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Original article

Physiological behavior of banana passionfruit [*Passiflora tripartita* var. *mollissima* (Kunth) Holms-Niels. & P.M. Jørg.] in two altitudinal conditions at Pasca municipality, Cundinamarca (Colombia)

Comportamiento fisiológico de la curuba [*Passiflora tripartita* var. *mollissima* (Kunth) Holms-Niels. & P.M. Jørg.] en dos condiciones altitudinales en el municipio de Pasca, Cundinamarca (Colombia)

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Abstract

Banana passionfruit (*Passiflora tripartita* var. *mollissima*) grows in the Andes. Given its biochemical and organoleptic properties, it has great potential for bioprospecting. There is little information about the plant's ecophysiological characteristics that may be useful to optimize its productive system. Here, we sought to identify the physiological behavior of banana passionfruit plants growing in two altitudinal conditions through their distinct phenological phases. We established crops of this species in low (2,006 m) and high altitudinal areas (2,498 m) in Pasca municipality in Cundinamarca (Colombia), and we monitored the climatic characteristics. We evaluated the water potential, gas exchange, and chlorophyll fluorescence in plants at different phenological stages, and we generated light photosynthetic response curves. We found that the higher altitude (2,498 m) area was colder, with higher photosynthetically active radiation (PAR) and relative humidity, but less vapor pressure deficit. The high-altitude plants showed higher rates of photosynthesis, water potential, stomatal conductance, water use efficiency, and reduced transpiration compared to the low zone (2,006 m) plants, while at this lower altitude, the plants showed better PSII performance and a higher photosynthetic efficiency. Photosynthetic rates decreased along the phenological stages. During flowering and the early stages of fruit development, the transpiration rates decreased, the water use efficiency improved, while leaf water potential increased. The plants showed physiological responses and adaptation to the different ecophysiological conditions at the two altitudes, but the climatic characteristics of the higher elevation allowed the banana passionfruit plants to develop a higher physiological performance.

Keywords: Phenology; Leaf water potential; Chlorophyll fluorescence-a; Gas exchange; Climatic factors.

Resumen

La curuba (*Passiflora tripartita* var. *mollissima*) es originaria de los Andes y tiene un alto potencial para la bioprospección debido a sus propiedades bioquímicas y organolépticas. Existe poca información sobre las características ecofisiológicas de la planta útiles para optimizar sus sistemas productivos. Nuestro objetivo fue determinar el comportamiento fisiológico de las plantas de curuba en sus distintas fases fenológicas en dos condiciones altitudinales. Se establecieron cultivos de la especie en una zona altitudinal baja (2.006 m) y en otra más alta (2.498 m) del municipio de Pasca, Cundinamarca, Colombia, y se monitorearon las características climáticas. Se evaluó el potencial

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hídrico, el intercambio gaseoso, y la fluorescencia de clorofila a en plantas en diferentes estados fenológicos y se generaron curvas de respuesta fotosintética a la luz. Se encontró que las condiciones de mayor altitud (2.498 m) fueron más frías, con mayor radiación fotosintéticamente activa (PAR) y humedad relativa, pero con menor déficit de presión de vapor. Las plantas de la zona alta presentaron mayores tasas de fotosíntesis, potencial hídrico, conductancia estomática y uso eficiente del agua, y menor transpiración que las plantas de la zona baja (2.006 m); en la altitud menor las plantas mostraron un mejor rendimiento del PSII y una mayor eficiencia fotosintética. Las tasas fotosintéticas se redujeron a lo largo de las etapas fenológicas. Durante la floración y los primeros estadios de desarrollo del fruto, las tasas de transpiración disminuyeron, el uso eficiente del agua mejoró, y el potencial hídrico foliar aumentó. Las plantas tuvieron respuestas fisiológicas de adaptación a las diferentes condiciones ecofisiológicas en las dos altitudes, pero las características climáticas de la mayor elevación permitieron a las plantas de curuba desarrollar un mayor rendimiento fisiológico.

Palabras clave: Fenología; Potencial hídrico foliar; Fluorescencia de la clorofila a; Intercambio gaseoso; Factores climáticos.

Introduction

In agricultural production, understanding the response of plants and their mechanisms to different environmental conditions contributes to the selection of crop establishment sites with optimal conditions for growth, development, and production (**Flórez-Velasco *et al.***, 2024; **Fischer *et al.***, 2024a; **Lambers & Oliveira**, 2019; **Melgarejo *et al.***, 2010). In tropical regions, climatic factors, among others, are influenced by elevation (**Fischer *et al.***, 2022**; Sandoval *et al.***, 2019), and they have effects on the physiological response of plants, their metabolite content, fruit ripening, and quality (**Mayorga *et al.***, 2020; **Solarte *et al.***, 2014; **Balaguera-López *et al.***, 2024). Climate change has led to increased interest in fruit production in tropical highland areas (**Fischer *et al.***, 2024b).

Depending on the plant species, physiological responses to certain environmental conditions may vary between phenological stages. The methods applied in ecophysiology are generally based on the study of *in situ* responses (**Crous *et al.***, 2016) and involve the evaluation of parameters such as stomatal aperture that vary continuously with diurnal changes in the environment (**Jones**, 2013), influencing photosynthesis, water status, biomass accumulation, crop yield, and carbon sequestration in agroecosystems (**Raquel *et al.***, 2016). Therefore, stomatal regulation in a changing environment is fundamental for plant adaptation (**Franks & Britton-Harper**, 2016; **Li *et al.***, 2015). Chlorophyll fluorescence, a fast and effective tool for analyzing light-dependent photosynthetic reactions in response to given conditions (**Aucique-Perez & Ramos**, 2024), allows the identification of possible causes of photosynthesis changes and plant development (**Maxwell & Johnson**, 2000; **Murchie & Lawson**, 2013). Knowing the dynamics in plant water potential facilitates an understanding of local water demand, availability of soil water, stomatal regulation, and plant internal hydraulic conductivity and its effect on plant development (**Choné *et al.***, 2001; **Larcher**, 2003).

