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Publication Date

DOI

Peer reviewed

Above- and below-ground plant traits are not consistent in response to drought and competition treatments

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- **Background and Aims** Our understanding of plant responses to biotic and abiotic drivers is largely based on above-ground plant traits, with little focus on below-ground traits despite their key role in water and nutrient uptake. Here, we aimed to understand the extent to which above- and below-ground traits are co-ordinated, and how these traits respond to soil moisture gradients and plant intraspecific competition.
- **Methods** We chose seedlings of five tropical tree species and grew them in a greenhouse for 16 weeks under a soil moisture gradient [low (drought), medium and high (well-watered) moisture levels] with and without intraspecific competition. At harvest, we measured nine above- and five below-ground traits of all seedlings based on standard protocols.
- **Key Results** In response to the soil moisture gradient, above-ground traits are found to be consistent with the leaf economics spectrum, whereas below-ground traits are inconsistent with the root economics spectrum. We found high specific leaf area and total leaf area in well-watered conditions, while high leaf dry matter content, leaf thickness and stem dry matter content were observed in drought conditions. However, below-ground traits showed contrasting patterns, with high specific root length but low root branching index in the low water treatment. The correlations between above- and below-ground traits across the soil moisture gradient were variable, i.e. specific leaf area was positively correlated with specific root length, while it was negatively correlated with root average diameter across moisture levels. However, leaf dry matter content was unexpectedly positively correlated with both specific root length and root branching index. Intraspecific competition has influenced both above- and below-ground traits, but interacted with soil moisture to affect only below-ground traits. Consistent with functional equilibrium theory, more biomass was allocated to roots under drought conditions, and to leaves under sufficient soil moisture conditions.
- **Conclusions** Our results indicate that the response of below-ground traits to plant intraspecific competition and soil moisture conditions may not be inferred using above-ground traits, suggesting that multiple resource use axes are needed to understand plant ecological strategies. Lack of consistent leaf–root trait correlations across the soil moisture gradient highlight the multidimensionality of plant trait relationships which needs more exploration.

Key words: Abiotic factors, biomass allocation, biotic factors, biotic interactions, drought, environmental factors, functional traits, leaf traits, plant–soil interactions, root traits, soil moisture gradient, seedlings.

INTRODUCTION

Functional traits have been used to explain plant responses to alterations in water availability. However, our understanding of plant water use strategies is still mostly based on above-ground plant traits (Lorts and Lasky, 2020; Anderegg *et al.*, 2021), with less attention to below-ground plant traits despite their key role in predicting plant responses to global change factors (Bardgett *et al.*, 2014; Laliberté, 2017). Due to the limited consideration of below-ground plant traits, a general view of plant water use strategies remains elusive. Accounting for below-ground plant

traits together with their above-ground counterparts may help to better understand mechanisms of plant adjustment to biotic and abiotic changes (de la Riva *et al.*, 2016; Weemstra *et al.*, 2016).

Empirical evidence on whether above- and below-ground traits co-ordinate in response to different soil water conditions is limited, despite the prediction of these traits being integrated in response to variable environmental conditions (Reich, 2014). The widely known leaf economics spectrum, based on above-ground traits, describes plant functional strategies ranging from acquisitive under adequate resource availability to conservative

in resource-limited environments (Wright *et al.*, 2004). A similar spectrum has also been proposed for roots (root economics spectrum, but to what extent leaf-based resource use trade-offs can be extended to below-ground plant traits has been poorly investigated, especially under different environmental conditions (Weemstra *et al.*, 2016). Consistent leaf–root trait correlations are expected across resource gradients if plant resource use spectra are common in both organs (Reich, 2014). Leaf and root traits are predicted to align and co-ordinate along a one-dimensional axis from resource-acquisitive to resource-conservative traits that maintain species metabolic processes providing support for the extension of leaf and root economics spectra to a whole-plant economics spectrum (Freschet *et al.*, 2010). Castorena *et al.* (2022) also indicated that leaves and roots should be aligned into a resource acquisitive–conservative strategy scaling up to the whole-plant economics spectrum because a fast–slow plant economics spectrum should arise from trait combinations whereby the amount of energy gained from autotrophic organs (leaves) and the amount of energy required for investment in heterotrophic organs (roots, stems and flowers) are similar over the life span of plants. The few studies that tested this hypothesis found diverse results, suggesting that plants may adopt alternative resource use strategies across resource gradients. For instance, Lozano *et al.* (2020) found a strong relationship between root traits and shoot biomass under drought conditions, compared with non-drought conditions, suggesting that root–leaf trait correlations are influenced by soil moisture conditions. Root traits have been found to drive leaf physiological activities of herbaceous plants in response to precipitation (Zhang *et al.*, 2020), providing support for leaf–root trait co-ordination. In contrast, some studies reported that root and leaf traits may not be co-ordinated in response to drought conditions due to different plant physiological and morphological adjustments (Brunner *et al.*, 2015; Weemstra *et al.*, 2016), indicating that traits from different plant organs may operate independently over variable environmental conditions. For instance, the leaf trait response to drought is similar for a large set of plant species while the root trait response is variable and highly dependent on the plant species identity (Lozano *et al.*, 2020), showing that above- and below-ground traits are not uniform in response to soil moisture availability.

Plants reveal a range of below-ground resource use strategies in response to changing water conditions (Bardgett *et al.*, 2014). Under dry conditions, plants largely invest in below-ground traits with greater root allocation, and thick, deep and long-lived roots following a conservative resource use strategy (Yang *et al.*, 2011; Larson and Funk, 2016). On the other hand, plants show an acquisitive resource use strategy by investing little energy below-ground, with thin and short-lived roots, under sufficient moisture conditions (Larson and Funk, 2016). This trade-off reflects a major axis of morphological trait variation in plant water use strategies. However, this pattern of water use strategy has not been consistently found among plant species. For instance, to maximize water acquisition under dry conditions, thinner roots with high specific root length (SRL) and specific root surface area (SRSA) have been observed (Comas *et al.*, 2013) while other species have been shown to develop thicker roots with low SRL and SRSA under dry conditions to minimize hydraulic failure (Larson and Funk, 2016). These contrasting results highlighted differences among species in water use strategies, as some plants may increase thinner roots while others may increase thicker roots as a strategy to face drought (Lozano *et al.*, 2020).

