

RESEARCH ARTICLE

Relationships between aboveground and belowground trait responses of a dominant plant species to alterations in watertable depth

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Abstract

Drought impacts to plant growth can be indicated by changes in key functional traits. However, previous research has focused on aboveground trait responses to precipitation deficits, with less emphasis on concomitant belowground impacts and deep soil drought from groundwater depletion. We assessed changes in a suite of aboveground and belowground traits of a dominant plant, *Phragmites communis*, in response to an experimental gradient of underground watertable depth. Our study occurred within the northeastern Inner Mongolia region, where changes to groundwater tables have been pervasive in recent years. In general, the results indicate that both aboveground and belowground traits responded positively, yet eventually negatively, to continual increases in watertable depth, indicative of reduced access to soil moisture as watertable depths increased. Key adjustments include changes to the ratio of coarse roots to fine roots, and the distribution of fine roots within the soil profile. These changes in belowground traits had strong correlations with changes in aboveground traits. In particular, specific root length of fine roots was positively correlated with leaf area, height, and aboveground biomass, whereas root biomass was linked to leaf area, specific root length of coarse roots, and root length density. Fine and coarse root production also had positive and negative relationships with aboveground biomass, respectively, suggestive of biomass allocation tradeoffs. We suggest that biomass production responses of this species to changes in watertable depths may largely be driven by interactions between the distribution of fine and coarse roots in the soil profile and changes to leaf area.

KEYWORDS

drought, fine roots, root traits, underground watertable

1 | INTRODUCTION

Plant functional traits are used to indicate the ability of plants to capture and retain essential resources (Kazakou et al., 2014; Kraft, Godoy, & Levine, 2015; Reich et al., 2003). However, much attention has historically focused on aboveground traits, leading to an increased recognition about the need to better understand the dynamics of

belowground traits (Laliberté, 2017). Theory predicts that plants with 'fast' traits such as high specific leaf area (SLA: the ratio of leaf area to leaf dry mass), photosynthetic rate, and leaf nitrogen content will rapidly acquire key resources, whereas plants with longer life span or in resource poor habitats may exhibit opposite patterns of 'slow' traits with more conservative resource use (Perez-Harguindeguy et al., 2013). It is uncertain whether root traits fall along the same ecological

trade-off spectrum of resource use and conservation, although there is evidence to suggest different mechanisms may operate between belowground and aboveground traits (Zemunik, Turner, Lambers, & Laliberté, 2015). Indeed, an understanding of root traits, their relationships with aboveground traits, and how this influences plant biomass production can also serve to constrain predictions of ecological models (Warren et al., 2014), particularly amid increasing levels of land use intensification and consequent degradation.

Changes to environmental conditions will impact root traits, with downstream impacts to key ecosystem processes and services. For example, low temperatures tend to increase the fraction of root biomass relative to aboveground biomass in forests yet decrease forest ecosystem productivity (Ostonen et al., 2007). Under drought stress, plants produce deeper and thinner roots to improve soil moisture acquisition (Debinski, Wickham, Kindscher, Caruthers, & Germino, 2010; Hoepfner & Dukes, 2012), with this plasticity differing considerably among species (Comas, Becker, Cruz, Byrne, & Dierig, 2013; Nippert & Knapp, 2007). Plants may also alter root morphology by decreasing root diameter to maintain water acquisition and productivity under drought conditions (Wasson et al., 2012), with higher growth rates of fine roots under drought conditions previously observed (Robinson, Hodge, Griffiths, & Fitter, 1999).

The 'balance growth' hypothesis predicts that plants will stimulate or maintain root growth but reduce shoot growth during drought (Bloom, Chapin, & Mooney, 1985), as maintenance of root growth will maintain plant hydraulic status under drought. These changes may be driven by shifts in the ratio of fine to coarse roots, as increased fine root production will increase root surface area for absorption, whereas increased coarse root production may increase the maximum root length to access deeper soil layers (Poorter et al., 2012), while also potentially allowing for greater soil C storage due to slower turnover of coarse versus fine roots. As a consequence, it is critical to consider the correlative drought responses between coarse and fine roots, as well as their linkages with other key functional traits, both aboveground and belowground.

In recent years, an increasing number of ecological studies have experimentally or observationally assessed how drought impacts plant communities, yet most approaches have only considered surface drought that is caused by precipitation deficits (Nippert & Holdo, 2015; Tombesi et al., 2015). With precipitation-driven surface drought, plants increase lateral branching to access more soil moisture (Comas et al., 2013). However, in 'deep' drought that is driven by alterations to the watertable, plants may preferentially seek moisture in deeper soil layers by increasing the depth of coarse roots. For example, some plants employing deep-rooting strategies, such as Phreatophytes, may become largely decoupled from precipitation variability due to acquisition of moisture from deep layers and thus limited reliance on precipitation inputs.

