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D.G. Williams · R.A. Black

Drought response of a native and introduced Hawaiian grass

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Abstract The alien grass, *Pennisetum setaceum*, dominates many of the lowland arid regions that once supported native *Heteropogon contortus* grassland on the island of Hawaii. Response to drought in a glasshouse was compared between these C₄ grasses to test if success as an invader is related to drought tolerance or plasticity for traits that confer drought tolerance. *Pennisetum* produced 51% more total biomass, allocated 49% more biomass to leaves, and had higher net photosynthetic rates (P_n) on a leaf area basis than *Heteropogon*. Plants of both species under drought produced less total biomass and increased their allocation to roots compared to well-watered plants, but there was no difference between the two species in the magnitude of these responses. The decline in P_n with decreasing leaf water potential (Ψ_l) was greater for *Pennisetum* compared to *Heteropogon*. Plasticity in the response of P_n to Ψ_l , osmotic potentials, and the water potentials at turgor loss in response to drought were not different between the two species. Stomata were more responsive to Δw in *Heteropogon* than in *Pennisetum* and for well-watered plants compared to droughted plants. Plasticity for the stomatal response to Δw , however, was not different between the species. There was no evidence that the alien, *Pennisetum*, had greater plasticity for traits related to drought tolerance compared to the native, *Heteropogon*. Higher P_n and greater biomass allocation to leaves resulted in greater growth for *Pennisetum* compared to *Heteropogon* and may explain the success of *Pennisetum* as an invader of lowland arid zones on Hawaii.

Key words Plant invasion · Drought acclimation
Hawaii · *Heteropogon contortus* · *Pennisetum setaceum*

D. G. Williams (✉)¹ · R. A. Black
Department of Botany, Washington State University,
Pullman, WA 99164, USA

Present address:

¹ Department of Biology, University of Utah,
Salt Lake City, UT 84112, USA

Introduction

Explanations for invasive ability in plants often stress the importance of genetic (Barrett and Richardson 1986; Gray 1986) and life history (Baker 1974; Mack and Pyke 1983; Groves 1986) characteristics. Ecophysiological characteristics that confer success on an invading plant, by contrast, have received less attention (Bazzaz 1986; Newsome and Noble 1986). Generalizations about the physiological attributes of invasive plants, such as those proposed by Bazzaz (1979, 1986) for early successional species, may be difficult to formulate because of the broad taxonomic diversity of invading plants that collectively display different growth forms, different environmental requirements, and different ecological roles in the communities they invade (Parsons 1972; Baker 1986; Heywood 1989; Mack 1989).

An invading species, by definition, is one that reproduces and spreads in a community in which it has not occurred before (Mack 1985). Baker (1974) argues that successful invading plants will have a high level of phenotypic plasticity allowing exploitation of resources in a new environment that may bear little resemblance to the home range. For example, in arid environments characterized by infrequent or unpredictable precipitation, a plant invader should have physiological plasticity to allow survival when water is limiting and rapid growth when water is abundant. Community dominance by the invader in this case may stem from the invader's greater physiological plasticity compared to natives. Addressing the importance of specific physiological traits as they relate to the invasive ability of plants, therefore, may be inadequate unless one also considers the plasticity of these traits.

Comparisons between ecologically similar native and alien taxa offer a preliminary assessment of those attributes that confer invasive ability. *Pennisetum setaceum* (Forssk.) Chiov, a perennial C₄ grass, was introduced to the Hawaiian islands early in this century and is now the dominant plant on barren lava flows, in coastal dry grasslands, and in coastal, montane and

subalpine dry shrublands on the arid (leeward) side of the island of Hawaii (Wagner et al. 1990; D.G. Williams, personal observation). While *Pennisetum* has proliferated on Hawaii, many native plants in the arid coastal zones have undergone a severe reduction in range and abundance (Cuddihy 1989) principally because of development by people and grazing. For example, *Heteropogon contortus* (L.) P. Beauv., a native perennial grass, was once abundant in the arid coastal zones of Hawaii, but is now dominant only on dry lowland cliffs and in scattered remnants in coastal areas (Degener and Degener 1968; Wagner et al. 1990).

In this study we compared drought responses of *Heteropogon* and *Pennisetum* to evaluate their drought tolerance and to test if *Pennisetum*, the alien, has greater plasticity for characters that confer drought tolerance compared to the native, *Heteropogon*.

