**Ecología en Bolivia** 61(1): 3-9. Abril 2026. ISSN 2075-5023.

Artículo

# Temporal variability of ecophysiological responses of cocoa (*Theobroma cacao* L.) are influenced by environmental variables and leaf traits

La variabilidad temporal de las respuestas ecofisiológicas del cacao (*Theobroma cacao* L.) están influenciadas por variables ambientales y caracteres de las hojas

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**Abstract**
The temporal variation of plant physiology is essential to understand plant responses to environmental conditions. We explored diurnal (24h) variation in microenvironmental conditions and key physiological processes of cacao (*Theobroma cacao* L. var. TSH-565) in two organic cultivation systems in Alto Beni, Bolivia: monoculture and successional agroforestry. We hypothesized that physiological responses (transpiration and $CO_2$ uptake) would be lower and less variable in agroforestry systems due to canopy buffering. In each system, we selected mature trees and measured temperature, relative air humidity, transpiration and $CO_2$ uptake hourly for 5 minutes on healthy canopy leaves placed in a sealed 3-L plastic chamber with wireless infrared sensors. We found that temperature and relative air humidity showed opposing bell-shaped patterns. Transpiration rate peaked at ~10:00 h and declined rapidly thereafter, while $CO_2$ uptake was highest at ~09:00 – 10:00 h and declined more slowly until 17:00 h in both systems. Transpiration rate was significantly influenced by temperature, relative air humidity, leaf area and cultivation system (lower in agroforestry, $p< 0.001$). $CO_2$ uptake was primarily driven by leaf area, with marginally lower rates in agroforestry ($p = 0.05$). Our results indicate that successional agroforestry systems may buffer extreme microclimatic conditions, reducing transpiration variability and potentially improving water-use efficiency under climate stress. Our findings support the use of diversified shade systems for climate adaptation in cacao production.
**Key words**: $CO_2$ uptake, Leaf area, Relative air humidity, Temperature, Transpiration.

**Resumen**
La variación temporal de la fisiología vegetal es esencial para comprender la respuesta de las plantas a las condiciones ambientales. Analizamos la variación diurna (24 h) en las condiciones microambientales y los procesos fisiológicos clave del cacao (*Theobroma cacao* L. var. TSH-565) en dos sistemas de cultivo orgánico: monocultivo y agroforestal en Alto Beni, Bolivia. Hipotetizamos que las respuestas fisiológicas (transpiración y absorción de $CO_2$) serán menores y menos variables en sistemas agroforestales debido al efecto amortiguador del dosel. En cada sistema, seleccionamos árboles maduros y medimos la temperatura, humedad relativa del aire, transpiración y absorción de $CO_2$ cada hora durante cinco minutos en hojas sanas del dosel colocadas en una cámara de plástico sellada de 3-L con sensores infrarrojos inalámbricos. Encontramos que la temperatura y la humedad relativa del aire mostraron patrones opuestos en forma de campana. La tasa de transpiración alcanzó su máximo a las 10:00 h y disminuyó rápidamente, mientras que la absorción de $CO_2$ fue máxima entre las 9:00 y 10:00 h y disminuyó lentamente hasta las 17:00 h en ambos sistemas. La tasa de transpiración se vio significativamente influenciada por la temperatura, humedad relativa del aire, área foliar y el sistema de cultivo, siendo menor en el sistema agroforestal ($p < 0,001$). La absorción de $CO_2$ estuvo impulsada principalmente por el área foliar, con tasas ligeramente inferiores en el sistema agroforestal ($p = 0,05$). Nuestros resultados indican que los sistemas agroforestales pueden amortiguar las condiciones microclimáticas extremas, reduciendo la variabilidad de la transpiración y mejorando potencialmente la eficiencia del uso del agua bajo estrés climático.
**Palabras clave** : Absorción de $CO_2$, Área foliar, Humedad relativa del aire, Temperatura, Transpiración.

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**Recibido**: 19.08.25, **Aceptado**: 28.11.25

## Introducción

How organisms respond to environmental conditions often creates patterns across different spatial and temporal scales (Adrian *et al.* 2012). Metabolic processes in plant species, such as transpiration and photosynthesis, exhibit both long and short-term temporal patterns (Lu *et al.* 2019). Although the mechanisms that shape these patterns were analyzed, there are gaps in our understanding of the influence of environmental variables, leaf traits and cultivation systems on shaping these patterns (Gómez-Yarce *et al.* 2020). By studying it, we can better understand the ecophysiological responses of cultivated tree species to different environmental conditions.

