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Potential growth and drought tolerance of eight desert grasses: lack of a trade-off?

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Abstract Eight perennial C-4 grasses from the Jornada del Muerto Basin in southern New Mexico show five-fold differences in relative growth rates under well-watered conditions (RGR_{max}). In a controlled environment, we tested the hypothesis that there is an inverse relationship (trade-off) between RGR_{max} and the capacity of these species to tolerate drought. We examined both physiological (gas exchange) and morphological (biomass allocation, leaf properties) determinants of growth for these eight species under three steady-state drought treatments (none=control, moderate, and severe). When well watered, the grasses exhibited a large interspecific variation in growth, which was reflected in order-of-magnitude biomass differences after 5 weeks. The species had similar gas-exchange characteristics, but differed in all the measured allocation and morphological characteristics, namely tiller mass and number, root:shoot ratio, dry-matter content, and specific leaf area (SLA). Drought affected tillering, morphology, and allocation, and reduced growth by 50 and 68% (moderate and severe drought, respectively) compared to the well-watered controls. With the exception of SLA, none of these variables showed a significant species-by-treatment interaction. We calculated three indices of drought tolerance, defined as the ratio in final biomass between all the possible “dry”/“wet” treatment pairs: severe/moderate, moderate/control, and severe/control. We found no significant correlation between these drought tolerance indices, on the one hand, and three indices of growth potential (greenhouse RGR_{max} , final biomass in the control treatment, and final:initial biomass ratio in controls), on the other. Based on these controlled-environment

results, we hypothesize that the commonly reported correlation between plant growth potential and drought tolerance in the field may in some cases be explained by differential effects of plants on soil-water content rather than by differences in species responses to drought.

Key words Chihuahuan Desert · C-4 photosynthesis · Water stress · Relative growth rate · Xerophytism

Introduction

A basic tenet of plant ecophysiology is the trade-off between the capacity of a genotype to grow when resources are abundant, and its capacity to tolerate resource shortages (Chapin 1980; Huston 1994; Bazzaz 1996). For arid environments, this paradigm predicts a negative interspecific association between xerophytism (the capacity to tolerate drought) and growth potential (e.g., the relative growth rate under well-watered conditions, RGR_{max}). Such a trade-off is depicted in Fig. 1, where the growth of a species with a high RGR_{max} (species *M*) steadily declines with increasing drought intensity (decreasing soil moisture), eventually dropping below that of a species with a low RGR_{max} (species *X*). If there was no trade-off, the growth of a high- RGR_{max} species would remain higher than that of a low- RGR_{max} species, regardless of drought intensity (species *F* and *S*, respectively, Fig. 1). Although both the trade-off and no trade-off responses may occur among different genotypes of the same crop species (Turner 1986), to our knowledge the trade-off hypothesis has not been tested among species.

Plants with a high growth potential have a suite of morpho-physiological traits that, in principle, should result in poor performance under intense drought conditions. For example, leaves of high- RGR_{max} species have a high SLA (specific leaf area, area:mass ratio), are usually thin and non-lignified (Van Arendonk and Poorter 1994), and have a low dry matter content (low “tissue

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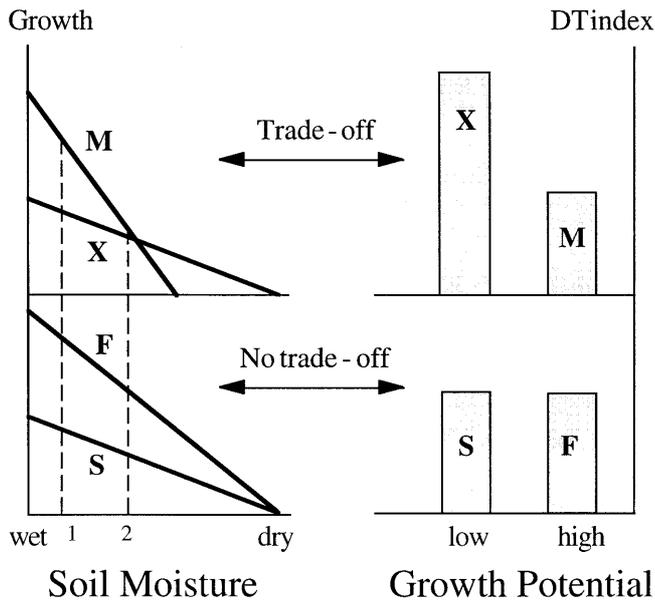


Fig. 1 Illustration of the trade-off hypothesis and a null (no trade-off) hypothesis for species differing in potential growth rate. For a given decrease in soil moisture (increasing drought intensity), the trade-off hypothesis predicts a proportionally smaller growth decline in species *X* than for species *M*; the null hypothesis predicts proportionally similar decreases in growth for both species *F* and *S*. These differences may be quantified with a drought-tolerance index: $DT = G''_{dry} / G''_{wet}$, where G is, e.g., biomass or growth, measured under both “dry” and “wet” soil moisture conditions (points 2 and 1, respectively)

density”: Poorter 1990; Ryser and Lambers 1995). In addition, leaf properties associated with high photosynthetic rates – such as a low resistance to gas diffusion – unavoidably result in high water loss and low water-use efficiency (Orians and Solbrig 1977; Turner and Kramer 1980; Cowan 1986). A high investment in leaf biomass is a prerequisite for a high RGR_{max} (Lambers et al. 1990) but is incompatible with a high investment in root

biomass, which may be critical for drought resistance (Orians and Solbrig 1977; Lambers et al. 1998).

