Chapter 6
Intraspecific Trait Variability of Emblematic Grass and Tree Species from Venezuelan Savannas Across Extended Physical Gradients

Zdravko Baruch

6.1 Introduction

Research on ecological gradients describe and examine gradual biotic shifts across geographic (elevation, latitude) or physical (irradiance, rainfall, fertility, disturbance). These studies are usually accomplished by surveys and samplings across the gradient of interest and offer significant advantages. For example, they capture environmental variability and detect phenotypic and genetic variation in target species. Also, gradients are proxies for climate and global changes (the space for time approach) and identify climate sensitive ecotypes or the range of intraspecific trait variation (ITV) (Caddy-Retalic et al. 2017). However, the true driver(s) of biotic change may be difficult to discern as many environmental variables (e.g., temperature and rainfall) may covary along single transects (Meirmans 2015).

Studies on ecological gradients in the tropics began with Humboldt's description of altitudinal zones in the Andes of Ecuador. Coincidentally, Humboldt also visited savannas in the Venezuelan Llanos during year 1800 but was unimpressed, referring to them as "being monotonous and with little scientific attraction" (Huber et al. 2006). Research on ecological gradients across Neotropical lowland savannas is scarce. Most studies come from the Brazilian cerrados (317 publications or 84% of total; Web of Science, searched on 18/09/2021) and few from the Venezuelan and Colombian Llanos. They typically discuss ecotones from open savanna to parklands

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"Environmental gradients are Nature's laboratory"

Z. Baruch (✉)
Universidad Simón Bolívar, Caracas, Venezuela

University of Adelaide, Adelaide, SA, Australia
e-mail: zdravko.baruchglaser@adelaide.edu.au

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or forests as well as those caused by fire or waterlogging taking place on a scale of a few kilometers (Araujo et al. 2021; Cassia-Silva et al. 2020; de Oliveira et al. 2021; Neves et al. 2017; Rossatto 2014) among the most recent.

This review of comparative ecology is a contribution to improve the understanding of the quantitative traits and ITVs responses to environmental demands as Neotropical savanna plants are poorly represented in databases (Kattge et al. 2020; Niinemets 2001; Reich et al. 1997; Siefert et al. 2015; Weigelt et al. 2020; Wright et al. 2004). Here, I merge and streamline previous studies to: (i) Characterize the Venezuelan seasonal savanna and its physical gradients; (ii) Portray the grass *Trachypogon spicatus* and the tree *Curatella americana* and establish the scale of their respective ITVs; (iii) Associate species ITVs to savannas physical gradients and; (iv) Discuss ITVs significance for savannas diversity, conservation, and management.

Neotropical savannas, which extend on 2.5 × 10^6 km^2, are warm and seasonally dry, unfertile, frequently burned, and dedicated to extensive cattle ranching (Huber 1987; Medina and Silva 1990; Sarmiento 1983; Solbrig 1996). In northern South America, the major continuous savannas are the Orinoco Llanos, which in Venezuela extend over 220,800 km^2, or 24.5% of the country (Huber and Alarcon 1988). The Andean and Coastal Mountains bound them to the west and north, and the Orinoco River to the south (Fig. 6.1). Physiognomically, the savannas are assembled by an herbaceous matrix of largely C_4 grasses and sedges with a variable proportion of trees (Fig. 6.2). Several sub-types of savanna, replace each other: from treeless grassland to wooded parkland and from drained to seasonally flooded savannas (Ramia 1967; Sarmiento 1983). Contingent on the connotation and area of savannas, they host a considerable floristic richness and diversity represented by either 555 (Ramia 1974) or > 3000 (Huber et al. 2006) Angiosperm species. However, compared to the much larger Brazilian savannas (Cerrados), the Llanos are species

