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RESEARCH ARTICLE

Root and shoot traits of two common herbs respond differently to drought and fertilization in a multifactorial global change experiment

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Abstract

Background Plants must adapt locally to the recent global change, such as increasing drought exposure or altering nutrient availability. In ecological theory, all functional traits of the plant move towards strategies of stability and resource conservation. In particular fine roots are responsible for water and nutrient uptake and they are highly plastic to stress. In contrast to shoot traits, the dynamics of root growth and the relationship between root and shoot trait responses are still understudied and poorly understood.

Methods Therefore, we investigated the shoot and root trait responses of two herbaceous plants, *Plantago lanceolata* and *Rumex acetosa,* growing in monoculture or in mixture in a *drought x nutrient* greenhouse experiment.

Results Low-nutrient stress, more than drought stress, led to a strong carbon allocation to the roots, because the root–shoot ratio increased to compensate for stress with improved root development. Roots responded with a more conservative resource use strategy, e.g., an actually decreasing biomass and surface area to drought and, in contrast, unexpectedly with acquisitive strategy by strongly increasing the root–shoot ratio in nutrient-poor conditions. Classical shoot traits such as the decreasing specific leaf area (SLA) indicated a more resource-conservative strategy in response to any stressor.

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Conclusions Understanding whole-plant responses to global change scenarios urgently requires a much more specific exploration of the adaptation and acclimatisation potential of roots in the application of ecological research. In view of climate-smart land management, the study highlights the importance of maintaining species-rich ecosystems in face of increasing likelihood of global change-type droughts.

Keywords Nutrient availability · *Plantago lanceolata* · Plant functional traits · *Rumex acetosa* · Species richness · Water availability

Introduction

On top of the unprecedented 1.1 °C warming during the last century, even intermediate climate change scenarios project a broad range of likely further increases in the surface temperature from 0.9 to 2.8 °C until the end of the century accompanied by increasing drought frequency and magnitude (Gulev et al. 2021; Lee et al. 2021). Due to this increasing climate stress, plant performance, i.e. their survival, fitness and growth, and populations will decline if plants do not adapt quickly enough to changing environmental conditions, which often means acclimatisation within a lifetime (Jump & Peñuelas 2005; Parmesan 2006).

Also, nutrient inputs to the biosphere increased in recent decades mainly due to the intensified application of N and P fertilizer in agriculture and due to the increased atmospheric nitrogen deposition from fossil fuel combustion (Peñuelas et al. 2020; Yuan & Chen 2015). It is hotly debated whether this increase in nutrient availability will actually mitigate the impacts of climate change on plant performance by enhancing average plant growth rates of certain species, or whether ongoing widespread eutrophication could in contrast enhance the climate vulnerability of ecosystems (Gentilesca et al. 2018; Hautier et al. 2020; Peñuelas et al. 2020). This debate is difficult to address, because soil weathering rates and nutrient release from microbial mineralization of organic matter are controlled by precipitation and temperature, while these climate factors also regulate plant productivity and thus competition for nutrients (Dieleman et al. 2012; Hou et al. 2018; Yuan and Chen 2015).

Anthropogenic biodiversity loss due to land use intensification, eutrophication, and habitat loss as a facet of global change is problematic in itself (Habel et al. 2013; Hautier et al. 2020; Wesche et al. 2012), and ecosystems with declining diversity are also likely to be more vulnerable to climate change stressors. This is because a higher species diversity is an insurance against extreme events to maintain more stable ecosystem productivity despite environmental variability, both through replaceability of species and complementary resource use (Brooker 2006; Grant et al. 2014; Tilman et al. 2006). According to the "stress gradient hypothesis" (Bertness & Callaway 1994), such complementary plant–plant interactions are especially emerging under harsh environmental conditions.

One possibility to measure plant responses to changing environmental conditions is to look in particular at plant functional traits, which are measurable plant features that have an impact on performance and fitness (Violle et al. 2007; Westoby 1998). Based on their functional traits, plant species arrange within spectra of economic life strategies. Within the leaf economics spectrum (LES), traits vary along a gradient from acquisitive to conservative resource use, facilitating high growth rates and fast nutrient uptake versus low growth rates and slow nutrient uptake, respectively (Reich 2014). Acquisitive strategies are linked with, e.g., higher specific leaf area (SLA) and higher leaf nitrogen and phosphorus content in comparison to the opposite conservative life strategy (Díaz et al. 2016). Regarding the root economics spectrum (RES), the acquisitive (fast) strategy associates for example with high root nitrogen content and the conservative (slow) strategy with high root tissue density (Bergmann et al. 2020; McCormack & Iversen 2019; Roumet et al. 2016).

The widely studied and highly plastic SLA represents the light capturing area per gram of leaf dry matter (Bruelheide et al. 2018; Westoby 1998). From a plant economics perspective, a low SLA represents smaller, thicker, structurally stronger, and thus more stress-resistant leaves. This resistance allows for a longer, conservative revenue stream, meaning that tissue longevity is preferred, in contrast to more labile, thinner, and larger, high SLA leaves representing an acquisitive resource use strategy (Reich 2014; Westoby 1998). However, the interpretation of SLA as a stress indicator can be very delicate, because its variation along ecological gradients is strongly coupled with the variation of other plant and leaf traits, too (Cunningham et al. 1999; Westoby 1998). Stress might further induce chloroplast decline because the allocation of N to the photosynthetic apparatus decreases and because reduced gas exchange results in oxidative stress (Bhargava and Sawant 2013; Evans 1989). In contrast to this, a drought-induced decrease of SLA causes leaf structures to become more densely packed too, potentially leading to an actual increase in the count of N-rich chloroplasts per leaf area (Cunningham et al. 1999). In analogy, stomates become also packed more densely, but also smaller, to maintain high water use efficiency under stress (Holland and Richardson, 2009; Xu and Zhou 2008). Overall, stress shifts most aboveground traits towards a conservative strategy in the plant economics spectrum, but for some specific traits, for example, leaf N concentration, the direction of change might depend more specifically on the type of stressor (Reich 2014).