Although general trends in plant architecture, leaf morphology, and gas-exchange characteristics along regional precipitation gradients are consistent with the trade-off hypothesis (Schulze and Hall 1982; Givnish 1986; Tilman 1988), there is limited direct evidence that such trends are attributable to ecophysiological trade-offs. In part, progress has been hindered by three specific experimental constraints: (1) plant effects on soil-water availability are difficult to distinguish from plant responses to soil-water availability (Goldberg 1990): the larger the plant in relation to rooting volume, the larger this effect; (2) when measuring plant response to increasing drought over time, it is difficult to distinguish drought-induced changes in plant morphology and physiology from size-dependent (ontogenetic) changes; and (3) comparisons between plant functional groups are confounded because of differences in, e.g., phenology, temperature optima, or growth habit.

In this paper, we report an experimental test of the trade-off hypothesis specifically designed to overcome these constraints. In a preliminary study, we found that eight perennial C-4 grasses from the northern Chihuahuan Desert (Jornada del Muerto Basin, New Mexico, USA) have substantial differences in growth potential under well-watered conditions, despite presumably belonging to the same functional group (Table 1). Sustained growth at these rates would result in large differences in the length of time required for a species to double its biomass (<1 week for *Eragrostis lehmanniana* to 4 weeks for *Scleropogon brevifolius*). The trade-off hypothesis predicts that species with such a wide range of RGR_{max} values will have considerable differences in drought tolerance; alternatively, the null hypothesis (no trade-off) predicts that the reduction in growth for a given increase in drought intensity will be proportionally similar for all species (Fig. 1, right panels). To test this,

Table 1 Taxonomy, physiology, and potential growth of eight perennial Chihuahuan Desert grasses. Relative growth rates under non-drought conditions (RGR_{max}) were estimated from greenhouse-grown seedlings (100–300 mg dry mass) during January–February 1996 in Durham, North Carolina (34°N). RGR was calculated as the slope of the ln-transformed total dry mass changes

over time ($n \geq 20$), and its coefficient of variation (CV) calculated through pairing by sequential size order (Causton and Venus 1981). Photoperiod was supplemented to 12 h; temperature ranged between 18°C during the night and 37°C during the day; plants were watered daily and fertilized 3 times a week with a half-strength Hoagland solution

SPECIES	Subfamily ^a	Photosynthesis sub-type (all C4) ^b	RGR_{max} (g g ⁻¹ day ⁻¹)	CV (no units)
<i>Eragrostis lehmanniana</i> Nees	Chloridoideae	NAD-me	0.158	0.06
<i>Sporobolus flexuosus</i> (Thurb.) Rydb.	Chloridoideae	NAD-me, PCK ^c	0.137	0.05
<i>Muhlenbergia porteri</i> Scribn. ex Beal	Chloridoideae	NAD-me, PCK ^c	0.119	0.04
<i>Panicum obtusum</i> Kunth	Panicoidaeae	NADP-me	0.104	0.10
<i>Aristida purpurea</i> Nutt.	Arundinoideae	NADP-me	0.100	0.28
<i>Bouteloua eriopoda</i> (Torr.) Torr.	Chloridoideae	PCK ^c	0.072	0.17
<i>Hilaria mutica</i> (Buckl.) Benth.	Chloridoideae	PCK ^c	0.067	0.14
<i>Scleropogon brevifolius</i> Phil.	Chloridoideae	Unknown	0.029	0.20

^a From Watson L, Dallwitz MJ (1999) Grass genera of the world: descriptions, illustrations, identification, and information retrieval (<http://biodiversity.bio.uno.edu/delta/grass/>)

^b *NAD-me* NAD-malic enzyme, *NADP-me* NADP-malic enzyme, *PCK* PEP carboxykinase; data from Buchmann et al. (1996), Gutiérrez et al. (1974), Hattersley (1987), Schulze et al. (1996)

^c Type is known for other specie(s) in the same genus

we examined the growth of these eight perennial grasses in response to simulated drought in a controlled environment. To elucidate mechanisms of response, we assessed both physiological (gas exchange) and morphological (biomass allocation, leaf properties) determinants of growth.

Materials and methods

The experiment was performed in a growth chamber at the Duke University Phytotron, with plants grown from seed collected at the Jornada Long Term Ecological Research (LTER) site, New Mexico (site information at: <http://jornada.nmsu.edu>). All eight species are perennial C-4 grasses and are native to the area, with the exception of *Eragrostis lehmanniana* which was introduced from South Africa (Table 1). Plants were grown free of competition, with individuals kept in separate pots, and subjected to one of three drought intensities.

