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High V_{cmax}, J_{max} and photosynthetic rates of Sonoran Desert species: using nitrogen and specific leaf area traits as predictors in biochemical models

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ABSTRACT

Dryland ecosystems largely control the inter-annual variability of the global carbon cycle. Unfortunately, there is a paucity of data on key biochemical parameters, such as maximum carboxylation velocity (V_{cmax25}) and electron transport rate (J_{max25}), from species in these ecosystems which limits our capacity to model photosynthesis across ecological scales. We studied six dominant C_3 shrub and tree species from the Sonoran Desert with different leaf traits and phenological strategies. We characterized V_{cmax25} and J_{max25} for each species and assessed which traits or trait combinations were the best predictors of these parameters for biochemical models of photosynthesis. All species had high values of V_{cmax25} and J_{max25}, mostly explained by high leaf nitrogen content (N_{area}) and high nitrogen allocation to photosynthetic enzymes comparable to those reported for herbs and crop species but higher than those of shrubs and other functional types in world databases. We found that the high values of V_{cmax25} and J_{max25}, by increasing rates of photosynthetic reactions, enhance photosynthetic water and nitrogen-use efficiencies and may favor carbon gain under typical conditions in drylands. Our findings provide novel implications to common findings of high N_{area} in dryland species and can help to improve the parameterization of photosynthesis models for drylands.

Keywords: V_{cmax}; J_{max}; Photosynthesis biochemical models; Leaf nitrogen content; Dryland species; Leaf traits; N_2-fixers.

1. INTRODUCTION

Photosynthesis is a fundamental biological process that influences the global carbon cycle, because it is the main flux responsible for the inter-annual variability of the global terrestrial CO_2 sink (Ahlstrom et al., 2015). Photosynthesis rates are widely described mechanistically (or semi-mechanistically), from sub-cellular to global scales (Farquhar et al., 2001), using principles of the biochemical model originally developed by Farquhar et al. (1980). This model integrates knowledge about photosynthesis biochemistry, stoichiometry, and the kinetic properties of key enzymes and processes. While most parameters of the model are fairly constant among C_3 species, day respiration (R_d), the carboxylation capacity (V_{cmax}), electron transport capacity (J_{max}), and rate of triose phosphate utilization (TPU) can vary substantially among species (von Caemmerer, 2000). Of these parameters, R_d tends to be correlated with V_{cmax}, and TPU is usually not limiting under natural conditions; therefore, V_{cmax} and J_{max} can be considered the key parameters of the model (von Caemmerer, 2000). It is known that V_{cmax} and J_{max} can vary up to two orders of magnitude among species (Kattge et al., 2009; Wullschleger, 1993), making large-scale estimates of photosynthesis highly sensitive to these parameters (Bonan et al., 2011). Thus, large scale modeling of photosynthesis requires accurate characterization of V_{cmax} and J_{max} across a wide range of species and functional types and vegetation types.

Current Earth System Models use various approaches to parameterize the variation in V_{cmax} and J_{max} across the biosphere. The most common is the plant functional type approach, where functional types are broad categories of plants, vegetation types, or biomes, which are considered to have similar physiology and therefore similar values of V_{cmax} and J_{max} (Rogers, 2014). In this way, the variation across plant diversity in these parameters can be simplified to a single value for each functional type. The limitation on how well each parameter represents this variation depends on the number of different functional types that are considered, as well as the extent to which these parameters represent the average or most probable local-to-global value (depending on the scale of the study). Other approaches include covariation of V_{cmax} and J_{max} with different leaf traits, or by integrating biogeochemical cycles and leaf traits (Rogers, 2014). Measurement of V_{cmax} and J_{max} is laborious and time-consuming, leaving a paucity of data when compared to other plant traits such as specific leaf area or leaf nitrogen content (Kattge et al., 2009; Kattge et al., 2011; Walker et al., 2014). Consequently, limited information on V_{cmax} and J_{max} challenge our capacity to represent the "real" variation of these parameters within models and lead to biases in regional and global estimates of carbon fluxes and net ecosystem productivity (Kattge et al., 2009).

Historically, dryland ecosystems have been underrepresented over the wealth of information available for tropical and temperate ecosystems. Consequently, V_{cmax} and J_{max} parameters for plant functional types from temperate and tropical forest ecosystems overwhelmingly dominate the Earth System Models (Rogers, 2014). Recent evidence has shown that dryland ecosystems have a dominant contribution to the positive trend (51-57% contribution) and inter-annual variation (39-47% contribution) in the land CO_2 sink (Ahlstrom et al., 2015; Biederman et al., in press; Fu et al., 2017; Poulter et al., 2014). However, data are scarce or null for typical functional types inhabiting dryland ecosystems such as sclerophyll and deciduous trees and shrubs, stem-succulent deciduous trees and shrubs, non-succulent trees, herbs, and winter and summer active annuals among others (Shreve 1942). Only a handful of published data can be attributed to dryland species and functional types in extant syntheses of V_{cmax} and J_{max} parameters. For example, Wullschleger (1993) report data for three species of desert annuals and perennials (2.8 % of total species), Kattge et al. (2009) included four desert evergreens and deciduous shrubs and annuals (unknown proportion), and Walker et al. (2014) reported six sclerophyll and deciduous tree species from open savannas (1.6 % of total); altogether ranging 64-127 μmol m^{-2} s^{-1} for V_{cmax} and 58-276 μmol m^{-2} s^{-1} for J_{max}. More data is needed to reflect actual variation in these parameters across species and functional types in the globally important biomes of drylands. This is a crucial step to improve our understanding, and accuracy of models of the photosynthetic processes occurring on them.

Even though there are few data for V_{cmax} and J_{max} in dryland species and functional types, other leaf traits (that are linked to V_{cmax} and J_{max}) have been sampled more extensively and could provide valuable information. For example, leaf traits such as specific leaf area (SLA), area-based nitrogen (N_{area}), and phosphorus (P_{area}) content, are known to be well correlated with V_{cmax} and J_{max} (Domingues et al., 2010; Kattge et al., 2009; Walker et al., 2014). Global syntheses indicate that increasing aridity tends to increase N_{area}, P_{area}, and light-saturated net photosynthesis rates (A_{area}), but increasing aridity decrease SLA and nitrogen content on a mass basis (N_{mass}) (Bagouse-Pinguet et al., 2016; Maire et al., 2015; Wright et al., 2005). In general, these observations could imply that conserving strategies such as low gas exchange rates and resource use predominate in drylands, or that dryland species have consistently high values of V_{cmax} and J_{max}.

Our overarching goal is to provide baseline information for key parameters relevant for modeling photosynthesis in dryland species and provide a discussion of its physiological implications. In this study, we characterized V_{cmax} and J_{max} from photosynthetic response curves, photosynthetic rates, SLA, and nitrogen content, for six dominant species from the Sonoran Desert. Although six species is a small number, this set comprises a wide array of functional types and leaf phenologies, spanning across the known range of values of these traits and parameters, thus allowing to get broad picture on these parameters, traits, and processes, for dryland species. We asked the following questions: what magnitudes and ranges of V_{cmax} and J_{max} does dominant species of the Sonoran Desert have? Which traits or trait combinations are the best predictors of V_{cmax} and J_{max}? What are the implications of the magnitudes and ranges of V_{cmax} and J_{max} for photosynthesis in drylands?

2. MATERIALS AND METHODS

2.1. Study site and species sampled

All gas exchange measurements and leaf material were obtained from plants growing under natural conditions at La Colorada, Sonora, Mexico. Field campaigns were conducted at locations associated with two sites participating with the Mexican eddy covariance network: Mexflux (Vargas et al., 2013, Hinojo-Hinojo et al., 2016), which are representative of the Southeastern part of the Sonoran

Desert. Predominant vegetation is a Sonoran Desert scrub characteristic of the Plains of Sonora composed by deciduous shrubs and low stature deciduous and evergreen trees (Shreve & Wiggins, 1964; Brown et al., 1994). Long term annual rainfall is 345 mm, 70 % of which occurs during the summer monsoon, while mean annual temperature is 20.7 ºC with a mean temperature of 13.2 ºC during January, the coldest month, and 28.1 ºC during July, the warmest month (station 26046 La Colorada, Servicio Meteorológico Nacional). Soils are calcic regosol and haplic phaeozem with loamy sand texture, 0.6-2.6 % organic matter content, 0.18-0.38 % nitrogen, and 0.05-0.1 % phosphorus content (Celaya et al., 2015).