Plants encounter not only abiotic stressors (soil moisture limitation) but also biotic stressors such as interacting with conspecific neighbours, leading to competition. The combined effects of soil moisture conditions and plant intraspecific competition on above- and below-ground traits have rarely been tested. Plants adjust their morphological and physiological traits in response to plant competition (Abakumova *et al.*, 2016). However, how intraspecific competition can affect plant traits' adjustment to drought is still unclear. Compared with interspecific competition, a stronger effect of intraspecific competition on traits is expected, particularly under limited water resources, due to ecological niche overlap among conspecifics (Hooper *et al.*, 2005). In terms of above-ground traits, plants have been shown to respond differently to competition under different soil moisture conditions, with an increase in specific leaf area (SLA) under drought while no effect was observed under well-watered conditions (Lorts and Lasky, 2020), showing a moisture-dependent effect of competition on plant traits. Also, under drought conditions, competition has been shown to favour both resource-acquisitive traits (Farrior *et al.*, 2013) and resource-conservative traits (Guo *et al.*, 2020), indicating that competition may promote diverse resource use strategies among plants. Beyer *et al.* (2013) indicated that intraspecific competition did not change the functional strategies of root morphological traits. However, the response of traits to plant intraspecific competition under different soil moisture conditions has not been widely tested. Therefore, investigating how local biotic (plant intraspecific competition) and abiotic (soil moisture) conditions interactively determine above- and below-ground resource use strategies of plants is important to predict future plant response to environmental change.

Plants also balance energy allocation between above- and below-ground organs to maximize efficiency of resource utilization (Veresoglou and Peñuelas, 2019), but it remains unclear how the allocation varies with plant competition under different soil moisture conditions. According to the functional equilibrium hypothesis, plants allocate more biomass to above-ground organs when there is above-ground resource limitation and to below-ground organs if there is below-ground resource limitation for growth (Brouwer, 1962). Regarding the effect of soil moisture on biomass allocation, contrasting results have been reported as research has found that root biomass increased (Bai *et al.*, 2010), decreased (Frank, 2007) or remain unaffected (Wilcox *et al.*, 2015) with increasing soil moisture availability, suggesting that multiple mechanisms are involved in soil moisture–biomass allocation relationships. Few studies have investigated plant biomass allocation in response to competition and how this depends on soil moisture availability. In one example, Lorts and Lasky (2020) found that the effect of competition on biomass allocation of arabidopsis genotypes was smaller under well-watered conditions, compared with dry conditions. However, how soil moisture availability mediates the effect of competition on plant biomass allocation, particularly for multiple species, remains to be tested. Therefore, investigating competition–biomass allocation relationships at different soil moisture levels may help to understand plant energy allocation strategies in response to biotic and abiotic changes.

The aim of this study was to examine and compare the response of above- and below-ground traits and patterns of biomass allocation to soil moisture and plant competition treatments. We addressed the following questions. (1) Do above- and below-ground traits show parallel responses to soil moisture, plant competition treatments and their combined effects? We hypothesized that above- and below-ground traits would be consistently correlated and have similar responses to soil moisture and plant competition treatments. Following resource use economics spectra, acquisitive and conservative leaf and root traits are expected to trade-off along a single functional axis if the plant economics spectrum is common in both organs, showing a unified functional strategy at the whole-plant level (Reich, 2014). (2) How do plant growth and biomass allocation change with soil moisture and plant intraspecific competition treatments? Consistent with the functional equilibrium hypothesis, we hypothesized that biomass allocation to above- and below-ground organs would shift with a soil moisture availability gradient, i.e. more biomass would be allocated to below-ground organs when there was soil moisture limitation and/or intraspecific competition, and to above-ground biomass under sufficient soil moisture and/or in the absence of intraspecific competition (Brouwer, 1962).

MATERIALS AND METHODS

Experimental design

We selected five common plant species in a 20 ha Xishuangbanna seasonal tropical rain forest dynamics plot in Yunnan, south-west China (21°37′08″N, 101°35′07″E, 869 m asl): *Aphananthe cuspidata* (Ulmaceae), *Breynia fruticosa* (Euphorbiaceae), *Macaranga denticulata* (Euphorbiaceae), *Mallotus barbatus* (Euphorbiaceae) and *Sapium baccatum* (Euphorbiaceae). These plant species have a range of ecological distributions spanning different local environments. For details on species characteristics, see Supplementary data Table S1. Seeds were randomly collected from different mature trees (multiple mother trees for each species) growing in the same field in 2018. The seeds were surface sterilized in 1 % potassium permanganate solution and stored at 4 °C. In a greenhouse under natural light conditions, we germinated the seeds in a seed bed filled with soil rich in sand. This experimental study was carried out in a greenhouse at Xishuangbanna Tropical Botanical Garden (21°54′30″N, 101°46′59″E, 580 m asl) which is characterized by a mean annual temperature and rainfall of, respectively, 21.8 °C and 1493 mm (Cao *et al.*, 2006).

We established three different soil moisture treatments representing low (considered as dry), medium (considered as control) and high (considered as wet) moisture contents, respectively, with 10, 25 and 35 % soil moisture content. These soil moisture treatments were selected to represent the soil moisture content in the field between the lowest and the highest rainfall period in Xishuangbanna tropical rain forests. i.e. in a nearby field site, the soil moisture content ranged from 10 % in the dry season to 40 % in the rainy season (Li *et al.*, 2012). We filled pots (24 cm diameter and 20 cm height) with a soil rich in sand that is similar to the soil where the plant species naturally grow. The soil was collected from a nearby field site

and it is characterized by low water-holding capacity. Since we are simulating the precipitation patterns of the region, we watered the seedlings daily to maintain 10, 25 and 35 % of the soil moisture. These moisture levels were kept throughout the experiment by measuring the volume water content (VWC) daily using a conductivity probe (Theta probe MPM-160B, ICT International Pty Ltd, Armidale, New South Wales, Australia) from ten randomly selected pots in each treatment. We used the average VWC from these pots to estimate the amount of water to be added to all pots to ensure that all individual plants grew under the selected soil water content. After watering, we re-measured the moisture content of the ten randomly selected pots in each water treatment to ensure that the target soil moisture content was maintained (Supplementary data Fig. S1).