Banana passionfruit [*Passiflora tripartita* var. *mollissima* (Kunth) Holms-Niels. & P.M. Jørg.] is a tropical semi-evergreen fruit belonging to the subgenus *Tacsonia*, genus *Passiflora* (Passifloraceae) (**Coppens *et al.***, 2001; **Segura *et al.***, 2005). The species originated in the Andes, and it grows in high tropical forests from Bolivia to Venezuela between 1,800 and 3,600 m of altitude. Due to its organoleptic and nutraceutical characteristics, the fruit is one of the most appreciated passionflower species (**Fischer *et al.***, 2020). It also has nutraceutical importance given its high antioxidant potential (**Simirgiotis *et al.***, 2013; **Rojano *et al.***, 2012) and the active principles in its leaves (**Costa *et al.***, 2016) containing pasiflorin (**Dhawan *et al.***, 2004), an alkaloid with sedative action.

Some aspects of *P. tripartita* var. *mollissima* cultivation ecophysiology are little known (**Fischer & Miranda**, 2021), as studies have been conducted mainly on other fruiting passionflower species such as *Passiflora ligularis* Juss. (**Fernández *et al.***, 2014; **Rodríguez-Castillo & Melgarejo**, 2015), *Passiflora edulis* Sims (**Pérez-Martínez & Melgarejo**, 2015; **Rodríguez *et al.***, 2019; **Rodríguez *et al.***, 2020), and *Passiflora edulis* Sims. f.

flavicarpa Degener (**Gama *et al.***, 2013; **Melo *et al.***, 2014; **Rodríguez *et al.***, 2019). In the present study, we determined the physiological response of *P. tripartita* var. *mollissima* plants at different phenological stages in two contrasting environmental conditions and estimated the effect of climatic variables on plant physiology as a contribution to the optimization of their productive system in constantly changing environmental conditions.

Materials and methods

Plant material and growth conditions

Three-month-old banana passion fruit seedlings, obtained from a nearby fruit nursery, were planted in two zones of the municipality of Pasca (Cundinamarca, Colombia). In the high altitude (2,498 m), we established the crop at El Refugio farm in Santa Teresita village, at 4°16’20.9’’N & 74°19’21.7’’W. In the low altitudinal zone (2,006 m), we established the crop at Bellavista farm in San Pablo village, at 4°18’45.52’’N, 74°19’58.3’’W. Fifty plants were planted at each site in a 600 m^2 area, at a distance of 4 m between plants and 3 m between rows. We used a single trellis trellising system with double wire (at 1.5 m and 2 m height). In the high-elevation site, the soil had a pH of 4.7 with a sandy loam texture, ECEC 4.53 meq/100 g, 9.57% OC, 0.82% N, 2.1 meq/100 g Ca, 0.51 meq/100 g K, 0.48 meq/100 g Mg, 33.9 mg kg^{-1} P, 11 mg kg^{-1} S, 1.19 mg kg^{-1} Cu, 103 mg kg^{-1} Fe, 1.53 mg kg^{-1} Mn, 2.05 mg kg^{-1} Zn, and <0.12 mg kg^{-1} B. In the lower-altitude site, the soil had a pH of 4.5, clay texture, ECEC 10.96 meq/100 g, 2.78% OC, 8.74 meq/100 g Ca, 0.31 meq/100 g K, 2.02 meq/100 g Mg, 0.34 mg kg^{-1} P, 24.56 mg kg^{-1} S, 0.033 mg kg^{-1} Cu, 2.51 mg kg^{-1} Fe, 0.18 mg kg^{-1} Mn, 0.17 mg kg^{-1} Zn, and 0.14 mg kg^{-1} B (**Mayorga**, 2017; **Mayorga *et al.***, 2020).

The cultivated sites were treated with dolomite lime; before planting, the seedlings were treated with a sulfur-based product. Each crop was fertilized seven times during the growing season, on average every 2 to 2.5 months, using compound edaphic fertilizers and foliar fertilizers. Given the limited information available for banana passion fruit cultivation, fertilization plans in each zone were based on soil analyses and nutritional levels reported as optimal for *Passiflora ligularis* L. (**Castro & Gómez**, 2010). The plants were irrigated when necessary, considering rainy or dry environmental conditions. Manual control of weeds and integrated pest and disease management was done through phytosanitary pruning, ethological control, and applications of biological and chemical products in rotation. Training pruning was done according to the established trellising system (**Mayorga**, 2017).

Climatic variables

Following the studies by **Mayorga** (2017) and **Mayorga *et al.*** (2020), we used a weather station (Coltein Ltda., Bogotá, Colombia; Hobo U12-006, Onset Computer Corporation, Bourne, USA) to record temperature, relative humidity (THR 102 sensors, USA) and photosynthetically active radiation (PAR; LI 190 B sensors, LI-COR, Lincoln, NE) in the two areas. Data recording was set every 15 minutes. Vapor pressure deficit (VPD) was determined from relative humidity and temperature data as recommended by **Allen *et al.*** (1998). We recorded the data at the high elevation zone from November 2014 to March 2016, and at the low elevation from April 2015 to March 2016.

Photosynthetic rate/photosinthetic photon flux density curves

The photosynthetic rate/photosynthetically photon flux density (A_N/PPFD) curves (**Mayorga**, 2017) were based on the BBCH (Biologische Bundesanstalt, Bundessortenamt, and Chemische Industrie) codes for three plants with stem heights between 80 and 160 cm (BBCH 34-38) in their vegetative stage, as applied to *Passiflora ligularis* by **Rodríguez-León *et al.*** (2015), and for three plants in their reproductive stage (flowering, BBCH 56-60) in each of the two study areas. Measurements were recorded between 8:00 and 13:00 h. We selected fully expanded leafs in optimal nutritional and phytosanitary state from the middle third of the plant at the vegetative stage or source leaves at the reproductive stage to measure the photosynthetic rate (A_N) at photosynthetically photon flux density (PPFD) levels of 1800, 1600, 1400, 1200, 1000, 800, 600, 400, 300, 200, 100, 50, 40, 30, 20, 10, and 0 µmol m^{-2} s^{-1} photons. Measurements for each PPFD level were registered using an infrared gas analyzer (ADC BioScientific Ltd., Hoddesdon, UK), taking six technical replicates in each PPFD level. The CO_2 flux was adapted to maintain a concentration of 400 µmol mol^{-1} s^{-1} inside the chamber at a constant temperature of 18°C. Data were adjusted to the Michaelis-Menten hyperbolic model by nonlinear regression to obtain the parameters of maximum photosynthetic rate (A_{max}), light saturation point (LSP), light compensation point (LCP), respiration in darkness (R_D), and apparent quantum yield (φ) (**Rodríguez *et al.***, 2019). We selected the curve with the best fit (R^2) for each zone and phenological stage.

