Wide Ranges of Functional Traits in the Flora from the Central Region of Sonora: A Diversity to be Explored

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Abstract*—Although the Sonoran Desert does not have the highest plant species richness, it has been documented with the highest growth form diversity from the North American deserts. It is not known if this high growth form diversity could also harbor a high functional diversity. In this study we characterize the ecophysiological functional traits of photosynthetic capacity, stomatal conductance, transpiration and resource use efficiency (water and nitrogen), as well as morphological and structural traits of specific leaf area and nitrogen content in 52 species that inhabit the arid and semiarid Central Region of Sonora. For all species and analyzed traits, we found a larger range of values compared to those reported from a recent world survey, which represent a very high functional diversity. Such large range and amplitude in functional trait values has not been reported for other regions of the world. This study presents evidence of the high functional diversity of the Sonoran Desert plants waiting to be described and documented.*

Introduction

Great efforts have been made to know the functional traits of species that inhabit the different biomes of the world during the past two decades. This information is important because it allows us to know and understand the biodiversity, not just from a taxonomic point of view but as functional diversity or, in other words, the functions, properties, and possible effects and responses of the species to the environment. Leaf traits are the most common and important plant functional traits because they are strongly related to various traits of other parts of the plants, to species ecological strategy, and even to various aspects of the ecosystem functioning (Cornwell and others 2008; Craine and others 2005; Díaz and others 2004; Vendramini and others 2002; Westoby 1998).

At a global level, the major effort so far to assess functional traits of plant species is the TRY database (online in http://try-db.org/) with over 3 million trait records from 69,000 species from all major biomes in the world. Kattge and others (2011) suggest that it is evident that plant traits from the warm deserts and, in general, most of the arid and semiarid zones floras of the world are still poorly represented in this database.

Arid and semiarid zones are important worldwide because they represent almost 50% of the terrestrial area (without considering the polar caps). Shreve (1942) and Stebbins (1952) recognized the large growth forms and trait diversity that existed in the plants from these ecosystems and the different ways in which they deal with extreme conditions of water scarcity, high temperatures, and high irradiance that characterize them. This can mean that arid and semiarid zones harbor a high functional diversity; however, this issue has been little explored.

The Sonoran Desert, as delimited by Shreve and Wiggins (1964), shows some climatic and floristic particularities compared to other deserts of the world. It possesses a bi-seasonal rainfall pattern for most of its extension, with abundant monsoon rains in summer and long duration and highly unpredictable low intensity rains during winter (Brito-Castillo and others 2010; Shreve and Wiggins, 1964; Schmidt 1989). Its flora has neartic and neotropical biogeographic influences (Castellanos 1992), which result in a great number of species that reach its most northern, southern, or western distribution limits in this region (Castellanos 1992; Castellanos and others 2010; Van Devender and others 2010). In the Central Region of Sonora, however, its major affinity is with the highly seasonal neotropical flora from the tropical deciduous forest ecosystems of Mexico (Rzedowski, 1973). Moreover, it has been found that the Sonoran Desert possesses the highest growth form diversity of the North American deserts (Shreve 1942; Cody 1991).

Due to the poor representation of warm deserts in plant functional trait studies, and to the climatic and floristic particularities above mentioned of the Sonoran Desert, the objective of this research was to conduct a characterization of leaf traits of species that inhabit the arid and semiarid area of the Central Region of Sonora. We assessed these through a large sampling in terms of number of species, growth forms, habitats, and habits. It is in this Central Region of Sonora, which comprises a gradient of arid and semiarid zones, where desert and subtropical vegetation integrates in ecotones creating interesting mosaics in terms of biota composition and physiognomy of plant communities.

The large sampling undertaken in this study was conducted where both "soft" leaf traits as the specific leaf area, leaf nitrogen content, and "hard" as various ecophysiological traits related to the photosynthesis and gas exchange were considered (Lavorel and Garnier, 2002)

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to represent the functional diversity of the flora from this region in a variety of leaf traits. It was expected that the species would show wide ranges in the leaf traits due to the great variety of strategies and traits of plants that inhabit these environments can develop to deal with the extreme conditions in the arid and semiarid zones, as suggested in Stebbins (1952).

Methodology

Study Sites

To include the more representative plant communities from the Central Region of Sonora, 14 localities were selected following a gradient in vegetation, aridity and disturbance level (table 1). These sites were located near the limits of the Plains of Sonora and Foothills Thornscrub subdivisions of the Sonoran Desert (Shreve and Wiggins 1964).

