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Growth and Resource Use of the Invasive Grass, Pampasgrass (*Cortaderia selloana*), in Response to Nitrogen and Water Availability

George L. Vourlitis and Joanna L. Kroon*

Exotic invasive species are nonnative species that thrive outside of their native habitat, and while it is difficult to determine which exotic plants will become invasive, successful invaders often share a wide range of traits including high growth rate and reproductive output, vegetative reproduction, high population growth rates, early reproductive age, phenotypic and physiological plasticity, and high resource use efficiency. Here we report on the response of pampasgrass, an important exotic invasive plant of the western United States, to experimental variations in soil nitrogen (N) and water availability. Given its ability to invade a wide variety of ecosystems in southern California, we hypothesized that pampasgrass would have higher water and N use efficiency under conditions of low water and N availability but rapid growth and resource use under conditions of high water and N availability. Our data support this hypothesis and indicate that pampasgrass exhibited large variations in growth, carbon allocation, morphology, and N and phosphorus (P) nutrition to variations in N availability and water table depth. Many of these traits are highly correlated with invasive performance, and the high N and P use efficiency observed under low soil N (control) and water table, coupled with the large increase in physiological performance and resource use under high N and water table, indicate that pampasgrass is highly flexible to soil resource levels that are typical for coastal sage scrub and riparian ecosystems of southern California. Such flexibility in resource use could allow pampasgrass to persist in low-resource environments and expand as resource levels increase.

Nomenclature: Pampasgrass, *Cortaderia selloana* (Schultes) Asch. & Graebner.

Key words: Coastal sage scrub, exotic species, Mediterranean-type ecosystems, resource use efficiency, riparian ecosystem.

Exotic invasive species are nonnative species that colonize a new area from accidental or intentional introduction and thrive outside of their native territory (Bossard et al. 2000; Mack et al. 2000; Rejmanek and Richardson 1996). It is difficult to determine which exotic plants will become invasive; however, invasive species often share a wide range of traits including high reproductive output, vegetative reproduction, high relative and population growth rates, early reproductive age, phenotypic and physiological plasticity, and high resource use efficiency (Burns 2004; Funk 2008; Mack et al. 2000; Osunkoya et al. 2010; Rejmanek and Richardson 1996). In particular, traits associated with maximizing carbon (C) gain, such as high leaf-area production, maximum photosynthesis, and specific leaf area (SLA; projected leaf area : leaf dry mass), appear to be positively correlated with invasive performance (Funk 2008). However, expression of these traits may be highly dependent on soil resource availability, especially soil N, water, or both (Burns 2004; Davis and Pelsor 2001; Sala et al. 1996). For example, the frequency of plant invasion is typically lower in resource-poor environments (Davis and Pelsor 2001), implying that invasive plant species may have little advantage over native species adapted to low resource availability. However, invasive species may be more efficient than native species at using limited resources (Funk and Vitousek 2007), and the ability to use limited resources efficiently, coupled with rapid physiological response to changes in resource availability, would allow invasive species to persist in low-resource environments and expand as resource levels increase.

Cortaderia selloana, commonly known as pampasgrass, is a perennial grass that is native to moist riparian areas of Argentina, Brazil, and Uruguay (Bossard et al. 2000). Pampasgrass has an upright growth habit up to 4 m in height

and 3.5 m in diam and produces dense clumps of evergreen leaves from a basal tussock (Bossard et al. 2000). The reproductive system of pampasgrass is gynodioecious, in which plants produce both female and hermaphroditic flowers (Connor 1973), and reproductive output is extensive with both types of flowers producing 10^5 to 10^6 wind-dispersed seeds from large plumes that are displayed apically (Domenech and Vila 2008a). Pampasgrass was used extensively as an ornamental landscape plant and became naturalized in California, the Mediterranean basin, New Zealand, the Hawaiian Islands, and South Africa (Brunel et al. 2010; Domenech and Vila 2008a; Lambrinos 2000). In southern California, pampasgrass has escaped urban landscapes (Okada et al. 2007) and has invaded coastal sage scrub drainages and riparian areas, where it forms dense, extensive, and monospecific stands (Bossard et al. 2000; Lambrinos 2001, 2002). These areas are typically moist to wet, suggesting that pampasgrass requires adequate moisture to become established; however, once established pampasgrass can tolerate moderate drought, winter frost, intense sunlight and warm summer temperatures (Bossard et al. 2000; Lambrinos 2002). Furthermore, pampasgrass is almost evenly distributed in coastal chaparral, seasonal wetland, and ruderal areas of southern California (Lambrinos 2001), suggesting that it has rather broad physiological requirements for soil resources.

A wide tolerance for environmental characteristics is presumably a main reason that pampasgrass is invasive in coastal southern California (Baker 1974; Lambrinos 2002). Wide tolerance for varying environmental characteristics, coupled with a capacity for rapid growth per unit resource, implies high resource-use efficiency (Funk 2008; Funk and Vitousek 2007; Hirose 1987). However, little is known about the growth and resource use response of pampasgrass to variations in soil resources. The wide variations in soil water and N availability between riparian and upland habitats in southern California (Coffman et al. 2010; Lambrinos 2002; Vourlitis et al. 2007a,b; Westman 1981), coupled with the ability of pampasgrass to exploit both habitats relatively

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equally (Lambrinos 2001), suggests that pampasgrass has significant potential for morphological and physiological plasticity. Thus, we hypothesized that pampasgrass would have higher water and N use efficiency under conditions of low water and N availability but significantly higher growth and resource use as water table depth and soil nitrogen content increased. These hypotheses were tested in a greenhouse experiment where the growth and physiology of pampasgrass juveniles were quantified in response to varying N and water availability.

Materials and Methods

Experimental Design. The experiment was performed over a 154-d period in a greenhouse located on the campus of California State University, San Marcos. Seedlings were purchased from a local nursery when plants were on average 8 cm tall and had two tillers per plant (a tiller is a genetically identical vegetative clone (ramet) that is produced from the basal tussock). Seedlings were used because we were interested in determining the effects of N and water availability during the seedling recruitment stage, which is often the most vulnerable stage in the plant life cycle (Harper 1977). Seedling recruitment success is reportedly high in sandy soil (Domech and Vila 2008b), thus we planted seedlings in riverbed sand where pampasgrass is known to occur. Plants were grown in 46 cm tall by 20 cm diam tree pots (Steuwe and Sons, Corvallis, OR), which were suspended in 19-L (5-gallon) buckets (one pot per bucket) with cut-out lids to create an artificial water table and minimize evaporation water loss.