We sampled the more abundant C_3 perennial species of the sites which comprised a diverse set of growth forms and leaf phenologies: *Olneya tesota* and *Prosopis velutina* (leguminous evergreen trees); *Mimosa laxiflora* (drought deciduous leguminous shrub); *Encelia farinosa* (drought deciduous shrub). We included other stem-succulent deciduous species with leaf phenology restricted to the summer: *Ipomoea arborescens* (a tree); and *Jatropha cardiophylla* (a shrub). Altogether, these species comprised about 80-90 % of perennial cover in the sites. In addition, the species have a wide distribution and are abundant throughout the Sonoran Desert and across other North American dryland regions.

2.2. Measurement of gas exchange and related leaf traits

We conducted gas exchange measurements at the study sites during multiple field campaigns for five consecutive years. All measurements were performed during the summer rainy seasons, from July to early October, in sun-exposed mature leaves. The following gas exchange measurements were performed in all studied species: a) response curves of leaf net photosynthesis to intercellular CO_2 concentrations (A-C_i curves); b) measurements of light-saturated net photosynthesis rates; c) measurements at various light levels through the use of neutral filters; and d) diurnal courses of gas exchange. Air flow in the chamber was set at 300-500 μmol s^{-1} in all measurements. No attempt was made to control conditions in the chambers, besides light in b) and c), or leaf temperature and

CO_2 concentration in A-C_i curves. Light saturated net photosynthesis (A_{max}) measurements and measurements at different light levels were performed with a LCi system (ADC Bioscientific Ltd., Herts, England), and A-C_i curves and A_{max} measurements with a Li-6400XT (LICOR Scientific, Lincoln, Nebraska, USA). Both systems gave comparable data across species. With this measurements, we aimed to derive V_{cmax} and J_{max} parameters for the biochemical model of photosynthesis (from A-Ci curves), and to have measurements of photosynthetic rates under a wide range of natural environmental conditions (from b-d measurements) to validate photosynthesis models.

A-C_i curves were measured in six to eleven individuals of each species with a Li-6400XT (LI-COR, Lincoln, NE, USA) following Long & Bernacchi (2001). Measurements were performed first time in the morning under saturating direct sunlight (PAR, photosynthetically active radiation flux density >1500 μmol m^{-2} s^{-1}) during clear, cloudless days. Leaf temperature was maintained close to the initial value as much as possible, although this value may had differ in different measurements. A-Ci curves were fitted using the "bilinear" method (see Duursma, 2015) with R software package "plantecophys" to obtain biochemical parameters (V_{cmax}, J_{max}, R_d and TPU) for the photosynthesis model. Temperature response functions and values for other parameters in the model followed Medlyn et al. (2002). R_d and TPU were used to fit V_{cmax} and J_{max} accurately. Only photosynthesis curves from unstressed leaves (with stomatal conductance above 0.05 mol m^{-2} s^{-1}, see Flexas et al., 2006) were considered in our analyses and modeling as quality control.

V_{cmax} and J_{max} values were scaled to its values at 25 ºC (V_{cmax25} and J_{max25}) using temperature response functions from Medlyn et al. (2002) with two widely-used sets of parameter values: those from Bernacchi et al. (2001, 2003) and those from Kattge & Knorr (2007). There is one essential difference between both sets of parameter values. When those from Bernacchi are used (called BRc hereafter), the value of V_{cmax} and J_{max} keep increasing exponentially with temperature. When those from Kattge & Knorr (called KKr hereafter) are used, the value of V_{cmax} and J_{max} initially increases exponentially until a peak is reached (temperature optimum) where the value decrease afterwards. The temperature at which this peak value occurs depends on the growth temperature (mean air temperature of the previous month).

To perform leaf area corrections of gas exchange data, all leaf samples were collected after measurements, sealed in bags with moist paper and stored in dark and cold conditions. In the lab, leaves were scanned and area measured using ImageJ software (version 1.50i, Wayne Rasband, National Institutes of Health, USA). Leaves were oven dried at 60-70 ºC for two days and weighted. Specific leaf area (SLA) was estimated as the fresh area to dry weight ratio in each leaf. Total nitrogen content per mass was measured either by the phenate method for Kjeldahl nitrogen with a rapid flow analyzer (RFA300, ALPKEM Corporation, Clackamas, Oregon, USA) or with an elemental analyzer (2400, PerkinElmer Inc., Waltham, MA, USA). Nitrogen content per mass (N_{mass}) was expressed as nitrogen per area (N_{area}) using the SLA of the same leaf. The proportion of leaf nitrogen allocated to Rubisco enzyme and to bioenergetics was estimated following equations from Niinemets & Tenhunen (1997). These equations estimate the amount of nitrogen within enzymes according to measured V_{cmax25} (for Rubisco) and J_{max25} (for bioenergetics), and compare it against total leaf nitrogen content.

2.3.Data analysis and photosynthesis modeling

Species mean V_{cmax25} and J_{max25} was compared using analysis of variance and Tukey HSD post-hoc test. Additionally, we assessed which single leaf trait or trait combinations were the best predictors for V_{cmax25} and J_{max25}. For this, simple linear regressions was performed for each single leaf trait (SLA or N_{area}) against either V_{cmax25} or J_{max25}. For assessing leaf trait combinations as predictors of V_{cmax25} and J_{max25}, we identified the best statistical model using backward and forward stepwise regression according to the minimal Akaike information criterion index, as follows: for V_{cmax25} we included SLA, N_{area}, and SLAxN_{area} interaction effects ($V_{cmax25}=\beta_1 SLA+\beta_2 N_{area}+\beta_3 SLA\cdot N_{area}$), and for J_{max25} we included SLA, N_{area}, V_{cmax25}, and all interaction terms

($J_{cmax25}=\beta_1 SLA+\beta_2 N_{area}+\beta_3 V_{cmax25}+\beta_4 SLA\cdot N_{area}+\beta_5 SLA\cdot V_{cmax25}+\beta_6 N_{area}\cdot V_{cmax25}+\beta_7 SLA\cdot N_{area}\cdot V_{cmax25}$). These statistical analyses were performed on JMP software (version 9.0.1, SAS Institute, 2010).

The net photosynthetic rate was modeled with the biochemical model of photosynthesis (Farquhar et al., 1980) using the "plantecophys" package (Duursma, 2015). The following approaches were used to parametrize V_{cmax25} and J_{max25} for the model: average values obtained from A-C_i curves for each species (species mean), average values obtained using the best models and all available trait values per species (trait mean), and calculating a V_{cmax25} and J_{max25} for each leaf using the best models and the trait values for each leaf (trait based). The first two approaches were to assess how well photosynthesis can be modeled by using a fixed value for V_{cmax} and J_{max}, and the third approach to assess whether allowing those parameters to vary with leaf traits enhances the accuracy of the model. Leaf temperature, photosynthetic photon flux density, and intercellular CO_2 concentration of each gas exchange measurement were entered into the model. The performance of each approach was evaluated using the mean absolute deviation of modeled versus measured data.

Light response curves of net photosynthesis rate for leaves under typical field conditions were simulated to determine the performance of leaves with the obtained values of V_{cmax25}, J_{max25} and leaf traits. This simulations were then compared to curves simulated using parameters for shrubs from Kattge and Knorr (2009) whose derivation included a poor representation of data for dryland species. For this, simulations were made for hypothetical leaves with contrasting trait values (high and low N_{area}) which would give a broad picture of the implications of having such parameter values for any generic leaf. Additionally, simulations were made for J. cardiophylla leaves. This species was the most extensively sampled and abundant in our study sites, and thus provides an opportunity to show the implications of the parameter values on the performance of a particular species.

3. RESULTS

3.1. V_{cmax}, J_{max} and leaf traits

After quality control, we obtained data for V_{cmax} and J_{max} from two to five curves for each species (Table 1). These curves yielded V_{cmax25} values between 86 and 212 μmol m^{-2} s^{-1} with BRc temperature parameters and 93-248 μmol m^{-2} s^{-1} with KKr temperature parameters. For J_{max25}, we found values of 83-312 μmol m^{-2} s^{-1} and 105-350 μmol m^{-2} s^{-1}, with BRc and KKr parameters respectively. V_{cmax25} and J_{max25} were on average 1.2 times higher with KKr than with BRc temperature parameters. The J_{max25}:V_{cmax25} ratio in the species had a range of 0.9-2.1 with an average of 1.4. *Prosopis velutina* was the species with the highest mean V_{cmax25} and J_{max25}, while other species had lower values, although there was a wide variation between individual values within each species (Table 1).