Gas exchange, leaf water potential, and chlorophyll fluorescence

As reported by **Mayorga** (2017), samples were collected at the following phenological stages using the BBCH commercial code: vegetative I (Veg_I) when plants' main stem had reached 60-70% of their maximum length (BBCH 36-37); vegetative II (Veg_II) when plants' main stem had 90-100% of their maximum length (BBCH 39); flowering (Flower) when flower buds reached 60% of their typical size (first open flowers; BBCH 56-60); fructification I (Fruit_I) when the fruits reached 30-40% of their final size (BBCH 73-74); fructification II (Fruit_II) when the fruits reached 60-70% of their final size (BBCH 76-77), and fructification III (Fruit_III) when the fruits reached 90-100% of their final size (BBCH 78-79).

In the vegetative phase, measurements were taken on leaves from the middle third of the plants' main stems; in the reproductive phase, they were made on source leaves of the reproductive organs (flowers or fruits) selected on secondary branches (productive branches). For the sampling in the reproductive phase, we considered that reproductive organs with the characteristics of the stage being evaluated predominated due to the overlapping of phenological stages of Passifloraceae, given their indeterminate growth habit.

In each phenological stage under evaluation, we took measurements at two-hour intervals from 8:00 to 18:00 h on eight plants, using three leaves per plant selected as described above. We recorded three measurements of photosynthetic rate (A_N), stomatal conductance (g_s), and transpiration (E) for each leaf using an infrared gas analyzer (IRGA) (ADC BioScientific Ltd., Hoddesdon, UK) with a narrow-leaf light chamber setting the PPFD equivalent to the LSP obtained from the A_N/PPFD curve corresponding to the phenological stage and zone. The CO_2 flow inside the chamber was adjusted to maintain a concentration of 380 µmol mol^{-1} and a constant temperature of 18°C. The extrinsic water use efficiency (WUE_e) was calculated as the ratio of A_N to E, while the intrinsic water use efficiency (WUE_i) was calculated as the ratio of A_N to g_s (**Fischer & Turner**, 1978; **Rodríguez *et al.***, 2019).

The maximum potential quantum efficiency of photosystem II (F_v/F_m) was determined using a modulated fluorometer (Hansatech FMS2, Norfolk, UK) on selected dark-adapted plants and leaves. The measurements were recorded at pre-dawn (4:00 h), ensuring dark-adapted leaves throughout the night.

We determined the leaf water potential (Ψ_{leaf}) on eight plants, one leaf per plant, using a Schöllander pressure chamber (model 1000, PMS Instruments Co., Albany, USA) at pre-dawn and midday, i.e., when the plants had the highest and lowest leaf water potential, respectively.

Statistical analysis

The A_N/PPFD curves were adjusted using the **R Core Team** (2024) statistical software (version 4.4.1). We validated normality and homoscedasticity assumptions on the model residuals and performed a factorial analysis of variance for each response variable ($P \leq 0.05$), taking the phenological stage and the zone as factors and using the SAS® software (version 9.4). For the gas exchange variables, we applied the square root transformation that allowed the adjustment of the data to the assumptions. We constructed models with the response variables based on the climatic variables, using longitudinal models in which the plant was taken as an individual and the phenological stages as time. This analysis allowed modeling the autocorrelation of the physiological variables of the plant in the different stages through the autoregressive structures of order 1 AR (1) and the symmetrical compound for F_v/F_m that showed the best fit. We limited the estimation method for the parameters using the restricted maximum likelihood (REML), and we used the Akaike information criterion (AIC) to fit the models. We performed these analyses using the R software, version 4.4.1 (**R CoreTeam**, 2024).

Results

Climatic conditions of the study zones

The high altitudinal zone (2,498 m) had lower daily minimum (11.9°C), average (14°C), and maximum temperatures (16°C). There, a high relative humidity close to 90% was maintained throughout the day. The highest average PAR (405.75 µmol photons m^{-2} s^{-1}) and low to medium VPD ranged between 0.3 and 0.5 kPa (**Figure 1**).

The lower altitudinal zone (2,006 m) had higher daily minimum (14.7°C), mean (17.9°C), and maximum temperatures (21.3°C), and lower relative humidity ranging from 75.9% at 16:00 h to 90.2% at 6:00 and 19:00 h. The lowest PAR was 352.4 µmol photons m^{-2} s^{-1}; the VPD was 0.4 kPa in the hours of high relative humidity and low temperature and reached 0.8 kPa in times of low relative humidity and high temperature (**Figure 1**).

In the two zones, the highest PAR level was recorded at 10:00 h, the lowest temperature at 6:00 h, and the highest one at 15:00 h. The differences between the minimum and maximum daily temperatures were greater in the lower altitude (6.6°C) compared to the high zone (4.1°C), indicating smaller temperature fluctuations at the higher elevation. Additionally, in the low zone, the VPD showed daily behaviors similar to that of the temperature and opposite to that of the relative humidity, while in the high altitude, VPD and relative humidity did not show marked oscillations during the day (**Figure 1**).

