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## Intraspecific variation in the resistance to flooding and drought in populations of *Paspalum dilatatum* from different topographic positions

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**Abstract** Many studies have analysed plant responses to flooding or drought separately, without addressing the relations between plant resistance to each of these factors. In this paper, we compare the responses to drought and flooding under glasshouse conditions of three populations of *Paspalum dilatatum*, a perennial C<sub>4</sub> grass dominant at different positions along a topographic gradient in the flooding pampa of Argentina. Our results showed that flooding effects on yield were negative on an upland, null on an intermediate, and positive on a lowland population, whereas drought reduced yield equally across populations, showing that resistance to flooding was not related to resistance to drought at a population level. Drought decreased height and aerenchyma, and increased the proportion of roots, while flooding had opposite effects on these traits. The responses of the single clones that made up each population showed a positive relation between the resistances to both factors: along the ecocline formed by 58 clones, those more resistant to drought were also more resistant to flooding. In addition, the combined resistance of each clone to both factors was negatively related to yield at field capacity, (i.e. the most resistant clones were less productive) and unrelated to the proportion of roots and aerenchyma. This result agrees with predictions of Grime's plant strategy theory and differs from a few previous studies, which showed negative relations between the resistances to flooding and drought among genera and species.

**Key words** Drought · Flooding · Intraspecific variation · Stress · *Paspalum dilatatum*

### Introduction

Most grassland ecosystems have heterogeneous water regimes in time and space (Knapp et al. 1993; Potvin 1993), with extreme situations ranging from drought to

flooding. This heterogeneity is matched by differences in plant community composition: many flooding-resistant species are not found in areas where drought is severe and drought-resistant species are usually absent in flooded environments (Bertness et al. 1992; McNaughton 1983; Medina and Motta 1990). However, some species show a generalist behavior, inhabiting areas with contrasting water regimes (Heathcote et al. 1987; Knapp et al. 1993). Such is the case of *Paspalum dilatatum*, a highly palatable C<sub>4</sub> grass that is found as co-dominant at different positions along drought-flooding gradients in the flooding pampa of Argentina (Burkart et al. 1990).

It has been shown that species of this sort achieve their generalist behavior by having either different ecotypes adjusted to the prevailing condition or a few similar genotypes with large phenotypic plasticity (Bradshaw 1965). Included in the first alternative is the situation where different ecotypes may shift habitats according to year-to-year climatic variation (Ehleringer 1988).

Flooding and drought have both similar and different effects on plants. Flooding, through the generation of hypoxia in the rhizosphere, reduces water absorption and stomatal conductance and causes wilting in flooding-sensitive plants in a way similar to drought (Kozlowski 1984). However, there are a number of differences in the physiological effects of the two factors and the potential selective pressures that they may exert on populations. Resistance to drought includes osmotic adjustment, reduced leaf area, increased leaf thickness, sclerophylly symptoms, increased root:shoot ratio and prostrate growth (Coughenour 1985; Pugnaire et al. 1993; Soriano 1982; Turner 1994). In contrast, flooding resistance includes increased plant height, ability to elongate shoots and petioles to avoid blade submergence, formation of adventitious roots aboveground, reduced root:shoot ratio, increased proportion of aerenchymatic tissue in roots, and the machinery that enables plants to cope with hypoxia (Blom et al. 1990; Davy et al. 1990; Jackson and Drew 1984).

Although physiological ecology has a long history of unveiling relationships between plant performance and

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variations in single environmental factors, it is only relatively recently that studies of response to multiple factors have become common (Chapin et al. 1987). These studies have been influential in the generation of broad theoretical generalizations on topics such as the relationships between resources and defenses, carbon and nitrogen economy, grazing and drought, competition and succession, etc. (Coley et al. 1985; Coughenour 1985; Milchunas et al. 1988; Tilman 1988).