The plant root system plays an important role as the connection between soil and plant, and plants respond to environmental change with a wide range of root trait responses (Vries et al. 2016). As mentioned, root functional traits can correspond to an acquisitive–conservative gradient (Reich 2014). During moderate drought, more carbon can be provided for deeper root growth to improve water uptake and enhanced fine root growth to compensate for higher fine root mortality (Hertel et al. 2013; Meier and Leuschner 2008a). This stress-induced increase in fine root growth should supposedly increase the root–shoot ratio; at least until strong drought-induced fine root mortality exceeds the potential for carbon investment into compensatory root growth, resulting in constant or even decreasing root–shoot ratio (Meier and Leuschner 2008a, b; Vries et al. 2016). In general, root traits even turned out to give a better explanation of several ecosystem processes and properties than leaf traits (Vries et al. 2016). In contrast to leaf traits, the stress response of root traits may be even more complex and in recent years a multidimensional root economic space has been proposed (Bergmann et al. 2020; McCormack and Iversen 2019). This is because the need for fast resource acquisition to compensate for nutrient and water limitation must be balanced against the need to increase root life span for resource conservation (Reich 2014). In general, root traits are classically understudied, and thus little is known about the relationship between above- and belowground traits and about their coordinated whole-plant stress responses (Kramer-Walter et al. 2016).

It is hotly debated whether typical response traits react individually to environmental changes or whether there are certain "controlling" traits (Reich 2014; Westoby 1998). However, the complex and presumably very decisive stress reactions of the root system are still largely unexplored. In this study, we investigated the impact of functional diversity, competition, water, and nutrient supply on plant responses above and below ground. The grassland species studied, *Rumex acetosa* (L.) and *Plantago lanceolata* (L.), are both generalists in their preferences regarding soil moisture (Ellenberg et al. 2010). *R. acetosa* prefers nutrient rich sites, while *P. lanceolata* is indifferent concerning nutrient availability (Ellenberg et al. 2010). Both, P. *lancelolata* and *R. acetosa* are native to temperate ecosystems in Eurasia, where they mostly inhabit both pastures and disturbed ruderal areas (Kew Royal Botanical Gardens 2025; Penczykowski & Sieg 2021). While native to Eurasia, records of both species can be found globally (Kew Royal Botanical Gardens 2025; Penczykowski and Sieg 2021).

We put this study in a global change context, combining treatments of altered nutrient availability and drought exposition. At least for aboveground traits, many studies have already addressed the impact of drought or fertilization separately (*e.g.*, DaMatta et al. 2002; Wu et al. 2008; Zahoor et al. 2017). However, more needs to be learned about the combined effect, that is, the possible mitigation of increasing drought exposure in the future by increased nutrient availability. In this context, a view on the role of plant interactions in plant communities as a controlling factor of ecosystem dynamics is essential to better estimate ecosystem responses and stability under environmental stress.

Thus, in an experimental manipulation of various global change drivers (*irrigation x fertilization x species richness*), we hypothesize that.

1) In variable environments, there is a stronger relationship between traits within the aboveground and within the belowground plant parts than between aboveground and belowground traits.

2) The separate effects of drought, nutrient scarceness, and interspecific competition induce "conservative" plant economic strategies, which means more stability in stressful environments, coordinated across traits.
3) Fertilization mediates drought stress and species admixture mediates nutrient and drought limitation.

Methods

Setting up of the experiment

We established a fully crossed 3-factorial global change simulation experiment, manipulating community composition, water availability, and nutrient availability. Our study organisms were two common grassland species, *Plantago lanceolata* and *Rumex acetosa*. The plants were potted in sandy substrate within 5.7 L pots, measuring $20 \times 20 \times 23\ \text{cm}^3$ (Fig. 1a). The experiment was conducted in a controlled greenhouse environment of approx. 25 m^2 size (Fig. 1b) belonging to the experiment facilities of the Experimental Botanical Garden (51.55°N, 9.95°E) of the University of Göttingen. Individuals of *P. lanceolata* and *R. acetosa* were cultivated from seed in October 2019 and assigned to either monoculture pots with two conspecifics or mixed pots with one plant of each species. In this way, we created two levels of species richness: a lower-diversity condition (monoculture) and a slightly higher-diversity condition (admixture of two species). While this is a simplified model of species diversity in ecosystems, it allows us to investigate fundamental plant interactions and trait responses.

After initially watering all plants each day, we simulated drought for half of the plants by restricting watering to every third day from the end of December 2019 until the final harvest at the end of February 2020, which caused recursive soil drying in the sandy soil substrate. The three-day interval brought the plants close to the wilting point and was based on many years of empirical experience from pre-trials on the plants'water requirements in our experimental system. Initially, all pots received universal NPK fertilizer (8–8–6 Wuxal Universal Fertilizer, Hauert MANNA GmbH, Nuremberg, Germany; diluted to 0.3% in water) to enable growth in the sandy substrate, while from January onward each half of the plants received no more fertilizer or a high weekly fertilizer input (45 mg total N equivalents of ammonium nitrate and urea, 19 mg total P equivalents of phosphate, 28 mg potassium per pot). The well-watered treatment has been defined as the "water control", and the non-fertilized treatment as the "fertilization control", as baseline reference for the global change scenarios with increasing drought exposure and increasing eutrophication.

We kept the temperature at 20 °C for 8 h during the day and at 15 °C at night. During the day, the lamps supplied a light source of around 95 $\mu\text{mol/m}^2\text{/s}$ (Fig. 1). The 12 treatment combinations were randomized within n = 10 blocks, resulting in 240 plants distributed across 120 plant pots (Fig. 1).

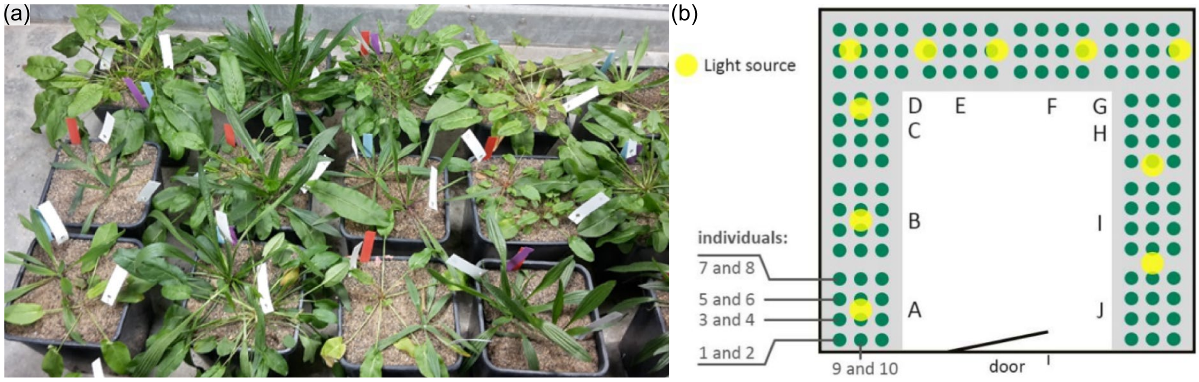


Fig. 1 Exemplary treatment block **a** and setup of the greenhouse experiment **b**. Each individual was labelled with a consecutive number from 1 to 240 on a plastic tag (visible in a), whereby we counted in rows from top left to bottom right in each pot and in one block after the other **b**