Drought was imposed using a modification of the method proposed by Haan and Barfield (1971), as described by Snow and Tingey (1985), which overcomes the first two experimental constraints of plant-soil water interactions described in the Introduction. The third constraint was overcome by our choice of eight species belonging to the same family and having the same perennial growth habit and photosynthetic pathway. We set open-bottom pots over a column of a uniform porous medium with a water table at different depths (Fig. 2). This procedure ensures a uniform and repeatable water potential in the pots (Wookey et al. 1991; Saulescu et al. 1995). Consequently, drought intensity becomes independent of plant size. Plants have access to an unlimited volume of water that, nonetheless, is always delivered at a predetermined water potential. The soil is kept constantly half-wet; hence, equilibrium moisture levels are reached in a few minutes – even starting with completely dry soil (B.D. Bovard and R.J. Fernández, unpublished work). The same effect could have been attained by the use of osmotica (such as poly-ethylene-glycol) but at the risk of undesirable side-effects (Kramer and Boyer 1996; Fan and Blake 1997).

The pots (height: 15 cm, volume: 0.7 l) were sand-filled and fitted at their base with a fine nylon cloth (20- μm "Nitex" mesh) to allow air and nutrient-solution exchange, yet prevent root passage. Twenty-four sets of eight pots (one pot per species, one plant per pot) were placed into 45-cm-tall, 20-l plastic containers housing a 35-cm-tall column of commercial Styrofoam (no. 0140; Smithers-Oasis; Kent, Ohio, USA) (Fig. 2). The foam had been repeatedly rinsed with nutrient solution as recommended by the manufacturer. The 20-l containers were randomly assigned to three drought treatments, with eight replications each. Based on a pilot experiment, we chose water levels so as to obtain three drought intensities (none, moderate, and severe), all compatible with survival but sufficient to reduce final growth by more than 50%. These stress levels were attained by partially filling the containers until the nutrient solution was either 5 cm (control; no drought), 15 cm (moderate drought), or 25 cm (severe drought) below the base of the pots (dimension z , Fig. 2). The nutrient solution (one-quarter-strength modified Hoagland's solution) was checked daily, and replenished as needed to maintain it within 1 cm of the target level.

The pots were placed in a growth chamber with temperatures of 33/20°C (day/night), which are within 2°C of the average maximum and minimum temperatures for the northern Chihuahuan Desert area in July, the first month of the typical 3-month rainy season (Conley et al. 1992). Photoperiod was set to 14 h; light intensity was 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$, combining fluorescent tubes with halogen lamps. Chamber vapour pressure deficit (VPD) was not controlled, but during the daytime remained close to 2.0 kPa. We did not assume that these conditions mimicked field conditions exactly, but rather that they were as close as feasible – except for drought – to the optimal environmental values for C-4 grasses

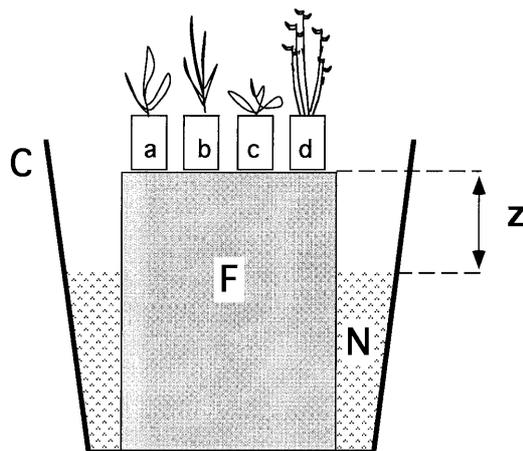


Fig. 2 Diagram of the drought-imposing method, based on Snow and Tingey (1985) [C 20-l plastic container, F hygroscopic foam, N nutrient solution, a,b,c,d 0.7-l, sand-filled pots with a nylon mesh at the bottom (4 more pots were at the back), z water-table depth (different for different treatments, see Table 2)]

(Ehleringer et al. 1997; Sage and Monson 1999). The experiment lasted 5 weeks, which was enough for these grasses to reach their mature size, and for some even the flowering stage (see Results).

The treatments were imposed when the plants had started to develop secondary roots, which occurred by the time they had a mean total dry mass of 80 mg (estimated from regressions on total leaf length per plant). No size differences were detectable within each species among treatments at that time ($P=0.40$). However, species did differ in initial size ($P<0.05$), with *E. lehmanniana* and *M. porteri* seedlings (average dry mass 160 mg) larger than the rest (55 mg). Moisture content in the growing medium was measured twice during the experiment using a reflectometry sensor (CS615, Campbell Scientific, Logan, Utah, USA) inserted for a few seconds in each pot to take a reading; each of these was then converted to soil gravimetric content. Leaf gas exchange was measured during the morning hours of the last week (1–4 h after the lights were turned on) with a closed photosynthesis system (LI6200, Li-Cor Inc., Lincoln, Neb., USA). Cuvette VPD during these measurements was similar to the daytime VPD in the chamber. Instantaneous water-use efficiency (WUE) was calculated as the ratio of net leaf CO_2 uptake (on an area basis) and stomatal conductance (Tissue et al. 1997). Pre-dawn leaf water potential (ψ_L) was assessed on the 2 days immediately preceding the final harvest using a pressure bomb (Soilmoisture Equipment, Santa Barbara, Calif., USA).