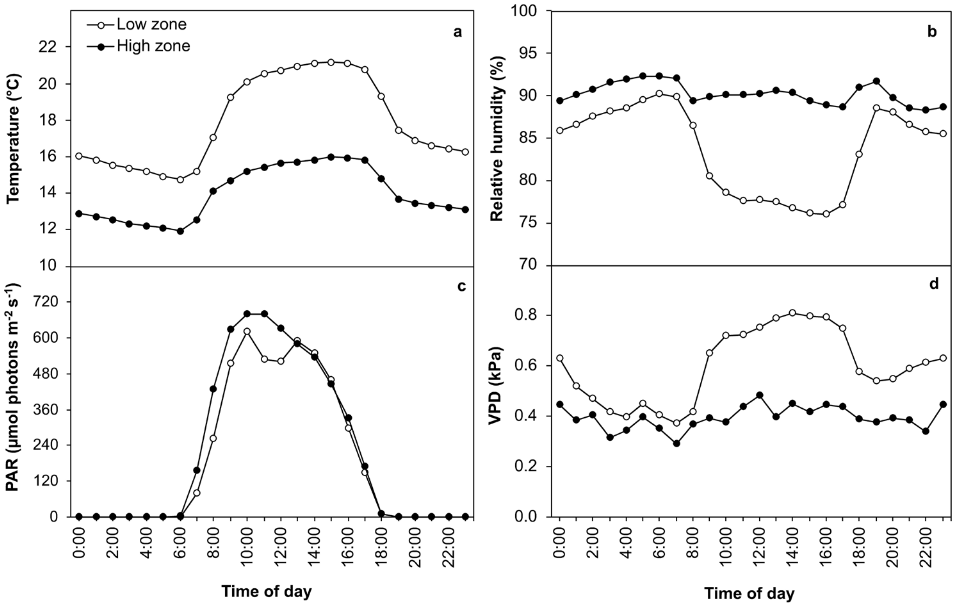

Figure 1. Average daily course of climatic variables in the two altitudinal zones for *P. tripartita* var. *mollissima* crops in Pasca, Cundinamarca (Colombia): high altitudinal zone (2,498 m) from November 2014 to March 2016, and low altitudinal zone (2,006 m) from April 2015 to March 2016. Temperature (**a**), relative humidity (**b**), photosynthetically active radiation (**c**), and vapor pressure deficit (**d**)

Photosynthetic response curves to light

The parameters derived from the A_N/PPDF curves indicated that plants grown in the low zone showed a higher A_{max} and apparent quantum yield φ than plants grown in the high zone (**Table 1**). In the two altitudes, we found differential photosynthetic responses to light between plants in the vegetative and reproductive stages; plants in the vegetative stages showed higher A_{max}, LSP, LCP, and R_D, while plants in the reproductive stage had a higher φ (**Table 1**).

Gas exchange and chlorophyll-a fluorescence

The A_N gradually decreased as phenological development progressed, showing the highest values in vegetative I stage (11.4-12.7 µmol CO_2 m^{-2} s^{-1}) and the lowest at fruit III reproductive stage (7.4-8 µmol CO_2 m^{-2} s^{-1}), when fruits showed harvest maturity (**Figure 2a**). A slight increase in A_N was recorded in plants from the low altitude at the early stage of fruit development and at the intermediate stage of fruit development in the high elevation (**Figure 2a**). The highest *E* rates in plants from the high altitude area occurred in the vegetative I stage (3.5 mmol H_2O m^{-2} s^{-1}) and fruit III stage (2.2 mmol H_2O m^{-2} s^{-1}), and the lowest rates occurred at flowering and fruit I stage (1.3 mmol H_2O m^{-2} s^{-1}). Although the behavior of *E* showed a similar behavior to that seen in the high altitude, in the low elevation, an increase in this variable was clear in the fruit I stage (3.3 mmol H_2O m^{-2} s^{-1}) (**Figure 2b**). In the two zones, the lowest g_s values were recorded in the vegetative I stage and the last stages of fruit development, at 0.2-0.3 mol H_2O m^{-2} s^{-1}. The highest g_s was seen in the flowering stage, with values of 0.6 and 0.36 mol H_2O m^{-2} s^{-1} for the high and low zones, respectively (**Figure 2c**).

Plants increased their WUE_e after the vegetative I stage. In the low zone, the maximum WUE_e occurred at the vegetative II stage and flowering (5.3 and 5.7 µmol CO_2 $mmol^{-1}$ H_2O). In the high altitude area, this maximum was obtained at flowering (8.1 µmol CO_2 $mmol^{-1}$ H_2O). In the two zones, WUE_e decreased after flowering, presenting levels of 2.4 and 3.8 µmol CO_2 $mmol^{-1}$ H_2O at fruit III stage for the low and high zones, respectively (**Figure 2d**). In the low zone, plants at the vegetative I stage presented a WUE_i of 47.1 µmol CO_2 mol^{-1} H_2O, which decreased to 33 µmol CO_2 mol^{-1} H_2O at flowering and fruit I stage and then increased during fruit development until reaching the maximum value of 50.9 µmol CO_2 mol^{-1} H_2O when the fruit showed harvest maturity. In the high zone, the WUE_i behavior was similar: plants in the vegetative I stage presented the highest WUE_i (65.1 µmol CO_2 mol^{-1} H_2O), then decreased until reaching the minimum value at flowering (16.5 µmol CO_2 mol^{-1} H_2O), and increased again during fruit development (**Figure 2e**).

Table 1. Parameters estimated from the photosynthetic response to the light (A_N/PPFD) curve fit on the Michaelis-Menten model in *P. tripartita* var. *mollissima* plants in the vegetative and the reproductive states grown in a high altitudinal (2,498 m) zone and a low altitudinal zone (2,006 m) in Pasca, Cundinamarca (Colombia). Photosynthetic rate at light saturation (A_{max}), light compensation point (LCP), respiration in darkness (R_D), light saturation point (LSP), and apparent quantum yield (**φ**). Values correspond to the mean (n=6) ± standard error.

Altitudinal zone	**Development state**	**R^2**	**A_{max} (µmol CO_2 m^{-2} s^{-1})**	**LCP (µmol photons m^{-2} s^{-1})**	**R_D (µmol CO_2 m^{-2} s^{-1})**	**LSP (µmol photons m^{-2} s^{-1})**	**φ (µmol CO_2 µmol $photons^{-1}$)**
High	Vegetative	0.99	19.19±0.19	24.05	1.25±0.10	689.96±28.38	0.030±0.0007
	Reproductive	0.99	16.09±0.11	19.07	0.99±0.08	584.78±18.82	0.031±0.0004
Low	Vegetative	0.99	24.71±0.38	38.64	2.31±0.14	748.78±40.04	0.039±0.0009
	Reproductive	0.99	20.55±0.34	11.25	0.82±0.13	542.18±21.24	0.045±0.0023

The F_v/F_m in plants in the vegetative phase in the low altitudinal zone (0.82-0.83) was slightly higher than that of plants in the high zone (0.81-0.82). In the reproductive stage, the F_v/F_m was similar in the two zones, except in the fruit II stage, with an F_v/F_m of 0.83 here in the high elevation and of 0.82 in the low one (**Figure 2f**).

Plants grown in the high altitudinal zone presented higher A_N, g_s, and WUE_e values than plants in the low zone, while in the latter, there were higher rates of *E*, WUE_i, and F_v/F_m (**Figure 2**).