Species Leaf Traits Characterization

Samplings in the 14 sites were carried out in September and the first half of October in 2010 to determine some species leaf traits. An effort was made to include a wide variety of species, growth forms, habitats, and habits. The sampling period was in the rainy season to avoid the limiting effects of the water stress on the photosynthetic capacity with measurements made between the 8:00 AM and 12:00 PM.

On each site and for each species, photosynthesis of leaves at high irradiances (generally 1500-2000 μmol photons m^{-2} s^{-1}) was determined at field natural conditions as a measure of the photosynthetic capacity (A_{area}), stomatal conductance to water vapor (g_s), transpiration rate (E), water use efficiency (EUA = Amount of fixed CO_2 per unit of transpired water), and intercellular concentration of CO_2 using a portable photosynthesis system LCi (ADC BioScientific, England) provided with the broad leaf chamber. Also, the dark respiration rate (R) was determined for some species by putting the leaves in complete darkness during the measurement period. At least three plants per species were measured, one leaf per plant, with three measurements per leaf, except in rare occasions where it was not possible to sample enough individuals. Each measured leaf was collected in paper envelopes and stored in ice for its transportation. The real area used in the measurements of gas exchange was determined using the image analyzing software ImageJ 1.43u (National Institutes of Health, USA). This value was used to correct the gas exchange measurements.

After the measurement of leaf area, each leaf was oven-dried at 70 ºC for 2 days to determine leaf dry weight. Using the leaf area and dry weight, the specific leaf area (SLA) was calculated. For those same leaves, nitrogen content per leaf weight (N_{mass}) was determined by the fenate method for Kjeldahl total nitrogen using a Digestor 2020 (Tecator, Spain) and a rapid flow analizer RFA (ALPKEM). The measure of specific leaf area was used as a conversion unit for expressing some leaf traits on a mass and area basis (mass and area subscripts). The nitrogen use efficiency was calculated for each measure of A_{area} as the A_{area}/N_{area} quotient. The complete list of leaf traits measured and their corresponding units are listed in the table 2.

Data Analysis

All the data were screened and those that showed any evidence of stress limitation weren't included in the analysis (e.g., stomatal conductance values below 0.05 mol H_2O m^{-2} s^{-1} (Flexas and others 2006) or individual trait values far from the trend of the rest of the values for the same species). A mean value for each measured leaf trait was obtained with the remaining data for each species. These mean values are those reported in the paper and compared with all of the world data (TRY database in Kattage and others 2011).

Results and Discussion

Leaf Traits of Species in the Central Region of Sonora

A total of 52 species was sampled that represent a wide variety of growth forms (with the exception of plants with CAM photosynthetic pathway) including those species that are the most commonly found in the flora of the Central Region of Sonora. All species were sampled under natural conditions except for *Cucurbita digitata*, *C. palmeri*, *Jatropha cinerea* and the exotic ruderal *Ricinus communis*, which were sampled under irrigated conditions. Photosynthesis and gas exchange data were obtained for 51 species. Only *Ipomoea nil*

Table 1—Geographic location, vegetation type, and annual rainfall for the study sites.

Site	Latitude	Longitude	Vegetation type[a]	Annual rainfall[b]
1	N 29.023°	O 111.137°	Abandoned agricultural field	200-300 mm
2	N 28.966°	O 110.961°	Subtropical scrub	200-300 mm
3	N 28.700°	O 110.540°	Subtropical scrub	400-500 mm
4	N 28.710°	O 110.540°	Induced buffel savanna	400-500 mm
5	N 29.563°	O 111.011°	Disturbed mezquital	300-400 mm
6	N 29.684°	O 110.145°	Disturbed mezquital	500-600 mm
7	N 29.559°	O 110.123°	Disturbed mezquital	500-600 mm
8	N 29.474°	O 110.217°	Subtropical scrub	500-600 mm
9	N 29.465°	O 110.248°	Subtropical scrub	500-600 mm
10	N 29.439°	O 110.315°	Riparian vegetation	400-500 mm
11	N 29.435°	O 110.334°	Mezquital	500-600 mm
12	N 29.346°	O 110.497°	Desert microphyllous scrub	400-500 mm
13	N 29.327°	O 110.561°	Riparian vegetation	400-500 mm
14	N 29.240°	O 110.726°	Mezquital	300-400 mm

[a]Following the INEGI's land use and vegetation classification for Mexico
[b]Following the isohyets map of Mexico by CONABIO. Online at: http://www.conabio.gob.mx/informacion/gis/

Table 2—Leaf traits characterized for the species, its abbreviations and measurement units.