Single leaf traits were significantly correlated with Vcmax25 and Jmax25 (Table 2). N_{area} was correlated with both V_{cmax25} and J_{max25} and explained 35-56% of the variance, and SLA was inversely related to J_{max25} and accounted for 18-21% of the variance. The N_{area} to V_{cmax25} relationship had a higher intercept compared to studies published in a recent global synthesis (Figure 1). The value of V_{cmax25} and J_{max25} for a given N_{area} in the studied species corresponds to a 36-46% nitrogen allocated to Rubisco enzyme and 4.9-5.8% to enzymes in bioenergetics in the studied species.

Combinations of traits in statistical models increased the explained variance of V_{cmax25} obtained with BRc parameters (Table 3). Only in this case, the stepwise regression showed that including the effects of SLA and N_{area} produced the best model and explained 10 % more variance than N_{area} alone. N_{area} explained similar amounts of variation for other parameters (J_{max25} with BRc parameters, and V_{cmax} and J_{max} with KKr parameters) than the best models (Table 2 and 3). By using the best models with all available data for SLA and N_{area} gathered over the years (leaves from A-C_i curves and leaves from all the other gas exchange measurements), we obtained a species average V_{cmax25} and J_{max25} (Table 4) which could be considered a more representative species average because of its larger sample number. It should be noted that these estimates carry the uncertainties associated with our best models. These species averages were used in the “trait mean” approach in the following section.

3.2. Photosynthesis modeling

The comparison between the species mean, trait mean, and trait-based approaches for modeling photosynthesis on each species is shown in Table 5. The error obtained in *M. laxiflora* and *P. velutina* species was substantially lowered with the trait-based approach, although the three approaches had similar errors (< 1 µmol m^{-2} s^{-1} of difference on its mean absolute deviation) in the remaining species (Table 5). Additionally, we found that models using V_{cmax25} and J_{max25} obtained with BRc temperature parameters had a better fit and lower error across all species (Table 5).

Modeled data tracked closely most of our gas exchange measurements (Figure 2). In four of the six species, error diminished when observations with leaf temperatures above 40 ºC were discarded (Figure 2, Table 5). Nonetheless, data modeled with BRc gave lower mean absolute deviation than data modeled with KKr when all data was considered, but had similar mean absolute deviation when data with leaf temperatures above 40 ºC were discarded (Table 5).

To assess the implications of the values of V_{cmax25}, J_{max25}, and V_{cmax25} per N_{area} generated in this study for the photosynthetic performance of leaves, we simulated net photosynthetic rates under typical conditions that leaves experience in the field (Figure 3). Using our parameters, net photosynthesis rates were about 7-10 µmol m^{-2} s^{-1} higher than those obtained with parameters from a global database (Kattge et al., 2009) for hypothetical leaves at full sunlight, high leaf temperatures and high, mid or low stomatal conductances (see Figure 3). For *J. cardiophylla* leaves, our parametrization gave similar photosynthesis rates to our actual measurements, and had rates 7-13 µmol m^{-2} s^{-1} above those obtained with parametrizations from the global data base (Figure 3). Additionally, photosynthetic rates with the parameters obtained in this study saturated at higher irradiances (Figure 3).

4. DISCUSSION

Global databases and large-scale flux modeling schemes still have poor representation of key biochemical (V_{cmax} and J_{max}) parameters of photosynthesis for dryland plant species and functional types (Kattge et al., 2009; Rogers, 2014; Wullschleger, 1993; Walker et al., 2014). In this study, we characterized V_{cmax25} and J_{max25} parameters for six dominant and widely distributed species in the Sonoran Desert, representing a wide range of functional types, leaf phenological strategies, and leaf trait values. By generating this set of biochemical parameters for dominant plant species and determining the relationship between these parameters and leaf traits, we aimed to contribute to have more accurate parameterizations for modeling carbon fluxes in Sonoran Desert ecosystems . The high values reported here for V_{cmax25} and J_{max25} in the studied species and the relationship between these biochemical parameters and leaf traits may have important implications for carbon flux models and the photosynthetic performance of plant species in dryland environments.

4.1. High V_{cmax} and J_{max} for dryland species

Global databases report a measured range of V_{cmax25} of 10-200 μmol m^{-2} s^{-1} (Kattge et al., 2009; Walker et al., 2014), but the bulk of data values are in the range of 35-63 μmol m^{-2} s^{-1} (interquartile range from Walker et al., 2014). V_{cmax25} for the species in our study (86-212 μmol m^{-2} s^{-1} with BRc dataset and 93-248 μmol m^{-2} s^{-1} with KKr dataset) fall above this global range of bulk data, and are higher than mean values for the most closely related functional types from global databases and modeling schemes (see Kattge et al., 2009; Rogers, 2014). For example, the global database of Kattge et al. (2009), which had a poor coverage of dryland species, reported a mean V_{cmax25} of 54-62 μmol m^{-2} s^{-1} for shrubs (mostly from temperate ecosystems) and 30-40 μmol m^{-2} s^{-1} for tropical trees. However, herbs and crops had a comparable range to our data (80-100 μmol m^{-2} s^{-1}), and high V_{cmax25} values (100-150 μmol m^{-2} s^{-1}) have also been found on few temperate broadleaved trees, coniferous trees, shrubs, herbs and crops species (Kattge et al., 2009). In agreement with our findings, the few measurements which have been reported for other dryland species from Australia, western Africa and North America also showed high V_{cmax25} values, ranging 60-130 μmol m^{-2} s^{-1} (Cernusak et al., 2011; Domingues et al., 2010; Ellsworth et al., 2004; Hamerlynk et al., 2002, Wullschleger, 1993). In addition, we found that most of our J_{max25} data were above the global median (89 μmol m^{-2} s^{-1}, Walker et al., 2014) and can also be considered somewhat high. The data summarized here indicates that dominant C_3 species from the Sonoran Desert (this study) and other dryland species which have been studied have consistently high V_{cmax25} and J_{max25} values. More importantly, this indicates that current global databases and modeling schemes (Kattge et al., 2009; Rogers, 2014; Walker et al., 2014) may be underestimating the V_{cmax25} and J_{max25} of species and functional types for the Sonoran Desert and probably in other dryland regions.

High V_{cmax25} and J_{max25} values may result from high N_{area} values. In our analysis N_{area} explained 35-56 % of the variation these parameters, thus help explaining differences across species and individual leaves (Table 2 and 3). In addition, we found values of N_{area} above the global median of 1.6 g N m^{-2} (from 12860 samples in Kattge et al., 2011) in all six species studied, with some above the global 97.5% quantile of 3.6 g N m^{-2} (Kattge et al., 2011). From global data bases of leaf trait measurements, studies have found that that N_{area} tends to increase with aridity (Bagouse-Pinguet et al., 2016; Maire et al., 2015; Wright et al., 2005), suggesting that high N_{area} values are common among dryland species. Our study shows a direct link between high N_{area} and high values of V_{cmax25} and J_{max25} for a dryland region, which has not been previously reported.

High values of N_{area} in dryland species have several possible causes. Species from these biomes tend to have similar (Killingbeck & Withford, 1996) or higher (Skujins 1981; West 1981; West & Skujins, 1978) nitrogen content on a mass basis (N_{mass}) than species from other biomes such that higher N_{area} values should arise from combinations of N_{mass} and SLA values ($N_{area}=N_{mass}/SLA$). For example, *O. tesota* had a mean N_{mass} of 2-3 %. In this case, high N_{area} occurred due to relatively low SLA (10-15 m^2 kg^{-1}). Species with high N_{mass} (3-5 %) and low SLA (5-15 m^2 kg^{-1}) such as *P. velutina* and *E. farinosa* had the highest N_{area}; and species with high SLA (15-30 m^2 kg^{-1}) need very high N_{mass} (3-6 %) to achieve high N_{area}, as observed for *I. arborescens*, *J. cardiophylla,* and *M. laxiflora*. Other mechanisms that may enable species to have high N_{area} are: 1) high efficiency of nutrient resorption (Killingbeck, 1993); 2) association with nitrogen-fixing symbionts, as in the three leguminous species *M. laxiflora*, *O. tesota,* and *P. velutina*, which may increase nitrogen availability during the growing season, unless water or phosphorus became limiting in the soil; 3) a relationship between non-nitrogen-fixing and nitrogen-fixing plant species in fertility islands (Garcia-Moya, 1974; Pugnaire et al., 1996), and that 4) nitrogen is not necessarily limiting in dryland ecosystems (0.18-0.38 % N_{mass} in the soil o our sites, Celaya et al., 2015; LeBauer & Treseder, 2008).