Plants are never subjected to flooding and drought simultaneously, but a single plant can experience both factors in sequence, or a single population, as explained above, may be affected by different flooding-drought regimes. Studying the adaptation of plants to flooding and drought is particularly interesting because of the conflicting effects of the two factors on root:shoot allocation and its relation to current theories on plant strategies (Grime 1979; Tilman 1988). We know of only three studies on the simultaneous adaptation to drought and flooding (Baruch 1994; Sultan and Bazzaz 1993; ter Steege 1994). The first two approached the problem by comparing different species or genera, whereas the third studied populations of a single species, but was more focused on theoretical aspects of phenotypic plasticity than on the interaction between the two factors *per se*. Studying populations of a single species is likely to be a better approach because of the elimination or reduction of other selective factors and potential phylogenetic constraints that might obscure the origin of the differences. We studied the responses to flooding and drought of populations of the grass *Paspalum dilatatum* from three positions along a fine-grained gradient: one drier and never flooded and two frequently flooded, though with different intensities and duration. *P. dilatatum* is an apomictic species (Davies and Cohen 1992), so gene flow among populations is highly restricted and the effect of natural selection at the intraspecific level may be more noticeable.

## Materials and methods

We performed a factorial experiment by exposing clones of *P. dilatatum* from three different sites along a topographic gradient to three experimental water regimes (drought, field capacity, and flooding). The clones were collected in three sites (upland, intermediate, and lowland) occupied by different plant communities. The *upland* site is occupied by a community denominated A by Burkart et al. (1990) and has a topographic position 50–100 cm higher than the *intermediate* site, which contains community B and is about 15 cm more elevated than the *lowland* site, where community C predominates (Chaneton 1995). The collection sites were located in the Estancia Las Chilcas, a livestock ranch in Pila County, in the central flooding pampa of Argentina (36°S, 58°30'W).

At each site we collected 20 ramets which, because of the tussock growth form of the species, are assumed to belong to different clones. The clones, collected in February 1994, were cultivated and propagated in a greenhouse until the start of the experiment in September 1994: each original ramet was vegetatively replicated into four or five ramets in June, and each of these was replicated into approximately three more ramets in August, resulting in about 15 ramets/clone. We believe that any influence from the original environment was erased during this process, for two reasons. First,

7 months of cultivation under greenhouse conditions is enough time for a fast-growing herbaceous C<sub>4</sub> plant like *P. dilatatum* to accumulate significant amounts of biomass and to senesce old tissue. These two processes combined greatly diluted the contribution of the original tissue to the final experimental plants. Second, vegetative propagation during that time meant that most tillers of the final plants originated under greenhouse conditions (we started the propagation with about 5 tillers per clone and ended it with 75).

The experiment was a 3×3 factorial. Water was the treatment factor and origin site was the classification factor (Hurlbert 1984). The water levels were drought, field capacity (control), and flooding. The origin site levels were plants originated in each of the three sites described above: the upland, the intermediate and the lowland site. Each combination of water × origin had 20 true replicates (clones) for the intermediate and lowland sites and 18 for the upland site, since two clones from this origin did not survive the propagation period. Each clone was represented by two ramets, which were considered subsamples to avoid pseudoreplication (Hurlbert 1984). Thus, we had three water treatments by three origins, two of them with 20 clones and one with 18 clones, which makes 174 experimental units. Since each experimental unit comprised two ramets, we had 348 ramets.

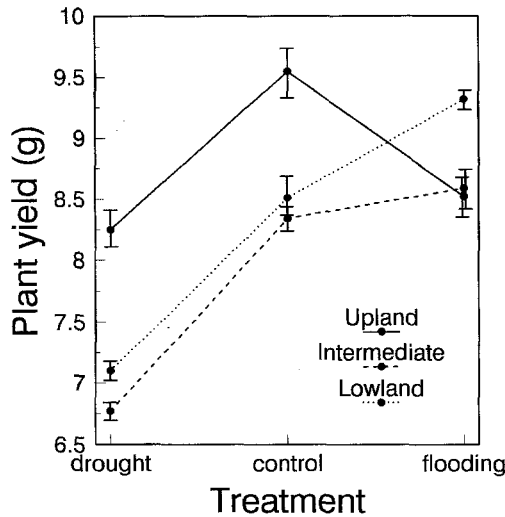
The experimental plants were grown on washed sand in 16 cm height × 11 cm diameter plastic pots without drainage holes. They were located in the same greenhouse where they had been propagated. The experiment began after a 15-day acclimation period. We randomly applied the water treatments within clones and segregated the treatments and origins in space to avoid aboveground competition among them (they were periodically rotated). We installed a pair of 15 cm steel rods in each pot in order to monitor volumetric water content (Θ) on a daily basis by means of a time domain reflectometry (TDR) apparatus (Trase System I, Soil Moisture Equipment Corp.). Pots of flooded plants had a permanent water film of about 2 cm above surface and Θ=34%. Pots of the drought treatment were maintained at Θ=2–5% by watering daily until reaching Θ=5%. Pots of control plants were held at Θ=8–11%, which corresponds to field capacity in sandy soils (Hillel 1971), by watering daily until reaching Θ=11%. All plants received 50 ml of Hoagland's solution number 2 weekly divided into five doses of 10 ml each. Midday leaf water potential was measured with a pressure bomb on a randomly chosen full expanded leaf 30 days after the start of the experiment.

