Studies

Functional plasticity of Capsicum annuum var. glabriusculum through multiple traits

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Abstract

The diversity of functional traits still has not been studied enough in model plant species, even less so in little-known species. This experiment was carried out under the extreme heat of Sonoran Desert, using shading nets and under conditions where the availability of water and nutrients was not a stress factor. We evaluated how the low, intermediate and high sunlight regimes impact survival and promote multiple alterations on the photosynthetic and ecophysiological response of cultivated Capsicum annuum var. glabriusculum plants. Extremely warm temperatures promoted a high heat sum in degrees days throughout plants development. Most plants grown in high sunlight regimes did not survive; under intermediate sunlight regimes survival was high and plants developed vegetative and reproductively; but under low sunlight regimes plants survival was high; however, they developed just vegetatively. Photosynthetic response to light suggests that plants are physiologically acclimated to low and intermediate irradiance, whereas the CO₂ assimilation curves suggest contrasting photosynthetic capacity traits. Under the intermediate sunlight regimes, plants strengthened their performance through multiple functional traits (e.g. CO₂ and water diffusion traits, photosynthetic capacity, respiration, among others). Consequently, their biomass gain was faster and proportionally higher by 76% with an investment of 14% in fruits development. The principal components analysis extracted the main explanatory functional traits: photosynthetic nitrogen allocation, stomatal conductance, Rubisco maximum carboxylation velocity, among others. In conclusion, phenological response and multiple functional traits determine plants acclimation to sunlight regimes and extremely warm temperatures in short term.

Keywords: C, plants; ecophysiology; phenology; photosynthesis; Sonoran Desert.

Introduction

The variability of plants’ functional traits in response to environmental shifts is largely determined by their phenotypic and ecophysiological plasticity traits; therefore, in different environments and among plants species, the ability of genotypes to produce different phenotypes is the main strategy for their adaptation and evolution in the short and long term (Valladares et al. 2014). The sunlight regimes and air temperature thresholds (together with other complementary cues such as the vapour pressure deficit, rainfalls, CO₂, soil biotic and abiotic traits) are the main drivers of plants phenological transitions and ecophysiological responses (Wadgymar et al. 2018; Fernández-Marin et al. 2020). For a robust analysis of phenological and ecophysiological traits either within individual species or among different species, microclimatic data sets are needed to provide realistic forecasts of plants’ fate under climate change pressures (Halbritter et al. 2020; Kattge et al. 2020). For such purposes, one of the main requirements is the tracking of environmental conditions, which implies recording mainly the sunlight regimes and air temperature thresholds, but also as many variables as possible during evaluations (e.g. CO₂, vapour pressure deficit, rainfalls frequency/amount, irrigation/fertilization frequency and amount, and many others) (Poorter et al. 2012a, b, 2016).

Measurements and descriptions must accurately reflect multiple functional traits related to plants behaviour, e.g. phenological development, photosynthetic traits, mineral nutrition and a long list of parameters (Poorter et al. 2015, 2016, 2019). The availability of such data sets has broad implications not only for the prediction of productivity (either in individual, populations or communities) but also because is the basic requirement for comparison purposes through meta-analysis focused on phenological events, the carbon feedbacks and patterns of biomass allocation (Niinemets et al. 2015; Halbritter et al. 2020). Current meta-analysis about the functional equilibrium model shows that plants significantly change the allometric distribution of their biomass (fruits, leaves, stems, roots) in response to sunlight regimes and air temperature.
regimes and temperatures (Poorter et al. 2012c, 2015, 2019). However, still, there are multiple knowledge gaps behind such a model, since meta-analyses clearly show that functional plasticity behind plants phenological and ecophysiological responses still has not been studied enough in model species, even less so in little-known species (Flexas and Gago 2018; Niinemets 2018). Furthermore, the current global estimates of leaves traits in response to sunlight and temperatures are biased due to the wide plasticity existing within and between plant species (Keenan and Niinemets 2016; Niinemets 2018). Currently, there is scientific consensus that basic research about the impact of environmental conditions at a local level on plants’ phenological and ecophysiological performance will provide reference data sets aimed to reveal the different functional plasticity attributes (Poorter et al. 2019; Kattge et al. 2020).

This survey combines various research methods applied in C₃ species (Martins et al. 2014; Sun et al. 2014; Sharkey 2016). We focused on a woody, perennial and deciduous shrub: Capsicum annuum var. glabriusculum, a little-studied C₃ species considered as the wild genetic ancestor of all varieties of domesticated and cultivated peppers worldwide (C. annuum), as well as a global priority species for in situ conservation programmes (Castañeda-Alvarez et al. 2016). Under the extreme heat of Sonoran Desert, we conducted an experiment where we used shading nets for plants cultivation under different sunlight, and in conditions where water and nutrient availability was not a stress factor. We addressed the following research question: Do the low, intermediate and high sunlight regimes drive a shift in survival rate and multiple alterations on the phenological and ecophysiological behaviour of cultivated plants? We hypothesized that under extremely warm temperatures, cultivated plants in low, intermediate and high sunlight regimes exhibit a positive survival rate, contrasting phenotypic attributes and multiple acclimation traits.

**Materials and Methods**

**Experimental site and modification of sunlight regimes to differentially shade plants**

This experiment was conducted under the extremely warm climate from Sonoran Desert (Hermosillo, Sonora, México; 29.128426 LN, −110.906437 LW). The historical trend of climatological conditions at the study site is described in Supporting Information A. For this experiment, we cultivated plants under the horticultural shading nets set to provide low, intermediate and high sunlight regimes (treatments). The daily photosynthetically active photons flux density (i.e. PPFD = sunlight regimes in mol m⁻² day⁻¹) was recorded throughout plants’ development by using a WatchDog™ ministration.

**Seeds germination, acclimation, transplanting, soil traits and growth conditions**

This experiment lasted 157 days. Seeds were sowed in germination trays towards mid-spring. After 49 days plants were transferred to wet soil contained in big pots and they were distributed in the following sunlight regimes: low (n = 36), intermediate (n = 36) and high (n = 36). After transplantation, plants developed in the treatments throughout the summer, under the influence of natural variations of climatic conditions. We fully avoided water and nutrients stress throughout plants’ development by applying daily irrigation as it was needed. Details of germination protocol, acclimation, soil physical and chemical profile, as well as growth conditions are described in Supporting Information A.