The experiment consisted of a two by three random factorial design with three levels of N addition and two levels of water level manipulation ($n = 13$ individuals in each treatment combination). The water level manipulation consisted of a low water table treatment, where the water level was maintained at 30 cm below the soil surface, and a high water table treatment, where the water level was maintained at 10 cm below the soil surface. These water table treatments simulate drier and wetter conditions, respectively, in riparian and drainage areas during the winter and spring seasons when pampasgrass would be expanding by seed germination, fragmentation, or both (Lambrinos 2002). Water level was measured every 7 to 21 d and maintained at the appropriate level by replacing the amount of water lost to a permanent mark made on each bucket, which corresponded to the 10- or 30-cm water level treatments. Because each bucket was affixed with a lid, free evaporation was minimized and the volume of water needed to restore the water to the original level was equivalent to the amount of water lost from transpiration.

The soil N availability treatments consisted of no N added (control), intermediate ($5 \mu\text{g N g dry soil}^{-1}$), and high ($10 \mu\text{g N g dry soil}^{-1}$) N availability. The control and intermediate N treatment levels are consistent with those observed from southern Californian riparian and coastal sage scrub ecosystems whereas the high treatment level is consistent with urban riparian and shrubland ecosystems exposed to high atmospheric N deposition (Coffman et al. 2010; Padgett et al. 1999; Vourlitis et al. 2007a,b, 2009; Westman 1981). Soil N was added once at the beginning of the experiment as NH_4NO_3 .

Response Variables. The photosynthetic light response was measured at the time of final harvest (154 d from the beginning of the experiment) for five randomly chosen plants

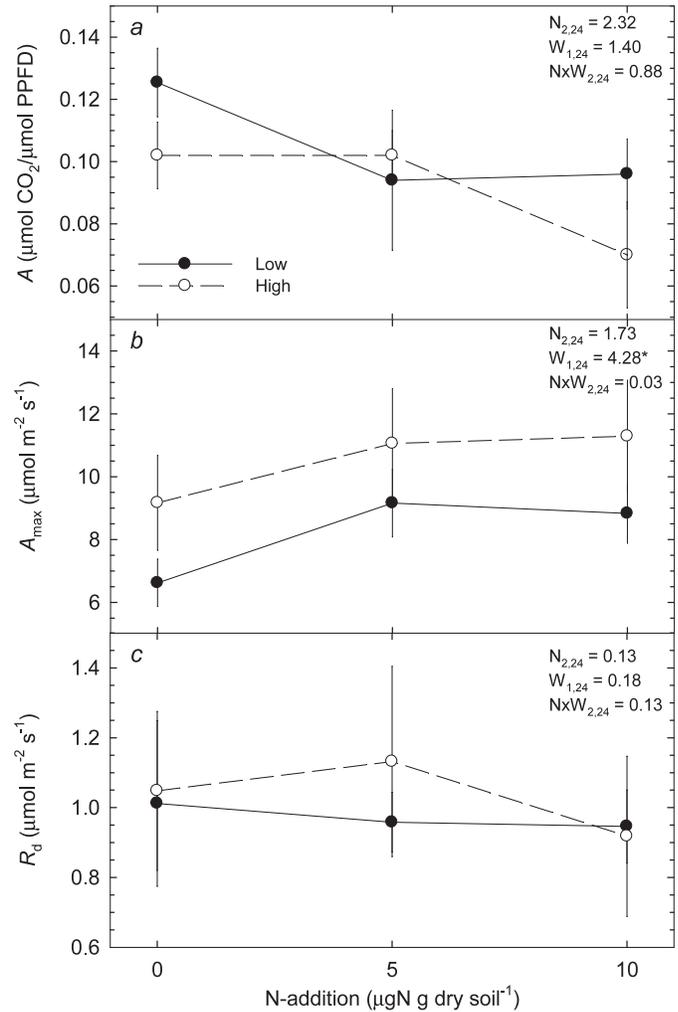


Figure 1. The effects of added nitrogen (N) on the mean (\pm SE, $n = 5$ plants per treatment combination) (a) quantum yield, (b) maximum rate of light-saturated photosynthesis, and (c) dark respiration for plants growing in low (black circles, solid lines) and high water table (white circles, dashed lines) at the end of the 154-d experiment. Also shown are the results of a two-way ANOVA (F -statistic and degrees of freedom) with N and water table (W) as fixed effects. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

from each treatment group using a portable photosynthesis system (LI-6400, LICOR, Inc., Lincoln, NE). Leaf CO_2 exchange was measured at 2,000, 1,000, 500, 200, 100, and $0 \mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic-photon-flux density (PPFD), 25 C, $370 \mu\text{mol mol}^{-1}$ ambient CO_2 concentration, and a relative humidity of 50%. Also during the final harvest, SLA (projected [one-sided] leaf area : leaf dry mass; Pearcy et al. 1989) was determined by (1) cutting a 10-cm-long section from the midpoint of each leaf harvested, (2) measuring the width of the leaf segment, (3) drying the leaf segment at 70 C for 1 wk, and (4) dividing the leaf area for each segment (fresh width by 10 cm) by the dry weight of the leaf cutting.

Plant height and the number of tillers per plant were measured at the start of the experiment and 67, 111, and 154 d into the experiment ($n = 13$ individuals in each treatment combination). Plant height was measured from the plant base to the tip of the longest leaf. Aboveground live (AGL) and dead (AGD) biomass and total below ground biomass (BG) were measured on a randomly selected subset of plants ($n = 10$) before the treatments were allocated and for

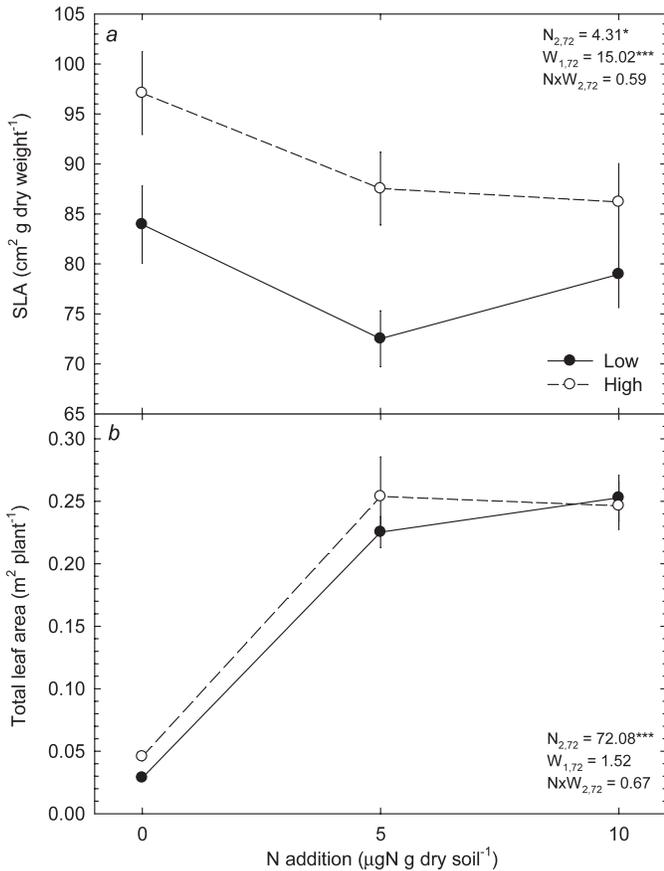


Figure 2. The effects of added nitrogen (N) on the mean (\pm SE, $n = 13$ plants per treatment combination) (a) specific leaf area and (b) total leaf area per plant for plants growing in low (black circles, solid lines) and high water table (white circles, dashed lines) at the end of the 154-d experiment. Also shown are the results of a two-way ANOVA (F -statistic and degrees of freedom) with N and water table (W) as fixed effects. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

