to defense mechanisms rather than latex synthesis [21]. Second, the substantially higher precipitation in this location (over 1000 mm more annually than location B) may have contributed to reduced latex yield by increasing the number of rainy days and consequently limiting tapping frequency. Together, these factors likely explain the lower productivity observed in location A.

The FX 3899 P1, FDR 4575 and GU 198 genotypes showed higher *EDRY* ($> 14 \text{ g tree}^{-1} \text{ tap}^{-1}$) compared to IAN 873 ($12.79 \text{ g tree}^{-1} \text{ tap}^{-1}$) during the first year of tapping. These findings are consistent with those reported in previous studies for both polyploid and non-polyploid FX 3899 and GU 198 clones [6, 21]. Moreover, the highest mean *EDRY* recorded in this study ($34.26 \text{ g tree}^{-1} \text{ tap}^{-1}$) exceeded that reported by Antony et al. [55] for Indian clones ($27.72 \text{ g tree}^{-1} \text{ tap}^{-1}$), although it was lower than the yield range reported by Ali et al. [61] for Malaysian clones (75 to $78 \text{ g tree}^{-1} \text{ tap}^{-1}$).

The *SC* and *IPC* variables are considered key physiological indicators in latex diagnosis analysis [65]. Moreover, they helped to clarify the differences in productivity, since *SC* concentration is essential for latex regeneration, and its level reflects the tree's production potential [36]. A negative correlation was also observed between *SC* and *IPC*, alongside a positive correlation between *IPC* and *EDRY*. In addition, a highly significant negative correlation was found between the *EDRY* and *SC* variables (Fig. 6), corroborating findings from previous studies [66, 67], where elevated sucrose concentrations were associated with reduced metabolic activity and lower yields [67].

Similarly, these relationships suggest that a reduction in latex sucrose content is linked to enhanced metabolic activity required for rubber particle synthesis, thereby increasing yield. Notably, FDR 4575, which exhibited high *IPC* (4.26 mM) and low *SC* (0.55 mM) values, demonstrated the most active physiological profile in latex metabolism, suggesting efficient use of sucrose for latex regeneration [65]. This is further supported by the lower *GIR* values observed in this genotype, indicating a higher allocation of photoassimilates to latex production.

Similarly, thiols (*TC*) act as enzymatic activators and contribute to the stability of the luteoid membrane, thereby extending latex flow [68]. Furthermore, a highly significant positive correlation was found between *TC* and *EDRY*, consistent with other reports [60, 69] especially during the rainy season in location B. Genotypes FX 3899 P1 and FDR 4575 formed a group characterised by both high yields and

elevated thiol concentrations ($> 0.22 \text{ mM}$). These genotypes likely increased their thiol levels during tapping as a defense mechanism against oxidative stress [60]. The positive correlation between *IPC* and *TC* further suggests that enhanced latex metabolic activity contributes to greater protection of laticiferous vessels from reactive oxygen species (ROS) [60].

Finally, the analysis of *DRC* and *TSC* provides insights into the dual physiological effects of stimulation in natural rubber trees: first, the improved import of water into the latex, reflected in a lower *DRC/TSC* ratio; and second, increased metabolic activity for rubber synthesis, associated with a higher *DRC/TSC* ratio [70]. Therefore, *TSC* and *DRC* are among the most critical indicators for fresh latex productivity [37, 71]. Although the *DRC* values were within the expected range (25% to 45%) [66], they had an impact on the latex flow of the genotypes. For instance, in this study, a positive correlation between *DRC* and *EDRY* was observed (Fig. 6). Specifically, the FX 3899 P1 genotype had the lowest *DRC* (35.25%) and the highest *EDRY*. In contrast, genotypes such as CDC 312 and CDC 56 showed higher *DRC* values ($> 38.20\%$) and lower yields ($< 11 \text{ g tree}^{-1} \text{ tap}^{-1}$). Based on the classification proposed by Yip [72], the evaluated genotypes can be grouped as follows: (i) medium *DRC* ($> 34\text{--}38\%$): GU 198, FDR 4575, MDF 180, IAN 873, FX 4098 and FX 3899 P1; and (ii) High *DRC* ($> 38\text{--}41\%$): FDR 5788, CDC 312, CDC 56 and FDR 5597 reflecting differences in yield potential.

According to D'Auzac et al. [69], *TSC* can, under certain conditions, reflect the biosynthetic activity of laticiferous system, with higher total solids content being positively correlated with latex yield. However, high *TSC* values (e.g., 43.60% in CDC 312) were associated with reduced yields. High *TSC* values may indicate excessive regeneration activity, resulting in latex with high viscosity and reduced flow due to increased sedimentary fractions (luteoids and Frey-Wyssling particles), ultimately limiting yield [69]. In contrast, the FX 3899 P1 genotype showed low *TSC* (36.89%) and high *EDRY* ($34.26 \text{ g tree}^{-1} \text{ tap}^{-1}$), suggesting that its latex has lower viscosity, which prolongs flow and enhances yield.

Conclusion

The results of this study clearly demonstrate that microclimatic variation (precipitation, relative humidity, temperature, photosynthetically active radiation and vapour pressure deficit) strongly shaped the physiology, vigour, and yield of *H. brasiliensis* across two Amazonian zones with seasonal water deficits. Under drier conditions (dry season and Location B), all genotypes showed reduced photosynthesis and

leaf water status, yet CDC 312, FX 3899 P1, FX 4098, and MDF 180 displayed better drought responses. Despite stronger water limitation, Location B exhibited higher latex yields and more active latex metabolism, with FX 3899 P1 and FDR 4575 scoring best in productive performance; FDR 5788, FDR 5597, FX 4098, and MDF 180 were consistent across seasons.

Agro-physiological and latex indicators converged on a set of desirable clones: FX 3899 P1, FDR 4575, and GU 198 combined high rainy-season photosynthesis with stable water-use efficiency and leaf water potential under stress, and a latex profile of lower sucrose, higher inorganic phosphorus, and elevated thiols—traits associated with faster regeneration and oxidative-stress mitigation. These genotypes (together with the seasonally stable FDR 5788, FDR 5597, FX 4098, MDF 180) are strong options for germplasm selection and deployment under recurrent water deficits.

Prioritising drought-tolerant clones and managing for soil moisture and tapping schedules can stabilise yields under seasonal dryness. Future work should extend to multi-year, post-tapping evaluations (years 4–5) of photosynthetic performance, post-tapping vigour, bark anatomy, yield stability, and latex biochemical/physical quality, coupled with high-frequency microclimate monitoring and genotype-by-environment trials to validate scalability across the region.

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Caucho del Caquetá Asoheca.

Data availability All data that were produced and analysed in this research are included in this manuscript.

Code availability No applicable.

Declarations

Conflict of interest The authors certify that no conflict of interest exists.

Ethical approval This research did not involve Human and/or Animal Participants. Informed consent does not apply to this research. This manuscript has not been published before or submitted to more than one journal for simultaneous consideration. This manuscript is original and is not under consideration for publication anywhere in any form or language (partially or in full). This manuscript has been approved by all co-authors and responsible authorities – tacitly or explicitly – at the institute where the work was carried out. The author group, Corresponding Author, and order of the authors are all correct.

Consent for publication The authors declare that they read and approved the manuscript.

Concept to participate Not applicable.

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