**Air temperature thresholds, heat sum in degrees days and phenology**

The daily minimum and maximum air temperature thresholds were recorded in the different sunlight regimes and open sky [see Supporting Information A]. The heat sum in degrees days (°D) was quantified throughout plants’ phenological development (Moreno et al. 2014). Plants’ phenological transition is shown in Table 2.

**Survival rate and gas exchange measurements**

Three days before gas exchange measurements, the survival rate (%) of plants was quantified at the stage of full vegetative and reproductive growth. Although there was no water and nutrients stress, in high sunlight regimes very few plants survived (Table 2). Therefore, all measurements were conducted only in plants grown in low and intermediate sunlight. The gas exchange measurements were conducted at the stage of full vegetative and reproductive growth in summer (Table 2); CO₂ assimilation curves in response to the photosynthetic photon flux density (A/PPFD) and CO₂ concentrations (A/C) were measured. Before this study, we conducted gas exchange measurements in wild plants to get reference values to compare those traits of cultivated plants. It was used a single portable infrared gas analyser system following standard procedures (LICOR 6400XT™). For details of gas exchange measurements, see Supporting Information A, while the raw gas exchange data set in Supporting Information B.

**Curves fitting, parameters validation and biochemical traits assessment**

Definitions and units from photosynthetic parameters are shown in Table 1. The measured A/PPFD curves and its photosynthetic parameters (i.e. Aₘₓ, Rₛₜₘₜ, Jₘₓ, others) were solved (i.e. validated) using different methods (Lobo et al. 2013; Sharkey 2016; www.landflux.org). The measured A/Cₑ curves were corrected to A/Cₑ curves by using the respective equation, removing by this way all diffusion resistance effects. Afterward, the A/Cₑ curves were solved by using two different curve fitting methods, e.g. the linear and rectangular mathematical methods (Sun et al. 2014; Sharkey 2016, 2019). From the A/Cₑ curves, multiple photosynthetic parameters were derived either directly or by using the corresponding equations (i.e. Vₑₓₘᵢₙ, Aₘₓ, Rᵢ/A, Cₑᵢ, others) (Martins et al. 2014; Sun et al. 2014; Sharkey 2016; www.landflux.org). To identify the photosynthetic plasticity traits, the gas exchange parameters recorded on wild plants were compared to cultivated plants in low and intermediate sunlight. A detailed description of curve fitting, and parameters validation is shown in Supporting Information A. Immediately after gas exchange measurements, leaves were freezing (−20°C) until analysis of total photosynthetic pigments, chlorophyll a, chlorophyll b, xanthophylls and carotenoids (Lichtenthaler and Buschmann 2001). All canopy leaves from harvested plants were dried, grounded to a fine powder and then subsamples were used to quantify the macroelements and microelements (FLASH 2000 analyser™, Thermo Scientific™; UV–visible
Afterward, the total content of each macroelement and microelement was calculated on a leaf area basis. To calculate the amount of nitrogen allocated to the main protein complexes of photosynthetic machinery (i.e. carboxylation, bioenergetics and light-harvesting), we applied the approach, equations and constants proposed by Niinemets and Tenhunen (1997). The leaf anatomical traits related to the gas exchange capacity were evaluated under the optical microscope (Leica BX51) by counting the abaxial and adaxial stomatal density, as well as the abaxial stomatal index (Martins et al. 2014).

We quantified plants’ growth rate, architectural development and their biomass allometry through different parameters: (i) relative growth rates, (ii) leaf area index, (iii) individual leaf area, (iv) specific leaf area, (v) leaf area ratio, (vi) total dry biomass, (vii) leaf mass per area, (viii) shoot/roots ratio, (ix) roots mass fraction, (x) stems mass fraction, (xi) leaf mass fraction and (xii) specific stem length (Poorter et al. 2012c, 2015). The reproductive yield was quantified by measuring the fruits’ fresh and dry weight, and the reproductive mass fraction on a dry basis.

Plants harvest, growth rate, biomass allometry and elemental analysis
Immediately after gas exchange measurements, plants harvest for growth assessment was conducted, six plants from the low sunlight and six plants from the intermediate sunlight.

| Symbol | Units | Definition |
|--------|-------|------------|
| PPFD  | µmol m⁻² s⁻¹ | Photosynthetically active photons flux density |
| VPD   | kPa   | Vapour pressure deficit |
| CO₂   | ppm   | Carbon dioxide |
| T_leaves | °C   | Temperature of leaf at the time of gas exchange measurements |
| Cᵢ    | —     | The most common metabolic pathway for carbon fixation through photosynthesis |
| R_dark | µmol CO₂ m⁻² s⁻¹ | Respiration rate in the dark, i.e. in absence of light |
| LCP   | µmol CO₂ m⁻² s⁻¹ | Light compensation point |
| PPFD₅₀ | µmol m⁻² s⁻¹ | Photosynthetically active photons flux density which half saturates CO₂ assimilation |
| PPFD₉₅ | µmol m⁻² s⁻¹ | Photosynthetically active photons flux density which saturates CO₂ assimilation by 95 % |
| gₛ    | mmol m⁻² s⁻¹ | Stomatal conductance |
| Tᵣ    | mmol H₂O m⁻² s⁻¹ | Transpiration rate |
| A/gₛ  | µmol CO₂ mmol H₂O | Intrinsic photosynthetic water use efficiency or the ratio between A/gₛ |
| A/Tᵣ  | µmol CO₂ mmol H₂O | Instantaneous photosynthetic water use efficiency or the ratio between A/Tᵣ |
| gₛₘ   | µmol CO₂ m⁻² s⁻¹ Pa⁻¹ | Mesophyll conductance |
| Cᵢ    | µmol mol⁻¹ | Ambient CO₂ concentration |
| Cᵢ    | µmol CO₂ mol⁻¹ or Pa | Intercellular CO₂ concentration or the CO₂ partial pressure at intercellular spaces |
| Cᵢ    | µmol CO₂ mol⁻¹ or Pa | Chloroplastic CO₂ concentration or the CO₂ partial pressure at the carboxylation sites of Rubisco |
| lₛ/lₘ/lᵦ | % | Stomatal, mesophyll and biochemical limitations of photosynthesis, respectively |
| A     | µmol CO₂ m⁻² s⁻¹ | net rate of CO₂ assimilation |
| R/A   | µmol CO₂/µmol CO₂ m⁻² s⁻¹ | The ratio between CO₂ respiration and CO₂ assimilation |
| Aₘ₈₉  | µmol CO₂ m⁻² s⁻¹ | The maximum CO₂ assimilation at high concentrations of CO₂ or at high levels of irradiance |
| Ru-bisco | — | Ribulose 1–5 bisphosphate carboxylase-oxidgenase |
| Rubp  | — | Ribulose 1–5 bisphosphate |
| Ac    | — | The portion of the photosynthetic process limited by the Rubisco activity |
| Aj    | — | The portion of the photosynthetic process limited by the Rubp regeneration |
| Cₑₑ   | Pa | The transitory portion between Ac and Aj evaluated at Cᵢ |
| J/4   | — | Four electrons are required for every assimilated CO₂ and every O₂ evolved |
| Vₑₑₙₙ | µmol CO₂ m⁻² s⁻¹ | Maximum velocity of Rubisco carboxylation |
| Jₑₑₙₙ | µmol e⁻ m⁻² s⁻¹ | Maximum electrons transport rate |
| J     | µmol e⁻ m⁻² s⁻¹ | Electrons transport rate |
| TPU   | µmol CO₂ m⁻² s⁻¹ | Triose phosphate utilization rate |
| Rₕ    | µmol CO₂ m⁻² s⁻¹ | Respiration rate in the day, i.e. in presence of light |
| Γ⁺    | µmol mol⁻¹ | Chloroplastic CO₂ photocompensation point or the CO₂ required to overcome photorespiration |
| Γ     | µmol mol⁻¹ | CO₂ compensation point or the CO₂ required to overcome Rₕ or where A = 0 |