all plants at the end of the experiment ($n = 13$ individuals in each treatment combination). Tissue samples were separated into their different components (AGL, AGD, and BG), washed, and dried at 70 °C; the dry weight of each plant part was measured using a digital balance.

The N and P concentration of AGL, AGD, and BG tissue was analyzed using Kjeldahl analysis (Bremner 1996). Tissue samples were ground to pass through a 40-mesh screen (Wiley Mill, Thomas Scientific; Swedesboro, NJ) and digested at 390 °C for 3 h using a block digester (BD-46, Lachat Instruments). Digests were analyzed for N and P using a flow injector analysis system (Quickchem 8000, Lachat Instruments).

Statistical Analysis and Derived Quantities. The photosynthetic light response was modeled using a nonrectangular hyperbola (Thornley 1976):

$$A_{net} = [(A \cdot \text{PPFD} \cdot A_{max}) / (A \cdot \text{PPFD} + A_{max})] - R_d \quad [1]$$

where A_{net} is the net rate of photosynthesis per unit leaf area ($\mu\text{mol m}^{-2} \text{s}^{-1}$); A = estimated quantum yield ($\mu\text{mol CO}_2 \mu\text{mol PPF D}^{-1}$), A_{max} is the maximum light-saturated rate of net photosynthesis ($\mu\text{mol m}^{-2} \text{s}^{-1}$), and R_d is the dark respiration rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$). Coefficients were estimated using the nonlinear curve-fitting routine available on NCSS 2004 (Number Cruncher Statistical Systems, Kaysville, UT).

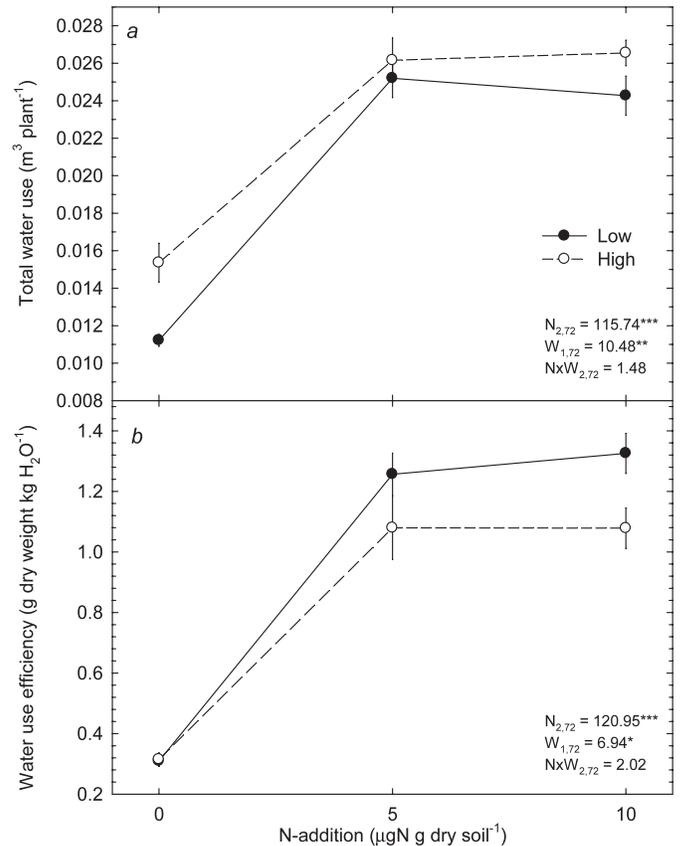


Figure 3. The effects of added nitrogen (N) on the mean (\pm SE, $n = 13$ plants per treatment combination) (a) total water use and (b) water use efficiency for plants growing in low (black circles, solid lines) and high water table (white circles, dashed lines). Total water use was calculated over the 154-d experimental period while water use efficiency was calculated as the total biomass at the end of the 154-d experiment divided by the total water use. Also shown are the results of a two-way ANOVA (F -statistic and degrees of freedom) with N and water table (W) as fixed effects. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Several indices of resource use efficiency were calculated to quantify pampasgrass resource use in response to variations in N and water availability. Nutrient resorption efficiency of aboveground tissue was calculated as the mass of nutrient per plant retained during tissue senescence (mass nutrient in live biomass – mass of nutrient in dead biomass) divided by the mass of nutrient in live biomass. This fraction was multiplied by 100 to express N and P resorption efficiency (NRE and PRE, respectively) as a percentage. Nutrient and water use efficiency was calculated using biomass production, tissue N and P concentration, and whole-plant water use data, respectively. N use efficiency (NUE; $\text{g dry weight g N}^{-1}$) was calculated according to Vásquez de Aldana and Berendse (1997) and Silla and Escudero (2004) where NUE is the product of the N productivity (A_N) and the mean residence time of N (MRT_N). A_N ($\text{g dry weight g N}^{-1} \text{wk}^{-1}$) was calculated as the rate of biomass production over the 154-d experiment ($\text{g dry weight plant}^{-1} \text{wk}^{-1}$) divided by the mean tissue N concentration (g N plant^{-1}), whereas MRT_N (wk^{-1}) was calculated as the ratio of whole plant N content divided by the N loss, which was derived from the dead biomass N concentration. P use efficiency (PUE) was calculated in a similar manner except P concentration was used in the calculations above instead of N concentration. Water use efficiency (WUE; $\text{g dry weight kg H}_2\text{O}^{-1}$) was calculated as

Table 1. Results of a repeated-measures ANOVA for plant height and tiller production of pampasgrass exposed to variations in water table depth (water) and added nitrogen (N). Shown are the degrees of freedom (df), sums of squares (SS), mean square (MS), *F*-statistic (*F*), and probability of type I error (*P*) with water table and N addition analyzed as fixed effects. NS = *P* > 0.05.