Materials and methods

Seeds of *Heteropogon contortus* were collected in March, 1991 from a population at Puuhonua 'o' Honaunau National Historical Park on the leeward side of Hawaii. The population was deliberately established in 1969, and the community in which it occurs is maintained to provide an example of a native *Heteropogon* grassland (Wagner et al. 1990; K. Domingo, personal communication). *Heteropogon contortus* is widespread throughout the tropics and subtropics and is a valuable pasture grass in many arid regions (Hitchcock 1950, Tothill 1968). The race of *Heteropogon contortus* on Hawaii, however, is cytogenetically and morphologically distinct and may be endemic to the islands (Degener and Degener 1968, Wagner et al. 1990). Seeds of *Pennisetum setaceum* were collected from greenhouse representatives of populations from 20, 960, and 1995 m elevation on Hawaii that we have used in related studies (Williams 1992; Williams and Black 1993). Seeds were sown in flats in a greenhouse at Washington State University, Pullman, WA, United States (740 m elevation) on 6 August 1991. After germination and growth for 2 weeks, 32 uniformly-sized seedlings with one primary tiller and three to five leaves, from each population (96 plants from *Pennisetum* and 32 from *Heteropogon*), were transplanted individually to 5.4 l peat pots filled with a mixture of crushed basalt and weathered granitic sand. Plants were grown at a constant 30°C on benches in a greenhouse under natural lighting, but received supplemental lighting from high pressure metal halide lamps. Average high temperatures in summer in coastal areas on leeward Hawaii are about 33°C (Atlas of Hawaii, 1983; Williams and Black 1993). Photosynthetic photon flux density at mid-day in the glasshouse was $1241 \pm 19 \mu\text{mol photons m}^{-2}\text{s}^{-1}$ on clear days.

All plants were watered daily with 500 ml water. After 4 weeks, plants from each species were randomly assigned to two watering treatments: (1) a well-watered treatment (W), where plants were watered daily with 500 ml water, and (2) a drought treatment (D), where plants were watered only every 6–8 days. A dilute fertilizer solution (Peter's 20-20-20; 100 ppm N and micronutrients) was used for all watering. The locations of pots on the greenhouse benches were randomized every 2 weeks.

Water relations

After the drought treatment had gone through five cycles, six plants from each species and watering treatment combination were randomly selected for pressure-volume analysis. One young, fully expanded blade (leaf) from each plant was used for analysis following rehydration overnight in a dark cabinet. Pressure-volume methods followed those of Robichaux (1984), where the

weight and water potential were measured periodically with a pressure chamber (PMS Instruments Co., Corvallis, Oregon) as the leaves dried on the laboratory bench. Non-linear regression models described by Schulte and Hinckley (1985) were used to estimate osmotic potential at full turgor ($\Psi_{\pi 100}$), osmotic potential at turgor loss ($\Psi_{\pi 0}$), relative water content at turgor loss (RWC₀), bulk modulus of elasticity (E), and symplastic water fraction (SWF).

Gas exchange

After six drought cycles, three to five plants from each species and watering treatment combination were randomly selected for measurement of the response of gas exchange to leaf-to-air vapor pressure difference (Δw) with a compensating, null-balance gas exchange system (Bingham et al. 1980) and an infrared gas analyzer (225-MK3, ADC Ltd., Herts, England). Plants were kept well-watered over the 2-day measurement period. Net photosynthesis (P_n), stomatal conductance (g_s), and the ratio of internal to ambient CO₂ concentration (c_i/c_a) were measured on six or seven young, fully expanded leaves placed in the cuvette. Measurements on each plant were made sequentially at Δw ranging from approximately 1.0 to 3.5 kPa at 0.5 kPa intervals. Leaf temperature and photosynthetic photon flux density (PPFD) were maintained at 30°C and 1800 $\mu\text{mol quanta m}^{-2}\text{s}^{-1}$, respectively. Carbon dioxide concentration of air in the cuvette was maintained at 350 $\mu\text{l l}^{-1}$.