At the end of the experiment, on the 50th day, we harvested the plants, measured leaf area with a Li-3000 leaf area meter (LICOR, Inc), and quantified gas-filled root porosity by means of the pycnometer method (Sojka 1988). We separated plant biomass into different organs, and weighed it after oven-drying for 72 h.

Data were analysed by two-way type III ANOVA, because of the unbalanced design due to the lower number of clones from the upland site. Since the clones cannot be crossed among origins, they were nested within them by a nested-factorial ANOVA model. The results of drought and flooding treatments were analysed by separate ANOVAs in order to discriminate their effects on the different populations. Data were checked for normality and homogeneity of variances and Tukey's tests were performed for *a posteriori* mean comparisons. The resistance of single clones to each factor was determined as  $(Y_t - Y_c)/Y_c$ , where  $Y_t$  is the yield of treated plants (drought or flooding), and  $Y_c$  is the yield of controls. The combined resistance to both factors was obtained by simple addition of the resistance to each factor. We determined resistance as relative differences in order to avoid possible spurious results due to potential differences of plant growth rate among clones. The relationships among resistances and yield of control plants were studied by correlation analysis. Although correlations between variables that share a common term are sometimes considered as spurious, this claim is currently regarded as a misconception if the assumptions of correlation analysis are satisfied, and if the variables are meaningful and do not share a large measurement error term (Prairie and Bird 1989).

**Table 1** ANOVA probability values for the effects of drought and flooding on different traits of three populations of the grass *Paspalum dilatatum* from an upland, an intermediate, and a lowland site. Main effects and interactions are considered significant at  $P < 0.05$

Variable	Control vs. drought contrast			Control vs. flooding contrast		
	Population	Drought	Population×drought	Population	Flooding	Population×flooding
Plant yield (g)	0.0001	0.0001	0.80	0.05	0.60	0.0005
Midday water potential (MPa)	0.9	0.0001	0.30	0.40	0.10	0.30
Blade (g)	0.05	0.0001	0.40	0.90	0.04	0.002
Leaf area (cm <sup>2</sup> )	0.05	0.0001	0.10	0.40	0.01	0.006
Sheath (g)	0.60	0.0001	0.05	0.15	0.02	0.0005
Standing dead (g)	0.10	0.0001	0.90	0.40	0.0004	0.60
Crown (g)	0.005	0.0001	0.90	0.0001	0.001	0.05
Root (g)	0.0001	0.10	0.02	0.0001	0.0001	0.004
Proportion of roots (g/g)	0.0001	0.0001	0.0001	0.0001	0.0001	0.10
Plant height (cm)	0.0005	0.0001	0.10	0.006	0.0001	0.01
Root porosity (%)	0.05	0.0005	0.65	0.001	0.0001	0.75