When we evaluated the daily behavior of gas exchange variables during the vegetative phase (**Figure 3 a,b,c,d,e**) in the high altitudinal zone, plants presented the maximum A_N (13.7 µmol CO_2 m^{-2} s^{-1}) and *E* (3. 3 mmol H_2O m^{-2} s^{-1}) between 12:00-14:00 h (**Figure 3a,b**), while g_s remained between 0.33 and 0.36 mol H_2O m^{-2} s^{-1} during most of the day, declining to 0.28 mol H_2O m^{-2} s^{-1} between 16:00-18:00 h (**Figure 3 c**). In the lower altitude, the maximum A_N (13 µmol CO_2 m^{-2} s^{-1}), *E* (2.4-2.5 mmol H_2O m^{-2} s^{-1}), and g_s (0.42 mol H_2O m^{-2} s^{-1}) were recorded between 8:00-10:00 h and decreased as the day progressed, except for g_s which, after showing a marked decrease between 10:00-12:00 h, increased again between 12:00-14:00 (**Figure 3 a, b, c**), times when PAR decreased and then increased in this zone (**Figure 1**).

WUE_e in plants in the low altitude area was high during the early hours of the day (5.9 µmol CO_2 $mmol^{-1}$ H_2O), coinciding with the time of highest A_N. It then remained constant during the rest of the day, at levels between 4.8-5.1 µmol CO_2 $mmol^{-1}$ H_2O. In

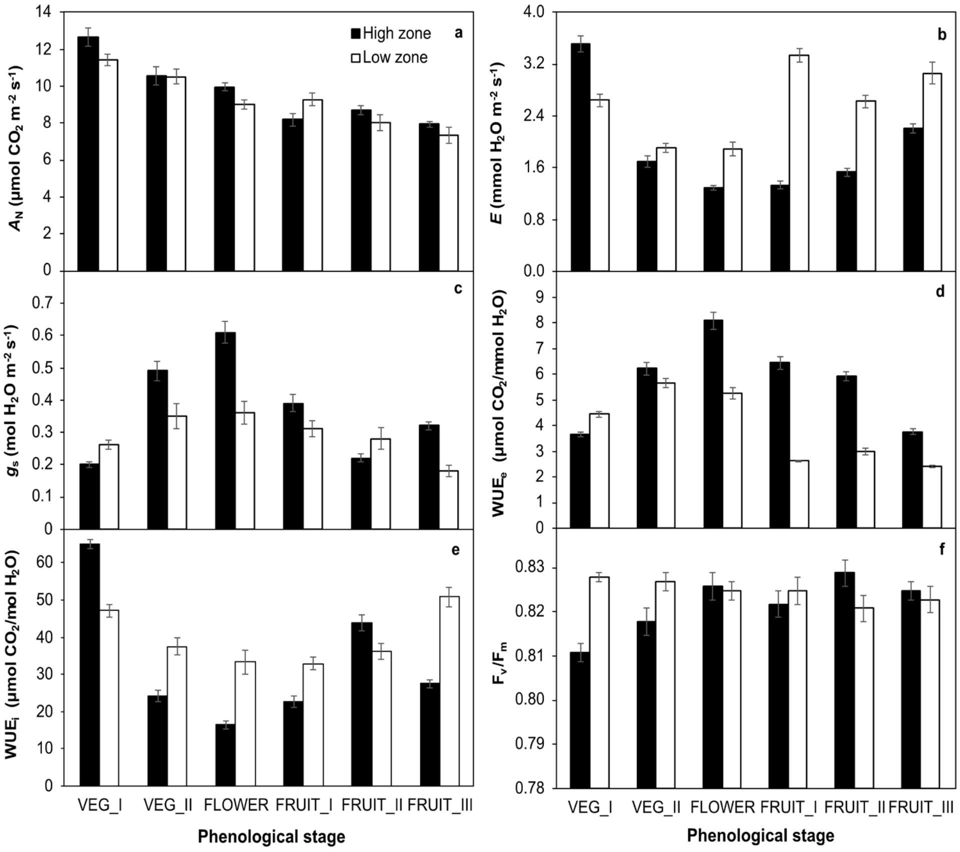

Figure 2. Gas exchange in *P. tripartita* var. *mollissima* plants at different phenological stages in a high altitudinal zone and a low one (2,498 and 2,006 m, respectively) in Pasca, Cundinamarca (Colombia). **(a)** Photosynthetic rate (A_N). **(b)** Transpiration (*E*). **(c)** Stomatal conductance (g_s). **(d)** Extrinsic water use efficiency (WUE_e). **(e)** Intrinsic water use efficiency (WUE_i). **(f)** Maximum potential quantum efficiency of photosystem II (F_v/F_m). Vertical error bars indicate standard error (n=8)

the high altitude, the highest WUE_e was also recorded in the early hours of the day (5.5 µmol CO_2 $mmol^{-1}$ H_2O) and the lowest (3.9 µmol CO_2 $mmol^{-1}$ H_2O) between 16:00-18:00 h (**Figure 3d**).

Plants in the high zone presented the highest WUE_i between 12:00-14:00 h (52.7 µmol CO_2 mol^{-1} H_2O) (Fig. 3e), suggesting a possible stomatal closure at this time of the day when there is a high VPD (**Figure 1d**). For the rest of the day, WUE_i remained between 43-