Source	df	Height				Tiller production			
		SS	MS	<i>F</i>	<i>p</i>	SS	MS	<i>F</i>	<i>P</i>
Water	1	4,410	4,410	19.2	< 0.001	23	23	8.1	< 0.005
N	2	85,417	42,708	186.0	< 0.001	753	377	135.0	< 0.001
Water × N	2	1,073	536	2.3	NS	31	16	5.6	< 0.005
Time	3	1,032,796	344,266	1499.4	< 0.001	651	217	77.8	< 0.001
Water × time	3	1,520	507	2.2	NS	49	16	5.8	< 0.001
N × time	6	29,123	4,854	21.1	< 0.001	278	46	16.6	< 0.001
Water × N × time	6	377	63	0.3	NS	45	8	2.7	< 0.05
Error	288	66,126	230			804	3		

the ratio of the aboveground biomass per plant produced over the experimental period divided by the total water loss per plant.

The effects of N availability and water table depth over time on plant height, tiller production, and total water use were analyzed using repeated-measures ANOVA. The effects of N and water table depth on biomass production (AGL, AGD, and BG) and the tissue N and P concentration were analyzed using Multivariate ANOVA (MANOVA) because of the highly correlated nature of these response variables. Those response variables that exhibited a significant MANOVA were then analyzed individually using a one-way ANOVA. The effects of N addition and water level on SLA, total leaf area, the root : shoot ratio, the N : P ratio, N and P resorption efficiency, nutrient use efficiency (NUE and PUE), N and P productivity and residence time, and plant water use and water use efficiency were assessed using two-way ANOVA with N and water level as fixed effects. All assumptions of the

ANOVAs and MANOVAs, such as random sampling and homogeneous variances were met. All statistical analyses were performed using NCSS-2004 (Number Cruncher Statistical Systems, Kaysville, UT).

Results and Discussion

Photosynthesis, Leaf Morphology, and Water Use. Estimated quantum yield (*A*) ranged between 0.07 $\mu\text{mol CO}_2 \mu\text{mol PPF D}^{-1}$ for plants exposed to high N (10 $\mu\text{g N g dry soil}^{-1}$) and high (10 cm) water table to 0.13 $\mu\text{mol CO}_2 \mu\text{mol PPF D}^{-1}$ for plants exposed to low N (control) and low (30 cm) water table (Figure 1a); however, treatment effects were not statistically significant. Estimated rates of A_{max} were significantly higher for plants exposed to higher water table (Figure 1b). Plants exposed to the low water table treatment had an A_{max} that ranged between 6.0 and 8.75 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for the control and high N treatments, respectively, whereas

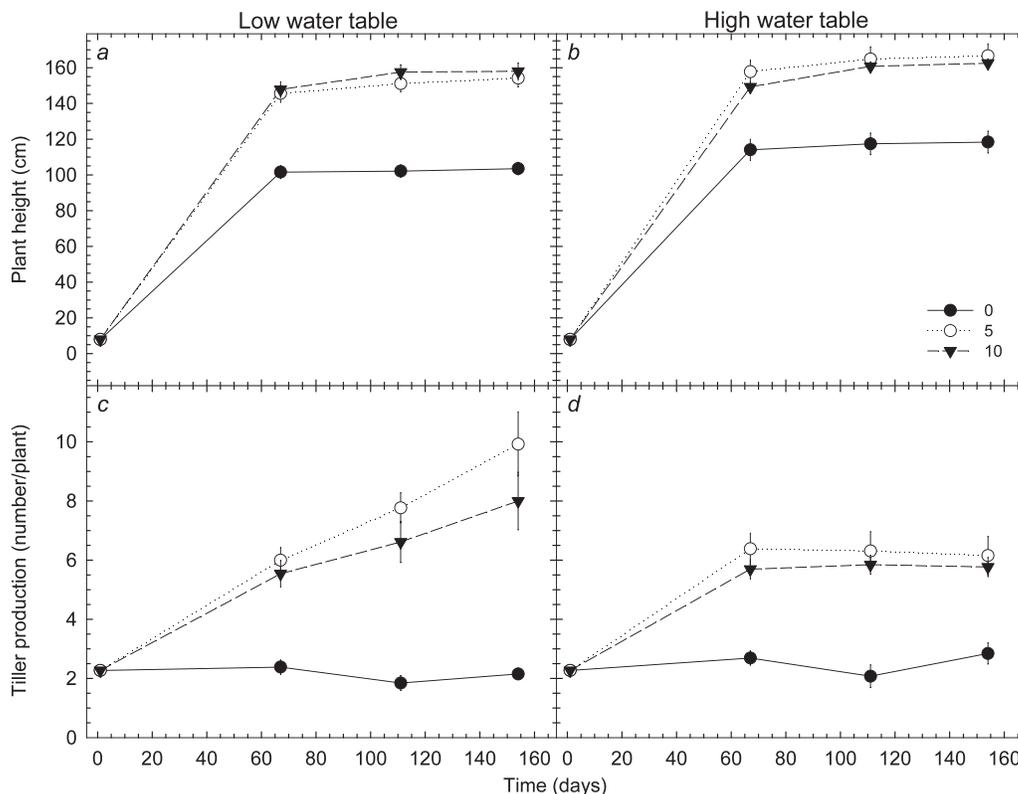


Figure 4. Temporal changes in (a and b) mean plant height and (c and d) tiller number for plants exposed to 0 (black circles, solid lines), 5 (white circles, dotted lines), and 10 $\mu\text{g N g dry soil}^{-1}$ (inverted triangles, dashed lines) in low (left-hand panels) and high water table (right-hand panels). Data are means (\pm SE; *n* = 10 plants per treatment combination).

Table 2. Results of a multivariate ANOVA for aboveground live biomass (AGL, g plant⁻¹), aboveground dead biomass (AGD, g plant⁻¹), and belowground live biomass (BGL, g plant⁻¹) of pampasgrass exposed to variations in water table depth (water) and added nitrogen (N). Shown are the degrees of freedom (df), multivariate (Hotelling-Lawley Trace), and univariate test statistics (*F*-statistics), *F*-ratio (*F*), and probability of type I error (*P*) with water table and N addition analyzed as fixed effects. NS = *P* > 0.05; NA = not applicable.