For each soil moisture treatment, 15 pots were used for each plant species. Ten of these pots were transplanted with one individual (30 d after germination) while in the other five pots we grew four conspecific individuals per pot (intraspecific competition). We thus have 5 plant species × 3 moisture treatments × 15 replicates which gives a total of 225 pots, i.e. 150 pots for individuals and 75 pots for the intraspecific competition. All seedlings were subjected to the same ambient temperature in the greenhouse throughout the experiment. As the seedling transplantation was finished in a day, the chosen seedlings had a similar height. The experiment lasted for 16 weeks (March to 22 July 2019) as this time period corresponded to the growing season of these species and also ensured maximum development of roots before exceeding pot boundaries.

Trait measurements

We measured leaf and root morphological traits of all individuals (see Table 1 for full trait names, abbreviations and their ecological roles). These traits are the key components of leaf and root economics spectra, thereby determining plant growth and ecological strategies (Wright *et al.*, 2004; Weemstra *et al.*, 2016).

To measure root functional traits, we carefully washed roots using tap water and gently separated the entire roots of each conspecific individual plant. Although roots of conspecific individuals intermingled when growing together in a pot, the sandy soil made the separation of the roots relatively easier for us for each conspecific individual seedling. We spread the roots in a transparent tray under water and scanned the entire root system of each individual seedling using a flatbed scanner, Epson Perfection V700 Photo Scanner. We used Win-RHIZO software (Regent Instruments Inc., Sainte-Foy, QC, Canada) to analyse the scanned root images for root average diameter (RAD), specific root length (SRL) and root branching index (RBI). For leaf trait measurements, three healthy and fully expanded young leaves from each individual plant were measured and average values were calculated. We dried all the leaves, stems and roots separately in an oven at 60 °C for 72 h to obtain above- and below-ground biomass and other trait estimations that required dry mass (e.g. SRL). We followed the protocol of Pérez-Harguindeguy *et al.* (2013) for measurement of leaf traits. Specifically, to measure leaf chlorophyll content, the average of three readings at the widest part of the leaf blade

Table 1. *List of traits measured with their abbreviations and ecological functions*

Traits	Abbreviations and units	Ecological functions	References
Leaf area	LA, cm^2	Energy balance	Poorter and Rozendaal (2008)
Specific leaf area	SLA, cm^2 g^{-1}	Light capture	Wright *et al.* (2004)
Leaf dry mass	LDM, g	Estimates leaf construction cost	Niinemets *et al.* (2007)
Leaf thickness	LT, mm	Leaf physical strength	Onoda *et al.* (2011)
Leaf dry matter content	LDMC, g g^{-1}	Leaf life span	Pérez-Harguindeguy *et al.* (2013)
Leaf chlorophyll content	Chl, SPAD meter	Photosynthesis	Coste *et al.* (2010)
Stem dry matter content	SDMC, g g^{-1}	Hydraulic and biophysical support	van Gelder *et al.* (2006)
Specific root length	SRL, cm g^{-1}	Resource absorption	Nicotra *et al.* (2002)
Root average diameter	RAD, mm	Hydraulic conductivities of roots	Kirfel *et al.* (2017)
Root branching intensity	RBI, tips cm^{-1}	Resource absorption	Comas and Eissenstat (2009)
Root dry matter content	RDMC, g g^{-1}	Root lifespan	
Leaf mass fraction	LMF, g g^{-1}	Energy allocation strategy	Poorter *et al.* (2015)
Root mass fraction	RMF, g g^{-1}	Energy allocation strategy	Poorter *et al.* (2015)
Stem mass fraction	SMF, g g^{-1}	Energy allocation strategy	Poorter *et al.* (2015)

was taken using a SPAD-502 Chlorophyll meter (Minolta Camera Co., Osaka, Japan) (Marenco *et al.*, 2009). Leaf area was computed using ImageJ software (Katabuchi, 2015). The SLA was measured as the area of one side of the leaf divided by its dry mass. Leaf dry mass content (LDMC) was calculated as dry mass divided by its fresh mass. Leaf thickness (LT) was measured using an electronic digital micrometer (CANY Co., Shanghai, China). We calculated SDMC and RDMC separately as the ratio of dry masses to their respective fresh masses. Leaf mass fraction (LMF), stem mass fraction (SMF) and root mass fraction (RMF) were calculated as the ratio of their respective dry masses to the total dry biomass. Total biomass (sum of the leaf, stem and root masses) was also calculated.

Data analyses

The first aim of this study was to test how traits vary with soil moisture and plant intraspecific competition treatments. We used linear mixed-effect models with soil moisture and plant intraspecific competition and their interactions as fixed effects, with species as a random effect, using the 'lmer' function in the lme4 package (Bates *et al.*, 2015). In order to fulfil the assumptions of normality and homoscedasticity in the analysis of variance (ANOVA), our variables were log transformed. We also used the *z*-score to standardize the data for ease of comparison and interpretation.

To determine whether root and leaf traits are co-ordinated in response to soil moisture and plant intraspecific competition, we tested co-ordination between above- and below-ground traits using Pearson correlation coefficients by applying the 'rcorr' function in the 'Hmisc' R package (Harrell, 2022). We used standardized major axis (SMA) regression to visualize the pair-wise relationships. We also further used principal component analysis (PCA) to visualize how leaf and root traits are associated in each soil moisture condition using the function 'dudi.pca' in the ade4 package (Dray and Dufour, 2007) and

'fviz_pca_var' in the factoextra package (Kassambara and Mundt, 2020).

We also tested variation of total biomass production and biomass allocation across soil moisture and plant intraspecific competition treatments. We built linear mixed-effect models with these two factors and their interaction as fixed effects, while plant species was considered as a random effect using the 'lmer' function in the lme4 package (Bates *et al.*, 2015). We used R 3.6.3 for all statistical analyses (R Core Team, 2020).