Response traits

We measured plant height (cm) of the 240 individuals as the total length of the shoot axis from the ground to the outermost leaf tip when the plants were still in the pot at the beginning of our sampling day. After harvesting the biomass in all pots within some hours, the biomass (g) was separated in root and shoot for all individuals, dried for 24 h at 70 °C and weighed in order to calculate the root–shoot ratio (g/g). To do so, we harvested the root biomass by carefully pouring the pots over a coarse mesh sieve after harvesting the shoot. We carefully removed the root system from the sandy substrate by hand. Then we successively washed the root in a washing line of several washbasins from dirty to clean, regularly changing the water. Finally, we used tweezers to remove the last remaining soil substrate from the root stump in clean water. The length of the tap root (cm) as the deepest elongation of the root in the soil was also measured on the whole harvested root system. Note that some of the harvested leaves and parts of the roots were used as fresh biomass for other measurements (see below) before they were also dried at 70 °C for 24 h to be added back to the dry biomass. Also note that plant height, aboveground biomass and root biomass were measured for both individuals of the same species in the monoculture pots, resulting in n = 20 pseudo-replicates (Table S1 in Appendix A1). These values were averaged at the pot level to align them with the experimental replication of n = 10 blocks.

The specific leaf area (SLA, cm^2/g) was determined using the first, third and fifth most developed leaves of each plant, dividing the sum of the leaf area, which was measured on scanned leaves at 150 dpi (WinFOLIA software, Régent Instruments, Quebec City, Canada), by their dry weight (g). The total leaf area (cm^2) of the plant was calculated by multiplying the SLA and the total biomass of the plant. The chlorophyll content per leaf area was approximated on the same three leaves in all individuals just before harvest using a chlorophyll meter (SPAD-502, Konica Minolta, Marunouchi, Japan).

For the morphology of the stomates, we sampled both individuals in the mixed species system and only one individual in each monoculture pots, resulting in n = 160 individuals sampled. The second, fourth and sixth most developed leaves were selected. Imprints on the lower surface of fresh leaves were produced with nail polish (trend'double volume and shine') and adhesive tape (Tesafilm'Crystal Clear'19 mm), and the imprints were digitalized using a stereo microscope system (SteREO Discovery.V20 with digital camera AxioCam MRc and software Axio Vision v.4.9, Zeiss Microscopy, Jena, Germany). On one high-resolution image (approximately 1 mm^2 at 1384 × 1036 pixels) per leaf, we measured the length (µm) of 5 stomates and calculated the stomate density (1/mm^2 leaf area) by measuring the average distance between stomates (one stomate and the five closest neighbours) in ImageJ v.1.53 k (National Institutes of Health, USA). A preliminary analysis of a smaller selection of leaves had shown that these approaches provide representative values for stomate size and density. To estimate the total leaf stomate area (cm^2 stomate area/cm^2 leaf area), we calculated the average radial stomate area from the average size of the stomates and multiplied it by the density of the stomates. The results obtained from the three leaves of each individual were then averaged.

The content of C and N (g C or g N/g dry matter) and C/N ratio of dried leaf and root material was determined with a gas chromatographer (vario EL III, Elementar, Hanau, Germany) for n = 80 pots (for logistic reasons only *R. acetosa*, 1 per mixed system, 1 per monoculture). Due to time constraints, we measured stomatal conductance (µmol H_2O loss/m^2/s) and photosynthetic rate (µmol CO_2 consumed/m^2/s) only in well-watered individuals of *R. acetosa* (n = 40), i.e. in the irrigation control, in order to compare the influence of fertilization and species richness in a two-factorial manner only. Measurements were performed on one leaf per individual with the LI-6400 Portable Photosynthesis System (LI-COR, Lincoln, USA). Both measurements were scaled to the whole individual (µmol/s) using the calculated total leaf area.

For each species in a pot, we performed a detailed analysis of the root architecture using a representative side strain of each root system, which was carefully washed as described above, focussing on all fine roots (< 2 mm diameter). Exclusively for this representative fine root side strain, the root surface was optically analyzed with WinRHIZO software (Régent Instruments, Quebec City, Canada) in a two-sided 3-D scan to determine the average diameter of the root (mm), the specific root length (cm root length/g dry matter), the specific root area (cm^2/g), and the total surface area of the root. For this optical analysis, the sample was placed in a special tray to float in distilled water.

Note that for all traits except plant height, aboveground biomass and root biomass, only one and always the same individual was sampled in each monoculture pot. In the diagonal arrangement of the plants in the pot, this was always the individual at the top left when viewed from the centre of the greenhouse (see Fig. 1a for diagonal planting). In order to avoid confusion from the outset, we first labelled each plant individual with a numbered plastic tag (visible in Fig. 1a), consecutively from 1 to 240 (indicated exemplarily for 1 to 8 in Fig. 1b), and always assigned the odd numbers to the individuals on the top left. The other conspecific in the monoculture pot was then not sampled, except for height and biomass, while in the admixture pots with the two different species we of course sampled both plants.

We used an overyield coefficient (*e.g.*, Hector et al. 2002) as a measure for inter-specific interaction. For each species, this coefficient compares plant performance (both shoot and root biomass growth separately) of the individual in the mixed pot with the respective value of a single plant in the monoculture pot in each block and treatment following Eq. (1). As described further above, the value for the single plant in the monoculture pot is the pot-average of both conspecifics in this pot. According to Eq. (1), overyield values above 0% indicate better performance in mixture than in monoculture ("complementarity"), values below indicate worse performance in mixture ("competition"). In each environment, we tested for significant overyield or underyield in mixture compared to monoculture by testing for a significant ($p < 0.05$) deviation from 0% using Student's two-sided t-Test.

$$\text{Overyield} = 100\% * \frac{Yield(mixture)}{Yield(monoculture)} - 100\% \quad (1)$$

Statistical modelling

To explore the trait–trait relationships across varying environmental conditions, we correlated (Pearson's r) all traits with each other and then performed a cluster analysis (based on Euclidian distance) on the resulting correlation matrix to group traits with similar responses (high correlation) together.