Source	Statistic	Test value	df	<i>F</i>	<i>P</i>
Water	Hotelling-Lawley	0.01	3,70	0.34	NS
	AGL	44.09	1,72	0.81	NA
	AGD	2.02	1,72	0.14	NA
	BGL	0.14	1,72	0.00	NA
N	Hotelling-Lawley	5.57	6,138	64.04	< 0.001
	AGL	6,012.23	2,72	110.47	< 0.001
	AGD	1,177.48	2,72	78.89	< 0.001
	BGL	1,466.18	2,72	40.29	< 0.001
Water × N	Hotelling-Lawley	0.09	6,138	1.07	NS
	AGL	40.52	2,72	0.74	NA
	AGD	6.15	2,72	0.41	NA
	BGL	95.76	2,72	2.63	NA

plants exposed to the high water table treatment had an A_{max} that ranged between 9.0 and 11.4 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for the control and high N treatments, respectively. Rates of dark respiration (R_d) were on average 1.0 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and were not affected by variations in N or water table (Figure 1c).

Plants exposed to the high water table (10 cm) had significantly higher SLA (Figure 2a), indicating that these plants produced thinner leaves with less structural C and lower resource-use efficiency (Knops and Reinhart 2000).

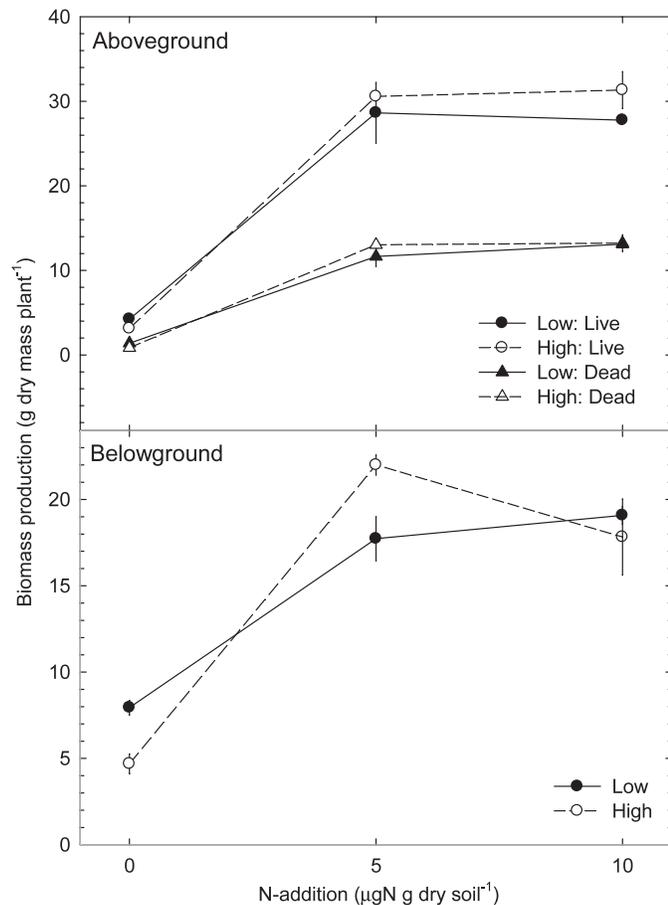


Figure 5. The effects of added nitrogen on the mean (\pm SE, $n = 13$ plants per treatment combination) aboveground live (circles) and dead (triangles) biomass and belowground live biomass production for plants growing in low (black symbols, solid lines) and high water table (white symbols, dashed lines) at the end of the 154-d experiment.

Thinner leaves would enhance the amount of light absorbed by leaf chloroplasts, which may have been limiting for greenhouse-grown plants, increasing rates of A_{max} (Terashima and Evans 1988). SLA was also significantly affected by N addition (Figure 2a); however, plants exposed to added N had a lower SLA, which is contrary to those reported for some grasses (Knops and Reinhart 2000) but not others (Van Der Werf et al. 1993). Unfortunately leaf structural properties were not measured, but typically leaves with a lower SLA have more structural C and an increase in longevity; traits that are often associated with species of resource-poor habitats (Knops and Reinhart 2000; Reich et al. 1998; Van Der Werf et al. 1993). This may be one reason why rates of leaf photosynthesis were not significantly affected by N addition (Figure 1).

Total leaf area production (projected [one-sided] leaf area per plant) increased significantly in response to N addition but not water table manipulation (Figure 2b). Leaf area was more than fivefold higher for plants exposed to the intermediate (5 $\mu\text{g N g dry soil}^{-1}$) N treatment than in the control, and as with biomass production, leaf area was similar

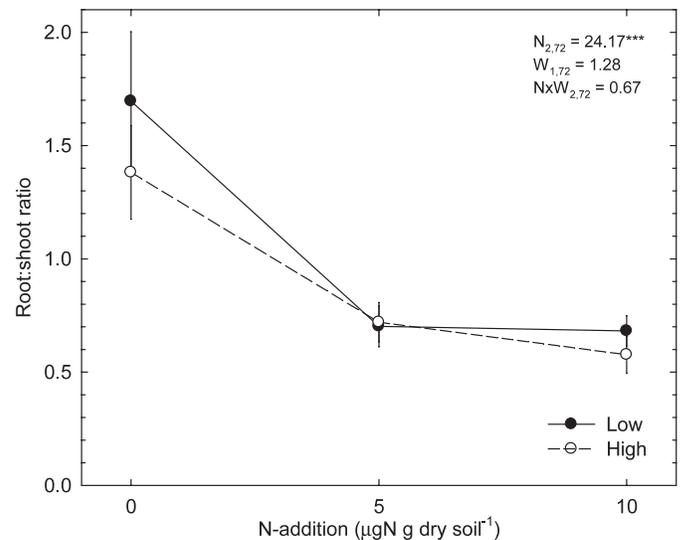


Figure 6. The effects of added nitrogen (N) on the mean (\pm SE, $n = 13$ plants per treatment combination) root : shoot ratio of live biomass for plants growing in low (black symbols, solid lines) and high water table (white symbols, dashed lines) at the end of the 154-d experiment. Also shown are the results of a two-way ANOVA (*F*-statistic and degrees of freedom) with N and water table (W) as fixed effects. * *P* < 0.05; ** *P* < 0.01; *** *P* < 0.001.

Table 3. Results of a multivariate ANOVA for the nitrogen (N) and phosphorus (P) concentration and N : P ratio of aboveground live biomass (AGL), aboveground dead biomass (AGD), and belowground live biomass (BGL) of pampasgrass exposed to variations in water table depth (water) and added nitrogen (N). Shown are the degrees of freedom (df), multivariate (Hotelling-Lawley Trace), and univariate test statistics (*F*-statistics), *F*-ratio (*F*), and probability of type I error (P) with water table and N addition analyzed as fixed effects. NS = *P* > 0.05.