We found a higher V_{cmax25} per amount of N_{area}, and thus a high allocation of nitrogen to photosynthetic enzymes, in our study species than typical values for shrubs and other functional types from a global database with a poor representation of dryland species, but comparable to those reported for herbaceous and crop species (Figure 1, Kattge et al., 2009). (Kattge et al., 2009). Our estimates show that Sonoran Desert species invest on average 36-46 % of nitrogen in Rubisco which is higher than the typical 10-30 % reported for C_3 plants (Evans, 1989; Evans & Seeman, 1989; Ghimire et al., in press). Nitrogen allocated to bioenergetics was 4.9-5.8 %, which is in the range that has been reported for shrubs and deciduous trees (Ghimire et al., in press). Together, our observations indicate that high V_{cmax25} and J_{max25} in Sonoran Desert species is mainly explained by high N_{area} and a high allocation of nitrogen to photosynthetic enzymes.

4.2. Implications for photosynthesis and productivity

Previous studies have found that high N_{area} in species from low-rainfall sites results in an important strategy for water conservation, allowing an increase in net photosynthesis for any given C_i and stomatal conductance compared to species from high-rainfall sites (Field et al., 1983, Wright et al., 2001). In agreement with this, here we showed than the a N_{area}, but also a high allocation of nitrogen to photosynthetic enzymes in dryland species, allow higher photosynthetic rates for a given C_i as compared to non-dryland species (Figure 3). In addition, our simulations and data comparisons provide novel biochemical and physiological evidence on how high values of N_{area}, nitrogen allocation to photosynthetic ezymes, and V_{cmax25}, and J_{max25}, can enhance the photosynthetic performance of species under typical abiotic conditions in drylands: 1) allowing very high photosynthetic rates during periods of high resource availability (soil water, light, air humidity, air CO_2 concentration) (see Figure 3 at C_i of 290 µmol mol^{-1}; Castellanos et al., 2010; Ehleringer & Cook, 1984; Mooney et al., 1976; Werk et al., 1983); 2) enhancing the carbon gain during periods of moderate stress conditions, e.g during the short periods between rainfall pulses or at the end of the rainy season, when high leaf temperatures and vapor pressure deficits limit stomatal conductance (see Figure 3 at C_i of 180 µmol mol^{-1}; Flexas et al., 2006 and references therein); and 3) rising the light saturation level of photosynthesis, which serves as a photoprotective mechanism, decreasing photosynthesis limitations under high light conditions (Mooney et al., 1974).

V_{cmax} and J_{max} derived here for dryland species may have important consequences for estimates of ecosystem production. Studies report that 70-90 % of annual net ecosystem productivity (NEP) in dryland ecosystems occur during relatively short periods when most of the annual rainfall is registered (Hinojo-Hinojo et al., 2016, Biederman et al. in press). Our V_{cmax25} and J_{max25} data were obtained during these periods. Dominant species have strategies to maximize the time when non-limiting conditions and the highest photosynthetic rates occur, by having deep roots (*O. tesota* and *P. velutina*) and performing hydraulic redistribution (i.e. water movement across soil layers via plant roots), nitrogen-fixing (leguminous species), positive plant-plant interactions (*O. tesota* and *P. velutina*), storing water and nutrients in succulent stems or tuberous roots (*I. arborescens* and *J. cardiophylla*), and deciduous phenology (*I. arborescens*, *J. cardiophylla*, *M. laxiflora* and *E. farinosa*). Failing to incorporate high values of V_{cmax} and J_{max} for species with these strategies will lead to important underestimation of carbon fluxes in large-scale Earth System Models in the Sonoran Desert and probably in other dryland regions.

4.3. Estimation of V_{cmax} and J_{max} and limitations for modeling photosynthesis

In this study, we assessed whether using leaf-specific V_{cmax25} and J_{max25} values (trait-based approach) instead of a fixed species-specific value (species mean and trait mean approaches) improved the accuracy of photosynthesis models. However, actual V_{cmax25} and J_{max25} values were highly variable among leaves, and thus using the trait-based approach resulted in comparable errors than using a single average value. The statistical models developed in this study (Table 3) should allow the estimation of V_{cmax25} and J_{max25} from N_{area} and SLA data for a wider range of species in warm dryland communities, given the ample range of biochemical and leaf N_{area} and SLA traits values, and the variety of functional types of the species included in this study.

We found that one of the factors affecting the accuracy of the model were leaf temperatures above 40 ºC in most species. However, the model using BRc parameters performed better than those using KKr when data with leaf temperatures above 40ºC were included (Table 5). Given that BRc parameters do not have a peak activity, this suggest that actual peak activity of V_{cmax} and J_{max} occurred at higher temperatures than those assumed by functions for the acclimation to growth temperature in KKr parametrization. It is important to note that temperature response parameters (such as BRc and KKr) for crops and temperate species have been derived from measurements spanning 5 to 40 ºC leaf temperatures, as most photosynthesis rates are assumed to occur within this range (Bernnacchi et al., 2001 and 2003; Kattge & Knorr, 2007; Medlyn et al., 2002; Wohlfahrt et al., 1999). Given that leaf temperatures higher than 40 ºC may be common in dryland species as were in our data, development of approaches that extend temperature response functions to higher temperatures should improve the performance of photosynthesis models in drylands (Table 5).

Our approach may have had additional limitations. Mesophyll conductance and TPU can limit photosynthesis rates under drought conditions (Díaz-Espejo et al., 2006; Flexas et al., 2006). We did not include mesophyll conductance nor TPU limitation in our models due to the lack of widely tested parameters and functions on its response to environmental conditions, especially temperature. Also, increased availability of leaf phosphorus content data should help to further constrain estimates of V_{cmax25} and J_{max25} with leaf traits (Domingues et al., 2010; Walker et al., 2014). Lastly, simulating photosynthesis rates above 40 μmol m^{-2} s^{-1} was difficult (see underestimated data for *Encelia* in Figure 2), even using very high values of V_{cmax25} and J_{max25}, but photosynthesis rates that high have been reported for desert annuals and shrubs species (Ehleringer & Cook, 1984; Mooney et al., 1976; Werk et al., 1983). More data of V_{cmax25} and J_{max25}, and information of mesophyll conductance, TPU and phosphorus content for species and functional types from dryland ecosystems will increase their representation in global databases and improve modeling schemes for photosynthesis to better assess the role of drylands in the global carbon and water cycles.

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6. REFERENCES

- Ahlstrom, A., Raupach, M.R., Schurgers, G., Benjamin, S., Arneth, A., Jung, M., Reichstein, M., Canadell, J.G., Friedlingstein, P., Jain, A.K., Kato, E., Poulter, B., Sitch, S., Stocker, B.D., Viovy, N., Wang, Y.P., Wiltshire, A., Zaehle, S. & Zeng, N. 2015. The dominant role of semi-arid ecosystem in the trend and variability of the land CO2 sink. Science, 348, 895–899.
- Bagousse-Pinguet, Y. Le, Liancourt, P., Gross, N., de Bello, F., Fonseca, C.R., Kattge, J., Valencia, E., Leps, J. & Maestre, F.T. 2016. Climate, topography and soil factors interact to drive community trait distributions in global drylands. Peer J Preprints, 4, e1913v1.
- Bernacchi, C.J., Pimentel, C. & Long, S.P. 2003. In vivo temperature response functions of parameters required to model RuBP-limited photosynthesis. Plant, Cell and Environment, 26, 1419–1430.
- Bernacchi, C.J., Singsaas, E.L., Pimentel, C., Portis Jr, A.R. & Long, S.P. 2001. Improved temperature response functions for models of Rubisco-limited photosynthesis. Plant, Cell and Environment, 24, 253–259.
- Biederman, J.A., Scott, R.L., Bell, T.W., Bowling, D.R., Dore, S., Garatuza-Payán, J., Kolb, T.E., Krishnan, P., Krofcheck, D.J., Litvak, M.E., Maurer, G.E., Meyers, T.P., Oechel, W.C., Papuga, S.A., Ponce-Campos, G.E., Rodriguez, J.C., Smith, W.K., Vargas, R., Watts, C.J., Yepez, E.A. & Goulden, M.L. 2017. CO2 exchange and evapotranspiration across dryland

ecosystems of southwestern North America. Global Change Biology DOI: 10.1111/gcb.13686 online version.