RESULTS

Above- and below-ground traits vary in response to soil moisture availability and plant competition

We found that both soil moisture and plant intraspecific competition influenced both above- and below-ground traits (Table 2). Soil moisture significantly affected all traits ($P < 0.05$), whereas competition only had a significant effect on selected traits, four above-ground and two below-ground traits (Table 2). With a trait variation being observed among species (Supplementary data Table S2), above- and below-ground traits responded differently to soil moisture and competition treatments (Supplementary data Figs S2 and S3). We found high LDMC, LT and SDMC under low soil moisture conditions, with high SLA and LA in both medium and high soil moisture conditions ($P < 0.05$), while SRL and RBI were found to be high and low, respectively, in low soil moisture conditions (Supplementary data Fig. S2).

Regarding above-ground–below-ground co-ordination of traits, we found mixed results of leaf and root trait correlations across soil moisture and plant competition treatments (Fig. 1; Supplementary data Figs S4 and S5). As expected, SLA was found to correlate positively and negatively with SRL and RAD, respectively, in all moisture conditions, although the strength of the correlations depends on soil moisture. For example, the SLA and RAD correlation was

TABLE 2. *Wald Type II tests of fixed effects in linear mixed-effect models showing the effects of soil moisture, plant intraspecific competition and their interactions on above- and below-ground traits in which species was a random effect*

Traits	Fixed effects	d.f.	χ^2	*P*-value
	Moisture	2	60.2	0***
	Competition	1	0.1	0.7951
LDMC	Moisture × Competition	2	4.6	0.1020
	Moisture	2	41.0	0***
SDMC	Competition	1	5.8	0.0163*
	Moisture × Competition	2	0.25	0.8835
	Moisture	2	30.7	0***
RDMC	Competition	1	0.01	0.9106
	Moisture × Competition	2	4.8	0.0868·
LDM	Moisture	2	168.0	0***
	Competition	1	304.8	0***
	Moisture × Competition	2	0.6	0.7256
LA	Moisture	2	193.6	0***
	Competition	1	347.2	0***
	Moisture × Competition	2	0.6	0.7526
SLA	Moisture	2	16.2	0.0003***
	Competition	1	0.03	0.8677
	Moisture × Competition	2	2.0	0.3663
	Moisture	2	19.0	0***
Chlorophyll	Competition	1	97.2	0***
	Moisture × Competition	2	4.8	0.0897·
LT	Moisture	2	19.4	0***
	Competition	1	0.7	0.4082
	Moisture × Competition	2	0.5	0.7643
	Moisture	2	8.2	0.0162*
RAD	Competition	1	105.0	0***
	Moisture × Competition	2	3.6	0.1619
SRL	Moisture	2	123.3	0***
	Competition	1	59.7	0***
	Moisture × Competition	2	13.3	0**
	Moisture	2	41.5	0***
RBI	Competition	1	3.6	0.0584·
	Moisture × Competition	2	0.5	0.7706

***$P < 0.001$; **$P < 0.01$; *$P < 0.05$; ·$P < 0.1$. Sample size for each trait is 417.

LDMC, leaf dry matter content; SDMC, stem dry matter content; RDMC, root dry matter content; LDM, leaf dry mass; LA, leaf area; SLA, specific leaf area; LT, leaf thickness; RAD, root average diameter; SRL, specific root length; RBI, root branching index.

significant at low and medium soil moisture but not significant at higher soil moisture. The direction and strength of the correlation between SLA and RBI were found to depend on moisture availability. A non-significant negative correlation of SLA and RBI was observed under low and medium soil moisture conditions, while this correlation shifted to a significantly positive relationship under high soil moisture conditions (Fig. 1). The LDMC was unexpectedly also found to be positively

correlated with SRL and RBI, in almost all soil moisture conditions (Fig. 1).

We also used PCA to further explore covariation between root and leaf traits in each soil moisture condition. As mentioned above, similar associations between root and leaf traits are observed across soil moisture conditions. For instance, SLA and SRL are positively associated along the first PCA axis, while LDMC and SRL are also positively correlated
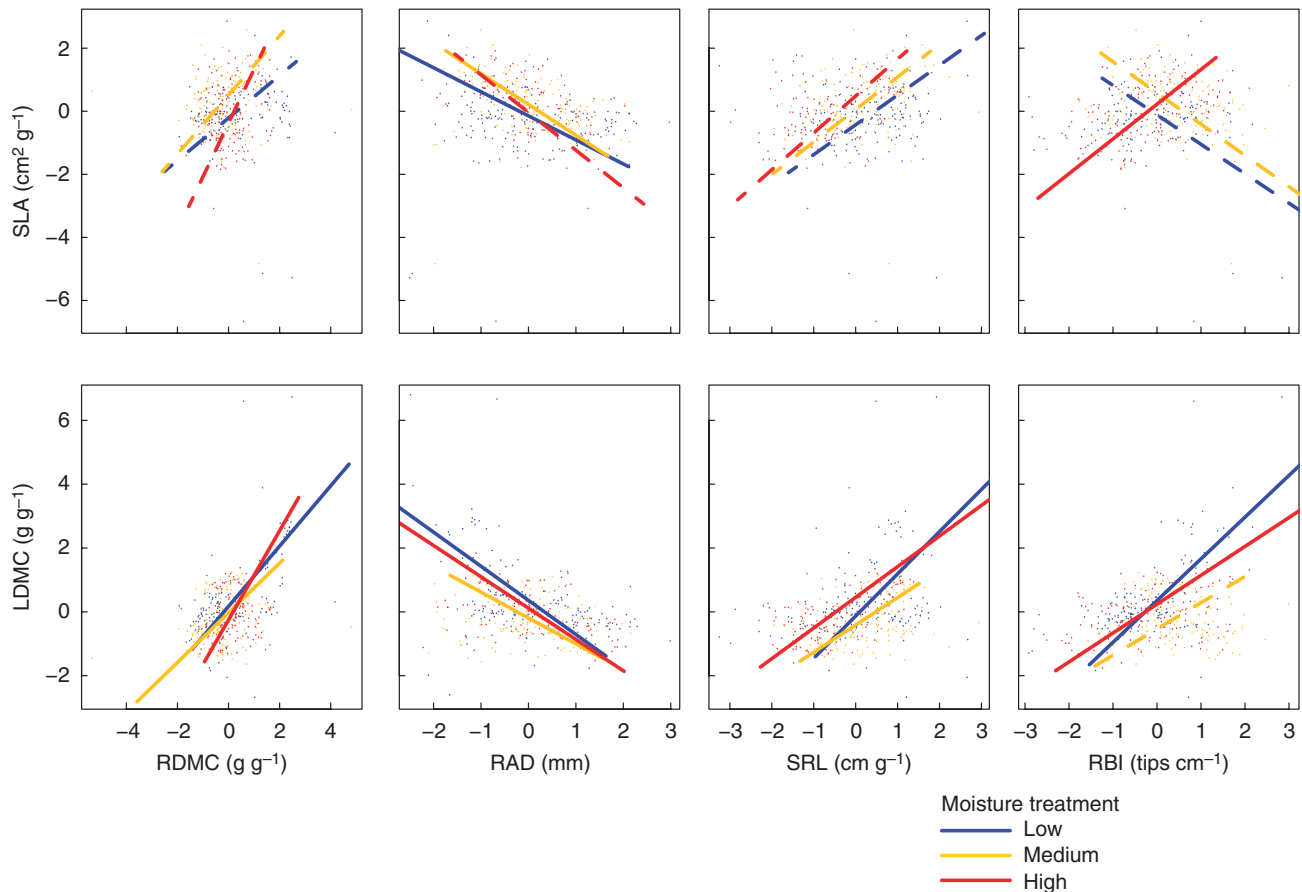
FIG. 1. Correlations of above- and below-ground traits across a soil moisture gradient. Solid lines show significant trait correlations while broken lines show no significant correlations. Traits are log transformed and *z*-standardized. For trait abbreviations, see Table 1.