At the end of the 5-week period, all pots were wetted to the level of the controls, allowing them to equilibrate overnight, in order to rehydrate the plants before taking leaf-blade samples to determine specific leaf area (SLA, leaf area per unit dry mass) and tissue density (dry mass per unit fresh mass) from fully expanded, non-senescent leaves. In this way, we avoided leaf-rolling errors in the determination of leaf area, and made our fresh-mass determinations at a similar (high) leaf hydration status. Each plant was then separated into roots, blades, and stems (including true stems, leaf sheaths, and in some cases inflorescences), to determine their dry mass. The number of total and flowering tillers was also recorded.

Data were analyzed as an ANCOVA, with a generalized linear model (GLM; Velleman 1995), which included drought treatment and species as the main factors. Initial biomass was included as a covariate in the GLM to control for initial plant size differences when analyzing responses in final biomass, biomass per tiller, and number of tillers. Final total biomass was included as a covariate when considering the contribution of different plant parts to total growth (allometric analyses). Transformations were conducted on biomass (log-transformed, both as variables and covariates) and tiller numbers (square root).

We explored the trade-off between potential growth and drought tolerance in two ways. First, we inspected the species-by-treatment interaction in the GLM for final total biomass and its components. Second, we calculated the Pearson product-moment correlation coefficient (r_s) between indices of potential growth and drought tolerance. There were three indices of potential growth: (1) greenhouse RGR_{max} from Table 1; (2) final control biomass; and (3) the ratio of final control biomass:initial control biomass. The indices of drought tolerance (DT, Fig. 1) were also three, in this case defined as the ratio in final control biomass (G) between all of the dry/wet treatment pairs, i.e., $DT = G_{dry}/G_{wet}$, where dry/wet corresponds to severe/moderate, moderate/control, and severe/control treatment pairs. DTs range from 1 for very tolerant species (similar growth under dry and wet conditions) to 0 for extremely intolerant ones (or for extreme drought intensities). The statistical power of these tests was assessed using guidelines described in Cohen (1988), and his tables for F and r_s ($\alpha=0.05$). For the F -test, effect size (ES) was determined based on the observed ratio between the standard deviation of the interaction term among treatment-species combinations (“cells”) and the “within-cell” mean standard deviation. For r_s , ES was calculated from the slope the relationship would have had if the trade-off hypothesis had been true. Implicit in these two analyses is the idea that a trade-off can be detected through a proportionally different response of the species to the same drought treatment. The opera-

tional advantage of this definition is that a crossover does not have to be observed to detect a trade-off, which means that drought does not have to be close to lethal to test the hypothesis.

Results

We were successful in producing consistent differences in soil moisture among the three treatments for the entire duration of the experiment ($P<0.0001$) (Table 2), with no differences among species ($P=0.58$). These soil moisture results were mirrored by pre-dawn leaf water potential values ($P<0.0001$ for treatment; $P=0.44$ for species effect; Table 2).

Drought levels were non-lethal but still had a marked effect on growth. Final biomass was reduced by an average of 50% (moderate drought) to 68% (severe drought) compared with the well-watered controls (Fig. 3). After factoring out initial size differences, we found that all species were affected by drought to a similar degree (non-significant interaction, Table 3). Drought effects on

Table 2 Effect of the experimental drought treatments upon soil-moisture content in the pots ($n=64$), and pre-dawn leaf-water potential (ψ_L ; $n=32$). Data are means, with SE in parentheses. Water-table depth refers to the dimension z in Fig. 2

Treatment	Water-table depth (cm)	Soil moisture (w/w)				Pre-dawn ψ_L (MPa)	
		Week 2		Week 5		Week 5	
Control (No drought)	5	0.085	(0.004)	0.073	(0.004)	-0.311	(0.084)
Moderate drought	15	0.044	(0.003)	0.043	(0.003)	-0.557	(0.092)
Severe drought	25	0.026	(0.004)	0.015	(0.002)	-0.800	(0.086)

Table 3 Generalized linear model results comparing the effects of experimental drought (3 levels), species (8 levels) and their interaction, on grass biomass, morphology and physiology ($n=8$). Biomass data, both as variables and covariates, were log-transformed; tiller numbers were square-rooted. Sequential (type 1) sum of squares used in the first eight analyses; partial (type 3) in the rest. Units as in Figs. 3,4,5

