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Research paper

Growth potential limits drought morphological plasticity in seedlings from six *Eucalyptus* provenances

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Water stress modifies plant above- vs belowground biomass allocation, i.e., morphological plasticity. It is known that all species and genotypes reduce their growth rate in response to stress, but in the case of water stress it is unclear whether the magnitude of such reduction is linked to the genotype's growth potential, and whether the reduction can be largely attributed to morphological adjustments such as plant allocation and leaf and root anatomy. We subjected seedlings of six seed sources, three from each of *Eucalyptus camaldulensis* (potentially fast growing) and *E. globulus* (inherently slow growing), to three experimental water regimes. Biomass, leaf area and root length were measured in a 6-month glasshouse experiment. We then performed functional growth analysis of relative growth rate (RGR), and aboveground (leaf area ratio (LAR), specific leaf area (SLA) and leaf mass ratio (LMR)) and belowground (root length ratio (RLR), specific root length (SRL) and root mass ratio (RMR)) morphological components. Total biomass, root biomass and leaf area were reduced for all *Eucalyptus* provenances according to drought intensity. All populations exhibited drought plasticity, while those of greater growth potential (RGR_{max}) had a larger reduction in growth (discounting the effect of size). A positive correlation was observed between drought sensitivity and RGR_{max}. Aboveground, drought reduced LAR and LMR; under severe drought a negative correlation was found between LMR and RGR_{max}. Belowground, drought reduced SRL but increased RMR, resulting in no change in RLR. Under severe drought, a negative correlation was found between RLR, SRL and RGR_{max}. Our evidence strongly supports the classic ecophysiological trade-off between growth potential and drought tolerance for woody seedlings. It also suggests that slow growers would have a low capacity to adjust their morphology. For shoots, this constraint on plasticity was best observed in partition (i.e., LMR) whereas for roots it was clearest in morphology/anatomy (i.e., SRL). Thus, a low RGR_{max} would limit plastic response to drought not only at the whole plant level but also at the organ and even the tissue level.

Keywords: allometry, *Eucalyptus camaldulensis*, *Eucalyptus globulus*, morphological plasticity, RGR_{max}, stress tolerance.

Introduction

Species are usually classified as fast or slow growers depending on their growth potential, as expressed by the relative growth rate (RGR) of seedlings under non-limiting conditions (RGR_{max}). Several studies have pointed out the different traits of plants belonging to these two extreme types, not only under optimal growth conditions (Evans 1998, Lambers and Poorter 2004) but also under stress, particularly lack of nutrients (Ryser and Lambers 1995, Li et al. 2012, Tripathi and Raghubanshi 2014). RGR_{max} is a useful integrative variable for classifying species because of its correlation with a large number of ecophysiological and morphological traits that have influence on stress tolerance (Lambers et al. 1998, Reich 2014). For instance, fast growers usually have a high shoot–root ratio, high specific leaf area (SLA), short tissue life span and low tissue density. Moreover, many of these same traits are subject to environmental influence, i.e., have phenotypic plasticity (Valladares et al. 2007). Water stress, for example, tends to reduce SLA (Fernández and Reynolds 2000, Von Arx et al. 2012).

Optimal allocation theory suggests that plants respond to resource deficiency in a plastic way, i.e., apportioning biomass differentially to different organs (Reynolds and Thornley 1982). This tends to optimize acquisition of the limiting resource and therefore to maximize the rate of growth under those conditions (Bloom et al. 1985). The larger a species' morphological plasticity, the larger the difference in patterns of biomass allocation as resources become more limiting. The existence of morphological plasticity has been documented for various types of stress: drought (e.g., Fernández et al. 2002, Magnani et al. 2002), CO_2 (e.g., Yoder et al. 2000), nutrients (e.g., Dawson et al. 2004, Jansen et al. 2005, Kume et al. 2006) and light (e.g., Robakowski et al. 2003, Bloor and Grubb 2004, Delagrange et al. 2004, Cardillo and Bernal 2006). Besides optimizing resource acquisition, these changes result in a lower actual plant growth rate (RGR; Chapin 1991), which might be adaptive in non-competitive situations because of the ensuing reduction in resource demand and a likely positive effect on survival (Chapin 1980, Mencuccini 2014). A rigorous assessment of stress impact upon RGR, however, requires considering plant developmental stage or, for vegetative growth, plant size (e.g., Gebauer et al. 1996, McConnaughay and Coleman 1999). If these allometric changes are not taken into account, it is easy to confuse plastic responses with developmental changes (Preston and Ackerly 2003, Maseda and Fernández 2006). Moreover, development modifies not only plant size, but also its ability to respond to changes in the environment (Delagrange et al. 2004, De Kroon et al. 2005).