Leaf trait	Abbreviation	Units
Specific leaf area	SLA	$m^2\ kg^{-1}$
Photosynthetic capacity per leaf area	A_{area}	μmol $CO_2\ m^{-2}\ s^{-1}$
Photosynthetic capacity per leaf dry mass	A_{mass}	nmol $CO_2\ g^{-1}\ s^{-1}$
Transpiration rate	E	mmol $H_2O\ m^{-2}\ s^{-1}$
Stomatal conductance to water vapor	g_s	mol $H_2O\ m^{-2}\ s^{-1}$
Dark respiration per leaf area	R_{area}	μmol $CO_2\ m^{-2}\ s^{-1}$
Dark respiration per leaf dry mass	R_{mass}	nmol $CO_2\ g^{-1}\ s^{-1}$
Leaf nitrogen content per leaf area	N_{area}	g N m^{-2}
Leaf nitrogen content per leaf dry mass	N_{mass}	%
Nitrogen use efficiency	NUE	μmol $CO_2\ g^{-1}$ N s^{-1}
Water use efficiency	WUE	μmol CO_2 $mmol^{-1}$ H_2O

did not give reliable data because plants were under stress. However, its leaves were included in the data for specific leaf area (SLA) and nitrogen content (N). Data were obtained on dark respiration (R) for 21 species. The SLA could be determined for all the species, while N and nitrogen use efficiency (NUE) could be determined for 48 and 46 species respectively. Compared to previous data (Wright and others 2004; Kattge and others 2011), this study had the largest number of species with an ecophysiological characterization from an arid or semiarid region and from the Sonoran Desert.

Trait mean values for all species grouped by growth form are shown in table 3. Evergreen trees presented the lowest values of gas exchange and SLA traits, herbaceous and grass species had the highest gas exchange values, vines had the highest SLA and high A_{masa}, N_{mass} and g_s but low A_{area}, , and shrubs had intermediate values on all traits. These patterns had the most traits that agree with previously reported values for these groups of plants (Larcher 1995; Castellanos 1991; Castellanos and others 1989).

Comparison of Leaf Traits From Species of the Central Region of Sonora with Those of the World

Several studies have addressed the issue of the leaf functional traits of species in different biomes of the world and, therefore, may serve to give a meaning to the values found in the species of the Central Region of Sonora. For example, the mean values of SLA and N of the species of the present study (fig. 1) agreed with values reported for species with the lowest leaf life spans (between 1-4 months) (Reich and others 1992; 1997), which may be related to the short seasonal character of species in the Central Region of Sonora. These values may be considered high in a global context of the species and in particular for those that could be expected in an arid region where the trend for species that inhabit the warmest and driest regions have the lowest SLA (Wright and others 2004) in contrast with our findings in this study. Wright and others (2005) report that species with the highest irradiances and lowest annual rainfall habitat conditions had highest values in N_{area}, which agrees with the high values found in the studied species, although in this study we also report high values of N_{mass} (fig. 1).

It is evident that all leaf traits from the species that we studied had a similar or larger range of values than those reported for all the species in the world that have been studied (fig. 1) in comparing the data for the species that we studied with those of the global compendium of the TRY database functional traits (Kattge and others 2011). In fact, the maximum value in all the trait ranges exceeds the value of the 97.5% quantile from the data of TRY database. Ranges this wide are not common and we have not found such amplitude in the literature from other ecosystems or regions of the world. According to Tilman's (2001) definition of functional diversity, those components of biodiversity that influence how an ecosystem operates or functions that we found for both ecophysiological and morphostructural traits or "hard" and "soft" traits *sensu* (Lavorel and Garnier 2002) in species that inhabit the arid and semiarid zones of the Central Region of Sonora represent, without any doubt, the high functional diversity that exists in the flora of the southwestern Sonoran Desert.

Previous studies that have documented a high biological diversity different from the taxonomic diversity in the Sonoran Desert are those of Shreve (1942) and more recently Cody (1991, which point out the highest growth form diversity of the North American deserts. Nilsen and others (1984) documented a wide diversity in ecophysiologic strategies in water use within a single functional type, the phreatophytes of the Sonoran Desert. Stebbins (1952) explains that the plant diversity in sites with aridity may be high, where an important factor is the high environmental (resources) and topographical heterogeneity, but plants show a wide variety of ways (strategies) and structures (organs) that can make it possible for a plant to inhabit arid conditions, which can be interpreted as a high functional diversity.