Although the ecological dynamics of groundwater depletion are largely uncertain (Antunes et al., 2018), previous research suggests that if precipitation is insufficient and groundwater table depth is gradually increasing, plants will produce longer coarse roots to explore soil moisture in deeper layers (Vandeleur et al., 2009). Because it is impossible to distribute a large number of fine roots in all soil layers, the most economic soil water acquisition strategy should be to

produce fine roots both in the surface (to absorb precipitation) and near the groundwater table (to absorb groundwater). This different type of human-driven soil drought has become increasingly important in developing regions (Laliberté, 2017) and is caused by the continuous increase of water usage for urban, industrial, and agricultural purposes (IPCC, 2012). As a result, increasing land use and consequent degradation of groundwater resources is an increasingly important, yet still poorly understood, aspect of how future water scarcity will impact ecosystems.

This project was located in the northeastern part of China's Inner Mongolia grassland region, where groundwater is the main source of industrial and agricultural water use. Overexpansion of well irrigation has produced sharp drops in ground water depths (Gao, Tang, & Tang, 2015), leading to shortages of water resources, biodiversity loss, and land degradation (Mao, Zhang, Li, Zhao, & Huang, 2012; Sun et al., 2018) that has exacerbated the process of desertification within the region. Our study focused on the plasticity of aboveground and belowground trait responses of the dominant plant species *Phragmites communis* to a gradient of increasing ground water depths, with an emphasis on understanding the consequences this trait plasticity has for biomass production.

Because of the wide adaptability, root structure, and physiological ecology of *P. communis*, this species can produce high levels of root biomass under drought conditions, which increases soil structural stability and colonization for species in early vegetation succession, and thus ameliorates land degradation (Zhao, Chang, Li, & He, 2003). Responses of dominant species to environmental change can serve as indicators of ecosystem sensitivity to environmental change (Gitlin et al., 2006; Liu et al., 2018), as such species often control biomass production and other ecosystem functions and services (Grime, 1998). We thus used *P. communis* as a model species to assess the responses and linkages among belowground and aboveground traits to 'deep' soil drought via changes to watertable levels at multiple depths. This approach can mechanistically improve forecasts of ecosystem sensitivity to an emerging pathway of water stress within this region: altered watertable depths. Our study sought to answer the following questions:

- 1) How do aboveground and belowground traits of *P. communis* respond to alterations in groundwater depth? Are trade-offs or linkages apparent among trait responses?
- 2) Which aboveground or belowground trait responses are most strongly linked with changes to biomass in response to changes in groundwater depth?

2 | MATERIALS AND METHODS

2.1 | Study site and species

We conducted this study within the Horqin Sandy Grassland of eastern Inner Mongolia, China (42°55'N, 120°42'E). The dominant plant species of this region are *Setaria viridis*, *P. communis*, *Chenopodium acuminatum*, and *Pennisetum centrasiticum* (Mao et al., 2012). Soil

nitrogen content is very low, approximately $0.057\text{--}0.199\text{ g kg}^{-1}$, and the soil bulk density can range from $1.29\text{ to }1.59\text{ g cm}^{-3}$ within the top 0–30 cm (Mao et al., 2012). We chose to assess the responses of *P. communis* because this species survives in various degraded habitats, especially in severely water stressed habitats, and plays an important role in maintaining soil structural stability and hindering land degradation (Luo et al., 2014).

2.2 | Experimental design

Five levels were produced to experimentally manipulate watertable depth, with three replicates per each treatment level. Manipulations were carried out in polyvinyl chloride barrels with a diameter of 30 cm and consisted of 40, 80, 120, and 180 cm underground water table depths (Figure 1). The control treatment has no seal at the bottom and was thus the local underground water level, which is near 700 cm (Ma, Zhang, Liu, Mao, & Yue, 2015). This experimental approach allowed us to produce a controlled treatment gradient (sensu Cottingham, Lennon, & Brown, 2005) to mechanistically assess impacts of gradually increasing watertable depths, all the way to the far deeper depths currently experienced in the region.

Polyvinyl chloride barrels were buried to 0.6, 1, 1.4, and 2 m according to each treatment level (Figure 1). We then loaded stones (diameter > 10 mm, thickness of 10 cm) into the experimental barrels, followed by sand to establish the watertable. At the bottom of each barrel, the free water layer was 20 cm. We selected adult *P. communis* individuals from the same sandy dune habitat, digging out the root system with the buds intact, and selected 4–6 rhizomes with two buds of ~5 mm diameters and ~15 cm lengths. We then planted all the selected rhizomes into the experimental barrels. Finally, we established a simple Mariotte bottle device to control the water levels (Thorel, Favraud, & Garnier, 2002) and record the amount of supplemental water when the Mariotte device was needed (see Ma et al., 2015 for detailed description). The experiment began on March 15, 2013. The soil moisture content between 0- and 180-cm soil depths was monitored using TRIME-FM-P3 (IMKO Micromodultechnik, Ettlingen, Germany) portable soil moisture meter every 2 weeks during the growing season from June 15 to August 15.