Variable	Covariate	Drought effect		Species effect		Drought×Species interaction	
		F	P	F	F	F	P
<i>Final biomass</i>							
Total	Initial biomass	4183.0	0.010	48.6	<0.001	2.2	0.160
Aboveground	Initial biomass	8408.0	0.007	57.6	<0.001	2.3	0.150
Belowground	Initial biomass	150.2	0.037	22.4	<0.001	3.0	0.089
<i>Tillering</i>							
Number of tillers	Initial biomass	158.0	0.050	14.2	0.001	3.2	0.075
Biomass per tiller	Initial biomass	10.2	0.193	58.6	<0.001	2.1	0.169
<i>Allocation-allometry</i>							
Blade biomass	Total final biomass	23.9	0.129	20.7	<0.001	1.3	0.371
Stem biomass	Total final biomass	0.1	0.855	16.5	<0.001	1.7	0.255
Root biomass	Total final biomass	15.1	0.160	10.2	0.003	2.0	0.190
<i>Leaf morphology</i>							
Specific leaf area	None	58.6	<0.001	21.8	<0.001	4.7	<0.001
Dry-matter content	None	85.2	<0.001	11.9	<0.001	1.6	0.154
<i>Gas exchange</i>							
Photosynthesis (mass)	None	44.9	<0.001	10.0	<0.001	2.7	0.014
Photosynthesis (area)	None	5.1	0.027	1.2	0.309	0.8	0.588
Stomatal conductance	None	2.1	0.148	0.7	0.672	0.5	0.826
Water-use efficiency	None	0.3	0.597	1.2	0.335	0.5	0.816

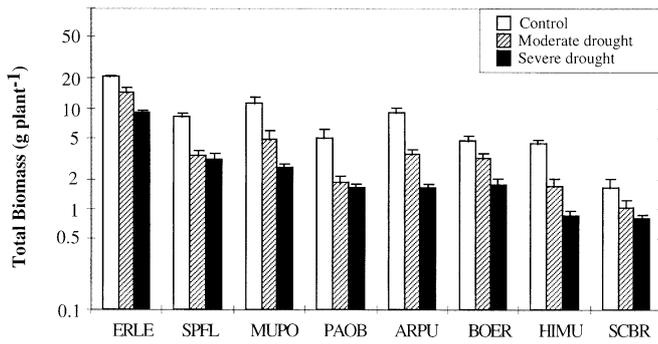


Fig. 3 Effect of drought on plant biomass after 5 weeks in a growth chamber (means+SE, $n=8$). *Four-letter codes* refer to the species in Table 1, which are shown here in decreasing order of RGR_{max} . Treatments as in Table 2. Note the *logarithmic scale*

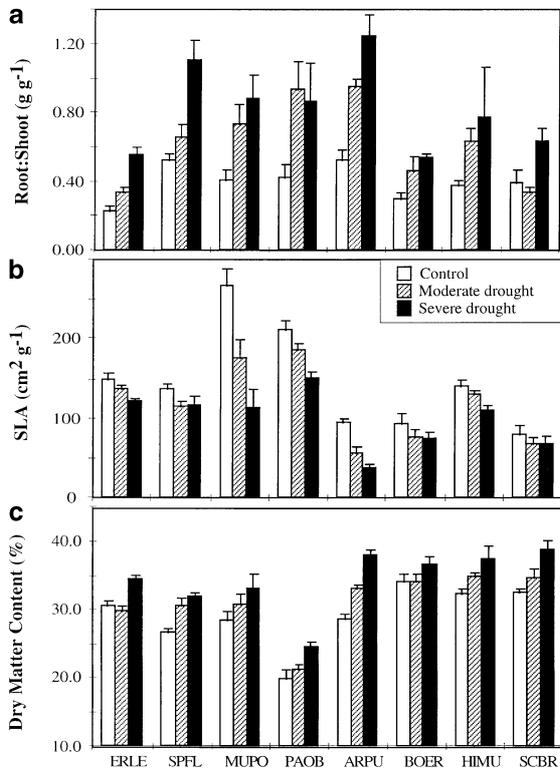


Fig. 4a-c Effect of drought on allocation and leaf morphology after 5 weeks in a growth chamber (means+SE; $n=8$). *Four-letter codes* refer to the species in Table 1, which are shown here in decreasing order of RGR_{max} . Treatments as in Table 2. Note the *magnified scale for c*

biomass were more pronounced above- than below-ground (Table 3), causing an increase in the root:shoot ratio (Fig. 4a). Allometric analyses show that, within species, the proportion of biomass in roots, stems and blades was the result of the effect of drought on total biomass (“ontogenetic drift”), rather than a direct response to the treatments (Table 3). Drought affected the number of tillers per plant, but not biomass per tiller. Specific leaf area (SLA) was markedly reduced by drought Fig. 4b. The parallel increase in dry-matter con-