A few efforts to understand the causes of high biological and functional diversity of the Sonoran Desert have been reported while a major emphasis has gone to describe its taxonomic diversity (Shreve and Wiggins, 1964; Turner and 1995; Molina and Van Devender 2010). We propose that the high diversity (e.g., functional diversity and growth form diversity) is found in the Central Region of Sonora may be due a number of factors including (1) the floristic affinity, influence and confluence of different contiguous biogeographic (Neartic and Neotropical) regions (Rzedowski, 1973; Castellanos, 1992; Castellanos

Table 3—Leaf trait mean values per species growth form.[a]

Type[b]	Subtype[b]	SLA	N_{mass}	A_{area}	A_{mass}	g_s	WUE	NUE
Trees	Evergreen (3)	9.14 ± 2.05	2.13 ± 0.61	14.42 ± 5.27	129.83 ± 22.88	0.27 ± 0.14	**2.09** ± 0.60	5.23 ± 1.25
	Deciduous (6)	15.29 ± 5.16	2.93 ± 0.76	20.99 ± 7.28	292.52 ± 117.59	0.60 ± 0.38	1.79 ± 0.47	10.54 ± 3.54
Shrubs	Deciduous (15)	12.77 ± 2.22	2.99 ± 0.83	22.44 ± 7.90	273.33 ± 106.84	0.69 ± 0.42	1.71 ± 0.51	8.63 ± 4.82
	Ferns (1)	14.01	**4.58**	19.44	272.38	**0.94**	0.86	5.94
Herbs	Summer annuals (5)	20.27 ± 10.85	2.35 ± 2.27	**36.97** ± 21.49	**721.86** ± 585.27	**0.72** ± 0.52	**2.49** ± 0.47	**122.71** ± 186.65
	Perennials (6)	15.57 ± 5.90	2.71 ± 1.29	23.66 ± 14.66	346.87 ± 218.18	0.60 ± 0.43	1.75 ± 0.32	**32.43** ± 58.01
	Grasses (6)	18.31 ± 3.71	2.49 ± 1.82	**35.05** ± 11.26	**603.40** ± 143.60	0.33 ± 0.25	**3.21** ± 1.64	**53.53** ± 48.74
	Vines (10)	**30.86** ± 19.40	**3.52** ± 1.24	14.83 ± 6.28	451.06 ± 279.52	0.67 ± 0.47	1.84 ± 0.84	13.52 ± 7.26

[a]Low values are underlined, and high values are in bold. Values after the symbol ± are 1 Standard deviation. Units are the same as in table 2.
[b]Numbers in parenthesis represent the number of species per growth form.