We analysed the separate effect of all treatment factors by multiple regression modelling for each species separately. Therefore, each trait was modelled as a function of *ecosystem* (1 vs. 2 species) *x water availability* (0: drought vs. 1: well watered) *x nutrition availability* (0: low vs. 1: high) and potential two-fold interactions. The predicted responses were then range-scaled (0–100%) to isolate the effect size of a single environmental factor on this percentage scale, while accounting for possible interactions between treatment factors. To test the significance ($p < 0.05$) of the treatment factors, we applied analysis of variance (ANOVA). We took the block effect into account by always including *block* as an additional model factor, which, however, was never significant. The model residuals were visually checked for normal distribution and homogeneity of the variances between the groups using histograms, Q-Q diagrams and residuals versus fits diagrams. If necessary, the response variable was log-transformed for modelling in a few cases. The model predictions were back-transformed by the exponential function accordingly. No other transformation was required.

We also used these multiple regression models for a more focused analysis of the interaction of treatment factors by comparing models with and without two-fold interaction terms based on Akaike's Information Criterion (Akaike 1974). In case of significant interactions, we expressed the different response slopes in the subgroups as effect size on a percentage scale. We consider changes as significant, if the 90% 1000-fold bootstrap confidence interval of the means clearly deviates from each other. All analyses were performed in R v.4.0.4 (R Foundation for Statistical Computing, Vienna, Austria).

Results

Trait–trait relationships

For both species, the cross-correlation and cluster analysis could not identify a specific trait controlling (strongly correlating to all other traits) the response to environmental variability throughout the plant organism. Instead, traits of aboveground productivity (biomass, height, photosynthetic rate) clustered together (Fig. 2). Since the total leaf area was found to be an exclusive function of aboveground biomass in the herbaceous study species ($r > 0.95$), it was not considered an independent signal in the further analysis. Interestingly, the root–shoot ratio was mostly controlled by the variability in aboveground biomass instead of root biomass in both species (Fig. 2). The root traits clustered only weakly together. The specific leaf area (SLA) varied independently of the other leaf traits, such as the stomate traits. Only chlorophyll content was weakly related to SLA in *P. lanceolata* (Fig. 2). The stomate traits, size and density, were weakly related to each other in *P. lanceolata* and strongly related in *R. acetosa*, while the leaf stomate area (proportion of stomate area per leaf area) was mostly controlled by the stomate size (Fig. 2). In *R. acetosa,* stomate traits were even more related to the cluster of root traits than to leaf morphology (SLA). Furthermore, the trait that suggests an aboveground–belowground coordination of responses to environmental variability is the C/N ratio, which was strongly correlated from roots to leaves (Fig. 2).

Responses to treatment factors

For most traits in both species, fertilizer application caused the strongest responses in comparison to the non-fertilized control treatment. Less traits responded to the irrigation regime and in most cases the responses to drought stress in comparison to the well-watered control treatment were less strong. The species richness had almost no influence compared to fertilization and irrigation (Fig. 3, Table S2–S4 in Appendix A1).

In *R. acetosa*, the traits that clustered together, mostly leaf traits (Fig. 2), showed a coordinated response. In detail, plants became larger in richly fertilized soil, shoot growth increased disproportionately compared to roots, leaves became larger and thinner (higher SLA), chlorophyll content and plant

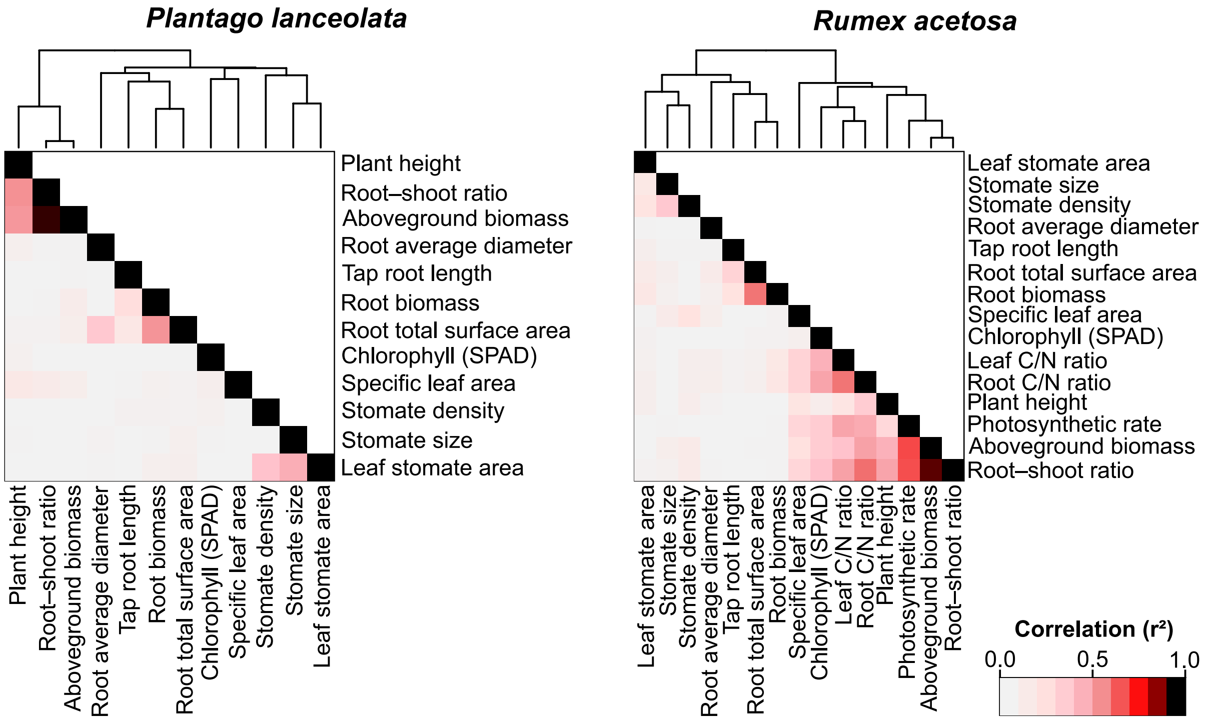


Fig. 2 Clustering of response variables based on their pairwise correlations. Highly correlated variables are sorted closely together in the cluster dendrogram and a short distance between variables in the dendrogram indicates a strong relationship between variables, a long distance indicates a weak relationship. The pairwise correlation strength (r^2) between each pair of response variables is shown in the lower left half of the heatmap