Gas exchange responses to decreasing soil and plant water potentials were evaluated at the end of the seventh drought cycle. Four days into the normal drying cycle for droughted plants, daily watering was terminated for well-watered plants. Gas exchange was measured on plants for both treatments three days later with a portable photosynthesis system (LCA-3, ADC Ltd., Herts, England). Soil water was depleted more rapidly in well-watered plants because of their greater leaf area and measurements were taken when approximately one-third of the plants from each treatment showed visible signs of water stress (e.g., leaf curling and fading color). Carbon dioxide concentration of the air in the chamber during these differential measurements averaged $349.5 \pm 1.4 \mu\text{l l}^{-1}$, while leaf temperature averaged $33.8 \pm 0.1^\circ\text{C}$. PPFD was maintained near 1000 $\mu\text{mol quanta m}^{-2}\text{s}^{-1}$, and Δw averaged 3.75 ± 0.05 kPa during measurements. All measurements were made on one day between 0930 and 1630 hours. One fully expanded leaf was placed in the cuvette and gas exchange measurements were recorded two minutes later. Water potential (Ψ_l) of an adjacent leaf from the same plant was measured with a pressure chamber concurrently with the gas exchange measurement. Specific leaf area (SLA) was determined from these samples after assessing leaf area and weighing oven dried samples to the nearest 0.1 mg.

Growth and carbon allocation

All plants were harvested after 14 weeks of growth, i.e., 8 weeks after the initiation of watering treatments. The number of living and dead tillers were counted, and plants were separated into root, culm (culm + sheath), and leaf fractions, and weighed after drying at 65°C for at least 48 h. The biomass allocated to roots or leaves was calculated as the fraction of root or leaf biomass to total plant biomass.

Statistical analysis

Data were analyzed using the GLM Procedure in the SAS statistical package (Freund et al. 1986). The species by watering treatment interaction was interpreted as a difference in plasticity between the two grasses (population variance for *Pennisetum* was factored out in the analyses). Water relations parameters were analyzed as a factorial experiment (species by watering treatment) in a completely randomized design. Gas exchange responses to Δw or Ψ_l were compared using regression models with species and

Table 1 Means, SEs (in parentheses), and significance of sources of variation for leaf water relations parameters in *Pennisetum* and *Heteropogon* subjected to drought and well-watered treatments in the greenhouse. Four to five plants were measured for each species and treatment combination. Osmotic potential at full turgor ($\Psi_{\pi 100}$), osmotic potential at turgor loss ($\Psi_{\pi 0}$), relative water content at turgor loss (RWC_0), bulk modulus of elasticity (E), and symplastic water fraction (SWF) were estimated from pressure-volume analysis 5 weeks after the start of watering treatments

	$\Psi_{\pi 100}$ (MPa)	$\Psi_{\pi 0}$ (MPa)	RWC_0 (%)	E (MPa)	SWF (%)
<i>Heteropogon</i>					
Well-watered	-1.32 (0.07)	-1.56 (0.12)	88.23 (2.06)	25.25 (8.59)	82.25 (4.76)
Drought	-1.51 (0.06)	-1.90 (0.08)	85.68 (1.78)	20.50 (2.86)	65.04 (4.86)
<i>Pennisetum</i>					
Well-watered	-1.02 (0.04)	-1.11 (0.05)	93.36 (1.13)	18.95 (3.51)	69.06 (5.49)
Drought	-1.23 (0.06)	-1.41 (0.10)	91.17 (2.60)	23.67 (6.96)	56.80 (5.58)
Sources of variation					
Species	***	***	*	ns	ns
Watering treatment	**	**	ns	ns	*
Species \times watering treatment	ns	ns	ns	ns	ns

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

watering treatment defined as class variables and Δw and Ψ_1 defined as continuous variables in SAS. This is equivalent to an analysis of covariance where a significant interaction between Δw or Ψ_1 and a class variable was interpreted as a difference in the regression coefficient (slope) of the response among class variables (Freund et al. 1986). Morphological data were analyzed as a factorial experiment (species by watering treatment). Data were transformed as necessary to comply with assumptions of analysis of variance.

Results

We found no differences among the three *Pennisetum* populations for their response to drought in this study. Furthermore, transplant and common environment studies (Williams 1992; Williams and Black 1993) and enzyme electrophoresis (D.G. Williams, unpublished observations) have provided data supporting the lack of genetic differentiation among these three populations. Data for the three *Pennisetum* populations, therefore, were pooled for comparison with *Heteropogon*.