Environmental variables such as temperature and relative air humidity are the most critical environmental variables influencing physiological plant responses (Grossiord *et al.* 2020) in natural and cultivated ecosystems. For example, short (temperature) and long (canopy cover) environmental variables could be modified in cultivation systems (e.g., Agroforestry systems) that consequently could influence the expression of functional leaf traits and physiological processes (Saavedra *et al.* 2020).

In plants, physiological processes are regulated by the expression of functional leaf traits (Medlyn *et al.* 2017). For instance, stomatal responses to changes in vapor pressure deficit (VPD) are influenced by air temperature and are the main regulators of daily transpiration rate (Grossiord *et al.* 2020). Similarly, leaf area (LA) and specific leaf area (SLA) are associated with the amount of photosynthetically active radiation (PAR) that leaves can intercept (Puglielli *et al.* 2017) and the $CO_2$ uptake rate per leaf area (Righetti *et al.* 2007) which are the main drivers of photosynthesis.

Despite all this information, the ecophysiological response patterns of cultivated trees over a daily period and their variation between cultivation systems remain unclear (Gómez-Yarce *et al.* 2020). This study aims to investigate how do physiological processes and environmental conditions change during a 24-hour period in two different cultivation systems? And which variables influence transpiration and $CO_2$ uptake rates? We hypothesize that in agroforestry systems, physiological responses such as transpiration and photosynthesis rates to environmental conditions will be lower and less variable than monocultures.

## Study area

Fieldwork was conducted in November 2022 and 2023 at the Sara Ana Research and Training Center in La Paz, Bolivia. The Sara Ana Center is located in the Alto Beni region (15°27'36" S – 67° 28'17" W, 450 m) at the bottom of the Bolivian Andes. In 2008, a long-term trial of different cocoa cultivation systems was established in a completely randomized block design with four repetitions of six cultivation systems: Organic monoculture (OM), Conventional monoculture (CM), Organic agroforestry (OA), Conventional agroforestry (CA) and Successional agroforestry (SA) (Armengot *et al.* 2016). (For more details see Figure 1 in Saavedra *et al.* 2020). Data were collected in the Organic monoculture (OM) and Successional agroforestry (SA). These two cultivation systems were similar in the density of planted trees, equivalent to 625 trees per hectare (4 x 4 density). They differ in the presence of a high density of trees occupying the middle and upper strata, with 602 trees per hectare. Agroforestry systems are characterized by fruiting trees such as: *Theobroma grandiflorum* (Copuazú), *Garcinia gardneriana* (Achachairu), *Averrhoa carambola* (Carambila), Nitrogen fixers like: *Erythrina fusca* (Ceibo) and *Inga spp.* (Pacay) and timber species, *Stryphnodendron purpureum* (Toco colorado), *Swietenia macrophyla* (Mara) and *Centrolobium microchaete* (Huasicucho) (Saj *et al.* 2025).

## Methods

### *Data collection*

To collect data, we selected two trees of the TSH 565 variety in each of the organic monoculture (OM) and successional agroforestry (SA) cultivation systems per year. From each tree, we selected one mature and healthy leaf from the top crown of the tree. Takin care not to detach from the plant, we placed the selected leaf inside a 3 L plastic container with infrared wireless sensors synchronized by bluetooth to a portable datalogger (SPARK LX, Pasco Scientific 2022) for real-time data recording (Saavedra *et al.* 2020). We recorded temperature, air humidity, $CO_2$ uptake, and transpiration data for five minutes per leaf. Data collection was conducted simultaneously in both cultivation systems and different leaves were used for recording data on physiological processes and environmental variables every hour for 24 hours.

### *Microenvironmental variables*

We used a weather wireless sensor (PS-3209, Pasco Scientific 2022) to record ambient temperature (°C) and relative air humidity (%) to illustrate the microclimate conditions in each cultivation system. Both variables were recorded before the weather sensor was placed in the plastic container. We averaged the data collected over five minutes to obtain a value for each variable at the leaf level. The same procedure was used for the physiological process.

### *Leaf gas exchange measurements*

We measured the absolute air humidity ($g/cm^3$) to estimate the net amount of water vapor produced at a specific temperature as an indicator of transpiration rate with a wireless sensor (PS-3209, Pasco Scientific 2022) (Pipitsunthonsan *et al.* 2018). The $CO_2$ uptake was measured simultaneously, using a $CO_2$ wireless sensor (PS-3208, Pasco Scientific 2022) calibrated to 400 ppm. To determine the transpiration and $CO_2$ uptake rate we divided the data by the leaf area (in $cm^2$) and multiplied the result by 3600 seconds.