Reich et al. (1998) proposed the *mirror image* theory of allocation, according to which, in the absence of stress, species with a high allocation to leaves (i.e., high RGR_{max}) must be balanced by a high total root system length to support their larger water and nutrient requirements. However, responses to stress can differ not only for different organs, but also for different levels of organization, for example, shoot vs leaf (Funk et al. 2007), or whole-plant vs root (Couso and Fernández 2012). Thus, the existence of coordination between above- and belowground plant part traits is far from being well understood (Liu et al. 2010).

This paper aims to advance our understanding of the plastic (ontogenic) above- and belowground responses to drought in eucalypt seedlings, using classical morphological growth analysis and taking allometry into account (Fernández et al. 2002). We have previously presented a hydraulic model of acclimation to drought (Maseda and Fernández 2006). Mitchell et al. (2013) have shown that fast growing eucalypts exhibit a less conservative (more anisohydric) hydraulic strategy in comparison with a slower growing species. Taking advantage of the wide RGR_{max} range of the genus *Eucalyptus*, here we seek to explore in further depth the influence of growth potential (RGR_{max}) by addressing three related issues: first, if *Eucalyptus* spp. genotypes that differ in their constitutive growth potential predictably differ in drought tolerance. Second, whether these species/genotypes also differ in their morphological adjustment in response to water stress. And, finally, we addressed whether aboveground morphological adjustments are mirrored belowground.

Materials and methods

Species

Seeds of *Eucalyptus globulus* ssp. *globulus* (Cradoc Hill, Tasmania, Australia), *E. globulus* ssp. *maidenii* (Wog Way Road, New South Wales, Australia), *E. globulus* ssp. *bicostata* (Tumbarumba, New South Wales), *Eucalyptus camaldulensis* ssp. *obtusa* (Lake Arrowsmith, Western Australia, Australia), *E. camaldulensis* ssp. *obtusa* (Wiluna, Western Australia), *E. camaldulensis* ssp. *obtusa* (Lake Coorong, Victoria, Australia) were obtained from Kylisa seeds Pty Ltd (Weston, ACT, Australia). The provenance of these populations represents humid, subhumid and semiarid environments (Table 1).

Plant culture

Several seeds from each of the six *Eucalyptus* provenances were sown on moistened filter papers in plastic boxes (10 × 25 cm) in a dark growth chamber at a constant temperature of 20 °C. Once seeds germinated (7–12 days) 200 seedlings of similar size were selected and transplanted to forestry trays (Dassplastic-40) in a refrigerated glasshouse with natural light regime. A coarse-fibrous cellulose-based forestry commercial substrate (Klasmann brand) was used and all the seedlings were kept at field capacity during the entire acclimation process. After 75 days (at the beginning of spring) 120 seedlings of similar size for each species were selected and transplanted to plastic pots (volume: 1000 cm^3), containing fine sand (<250 µm). Transplanting date was considered as time zero for the experiment. The base of each pot was fitted with a fine nylon cloth to allow air and nutrient solution exchange, while preventing root

Table 1. Mean annual precipitation at the seed collection site of the six *Eucalyptus* provenances.

Provenance	Code	Latitude	Longitude	Mean annual precipitation (mm)
E. globulus ssp. *bicostata* (Tumbarumba)	Egb	35°45′S	148°00′E	982
E. globulus ssp. *globulus* (Cradoc Hill)	Egg	43°07′S	147°05′E	878
E. globulus ssp. *maidenii* (Wog Way Road)	Egm	37°11′S	149°28′E	1050
E. camaldulensis ssp. *obtusa* (Lake Coorong)	Ecc	35°44′S	142°23′E	400
E. camaldulensis ssp. *obtusa* (Wiluna)	Ecw	26°35′S	120°14′E	250
E. camaldulensis ssp. *obtusa* (Lake Arrowsmith)	Eca	29°33′S	115°05′E	600

passage. All plants had been kept well watered until drought treatments began, at Week 2. Drought was imposed using a modified version of the method proposed by Snow and Tingey (1985), as described by Fernández and Reynolds (2000). This is a sub-irrigation technique which allows constant and uniform water potential in pots that sit on top of a column of hygroscopic foam along which the nutrient solution rises through capillary action. A hydrosoluble commercial fertilizer (KSC phitactyl II, Roullier s.a.) containing N : P : K (23 : 5 : 5) and micronutrients was used for mineral nutrition of plants at 3 g l^{-1}.