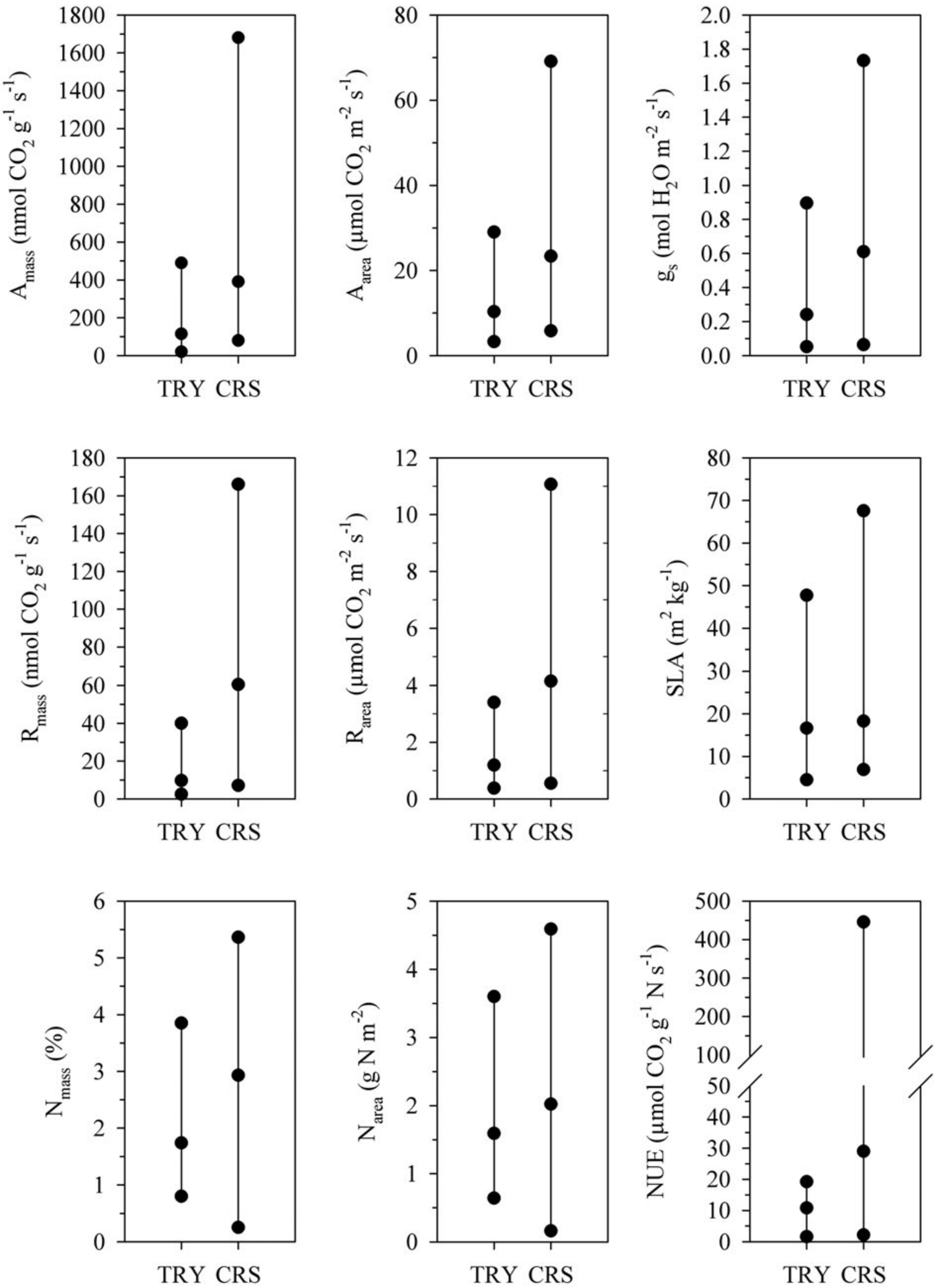

Figure 1—Comparison of leaf trait ranges between the species of the Central Region of Sonora (CRS) and the the world species included in the TRY database (TRY). Data points for the TRY species correspond to the 2.5% quantil (lowest point), mean value (mid point), and 97.5% quantil (highest point), and for the CRS species are the minimum (lowest point), mean (mid point) and maximum values (highest point).

and others 2010; Van Devender, 2010); (2) a large environmental heterogeneity in a short distance (Castellanos and others 1992); and (3) the interspecific positive ecological interactions (e.g., facilitation, nursing, symbiosis, mutualism, fertility islands, etc.) that can allow that species with different ecological strategies and stress tolerance levels to coexist in the same ecosystem.

Conclusions

Ecophysiologic and morphostructural leaf traits of 52 species were characterized, which makes this study the largest for the ecophysiologic characterization from an arid and semiarid and from the Sonoran Desert species. The ranges found in all leaf traits characterized for the studied species of the Central Region of Sonora had a similar and even larger range of values than those reported for all the species in the world. This wide amplitude in the ranges of leaf trait values is an indicator of a very high functional diversity in the species that inhabit the arid and semiarid gradient of the Central Region of Sonora. This work is evidence of the high functional diversity in the Sonoran Desert plants waiting to be described and documented.

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References

Brito-Castillo, L.; Crimmins, M. A.; Díaz, S. C. 2010. Clima. In: Molina-Freaner, F. E. and Van Devender, T. R, eds, Diversidad Biológica de Sonora. México D. F. UNAM: 73-96.

Castellanos, A. E. 1991. Photosynthesis and gas Exchange of vines. In: Putz, F. E.; Mooney, H. A. (eds.), The Biology of Vines. Cambridge. Cambridge University Press. 171-214.

Castellanos, A. 1992. Ecología, utilizacion y conservacion de las comunidades vegetales en el estado de Sonora: un analisis. In: Moreno, J. L., ed. Ecología, Recursos Naturales y Medio Ambiente en Sonora. Hermosillo. Secretaria de Infraestructura Urbana y Ecología: 25-37.

Castellanos, A. E.; Mooney, H. A.; Bullock, S. H.; [and others] 1989. Leaf, stem, and metamer characteristics of vines in a tropical deciduous forest in Jalisco, Mexico. Biotropica. 21(1): 41-49.