Water relations

Heteropogon and *Pennisetum* responded to the drought by lowering osmotic potentials 0.2–0.3 MPa (Table 1). *Heteropogon* had significantly lower $\Psi_{\pi 100}$ and $\Psi_{\pi 0}$ (0.3–0.5 MPa lower, respectively) than did *Pennisetum* (Table 1). There was no difference in the amount of reduction of $\Psi_{\pi 100}$ and $\Psi_{\pi 0}$ between the two species (Table 1, ANOVA, $\Psi_{\pi 100}$: $F = 0.02$, $P = 0.88$, $\Psi_{\pi 0}$: $F = 0.08$, $P = 0.78$). Bulk modulus of elasticity (E) was similar between the two species, and did not change in response to drought (Table 1, ANOVA, $F = 0.74$, $P = 0.40$). Relative water content at turgor loss (RWC_0) was lower in *Heteropogon* than in *Pennisetum* (Table 1), but was not affected by watering treatment (Table 1, ANOVA, $F = 1.56$, $P = 0.23$). There was no significant difference in the symplastic water fraction (SWF) between the two species (Table 1, ANOVA, $F = 3.95$, $P = 0.07$). SWF was reduced by the drought treatment but the species by

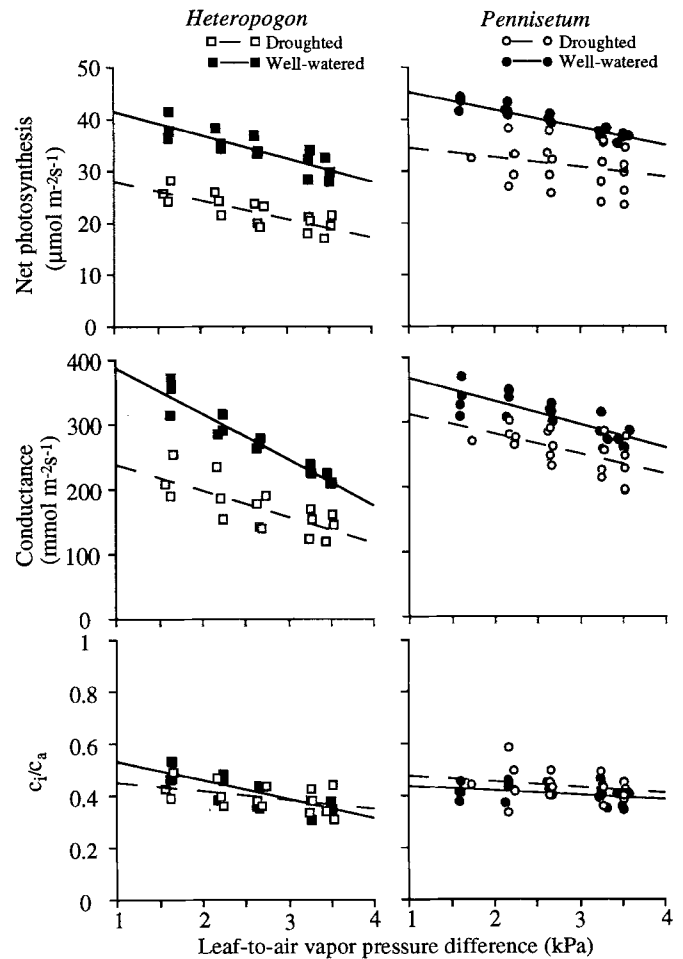
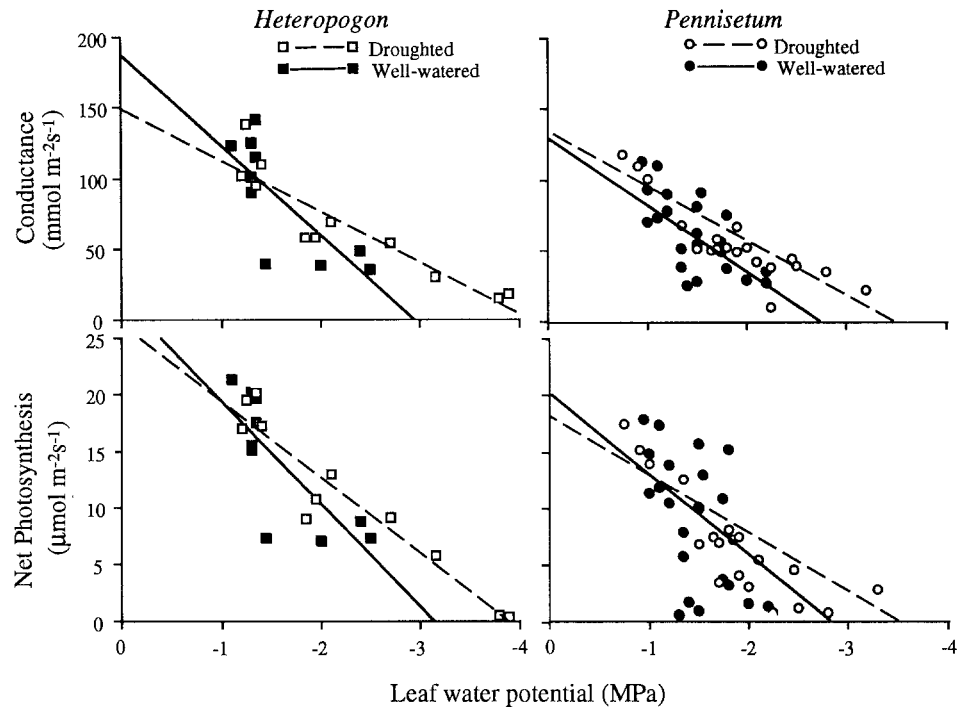