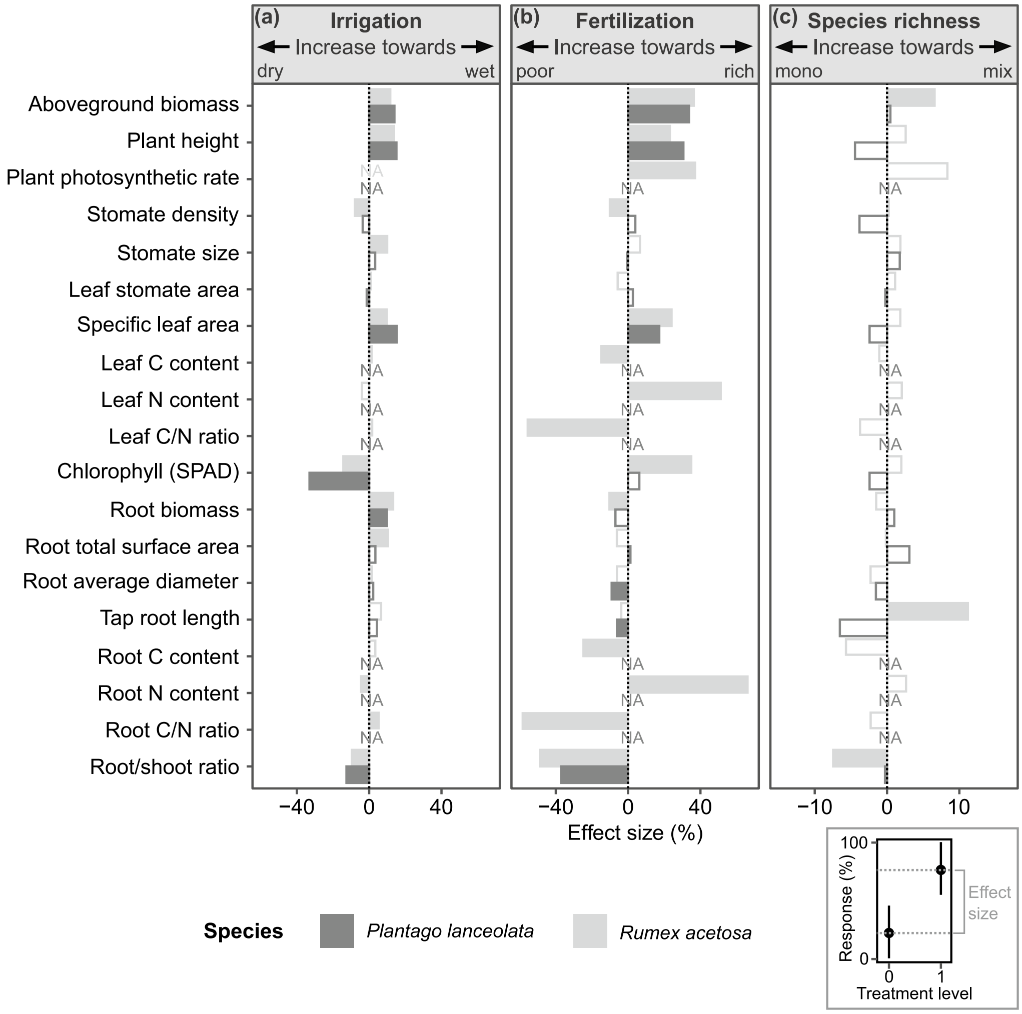


Fig. 3 Predicted responses of plant traits for each of the applied treatment factors. The predictions originate from the multiple linear regression model including all treatment factors and their potential interactions as explanatory variables. Effect size refers to the predicted change of range-scaled (0–100%; negative values if the response to treatment was a decrease) response trait variables when comparing the binary levels of each treatment factor (irrigation: dry vs. wet, soil fertility: poor vs. rich, species richness: monoculture vs. admixture). Note that there is a different scale on the x axis for the effects of species richness, while irrigation and fertilization have the same scale. Filled (empty) bars are (non-)significant responses at $p < 0.05$

photosynthetic rate increased, the C/N ratio became narrower in both shoot and root due to the strongly increasing tissue N content (Fig. 3b). The responses of the root and stomate trait cluster (compare Fig. 2) were less coordinated and rather diverse, even between the stomate traits. The stomate density increased under dry conditions and decreased in fertilized soil, the stomate size decreased in the dry treatment, and the leaf stomate area remained constant under all conditions (Fig. 3a&b). Root total surface area and root biomass were higher in the well-watered control treatment than under drought conditions. (Fig. 3a). The high input of fertilizer had a negative influence on root biomass (Fig. 3b). The root average diameter was not influenced by any treatment factor and the tap root length increased weakly due to the admixture of species (Fig. 3c).

For *P. lanceolata*, a coordinated response of cluster groups (compare Fig. 2) to a specific treatment factor could hardly be observed, because fertilizer input caused responses across all cluster groups (Fig. 3). The non-fertilized control treatment was related to thicker roots, longer tap roots, smaller plants, and the root–shoot ratio shifted towards roots (Fig. 3b). This was mainly due to the decline of aboveground biomass, because root biomass was not affected by fertilization (Fig. 3b). Although fertilizer application was the most influential factor for aboveground biomass, drought exposure also had a significant influence on aboveground production, which was greater than the effect on belowground biomass (Fig. 3a&b). However, as a result of water limitation, root biomass decreased (Fig. 3a). Chlorophyll content per leaf area increased under drought, while SLA decreased (Fig. 3a). SLA increased in the fertilized treatment. (Fig. 3b). No trait in *P. lanceolata* was affected by interspecific competition (Fig. 3c).

Interaction effects of treatment factors

In *R. acetosa*, only three traits were influenced by the interaction effects of the treatment factors (Fig. 4a–c; see Appendix A2 for a complete overview of mean responses in all possible two-fold interactions). For the chlorophyll content per leaf area, *R. acetosa* showed a much stronger drought response in admixture with *P. lanceolata* (Fig. 4a) compared to monoculture. Fertilization increased photosynthesis much more in species admixture compared to the monoculture (Fig. 4b) and the negative effect of fertilization on root biomass prevailed only in monoculture (Fig. 4c).