Experimental design and statistical analysis
All statistical tests were conducted in NCSS 2007. Before statistical analysis, the Skewness and Kurtosis tests were used to check normality, as well as to evaluate the variance homogeneity, Levene’s test was applied. A one-way analysis of variance and a Fisher LSD test (P < 0.05) were performed with the
Table 2. Degrees days (°D) throughout phenological stages of Capsicum annuum var. glabriusculum plants grown in high, intermediate and low sunlight regimes. Survival rate after 157 days of growth is also shown (n = 36 plants per treatment). The chronological timescale in days, the day of year, months and seasons are shown. *Indicates the day of plants transplantation.

| Phenological stages | Sowing time | Seedling birth | *Early vegetative growth | Early flowering | Full vegetative or reproductive growth | Survival rate | Flowers and Fruits |
|---------------------|-------------|----------------|--------------------------|----------------|---------------------------------------|---------------|--------------------|
| Treatments          | (°D) Degrees days throughout phenological stages |               |                          |                |                                       |               |                    |
| High sunlight regimes| 0 521       | 1042           | 1401                     | 4035           | 5.5                                   |               | No                 |
| Intermediate sunlight regimes | 0 516       | 1032           | 1397                     | 3857           | 86.1                                  |               | Yes                |
| Low sunlight regimes | 0 482       | 964            | 1284                     | 3441           | 91.6                                  |               | No                 |
| Timescale in days   | 0 15        | 49             | 63                       | 157            |                                       |               |                    |
| Day of year         | 108         | 123            | 171                      | 265            |                                       |               |                    |
| Months              | April, May, June |            | June, July, August, September |                |                                       |               |                    |
| Season              | Spring      |                |                          |                |                                       |               |                    |

photosynthetic parameters derived with different curve fitting methods. Reference gas exchange parameters from wild plants (n = 4) were compared to those derived from cultivated plants (n = 6). Simultaneously, gas exchange parameters from plants grown in low sunlight (n = 6) were compared to those of plants grown under intermediate sunlight (n = 6). Likewise, the architectural, anatomical, biochemical and growth traits from cultivated plants (n = 6) were analysed. We conducted a multiple correlation analysis by using the significant traits [see Supporting Information B]. We also applied a principal components analysis through the varimax method, by using the raw data of multiple traits to extract those most meaningful from the statistical point of view [see Supporting Information B].

Results

Climatological trend and phenological response throughout the ecophysiological timeline

At open sky the climatological conditions (i.e. sunlight regimes, air temperatures, rainfalls and relative humidity) were contrasting throughout the experiment during spring and summer [see Supporting Information A—Fig. S2]. Under the different shading nets, plants developed under contrasting sunlight regimes and extremely warm air temperature thresholds [see Supporting Information A—Table S2]; therefore, a high heat sum was rapidly accumulated throughout plants phenological stages from seeds sowing until the full vegetative and reproductive growth (Table 2). The daily maximum air temperature thresholds recorded under the different sunlight regimes were significantly higher than the daily maximum air temperature thresholds recorded at the open sky. During the summer, the extremely warm air temperature thresholds recorded at the different sunlight regimes promoted warm soil temperatures [see Supporting Information A—Table S3]. Plants showed a contrasting phenological response and survival rate. Under the high sunlight regimes, there were not flowers and fruits production since most plants did not develop, but on the contrary almost all died, i.e. there was only 5 % of survival in this treatment (Table 2; Fig. 1). By contrast, under intermediate sunlight regimes plants developed vegetatively, the survival rate was high (86 %) and production of flowers and fruits was positive. In the low sunlight regimes plants developed vegetatively, the survival rate was high (91 %), but there were not flowers and fruits production (Table 2; Fig. 1).

Curves validation and photosynthetic traits

The measured data from the photosynthetic curves in response to light and CO₂ (i.e. A/PPFD, A/Ci curves) (Figs. 2 and 3) fitted mathematically to data predicted by the biophysical and biochemical model of photosynthesis. In the case of photosynthetic curves in response CO₂ (Fig. 3), when two different mathematic fitting methods were applied, the derived photosynthetic parameters were similar [see Supporting Information A—Table S5]. The photosynthetic curves in response to light (Fig. 2) showed different traits at different conditions. The curves initial slope and the curvature were similar in wild and cultivated plants (Table 3; see Supporting Information A—Table S4). As compared to cultivated plants, wild plants showed higher maximum CO₂ assimilation (A max), and maximum electrons transport efficiency (J 4) (Fig. 2; Table 3). The dark respiration (R dark) was similar in wild and cultivated plants under the intermediate sunlight regimes, but respiration tended to be higher in plants grown in low sunlight regimes (Table 3). The light compensation point (LCP) from wild versus cultivated plants was lower. On average, the CO₂ assimilation reached the 50 % of light saturation between 80 and 111 μmol m⁻² s⁻¹ of irradiance (PPFD 50), it reached 95 % light saturation between 256 and 491 μmol m⁻² s⁻¹ (PPFD 95), it showed the asymptotic trend between 500 and 1000 μmol m⁻² s⁻¹ and its declination at irradiance levels between 1200 and 1400 μmol m⁻² s⁻¹ (Fig. 2; Table 3). The derived parameters from the photosynthetic curves in response to light (Fig. 2) and the photosynthetic curves in response to CO₂ (Fig. 3) reflected the maximum functional capacity of plants in summer just at the stage of full growth (Table 2). In addition, multiple photosynthetic acclimation traits were recorded (Table 4).