Fig. 1 The response of stomatal conductance, net photosynthesis, and the ratio of internal to ambient CO_2 concentration (c_i/c_a) to leaf-to-air vapor pressure difference (VPD) in *Heteropogon* and *Pennisetum* subjected to drought (open symbols) and well-watered (closed symbols) treatments. Symbols are individual measurements from plants measured over the range of VPDs. Three to four plants were measured for each species and treatment combination

Fig. 2 The response of stomatal conductance and net photosynthesis to leaf xylem water potential in *Heteropogon* and *Pennisetum* subjected to drought (open symbols) and well-watered (closed symbols) treatments. Each symbol represents the measurement on one plant 4 days after watering for both treatments



treatment interaction was not significant (Table 1, ANOVA, $F=0.21$, $P=0.65$).

Gas exchange

Stomatal conductance (g_s) and net photosynthesis (P_n) were higher in *Pennisetum* than in *Heteropogon* (ANCOVA, g_s : $F=142.7$, $P<0.0001$, P_n : $F=151.8$, $P<0.0001$). Well-watered plants of both species also exhibited higher g_s and P_n than did plants that had experienced drought (Fig. 1, ANCOVA, g_s : $F=204.6$, $P<0.0001$, P_n : $F=328.1$, $P<0.0001$). Both species responded to increasing leaf-to-air vapor pressure difference (Δw) by reducing g_s and consequently P_n (Fig. 1, ANCOVA, g_s : $F=113.9$, $P<0.0001$, P_n : $F=47.0$, $P<0.0001$). Stomatal conductance responded more to Δw in *Heteropogon* than in *Pennisetum* (ANCOVA, $F=4.1$, $P<0.05$) and in well-watered plants compared to droughted plants (Fig. 1; ANCOVA, $F=5.5$, $P<0.05$). Watering treatments, however, did not differentially affect the two species' stomatal response to Δw as indicated by a lack of a Δw by species by watering treatment interaction (ANCOVA, $F=1.6$, $P=0.21$). Conversely, there were no differences in the response of P_n to Δw between the two species or watering treatments (ANCOVA, Δw by species: $F=1.2$, $P=0.29$, Δw by treatment: $F=1.9$, $P=0.17$). c_i/c_a decreased at higher Δw (Fig. 1, ANCOVA, $F=25.4$, $P<0.0001$). The response of c_i/c_a to Δw , however, was not different between the two species (ANCOVA, $F=2.47$, $P=0.12$) or watering treatments (ANCOVA, $F=0.95$, $P=0.33$) and the watering treatments did not differentially alter the two species' responses to Δw for both P_n (ANCOVA, $F=1.02$, $P=0.32$) and c_i/c_a (ANCOVA, $F=3.19$, $P=0.08$).