Source	Statistic	df	N concentration			P concentration			N:P ratio		
			Test value	<i>F</i>	P	Test value	<i>F</i>	P	Test value	<i>F</i>	P
Water	Hotelling-Lawley	3,70	0.28	6.45	< 0.001	0.39	9.07	< 0.001	1.22	28.37	< 0.001
	AGL	1,72	0.29	0.11	NS	0.50	24.24	< 0.001	959.23	11.98	< 0.001
	AGD	1,72	41.07	16.19	< 0.001	0.00	0.01	NS	39,145.92	34.25	< 0.001
	BGL	1,72	6.51	2.04	NS	0.03	10.67	< 0.001	113.52	2.21	NS
N	Hotelling-Lawley	6,138	7.85	90.30	< 0.001	9.32	107.20	< 0.001	7.31	84.02	< 0.001
	AGL	2,72	503.22	186.19	< 0.001	5.62	271.68	< 0.001	15,450.13	193.02	< 0.001
	AGD	2,72	476.94	188.01	< 0.001	0.90	113.39	< 0.001	127,484.95	111.53	< 0.001
	BGL	2,72	479.97	150.44	< 0.001	0.38	147.50	< 0.001	9,614.02	187.30	< 0.001
Water × N	Hotelling-Lawley	6,138	0.50	5.79	< 0.001	0.79	9.10	< 0.001	0.72	8.26	< 0.001
	AGL	2,72	5.86	2.17	NS	0.42	20.49	< 0.001	111.88	1.40	NS
	AGD	2,72	36.28	14.30	< 0.001	0.07	9.32	< 0.001	14,902.52	13.04	< 0.001
	BGL	2,72	6.82	2.14	NS	0.04	16.08	< 0.001	163.50	3.19	< 0.05

in the intermediate and high N treatments (Figure 2b). The increase in leaf area has implications for whole-plant C gain and soil water availability in areas invaded by pampasgrass. Indeed, water loss per plant increased by nearly twofold between the control and intermediate N treatments but leveled off thereafter, and plants exposed to the high water table treatment lost approximately 2 kg H₂O plant⁻¹ more than plants exposed to the low water table treatment over the course of the experiment (Figure 3a). WUE increased as a function of N addition, but as with water loss, WUE leveled off between the intermediate and high N treatment (Figure 3b). In contrast, plants exposed to the high water table had a significantly lower WUE than plants exposed to the low water table treatment (Figure 3b). An increase in water use will result in a reduction in soil water availability, and thus, potential recruitment for other riparian species in

semiarid environments where spatial and temporal variations in soil water availability are crucial for germination and recruitment success (Domenech and Vila 2008b; Lambrinos 2002; Ward et al. 2006).

Plant Growth and Carbon Allocation. Pampasgrass plants exposed to N enrichment and a high water table grew significantly taller and produced more tillers than plants exposed to ambient levels of N and a low water table (Table 1; Figure 4). Plant height (Figures 4a and 4b) and tiller production (Figures 4c and 4d) were substantially higher for plants exposed to intermediate and high N; however, increases in plant height and tiller production beyond the intermediate N treatment were negligible. The significant increase in tiller production is particularly relevant for the vegetative reproduction of pampasgrass, which is an important mechanism for

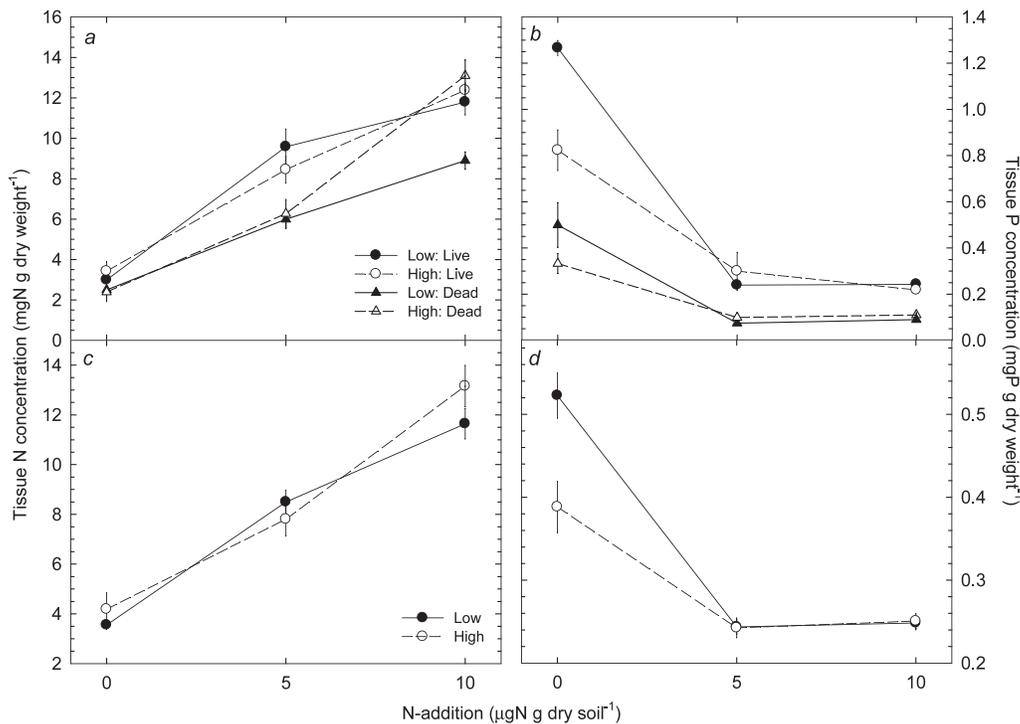


Figure 7. The effects of added nitrogen on the mean (\pm SE, *n* = 13 plants per treatment combination) aboveground live (circles) and dead (triangles) and the belowground live tissue (a and c) nitrogen and (b and d) phosphorus concentration for plants growing in low (black symbols, solid lines) and high water table (white symbols, dashed lines) at the end of the 154-d experiment.

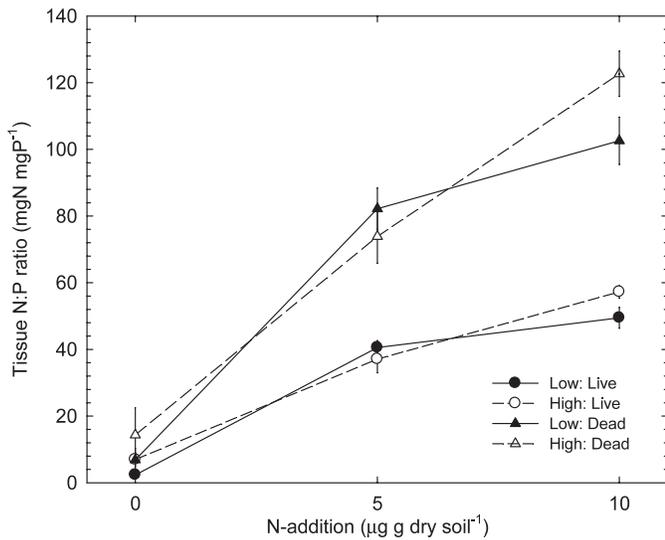


Figure 8. The effects of added nitrogen on the mean (\pm SE, $n = 13$ plants per treatment combination) aboveground live (circles) and dead (triangles) tissue nitrogen : phosphorus ratio for plants growing in low (black symbols, solid lines) and high water table (white symbols, dashed lines) at the end of the 154-d experiment.

the expansion in the spatial distribution of this species (Davies et al. 1990; Lambrinos 2001). Plants exposed to a higher water table grew taller (Figures 4a and 4b) but produced fewer tillers than plants exposed to a lower water table, especially by the end of the experiment (Figures 4c and 4d). Presumably, the higher water table inhibited leaf production, which has been observed for many trees and shrubs exposed to flooding (Ishida et al. 2002; Mielke et al. 2003).