Contrasting traits were recorded from the wild versus cultivated plants (Table 4; see Supporting Information A—Table S6). First, as compared to wild plants, in the low and intermediate sunlight regimes, the cultivated plants photosynthetically responded to warmer temperatures, different irradiance
Figure 1. *Capsicum annuum* var. *glabriusculum* plants harvested in low (A), and intermediate (C) sunlight regimes, after 157 days of development. In the high sunlight regimes (E–G) there was no harvest since most plants died. In (A) vegetative growth (stems and leaves) and (B) a sample of roots. In (C) the vegetative and reproductive growth (stems, leaves and green fruits), and (D) a sample of roots.

Figure 2. CO₂ assimilation curves in response to photosynthetic photons flux density (i.e. A-PPFD) measured on wild plants (A, D, n = 4) and cultivated plants in low and intermediate sunlight regimes (B, C, E, F, n = 6). In (A–C): □ Aobs refers to the averages from measured points. ◇ refers to measured data. ■ refers to averages from calculated J/4. ▲ refers to the raw data from calculated J/4. In (A–C): the continuous line refers to the modelled J/4. In (A–C): the curvature point and saturation of curves are shown. In (A–C): arrows indicate the declination of A at high PPFD. The LCP and Rdark are shown in the linear portion of curves (D–F). The measured points and those predicted by the model are shown in the linear portion of the curves (D–F).
and different vapour pressure deficit. Some traits were higher in wild versus cultivated plants, e.g. photosynthetic capacity ($A_{\text{max}}$, $A$, $J$, triose phosphate utilization [TPU]), the photosynthetic water use efficiency ($A/g_s$, $A/T_r$), the ratio between mesophyll and stomatal conductance ($g_m/g_s$ ratio), as well as the stomatal limitation ($l_s$). However, other specific traits were lower in wild versus cultivated plants, e.g. the ratio between CO$_2$ respiration and CO$_2$ assimilation ($R_d/A$), respiration ($R_d$), CO$_2$ compensation and photocompensation point ($\Gamma$, $\Gamma^*$), as well as the proportional mesophyll and biochemical limitations ($l_m$, $l_b$). In wild plants, the mean CO$_2$ concentration drawdown from intercellular spaces ($C_i$) towards chloroplastic spaces ($C_c$) (74 µmol CO$_2$ mol$^{-1}$) was lower than those from ambient towards intercellular spaces ($C_i$) (148 µmol CO$_2$ mol$^{-1}$) (Table 4). In plants grown under intermediate sunlight, the mean CO$_2$ concentration drawdown from intercellular spaces towards chloroplastic spaces ($C_c$) (78 µmol CO$_2$ mol$^{-1}$) was higher than those from ambient towards intercellular spaces (32 µmol CO$_2$ mol$^{-1}$). Similarly, in leaves plants grown in low sunlight, the mean CO$_2$ concentration drawdown from intercellular spaces towards chloroplastic spaces (29 µmol CO$_2$ mol$^{-1}$) was lower than those from ambient towards intercellular spaces (48 µmol CO$_2$ mol$^{-1}$) (Table 4). In response to low and intermediate sunlight regimes, cultivated plants exhibited contrasting traits, e.g. the CO$_2$ and water diffusional efficiency ($g_s$, $T_s$, $A/g_s$, $g_s/g_r$ ratio), photosynthetic capacity traits ($A_{\text{max}}$, $R_d/A$ ratio, $V_{\text{cmax}}$) and proportional limitation in stomata and mesophyll ($l_m$, $l_b$). However, other specific photosynthetic traits were similar in cultivated plants ($T$, $A/T_s$, $l_s$, $A/J/V_{\text{cmax}}$, $C_{\text{cavg}}$, $\Gamma$, $\Gamma^*$).

Architectural, anatomical and biochemical traits

The specific and individual leaf area, and the leaf area ratio were higher in plants grown in low sunlight regimes (Table 5; see Supporting Information A—Table S7). The leaf mass per area, adaxial and abaxial stomatal density, as well as the stomatal index were higher in plants grown under intermediate sunlight regimes, which also increased their photosynthetic pigments, nitrogen allocation to photosynthetic components and the content of macroelements and microelements (e.g. C, H, S, P, Mg, Ca, Fe, Ni, Cu). However, the content of some specific elements was similar in plants grown under the different sunlight regimes (e.g. N, K, Na, Zn and Mn).

Growth rate and biomass allometry

The relative growth rate of plants grown under intermediate sunlight regimes was higher; consequently, their total biomass, fruits fresh and dry weight, roots and reproductive mass fraction were higher. By contrast, the ratio of shoots and roots, leaf mass fraction and specific stems length were higher in plants grown in low sunlight regimes. The leaf area index and stems mass fraction were similar (Table 6; see Supporting Information A—Table S8).

Principal components analysis

The principal components analysis through the varimax method showed that the accumulated eigenvalues from four principal components explained 90% of the total experimental variance (PC1 = 35%, PC2 = 31.7%, PC3 = 16.3%...
Table 3. Photosynthetic traits (A/PPFD) measured on leaves from wild and cultivated Capsicum annuum var. glabriusculum plants. Average contrast is by column. Averages with different letters were significant at P < 0.05. SSE: sum of square error.