The relationship between leaf water potential (Ψ_1) and g_s or P_n varied between the two species and watering treatments. With decreasing Ψ_1 the decline in g_s and P_n was greater for *Pennisetum* than for *Heteropogon* (Fig. 2, g_s : ANCOVA, $F=12.8$, $P<0.001$, P_n : ANCOVA, $F=5.07$, $P<0.05$). For *Pennisetum*, photosynthetic rates were near zero at Ψ_1 of -2.5 to -3.5 MPa, while P_n in *Heteropogon* reached zero at -3 to -4 MPa. Watering treatments also influenced the response of g_s and P_n to decreasing Ψ_1 . Plants exposed to drought had higher g_s and P_n at low Ψ_1 compared to well-watered plants. The magnitude of stomatal adjustment to watering treatment, however, was not different between the two species (ANCOVA, $F=0.01$, $P=0.93$). The slope of the regression of P_n on g_s , the intrinsic water-use efficiency, was greater for *Pennisetum* than for *Heteropogon* (Fig. 3, ANCOVA, $F=7.3$, $P<0.01$). Watering treatments did not significantly influence the slope of the relationship between g_s and P_n (ANCOVA, $F=0.40$, $P=0.53$) and *Heteropogon* and *Pennisetum* did not respond differentially to the watering treatments (Fig. 3, ANCOVA, $F=2.93$, $P=0.09$). Specific leaf area (SLA) was significantly higher in *Heteropogon* than in *Pennisetum* (ANOVA, $P<0.05$) and the response of SLA to drought was different between the two species (ANOVA, $P<0.05$). Specific leaf area was 276.79 ± 11.11 and 301.66 ± 8.78 $\text{cm}^2 \text{g}^{-1}$ in well-watered and droughted plants of *Heteropogon* and 261.93 ± 8.59 and 233.74 ± 5.08 $\text{cm}^2 \text{g}^{-1}$ in *Pennisetum*.

Growth and biomass allocation

Total biomass at harvest was lower in droughted plants of *Heteropogon* and *Pennisetum*, but *Pennisetum* pro-

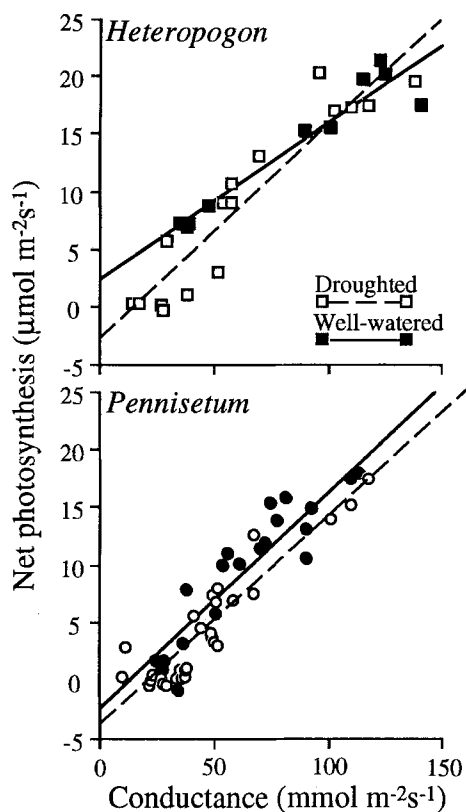


Fig. 3 The relationship between stomatal conductance and net photosynthesis in *Heteropogon* and *Pennisetum* subjected to drought (open symbols) and well-watered (closed symbols) treatments. Data are the same as for Fig 2

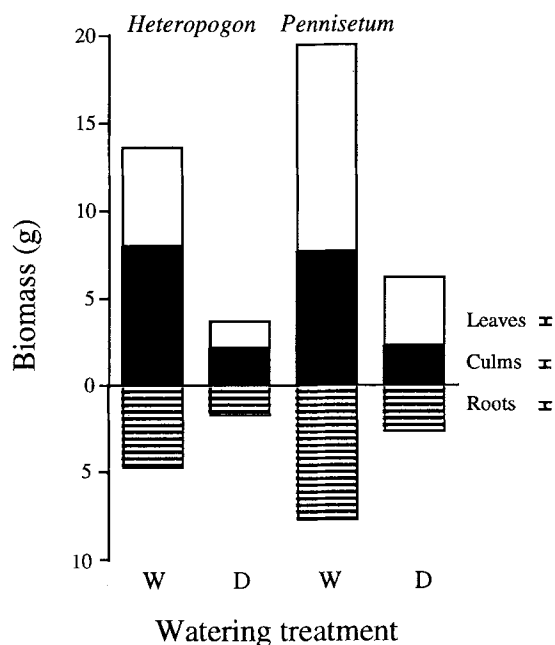


Fig. 4 The distribution of biomass among roots, culms, and leaves at harvest in *Heteropogon* and *Pennisetum* subjected to drought (D) and well-watered (W) treatments. For each treatment for *Pennisetum* 48 plants were harvested and 16 plants were harvested for each treatment for *Heteropogon*

Table 2 Means, SEs (in parentheses), and significance of sources of variation for morphological characters in *Pennisetum* and *Heteropogon* subjected to droughted and well-watered treatments in the glasshouse at harvest