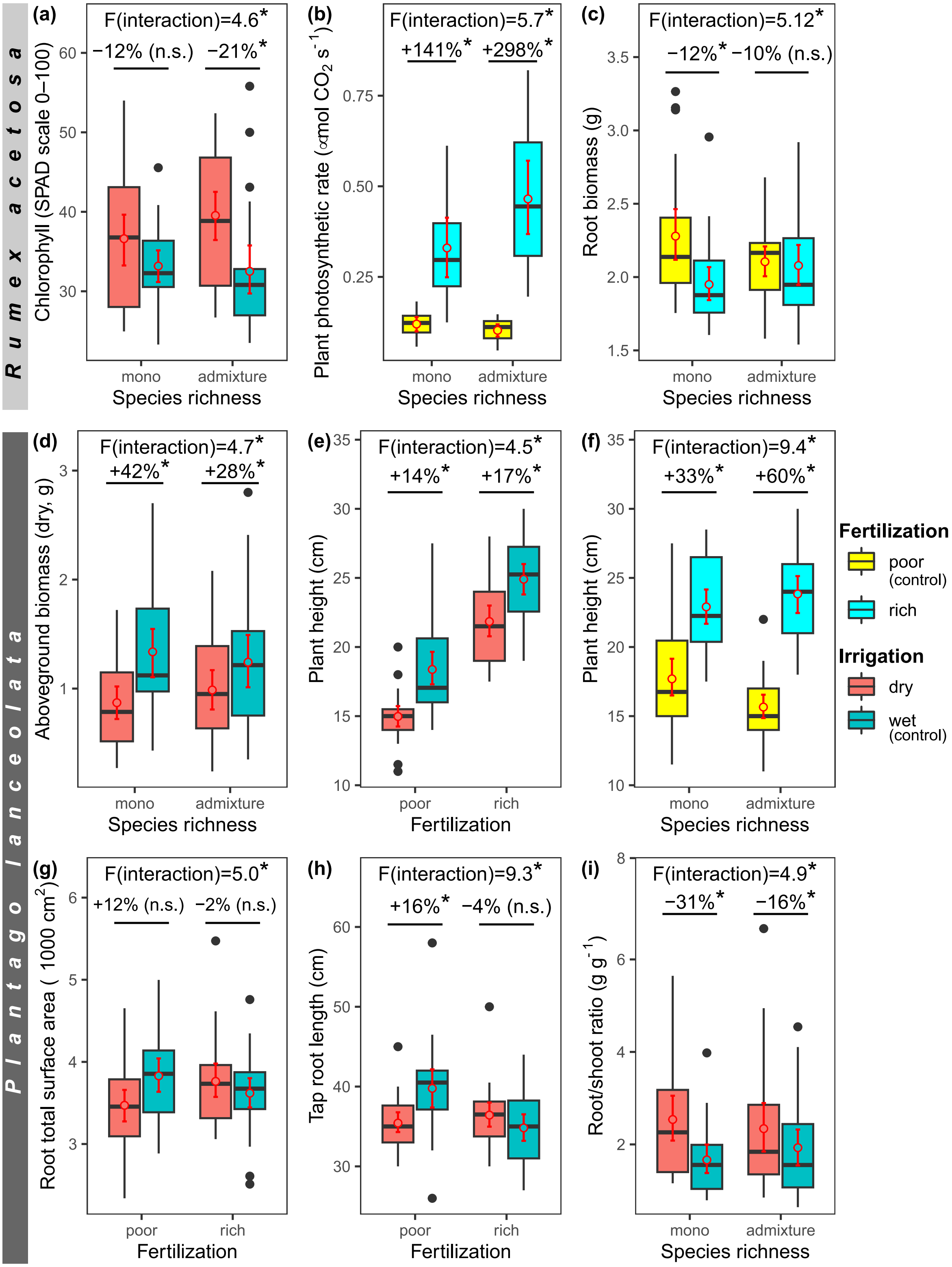
The effects of treatment interaction occurred more frequently in *P. lanceolata*. The production of root biomass was more sensitive to the availability of water in monoculture compared to species in admixture (Fig. 4d). For plant height, the effects of both water and nutrient availability interacted in our plants in the way that plant height continuously increased from dry and poor, to poor and wet, to rich and dry, and then to wet and rich substrate conditions (Fig. 4e). Plant height also showed a stronger response to low-nutrient stress when species were mixed, because plant height was similar in rich substrate regardless of competition, whereas plants became smaller in poor substrate, especially under interspecific competition (Fig. 4f). Although the models predicted an interaction between irrigation and fertilization on the total surface area of the roots, the mean responses and their confidence bands did not differ between groups (Fig. 4g). Tap root length decreased due to drought only in poor substrate (Fig. 4h) and the root–shoot ratio increased much stronger due to drought in monoculture compared to species admixture (Fig. 4i).

In terms of aboveground and root biomass, plants in the admixture of species never performed worse than the respective growth in monoculture (Fig. 5). However, significant overyield was only detected for the aboveground biomass under dry conditions for both species (Fig. 5a&b). In addition, *R. acetosa* showed clear overyield under high fertilization (Fig. 5d).

Discussion

Stronger association between root traits than between aboveground traits

Theoretically, plant species in more stressful environments should coordinate their trait responses towards a conservative economic strategy, i.e., resource acquisition and growth are slowed down in favour of higher organ longevity through, *e.g.*, smaller and thicker leaves, lower photosynthetic capacity, smaller size, and higher C/N ratio in plant tissue (Kramer-Walter et al. 2016; Reich 2014; Westoby 1998). Across the variable environments in our experiment, plant height and aboveground biomass in both studied herb species were well related and aboveground biomass and root–shoot ratio were the most closely linked trait responses. Plant size is a key trait in terms of competitive abilities, because plant individuals have to outsize their neighbours to secure their own light and carbon gain (Westoby 1998). This competition for light is probably more important in generally favourable environments, while larger plants are in contrast more sensitive to dry conditions (Olson et al. 2018; Westoby 1998). Thus, the carbon source activity, regulated by plant size and aboveground biomass, has to respond strongly plastic along stress gradients (Olson et al. 2018; Westoby 1998). Likely, the high importance of this plastic source regulation explains that the root–shoot regulation was not related to the regulation of the carbon sink activity (root biomass) in our data.


Rumex acetosa
Plantago lanceolata
(a)
F(interaction)=4.6*
−12% (n.s.)
−21%*
Chlorophyll (SPAD scale 0–100)
60
50
40
30
mono
admixture
Species richness
(b)
F(interaction)=5.7*
+141%*
+298%*
Plant photosynthetic rate (∝mol CO2 s-1)
0.75
0.50
0.25
mono
admixture
Species richness
(c)
F(interaction)=5.12*
−12%*
−10% (n.s.)
Root biomass (g)
3.5
3.0
2.5
2.0
1.5
mono
admixture
Species richness
(d)
F(interaction)=4.7*
+42%*
+28%*
Aboveground biomass (dry, g)
3
2
1
mono
admixture
Species richness
(e)
F(interaction)=4.5*
+14%*
+17%*
Plant height (cm)
35
30
25
20
15
10
poor
rich
Fertilization
(f)
F(interaction)=9.4*
+33%*
+60%*
Plant height (cm)
35
30
25
20
15
10
mono
admixture
Species richness
Fertilization
poor
(control)
rich
Irrigation
dry
wet
(control)
(g)
F(interaction)=5.0*
+12% (n.s.)
−2% (n.s.)
Root total surface area (1000 cm2)
6
5
4
3
poor
rich
Fertilization
(h)
F(interaction)=9.3*
+16%*
−4% (n.s.)
Tap root length (cm)
60
50
40
30
poor
rich
Fertilization
(i)
F(interaction)=4.9*
−31%*
−16%*
Root/shoot ratio (g g-1)
8
6
4
2
mono
admixture
Species richness