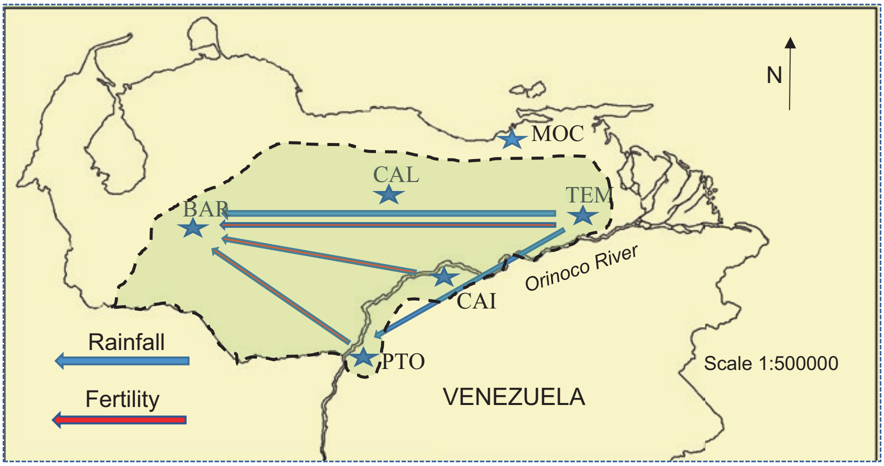

Fig. 6.1 Map of Venezuela displaying population locations and path of rainfall and fertility gradients. Green shaded area corresponds approximately to the Llanos region. Acronyms as in Table 6.1

Fig. 6.2 Vista of a typical savanna with a canopy of *Curatella americana* within a matrix of *Trachypogon spicatus*

poor (Sarmiento 1996). Functionally, nonflooded savannas display a relatively low primary productivity by unit area, attributed to unfertile soils, seasonal droughts, and frequent fires (Medina and Silva 1990).

In Venezuela, lowland savannas overlay recent alluvial and eolian plains resulting from the recess of an ancient inland sea. Most soils are Ultisols or Oxisols, which are acidic, oligotrophic, and low in organic matter (Schargel 2011). Climate is uniformly warm and rainfall is strongly seasonal (from May to November). Within this apparent environmental uniformity, local soil fertility and rainfall vary several fold. Across this extended Llanos landscape, with its significant level of environmental heterogeneity, a group of widespread emblematic plant species offer a first-rate opportunity to study interspecific trait variation of populations from woody and herbaceous species that replace each other across long climatic and edaphic gradients. Savannas are traditionally devoted to cattle ranching, with a mosaic of low-level agriculture in the more fertile sites. Recently, human pressure encouraged deforestation to grow crops or African pasture grasses. Spontaneous invasion of the African grass *Hyparrhenia rufa*, oil exploitation, and Caribbean pine plantations are displacing native savannas (Baruch 1996; Gómez et al. 2008; Ojasti 2001; Rodriguez et al. 2010; Williams and Baruch 2000). Currently and in the near future, Neotropical savannas will also be impacted by hotter and drier climate with increased atmospheric CO_2 (Hoffmann and Jackson 2002) which promotes woody encroachment (Archer et al. 2017) as reported from the CAL site (San Jose and Fariñas 1991; Silva et al. 2001).

From east to west, lowland savanna gradient extends continuously over more than 1000 km that broadens slightly to a narrow strip south of the Orinoco River. Undisturbed populations of both species are named after the nearest inhabited