under each soil moisture condition (Supplementary data Fig. S6).

Competition × soil moisture interactive effect on traits

Plant intraspecific competition interacted with soil moisture to influence a below-ground trait (SRL), but not above-ground traits ($P < 0.05$; Table 2). The effect of intraspecific competition varied for root and leaf traits, as it increased SRL under low and medium soil moisture levels but showed no effect on SLA across a soil moisture gradient (Fig. 2). However, each individual trait response to intraspecific competition did not differ along the soil moisture gradient, except SRL and RDMC due to the significant interaction effect of competition and soil moisture (Fig. 2; Table 2).

Total biomass and biomass allocation varied with soil moisture availability and plant competition

While soil moisture and plant intraspecific competition independently influenced total biomass and biomass allocation ($P < 0.05$; Table 3), they interacted only to influence SMF ($P < 0.001$; Table 3). Under each soil moisture condition, plant intraspecific competition reduced total biomass and LMF but

it increased RMF (Fig. 3). Regardless of soil moisture levels, intraspecific competition was also found to significantly reduce total biomass (Supplementary data Fig. S7). Total biomass of the seedlings decreased with decreasing soil moisture availability (Supplementary data Fig. S8).

DISCUSSION

Our results show that above- and below-ground traits have heterogeneous responses and inconsistent correlations to soil moisture availability and plant competition. These results suggest a lack of functional co-ordination between traits belonging to different plant organs and that a whole-plant economics spectrum is not supported. Biomass allocation to above- and below-ground plant organs across our soil moisture gradient, however, does support a functional equilibrium theory where relatively larger proportions of biomass were allocated in organs capturing limited water resource for growth.

Above- and below-ground traits vary in response to soil moisture availability and plant competition

Following plant economics spectrum theory, high values of acquisitive functional traits are expected under high moisture
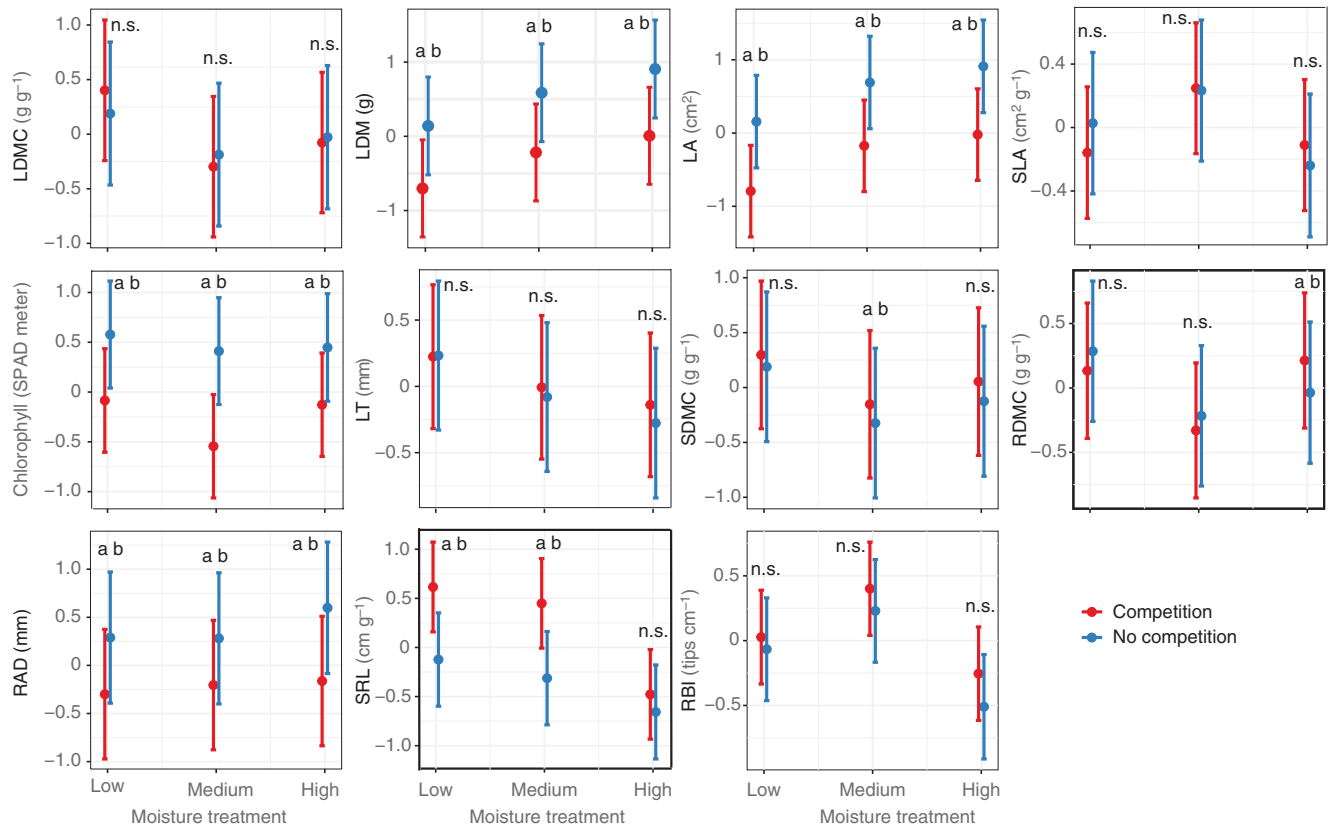
FIG. 2. Effect of plant intraspecific competition on above- and below-ground traits across a soil moisture gradient. Letters identify significant trait variations between competition and no competition treatment at each soil moisture level ($P < 0.05$). Values are means with their 95 % confidence intervals derived from the linear mixed-effect models in which species was a random effect. n.s., not significant. The bold outline shows traits with a significant interaction effect of competition and moisture (SLA and RDMC). For trait abbreviations, see Table 1. This figure depicts the result of the interaction effect of intraspecific competition and soil moisture on root and leaf traits (see Table 2 for the result). It shows how competition between conspecifics is changing with soil moisture availability, testing the assumption that the resource availability gradient (such as water) determines the strength of competition between organisms and thereby changes their trait values. The figure conveys two messages. First, above- and below-ground traits respond differently to intraspecific competition across a moisture gradient, perhaps showing lack of co-ordination in response to biotic interaction. Second, plants did not change most of their trait values for intraspecific competition across a moisture gradient, except SRL, suggesting that competition for water may not be enough for adaptive plasticity.