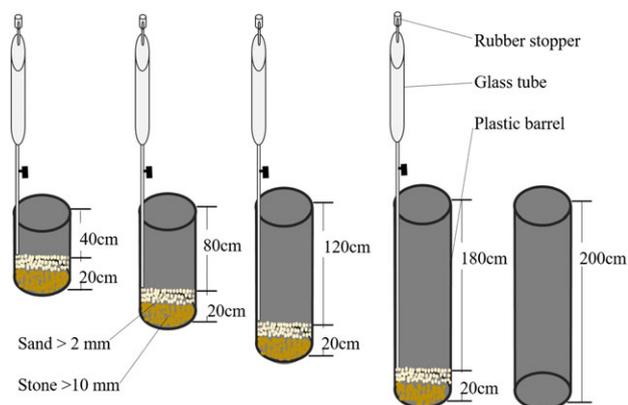


FIGURE 1 Schematic representation of the equipment utilized to control and maintain different underground water table depths among our treatments [Colour figure can be viewed at wileyonlinelibrary.com]

2.3 | Trait analyses

Photosynthetic rates per leaf area were measured mid-August utilizing an LI-6400 portable gas exchange system and infrared gas analyzer (LI-COR Industries, Lincoln Nebraska). We measured the leaf area used inside the IRGA chamber for photosynthetic measurements to calculate light-saturated photosynthesis on an area basis (P_{area}). Similarly, both aboveground and root biomass samples were collected mid-August, as this is when peak biomass is typically reached. Plant height and leaf area were also measured in the middle of August. For leaf area, we selected three individuals to measure the area per leaf on 3–5 mature and healthy leaves for each treatment. Fresh leaf area was scanned and calculated using SCION IMAGE (version 4.0.2; Scion Corp., Frederick, MD, USA). For aboveground biomass, we summed together and analyzed all components of aboveground structures, which included leaves, stems, and reproductive organs. Aboveground and root biomass were dried to 80°C for 48 hr after harvesting and were expressed as grams (g) of dry weight.

For belowground responses, root length, and biomass were measured separately, which allowed us to explore multiple root trait responses to our experimental gradient. In these measures, 2 mm or greater diameter roots were defined as coarse roots, whereas those less than 2 mm in diameter were defined as fine roots (Silver & Miya, 2001). Specific root length of fine roots (SRL-fine root) was quantified as the ratio of fine root length and fine root biomass, and SRL-coarse root was quantified as the ratio of coarse root length and coarse root biomass. Root length density (RLD) was defined as the length of all roots in the soil per unit volume, whereas total root length (TRL) was defined as the sum of fine root length plus coarse root length (Perez-Harguindeguy et al., 2013). In addition, the root length ratio was defined as the ratio of fine root length to coarse root length, and the root biomass ratio was calculated as the ratio of fine root mass to coarse root mass. Root-to-shoot ratio was quantified as the ratio of root biomass to shoot biomass. Vertical distributions of fine and coarse roots were determined via assessments of their biomass ratios at 20-cm increments across the watertable depth gradients. All measurements derived from scanned root images were conducted in SCION IMAGE.

2.4 | Statistical analyses

One-way analysis of variance was used to analyze data utilizing SPSS19.0 statistical analysis software. Plant height, leaf area, aboveground biomass, photosynthetic rate, RLD and SRL-fine root, SRL-coarse root, mass ratio, length ratio, and root biomass were compared by utilizing the least significant difference method for different treatment levels. Correlations between aboveground and belowground traits were quantified by calculating the Pearson correlation coefficient between each trait in SPSS. Because of potential high correlation between these traits, we first ran a principal component analysis (PCA) for the different aboveground and belowground traits. We then conducted stepwise model selection for trait correlates of aboveground and root biomass responses, with Akaike information criteria as our selection metric, as Akaike information criteria balances model parsimony with descriptiveness to find the best model fit. We utilized this

method in order to find the trait combination that best predicted the response of biomass production to changes in watertable depth, using Matlab 8.0. Both the PCA and multiple regression analyses as well as all graphs were plotted using Matlab.

3 | RESULTS

Soil moisture in the upper 40 cm of the soil profile was primarily driven by precipitation inputs. However, treatments were effective at manipulating soil moisture at different target depths, as underground watertable treatments impacted soil water content at different layers, especially in the deep soil layers (Figure 2). The results show that the shallower the underground watertable, the higher the soil water content in the topsoil layers, and vice versa. For 40-cm watertable depths (the shallowest), the soil moisture content of all soil layers was consistently high, whereas in the control depths (the deepest), the soil water content of 0-to 180-cm soil layers was consistently low. Moreover, in the 40, 80, 120, and 180 cm treatments, the soil water content reached its peak in the deepest soil layers (Figure 2).