| Plants                      | Photosynthetic traits | RH (%) | VPD (kPa) | $T_{ad}$ (°C) | LCP (µmol m$^{-2}$ s$^{-1}$) | $A_{max}$ (µmol CO$_2$ m$^{-2}$ s$^{-1}$) | Initial slope | Curvature | PPFD95 (µmol m$^{-2}$ s$^{-1}$) | PPFD60 (µmol m$^{-2}$ s$^{-1}$) |
|-----------------------------|-----------------------|--------|-----------|---------------|-----------------------------|------------------------------------------|---------------|-----------|---------------------------------|-------------------------------|
| **Wild plants**             |                       |        |           |               |                             |                                          |               |           |                                 |                               |
| Low sunlight                | 34 ± 0.9$^c$          | 4 ± 0.4 | 25 ± 5$^c$| 12 ± 0.6$^c$  | 17 ± 2$^a$                  | 111 ± 8°C                                | 0.39 ± 0.04$^e$| 0.8 ± 0.4 | 491 ± 97$^d$                      | 451 ± 93$^d$                  |
| Intermediate sunlight       | 36 ± 1$^b$            | 2 ± 0.4 | 64 ± 4$^b$| 18 ± 0.2$^b$  | 40 ± 3$^b$                  | 80 ± 18$^b$                              | 0.75 ± 0.1$^f$| 0.75 ± 0.1 | 251 ± 69$^b$                      | 256 ± 68$^b$                 |
| High sunlight               | 40 ± 2$^c$            | 2 ± 0.2 | 65 ± 7$^c$| 14 ± 0.3$^c$  | 48 ± 12$^c$                | 99 ± 31$^c$                              | 0.36 ± 0.1$^h$| 0.36 ± 0.1 | 303 ± 176$^c$                     | 303 ± 176$^c$               |
| **Cultivated plants**       |                       |        |           |               |                             |                                          |               |           |                                 |                               |
| Low sunlight                | 34 ± 0.9$^c$          | 4 ± 0.4 | 25 ± 5$^c$| 12 ± 0.6$^c$  | 17 ± 2$^a$                  | 111 ± 8°C                                | 0.39 ± 0.04$^e$| 0.8 ± 0.4 | 491 ± 97$^d$                      | 451 ± 93$^d$                  |
| Intermediate sunlight       | 36 ± 1$^b$            | 2 ± 0.4 | 64 ± 4$^b$| 18 ± 0.2$^b$  | 40 ± 3$^b$                  | 80 ± 18$^b$                              | 0.75 ± 0.1$^f$| 0.75 ± 0.1 | 251 ± 69$^b$                      | 256 ± 68$^b$                 |
| High sunlight               | 40 ± 2$^c$            | 2 ± 0.2 | 65 ± 7$^c$| 14 ± 0.3$^c$  | 48 ± 12$^c$                | 99 ± 31$^c$                              | 0.36 ± 0.1$^h$| 0.36 ± 0.1 | 303 ± 176$^c$                     | 303 ± 176$^c$               |

Discussion

Climatological trend, survival rate and phenological response

The climatological record during plants development is fundamental in phenological and ecophysiological terms (Wadgymar et al. 2018; Poorter et al. 2019). In this study, the extreme climatological conditions at open sky [see Supporting Information A—Fig. S2] reflected the typical seasonal trend of the Sonoran Desert (CONAGUA 2014). In a window of 157 days of growth, the sum of heat in degrees days was extremely high in the low, intermediate and high sunlight regimes (Table 2). Such extreme heating under the shading nets was promoted by the warm air temperature thresholds recorded at open sky throughout spring and summer. During summer, the extremely warm temperatures plants tolerated under the shading nets were higher than temperatures recorded in the open sky (11–38 °C). It can be attributed to a heat-trapping effect caused by the shading nets (Pérez et al. 2006). Jiménez-Leyva et al. (2017) successfully cultivated the same species under intermediate sunlight regimes and extremely warm temperature thresholds with a fast accumulation of heat in degrees days.

Although plants developed without hydric and nutritional stress, their phenological response and survival were contrasting. The high sunlight regimes and extremely warm temperature thresholds promoted a fast detrimental effect for plants because they induced growth arrest, progressive yellowing and defoliation until eventually most plants died (Fig. 1; Table 2). By contrast, plants grown under the intermediate sunlight regimes and extremely warm temperatures showed a fast vegetative and reproductive growth with high survival. Unexpectedly, plants grown in low sunlight regimes and extremely warm temperatures showed a fast vegetative growth and even higher survival, but their reproductive capacity was completely nullified (Fig. 1; Table 2). Such a trend indicates that in the short term, the different sunlight regimes, and extremely warm temperature thresholds, promote a deep alteration in plants phenological responses. Likely, this contrasting response could be strongly linked to different ecophysiological ability within plants to quickly adapt to the extreme growing conditions above ground.
Photosynthetic acclimation traits
Photosynthesis of many C₃ plants responds linearly to low light intensities, but rapidly towards the 500 μmol m⁻² s⁻¹ of irradiance (i.e. 25% of total possible irradiance PPFD = 2000 μmol m⁻² s⁻¹), the linear relationship between absorbed quanta and photosynthetic assimilation begins to plateau, to then decline if the irradiation continues to increase to saturation levels (Marino et al. 2010). In this study, interesting photosynthetic acclimation traits are highlighted. The photosynthetic curves in response to light suggest that the maximum CO₂ assimilation (A_max) saturates rapidly at low irradiance flux between 12 and 24% (PPFD 50), remain saturated towards an intermediate irradiance flux between 25 and 50% (PPFD 95), until its decline to a high irradiance flux >60%. Wild versus cultivated plants have higher photosynthetic capacity traits, because their CO₂ assimilation capacity and electrons transport efficiency were higher towards the asymptotic trajectory of photosynthetic curves ~500 μmol m⁻² s⁻¹ (Fig. 2; Table 3). Due to that A_max in response to high irradiance flux can be limited both by Rubisco activity and TPU, the calculated values for maximum electrons transport (J_max) could not reflect their maximum possible rate. In this study, following the recommendations provided by Buckley and Diaz-Espejo (2015), to avoid ambiguity for J_max (Fig. 2), we presented the value of irradiance at which J_max was reached. Namely, J_1000 and J_1400 for leaves from wild and cultivated plants, respectively (Table 3).

In addition to A_max and J_max, other photosynthetic traits are highlighted. Data set suggests that wild plants could maximize their CO₂ assimilation even at low light levels, since the dark respiration (Rdark) was overtaken at a low irradiance flux; therefore, wild versus cultivated plants could have a lower LCP (Fig. 2; Table 3). The low LCP, higher photosynthetic capacity and electrons transport efficiency recorded in wild plants could be related to an efficient acclimation strategy for maximize the sunlight photosynthetic capture at shade gradients in the understory. By contrast, data set suggests that under extreme cultivation conditions, plants could have lower photosynthetic capacity per each quantum absorbed. Besides, the higher LCP recorded in cultivated plants suggests that respiration could be a significant limiting factor for carbon gain when light availability is lower. Regardless the different LCP, the optimal functioning of photosynthesis could occur in a low to intermediate range of irradiance.