TABLE 3. *Wald Type II tests of fixed effects in linear mixed-effect models showing the effects of soil moisture, plant competition and their interactions on total biomass and biomass allocation in which species was a random effect*

Traits	Fixed effects	d.f.	χ^2	*P*-value
Total biomass	Moisture	2	230.7	0***
	Competition	1	273.0	0***
	Moisture × Competition	2	1.5	0.4757
LMF	Moisture	2	40.2	0.0002***
	Competition	1	40.1	0.0002***
	Moisture × Competition	2	1.6	0.4383
SMF	Moisture	2	9.99	0.0067**
	Competition	1	4.7	0.0305*
	Moisture × Competition	2	16.3	0.0003***
RMF	Moisture	2	70.1	0***
	Competition	1	25.8	0.0004***
	Moisture × Competition	2	5.1	0.0776.

***$P < 0.001$; **$P < 0.01$; *$P < 0.05$; $P < 0.1$. Sample size for each trait is 417.

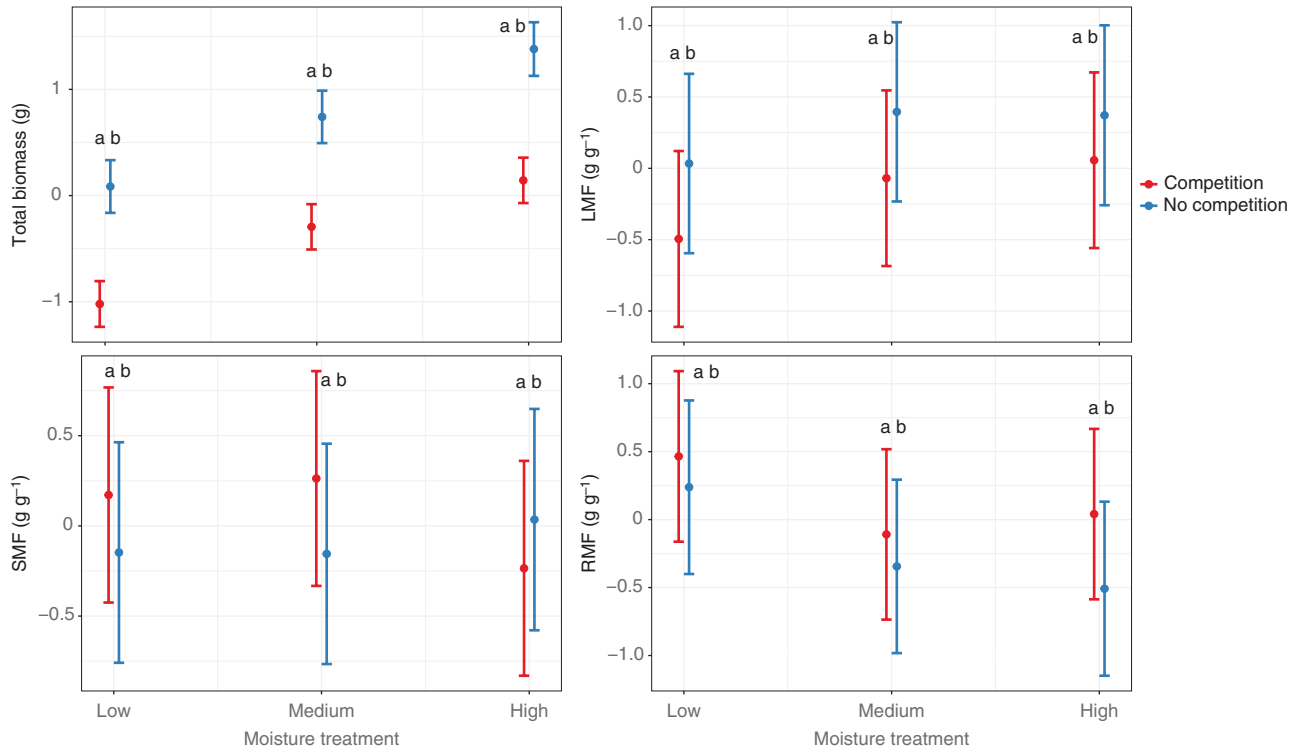LMF, leaf mass fraction; SMF, stem mass fraction; RMF, root mass fraction.