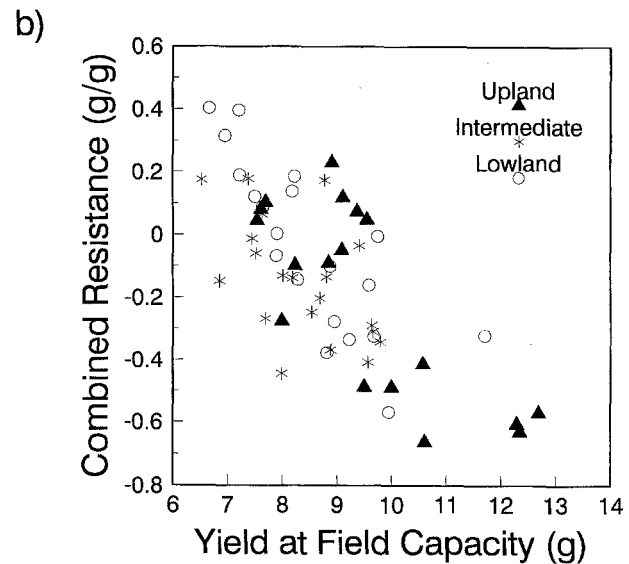
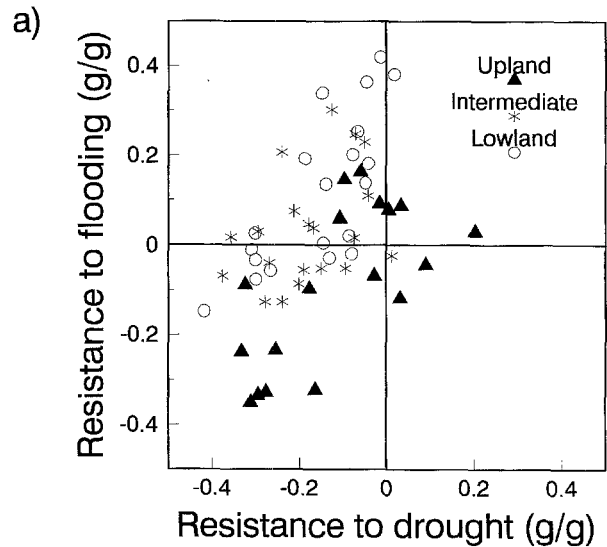


**Fig. 1** Final plant yield of three populations of *Paspalum dilatatum* from an upland, an intermediate, and a lowland site under different water conditions: drought, field capacity, and flooding. Bars indicate standard errors

**Results**

The populations showed similar yield responses to drought, but responded contrastingly to flooding. Drought reduced total yield by 16% in the three populations (Table 1, Fig. 1), whereas flooding had a negative effect (-11%) on the upland population, a non-significant effect (+3%) on the intermediate population, and a positive effect (+10%) on the lowland population (Fig. 1).

These responses at the population level were the result of a diverse pattern of response of the individual clones that made up each population. In Fig. 2a, the rela-



**Fig. 2** Relationships between **a** resistance to drought and resistance to flooding, and **b** the combined resistance to both factors and yield at field capacity among clones of *P. dilatatum* originating from an upland (black triangles), an intermediate (asterisks) and a lowland site (open circles). For **a** correlation coefficients between resistance to drought and resistance to flooding were 0.67 ( $P < 0.005$ ) for the upland population, 0.38 ( $P = 0.09$ ) for the inter-

mediate population, 0.74 ( $P < 0.0001$ ) for the lowland population, and 0.48 ( $P < 0.0001$ ) overall. For **b** correlation coefficients between the combined resistance and yield at field capacity were -0.77 ( $P < 0.0005$ ) for the upland population, -0.54 ( $P < 0.01$ ) for the intermediate population, -0.79 ( $P < 0.0001$ ) for the lowland population, and -0.72 ( $P < 0.0001$ ) overall

**Table 2** Values of different traits of three populations of *P. dilatatum* from an upland, an intermediate, and a lowland site under different water conditions: drought, field capacity, and flooding. Values are means and standard errors (in brackets)