Table 6.1 Climate and soil physico-chemistry of the research sites

		Rainfall	HI	Sand	Tot. N	P	CEC	O. M.	Fertility	WHC	WAI
Populations (acronyms)	Coordinates	(mm)		(%)	(%)	(ppm)	Meq/100g	(%)	Index	(%)	Index
BARINAS (BAR)	8° 38′ 40″ N 70° 16′ 32″ W	1582	0.79	64.1	0.21	3.33	8.2	4.13	300.0	6.74	106.6
CAICARA (CAI)	7° 35′ 21″ N 66° 08′ 23″ W	1511	0.67	65.1	0.04	1.83	4.5	0.98	150.7	3.61	54.5
CALABOZO (CAL)	8° 51′ 13″ N 67° 22′ 09″ W	1328	0.48	53.1	0.07	1.67	4.4	1.67	165.9	6.27	83.2
MOCHIMA (MOC)	10° 21′ 12″ N 64° 16′ 57″ W	466	0.21	76.5	0.08	0.67	6.6	2.38	135.6	6.57	30.6
PUERTO AYACUCHO (PTO)	5° 41′ 36″ N 67° 34′ 59″ W	2270	1.16	80.5	0.04	1.00	2.0	1.04	96.4	3.10	70.3
TEMBLADOR (TEM)	8°59′ 44″ N 62° 43′ 34″ W	1108	0.51	35.5	0.09	0.83	3.0	2.40	115.8	9.00	99.7

Climate data are from the Venezuelan Ministerio del Ambiente and soils were analyzed with standard laboratory methods

HI Humidity index (Evaporation/Rainfall). Fertility index = Relativized Σ N, P, K, *CEC* Cation exchange capacity, *WHC* Soil water holding capacity, *WAI* Water Availability Index = (Rainfall × ΔH_2O)/100 locality (Fig. 6.1 and Table 6.1). Except the MOC site, populations conform a continuum selected to encompass the range of variation in rainfall and fertility (Fig. 6.1). All sites are below 200 masl and their vegetation was surveyed in another study (Baruch 2005b). Within the savanna warm climate (mean 26.0–27.5 °C), rainfall varies almost fourfold between the wettest (PTO) and the driest (MOC) sites (Table 6.1). There is a gradient of increasing rainfall from east toward the west-southwest (Table 6.1 and Fig. 6.1). The rainy season starts first in the western Llanos at the Andes piedmont and progresses toward the east. The soils are sandy and low in organic matter influencing soil water holding capacity (WHC) that differs up to three times between sites (Table 6.1). By agricultural standards, soil N and P contents are low but large variation exists among sites and their pH is uniformly acidic (4.5–5.2). Soil nutrient content and fertility increase from east to west and it is highest in the piedmont BAR site (Table 6.1 and Fig. 6.1). Vegetation responds to climate and soil gradients with changes in species richness and diversity and with the density of the woody component (Baruch 2005b). As well as rainfall, water available for plants also depends on soil WHC which in turn is reliant on the proportion of sand in the profile. Therefore, the synthetic Water Availability Index [WAI = (Rainfall × WHC)/100] seems to be a better estimator of water availability. The grouping of relative water availability (WAI) and soil fertility (SF) settings generates four population groups: High WA and SF (BAR); High WA and low SF (PTO and CAI); Low WA and high SF (CAL and MOC); Low WA and SF (TEM). Across our study sites, the water availability and soil fertility gradients are not correspondent. For example, the PTO site, with the highest rainfall displays one of the lowest soil N and P contents and fertility due to sandier soils. The opposite example is MOC with the lowest rainfall but relatively fertile soils. In consequence, the effects that both gradients and their interaction have on ITVs are complex and challenging to infer.

6.2 The Emblematic Study Species

Trachypogon spicatus (L.f.)Kuntze, (formerly *T. plumosus* (Humb. and Bonpl. ex Willd.) Nees and henceforth Trachypogon) is a cespitose and perennial C_4 grass of medium height (1.0–1.5 m) dominant in many Neotropical savannas (Ramia 1967; Baruch 2005b; Huber et al. 2006) (Fig. 6.2). Its annual growth cycle starts rapidly with the rains in May, flowers in August- September, and seed dispersal occurs before the dry season (Ramirez 2002) when aerial biomass senesces but remains standing (Baruch and Fernandez 1993; Baruch et al. 1989). In Venezuela, populations of Trachypogon inhabit natural and anthropogenic lowland savannas, but extend to the Guyana plateau in the south-east and to intermediate elevations in the Andes and Coastal Mountains (Baruch 2005b). Although of limited nutritional quality, native savannas dominated by Trachypogon are essential for extensive cattle ranching.