◂**Fig. 4** Significant two-way interactions that affect trait responses for *R. acetosa* (**a**–**c**) and *P. lanceolata* (**d**–**i**). The slopes of the trait responses within subgroups are indicated by the given percentage change from median poor to rich or dry to wet conditions, with the asterisk indicating significant differences at $p < 0.05$, "n.s." indicating non-significant differences. The red error bars indicate the 1000-fold bootstrapped 90% confidence interval of the data mean. "mono" stands for "monoculture"

Apart from this, we mostly observed different patterns for the trait–trait relationships in the two herb species studied, which contrasts the hypothesized (H1) generality of trait correlations within shoot and within root. In *P. lanceolata*, SLA was clearly related to chlorophyll content only, which might be due to the fact that plants in more stressful environments form thicker and more resistant leaves while trying to maintain photosynthetic capacity with a higher chlorophyll content on a smaller leaf area (Westoby 1998). Furthermore, SLA in both species studied did not appear as the type of coordinating trait as it does in more large-scale trait analyses across many species and biomes (Bruelheide et al. 2018; Reich 2014). Indeed, leaf morphology regulation for drought adaptation may well correlate with global turnover in plant functional types across large gradients from cold-wet to hot-dry biomes (Olson et al. 2018). However, within species and within biomes where this global cold-wet–hot-dry trait axis is not as strong, the plastic response of leaf morphology likely also reflects other factors, for example, the need to maintain radiation gain despite varying water availability (Niinemets & Kull 1998; Puglielli et al. 2021; Reich 2014). In contrast, the stronger relationship of stomate traits, regulating water transpiration, with root traits, related to water absorption, in *R. acetosa* also contrasts our hypothesis (H1) and is likely due to their weak but common variance along a wet–dry trait axis (Reich 2014).

Partly coordinated trait response to fertilization in *R. acetosa* and separate shoot versus root trait responses in *P. lanceolata*

For *R. acetosa*, at least most of the aboveground traits showed a strong and coordinated response to nutrient availability along an acquisitive–conservative spectrum sensu Reich (2014).This acclimatisation showed, in particular, the down-regulation of the nutrient sink (leave matter) in relation to the nutrient source (root matter), decreased photosynthetic capacity, a higher C/N ratio in plant tissue, and thicker and stronger leaves with lower chlorophyll content. All this clearly reflects typical strategies for resource conservation in the face of low-nutrient stress, because longevity and slow but continuous resource acquisition are then favoured (Kramer-Walter et al. 2016; Reich 2014). However, plastic trait responses did not mirror each other in all plant organs from root to shoot, which contradicts the postulation of coordinated trait responses to stress (Reich 2014). In summary, there was a coordinated response in *R. acetosa* along the acquisitive–conservative plant economic spectrum, but contrasting our hypothesis (H2), only along a nutrient stress axis and not for all traits across the whole plant, because some traits showed equal or greater sensitivity to drought stress or no response at all.

In *P. lanceolata*, trait responses were even more diverse. The root versus shoot trait responses across variable environments were generally not related to each other. In a whole-plant perspective like here, it appears that in absolute contrast to our hypothesis (H2) there was not a single strategy to vary traits along stress gradients. Instead, organ- and trait-specific responses differ due to the type of environmental gradient. For example, the size of the plant decreased and the root–shoot ratio increased due to water or nutrient limitation in our study, indicating resource conservatism due to stress (Bruelheide et al. 2018; Reich 2014; Westoby 1998). However, water limitation caused our plants to become smaller overall, affecting the shoot mass more than the root mass, which indicates both resource conservation at the whole-plant level as well as a more favourable water absorption–transpiration ratio (Hertel et al. 2013). Under nutrient limitation, on the contrary, the root biomass of *P. lanceolata* actually increased. This probably indicates that roots switch to a compensatory strategy of fast resource acquisition despite or precisely because of nutrient deficiency, regardless of the aboveground traits (Kramer-Walter et al. 2016). This independent response strategy of root traits contrasts with previous ideas that selected aboveground traits, such as plant height and SLA, are representative of specific ecological strategies of plants as a whole (Cunningham et al. 1999; Fonseca et al. 2000; Westoby 1998). Thus, global change studies in plant