Experimental conditions

The experiment was performed in a refrigerated glasshouse under natural photoperiod (mean ± SE noon inside PAR = 663 ± 369 μmol m^{-2} s^{-1}) at Facultad de Agronomía, Universidad de Buenos Aires (latitude 34°35′S, longitude 58°28′W), for a duration of 18 weeks. Daily maximum and minimum temperatures and relative humidity (mean ± SE) were: 33.2 ± 10.8 and 17.1 ± 3.0 °C, and 90.3 ± 10.8 and 45.2 ± 22.4%, respectively. This experiment was a 3 × 6 factorial, with five replications. A split-plot design was used, with three levels of drought as main plots and six provenances of *Eucalyptus* as sub-plots. Fifteen groups of 36 pots each (six pots per provenance, one plant per pot) were placed in a 140-l plastic container housing a 28-cm-tall column of commercial Styrofoam (no. 0140; Smithers-Oasis; Kent, OH, USA). The foam was repeatedly rinsed with water as recommended by the manufacturer before the installation of plants. The 15 containers were randomly assigned to the three drought treatments, with five replications each. Based on a previous pilot experiment (unpublished), we chose water levels so as to obtain three drought intensities: 100% (control, C), 72% (moderate drought, DI) and 51% (severe drought, DII) of field capacity. These stress levels were attained by partially filling the containers until the nutrient solution was 5 cm (control; no drought), 10 cm (moderate drought), and 17.5 cm (severe drought) below the base of the pots. Keeping a constant nutrient solution height ensures uniform and repeatable water availability in the pots (Saulescu et al. 1995).

Morphological variables

Before transplanting, an initial harvest of 30 seedlings of each provenance was made. The other two harvests involved 15 plants per treatment each, and were carried out at Weeks 13 and 18. Each plant was separated into leaves, stems and roots; then, all plant material was dried at 80 °C until constant weight. Before drying the leaves, their area was measured using a leaf-area meter (Li-Cor 3100; LI-COR Inc., Lincoln, NE, USA). Subsamples of the root system were immediately scanned with an image-device system to determine their length. Finally, total biomass for each treatment was calculated.

Data analyses

We performed functional growth analyses (Hunt 1982) by fitting a second-order polynomial of log-transformed total biomass (ln W_T), log-transformed leaf area (ln LA), and log-transformed root length (ln RL) over time. Following equations shown in Table 2, we then calculated relative growth rate (RGR), leaf area ratio (LAR), root length ratio (RLR), leaf-based net assimilation rate (NAR_L), and root-based net assimilation rate (NAR_R).

Maximum relative growth rate (RGR_{max}) was calculated as the maximum slope of the ln W_T–time function for the 'no drought' treatment (control; Fernández et al. 2002). To eliminate the size effect on RGR with ontogeny (i.e., allometric effect), we calculated the RGR for a fixed development time (i.e., at same size, assuming *size* is a good predictor for development stage during vegetative growth) for all of the water availability levels. In addition, we calculated a water availability index (sensu Stearns 1992) to characterize the drought intensity: this was, at equal plant size, the average RGR for all *Eucalyptus* provenances at each drought treatment. Afterwards, for each provenance, we adjusted a linear regression between fixed-size RGR and the water availability index. Then we calculated, for each treatment

Table 2. Growth-analysis terms and relationships, based on Hunt (1982).

Organ	Abbreviation	Meaning	Equation
Whole plant	W_T	Total biomass	
	RGR	Relative growth rate	$(dW_T/dt)\ 1/W_T = LAR \times NAR_L$ or $(dW_T/dt)\ 1/W_T = RLR \times NAR_R$
	LAR	Leaf area ratio	$LA/W_T = LMR \times SLA$
	NAR_L	Leaf-based net assimilation rate	$(dW_T/dt)\ 1/LA = RGR/LAR$
	RLR	Root length ratio	$RL/W_T = RMR \times SRL$
	NAR_R	Root-based net assimilation rate	$(dW_T/dt)\ 1/RL = RGR/RLR$
Leaf	LA	Leaf area	
	M_L	Leaf mass	
	LMR	Leaf mass ratio	M_L/W_T
	SLA	Specific leaf area	LA/M_L
Root	RL	Root length	
	W_R	Root mass	
	RMR	Root mass ratio	M_R/W_T
	SRL	Specific root length	RL/M_R

modelled, the specific leaf area and leaf mass ratio (SLA and LMR; Table 2) at equal plant size, to eliminate the effect of size. Analogously, we calculated the specific root length and root mass ratio (SRL and RMR; Table 2). Then we adjusted a linear regression between morphological components and RGR_{max}.