The negative growth response and almost null survival recorded in plants grown in high sunlight regimes and extremely
Table 5. Architectural, anatomical and biochemical traits from Capsicum annuum var. glabriusculum plants grown under different sunlight regimes. Average contrast is by row. Averages with the different letters were significant \( P < 0.05 \).

| Traits                                      | Treatments                      |
|---------------------------------------------|---------------------------------|
|                                             | Low sunlight regimes            | Intermediate sunlight regimes |
| Specific leaf area (SLA = m² g⁻¹)           | 0.07 ± 0.01a                    | 0.03 ± 0.004b                 |
| Leaf area ratio (LA = m² g⁻¹)               | 0.02 ± 0.004a                   | 0.005 ± 0.001b                |
| Individual leaf area (ILA = cm²)            | 18 ± 4a                         | 4.6 ± 1b                      |
| Leaf mass per area (LMA = g m⁻²)            | 13 ± 1a                         | 32 ± 5b                       |
| Adaxial stomatal density per cm²            | 0                               | 127 ± 2                       |
| Abaxial stomatal density per cm²            | 191 ± 52a                       | 438 ± 57b                     |
| Stomatal index (%)                          | 12 ± 4a                         | 25 ± 1b                       |
| Total photosynthetic pigments (TPP = g m⁻²) | 0.4 ± 0.05a                     | 1.5 ± 0.1b                    |
| Chlorophyll a (Chla = mg m⁻²)               | 277 ± 33a                       | 770 ± 102b                    |
| Chlorophyll b (Chlb = mg m⁻²)               | 127 ± 14a                       | 501 ± 91b                     |
| Xanthophylls plus carotenoids (mg m⁻²)      | 72 ± 9a                         | 237 ± 45b                     |
| Nitrogen (N = g m⁻²)                        | 0.51 ± 0.1a                     | 0.66 ± 0.1b                   |
| Nitrogen to carboxylation (NC = mg g⁻¹)     | 118 ± 7a                        | 187 ± 58b                     |
| Nitrogen to bioenergetics (NB = mg g⁻¹)     | 14 ± 1a                         | 22 ± 4b                       |
| Nitrogen to light-harvesting (NL = mg g N⁻²)| 35 ± 9a                         | 133 ± 23b                     |
| Nitrogen to photosynthetic components (NP = mg g N⁻²) | 169 ± 14a                      | 343 ± 62b                     |
| NL/NP (mg g⁻¹)                              | 0.20 ± 0.04a                    | 0.39 ± 0.09b                  |
| Carbon (g m⁻²)                              | 5.9 ± 0.9a                      | 14 ± 2b                       |
| Sulphur (S = g m⁻²)                         | 0.07 ± 0.02a                    | 0.23 ± 0.07b                  |
| Hydrogen (H = g m⁻²)                        | 0.8 ± 0.1a                      | 1.9 ± 0.2b                    |
| Phosphorus (P = g m⁻²)                      | 0.05 ± 0.02a                    | 0.13 ± 0.02b                  |
| Magnesium (Mg = g m⁻²)                      | 0.06 ± 0.01a                    | 0.18 ± 0.04b                  |
| Calcium (Ca = g m⁻²)                        | 0.19 ± 0.03a                    | 0.34 ± 0.1b                   |
| Potassium (K = g m⁻²)                       | 0.04 ± 0.01a                    | 0.04 ± 0.01b                  |
| Sodium (Na = g m⁻²)                         | 0.09 ± 0.03a                    | 0.1 ± 0.02b                   |
| Manganese (Mn = mg m⁻²)                     | 1.3 ± 0.3a                      | 1.5 ± 0.2b                    |
| Iron (Fe = mg m⁻²)                          | 6.4 ± 1.5a                      | 8.7 ± 0.9b                    |
| Nickel (Ni = mg m⁻²)                        | 0.03 ± 0.02a                    | 0.14 ± 0.02b                  |
| Zinc (Zn = mg m⁻²)                          | 0.6 ± 0.2a                      | 0.9 ± 0.4b                    |
| Copper (Cu = mg m⁻²)                        | 0.2 ± 0.07a                     | 0.51 ± 0.1b                   |

Table 6. Growth rate and biomass allometry of Capsicum annuum var. glabriusculum plants grown in different sunlight regimes. Average contrast is by row. Averages \((n = 6)\) with different letters were significant \( P < 0.05 \).

| Growth and biomass allometry                | Treatments                      |
|---------------------------------------------|---------------------------------|
|                                             | Low sunlight                    | Intermediate sunlight         |
| Relative growth rate (RGR = g g⁻¹ day⁻¹)    | 0.04 ± 0.03a                    | 0.19 ± 0.1b                   |
| Total biomass (TB = g)                      | 4.9 ± 2.8a                      | 21 ± 13b                      |
| Leaf area index (LAI = m² m⁻²)               | 0.13 ± 0.06a                    | 0.10 ± 0.06c                  |
| Fruits fresh weight (FFW = g)               | 0                               | 5.5 ± 3                       |
| Fruits dry weight (FDW = g)                 | 0                               | 2.02 ± 1                      |
| Shoots/roots ratio (S/R ratio = g g⁻¹)      | 3.8 ± 0.8a                      | 2 ± 0.3b                      |
| Roots mass fraction (RMF = g g⁻¹)           | 0.21 ± 0.03a                    | 0.3 ± 0.03b                   |
| Stems mass fraction (SMF = g g⁻¹)           | 0.41 ± 0.07a                    | 0.39 ± 0.07a                  |
| Leaves mass fraction (LMF = g g⁻¹)          | 0.37 ± 0.06a                    | 0.15 ± 0.02b                  |
| Reproductive mass fraction (REMF = g g⁻¹)   | 0                               | 0.14 ± 0.1                    |
| Specific stem length (SSL = cm g⁻¹)         | 36 ± 14a                        | 6 ± 4b                        |

Warm temperatures (Fig. 1; Table 2) could be attributable to an abrupt disruption of photosynthetic acclimation mechanisms caused by the excessive photonic energy and extreme thermal thresholds. This specific hypothesis is partially supported by the rapid photosynthetic saturation at low irradiance and photosynthetic declining trend to high irradiance (Fig. 2; Table 3), as well as by different studies about photosynthetic acclimation (Zhu et al. 2018; Fernández-Marín et al. 2020). The functional traits recorded in cultivated plants under different sunlight regimes and extremely warm temperatures clearly suggest that their acclimation plasticity

depends both on biophysical regulation and photosynthetic capacity traits (Table 4). They efficiently cope heat stress through higher stomatal conductance that at expense of excessive water loss, minimize the risk of heat damage on their photosynthesis through cooling by high transpiration and inner cooling mechanisms, because leaf temperature reached very warm thresholds even under the shade (Table 4). This hypothesis is well supported by different studies addressing the causes and consequences of photosynthetic thermal acclimation (Liguori et al. 2017; Niinemets 2018).