Castellanos-Villegas, A. E.; Bravo, L. C.; Koch, G. W.; [and others]. [In press]. Impactos ecológicos por el uso del terreno en el funcionamiento de ecosistemas áridos y semiáridos. 157-186 p. In: Molina-Freaner, F. E. y Van Devender, T. R., eds. Diversidad Biológica de Sonora. México D. F. UNAM.

Cody, M. L. 1991. Niche theory and plant growth form. Plant Ecology. 97(1):39-55.

Cornwell, W. K.; Cornelissen, J. H. C.; Amatangelo, K.; [and others]. 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecology Letters. 11: 1065-1071.

Craine, J. M.; Lee, W. G.; Bond, W. J.; Williams, R. J.; Johnson, L. C. 2005. Environmental constraints on a global relationship among leaf and root traits of grasses. Ecology. 86(1): 12-19.

Díaz, S.; Hodgson, J. G.; Thompson, K.; [and others]. 2004. The plant traits that drive ecosystems: Evidence from three continents. Journal of Vegetation Science. 15: 295-304.

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(3): 343-352.

Kattge, J.; Díaz, S.; Lavorel, S.; [and others]. 2011. TRY—a global database of plant traits. Global Change Biology. 17(9): 2905-2935.

Larcher, W. 1995. Physiological Plant Ecology. 3rd ed. Berlin-Heidelberg: Springer-Verlag.

Lavorel, S.; Garnier, E. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holi Grail. Functional Ecology. 16(5): 545-556.

Molina-Freaner, F. E. y Van Devender, T. R.2010. Diversidad Biológica de Sonora. México D. F. UNAM.

Nilsen, E. T.; Sharifi, M. R.; Rundel, P. W. 1984. Comparative water relations of phreatophytes in the Sonoran Desert of California. Ecology. 65(3): 767-778.

Reich, P. B., Walters, M. B.; Ellsworth, D. S. 1992. Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. Ecological Monographs. 62(3): 365-392.

Reich, P. B., Walters, M. B.; Ellsworth, D. S. 1997. From tropics to tundra: Global convergence in plant functioning. Proceedings of the National Academy of Sciences. 94: 13730-13734.

Rzedowski, J. 1973. Geographical relationships of the flora of mexican dry regions. 61-72 p. En: Grahan, A (Ed.), Vegetation and Vegetational History of Northern Latin America. Elsevier. Amsterdam.

Shreve, F. 1942. The desert vegetation of North America. The Botanical Review. 4(3): 195-246.

Shreve, F.; Wiggins, I.L. 1964. Vegetation and Flora of the Sonoran Desert. Part I: Vegetation of the Sonoran Desert. Original Edition. Stanford: Stanford University Press.

Schmidt R. H., Jr. 1989. The arid zones of Mexico: climatic extremes and conceptualization of the Sonoran Desert. Journal of Arid Environments. 16: 241-256.

Stebbins, G. L. 1952. Aridity as a stimulus to plant evolution. American Naturalist. 86: 33-44.

Tilman, D. 2001. Functional diversity. In: Levin, S. A., ed. Encyclopedia of Biodiversity. Vol. 3. San Diego: Academic Press: 109-120.

Turner, R. M.; Bowers, J. E.; Burgess, T. L.; Hastings, J. R. 1995. Sonoran Desert Plants: An Ecological Atlas. Tucson. The University of Arizona Press.

Van Devender, T. R.; Felger, R. S.; Fishbein, M.; [and others]. 2010. Biodiversidad de plantas vasculares. In: Molina-Freaner, F. E. and Van Devender, T. R., eds. Diversidad Biológica de Sonora. México D. F.: UNAM: 229-255.

Vendramini, F.; Díaz, S.; Gurvich, D. E.; Wilson, P. J.; Thompson, K.; Hodgson, J. G. 2002. Leaf traits as indicators of resource-use strategy in floras with succulent species. New Phytologist. 154: 147-157.

Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. Plant and Soil. 199: 213-227.

Wright, I. J., Reich, P. B.; Westoby, M.; [and others]. 2004. The worldwide leaf economics spectrum. Nature. 428: 821–827.

Wright, I. J., Reich, P. B.; Cornelissen, J. H. C.; [and others]. 2005. Modulation of leaf economic traits and trait relationships by climate. Global Ecology and Biogeography. 14: 411–421.