To assess the effects of provenance and water regime, we performed an analysis of variance (ANOVA) and linear regressions using Prism (Version 4.0, GraphPad Software Inc., San Diego, CA, USA) data analysis software. Departure from normality and homogeneity of variances were also tested for each variable. All statistically significant differences were tested at the $P < 0.05$ level. Further details are given in figure and table legends.

Results

A threefold range of seedling RGR_{max} was found among our six *Eucalyptus* provenances (last column of Table 3). *Eucalyptus camaldulensis* behaved as the fastest growing species; all its genotypes showed larger RGR_{max} than those of *E. globulus*. There was no significant relationship ($P = 0.073$) between RGR_{max} and mean annual precipitation at the seed collection site.

RGR_{max} and drought tolerance

For all provenances, total biomass, belowground biomass and total leaf area were reduced as the intensity of drought increased (Table 3). At the end of the experiment, the three *E. globulus* provenances decreased, on average, total biomass (64%) and root biomass (41%) to a lesser degree than the three *E. camaldulensis* provenances (73 and 62%, respectively). Specifically, Egb was the material that reduced total biomass (60%) and root biomass (33%) the least, while Eca reduced them the most (74 and 63%, respectively). These provenances were also the two extremes regarding growth potential with the former almost doubling the latter Egb: 115 mg g^{-1} day^{-1}; Eca: 301 mg g^{-1} day^{-1}; Table 3). For leaf area, on the other hand, the average reduction by severe drought with respect to controls was very similar between species (73% *E. globulus* vs 76% *E. camaldulensis*).

Actual RGR diminished during ontogeny for all the *Eucalyptus* provenances, and this reduction was strongest for seedlings cultivated under drought (Figure 1). Moderate drought (DI) caused RGR reductions for all *E. camaldulensis* provenances (Figure 1d–f), but none of the *E. globulus* provenances (Figure 1a–c). The severe-drought treatment (DII) reduced RGR significantly for all materials. At equal biomass size (i.e., 3000 mg DM), RGR diminished with drought intensity for all *Eucalyptus* provenances (Figure 2a). Ecw and Eca were the provenances with the strongest reduction in growth (i.e., more sensitivity to drought), whereas Egb and Ecl were the provenances with the least reduction. A positive correlation was observed between drought sensitivity and growth potential: high RGR_{max} provenances were more affected than lower RGR_{max} provenances (Figure 2b).

Drought and morphological plasticity

For all provenances, the reduction of RGR by drought was explained by a proportional reduction of both LAR and NAR (data not shown). Insets in Figure 3 summarize the main effects of drought on morphological variables pooling all species/genotypes. Drought reduced LAR significantly (inset in Figure 3a_1), yet did not affect the SLA subcomponent (inset in Figure 3a_2). The reduction in LAR was explained by the proportion of total biomass allocated to leaves (inset in Figure 3a_3). Drought did not reduce RLR (inset in Figure 3b_1). Both SRL and RMR were significantly affected by drought, but in opposite directions (compare insets in Figure 3b_2 and b_3). The high reduction of SRL under drought was compensated by a significant increase in RMR (the belowground allocation subcomponent), with the result that no change in RLR occurred (the belowground morphological component; see Table 2).

Aboveground vs belowground plasticity

After correcting for allometry, and analysing only the morphological component of growth for above- and belowground parts (LAR and RLR, respectively), differences were also found in response to water stress. Aboveground, although higher RGR_{max} species tended to show greater morphological plasticity, there was not a significant correlation between LAR and RGR_{max} (Figure 3a_1), nor between SLA and RGR_{max} (Figure 3a_2). However, a significant negative correlation was found between LMR

Table 3. Morphological variables at the end of the experiment (125 days of treatment), and estimated maximum relative growth rate (RGR_{max}) for the six *Eucalyptus* provenances. C, control, no drought; DI, moderate drought; DII, severe drought. Different letters within each provenance and variable indicate significant difference with $P < 0.05$. Ordered by RGR_{max}.