Variable	Population								
	Upland site			Intermediate site			Lowland site		
	Drought	Control	Flooding	Drought	Control	Flooding	Drought	Control	Flooding
Midday water potential (MPa)	-3.7 (0.2)	-2.0 (0.2)	-1.6 (0.2)	-4.0 (0.0)	-1.7 (0.2)	-1.6 (0.0)	-4.0 (0.0)	-1.9 (0.4)	-1.8 (0.1)
Blade (g)	0.83 (0.03)	1.43 (0.07)	1.17 (0.06)	0.76 (0.03)	1.32 (0.03)	1.24 (0.05)	0.77 (0.02)	1.26 (0.04)	1.34 (0.04)
Leaf area (cm <sup>2</sup> )	193 (8)	356 (15)	299 (13)	158 (8)	356 (9)	327 (14)	172 (7)	330 (9)	347 (9)
Sheath (g)	0.88 (0.04)	1.52 (0.12)	1.36 (0.07)	0.98 (0.06)	1.50 (0.07)	1.63 (0.08)	1.01 (0.05)	1.34 (0.05)	1.69 (0.07)
Standing dead (g)	1.02 (0.05)	0.87 (0.04)	1.00 (0.05)	0.96 (0.04)	0.82 (0.04)	0.95 (0.03)	1.03 (0.03)	0.87 (0.03)	0.94 (0.03)
Crown (g)	1.99 (0.08)	2.40 (0.09)	2.52 (0.11)	2.07 (0.09)	2.50 (0.10)	2.67 (0.12)	2.29 (0.07)	2.67 (0.14)	3.20 (0.10)
Root (g)	3.53 (0.13)	3.33 (0.19)	2.48 (0.11)	2.00 (0.07)	2.20 (0.11)	2.08 (0.08)	1.97 (0.11)	2.37 (0.11)	2.14 (0.06)
Proportion of roots (g/g)	0.49 (0.01)	0.38 (0.01)	0.33 (0.01)	0.35 (0.01)	0.29 (0.01)	0.27 (0.01)	0.33 (0.01)	0.31 (0.01)	0.26 (0.00)
Plant height (cm)	6.53 (0.34)	9.36 (0.34)	12.30 (0.48)	5.93 (0.28)	7.55 (0.38)	12.75 (0.54)	5.68 (0.39)	7.08 (0.41)	11.98 (0.57)
Root porosity (%)	29.9 (1.1)	34.4 (0.7)	45.0 (1.1)	33.1 (1.0)	35.7 (0.8)	48.6 (0.9)	33.2 (0.9)	35.9 (1.2)	47.8 (0.8)

tive differences in total yield between flooding and control plants (i.e. flooding resistance) are plotted against the relative differences in yield between drought and control plants (i.e. drought resistance) of each clone. The figure shows that the three populations had some clones whose yield was unaffected by either drought or flooding (data points in the centre of the figure). In addition to these clones, the upland population showed a group of clones that were sensitive to both flooding and drought, and the intermediate and lowland populations showed a range of responses from clones negatively affected by drought and not much affected by flooding to clones little affected by drought and positively affected by flooding. This generates an overall pattern in which resistance to drought and flooding appear positively related, since the clones most affected by flooding were most affected by drought and those favored by flooding were insensitive to drought. This pattern could not be seen at the population level shown by Fig. 1, since the three populations as a whole were equally sensitive to drought. Fig. 2a also shows that rather than being discrete entities, the populations form a continuum of response to both factors and mainly differ in the proportion of clones with particular responses. The combined resistance of each clone to both factors (see methods) was negatively related to total yield at field capacity (Fig. 2b). Other allometric or morphological variables were much less related to resistance.

The negative effects of drought on plant yield (Fig. 1) were accompanied by similar decreases of leaf water potentials at midday, blade biomass and area, sheath biomass, and crown biomass in the three populations (Ta-

bles 1 and 2). Root biomass was less reduced by drought than the other compartments and the extent of reduction increased from upland through lowland (significant interaction, Tables 1 and 2). This resulted in a significant increase of the proportion of root biomass under drought in the three populations, with this increase being greater in the upland population and lower in the lowland population.

The more complex responses to flooding observed in total yield were also registered in different plant traits, but they were not accounted for by leaf water potential, since it was not affected by flooding (Tables 1 and 2). The negative effects of flooding on the yield of the population from the upland site was the result of reductions in blade, sheath and root biomass. The neutral effect of flooding on yield of the intermediate population was the result of no changes in any of the different compartments. Finally, the positive effects of flooding on total yield of the lowland population was accounted for by a conspicuous increase in sheath and crown biomass that overcompensated for a reduction in root growth. Contrasting to the response to drought, the proportion of root biomass was reduced by flooding equally in the three populations.

Two morphological variables usually associated with flooding resistance (height and root porosity) had different means and plasticities among the populations (Tables 1 and 2). Drought reduced plant height by 24% in the three populations. Flooding, in contrast, increased height by 31% in the upland population and by 68% in the other two populations (Tables 1 and 2). Gas-filled root porosi-

ty, an estimation of the proportion of aerenchymatic tissue in the roots, was reduced by drought and increased by flooding similarly across populations (Tables 1 and 2).

At field capacity (control), the plants from the upland population grew faster, had a higher proportion of root biomass, were taller, and their roots had lower porosity than the plants from the intermediate and lowland populations. These two populations were quite similar under control conditions and only differed in their reaction norms to flooding as described above.