### *Leaf area measure*

Those leaves where transpiration and $CO_2$ uptake rates measured were collected and transported to laboratory to estimate the leaf area (LA, $cm^2$). The leaves were processed each day after the physiological data was recorded in field. We used the method of Perez-Harguindeguy *et al.* (2016) to measure the leaves. The leaves were dehydrated in an electric dryer for two days at the Herbario Nacional de Bolivia (LPB). Subsequently, we scanned the dried leaves to estimate the leaf area and obtained digital photos processed with Image J software.

### *Statistical analysis*

For data analysis que applied Linear Mixed Models (LMMs) because data do not follow normality and independence. In separate models, we tested the effect of microenvironmental variables (temperature and relative air humidity), leaf area and cultivation systems as fixed factors on transpiration and $CO_2$ uptake rates. We included hour as a random variable. In both models, we started with a full model. After that, we created reduced models by simplifying the full model using the Dredge function. We compared models with the corrected Akaikes's Information Criterion (AICc) (Symonds & Moussalli 2011). All the reduced models, whose ΔAICc was less than 2, were considered the best. We carried out statistical analyses with the R software version 3.6.0 (R Core Team 2019).

## Results

We found that environmental variables (i.e., temperature and relative air humidity) and leaf area shaped the daily patterns of transpiration and $CO_2$ uptake (Fig. 1). Temperature and relative air humidity followed opposite bell-shaped patterns throughout the day. The highest temperature and relative air humidity occurred between 11:00 and 13:00 h in both cultivation systems (Figure 1a, b).