Code	Treatment	Total biomass (g DM $plant^{-1}$)	Root biomass (g DM $plant^{-1}$)	Leaf area (cm^2)	RGR_{max} (mg g^{-1} day^{-1})
Egb	C	10.89[a]	2.09[a]	936[a]	115
	DI	8.92[b]	2.17[a]	673[a]	
	DII	4.43[c]	1.41[b]	286[b]	
Egg	C	14.78[a]	3.22[a]	1297[a]	145
	DI	11.07[b]	2.72[a]	846[b]	
	DII	5.00[c]	1.83[b]	338[c]	
Egm	C	13.32[a]	3.05[a]	1251[a]	160
	DI	9.54[b]	2.29[b]	843[b]	
	DII	4.50[c]	1.58[c]	313[c]	
Ecc	C	16.42[a]	4.52[a]	584[a]	223
	DI	9.83[b]	2.99[b]	351[b]	
	DII	4.56[c]	1.71[c]	152[c]	
Ecw	C	11.46[a]	3.66[a]	444[a]	258
	DI	6.82[b]	2.47[b]	266[b]	
	DII	3.08[c]	1.43[c]	101[c]	
Eca	C	11.43[a]	3.73[a]	573[a]	301
	DI	8.05[b]	2.71[b]	444[a]	
	DII	2.94[c]	1.38[c]	132[b]	