Change of groundwater depth had widespread effects on aboveground traits of *P. communis* (Figure 3). All aboveground traits, except the saturating response of P_{area} , showed a tendency to increase first and then decrease with increasing watertable depth. Leaf area and aboveground biomass of *P. communis* were highest at the groundwater depth of 120 cm, and lowest in the control treatment, which had by far the lowest underground watertable depths. P_{area} was highest in the groundwater depths of 80 and 120 cm and lowest in the groundwater depth at 40 cm. However, P_{area} did not significantly differ for depths beyond 80 cm (Figure 3d). Height of *P. communis* was highest at groundwater depth of 80 cm and lowest at control treatment

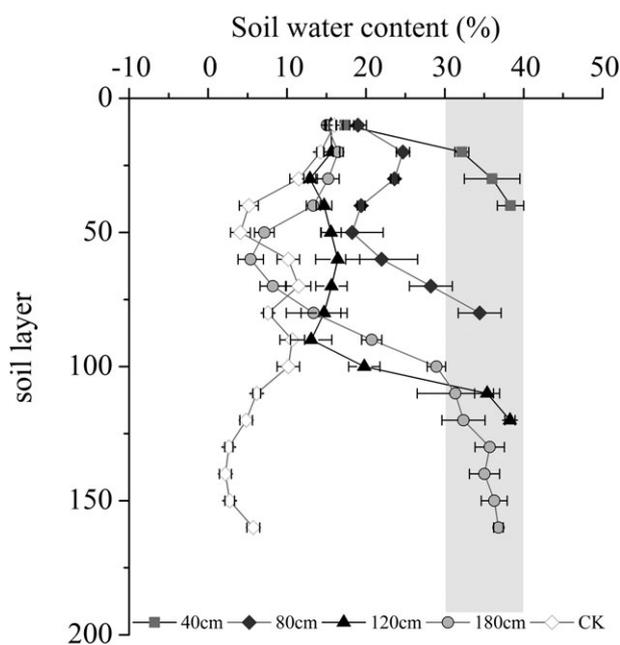


FIGURE 2 The soil water content of different soil layers within different watertable depths. Values are integrated over the course of the whole growing season. For all treatments, the greatest soil moisture availability occurred at the deepest depths, yet this dynamic was not evident for the 'ambient' controls

(Figure 3). Leaf area and aboveground biomass were more consistent among different treatments, and the variation and thus plasticity between the highest and lowest was higher, reaching 5.14- and 6.7-fold differences, respectively.

There were similar response patterns of root traits as compared with aboveground traits (Figures 3 and 4). For instance, root length and root biomass showed an initial increase then decrease as groundwater table depth increased. TRL and RLD were the highest at 80 cm and the lowest at control treatment. Total root biomass was highest at 120 cm and lowest at the control treatment (Figure 4a), with biomass at 120 cm depths 9.47 times higher than at control levels. Moreover, plasticity of root biomass was highest among all traits measured. However, SRL-fine root and SRL-coarse root had different patterns of responses than other root traits. These two traits did not show a tendency to increase first and then decrease with the increase of underground watertable depths. For instance, SRL-fine root was highest at 180 cm and lowest at control treatment, whereas coarse roots were lowest at 120-cm and highest at the 180-cm treatment. In the 40-cm treatment, the mass ratio of fine root to coarse root was higher than at other treatment levels, suggesting a preferential allocation to fine root production.

Pearson correlation analyses demonstrated that aboveground and root traits had high correlations (Table 1). Leaf area had strong relationships with almost every aboveground and belowground trait, except with the mass ratio of fine root to coarse root and P_{area} . For belowground traits, the RLD was positively correlated with all aboveground traits, except P_{area} (Table 1). SRL-fine roots and SRL-coarse root exhibited different patterns of correlations with aboveground traits, and PCA analysis (Figure S1) showed poor correlation between SRL-fine and SRL-coarse root values (Table 1). SRL-fine root was positively correlated with TRL, leaf area, and aboveground biomass, whereas SRL-coarse root was negatively correlated with leaf area and aboveground biomass. RLD was largely correlated with SRL-fine root, which had no significant relationship with SRL-coarse root. Moreover, in the 40-, 80-, and 120-cm treatments, plants tended to distribute more roots in the deepest layers to access underground water (Figure 5).

Leaf area, SRL-fine root, and height were selected as the best predictors for aboveground biomass, whereas for root biomass, the most important traits selected were leaf area, SRL-coarse root, and RLD (Figure S2). Given the differences in coarse and fine roots, we used these two belowground traits in combination with the best predictors selected from the stepwise regressions to gain inference on how these traits may interact to predict aboveground and root biomass (Figure 6). When RLD is held constant, for example, at 40, 400, and 800 m/m^{-3} for a given leaf area, SRL-coarse root exhibits a negative relationship with root biomass. In addition, when height is set as constant for a given leaf area, the higher value SRL-fine root is, the smaller aboveground biomass is.