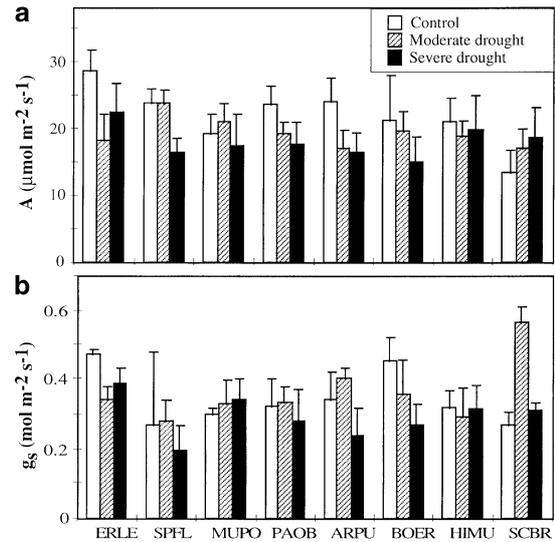


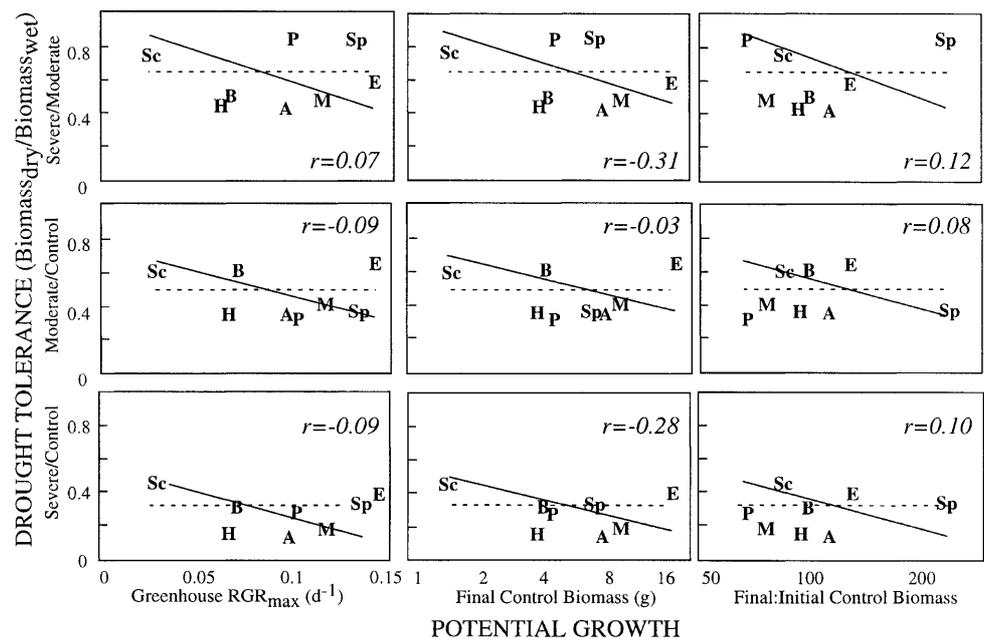
Fig. 5a,b Effect of drought on morning gas-exchange parameters in the final week of a 5-week growth chamber experiment (means+SE; $n\geq 5$). *Four-letter codes* refer to the species in Table 1, which are shown here in decreasing order of RGR_{max} . Treatments as in Table 2

tent (Fig. 4c) indicates that leaf thickness changes were relatively unimportant; therefore, SLA reduction had to have involved cell-size and/or dry-matter composition changes (cf. Lambers et al. 1990). SLA was the only variable that showed a species-specific response to drought (interaction in Table 3): *Muhlenbergia porteri* had a larger reduction ($P<0.001$), and *Scleropogon brevifolius* a smaller reduction ($P=0.04$) than the other species (Fig. 4b).

Unlike morphology and growth, gas-exchange characteristics tended to be similar among species, and not very responsive to drought. Photosynthetic rate per unit area (A), stomatal conductance (g_s), and WUE showed neither a species nor a species-by-drought effect (Fig. 5, Table 3). The significant interaction effect for photosynthesis per unit of leaf mass (the product of SLA and photosynthesis per unit leaf area) mirrored differences in SLA (Table 3); again, *M. porteri* was more affected and *S. brevifolius* less affected than the rest of the species ($P<0.01$ in both cases). Photosynthetic rate per unit leaf area was in general reduced by drought (Fig. 5a, Table 3). Stomatal conductance (Fig. 5b) and water-use efficiency (Table 3) were not affected. The contrast between these moderate or null gas-exchange responses, compared to strong biomass responses, may be partially explained by our choice of morning measurements for the former; afternoon measurements could have produced different results.