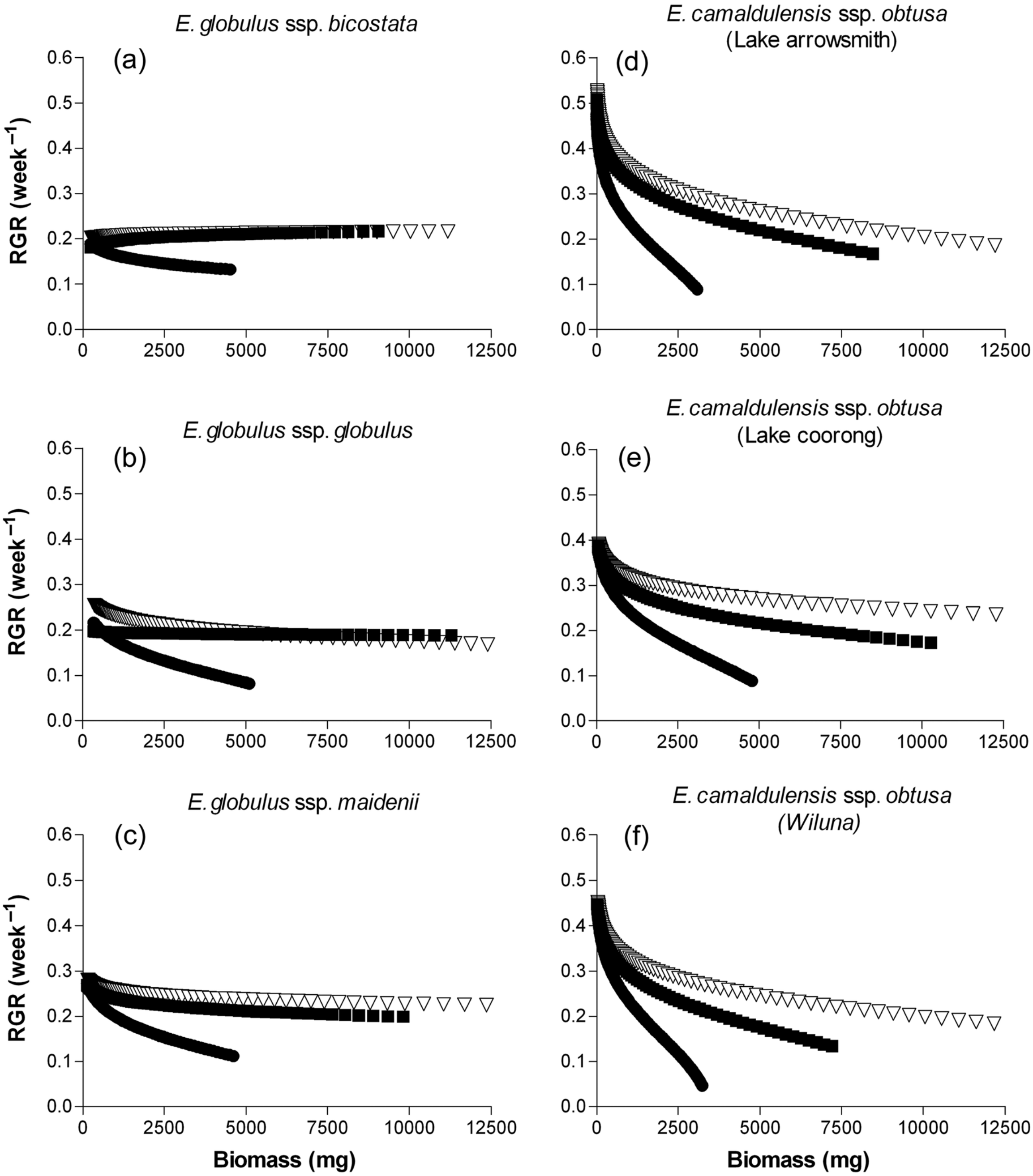

Figure 1. Dynamics of relative growth rate as a function of plant size for six *Eucalyptus* provenances growing under three water availability levels: open triangles: C, no drought; closed squares: DI, moderate drought; closed circles: DII, severe drought. The last point of each curve represents the same time: end of the experiment after 125 days of treatment.

and RGR_{max}, although only for the severe-drought treatment (Figure 3a_3). Belowground, again, only the severe-drought treatment showed a significant negative correlation between RLR and RGR_{max} (Figure 3b_1). Specific root length also showed a significant negative correlation with RGR_{max} for the severe-drought treatment (Figure 3b_2). No significant correlations with growth potential were found for RMR (Figure 3b_3). In other words, for LMR and SRL, the drought intensity and growth potential of the genotype conditioned the level of response.

Discussion

We wondered whether drought responses at the seedling stage differed among genotypes of *Eucalyptus* with different growth potential, and the answer was affirmative (Figure 2b). The eucalypt genus turned out to be a good study system because of its large variability in seedling RGR_{max} (Table 3), as previously reported by Warren and Adams (2005). Figure 2a is a size-corrected norm of reaction showing the provenances' response to drought. A genetic component in the phenotypic variation was

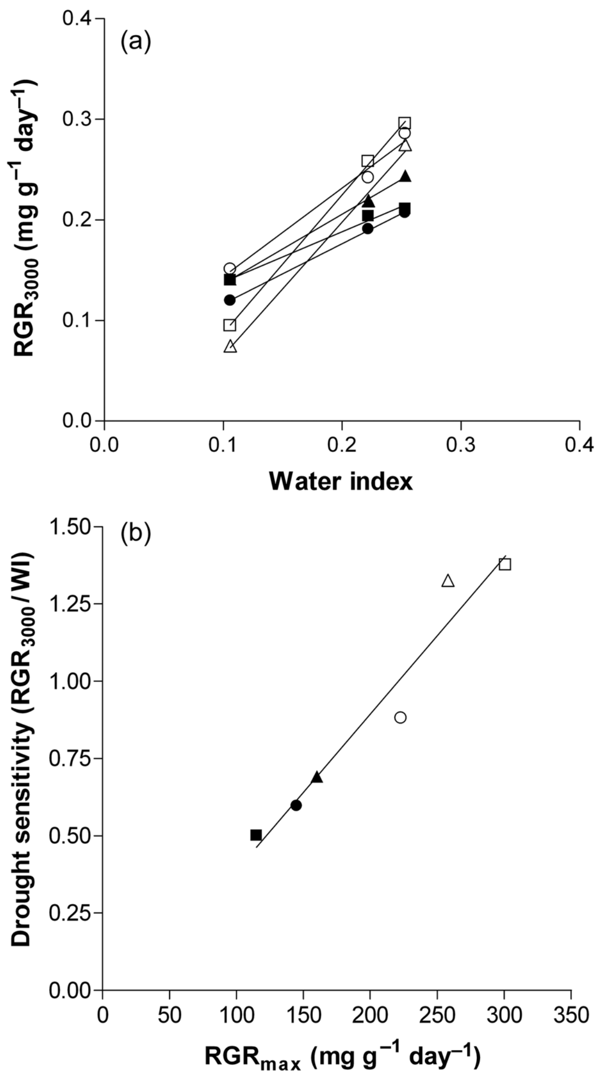

Figure 2. (a) Fixed-size relative growth rate for six *Eucalyptus* provenances as a function of drought intensity. The water index was calculated as the RGR average of all provenances at each drought treatment. Open triangles: *E. camaldulensis* ssp. *obtusa* (Wiluna): $r^2 = 0.99$, $P = 0.05$; open circles: *E. camaldulensis* ssp. *obtusa* (Lake Coorong): $r^2 = 0.98$, $P = 0.09$; open squares: *E. camaldulensis* ssp. *obtusa* (Lake Arrowsmith): $r^2 = 0.99$, $P = 0.01$; closed circles: *E. globulus* ssp. *maidenii* (Wog Way Road): $r^2 = 0.99$, $P = 0.02$; closed circles: *E. globulus* ssp. *globulus* (Cradoc Hill): $r^2 = 0.99$, $P = 0.02$; closed squares: *E. globulus* ssp. *bicostata* (Tumbarumba): $r^2 = 0.99$, $P = 0.07$. (b) Drought sensitivity (slope of (a)) for six *Eucalyptus* provenances related to potential growth rate. $y = 23.48 + 0.005x$, $r^2 = 0.94$. Symbols are the same as in (a).