4 | DISCUSSION

In this study, we sought to assess how aboveground and belowground plant traits respond to continual increases in watertable depth and to

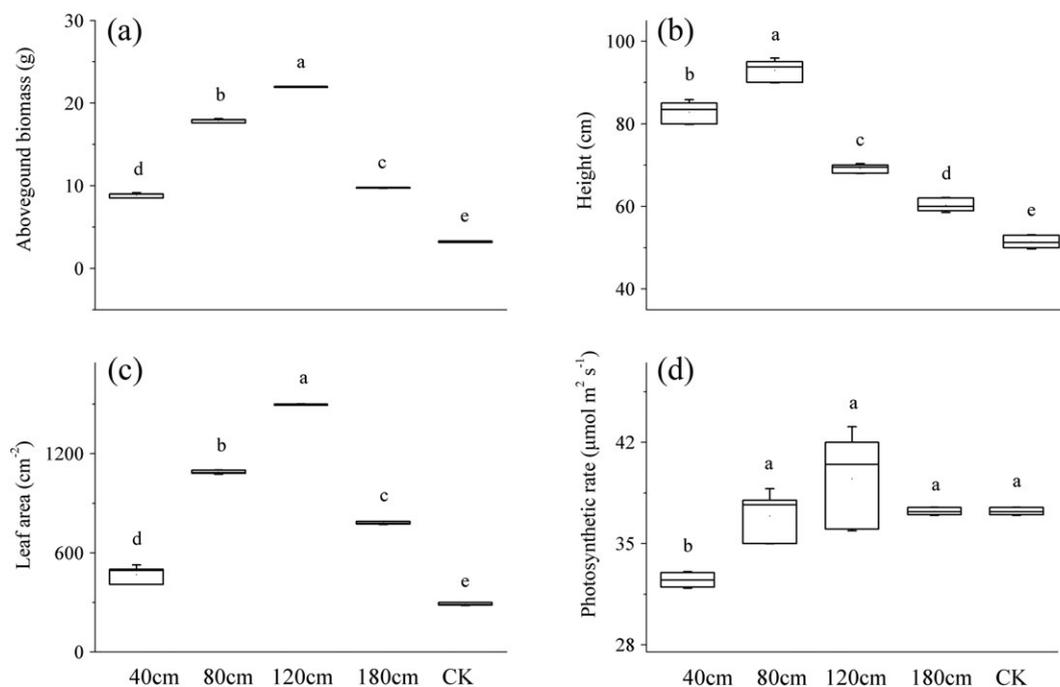


FIGURE 3 Changes in aboveground traits at different underground watertable depths. Although most traits initially responded positively to deeper levels of water table depth—potentially indicative of increases in space availability—processes tended to saturate, such as photosynthesis (d) or become negatively impacted (a–c) at the deepest depths, potentially reflecting increasing water stress as deeper soil water becomes increasingly inaccessible. Different letters indicate significant differences at $p < 0.05$