Curatella americana L. (henceforth, Curatella) is an evergreen medium sized (3–5 m high), fire-tolerant tree with twisted and branched trunks, thick bark, and deep roots. Its sclerophyllous leaves last roughly 12 months (Foldats and Rutkis 1975; Goldstein et al. 1986; Medina and Francisco 1994; Sobrado 1996) (Fig. 6.2). Curatella flowers during the dry season, it is insect pollinated with seeds dispersed by frugivores (Ramirez 2002). Curatella is the dominant tree in Venezuelan non-flooded seasonal savannas (San Jose and Fariñas 1991; Silva et al. 2001). As the most abundant savanna tree, Curatella probably controls a large part of the energy, carbon, and water budgets of the savanna (San Jose and Garcia 1981).

By itself, the dominance and widespread distribution of both species in the savanna suggests substantial interpopulation variation.

6.3 Intrapopulation Variability and Responses to Physical Demands

6.3.1 Field Sampling, Trait Assessment, and Analysis

Six populations of both species, identified by the first three letters of their shared localities (Table 6.1) were sampled at the peak growth during the rainy season during several years for ecophysiological and reproductive traits. Except for MOC, which is a patch in the Coastal Mountains, the rest of the populations conform a continuum of savannas. Care was taken to collect enough samples and/or measurements to make meaningful statistically tests following the recommended methods (Pérez-Harguindeguy et al. 2013). In brief, field work started with gas exchange measurements with portable equipment followed by phenology and plant dimensions appraisal. Finally, soil and leaf samples, plant biomass, and seeds were collected and preserved for laboratory analysis. Soil physico-chemistry and water retention capacity were assessed by standard soil methods. Iconic traits such as specific leaf area (SLA), leaf N and P contents, and photosynthetic rate (Amax) (Funk et al. 2017) plus the ^{13}C isotopic signature, as a proxy to water use efficiency, were appraised in both species. Nitrogen use efficiency (NUE) was calculated from SLA, Amax, and leaf N content. For Trachypogon, above ground biomass, awn length of diaspore, seed mass, and germination percentage are also included in the study. Detailed methods are in the respective publications (Baruch 2005a, 2011; Baruch et al. 2004). The relationships between physical variables and population traits are represented by linear models and principal component analysis.

6.3.2 Species Traits

Trachypogon and Curatella differ in growth form, life history, and metabolism routes and diverge in most traits across the entire environmental gradient (Table 6.2). Trachypogon displays higher SLA and Amax and lower leaf N content that are associated to rapid use of resources caused by fast and high growth rate during the rainy season and prompt senescence afterwards. In contrast, Curatella traits display opposite features that are geared to a more conservative use of resources evidenced by much slower growth rate, with long-lived and denser leaves (Foldats and Rutkis 1975; Medina and Francisco 1994; Sobrado 1996). Therefore, they represent opposite ends of the "fast-slow" growth continuum of resource use strategies (Wright et al. 2004). Within each species, trait-trait links are typical of the leaf economics spectrum predictions (Wright et al. 2004) where SLA, Amax, and leaf nutrient content are interdependent and stronger in Trachypogon. The reproductive and ecophysiological traits of Trachypogon populations are also linked such as seed mass is positively linked to Amax and leaf N content. Also, diaspore awns are shorter in late flowering populations that also germinate poorly.

6.3.3 Species Response Across the Physical Gradients

Quantitative traits of both species differed significantly among populations (Table 6.2) and share similar responses to water availability and fertility gradients (Table 6.3). In both species, water availability, either as rainfall or HI, was consistently and positively correlated to SLA, NUE, and the ^{13}C isotopic signature (Table 6.3). Among the fertility variables, soil N was correlated to more Trachypogon traits whereas soil P displayed more links with Curatella traits (Table 6.3). Leaf N and P were positively associated to the respective soil nutrient contents. By itself, Amax was uncorrelated to physical gradients. However, as a component of the NUE variable, it was positively associated to water availability and soil P content (Table 6.3). The ^{13}C isotope signature of both species, as in lieu of water use efficiency, was correlated to water availability showing that in drier sites water is used more efficiently.