Biomass production was also significantly affected by added N but not water table depth (Table 2; Figure 5), and the lack of a water table effect on biomass production is consistent with previous results on the growth of pampasgrass under a variety of soil water regimes (Domenech and Vila 2008b; Stanton and DiTomaso 2004). AGL biomass production was nearly seven times higher for plants exposed to the intermediate N treatment than for plants exposed to ambient N; however, higher levels of N addition failed to increase aboveground biomass production (Figure 5). The magnitude of the growth and allocation response of pampasgrass to N was similar in magnitude to that reported for other invasive species (Burns 2004; Funk 2008), and it is important to note that these large increases in growth and allocation occurred over a range of soil extractable N concentration ($5 \mu\text{g N g dry soil}^{-1}$) that is typical for coastal sage scrub and riparian ecosystems (Coffman et al. 2010; Vourlitis et al. 2007a,b). Similar patterns were observed with AGD biomass and root production (Figure 5). At ambient N, root biomass was on average 1.5 times higher than aboveground biomass production, but as N availability increased, biomass allocation to aboveground tissue increased significantly and the root : shoot ratio was on average 0.7 for both the intermediate and high N treatments (Figure 6). These data indicate flexible C allocation patterns as soil resource levels varied, which is a hallmark of many invasive exotic plant species (Funk 2008).

Tissue N and P Concentration and Nutrient Use Efficiency.

Tissue N concentration increased significantly with added N, but only the tissue N concentration of dead aboveground

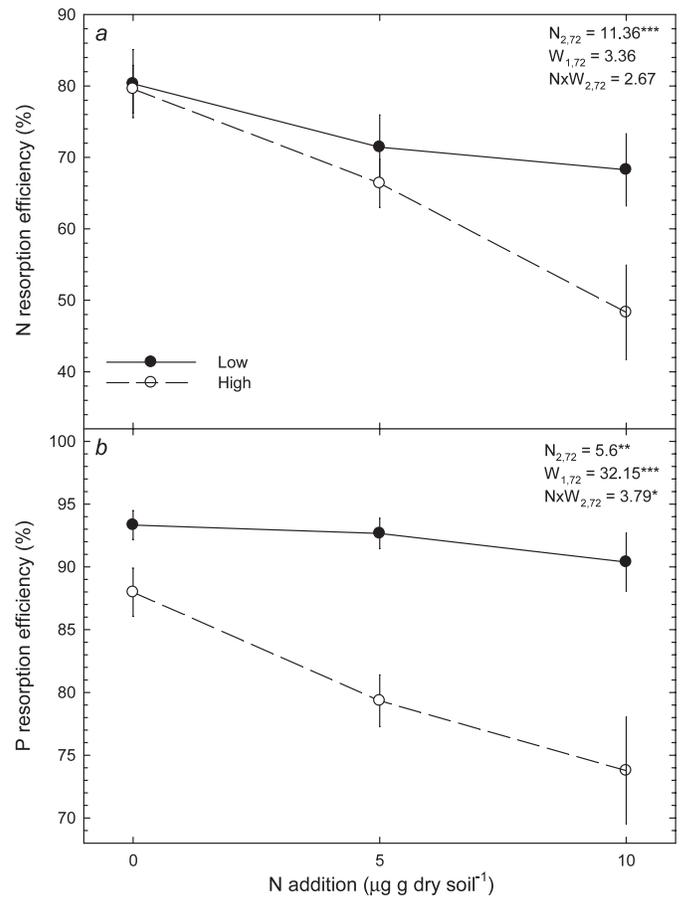


Figure 9. The effects of added nitrogen (N) on the mean (\pm SE, $n = 13$ plants per treatment combination) (a) aboveground N and (b) phosphorus resorption efficiency for plants growing in low (black symbols, solid lines) and high water table (white symbols, dashed lines) at the end of the 154-d experiment. Nutrient resorption efficiency was calculated as the mass of nutrient per plant retained during tissue senescence (mass nutrient in live biomass – mass of nutrient in dead biomass) divided by the mass of nutrient in live biomass. Also shown are the results of a two-way ANOVA (F -statistic and degrees of freedom) with N and water table (W) as fixed effects. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

tissue was significantly affected by water table depth (Table 3). The N concentration increased in an almost linear fashion with added N for both above- (Figure 7a) and belowground (Figure 7b) tissue fractions. However, the N concentration of AGD tissue exposed to the high water table increased in an exponential fashion to added N causing a significant N by water table interaction (Table 3). In contrast, the P concentration of above- (Figure 7b) and belowground (Figure 7d) tissue declined significantly as a function of N addition, but only between the control and intermediate N treatments. Considering aboveground tissue only, the increase in tissue N concentration with added N, coupled with a decline in tissue P concentration, caused the N : P ratio of both live and dead tissue to increase significantly as a function of added N (Table 3; Figure 8). Plants exposed to ambient N had an N : P ratio of 2 to 5 for live and dead aboveground tissue, but with added N the N : P ratio for live and dead tissue increased to 40 and 80, respectively, in the intermediate N treatment and 55 and 110, respectively, in the high N treatment (Figure 8). Assuming that an N : P ratio ≥ 15 indicates the potential for P deficiency (Koerselman and Meuleman 1996), these data suggest that the productivity of pampasgrass became P-limited as N availability increased.