observed, and the fact that some of them were not parallel (i.e., had different slopes) suggests a strong genotype × environment interaction (Stearns 1992). The positive correlation found between those slopes and the RGR_{max} of each provenance (Figure 2b) upholds the classic ecophysiological tenet, largely untested for water deficits, about the existence of a *trade-off* between growth potential and drought tolerance (Bazzaz 1996). This would reflect a morpho-physiological constraint on evolutionary time, i.e., on the adaptation to drought.

We have also asked whether these species/genotypes differed in morphological adjustment in the face of drought, and we showed that they do: slow growers (low RGR_{max}) displayed a lower capacity than fast growers to adjust morphology (see Couso and Fernández 2012). The investment in light-intercepting area (LAR) was significantly reduced by drought, while the capacity to absorb water (RLR) was unchanged (Figure 3a_1 and b_1). Since slow growers did not show LAR differences between drought levels (Figure 3a_1), it seems that growth potential constrains aboveground plasticity. Warren and Adams (2005) have shown that slow-growing *Eucalyptus* species constitutively allocate more biomass to roots and described this response as an adaptation to soil water deficits, which was confirmed in our study (Figure 3b_1).

Specific leaf area and SRL describe the geometry of plant acquisition surfaces, both also associated with anatomy, because of their dependence on organ thickness and tissue density (Cambridge and Lambers 1998). Under drought, no provenance showed a significant reduction in SLA at a common plant size (Figure 3a_2). Perhaps, this lack of plasticity for SLA was conditioned by *Eucalyptus*' naturally long leaf life span (Reich 1998), as expected from the high correlation observed between life span and tissue density (Ryser 1996), and the importance of the latter in the determination of SLA (Lambers et al. 1998). Marron et al. (2002) working with *Populus* sp. clones (a species with relatively short leaf life span) found a drastic reduction in SLA under drought. In contrast with SLA responses, the reduction in SRL under severe drought was strongest for fast growing genotypes (Figure 3b_2), which reflects their higher plasticity. These results are consistent with the notion that a high SRL confers more efficiency for depleting soil moisture under high availability of water. Likewise, a low SRL could reduce the amount of water lost to the soil if soil water potential falls below root water potential (Trillo and Fernández 2005), as could have happened in the severe drought level of this experiment. Regarding allocation behaviour, the reduction of LMR under severe drought was again strongest for fast growing genotypes (Figure 3a_3); in contrast, there was a lack of response for RMR (Figure 3b_3). The change in allocation promoted by drought is a commonly expected acclimation response as previously shown for seedlings of *Eucalyptus* (Costa e Silva et al. 2004), *Pinus* and *Quercus* (Baquedano and Castillo 2006), which in our study occurred along the entire RGR_{max} range.

Finally, we wondered whether seedling root morphological responses to drought mirror shoot responses: the answer was negative. While aboveground adjustments were mainly explained by changes in biomass allocation, belowground responses involved changes not only in allocation but also in morphology/anatomy. This could be interpreted as a balancing, homeostatic response resulting in a similar root length per unit of plant biomass (RLR).

A growing body of evidence suggests that plants coordinate their response to drought at different levels of organization