A recent study shows that maintenance of non-lethal temperature in leaves imposes constraints on stomatal regulation (Blonder and Michaletz 2018). Our data suggest that the contrasting CO₂ diffusion traits (Table 4) could represent not only the reflection of different gas exchange traits by themselves, but also an efficient photosynthetic response to the exposure of leaves to extremely warm temperatures (Niinemets 2018; Zhu et al. 2018). Studies suggest that plant species whose photosynthesis responds at low intercellular CO₂ concentration tend to display a high ratio between the mesophyll and stomatal conductance. Under such conditions, an improvement in the photosynthetic water use and positive carbon assimilation could prevail, given that stomatal limitations are not only the reflection of different gas exchange traits by themselves, but also an efficient photosynthetic response to the exposure of leaves to extremely warm temperatures (Niinemets 2018; Zhu et al. 2018).
depend on the simultaneous interplay of several traits: for instance, the increase of electrons transport and nitrogen allocation, and others (Supporting Information B). The different photosynthetic capacity and the lower photosynthetic water use efficiency recorded in cultivated plants (Table 4) could be traits related to the functional acclimation for maximizing CO₂ assimilation and carbon gain in response to the harsh growing conditions. Similarly to the findings of Martins et al. (2014), our data suggest that at different irradiance flux and warm temperatures, the net CO₂ assimilation could be constrained mostly by the Rubisco activity, since the estimated chloroplastic CO₂ concentration was lower than those in the transitory point towards the Rubp regeneration in curves, which is mostly regulated by the electrons transport rate and trioses utilization rate (Fig. 3; Table 4). Intriguingly, although the low sunlight constrained the photosynthetic capacity of plants, the ratio between the electrons transport rate and Rubisco carboxylation velocity was similar in wild and cultivated plants under different sunlight regimes (Table 4).

Data set suggests that the carbon economic spectrum of leaves could be significantly altered in response to intermediate sunlight regimes and extremely warm temperatures, because plants increase their respiratory level and consequently the ratio between respiration and assimilation (Table 4). Several closely related metabolic process during photosynthesis and respiration could simultaneously improve plants performance specifically when they grow under intermediate sunlight regimes and extremely warm temperatures. This hypothesis is partially supported by our multiple correlation analysis (Supporting Information B). Carbon and nitrogen economic spectrum recorded in plants under extreme cultivation conditions could be explained not only by the significant interplay between respiration and specific photosynthetic capacity traits (Tables 4 and 5), but also complementary metabolic processes, e.g. production of carbon precursors, redox balancing, among others (O’Leary et al. 2018; Scafaro et al. 2021).

The displacement of CO₂ compensation and photocompensation points recorded in photosynthetic curves from cultivated plants (Fig. 3; Table 4) could be strongly influenced not only by environmental conditions and CO₂ diffusive constraints, but also by the interplay between respiration rate, photosynthetic capacity and photosynthetic nitrogen economy (Tables 4 and 5). This hypothesis is strongly supported by studies which show that carbon gain is enhanced by alternate metabolic pathways that feed the CO₂ reasimilation by Rubisco enzyme through recycling mechanisms of photorespired and respired CO₂ (Busch 2020; Busch et al. 2020). It is expected that under a warmer climate with rising CO₂ levels (https://climate.nasa.gov/vital-signs/carbon-dioxide), natural selection may differentially favour those plants genotypes and phenotypes which have thermal and photonic tolerance in their cell walls, membranes and their proteins for provide stability and efficient balance between the CO₂ diffusion, assimilation, respiration, photorespiration and recycling rate of photorespired and respired CO₂ (Niinemets 2018; Clemente-Moreno et al. 2019).

Architectural, anatomical and biochemical traits

Differential expansion of leaf surface enables ecophysiological acclimation to shifts on sunlight regimes or shade gradients (Madeline et al. 2012). To maximize their sunlight photosynthetic interception surface, plants grown at low sunlight regimes could simultaneously increase the specific, individual and total leaf area with respect of total biomass (Table 5), but at expense of developing thinner leaves with a low mass per area (Table 5). Besides, the multiple correlation analysis suggests that the increase of photosynthetic interception surface negatively correlates to all photosynthetic capacity traits (Supporting Information B). Studies show that as the sunlight regimes increase, plants develop thicker leaves with extra palisade cells layers, containing thousands of chloroplasts and photosynthetic enzymes, which consequently enhance the photosynthetic capacity per unit of leaf area (Poorter et al. 2019). Under intermediate sunlight regimes, the balance between architectural and leaf structural traits could be linked to a cost-effective functional strategy because plants modify their photosynthetic assimilation surface, while prioritize mass gain in leaf, since photosynthetic capacity significantly increases (Tables 4–6).

The multiple correlation analyses suggest that the increment of leaf mass per area is strongly linked to increasing of abaxial stomatal index and density (Table 5 and Supporting Information B). It has been shown in other studies, the simultaneous increase of leaf mass per area and stomatal density could be also strongly linked to modifications of other anatomical, metabolic and biophysical parameters (Martins et al. 2014; Clemente-Moreno et al. 2019). It could be also related to a systemic stimulus promoted by changes in the spectral composition of sunlight and thermal acclimation (e.g. Red/
Far-red ratio plus warm temperatures and its effect in phytochromes signalling for morphogenesis (Jung et al. 2016; Matthews et al. 2020). Data set shows that plants grown under intermediate sunlight regimes increase the photosynthetic pigment content. Pigments are functional ecophysiological indicators of plants acclimation light availability (Lichtenthaler and Buschmann 2001; Liguori et al. 2017).

Plants grown under intermediate sunlight regimes allocated a lower ratio of chlorophyll a and chlorophyll b (~1.5), while those under low sunlight regimes (~2.1) (Table 5). The higher content of chlorophylls, xanthophylls and carotenoids in plants grown under intermediate sunlight regimes and extremely warm temperatures (Table 5; see Supporting Information A—Table S2) suggests a systemic effect on the light-harvesting protein complexes, the reaction centres and the inner energy dissipation mechanisms of excessive thermal and photonic energy (Lichtenthaler and Buschmann 2001; Liguori et al. 2017). The increase of photosynthetic pigments under the intermediate sunlight regimes may occur along with other intriguing biochemical modifications such as the nitrogen partition towards photosynthetic components (Table 5). The total fraction of nitrogen per unit of leaf area and the proportional fraction allocated to carboxylation, bioenergetics and light-harvesting are like findings of other studies (Niinemets and Tenhunen 1997; Niinemets 2007).