- Bonan, G.B., Lawrence, P.J., Oleson, K.W., Levis, S., Jung, M., Reichstein, M., Lawrence, D.M. & Swenson, S.C. 2011. Improving canopy processes in the Community Land Model version 4 (CLM4) using global flux fields empirically inferred from FLUXNET data. Journal of Geophysical Research, 116, 1–22.
- Brown, D.E. 1994. Biotic Communities: Southwestern United States and Northwestern Mexico. University of Utah Press, Salt Lake City.
- Castellanos, A.E., Bravo, L.C., Koch, G.W., Llano, J.M., Lopez, D., Mendez, R., Rodriguez, J.C., Romo, J.R., Sisk, T., Yanes, G. 2010. Impactos Ecologicos por el Uso del Terreno en el Funcionamiento de Ecosistemas Aridos Semi-Aridos de Sonora. In: Molina-Freaner F, Van Devender TR (eds) Diversidad Biologica del Estado de Sonora. CONABIO - UNAM., México, D. F., pp 157 - 186
- Celaya-Michel, H., García-Oliva, F., Rodríguez, J.C. & Castellanos-Villegas, A.E. 2015. Cambios en el almacenamiento de nitrogeno y agua en el suelo de un matorral desertico transformado a sabana de buffel (Pennisetum cialiare (L.) Link). Terra Latinoamericana, 33, 79–93.
- Cernusak, L.A., Hutley, L.B., Beringer, J., Holtum, J.A.M. & Turner, B.L. 2011. Photosynthetic physiology of eucalypts along a sub-continental rainfall gradient in northern Australia. Agricultural and Forest Meteorology, 151, 1462–1470.
- Diaz-Espejo, A., Walcroft, A.S., Fernandez, J.E., Hafidi, B., Palomo, M.J. & Giron, I.F. 2006. Modeling photosynthesis in olive leaves under drought conditions. Tree Physiology, 26, 1445–1456.
- Domingues, T.F., Meir, P., Feldpausch, T.R., Saiz, G., Veenendaal, E.M., Schrodt, F., Bird, M., Djagbletey, G., Hien, F., Compaore, H., Diallo, A., Grace, J. & Lloyd, J. 2010. Co-limitation of photosynthetic capacity by nitrogen and phosphorus in West Africa woodlands. Plant, cell & environment, 33, 959–80.
- Duursma, R.A. 2015. Plantecophys - An R package for analysing and modelling leaf gas exchange data. PLoS ONE, 10, 1–13.
- Ehleringer, J.R. & Cook, C.S. 1984. Photosynthesis in Encelia farinosa Gray in response to decreasing leaf water potential. Plant Physiology, 75, 688–693.
- Ellsworth, D.S., Reich, P.B., Naumburg, E.S., Koch, G.W., Kubiske, M.E. & Smith, S.D. 2004. Photosynthesis, carboxylation and leaf nitrogen responses of 16 species to elevated pCO2 across four free-air CO2 enrichment experiments in forest, grassland and desert. Global Change Biology, 10, 2121–2138.
- Evans, J.R. 1989. Photosynthesis and nitrogen relationship in leaves of C3 plants. Oecologia, 78, 9–19.
- Evans, J.R. & Seemann, J.R. 1989. The allocation of protein nitrogen in the photosynthetic apparatus: costs, consquences, and control. In: W. R. Briggs ed. Photosynthesis, Alan Liss, Inc, New York, pp. 183–205.
- Farquhar, G.D., Caemmerer, S. & Berry, J.A. 1980. A biochemical model of photosynthetic CO2 assimilation in leaves of C3 species. Planta, 149, 78–90.
- Farquhar, G.D., Caemmerer, S. Von & Berry, J.A. 2001. Models of Photosynthesis. Plant Physiology, 125, 42–45.
- Field, C., Merino, J. & Mooney, H.A. 1983. Compromises between water-use efficiency and nitrogen-use efficiency in five species of California evergreens. Oecologia, 60, 384–389.
- Flexas, J., Bota, J., Galmés, J., Medrano, H. & Ribas-Carbó, M. 2006. Keeping a positive carbon balance under adverse conditions: responses of photosynthesis and respiration to water stress. Physiologia Plantarum, 127, 343–352.
- Fu, Z., Dong, J., Zhou, Y., Stoy, P.C. & Niu, S. 2017. Long term trend and interannual variability of land carbon uptake—the attribution and processes. Environmental Research Letters, 12, 14018.

- García-Moya, E., McKell, C.M. 1970. Contribution of shrubs to the nitrogen economy of a desert-wash plant community. Ecology 51:81-88.
- Ghimire, B., Riley, W.J., Koven, C.D., Kattge, J., Rogers, A., Reich, P.B. & Wright, I.J. 2017. A global trait based approach to estimate leaf nitrogen functional allocation from observations. Ecological Applications. DOI: 10.1002/eap.1542 online version
- Hamerlynck, E.P., Huxman, T.E., Charlet, T.N. & Smith, S.D. 2002. Effects of elevated CO2 (FACE) on the functional ecology of the drought-deciduous Mojave Desert shrub, Lycium andersonii. Environmental and Experimental Botany, 48, 93–106.
- Hinojo-Hinojo, C., Castellanos, A.E., Rodriguez, J.C., Delgado-Balbuena, J., Romo-León, J.R., Celaya-Michel, H. & Huxman, T.E. 2016. Carbon and water fluxes in an exotic buffelgrass savanna. Rangeland Ecology & Management, 69, 334–341.
- Kattge, J., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Bönisch, G., Garnier, E., Westoby, M., Reich, P.B., Wright, I.J., Cornelissen, J.H.C., Violle, C., Harrison, S.P., Van BODEGOM, P.M., Reichstein, M., Enquist, B.J., Soudzilovskaia, N.A., Ackerly, D.D., Anand, M., Atkin, O., Bahn, M., Baker, T.R., Baldocchi, D., Bekker, R., Blanco, C.C., Blonder, B., Bond, W.J., Bradstock, R., Bunker, D.E., Casanoves, F., Cavender-Bares, J., Chambers, J.Q., Chapin III, F.S., Chave, J., Coomes, D., Cornwell, W.K., Craine, J.M., Dobrin, B.H., Duarte, L., Durka, W., Elser, J., Esser, G., Estiarte, M., Fagan, W.F., Fang, J., Fernández-Méndez, F., Fidelis, A., Finegan, B., Flores, O., Ford, H., Frank, D., Freschet, G.T., Fyllas, N.M., Gallagher, R. V, Green, W.A., Gutierrez, A.G., Hickler, T., Higgins, S.I., Hodgson, J.G., Jalili, A., Jansen, S., Joly, C.A., Kerkhoff, A.J., Kirkup, D., Kitajima, K., Kleyer, M., Klotz, S., Knops, J.M.H., Kramer, K., Kühn, I., Kurokawa, H., Laughlin, D., Lee, T.D., Leishman, M., Lens, F., Lenz, T., Lewis, S.L., Lloyd, J., Llusià, J., Louault, F., Ma, S., Mahecha, M.D., Manning, P., Massad, T., Medlyn, B.E., Messier, J., Moles, A.T., Müller, S.C., Nadrowski, K., Naeem, S., Niinemets, Ü., Nöllert, S., Nüske, A., Ogaya, R., Oleksyn, J., Onipchenko, V.G., Onoda, Y., Ordoñez, J., Overbeck, G., Ozinga, W.A., Patiño, S., Paula, S., Pausas, J.G., Peñuelas, J., Phillips, O.L., Pillar, V., Poorter, H., Poorter, L., Poschlod, P., Prinzing, A., Proulx, R., Rammig, A., Reinsch, S., Reu, B., Sack, L., Salgado-Negret, B., Sardans, J., Shiodera, S., Shipley, B., Siefert, A., Sosinski, E., Soussana, J.-F., Swaine, E., Swenson, N., Thompson, K., Thornton, P., Waldram, M., Weiher, E., White, M., White, S., Wright, S.J., Yguel, B., Zaehle, S., Zanne, A.E. & Wirth, C. 2011. TRY - a global database of plant traits. Global Change Biology, 17, 2905–2935.
- Kattge, J. & Knorr, W. 2007. Temperature acclimation in a biochemical model of photosynthesis: A reanalysis of data from 36 species. Plant, Cell and Environment, 30, 1176–1190.
- Kattge, J., Knorr, W., Raddatz, T. & Wirth, C. 2009. Quantifying photosynthetic capacity and its relationship to leaf nitrogen content for global-scale terrestrial biosphere models. Global Change Biology, 15, 976–991.
- Killingbeck, K.T. 1993. Nutrient Resorption in Desert Shrubs. Revista Chilena De Historia Natural, 66, 345–355.
- Killingbeck, K.T. & Whitford, W.G. 1996. High foliar nitrogen in desert shrubs: An important ecosystem trait or defective desert doctrine? Ecology, 77, 1728–1737.
- Lambers, H., Chapin, F. S. & Pons, T. L. 2008. *Plant Physiological Ecology*. Springer New York. 604 pp.
- LeBauer, D.S. & Treseder, K.K. 2008. Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. Ecology, 89, 371–379.
- Long, S.P. & Bernacchi, C.J. 2003. Gas exchange measurements, what can they tell us about the underlying limitations to photosynthesis? Procedures and sources of error. Journal of Experimental Botany, 54, 2393–401.
- Maire, V., Wright, I.J., Prentice, I.C., Batjes, N.H., Bhaskar, R., van Bodegom, P.M., Cornwell, W.K., Ellsworth, D., Niinemets, Ü., Ordonez, A., Reich, P.B. & Santiago, L.S. 2015. Global effects of soil and climate on leaf photosynthetic traits and rates. Global Ecology and Biogeography, 24, 706–717.