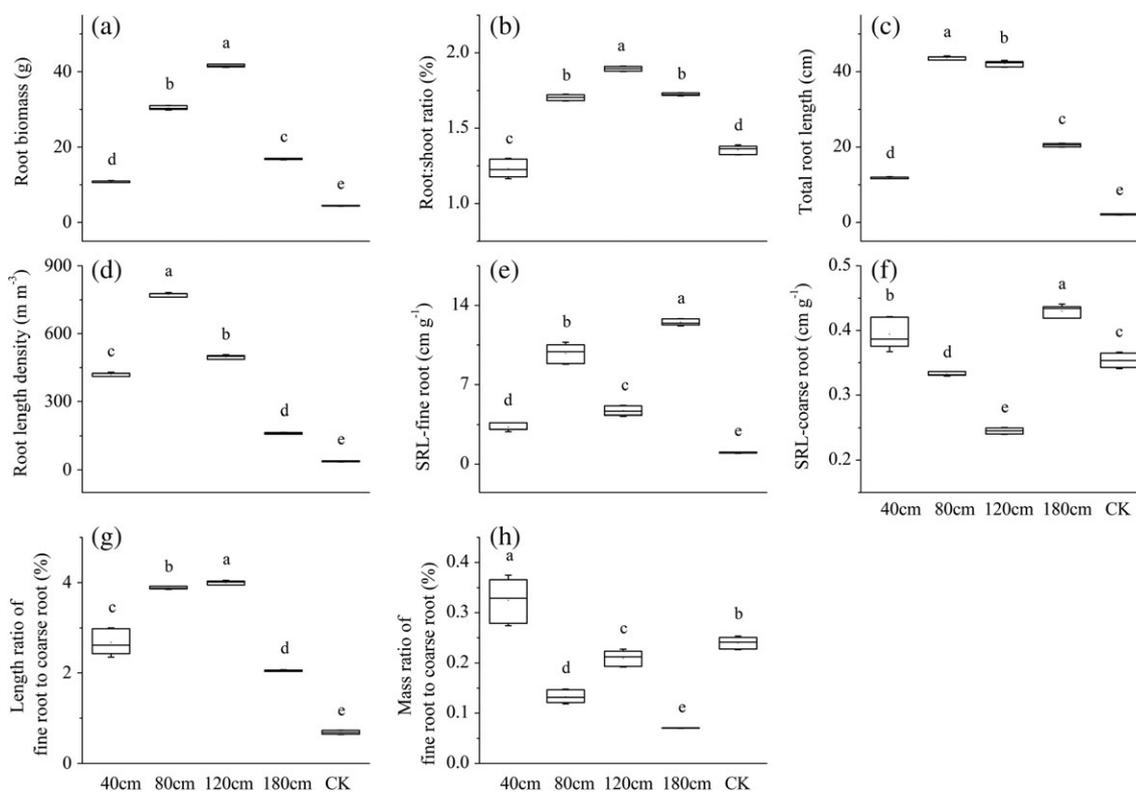


FIGURE 4 Belowground trait responses at different underground watertable depths. In general, belowground traits responded to increasing water table depth in a similar way as aboveground traits (a–d, g), yet overall exhibited more variable and less consistent responses. Different letters indicate significant differences at $p < 0.05$

elucidate which of these traits may explain changes in plant biomass production. Morphological characteristics of the dominant plant species *P. communis* showed strong plasticity in response to changes in

underground watertable depths (Figure 3b,c), yet this was not evident for our physiological metric of photosynthetic responses (Figure 3d). High phenotypic plasticity can represent an adaptive advantage when

TABLE 1 Pearson correlation coefficients between aboveground and belowground traits

| Root traits Aboveground plant traits | Total root length | SRL- fine root | SRL- coarse root | Root l ength density | Length ratio | Mass ratio | Root: shoot ratio | Root biomass | P_{area} | Leaf area | Height | Aboveground biomass |
|--|-------------------------|----------------------|------------------------|----------------------------|-----------------|---------------|-------------------------|-----------------|------------|--------------|--------|------------------------|
| Total root length | 1 | 0.84** | -0.37 | 0.90** | 0.96** | -0.39 | 0.72** | 0.98** | 0.21 | 0.95** | 0.68** | 0.98** |
| SRL-fine root | | 1 | 0.13 | 0.65** | 0.72** | -0.76** | 0.63* | 0.74** | 0.12 | 0.73** | 0.5 | 0.73** |
| SRL-coarse root | | | 1 | -0.33 | -0.39 | -0.32 | -0.53* | -0.55* | -0.54* | -0.57* | -0.11 | -0.52* |
| Root length density | | | | 1 | 0.98** | -0.02 | 0.38 | 0.84** | -0.11 | 0.77** | 0.91** | 0.91** |
| Length ratio | | | | | 1 | -0.13 | 0.53* | 0.92** | 0.018 | 0.86** | 0.81** | 0.97** |
| Mass ratio | | | | | | 1 | -0.61* | -0.33 | -0.37 | -0.39 | 0.1 | -0.24 |
| Root:shoot ratio | | | | | | | 1 | 0.80* | 0.71** | 0.87** | 0.06 | 0.71** |
| Root biomass | | | | | | | | 1 | 0.35 | 0.99** | 0.59* | 0.99** |
| P_{area} | | | | | | | | | 1 | 0.45 | -0.34 | 0.24 |
| Leaf area | | | | | | | | | | 1 | 0.48 | 0.96** |
| Height | | | | | | | | | | | 1 | 0.68** |
| Aboveground biomass | | | | | | | | | | | | 1 |

Note. Trait correlation values integrate trait responses across levels of watertable depth. P_{area} is photosynthesis per area, mass ratio is the ratio of fine root mass to coarse root mass, length ratio is ratio of fine root length to coarse root length, and SRL refers to specific root length.

* $p < 0.05$. ** $p < 0.01$.