Flowering responses were extremely variable. *Hilaria mutica*, *Panicum obtusum*, and *Scleropogon brevifolius* had not flowered by the end of the experiment. With one exception, the rest of the species had uneven flowering across replicates, with no apparent treatment effects ($P>0.05$; data not shown). The exception was *Eragrostis lehmanniana*, for which the number of reproductive

Fig. 6 Comparison between the observed drought tolerance of 8 Chihuahuan Desert grasses and predictions from the trade-off and the null hypothesis in Fig. 1. Letter codes refer to the species in Table 1. X axes represent three different indexes of potential growth. Y axes represent drought tolerance (DT), which was calculated as the ratio of final biomass between the 3 indicated dry/wet treatment pairs. The trade-off (solid) line assigns the maximum observed value of DT to the species with less growth potential, and the minimum observed value of DT to the species with most growth potential; the null-hypothesis (dashed) line represents the average drought tolerance. All nine correlations (Spearman's r) are statistically non-significant ($P > 0.10$). See Table 4



tillers (present in all the individuals at harvest) was less reduced by drought than the total number of tillers, resulting in an increased proportion of reproductive tillers with drought: 0.41 in controls, 0.65 in moderately droughted, and 0.73 in severely droughted plants ($P=0.03$).

If there were a trade-off between RGR_{max} and the capacity of a species to tolerate drought, we would expect to find: (1) a significant species-by-drought interaction for total biomass, or at least for some of its components; and (2) significant negative correlations between drought tolerance and growth potential. As described above, the species-by-drought interaction was not significant (Table 3). To examine relationships between drought tolerance and growth potential, we performed nine separate comparisons, taking all the possible pairs between indices of growth potential, on the one hand, and indices of drought tolerance, on the other (summarized in Fig. 6; see Methods). None of the correlation coefficients was statistically significant. However, the reason why the ANCOVA and the correlation test both failed to reject the null hypothesis was not a lack of statistical power: The probability of correctly rejecting the null hypothesis was 94% for the species-by-treatment interaction in the ANCOVA, and close to 80% for most of the r_s comparisons (Table 4).

Discussion

Under well-watered conditions, the eight Chihuahuan Desert grasses exhibited a large variation in growth, which was reflected in very large differences in final biomass between the fastest and the slowest growers (Fig. 3). The members of this perennial, C-4 functional

Table 4 Power analysis for the analyses in Fig. 6. Numbers represent $1-\beta$, i.e., the probability of correctly rejecting the null hypothesis (dashed lines in Fig. 6), under the assumption of a true alternative (trade-off) hypothesis as illustrated by the solid lines in Fig. 6

Drought tolerance index	Greenhouse RGR_{max}	Final biomass controls	Final/initial biomass
Severe/Moderate	0.786	0.722	0.797
Moderate/Control	0.754	0.693	0.765
Severe/Control	0.891	0.819	0.904

group did not differ in gas-exchange characteristics but did differ in all the measured allocation and morphological characteristics (Table 3). According to the trade-off hypothesis (Chapin 1980; Huston 1994; Bazzaz 1996), a set of species with such a wide range of morphologies and RGR_{max} should also have large differences in drought tolerance, with the potentially fast-growing (high- RGR_{max}) species being least tolerant to low soil moisture. In stark contrast to this prediction, we found a similar proportional reduction in growth for all species when subjected to similar drought treatments. In other words, we failed to reject the null (no-trade-off) hypothesis in Fig. 1. As with any such “negative” (lack-of-effect) result, an important question is (Peters 1991): had a true effect existed, were our experimental protocol and analyses capable of detecting it? We are confident that they were, because of two partially related considerations: the intensity of the imposed drought, and the statistical power of our analyses.

The low-moisture regimes, while not as intense as the most extreme values observed in the field (cf. Moorhead et al. 1989; Kemp et al. 1997), were applied throughout the 5 weeks of the experiment, starting when the plants

were seedlings and maintained until they were close to maturity. There are two reasons to suggest that these treatments were intense enough to detect any interspecific differences in xerophytism had they existed. First, the severe-drought treatment reduced final biomass, on average, to one-third of that of the controls (Fig. 6); secondly, leaf water potential (ψ_L) values in Table 2 represent only the minimum stress that these plants experienced during the day. For a drought treatment similar to ours (water table at 20 cm) in a cooler, less illuminated environment, Snow and Tingey (1985) reported a dawn-to-midday drop in sunflower ψ_L of c. 0.4 MPa. From this, we infer that daytime ψ_L during our experiment was ≤ 1 MPa even in the moderate-drought treatment. Was this degree of stress too mild for these desert plants, thus explaining the general lack of gas-exchange responses to our treatments? This is, of course, possible: in the field, some of these grasses maintain a fairly high leaf conductance while noon ψ_L is as low as -13 MPa (Senock et al. 1994). However, considering the strong biomass responses observed, we are inclined to attribute the lack of an observed response to our gas-exchange measurement protocol. As noted earlier, the timing of these measurements may partially explain the relatively moderate reductions in photosynthesis (and no effect on stomatal conductance) compared with the much greater relative effects on total biomass and root-to-shoot ratio. These morphological indicators of drought are integrative over the course of the experiment, whereas the leaf gas exchange measurements are instantaneous, and treatment effects may have been much larger had the observations been done in the afternoon.