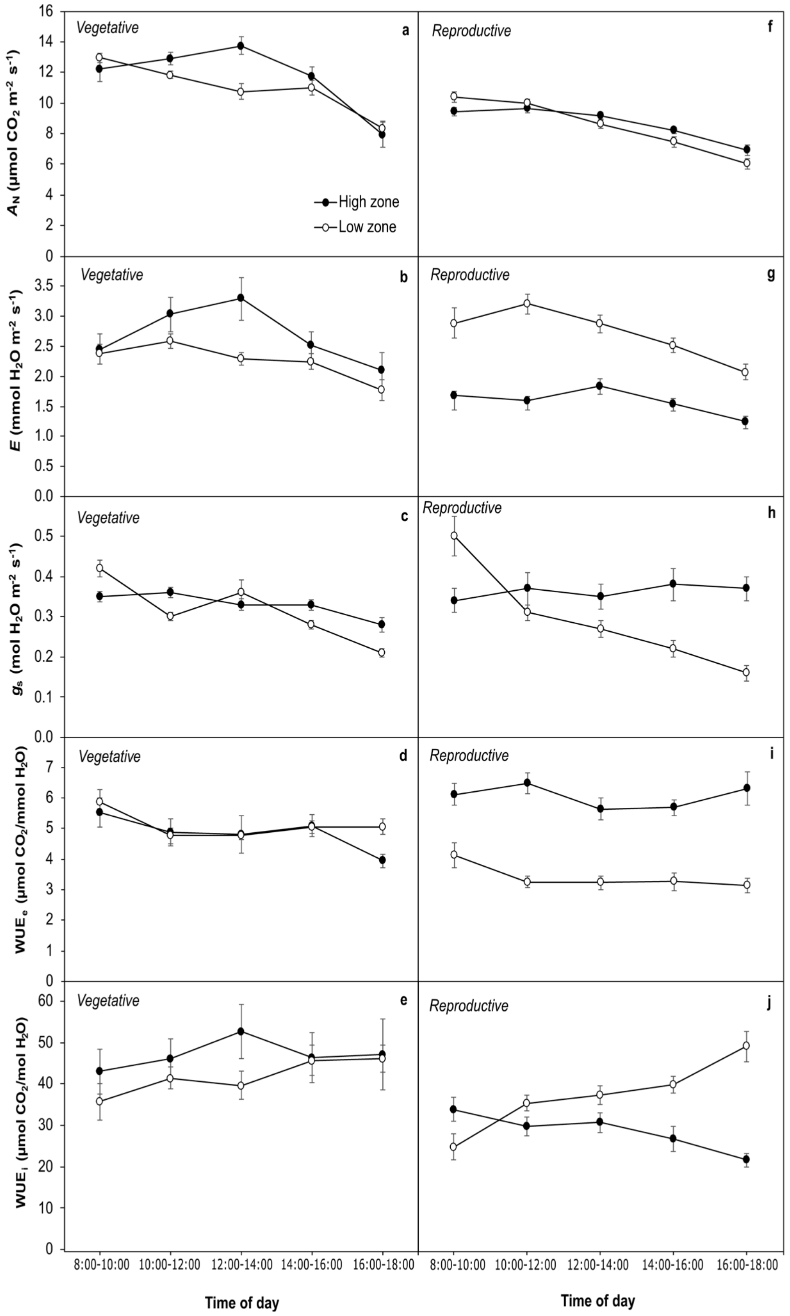

Figure 3. Daily behavior of gas exchange in *P. tripartita* var. *mollissima* plants in the vegetative (**a, b, c, d, e**) and the reproductive (**f, g, h, i, j**) stages in a high (2,498 m) and a low altitudinal zone (2,006 m) in Pasca, Cundinamarca (Colombia). Photosynthetic rate (A_N) (**a** and **f**), transpiration (*E*) (**b** and **g**), stomatal conductance (g_s) (**c** and **h**), extrinsic water use efficiency (WUE_e) (**d** and **i**), intrinsic water use efficiency (WUE_i) (**e** and **j**). Vertical bars indicate standard error (n=8).

46.1 µmol CO_2 mol^{-1} H_2O. In the low altitude area, WUE_i gradually increased throughout the day, except between 12:00-14:00 h, when a slight decrease in WUE_i coincided with an increase in g_s (**Figure 3e**).

In the reproductive phase (**Figure 3f,g,h,I,j**), plants grown in the low altitude area had the highest A_N (10.4 µmol CO_2 m^{-2} s^{-1}) and g_s (0.5 mol H_2O m^{-2} s^{-1}) between 8:00-10:00 h. These values decreased as the day progressed. In the high elevation area, the highest A_N was recorded between 10:00-12:00 h (10 µmol CO_2 m^{-2} s^{-1}), and g_s was maintained at levels between 0.34-0.38 mol H_2O m^{-2} s^{-1} over the day (**Figure 3f,h**). In the low altitudinal zone, the highest *E* rate (3.2 mmol H_2O m^{-2} s^{-1}) was recorded between 10:00-12:00 h, while in the high zone, the highest *E* rate (1.8 mmol H_2O m^{-2} s^{-1}) occurred between 12:00-14:00 h (**Figure 3g**). In the two altitudes, plants in the fruiting phase had the highest WUE_e at the time of day when they had the highest A_N: 4.1 µmol CO_2 $mmol^{-1}$ H_2O for the low zone and 6.5 µmol CO_2 $mmol^{-1}$ H_2O for the high zone (**Figure 3i**), with WUE_i behaving inversely to the g_s (**Figure 3j**).

Leaf water potential

The Ψ_{leaf} was higher at pre-dawn than at midday in all phenological stages evaluated in the two altitudes (**Figure 4**). Under pre-dawn conditions, Ψ_{leaf} in the high elevation at the vegetative I stage was -0.38 MPa, then it increased during the phenological development of the plants until reaching the highest value at the fruit II stage (-0.24 MPa) to subsequently decrease at the fruit III stage (-0.62 MPa). In the lower altitude, a gradual increase of Ψ_{leaf} was also observed in the early stages of plant development, from vegetative I stage (-0.53 MPa) to flowering (-0.2 MPa); then, Ψ_{leaf} decreased during fruit formation and growth until