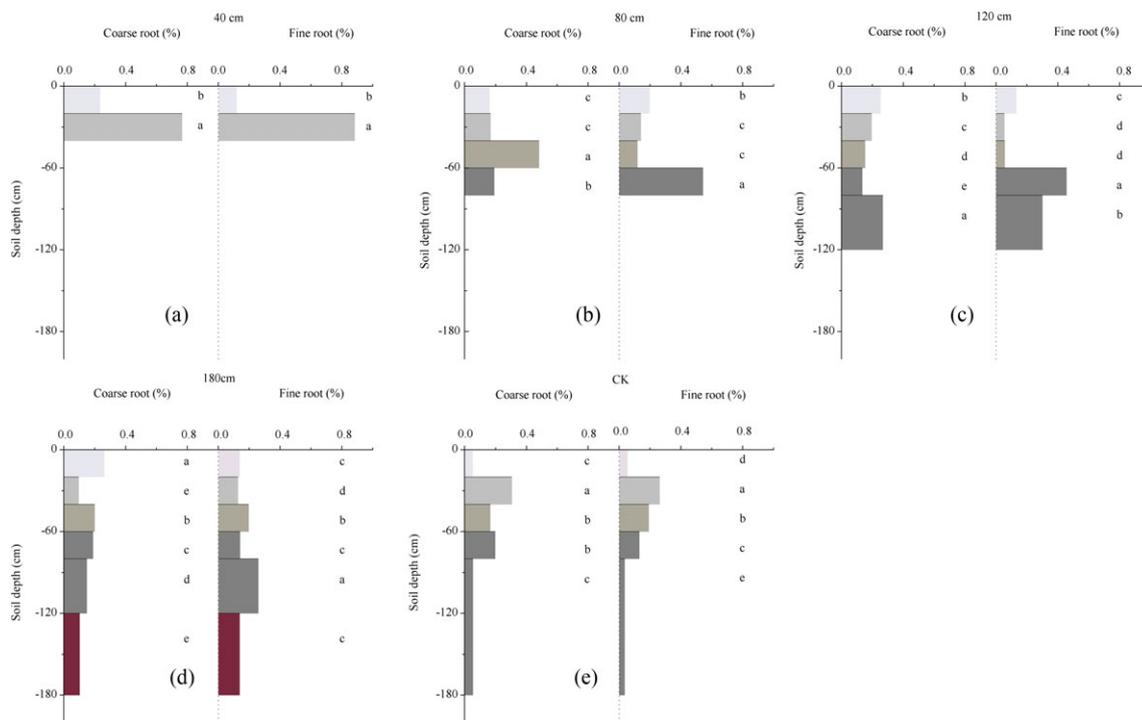


FIGURE 5 The vertical distribution of coarse and fine roots within the soil profile under varying levels of watertable depth. The x-axis indicates the ratio of root biomass in each 20 cm. Different letters indicate significant differences among different soil level at $p < 0.05$. Changing underground watertable depth altered root vertical pattern of *P. communis*. In the 40-, 80-, and 120-cm treatments, plants tended to distribute more roots in the deepest layers to access moisture, whereas in the 180-cm and control treatments (CK) that were over the apparent threshold, plants did not distribute a high ratio of roots in deeper soil layers [Colour figure can be viewed at wileyonlinelibrary.com]

resource availability varies rapidly in time and space (Davidson, Jennions, & Nicotra, 2011). For aboveground traits, leaf area and biomass showed large plasticity, increasing initially then decreasing with increases in watertable depths. This suggests an initial plastic response to water depth changes until a potential overriding impact of an increasing limitation of accessing soil moisture at deeper depths.

Interestingly, the highest trait values were at 120-cm depths, whereas the lowest value were for the 40 cm and control treatments (Figure 3). We suggest this dynamic reflects trade-offs between soil space occupation at the shallowest depths and soil moisture access at the deepest depths. In addition, waterlogged soils at shallow watertable depths may also lead to hypoxic conditions that reduce oxygen

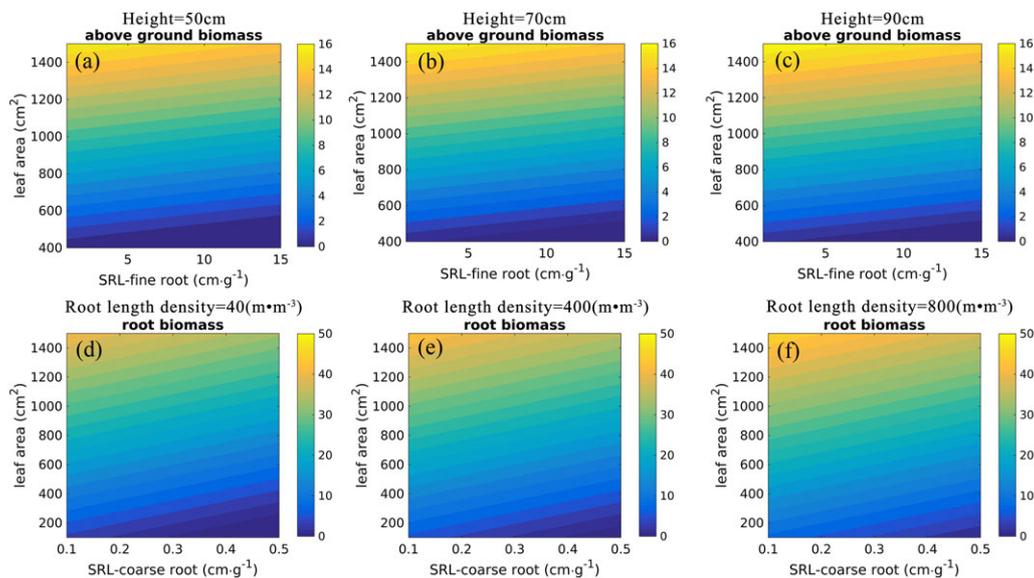


FIGURE 6 Linear functions of biomass with three variables: SRL-coarse root, SRL-fine root, and leaf area at standardized plant heights and root length densities. Colors represent biomass and grams of (a–c) above and (d–f) root biomass. SRL-fine root was negatively correlated with aboveground biomass, whereas SRL-coarse root was negatively correlated with root biomass. According to the minimum, mean, and maximum values of plant height, aboveground biomass was predicted by leaf area and SRL-fine root, with root biomass was predicted by leaf area, root length density, and SRL-coarse root [Colour figure can be viewed at wileyonlinelibrary.com]