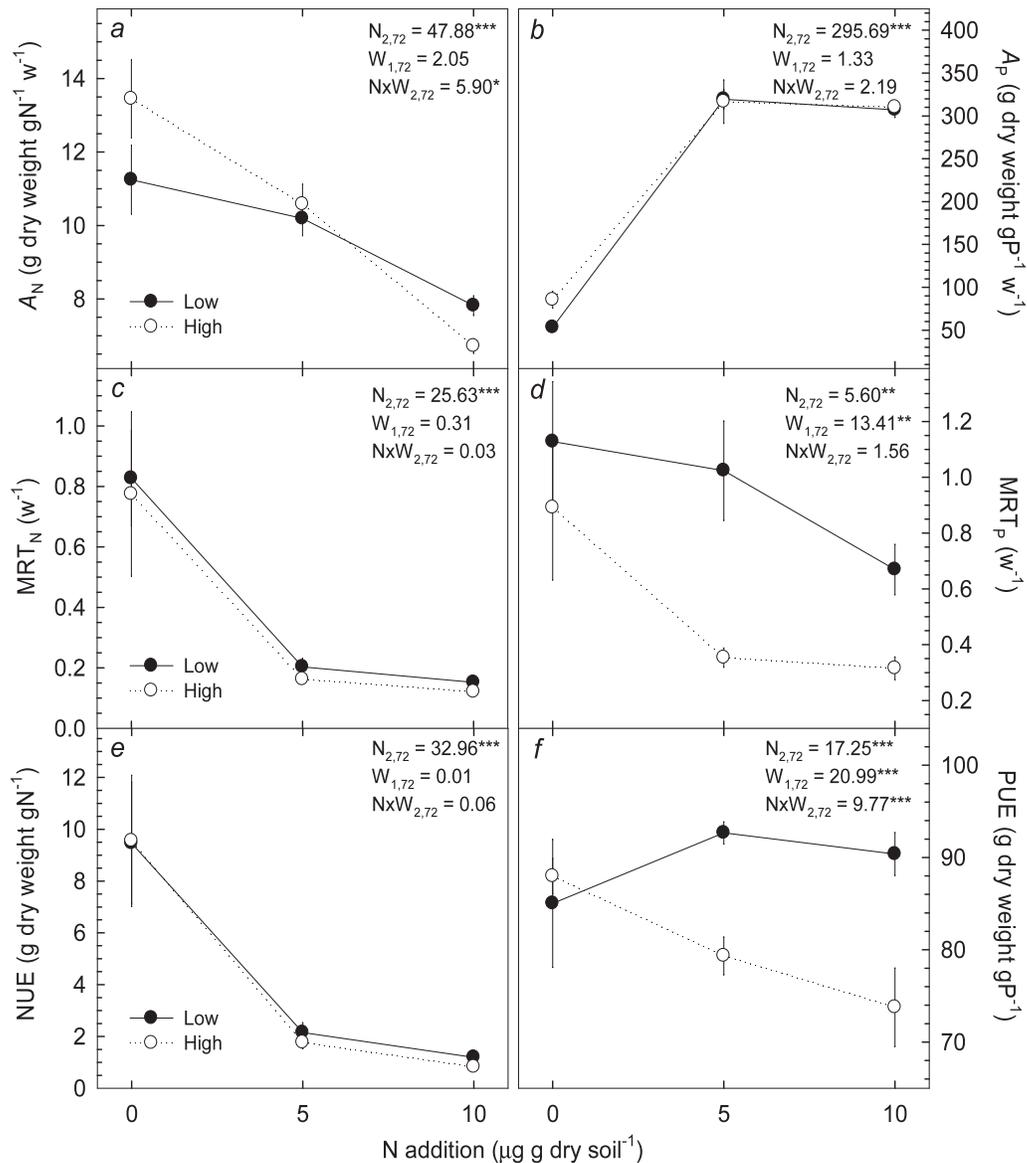


Figure 10. The effects of added nitrogen (N) on the mean (\pm SE, $n = 13$ plants per treatment combination) on (a) nitrogen and (b) phosphorus (P) productivity, (c) residence time for N and (d) P, and (e) N and (f) P use efficiency for plants growing in low (black symbols, solid lines) and high water table (white symbols, dashed lines) at the end of the 154-d experiment. Nutrient use efficiency was calculated as the product of the nutrient productivity (A_N and A_P) and the mean nutrient residence time (MRT_N and MRT_P). Nutrient productivity was calculated as the rate of biomass production over the 154-d experiment ($\text{g dry weight plant}^{-1} \text{wk}^{-1}$) divided by the mean tissue N or P concentration (g N plant^{-1}), while the mean nutrient residence time was calculated as the ratio of whole plant N or P content divided by the N or P loss, which was derived from the dead biomass N or P concentration. Also shown are the results of a two-way ANOVA (F -statistic and degrees of freedom) with N and water table (W) as fixed effects. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

The NRE declined significantly with added N, and although the decline in NRE appeared to be higher in plants exposed to a high water table depth, the N by water table interaction was not statistically significant (Figure 9a). Plants exposed to ambient N were found to retain approximately 80% of N from senescent tissue; however, the percentage of tissue N retained declined to 50 to 70% in the highest N treatment depending on water table depth (Figure 9a). PRE, however, was significantly affected by both N addition and water table depth, and there was a significant N by water table interaction (Figure 9b). For plants exposed to a low water table the PRE was on average 92% regardless of N treatment, but for plants exposed to the high water table treatment the PRE declined from 87% in the control treatment to 79 and 70% in the intermediate and high N treatments, respectively (Figure 9b).

Under low N availability, pampasgrass exhibited significantly higher A_N , longer MRT_N , and higher NUE (Figure 10), indicating efficient use of N and a high potential to respond to an increase in N availability (Berendse and Aerts 1987; Burns 2004; Silla and Escudero 2004). However, A_N , MRT_N , and NUE declined significantly with added N suggesting that pampasgrass may have become N-saturated (Fenn et al. 2003, 2008; Gundersen et al. 1998). In contrast, P productivity (A_P) increased significantly as a function of added N but not water table, and the largest increase in A_P occurred between the control and intermediate N treatment (Figure 10b). The mean residence time for P (MRT_P) also declined as a function of added N; however, water table depth had a significant effect on the MRT_P with plants exposed to the low water table having higher MRT_P than plants exposed to the high water table depth

(Figure 10d). As a result, the PUE was a complex function of the N treatment level and water table depth, with plants exposed to low water table exhibiting a significant increase in PUE as a function of N and the plants exposed to high water table exhibiting a significant decline in PUE with N addition (Figure 10f). Presumably, the higher physiological activity (A_{max}) and SLA observed in the high water table reflects an increase in the rate of tissue turnover (lower tissue lifespan) and an associated decline in P resorption and PUE (Knops and Reinhart 2000).

In conclusion, we hypothesized that pampasgrass would have high WUE and NUE under conditions of low water and N availability but significantly higher growth and resource use in response to increases in water table depth and soil N content. Our data support this hypothesis and indicate that pampasgrass has the capacity for high morphological and physiological plasticity in response to variations in N availability and water table depth, variations that are typical for coastal sage scrub and riparian ecosystems of southern California. The ability to use limited resources efficiently, coupled with rapid physiological response to changes in resource availability, could allow pampasgrass to persist in low-resource environments and expand as resource levels increase.

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