	Total number of tillers	Number of live tillers	Total biomass (g)	Root fraction (g g^{-1})	Leaf fraction (g g^{-1})
<i>Heteropogon</i>					
Well-watered	69.22 (7.09)	69.22 (7.09)	18.37 (1.75)	0.26 (0.01)	0.31 (0.01)
Droughted	18.75 (1.85)	16.58 (2.18)	5.42 (0.55)	0.32 (0.02)	0.28 (0.01)
<i>Pennisetum</i>					
Well-watered	107.97 (2.93)	107.97 (2.93)	27.24 (0.79)	0.28 (0.01)	0.44 (0.01)
Droughted	32.49 (1.17)	28.45 (1.33)	8.78 (0.44)	0.30 (0.01)	0.44 (0.01)
Sources of variation					
Species	***	**	***	ns	***
Watering treatment	***	***	***	*	ns
Species \times watering treatment	ns	ns	ns	ns	ns

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

duced more biomass than *Heteropogon* regardless of watering treatment (48 and 62% more in the well-watered and drought treatments, respectively) (Fig. 4, Table 2). The effect of watering treatment on biomass was similar for the two species (species by watering treatment interaction, ANOVA, $F = 0.34$, $P = 0.56$). Greater biomass in *Pennisetum* was accompanied by greater biomass allocation to leaves compared to that in *Heteropogon*, but biomass allocation to roots was not different between the two species (Table 2, ANOVA, $F = 0.31$, $P = 0.58$). *Heteropogon* and *Pennisetum* responded to drought by increasing biomass allocation to roots (23% and 7% increase, respectively), but there was no difference in the magnitude of response between the two species (Table 2, ANOVA, $F = 0.12$, $P = 0.73$). Both the total number of tillers and the number of living tillers at harvest for both species were significantly greater in plants from the well-watered treatment compared to plants from the drought treatment (Table 2). *Pennisetum* produced 55 and 68% more total tillers than *Heteropogon* in the well-watered and drought treatments, respectively (Table 2), but the species by treatment interaction was not significant (ANOVA, $F = 0.97$, $P = 0.33$).

Discussion

High photosynthetic capacity and high allocation to leaves may be common attributes of aggressive alien grasses in arid environments. Maximum photosynthetic rates were higher and biomass allocation to leaves was greater in *Pennisetum* compared to *Heteropogon*, re-

ardless of the watering treatment. These characteristics allowed *Pennisetum* to accumulate more biomass than *Heteropogon* even under drought in our glasshouse study. Similarly, Baruch et al. (1985) found that invasive C_4 grasses in the tropical savannas of Venezuela have higher photosynthetic rates, allocate more biomass to leaves and have higher growth rates than the native grass, *Trachypogon plumosus*. Even the greater productivity of the alien C_3 grass *Ammophila arenaria* compared to the native C_3 *Elymus mollis* of dunes along the Pacific coast of North America apparently relates to the alien's greater allocation of biomass to leaves (Pavlik 1983).

Accumulating more biomass is positively correlated with competitive ability and fitness in plants (Harper 1977). Greater vegetative growth when water is plentiful as well as under recurring drought may allow *Pennisetum* to maintain dominance in the arid zones on Hawaii. In addition, high photosynthetic rates and high allocation to leaves may be advantageous in these environments where disturbance by fire and grazing is frequent (Cuddihy 1989) and the availability of water is infrequent and seasonal (Atlas of Hawaii 1983; Williams and Black 1993). Although our experiment was conducted under lower light levels than those that *Heteropogon* and *Pennisetum* experience in the field (1250 $\mu\text{mol photons m}^{-2}\text{s}^{-1}$ compared to about 2200 $\mu\text{mol photons m}^{-2}\text{s}^{-1}$ for field sites on Hawaii), the relative photosynthetic and growth rate differences between the two grasses under natural conditions on Hawaii is likely similar.