The response of Trachypogon reproductive traits to physical gradients mirrors those of the ecophysiological traits. They were correlated to water availability such as that in rainier sites flowering took place earlier in the season ($R^2 = 0.52$), diaspore awns were longer ($R^2 = 0.49$), and germination percentage was higher ($R^2 = 0.80$). On the other hand, seed mass was uncorrelated to physical variables. Soil fertility, mostly soil P content, was only correlated to aerial biomass ($R^2 = 0.44$). The positive correlation of awn length and water availability was unexpected as awn length is associated to depth of seed burial into the soil as an avoidance response to fire damage that is more frequent and severe in the driest sites (Baruch 2005b; Johnson and Baruch 2014).

Although the ecophysiological traits of Trachypogon and Curatella are plainly different, the relationship among populations of both species within the multivariate trait space is alike in regard to responses to physical demands. The populations from the extremes of water availability (MOC and PTO) and fertility gradients (BAR) occupy the ends of both ordination axes (Fig. 6.3). Populations from the intermediate physical ranges (CAL and TEM) are at midway positions along the ordination

Table 6.2 Traits of populations of study species

(a) Ecophysiological traits

	Trachypogon spicatus						*Curatella americana*					
	SLA	Leaf N	Leaf P	Amax	NUE		SLA	Leaf N	Leaf P	Amax	NUE	
Populations	(cm^2g^{-1})	(%)	(ppm)	($\mu mol\ m^{-2}\ s^{-1}$)	($\mu mol\ g^{-1}\ s^{-1}$)	^{13}C	($cm2g^{-1}$)	(%)	(ppm)	($\mu mol\ m^{-2}\ s^{-1}$)	($\mu mol\ g^{-1}\ s^{-1}$)	^{13}C
BARINAS	157.1	0.99	0.08	19.10	30.07	–12.1	103.3	1.22	0.08	14.70	12.45	–29.1
CAICARA	164.5	0.82	0.06	17.38	34.56	–12.5	99.0	0.91	0.08	11.19	12.18	–29.3
CALABOZO	148.9	0.95	0.06	22.18	34.49	–12.1	101.4	1.1	0.05	11.28	10.39	–28.0
MOCHIMA	144.6	0.96	0.07	21.77	32.81	–12.4	79.5	1.18	0.04	14.20	9.56	–27.9
P.AYACUCHO	166.9	0.92	0.05	20.36	36.73	–12.9	98.3	1.36	0.04	17.06	12.33	–29.0
TEMBLADOR	133.0	0.89	0.08	22.14	32.92	–12.6	80.9	1.24	0.07	14.88	9.71	–27.9

(b) Biomass and reproductive traits

	Trachypogon spicatus				
Populations	Aerial biomass	Days to flowering	Awn length	Seed mass	Germination
	(g)	[a]	(mm)	(mg)	(%)
BARINAS	143.2	225	56.1	0.74	41.6
CAICARA	103.3	270	49.3	0.61	44.8
CALABOZO	114.4	225	55.1	0.70	38.4
MOCHIMA	141.1	285	45.7	0.78	54.4
P.AYACUCHO	93.6	180	60.8	0.78	24.8
TEMBLADOR	112.1	210	58.9	0.74	40.0

Acronyms are: *SLA* specific leaf area, *Amax* photosynthesis rate, *NUE* nitrogen use efficiency, *13C* isotopic signature

[a] After January 1st

Table 6.3 Slope (β) and correlation coefficient between physical variables and ITVs of research species