Statistical power analyses of biomass responses showed a high probability, relative to the customary value of 80%, of rejecting the null hypothesis had a trade-off existed. In the ANCOVA comparisons, even a modest species-by-treatment interaction could have been detected thanks to the low intra-treatment variability for each species (error bars in Fig. 3). In the r_s comparisons, those using the severe-drought versus control DT index were especially powerful, between 82 and 90% (Table 4).

Therefore, we conclude that all the grasses were affected by water shortage to a similar degree. Somewhat surprisingly, this conclusion also applies to the two species of known NADP malic enzyme physiology (*Panicum obtusum* and *Aristida purpurea*; Table 1). Regional studies have shown that the abundance of this particular metabolic subtype decreases with decreasing precipitation (Vogel et al. 1986; Hattersley 1992; Schulze et al. 1996), and from this perspective we would have expected *P. obtusum* and *A. purpurea* to be more drought prone than the rest. Still, regardless of their photosynthetic physiology, all eight species apparently responded to drought via the same mechanisms, with morphological (e.g., SLA) and allocation (e.g., root:shoot) adjustments that reduce water loss – and are likely to increase field survival – at the cost of reduced growth.

Ours is not the first study to report similar drought tolerance in C-4 grasses differing in growth potential. At

least two greenhouse studies have compared the drought response of a native, relatively slow-growing species vs. a coexisting, exotic fast grower. From data in these papers, we computed values for DT of 0.46 and 0.50 for a pair of Venezuelan species (Simoes and Baruch 1991; their Fig. 1a, unclipped plants) and of 0.31 and 0.33 for a pair of Hawaiian species (Fig. 4 in Williams and Black 1994). In each case, the lower DT corresponded to the slow-growing species of the pair, and the small intra-study differences likely indicate the absence of any differential drought sensitivities. Field studies, on the other hand, have often reported considerable differences in drought resistance, sometimes even for species that behave similarly under more controlled conditions. For example, for the Venezuelan species discussed above, Baruch and Fernández (1993) concluded that the native grass was more drought-tolerant than the invading one. Also, in contrast with our growth-chamber results, Senock et al. (1994) found *Hilaria mutica* to be more drought tolerant than *Bouteloua eriopoda*. In a longer-term study, Herbel et al. (1972) observed that after a series of very dry years in the Jornada Basin, *Sporobolus* spp. and *Aristida* spp. (genera with a relatively high RGR_{max} ; Table 1) had high mortality, whereas *Scleropogon brevifolius* and *H. mutica* (slow growers) had almost no mortality.

The most parsimonious way of reconciling these apparently conflicting results from field and controlled-environment studies is to consider the distinction between plant responses to, and plant effects on, soil resources (Goldberg 1990). Field studies, unlike controlled environment experiments, are usually unable to separate these effects. We argue that interspecific differences observed in the field are not necessarily a manifestation of different physiological tolerance to drought, and that not even differences in potential transpiration rates per unit leaf area have to be invoked. Green-grass biomass is one of the most dynamic attributes of semiarid landscapes (Peters et al. 1993). It may be that, following a precipitation event, rhizosphere soil water potential drops faster in patches dominated by fast-growing species than in patches dominated by slow-growing ones, owing mainly to a difference in green biomass and leaf area between the patches (greater in patches dominated by fast-growing species as a result of fast growth). This would result in the observed interspecific differences in growth and mortality. Acknowledging the differences between water and other soil resources, the slow growth of some of these grasses under non-limiting water conditions resembles what was first proposed as an adaptation to cope with nutrient shortages (Chapin 1980; Poorter 1990): that a low potential growth rate would be advantageous under stress because it reduces resource requirements.

The functional importance of species diversity is a topic of current debate (e.g., De Leo and Levin 1997), and the question of redundancy within functional groups has been raised. Warm-season perennial grasses have been traditionally considered as an homogeneous functional group

(Kemp 1983; Reynolds et al. 1997), but we have shown that those of the Chihuahuan Desert exhibit a diverse resource-use capacity mostly explained by their diverse morphology. In this sense, the species differed more than expected. On the other hand, we found these grasses to be very similar in their drought tolerance. Based on these two findings, we propose that a classification into mesic versus xeric species (labels frequently used to describe species such as *M* and *X* in Fig. 1) does not adequately portray the functional diversity of this group, which can be better described in terms of (relatively) fast- versus slow-growing species (*F* and *S*, Fig. 1).

There seems to be a consensus that the xerophytism versus growth potential trade-off is necessary to explain plant species diversity in arid and semiarid communities (Orians and Solbrig 1977; Huston 1994). Our controlled-environment results do not support the commonly assumed negative correlation between growth potential and drought tolerance. Obviously, a more complete, quantitative understanding of this problem must entail field measurements, and include factors such as the effects of losses to evaporation and competitors, dissimilar rooting patterns, and resources other than water. Still, if our results are confirmed for other plant groups, then the coexistence of species of contrasting RGR_{max} in water-limited environments will require an explanation more focused on the spatial and temporal variability in resource supply than on physiological or allocation trade-offs.

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