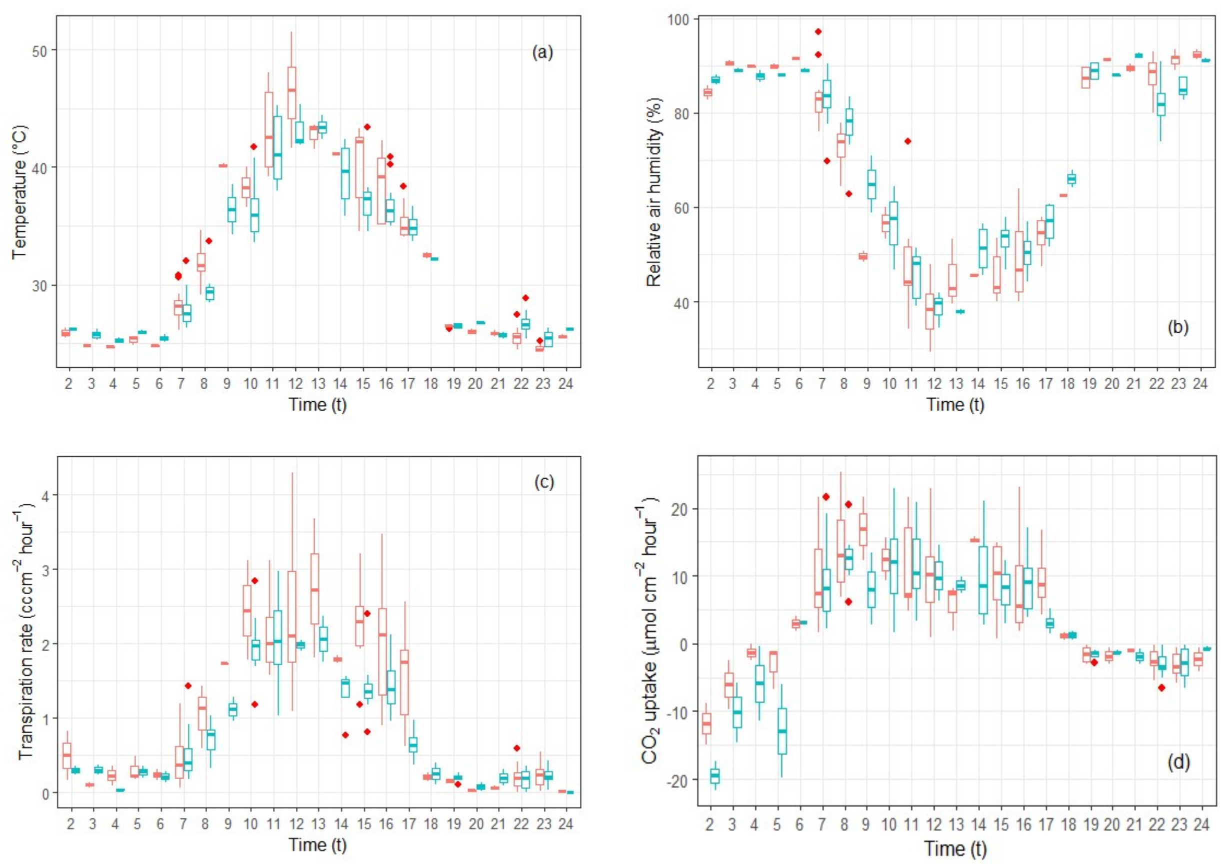


Figure 1. Daily patterns of (a) temperature (°C), (b) relative air humidity (%), (c) transpiration (cc/$cm^2$/hour) and (d) $CO_2$ uptake (umol/$cm^2$/hour) are compared between cultivation systems. In boxplots dark horizontal lines are median, boxes indicate 25th and 75th percentiles and whiskers show data variability. Boxplots in red correspond to cocoa monoculture and blue light denote agroforestry system. The red dots represent outliers.

We discover that transpiration rate along the day followed a bell-shaped pattern with a peak between 10:00 to 14:00 h in both cultivation systems (Figure 1c). Transpiration rate declined rapidly until 17:00 h. The best model results show that temperature, relative air humidity and leaf area were the main factors determining transpiration rate values (Table 1a). When comparing cultivation systems, the transpiration rate along the day was higher in monocultures than in agroforestry systems (Table 2a, Figure 1c).

We observed that there was no clear peak for $CO_2$ uptake. Higher values of $CO_2$ uptake were recorded at 9:00 and slowly declined until 17:00 h in both cultivation systems (Figure 1d). $CO_2$ uptake was mainly influenced by leaf area (Table 1b) and showed partial differences between monoculture and agroforestry systems (Table 2b) with a clear tendency showing slightly higher $CO_2$ uptake rates in monocultures than agroforestry systems (Table 2b, Figure 1d).

Table 1. Model comparison for testing effects of explanatory variables on (a) Transpiration and (b) $CO_2$ uptake. Hours were included as random effects in the models. We considered models with a ΔAIC less than 2.

| Response variable ~ predictor variables | *df* | AICc | ΔAIC | Weight |
|---|---|---|---|---|
| a) **Transpiration rate** | | | | |
| Transpiration ~ leaf area + temperature + relative air humidity + cultivation systems | 7 | 328.3 | 0.00 | 0.881 |
| Transpiration ~ hour (null model) | 3 | 439.8 | 111.51 | 0.000 |
| b) **$CO_2$ uptake rate** | | | | |
| $CO_2$ uptake ~ leaf area + cultivation systems | 5 | 1569.8 | 0.00 | 0.360 |
| $CO_2$ uptake ~ leaf area | 4 | 1571.3 | 1.52 | 0.168 |
| $CO_2$ uptake ~ leaf area + relative air humidity + cultivation systems | 6 | 1571.7 | 1.89 | 0.140 |
| $CO_2$ uptake ~ leaf area + cultivation system + temperature | 6 | 1571.8 | 2.00 | 0.133 |
| $CO_2$ uptake ~ hour (null model) | 3 | 1592.4 | 22.60 | 0.000 |

**Table 2.** Results from the best linear mixed model for (a) Transpiration (AICc= 327.9) and (b) $CO_2$ uptake (AICc= 1569.8). Hours were included as random effects in the models. Significant values are highlighted in bold.

| | Estimate | Std. Error | t-value | P(>\|t\|) |
|---|---|---|---|---|
| a) **Transpiration rate** | | | | |
| Intercept | 1.5828 | 1.0830 | 1.461 | 0.145 |
| Leaf area | -0.003 | 0.0005 | -5.197 | **<0.001** |
| Temperature | 0.0512 | 0.0188 | 2.725 | **0.007** |
| Relative air humidity | -0.0209 | 0.0069 | -3.031 | **0.002** |
| Cultivation system | -0.2222 | 0.0569 | -3.904 | **<0.001** |
| b) **$CO_2$ uptake rate** | | | | |
| Intercept | 11.0503 | 2.2170 | 4.984 | **<0.001** |
| Leaf area | 0.0323 | 0.0063 | -5.080 | **<0.001** |
| Cultivation system | -1.1312 | 0.5931 | -1.907 | **0.05** |

## Discussion

Our study provides insights into how cocoa (*Theobroma cacao*) modulates daily patterns of transpiration and $CO_2$ uptake in response to environmental conditions, leaf traits and cultivation systems. By linking physiological responses to cultivation systems our findings enhance our comprehension of plant-environmental interactions in a changing climate. Currently, the physiological responses of cultivated trees to environmental stress have received significant attention, because of the rising temperatures and drought conditions across the cocoa belt production as a result of climate change (Schroth *et al.* 2016). However, there is limited information about the factors that influence daily patterns of transpiration and $CO_2$ uptake rates as well as their variability between different cocoa cultivation systems, such as agroforestry and monoculture. The findings of this study contribute to improving our understanding of daily patterns that could be essential for assessing water use efficiency, cultivation practices and the productivity of cocoa trees.