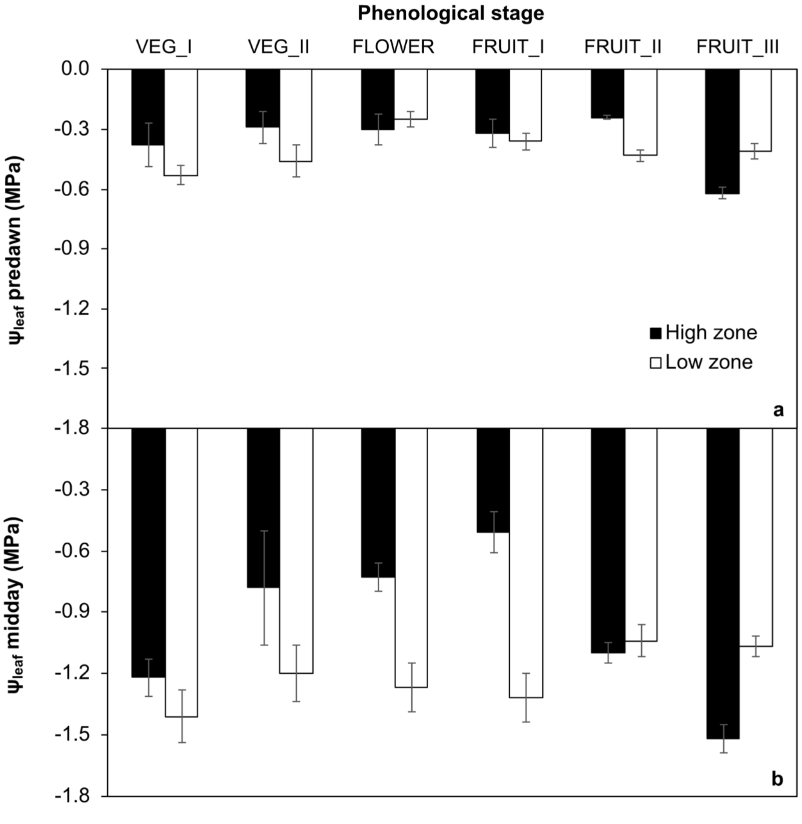

Figure 4. Leaf water potential at different phenological stages of *P. tripartita* var. *mollissima* plants at pre-dawn (**a**) and midday (**b**) in the high (2,498 m) and the low altitudinal zone (2,006 m) in Pasca, Cundinamarca (Colombia). The vertical bars indicate the standard error (n=8).

it reached -0.43 MPa (**Figure 4a**). In midday conditions, this trend was also seen in plants of the high zone, with Ψ_{leaf} increasing during the phenological development until reaching a maximum at fruit I stage (-0.51 MPa) and, then, decreasing in fruit III stage (-1.52 MPa). In the low altitudinal zone, Ψ_{leaf} was constant during the crop cycle, except in the last stages of fruit development, when the highest Ψ_{leaf} (-1.07 MPa) was reached but lower than in the higher zone for these stages of development at this time of the day. For the other stages, Ψ_{leaf} was higher in the high-altitude plants (**Figure 4b**).

The ecophysiological variables related to gas exchange, chlorophyll fluorescence, and water potential showed statistically significant differences between phenological stages and zones, and the interaction between stage and zone ($P \leq 0.05$). The only exception was the C_i/C_a ratio, which did not show significant differences between zones but did between stages and in the interaction of both factors (**Table 2**).

Effects of climatic conditions on physiological variables

Longitudinal analyses indicated that PAR only had a significant impact on the variable related to chlorophyll fluorescence ($P \leq 0.05$) (**Table 3**). In general, with a one-unit increase

Table 2. Analysis of variance for gas exchange variables, chlorophyll fluorescence, and water potentials. *P≤0.05; **P≤0.01; ***P≤0.001; ns: not significant

Source of variation	A_N	E	g_s	C_i/C_a	WUE_e	WUE_i	Φ_{PSII}	F_v/F_m	$\Psi_{leaf\ predawn}$	$\Psi_{leaf\ midday}$
Stage	***	***	**	***	***	***	**	***	***	**
Zone	**	***	***	ns	***	***	***	***	***	***
Stage × Zone	**	***	***	***	***	***	**	***	***	***

Table 3. Estimation and significance of the longitudinal model parameters for the physiological variables in *P. tripartita* var. *mollissima* plants at different phenological stages in the high (2,498 m) and low altitudinal zones (2,006 m) in Pasca, Cundinamarca (Colombia). The upper value of each cell expresses the parameter value ± EE (n=8), and the lower value in italics indicates the significance level. ns: not significant (P≤0.1)

Variable	A_N	E	g_s	F_v/F_m	Ψ_{leaf}
PAR	ns	ns	ns	-0.0003±0.00001 *0.028*	ns
Temperature	0.08±0.02 *0.0003*	0.05±0.02 *0.0029*	-0.02±0.01 *0.0216*	-0.006±0.003 *0.0338*	-0.06±0.02 *0.0091*
Relative humidity	-0.02±0.01 *0.06*	-0.05±0.01 *0.0000*	0.02±0.01 *0.0005*	0.01±0.002 *0.0047*	ns
VPD	-1.36±0.49 *0.0052*	-1.9±0.37 *0.0000*	0.54±0.21 *0.0110*	0.47±0.15 *0.0025*	ns
Stage	-0.32±0.08 *0.0000*	-0.34±0.07 *0.0000*	0.12±0.04 *0.0007*	0.003±0.0006 *0.0338*	0.31±0.08 *0.0001*
Zone	0.2±0.07 *0.0021*	-0.09±0.05 *0.0927*	ns	ns	ns

in PAR, F_v/F_m decreased 0.0003 units if the other variables remained constant. Temperature also had a significant impact on all the variables evaluated ($P\leq0.05$). With a one-unit increase in temperature, A_N and *E* increased 0.08 and 0.05 units, respectively, while g_s decreased 0.02 units, F_v/F_m 0.006 units, and Ψ_{leaf} 0.06 units when the other variables remained constant. Relative humidity influenced all the variables, except Ψ_{leaf}, with a 10% significance for A_N and 5% for the other variables. With a one-unit increase in relative humidity, A_N and *E* decreased 0.02 and 0.05 units, respectively. In contrast, g_s increased 0.02 units and F_v/F_m 0.01 units when the other variables remained constant. The VPD had a significant effect on gas exchange variables and F_v/F_m ($P\leq0.05$): with a one-unit increase in the VPD, A_N and *E* decreased 1.36 and 1.9 units, respectively, while g_s increased 0.54 units and F_v/F_m 0.47 units when the VPD had the greatest impact on the physiological variables evaluated. The phenological stage had a significant effect on all evaluated variables ($P\leq0.05$). For each plant developmental stage, the square root of A_N decreased by 0.32 units, the square root of *E* by 0.34 units, while the square root of g_s increased by 0.12 units, the F_v/F_m by 0.003 units, and the Ψ_{leaf} by 0.31 units when all the other variables remained constant. The zone had a significant effect only on A_N ($P\leq0.05$) and *E* ($P\leq0.1$). A plant growing in the high zone gained 0.2 units in the A_N square root and lost 0.09 units in the *E* square root compared to plants growing in the low zone (**Table 3**).