Pennisetum and *Heteropogon* had contrasting patterns of stomatal response to drought. While *Pennisetum* had a stronger stomatal response to decreased leaf water potential than *Heteropogon*, *Heteropogon* exhibited greater stomatal response to Δw than did *Pennisetum*. These contrasting responses may reflect different, but not mutually exclusive processes that limit water loss and protect tissues from rapid dehydration during drought. The capacity to limit transpiration by closing stomata under conditions of high evaporative demand apparently is not related to invader status for *Pennisetum* and *Heteropogon*. Stomatal conductance declined 20–35% in *Heteropogon* but only 15% in *Pennisetum* over a range of Δw . Furthermore, prior exposure to soil drought reduced the stomatal response to Δw for both grasses. Reductions in P_n with increasing Δw were apparently due to stomatal limitations and not reductions in photosynthetic capacity since c_i/c_a declined concomitantly with g_s . Stomatal response to Δw may minimize water loss and tissue dehydration under extreme evaporative demand (Hall et al. 1976) and variation among species in stomatal response to Δw has been found in other studies (Jarvis 1980; Losch and Tenhunen 1981; Turner et al. 1984). Our results show that the native, *Heteropogon*, has a greater capacity to respond to leaf-to-air vapor pressure difference than does the alien, *Pennisetum*. Other comparisons between introduced and native C_4 grasses (Baruch et al. 1985), however, have shown no such differences.

The capacity for stomatal adjustment was not an important characteristic distinguishing *Heteropogon* and *Pennisetum*. Both species showed stomatal adjustment to water deficits; the magnitude of stomatal adjustment, however, did not vary between the two species. Maintenance of photosynthesis at low Ψ_1 is an important characteristic of drought tolerant plants (Ludlow et al. 1983; 1985) and *Heteropogon* maintained higher photosynthetic rates at lower Ψ_1 than did *Pennisetum*. However, stomatal closure in response to decreasing Ψ_1 may protect leaf tissues from damage by limiting water loss (Schulze and Hall 1982) and *Pennisetum* exhibited more rapid stomatal closure in response to decreasing Ψ_1 than did *Heteropogon*.

Stomatal adjustment, or the change in the response of stomata to decreases in Ψ_1 , is likely a consequence of tissue osmotic adjustment to maintain turgor at low Ψ_1 (Turner and Jones 1980). *Pennisetum* and *Heteropogon* showed some ability to adjust osmotically, however, the degree of this adjustment was small compared to that for other C_4 grasses (Wilson et al. 1980; Ludlow et al. 1985). Solute accumulation in the guard cells and/or maintenance of turgor in the bulk leaf tissue, or both, could result in stomatal adjustment to water deficits (Pierce and Raschke 1980; Ludlow et al. 1985). The small degree of osmotic adjustment observed in this experiment may have been a consequence of the artificial conditions under which plants were grown, which may have limited full drought acclimation (Ludlow et al. 1985).

Heteropogon and *Pennisetum* maintained positive carbon gain at Ψ_1 values well below our estimate of the point of turgor loss in the bulk tissue. Overnight tissue rehydration, which is often performed prior to pressure-volume analysis, has been shown to increase estimates of osmotic potential (Evans et al. 1990) and may have influenced our measurements of $\Psi_{\pi 100}$ and $\Psi_{\pi 0}$. Alternatively, guard cells may maintain turgor at lower Ψ_1 than the bulk tissue or stomatal closure may be responsive to signals other than leaf water potential, such as symplast volume (Meinzer et al. 1990; Saliendra and Meinzer 1991) or root water potential (Gollen et al. 1985, Turner 1986, Chaves 1990). In addition, gas exchange was measured 2 weeks (and two drought cycles) after analysis of pressure-volume relationships; plants may have further acclimated to growing conditions which could have led to discrepancies between Ψ_{π} and gas exchange responses to Ψ_1 .

The alien, *Pennisetum*, showed no greater capacity for physiological acclimation or plasticity in response to drought than the native, *Heteropogon*. Only a few studies have compared physiological plasticity of alien and native plants. Caldwell et al. (1981) found that the alien tussok grass *Agropyron desertorum* had greater flexibility of carbon allocation following simulated grazing than did the native *A. spicatum*, which partially accounted for the alien's greater grazing tolerance. Black et al. (1994), working with the same two *Agropyron* species found that the alien *A. desertorum* also possesses greater flexi-

bility for root growth and activity when exploiting soil nutrient patches. In contrast, *Pennisetum* and *Heteropogon* from Hawaii shared a similar capacity to adjust physiologically to drought; the more vigorous growth of *Pennisetum* across both watering treatments could not be accounted for by greater physiological plasticity. Alternatively, the higher photosynthetic rates and proportionately greater allocation of biomass to leaves in *Pennisetum* more adequately explains its greater growth compared to *Heteropogon*. Successful invasions by tropical grasses in aridlands, therefore, may be related to their capacity to persist through drought, but rapidly exploit water when it is available.

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