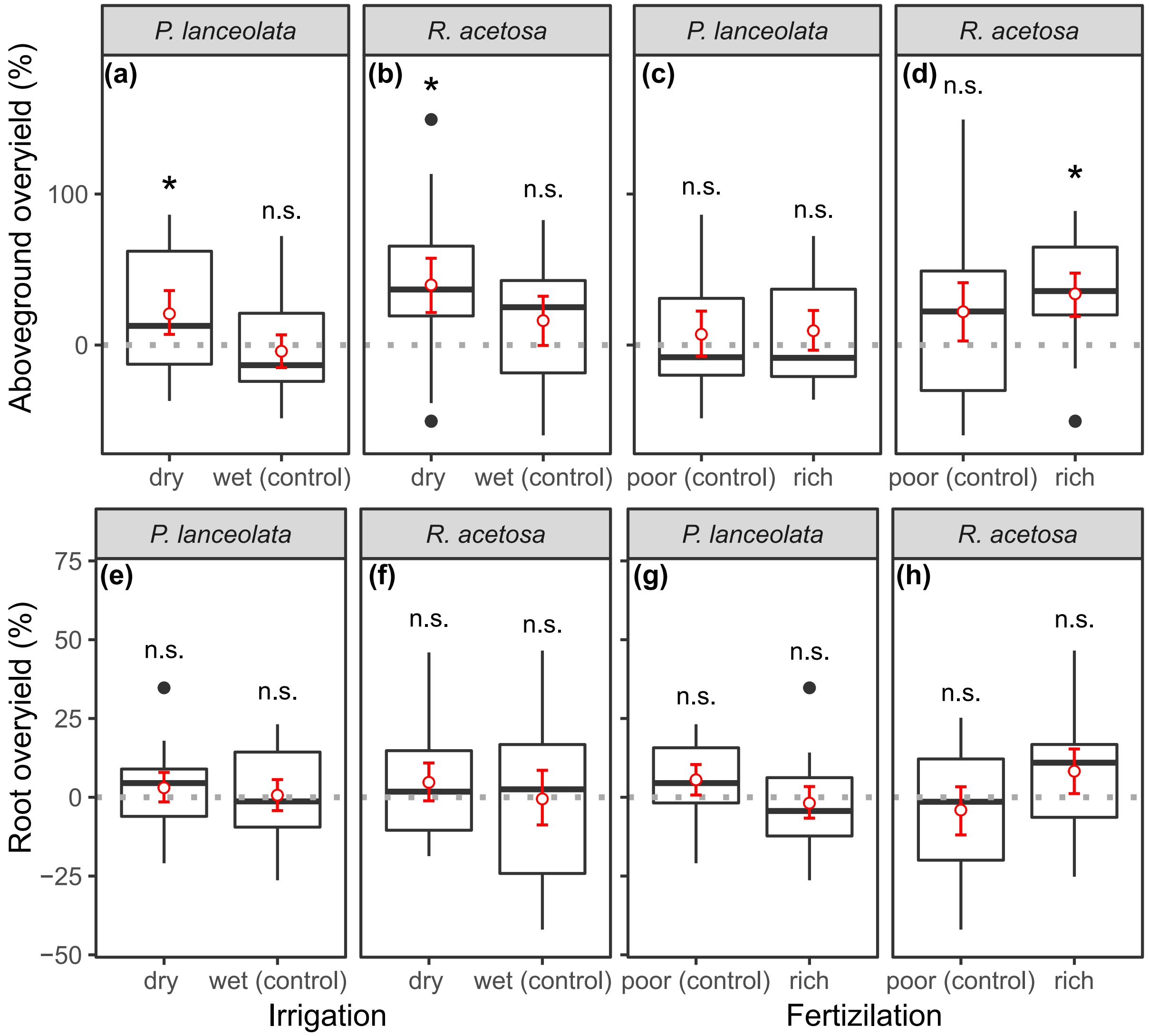


Fig. 5 Biomass overyield of mixed cultures in relation to monocultures for the different study species and different experimental treatments. Positive values (with asterisk) indicate a (significant) overyield in the admixture compared to monoculture, negative values an underyield. "n.s" means no significant difference from 0 at $p < 0.05$. The red error bars indicate the 1000-fold bootstrapped 90% confidence interval of the data mean

ecology urgently require a whole-plant perspective, properly including the rhizosphere. Furthermore, the unexpected, divergent root responses to water versus nutrient limitation in our study show that trait responses to global change drivers must be evaluated in environments where the influence of different stress factors can be well separated, as is the case in a controlled experimental setting (De Boeck et al. 2015; Peñuelas et al. 2020).

Fertilization mediates drought stress, but stress has varying influence on complementary resource use

At least partly for *P. lanceolata*, higher fertilization rates mediated drought stress as hypothesized (H3) and as expected (Gentilesca et al. 2018), because the well-fertilized individuals that were drought exposed grew larger than those that were well watered and nutrient limited. Furthermore, tap root growth was only affected by drought under poor substrate conditions. However, the observed importance (F-ratios) of these *irrigation x fertilization* interactions was quite low compared to the isolated drought effects on plant size. We must note that we applied an NPK fertilizer and controlled for diversity in the experiment. Therefore, we also excluded negative impacts of fertilization on the drought resilience of ecosystems that could indirectly result from a decline in biodiversity due to nitrogen eutrophication currently observed worldwide (Hautier et al. 2020; Peñuelas et al. 2020). Still, by controlling for these indirect effects, our experiment shows that fertilization can mitigate drought impacts as hypothesized (H3), but in our case only in selected species and few traits.

Overall, the influence of species richness on the measured traits was quite low in our study, which may very well be due to the relatively short duration of our experiment, because biodiversity effects on overyield, stability of productivity and ecosystem functioning often only become stronger after years (Meyer et al. 2016; Wagg et al. 2022; Zheng et al. 2024). However, we did indeed find signs of interspecific complementary resource use, which was indicated by a higher accumulation of biomass in the mixture compared to monoculture (Hector et al. 2002). Remarkably, this was found for both species under drought, but not under well-watered conditions, and for *P. lanceolata* the aboveground growth as well as the adjustment of the root–shoot ratio were not as sensitive to drought in the admixture of species as in monoculture. This is in line with the stress gradient hypothesis, which expects interspecific complementary resource use, especially in harsh environments (Bertness and Callaway 1994). Since the strong tap root system of *R. acetosa* and the more fibrous roots of *P. lanceolata* (Figure S1 in Appendix A1) may complement each other, the effect is possibly due to hydraulic redistribution, which is classically described as more important in more arid systems (Neumann & Cardon 2012). However, our results also show that this pattern depends on the type of stressor, because the results fit the stress gradient hypothesis and our hypothesis (H3) for drought but not for low-nutrient stress. In conclusion, our experiment is another strong case highlighting the stabilizing effect of plant diversity, particularly diversity of root morphology in our case, and complementary resource use for mitigating the impact of global change-type droughts (Brooker 2006; Grant et al. 2014).

Conclusion

This plant experiment offered a simplified but controlled view on the world under global change to understand the separate effects of varying water and nutrient availability on both shoot and root traits. Our experiment clearly showed that trait responses were often not coordinated from shoot to root, contrasting previous expectations. Root traits even showed unexpected multidimensional behaviour, with a ‘slow’ strategy due to water limitation, but a ‘fast’ strategy due to nutrient limitation. Thus, refining the concept of a whole-plant trait spectrum requires many more studies that include root traits in controlled environments where the influence of specific environmental factors can be experimentally separated. Relating the response of root and shoot traits more closely will certainly shed new light on many general assumptions that have been based heavily on observation of the more accessible aboveground plant organs. For example, our study shows that increasing nutrient availability has the potential to mitigate drought-induced aboveground growth decline, while, in contrast, high nutrient loads and drought in combination have a double negative effect on carbon allocation belowground. More generally, the study findings also highlight the importance of maintaining species richness in grassland systems to promote drought resilience, which is a challenging task due to the increasing global eutrophication that can lead to the decline of species diversity.

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Author contributions LM and RW conceived of and designed the study. KA, WB, CHD, TN, MS, AW, LW, and KZ performed the research. RW harmonized and analyzed the data. LM, RW, AW, LW, and KZ wrote the manuscript based on the first draft of RW. All authors improved the manuscript significantly by their critical comments.

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Data availability The replication data and all R scripts used for the analyses in this manuscript are published on the open research data server of the University of Goettingen, Goettingen Research Online (https://doi.org/10.25625/TBARNX).

Declarations

Competing interests None to report.

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