Consequently, the proportional nitrogen partition recorded (Table 5) could reflect the actual nitrogen economy in leaves and thus, lends support to explain why photosynthetic performance of plants grown under intermediate versus low sunlight regimes could be remarkably different (Table 4). However, from the total nitrogen allocated to photosynthetic protein complexes, a higher amount of nitrogen allocated to both carboxylation and bioenergetics could play a central role for carbon gain since they significantly correlated to Rubisco carboxylation velocity, electrons transport rate, TPU rate and respiration (see Supporting Information B). Photosynthetic performance also depends on alternate metabolic pathways (enzymatic or non-enzymatic), which involve the translocation and storage of carbon, hydrogen, nitrogen and multiple mineral nutrients (Niinemets 2007; Szabó and Speeta 2017). The multiple correlation analysis (see Supporting Information B) suggests that increase of several and specific nutrients (Table 5) could be mostly explained by the nitrogen allocation to light-harvesting protein complexes. Besides the significant correlations between the increase of iron in leaves and the increase of phosphorous and copper (Table 5) could related to the accumulation of ferritin in the chloroplasts, because this biochemical process directly responds to light availability, circadian clock and signalling pathways which regulate the nutritional homeostasis of iron and phosphorous (Bournier et al. 2013).

**Growth rate and biomass allometry**

In general terms, plants grown at low sunlight can fix a relatively fewer amount of carbon during photosynthesis due to lower stomatal conductance and lower photosynthetic water use efficiency; consequently, biomass gain and nutrient requirement are lower (Poorter et al. 2012c, 2015). Therefore, according to the functional equilibrium model, plants grown at a low light level should show higher biomass allocation to stems and especially leaves at the expense of roots (Poorter et al. 2012c, 2015). Our data set is consistent with such principle because the lower photosynthetic capacity of plants grown in low sunlight regimes (Table 4) was reflected in their low biomass gain and their significant allometry towards stems and leaves at the cost of less investment in roots development (Tables 5 and 6). Therefore, the growth strategy of plants under low sunlight regimes is to lengthen their stems maximizing leaves expansion (Tables 5 and 6), compensating by this way the gas exchange restrictions and lower photosynthetic capacity (Tables 4 and 5).

By contrast, the multiple correlation analysis suggests that under intermediate sunlight regimes, the increase of growth rate, biomass gain and reproductive mass fraction significantly depend on the rise of most important photosynthetic capacity traits, respiration rate and the enhancement of the nitrogen economy in leaves (see Supporting Information B). The impulse of the above-ground and below-ground vegetative biomass gain, as well as the reproductive development recorded in plants grown under intermediate sunlight regimes and extremely warm temperatures could also be attributed to a systemic response to the spectral composition of sunlight regimes (i.e. Red/Far-red ratio) and thermal thresholds, since recent studies suggest that the spectral quality of light and temperatures activate the phytochromes triggering signalling pathways for promoting the above-ground and below-ground development (vegetative and reproductive growth plus roots development) (Jung et al. 2016).

**Principal components analysis**

Determination of most sensitive indicators during plants development is fundamental to evaluate the conditions of plants in ecological systems. The principal components analysis is an effective statistical tool to reveal meaningful ecophysiological or biochemical parameters linked to acclimation plasticity and adaptive strategies among plants species when thriving in different environmental contexts (Füzy et al. 2019). The principal components analysis suggest that the main explanatory traits in response to the low sunlight regimes could be the specific leaf area, and some traits related to CO₂ diffusion, e.g. the stomatal limitation, the mesophyll conductance and the chloroplastic CO₂ concentration (Fig. 4). By contrast, the main explanatory traits in response to intermediate sunlight regimes could be the photosynthetic pigments, the nitrogen allocation to light-harvesting and carboxylation, the Rubisco V₄₅max, stomatal conductance, total biomass gain, among others. The significant traits recorded (Tables 4–6), as well as the main explanatory traits extracted by the principal components analysis (Fig. 4) could be useful in comparative studies about acclimation strategies among different C₃ species adapted to similar or different habitats.

**Conclusions**

Under the extreme heat of Sonoran Desert, by using shading nets for plants cultivation, and where water and nutrients availability was not a stress factor, dataset suggests that low, intermediate and high sunlight regimes could drive significant alterations on the survival rate, growth, reproductive capability and functional acclimation traits. This study provides multiple reference traits from a C₃ species and useful insights for future research about functional plasticity traits to cope with environmental stress factors occurring in semi-arid habitats under the context of a warmer climate and rising CO₂ levels.
Supporting Information

The following additional information is available in the online version of this article—

Supporting Information A.

Figure S1. Cultivated plants.

Figure S2. Summary of weather conditions at open sky during cultivation of plants.

Figure S3. Stomatal density.

Table S1. Physical and chemical profile of the experimental soil.

Table S2. Sunlight regimes and air temperatures thresholds.

Table S3. Summary of soil temperatures.

Table S4. Results of the analysis of variance of the photosynthetic traits.

Table S5. Photosynthetic parameters derived from the A/C\textsubscript{c} curves fitting.

Table S6. Results of analysis of variance of photosynthetic traits.

Table S7. Results of the analysis of variance of architectural, anatomical and biochemical traits.

Table S8. Results of the analysis of variance of growth traits.

Supporting Information B. Results of the principal components analysis and multiple correlation analysis; as well as the raw data set of photosynthetic curves.

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Conflict of Interest

None declared.

Contributions by the Authors

A.J.-L., E.M., A.G. and G.V. contributed with periodic seminars to discuss research progress. A.J.-L. conceived the main idea, designed and executed the experimental protocol, applied the mathematical model for gas exchange curves fitting, analysed data set, conducted data visualization and wrote (original draft), reviews & editing. A.J.-L., A.G., J.O.-A. and G.V. contributed with technical support in the laboratory and/or field measurements. A.J.-L., E.S. and M.E. contributed to nutrients measurements. This work was part of the PhD dissertation of A.J.-L.

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Data Availability

The raw data are available in Supporting Information B (excel file). Please contact the author for additional data requests, and the data will be made available upon your request.

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