Traits	Species	Physical variables					
		Rainfall	HI	Soil N	Soil P	Fertility	CEC
SLA	*T. spicatus*	**$\beta = 0.016$** **$R^2 = 0.53$**	**$\beta = 28.3$** **$R^2 = 0.52$**	–	**$\beta = 4.9$** **$R^2 = 0.14$**	–	–
	C. americana	**$\beta = 0.012$** **$R^2 = 0.51$**	**$\beta = 20.2$** **$R^2 = 0.37$**	–	**$\beta = 7.99$** **$R^2 = 0.54$**	–	–
Leaf N	*T. spicatus*	–	–	**$\beta = 0.63$** **$R^2 = 0.44$**	–	–	–
	C. americana	–	–	–	–	–	–
Leaf P	*T. spicatus*	–	–	**$\beta = 0.16$** **$R^2 = 0.61$**	–	–	–
	C. americana	–	–	–	**$\beta = 0.01$** **$R^2 = 0.43$**	**$\beta = 0.01$** **$R^2 = 0.31$**	–
Amax	*T. spicatus*	–	–	–	–	–	–
	C. americana	–	–	–	–	–	–
NUE	*T. spicatus*	–	**$\beta = 2.70$** **$R^2 = 0.15$**	–	–	–	–
	C. americana	**$\beta = 0.001$** **$R^2 = 0.67$**	**$\beta = 3.51$** **$R^2 = 0.69$**	–	**$\beta = 0.88$** **$R^2 = 0.40$**	–	–
^{13}C	*T. spicatus*	**$\beta = 0.001$** **$R^2 = 0.13$**	**$\beta = 0.44$** **$R^2 = 0.21$**	**$\beta = -3.2$** **$R^2 = 0.41$**	–	**$\beta = -0.01$** **$R^2 = 0.62$**	**$\beta = -0.10$** **$R^2 = 0.57$**
	C. americana	**$\beta = 0.001$** **$R^2 = 0.49$**	**$\beta = 1.48$** **$R^2 = 0.52$**	–	–	–	–

Acronyms as in Table 6.1

axes whereas CAI, from a site with high water availability but low fertility is set in a peripheral spot. The ordination of Trachypogon populations within the reproductive trait space displays a similar population arrangement except that soil fertility plays a lesser role (Fig. 6.3).

6.4 Recapitulation

Substantive ITV, and the adjustment of functional traits, through structural, biochemical, and physiological adaptations and trade-offs, support and explain the presence and dominance of our savanna emblematic species across long and steep gradients of physical demands. This type of variation is to be expected in populations inhabiting a set of diverse climatic and edaphic environments, like the Venezuelan savannas. Furthermore, the same abilities and capacities may determine species persistence and success in a rapidly changing and unstable planet. At the community level, dominant plant species control vegetation composition, diversity, and interactions. Functionally, plant traits of dominant species regulate energy and mass transfers as well as nutrient cycling of the ecosystems (Chapin 2004; Funk