- Medlyn, B.E. & Dreyer, E. 2002. Temperature response of parameters of a biochemically based model of photosynthesis. II. A review of experimental data. Plant, Cell &Environment, 61, 1167–1179.
- Mooney, H.A., Ehleringer, J.R. & Berry, J.A. 1974. High photosynthetic capacity of a winter annual in Death Valley. Science, 194, 322–324.
- Niinemets, U. & Tenhunen, J.D. 1997. A model separating leaf structural and physiological effects on carbon gain along light gradients for the shade-tolerant species Acer saccharum. Plant, Cell and Environment, 20, 845–866.
- Poulter, B., Frank, D., Ciais, P., Myneni, R.B., Andela, N., Bi, J., Broquet, G., Canadell, J.G., Chevallier, F., Liu, Y.Y., Running, S.W., Sitch, S. & van der Werf, G.R. 2014. Contribution of semi-arid ecosystems to interannual variability of the global carbon cycle. Nature, 509, 600–603.
- Pugnaire, F.I., Haase, P. & Puigdefábregas, J. 1996. Facilitation between higher plant species in a semiarid environment. Ecology, 77, 1420–1426.
- Rogers, A. 2014. The use and misuse of Vcmax in Earth System Models. Photosynthesis Research, 119, 15–29.
- SAS Institute, 2010. JMP ® *9 User's Guide*. Cary, NC: SAS Institute Inc
- Shreve, F. 1942. The desert vegetation of North America. The Botanical Review, 8, 195–246.
- Shreve, F., Wiggins, I.L. 1964. Vegetation and Flora of the Sonoran Desert. Stanford University Press, Stanford
- Skujins, J.J. 1981. Nitrogen cycling in arid ecosystems. In: Clark FE, Rosswall T (eds) Terrestrial nitrogen cycles. Processes, ecosystem strategies and management impacts, vol 33. Ecological Bulletin, Stockholm, pp 477 - 491
- Vargas, R., Yépez, E.A., Andrade, J.L., Ángeles, G., Arredondo, T., Castellanos, A.E., Delgado-Balbuena, J., Garatuza-Payán, J., González del Castillo, E., Oechel, W., Rodríguez, J.C., Sánchez-Azofeifa, A., Velasco, E., Vivoni, E.R. & Watts, C. 2013. Progress and opportunities for monitoring greenhouse gases fluxes in Mexican ecosystems: The MexFlux network. Atmósfera, 26, 325–336.
- von Caemmerer, S. 2000. Biochemical Models of Leaf Photosynthesis. CSIRO Publishing, Australia.
- Walker, A.P., Beckerman, A.P., Gu, L., Kattge, J., Cernusak, L.A., Domingues, T.F., Scales, J.C., Wohlfahrt, G., Wullschleger, S.D. & Woodward, F.I. 2014. The relationship of leaf photosynthetic traits - Vcmax and Jmax - to leaf nitrogen, leaf phosphorus, and specific leaf area: A meta-analysis and modeling study. Ecology and Evolution, 4, 3218–3235.
- Werk, K.S., Ehleringer, J., Forseth, I.N. & Cook, C.S. 1983. Photosynthetic characteristics of Sonoran Desert winter annuals. Oecologia, 59, 101–105.
- West, N.E. 1981. Nutrient cycling in desert ecosystems. In: Goodall DW, Perry RA, Howes KMW (eds) Arid-land ecosystems: Structure, functioning and management. V.2. Cambridge University Press, Cambridge, pp 301 - 324
- West, N.E., Skujins J. 1978. Nitrogen in desert ecosystems. US/IBP Synthesis series. 9. Dowden, Hutchinson and Ross, Inc., Stroudsburg
- Wohlfahrt, G., Bahn, M., Haubner, E., Horak, I., Michaeler, W., Rottmar, K., Tappeiner, U. & Cernusca, A. 1999. Inter-specific variation of the biochemical limitation to photosynthesis and related leaf traits of 30 species from mountain grassland ecosystems under different land use. Plant, Cell and Environment, 22, 1281–1296.
- Wright, I.J., Reich, P.B. & Westoby, M. 2001. Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats. Functional Ecology, 15, 423–434.
- Wright, I.J., Reich, P.R., Cornelissen, J.H.C., Falster, D.S., Groom, P.K., Hikosaka, K., Lee, W., Lusk, C.H., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Warton, D.I. & Westoby, M. 2005. Modulation of leaf economic traits and trait relationships by climate. Global Ecology and Biogeography, 14, 411–421.

- Wullschleger, S.D. 1993. Biochemical Limitations to Carbon Assimilation in C 3 Plants—A Retrospective Analysis of the A/C i Curves from 109 Species. Journal of Experimental Botany, 44, 907–920.

FIGURES:

Figure 1: Relationship between V_{cmax25} and N_{area} found in this study using Bernacchi's (BRc) temperature response parameters (thick continuous lines) and those of Kattge and Knorr (KKr) (thick dashed line) using linear regressions. Grey areas represent 95% confidence intervals for both linear regressions, and a darker gray color indicates the area where 95 % confidence intervals overlap. For comparison, thin lines show N_{area} and V_{cmax25} relationship for shrub and crop functional types from Kattge et al. (2009), which were derived from a global database with poor representation of dryland species.

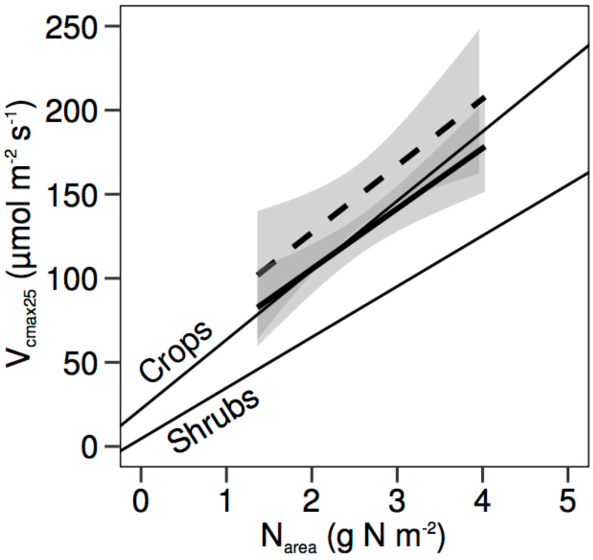


Figure 2: Modeled versus measured net photosynthesis rate for all available data and excluding data with leaf temperature > 40 ºC. Solid line corresponds to the 1:1 line. Photosynthesis rates were modeled using V_{cmax25} and J_{max25} for each leaf derived from our best models and trait values for each leaf (trait-based approach).