### *Temperature and relative air humidity patterns*

We found that temperature was lower in agroforestry than in monoculture systems, while relative air humidity was higher in agroforestry. Previous studies by Hebbar *et al.* (2020) have also observed similar patterns in open-top chambers. The negative correlation between temperature and air humidity may explain this opposite pattern (Pipitsunthonsan *et al.* 2018) and the shade created by canopy cover species such as *Theobroma grandiflorum* (Copuazú), *Garcinia gardneriana* (Achachairu), *Erythrina fusca* (Ceibo), *Inga* spp. (Pacay) and *Stryphnodendron purpureum* (Toco colorado) in agroforestry systems could account for the differences between cultivation systems (Niether *et al.* 2018).

*Micronvironmental drivers of transpiration pattern*

Our data further confirm that the long exposure of cacao trees to solar radiation in monoculture systems, increase temperature and consequently transpiration rate (Saavedra *et al.* 2020), supporting a positive relationship between these variables. Kirschbaum (2004) observed that with the increase of temperature values, vapor pressure deficit of the air may also increase, with a consequent increase in the transpiration rate. By contrast, the canopy-induced shading in agroforestry systems, reduce solar radiation and temperature (Niether *et al.* 2020, Suárez-Salazar *et al.* 2018, 2021), reducing the transpiration rate and its variability throughout the day. This lower variability suggests that agroforestry systems could be acting as a buffer against extreme environmental conditions, such as high temperatures and low relative air humidity, due to the effects of climate change. Previous studies have reported the contribution of agroforestry systems to reduce transpirations rates of cocoa (Saavedra *et al.* 2020) suggesting that water use efficiency of cocoa trees could be better managed in agroforestry systems.

*$CO_2$ uptake patterns*

The absence of a clear peak could be explained by other factors related with photosynthesis regulation. For instance, $CO_2$ uptake is regulated by environmental factors such as solar irradiance and photosynthetically active radiation (PAR) (Jaimez *et al.* 2008; Suárez-Salazar *et al.* 2018), functional leaf traits such as the opening and closing of stomata (Buckley 2019), and biochemical and genetic pathways that regulate the function of stomata and the activation of photosynthetic proteins (Eberhard *et al.* 2008). The similar pattern between cultivation systems could be explained by the compensation between the shade provided by companion trees in agroforestry systems (Ávila-Lovera *et al.* 2021) and the light saturation point of $CO_2$ uptake that induces photoinhibition (Verryckt *et al.* 2020) in monocultures. We trust that these two factors could drive a similar pattern between cultivation systems; however, more studies are needed to disentangle the main drivers of $CO_2$ uptake.

Our findings enhance our understanding of the biotic and abiotic factors that influence daily transpiration and $CO_2$ uptake patterns and how cultivation systems might change these patterns. This information could be valuable for future research and applications related to cocoa growth, yield, and environmental challenges such as drought and heat waves. Additionally, it supports numerous studies that highlight the importance of agroforestry systems as a successful approach to climate change adaptation.

## Conclusions

Temporal variability of environmental variables and physiological process show a bell-shape pattern with a peak near midday. Transpiration rate is influenced by environmental variables and functional leaf traits. $CO_2$ uptake is specially driven by functional leaf traits. Our findings suggest that agroforestry systems can buffer the impact of abiotic stress over the ecophysiological responses of cocoa trees.


## Acknowledgments

We would like to express our gratitude to all the staff at the Sara Ana experimental station for their support and guidance during fieldwork. We also want to thank the staff of the Herbario Nacional de Bolivia (LPB) and the Jardín Botánico La Paz (JBLP) of the Instituto de Ecología for their assistance with processing leaf data. We thank to Cristina Armas for reviewing early preliminary versions of the manuscript. The study was funded by the Swiss Agency for Development and Cooperation (SDC), the Liechtenstein Development Service (LED), the Biovisión Foundation for Ecological Development and the Coop Sustainability Fund and implemented in cooperation with the Research Institute of Organic Agriculture (FiBL) and Ecotop Foundation.


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