FIG. 3. Effect of intraspecific competition on total biomass and biomass allocation at each soil moisture level. Letters identify significant differences between competition and no competition treatment at each soil moisture level ($P < 0.05$). Values are means with their 95 % confidence intervals derived from the linear mixed-effect models in which species was a random effect. A significant effect of soil moisture treatments on total biomass and biomass allocation was also detected (Supplementary data Fig. S8). For trait abbreviations, see Table 1.

availability, while a conservative resource use strategy should be favoured in moisture-limited conditions (Wright *et al.*, 2004). Accordingly, our results showed that, across individuals of all species, traits respond to a soil moisture availability gradient but with contrasting responses between above- and below-ground traits, indicating that different plant organ traits diverge in position along the plant economics spectrum. The above-ground traits LA and SLA increased with soil moisture availability (Supplementary data Fig. S2), suggesting that an acquisitive strategy may allow seedlings to rapidly use resources promoting a fast growth rate (Wright *et al.*, 2004). We also found seedlings with high leaf thickness and LDMC under low moisture conditions promoting biomass production through less construction costs, a syndrome mostly linked with a conservative resource strategy. Fajardo and Siefert (2018) also reported that, consistent with the leaf economics spectrum, trait values shift with resource gradients at both the intraspecific and species levels. Our results also support the leaf economics spectrum whereby soil moisture availability drives above-ground trait variation, causing seedling individuals to develop an acquisitive strategy under well-watered conditions and a conservative strategy under water-limited environments (Reich, 2014).

However, the acquisition–conservation ecological axis of above-ground traits along the soil moisture gradient was not extended to below-ground traits as we found small RAD in the moisture-limited environment. Low SRL and RBI along with high RAD are expected in a moisture-limited environment if roots are the below-ground equivalent of leaves (de la

Riva *et al.*, 2016). According to the root economics spectrum, moisture-limited environments are mostly characterized by plants with thicker roots as an adaptive mechanism to maximize their survival (Larson and Funk, 2016; Kong *et al.*, 2019; Zhou *et al.*, 2019; Lozano *et al.*, 2020). However, this may not always be the case, as research has shown that instead of investing largely in root systems (thicker and long-lived roots) in response to dry conditions (Nicotra *et al.*, 2002), plants may invest in other organs such as leaves to be small and thickened, for which our finding is supportive. Likewise, plant below-ground responses may not be aligned to a single axis of ecological variation, indicating the presence of multiple resource use strategies (Laliberté, 2017; de la Riva *et al.*, 2018). Our results in general demonstrate that below-ground traits may not exclusively explain plant distributions across a range of moisture availability. Indeed, above- and below-ground traits should be integrated to better understand the effects of soil moisture availability on plant ecological strategies.

Above-ground traits, indicative of an acquisitive functional strategy, should be correlated with similar acquisitive below-ground traits (Reich, 2014). As a result, a consistent co-ordinated response of leaf and root traits is expected along resource gradients. However, we found mixed results of leaf–root trait correlations, suggesting that a unified functional strategy at the whole-plant level may not be identifiable. As predicted, we found SLA to be positively and negatively correlated, respectively, with SRL and RAD, which is consistent with previous studies (Reich *et al.*, 1998; Withington *et al.*, 2006; Holdaway *et al.*, 2011; de la Riva *et al.*, 2016), indicating co-ordination

of leaf and root traits for resource acquisition. However, this co-ordination was not extended to other resource economic traits, as LDMC was significantly positively correlated with SRL and RBI at almost all soil moisture levels. This indicates that above-ground resource use strategies do not necessarily reflect those below-ground (Withington *et al.*, 2006; Weemstra *et al.*, 2016) as plants may develop conservative root traits to retain water and acquisitive leaf traits to maximize photosynthesis (Birhane *et al.*, 2015). Weigelt *et al.* (2021) reported that multiple resource use dimensions are required to understand plant ecological strategies. Also, SLA negatively correlated with RBI under low soil moisture conditions while this relationship shifted to a positive correlation at a high soil moisture level, supporting the assumption that leaf–root trait correlations could shift under different environmental conditions due to trait variation across a resource gradient (Weigelt *et al.*, 2021). Plant species identity and the type of traits measured may contribute to inconsistencies in leaf–root trait correlations (Kembel and Cahill, 2011; Lozano *et al.*, 2020), as we found that traits vary among species (Supplementary data Table S2), which deserves further investigation. Our result showed no consistent leaf–root trait correlations, suggesting that plant below-ground functions may not be accurately estimated using above-ground traits.

Plant competition × soil moisture interactive effect on traits

Our results showed that soil moisture and plant intraspecific competition interactively affect only below-ground traits, indicating the importance of root traits for regulating underground resources. The SRL and RDMC were significantly influenced by their combined effect. Plant competition increased RDMC, compared with non-competition treatment, under high soil moisture conditions, whereas it enhanced SRL irrespective of soil moisture conditions. This interdependence of soil moisture and plant competition was also reported by Lorts and Lasky (2020), as competition increased leaf C:N under well-watered conditions while it had no effect under drought conditions. Plants may produce thin, soft and absorptive root tissues in high soil moisture conditions (Markesteijn and Poorter, 2009; Larson and Funk, 2016). However, our results suggest that when they are under competition for limited resources, plants develop high root tissue density (high RDMC) perhaps to maximize survival. Similarly, intraspecific competition for a limited water resource caused plants to allocate more energy to roots (Weigelt *et al.*, 2005).

Our result thus highlights the soil moisture-dependent effect of plant competition on the root system. The exclusive response of root traits to the combined effect of biotic and abiotic factors may highlight the importance of underground community assembly processes in explaining the shift in plant resource use strategies under changing environments.