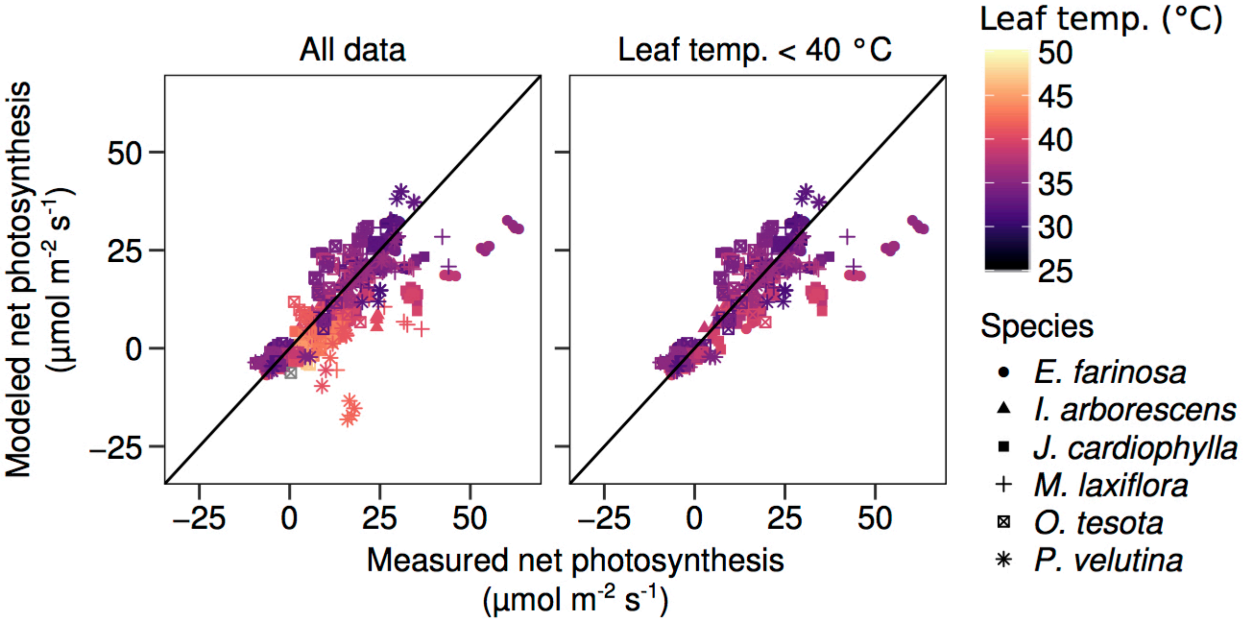
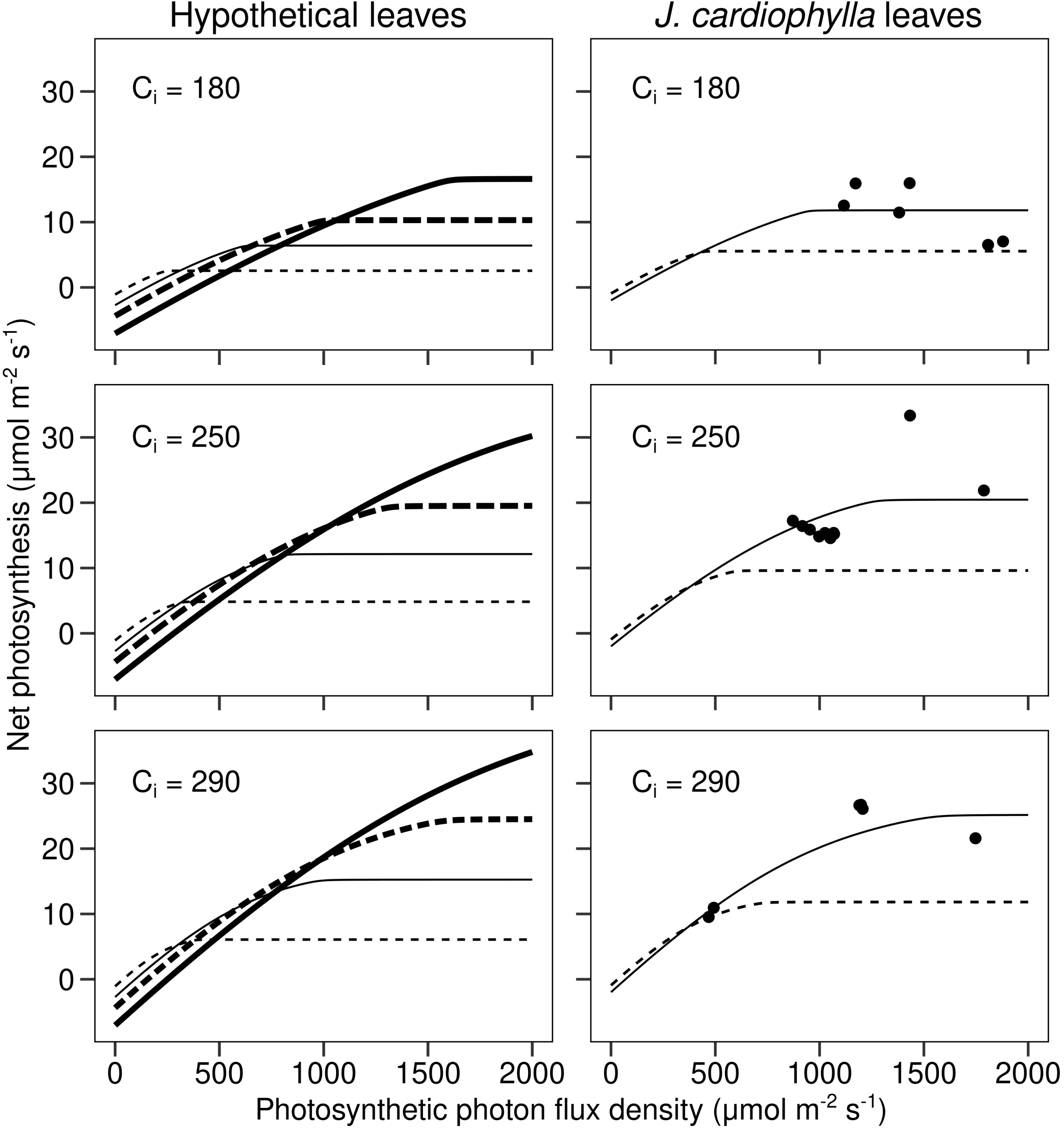
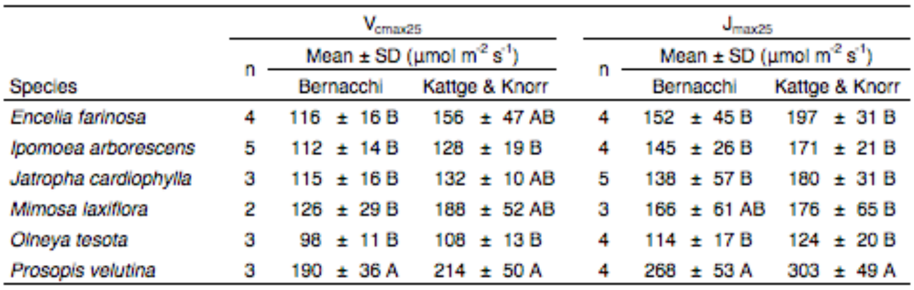


Figure 3: Comparison of simulated light response curves of net photosynthesis obtained using the parameterizations derived in this study for Sonoran Desert species (solid lines) and parametrizations for the shrub functional type from Kattge et al. (2009) (dashed lines). Simulations were performed for hypothetical leaves with high N_{area} (4.5 g N m^{-2}, thick lines) and low N_{area} (1 g N m^{-2}, thin lines) and for *J. cardiophylla* leaves, under high leaf temperatures (37 ºC) and acclimated to typical July temperatures of our study locations. We used three levels of intercellular CO_2 concentration (C_i) corresponding to typical values found at low and high stomatal conductance: 180 µmol mol^{-1} for stomatal conductances of 0.1-0.2 mol m^{-2} s^{-1}, and 290 µmol mol^{-1} for stomatal conductances of 0.6-1 mol m^{-2} s^{-1}, respectively). Also included was a typical intercellular CO_2 concentration for C_3 species (250 µmol mol-1) which is about the mean value of our data (Lambers et al. 2008). Data measured under similar conditions (dots) were included for *J. cardiophylla* leaves.