Discussion

The parameters derived from the A_N/PPFD curve in *P. tripartita* var. *mollissima* plants in the vegetative phase were close to those reported for ornamental passionflower species (**Abreu *et al.***, 2014; **Pires *et al.***, 2011), while in the reproductive phase, they remained in the ranges reported for passionflowers of fruiting interest (**Fernández *et al.***, 2014; **Pérez-Martínez & Melgarejo**, 2015; **Rodríguez *et al.***, 2019). The higher A_{max} and φ in plants from the lower zone could be explained by the higher temperatures and lower PAR characteristic of the zone (**Greer & Weedon**, 2012a, 2012b). High A_{max} and φ are associated with high night-time temperatures due to increased R_D and, therefore, decreased carbohydrate concentrations in the leaves (**Lin *et al.***, 2021; **Flórez-Velasco *et al.***, 2024), which increases the strength of sinks (**Turnbull *et al.***, 2002). However, some plants improve efficiency in light uptake and use it as an adaptation strategy to low PAR environments (**Abreu *et al.***, 2014).

A_{max} and LSP higher values in plants in the vegetative stages have also been reported, related to growth during this period and its interaction with the environment. Plant processes that enhance carbohydrate demand promote the photosynthetic rate (**Lambers & Oliveira**, 2019). Lower R_D and LCP and higher φ in plants in the reproductive stage could answer to a minimization of carbon losses via low respiration rates as a strategy of plants requiring high efficiency in carbon use at this stage of development to meet the high demand of sinks. An example of this could be fruits of higher weight in banana passionfruit plants grown at higher altitudes with lower night temperature (**Mayorga *et al.***, 2020). Besides allowing a positive carbon balance, low LCP values associated with low R_D levels are indicators of a successful acclimatization, as also seen from high φ (**Abreu *et al.***, 2014).

A_N tendency to decrease as phenological development progresses may be due to increased leaf age and development (**Jahan *et al.***, 2023; **Salazar-Parra *et al.***, 2012). The slight increase in A_N observed in the lower zone at fruit I stage and in the upper zone at fruit II stage coincides with high A_N rates reported in other species at fruit set and post fruit set stages (**Hunter & Visser**, 1988; **Lebon *et al.***, 2005) in response to a high demand for photoassimilates in the sinks. This suggests that the decrease in photosynthesis due to leaf age is arrested by the presence of fruit (**Poni *et al.***, 1994).

In the two study areas, flowering was the stage with the lowest *E* levels, the highest g_s and WUE_e levels, and high Ψ_{leaf} because it is a phenological stage with high water and carbon demand to ensure the supply of photoassimilates for the sinks. Additionally, the continuous A_N decrease and high g_s at the flowering stage indicate A_N non-stomatal limitations, possibly due to biochemical changes (**Sawicki *et al.***, 2015). The highest diurnal

A_N levels in each zone coincide with high-PAR times, as the increase of this environmental factor is determinant on stomatal opening. In the low zone, the A_N decrease throughout the day may respond to temperature and VPD (>0.7 kPa) increases in early morning hours that gradually induce stomatal closure to avoid water loss through *E* (**Cuevas *et al.***, 2006). In the high altitude area, the high *E* rate and low Ψ_{leaf} at midday were related to a 0.5 kPa VPD that induced stomatal opening. In this sense, grape cultivars have shown lower A_N, g_s, and *E* values in growing seasons with high cloudiness conditions (lower PAR) (**Evangelista *et al.***, 2023).

Generally, changes in *E* answer to temperature variations and Ψ_{leaf} (**Farquhar & Sharkey**, 1982). However, in our study, we found a marked dependence of *E* on VPD. The initial response was characterized by an increase in *E* as VPD increased, until reaching a limit (0.7 kPa) where it began to decrease (**Abreu *et al.***, 2014; **Monteith**, 1995) as a result of stomatal closure to minimize water loss or a possible limitation in the plants' hydraulic conductivity (**Duursma *et al.***, 2014; **Macfarlane *et al.***, 2004).

The F_v/F_m values found in *P. tripartita* var. *mollissima* plants were similar to those reported for common passionflowers (**Fernández *et al.***, 2014; **Gomes *et al.***, 2012; **Pires *et al.***, 2011; **Rodríguez *et al.***, 2019; **Rodríguez-Castillo & Melgarejo**, 2015). They were in an optimal range of 0.8-0.83, indicating an efficient conversion of PSII light energy for ATP and NADPH production (**Abreu *et al.***, 2014). Likewise, they indicate good functioning of the photosystem that directly influenced A_N, since the energy captured and transported in the photochemical pathway favored CO_2 fixation capacity (**Gama *et al.***, 2013).

High Ψ_{leaf} during flowering in the low altitude and fruit development in the high elevation may indicate the need for plants to maintain optimal water status at these stages of high photoassimilate mobilization to sinks. In the high altitudinal zone, water losses were minimized by decreasing *E* rates and g_s, thus maintaining high WUE_e levels, while in the low zone, there would only be a reduction in *E* rate with a consequent increase in WUE_e. Ψ_{leaf} decrease at pre-dawn in the two study zones during the fruit ripening stage (fruit III) is a behavior also observed in other species (**Leibar *et al.***, 2015) that, together with the increase in *E*, the decrease in WUE_e, and the trend in WUE_i, would indicate low stomatal control at this phenological stage.

Conclusions

Passiflora tripartita var. *mollissima* plants showed to be physiologically adapted to the differential ecophysiological conditions in the two altitudes, as reflected in the A_{max}, LCP, R_D, LSP, and φ levels consistent with the plants' phenology, and the good photosystems functioning with F_v/F_m optimal values, appropriate water potentials, and daily behavior of gas exchange parameters dependent on the climatic conditions of each zone. The low temperature, high relative humidity, and low vapor pressure deficit in the high zone contributed to maintaining a better water status for the plants, given the lower *E* rates, A_N, g_s, Ψ_{leaf} higher levels, and better WUE_e. As the phenological development of the plants progressed, there was a decrease in A_N due to age and leaf development; however, in the initial stages of the fruiting phase, CO_2 and WUE uptake and assimilation were optimized, and there was also a higher Ψ_{leaf}.

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Author contributions

Study design and conceptualization: LMM, MM, GF. Field work: MM, LMM. Provision of data for the study: MM. Data analysis: SEM, MM. Writing and correction of preliminary manuscripts: MM, GF, SEM, LMM. Reading and editing of final manuscript: MM, GF, SEM, LMM. Resources, project administration, and funding acquisition: LMM.

Conflict of interest

The authors declare that there is no conflict of interest related to the publication of this article.

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