## Discussion

Previous studies that compared the response of different taxa (genera and species) to flooding and drought suggested that the resistance to one factor was negatively related to the resistance to the other. Baruch (1994) showed that the biomass of *Hyparrhenia rufa* and *Andropogon gayanus*, from African drylands, was reduced to a greater extent by flooding than by drought. In contrast, drought was more negative than flooding for the wetland grasses *Echinochloa polystachya* and *Brachiaria mutica*. In addition, ter Steege (1994) found a negative relation between the effects of flooding and the effects of drought on germination and survival of two species of the genus *Mora* which occupied different positions along a topographic gradient.

Our results contradict these previous findings for two reasons. First, when the three populations of *P. dilatatum* were compared, we could not observe any trade-off between the resistance to the two factors, because the three populations were equally sensitive to drought. Second, when the entire ecocline formed by the 58 clones was considered, resistance to each of the two factors appeared positively related: the clones that were more sensitive to flooding were also very sensitive to drought and those that were favored by flooding were unaffected by drought. This agrees with the intraspecific analysis of two populations of *Polygonum persicaria* made by Sultan and Bazzaz (1993), who found that resistance to drought and flooding was similar in genotypes from both populations, although only one of them lived in a flooded environment. Thus, the conclusion from intergeneric and interspecific comparisons, which may be reflecting a number of selective factors and historical constraints rather than the effects of flooding and drought alone (Stearns 1992), does not apply to the variation found within a single population: maximum resistance to both factors in *P. dilatatum* can be found simultaneously in a single genotype.

The negative relationship between yield at field capacity and the combined resistance to drought and flooding suggests that the mechanisms leading to a combined flooding-drought resistance have a cost in terms of growth capacity. This agrees with predictions from Grime's plant strategy theory, which propose both a positive correlation between the resistances to different

types of stress and a trade-off between resistance and growth potential (Grime 1979). In contrast, the negative relation between the resistances to flooding and drought among genera or species (e.g. Baruch 1994; ter Steege 1994) strongly supported the predictions of the resource ratio hypothesis, which say that resistance to factors that have opposite effects on allocation should represent a conflict that would result in strategies adapted to either factor (Tilman 1988). Although flooding and drought caused opposite effects on biomass allocation to roots and shoots, the proportion of roots did not explain the differences in resistance to either factor in *P. dilatatum*.

The positive association between flooding and drought resistance among clones should not be interpreted as a consequence of similar physiological effects of flooding and drought. Both our results and those in the literature show that the effects overlap only partially (Jackson and Drew 1984), particularly in the case of flooding-resistant species like *P. dilatatum*. For instance, flooding had no effect on midday leaf water potential (this experiment), stomatal conductance, and photosynthetic rates of *P. dilatatum* (Loreti et al. 1994), and leaf water status of flooding-resistant *Sporobolus virginicus* (Naidoo and Naidoo 1992).

The populations of *P. dilatatum* differed in some traits usually associated with the resistance to flooding or drought. The proportion of root biomass had larger mean and plasticity in the population from the upland site. On the other hand, flooding increased plant height to a larger extent in the intermediate and lowland populations than in the upland population. The ability to increase plant height is common in species from flooded environments (Naidoo and Naidoo 1992; Oosterheld and McNaughton 1991) and has been recognized as a trait conferring adaptation to flooding, since it leads to avoidance of submergence of leaf tissue by flooding water (Laan and Blom 1990). Gas-filled root porosity is one of the most important traits governing flooding resistance (Davy et al. 1990; Jackson and Drew 1984; Pezeshki 1994). Thus, the high baseline porosity values of *P. dilatatum*, which are comparable to those of typical wetland species (Justin and Armstrong 1987), may contribute to its ability to inhabit flooded sites without having conspicuous costs in terms of resistance to drought.

Finally, previous studies have shown conflicting results about the effect of flooding on the growth of *P. dilatatum*: one showed a lack of effect (Loreti et al. 1994) and another a slight promotion (Rubio et al. 1995). Each study utilized ramets of a single (but different between studies) clone from the intermediate site. Our results showed that these different responses are likely to be due to intrinsic differences between clones. Clearly, the responses to water treatments in one clone of *P. dilatatum* cannot be generalized to the whole species.

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