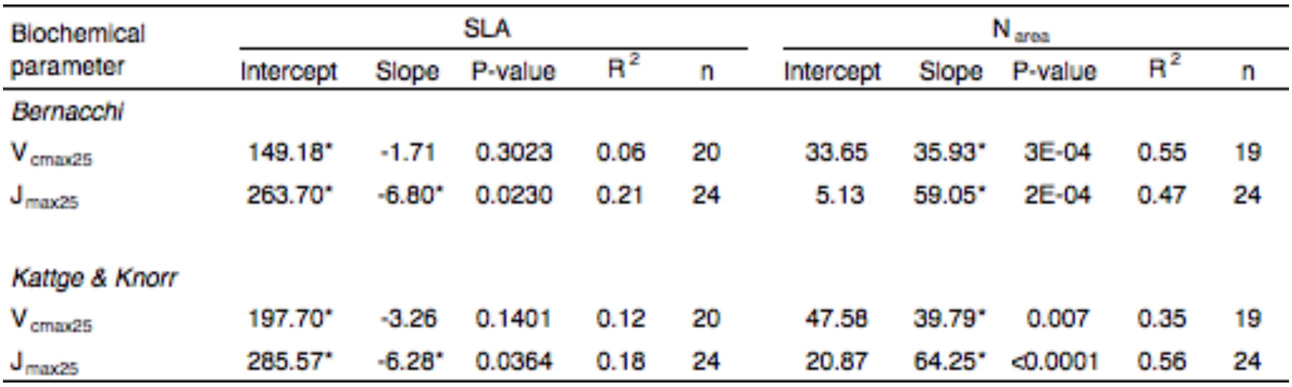
TABLES:

Table 1: V_{cmax25} and J_{max25} derived from response curves of net photosynthesis to intercellular CO_2 concentration. Values obtained with Bernacchi (BRc) and Kattge & Knorr (KKr) parameterizations are presented. n refers to the number of curves from which V_{cmax25} and J_{max25} were derived.



	V_{cmax25}			J_{max25}		
	n	Mean ± SD (µmol m^{-2} s^{-1})		n	Mean ± SD (µmol m^{-2} s^{-1})	
Species		Bernacchi	Kattge & Knorr		Bernacchi	Kattge & Knorr
Encelia farinosa	4	116 ± 16 B	156 ± 47 AB	4	152 ± 45 B	197 ± 31 B
Ipomoea arborescens	5	112 ± 14 B	128 ± 19 B	4	145 ± 26 B	171 ± 21 B
Jatropha cardiophylla	3	115 ± 16 B	132 ± 10 AB	5	138 ± 57 B	180 ± 31 B
Mimosa laxiflora	2	126 ± 29 B	188 ± 52 AB	3	166 ± 61 AB	176 ± 65 B
Olneya tesota	3	98 ± 11 B	108 ± 13 B	4	114 ± 17 B	124 ± 20 B
Prosopis velutina	3	190 ± 36 A	214 ± 50 A	4	268 ± 53 A	303 ± 49 A

Table 2: Results of linear regression analysis between parameters V_{cmax25} and J_{max25} and the leaf traits SLA and N_{area}, obtained with the two sets of temperature response parameters used (Bernacchi and Kattge & Knorr).



Biochemical parameter	SLA					N_{area}				
	Intercept	Slope	P-value	R^2	n	Intercept	Slope	P-value	R^2	n
Bernacchi										
V_{cmax25}	149.18*	-1.71	0.3023	0.06	20	33.65	35.93*	3E-04	0.55	19
J_{max25}	263.70*	-6.80*	0.0230	0.21	24	5.13	59.05*	2E-04	0.47	24
Kattge & Knorr										
V_{cmax25}	197.70*	-3.26	0.1401	0.12	20	47.58	39.79*	0.007	0.35	19
J_{max25}	285.57*	-6.28*	0.0364	0.18	24	20.87	64.25*	<0.0001	0.56	24

Table 3: Best models for describing the parameters V_{cmax25} and J_{max25} using combinations of leaf traits and two sets of temperature response parameters (Bernacchi and Kattge & Knorr). SE is the standard error. Some terms included in the original statistical model were excluded in the best models by the step-wise regression procedure according to Akaike information criterion

Biochemical parameter	Best model effects	Coefficient	SE	t	P	R^2
Bernacchi						
V_{cmax25}	Intercept	-56.28	46.58	-1.21	0.2445	0.65
	SLA	3.28	1.55	2.12	0.0503	
	N_{area}	51.92	10.43	4.98	0.0001	
J_{max25}	Intercept	-22.00	45.04	-0.49	0.6327	0.58
	V_{cmax25}	1.55	0.35	4.38	0.0006	
Kattge & Knorr						
V_{cmax25}	Intercept	47.58	34.70	1.37	0.1882	0.35
	N_{area}	39.79	13.07	3.04	0.0073	
J_{max25}	Intercept	-7.27	49.80	-0.15	0.8862	0.57
	N_{area}	39.28	19.10	2.06	0.0603	
	V_{cmax25}	0.71	0.31	2.32	0.0376	

Table 4: Species average V_{cmax25} and J_{max25} derived from using the best models and all available leaf trait values and two sets of temperature response parameters (Bernacchi and Kattge & Knorr). SD is the standard deviation.

	V_{cmax25}			J_{max25}			SLA		N_{area}	
	n	Mean ± SD (μmol m^{-2} s^{-1})		n	Mean ± SD (μmol m^{-2} s^{-1})		n	Mean ± SD	n	Mean ± SD
Species		Bernacchi	Kattge & Knorr		Bernacchi	Kattge & Knorr		(m^2 kg^{-1})		(g N m^{-2})
Encelia farinosa	12	136 ± 31	157 ± 23	12	189 ± 49	213 ± 39	16	13 ± 3.5	13	2.8 ± 0.6
Ipomoea arborescens	17	106 ± 23	117 ± 21	17	142 ± 36	144 ± 35	21	22 ± 4.5	17	1.7 ± 0.5
Jatropha cardiophylla	31	102 ± 28	125 ± 22	31	137 ± 44	158 ± 37	38	18 ± 3.2	31	1.9 ± 0.5
Mimosa laxiflora	15	124 ± 21	143 ± 14	15	171 ± 33	189 ± 24	19	18 ± 5.8	15	2.4 ± 0.4
Olneya tesota	30	106 ± 22	137 ± 23	30	143 ± 34	179 ± 38	39	14 ± 5.6	30	2.3 ± 0.6
Prosopis velutina	11	191 ± 37	215 ± 32	11	276 ± 57	312 ± 55	16	9 ± 1.7	11	4.2 ± 0.8

Table 5: Mean absolute deviation of modeled versus measured net photosynthesis rates using three approaches for obtaining V_{cmax25} and J_{max25} and two temperature response parameters datasets (BRc and KKr). Mean absolute deviation is reported in the same units as net photosynthesis rates (μmol m^{-2} s^{-1}).

	Bernacchi			Kattge & Knorr		
Species	Species mean	Trait mean	Trait based	Species mean	Trait mean	Trait based
All available data						
Encelia farinosa	6.81	6.43	6.68	7.39	7.35	6.76
Ipomoea arborescens	2.86	2.8	2.65	3.28	3.02	2.72
Jatropha cardiophylla	4.88	5.14	4.68	5.47	5.65	5.33
Mimosa laxiflora	5.69	5.64	4.69	5.71	5.54	4.85
Olneya tesota	3.58	3.93	4.29	3.84	4.59	5.08
Prosopis velutina	7.58	7.65	6.37	8.09	8.15	7.22
Leaf temperatures < 40 °C						
Encelia farinosa	7.02	6.71	6.76	6.61	6.57	6.77
Ipomoea arborescens	2.61	2.49	2.3	2.67	2.35	2.01
Jatropha cardiophylla	5.08	5.46	5.01	5.69	5.89	5.46
Mimosa laxiflora	5.01	4.95	3.99	4.86	4.65	3.84
Olneya tesota	2.95	3.21	3.61	2.8	3.88	4.76
Prosopis velutina	4.49	4.58	3.2	4.57	4.64	3.74

Authors’ contributions

CHH and AEC collected the data and led the writing of the manuscript

AECV and JRRL Conceived the ideas and designed research project

JP, RV and AECV provided research and writing inputs

JMLLS analyzed and interpreted nutrient data