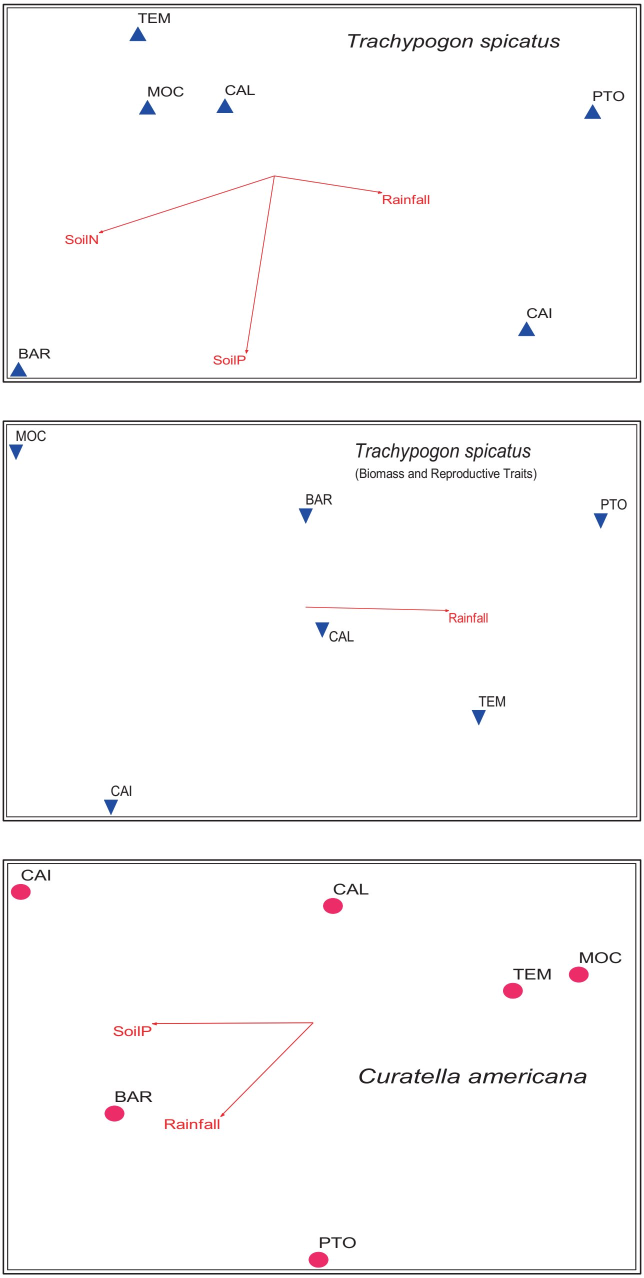

Fig. 6.3 PCA ordination of populations of study species in trait space. Variances explained for X and Y axes: *T. spicatus:* 52.2% and 25.4%; *C. americana*: 50.4% and 33.3%. *T. spicatus* Biomass and reproductive traits: 64.4% and 20.7%. Population acronyms as in Table 6.1

et al. 2017; Westerband et al. 2021). In addition to water and soil fertility limitations, the incidence of frequent fires is another stressor in the Llanos. The responses include rapid regrowth from the basal meristems and increased inflorescence production in Trachypogon (Baruch and Bilbao 1999) and thick cortex protecting the trunk in Curatella (Foldats and Rutkis 1975).

Despite their contrasting life forms, photosynthetic metabolism and with differently scaled ITVs, Trachypogon and Curatella respond similarly to physical demands although at different rates. Trachypogon-high SLA, Amax, and low leaf N content are geared to fast growth and opportunistic responses to resource availability. In contrast, Curatella, with low SLA and Amax, long-lived and high N leaves, grows slowly and uses resources more conservatively. These contrasting traits and responses frame Trachypogon at the fast end and Curatella at the slow end of the leaf economics spectrum (Wright et al. 2004). Genetic variability in Trachypogon differs among populations and their associations across the Llanos are similar to those of its ecophysiological traits (Baruch et al. 2004). Genetic and phenotypic levels of variation could promote selection events and the generation of local ecotypes. The wealth of ITV and genetic variation in Trachypogon represent valuable tools for selection of material to revegetate or restore physically damaged or polluted savanna sites in Venezuela (Rosales et al. 1997).

A plot-based survey of a large portion of Venezuelan savannas found 293 species in the herbaceous stratum and 25% of them inhabit all Venezuelan savanna types (Baruch 2005b). If the patterns of ITVs in most of these species are similar to those shown by Trachypogon and Curatella, then the phenotypic richness of the Llanos should be significantly higher than the relatively low species richness signed for them compared to the much larger Brazilian Cerrados (Sarmiento 1996).

Consequent from the above facts and discussion is the co-existence of Trachypogon and Curatella under the limited offer of savanna resources. Answers to queries such as “Which ITVs are essential for co-existence?” and “Are ITV roles similar under drier or wetter conditions?” are challenging and worth of research.

6.5 Conclusions

- The physical gradients of water availability and soil fertility in the Venezuelan Llanos are long and steep.
- The joint presence and dominance of two species of contrasting growth forms along such physical gradients is unusual.
- The absolute values of all ecophysiological traits are higher in Trachypogon than in Curatella.
- The populations of both species differ significantly across all ecophysiological traits analyzed.
- The populations of both species respond likewise to demands of the physical gradients.

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