The direction and magnitude of the effect of intraspecific competition varied with plant traits, as the response of above- and below-ground traits to intraspecific competition was different, suggesting that traits in different plant organs operate independently in response to plant competition. All below-ground traits responded to intraspecific competition, indicating that these traits are key and relevant to understand plant below-ground resource use strategies, a result consistent

with the idea that a strong effect of intraspecific competition on traits is expected due to niche overlap among conspecifics (Hooper *et al.*, 2005). We found that intraspecific competition reduces RAD while increasing SRL, regardless of soil moisture availability, as competition may favour acquisitive traits in resource-limited environments to promote efficient use of resources (Novoplansky, 2009; Farrior *et al.*, 2013). Competition for soil moisture triggers plant roots to be more responsive as roots are directly involved in soil water acquisition. Minden and Venterink (2019) also showed that root traits are more sensitive to plant competition, and thereby more important in capturing plant below-ground ecological functions. However, in contrast to our results, root morphological traits were found not to be responsive to intraspecific competition (Beyer *et al.*, 2013; Fruleux *et al.*, 2016), suggesting that species identity may play a role in these contradictory findings. A species-specific response of root traits to competition and soil moisture content was reported (Weigelt *et al.*, 2005), implying that root traits of different species vary, thus highlighting the importance of species identity to capture species-specific mechanisms for root trait variation. Our result also showed that trait variation was observed among species in each soil moisture condition (Supplementary data Table S2; Fig. S9), indicating that species-specific mechanisms are important for community assembly. Thus, different plant species and root traits should be considered when analysing plant responses to global change factors, such as drought. In terms of above-ground traits, intraspecific competition decreased leaf area and chlorophyll content across the soil moisture availability gradient. The reduction of leaf acquisitive traits and promotion of leaf thickness due to plant competition, especially in soil moisture-limited environments, might be an adaptive strategy that could enhance species survival through development of rigid cell walls and reduction of photosynthetic activities (Markesteijn *et al.*, 2011).

Total biomass and biomass allocation vary with soil moisture availability and plant competition

Our results showed that more biomass was invested in below-ground parts (RMF) than in above-ground parts in a soil moisture-limited environment, supporting the hypothesis that high biomass allocation is expected in plant roots when below-ground resources are limited (Levang-Brilz and Biondini, 2003). Larson and Funk (2016) reported that plants allocated high biomass to roots in soil moisture-limited environments, highlighting that drought may cause significant loss of above-ground investment. Our results reveal that plants reduce shoot mass compared with root mass in soil moisture-limited environments, for which Franco *et al.* (2020) similarly reported higher allocation of biomass to roots under drought conditions. The investment of more biomass in the root system has been suggested as a strategy to tolerate soil moisture-deficient conditions (Tomlinson *et al.*, 2012). Increasing root biomass at low soil moisture levels could be related to the reduction of root respiration (Thorne and Frank, 2009). High above-ground investments (LMF and SMF) were observed under medium and high moisture levels, suggesting high investment in photosynthetic tissues that favour plants cheaply building structures with high

leaf turnover but which are able to carry out sufficient photosynthesis (Wigley *et al.*, 2009). Markesteijn and Poorter (2009) also found that seedlings in a wet forest ecosystem invested greater biomass into their leaves and stems, compared with seedlings in a dry forest.

The effect of plant intraspecific competition on biomass allocation did not vary with soil moisture gradients, inconsistent with findings in other studies (Poorter and Nagel, 2000). This might be linked with the duration of the experiment in that biomass allocation differences might have been observed with soil moisture gradients if more time would have been given for the competition to occur. If competition among plant individuals leads to resource depletion, high biomass allocation to roots would be expected at the expense of leaves (Poorter *et al.*, 2012). Regardless of soil moisture gradients, plant competition reduced the amount of biomass allocated to leaves, while it favoured high biomass allocation to roots and stems. Similarly, Fruleux *et al.* (2016) also found that intraspecific competition for water favoured high biomass allocation to the root system. The organ-specific allocation strategies in response to competition could be attributed to the optimization of acquiring and conserving resources (Poorter *et al.*, 2012). Large root investment might be needed for water and nutrient acquisition under biotic pressure, preventing high allocation to the leaf biomass (Berendse and Möller, 2009). In other words, rapid carbon assimilation could occur in the absence of competition by allocating more resources to the photosynthetic tissues. Overall, our results reveal that soil moisture did not modulate the effect of intraspecific competition on plant biomass allocation while competition alone influences plant biomass distribution, implying that plant competition drives energy allocation strategies.

Conclusion

In this study, we showed variation in above- and below ground traits, plant biomass production and allocation in response to soil moisture and competition treatments. Lack of consistent correlations between above- and below-ground traits across soil moisture gradients may limit the utility of the plant economics spectrum across plant communities. Our findings are consistent with the functional equilibrium hypothesis that plants allocate relatively more biomass to the organ that encounters limited resources for growth. Overall, our results demonstrate that plants may use a range of ecological strategies in response to varying environmental changes, which is consistent with the finding of Castorena *et al.* (2022) that species have different ways to co-ordinate traits to use resources in which, on average, they gain a similar amount of carbon per body mass over their life spans. Placing more above- and below-ground physiological and anatomical traits in the context of multiple biotic and abiotic factors will help to better understand plant functional strategies under global environmental change.

SUPPLEMENTARY DATA

Supplementary data are available online at https://academic.oup.com/aob and consist of the following. Table S1: species characteristics. Table S2: trait variation among species. Figure S1: average volumetric water content of pots with low, medium and high soil moisture levels. Figure S2: above- and below-ground trait responses to a soil moisture gradient. Figure S3: above- and below-ground trait responses to plant competition. Figure S4: correlations of above- and below-ground traits across a soil moisture gradient. Figure S5: correlations of above- and below-ground traits between competition and no-competition treatments. Figure S6: PCA showing trait correlations. Figure S7: response of total biomass and biomass allocation to plant competition. Figure S8: response of total biomass and biomass allocation to a soil moisture gradient. Figure S9: species response to moisture treatments.

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