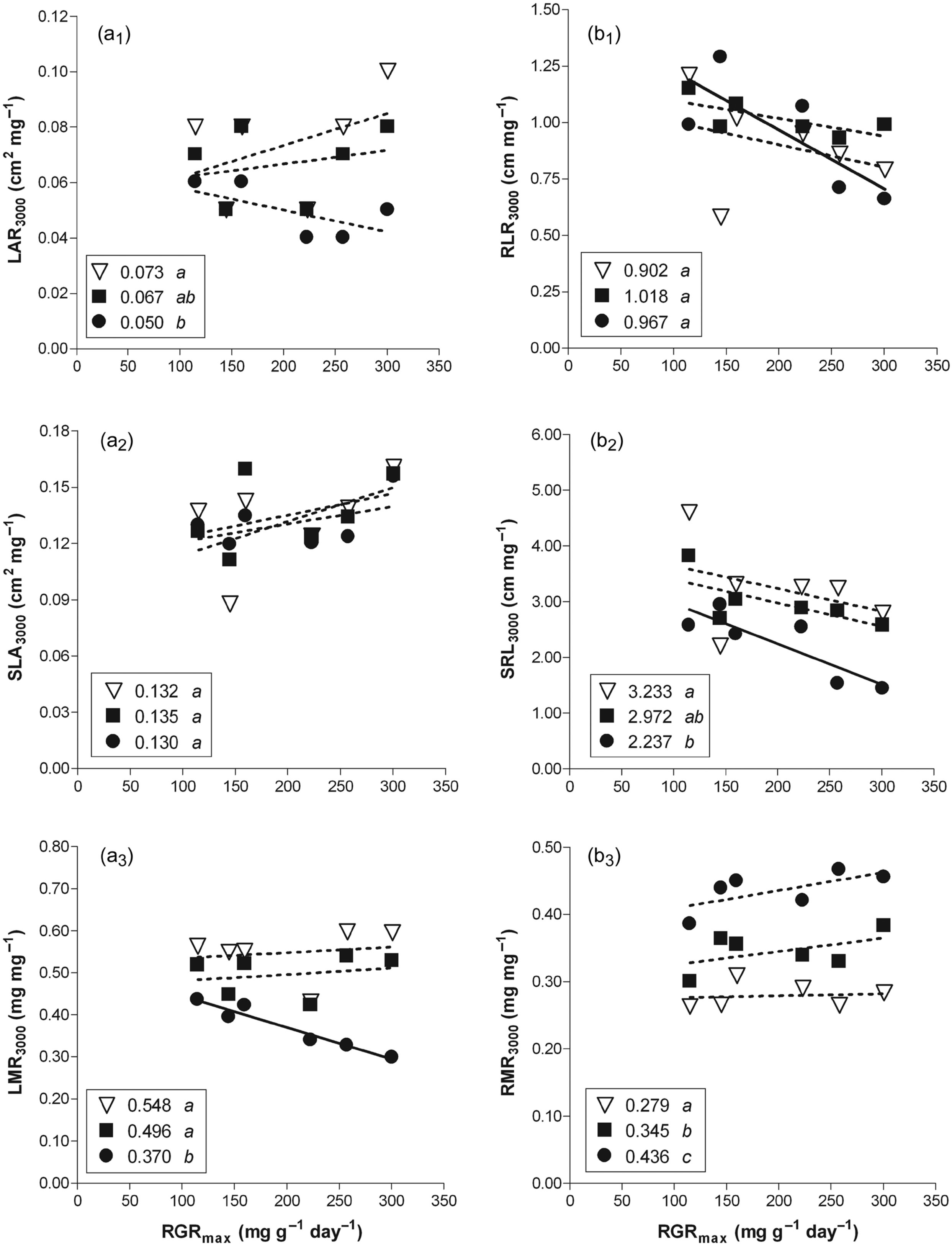

Figure 3. Drought effect on above- (a) and belowground (b) morphological components in six *Eucalyptus* provenances with different growth potential. Open triangles: C, no drought; closed squares: DI, moderate drought; closed circles: DII, severe drought. LAR, leaf area ratio; RLR, root length ratio; SLA, specific leaf area; SRL, specific root length; LMR, leaf mass ratio; RMR, root mass ratio. All points show plants of 3000 mg; continues line: significant regression; dotted line: non-significant regression. Insets display the mean for each drought treatment. Different letters on the same box indicate significant ($P < 0.05$) differences.

(Mencuccini 2014) and, in similar ways, across time scales (Chapin et al. 1993). For inter-species comparisons, Reich (2014) has recently proposed that the general leaf economics spectrum can be condensed in a fast–slow summarizing axis that includes wood density and plant hydraulic properties. Our previous model of whole-plant hydraulic plasticity (Maseda and Fernández 2006) hypothesized that the degree of leaf area adjustment is linked to stomatal behaviour, with rather fixed phenotypes expected to be isohydric (tight control of leaf water potential) and plastic ones expected to be anisohydric (looser stomatal control). Here we speculate that, under drought, high RGR_{max} genotypes or species will be anisohydric while maintaining both leaf area and water-transport capacity (leaf-specific hydraulic conductivity), whereas low RGR_{max} genotypes or species will tend to be isohydric while having a higher reduction of both leaf area and water-transport capacity. Thus, RGR_{max} would be a predictor not only of whole-plant responses to drought but also of tissue-level plasticity in properties such as xylem resistance to cavitation and therefore wood density.

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Conflict of interest

None declared.

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