diffusion through soil and thus negatively impact root growth. Waterlogged soils may also lead to stomatal closure that reduces gas exchange, producing downstream reductions in aboveground growth (Tombesi et al., 2015). As a result, the 40-cm treatment, where space was limited and soil moisture was likely near saturated from 20- to 40-cm depths (Figure 2), may have also inhibited plant growth.

Belowground trait responses tended to be more variable than aboveground trait responses. The TRL, RLD, and root biomass increased first and then decreased with the increase of groundwater depth, which is generally consistent with aboveground trait responses. However, the specific root length of fine roots (SRL-fine root) and SRL-coarse responses diverged from this dynamic. In deeper groundwater levels, where plant water-transport distance is inherently longer, more resources may be geared towards producing coarse roots to explore soil water in deep soil layers. This would then reduce the proportion of fine roots in a given soil volume, eventually leading to decreases of TRL. As a result, we posit that the root system of *P. communis* altered the proportion of fine and coarse roots to fully use soil water at different soil layers to optimize resource inputs.

Coarse and fine roots perform both similar and different functions for plants (Comas et al., 2013). Coarse roots can take up water like fine roots, but at a lower rate per surface area than fine roots. Instead, coarse roots of herbaceous species typically serve as anchorage and to establish the overall root system architecture and may control the ultimate rooting depth and the distance of soil water acquisition (Henry et al., 2011). Fine roots significantly increase soil moisture access for root systems due to increasing overall root surface area and root length in both herbaceous and woody plants (Bauhus & Messier, 1999; Rewald, Ephrath, & Rachmilevitch, 2011).

As groundwater depth increased, soil moisture produced via precipitation may not have met plant growth demands, and thus, *P. communis* may have increased fine root production in the surface and underground watertable area, partitioning root production to these areas of the profile instead of fully expanding production in every soil layer. Yet to increase rooting depth, plants will generally increase coarse root length (Lynch, 2007). In addition, according to the distribution of available water in the soil, plants may produce thinner and deeper coarse roots to access soil water under drought (Debinski et al., 2010; Hoepfner & Dukes, 2012). Shifting watertable depths, our experimental design likely resulted in an unintended yet concurrent shift from space limiting growth to moisture limiting growth, as deep water becomes increasingly inaccessible, and thus greatest increases in trait values, such as leaf area; at intermediate depths (e.g., 120 cm), depths may reflect neither space nor moisture limiting growth.

4.1 | Relationships between aboveground and belowground traits

Optimal partitioning theory predicts that plants are adapted to produce a particular root:shoot ratio to optimize whole plant growth under different levels of resource availability. In this study, root:shoot ratio was relatively high in the mid-range of underground watertable depths (Figure 4), whereas in the shallowest (saturated) and deepest (drought) watertable conditions, plants tended to produce low root:shoot ratios, which contrasts with previous findings (Gargallo-Garriga et al., 2014). Increased root versus shoot growth should improve plant hydraulic status under mild or moderate drought stress due to increased capacity for acquiring water to support new growth (Shipley & Meziane, 2002). However, if drought is over a water stress

threshold, hydraulic failure may ensue leading to an apparent low root: shoot ratio (McDowell et al., 2008), much like we observed in the deepest watertable depths. As a consequence, although there is considerable plasticity in this species' ability to respond to increasing watertable depths, this only operates up to a certain depth, whereby growth may then become entirely limited by precipitation inputs at the soil surface.

Plants have highly plastic root responses to a variety of soil conditions that can covary with aboveground traits (Ravenek et al., 2016). Because belowground traits are directly in contact with soil moisture and nutrients, such traits may be more sensitive, that is, respond faster or in greater magnitudes, to changes in the soil environment than aboveground traits (Hsiao & Xu, 2000). For aboveground traits, leaf area, and belowground traits were closely linked in our study, suggesting clear feedbacks as watertable depth increases. Due to the leaf being the primary photosynthetic organ (McEvoy, Gascon, Batista, & Brudvig, 2005), leaf area affects whole-plant capture of light quantum and thus carbon fixation capacity. Therefore, in cases where energy demand is high, we posit that *P. communis* increases leaf area to increase carbon fixation capacity (Jones, Hodge, & Kuzyakov, 2004), which may then be allocated towards root production.

Feedbacks between aboveground and belowground trait dynamics in this study were also reflected in RLD being positively correlated with aboveground biomass and height. Previous studies have shown that RLD characterizes the ability of plant roots to obtain water and that RLD can be a good predictor of species competitive ability (Ravenek et al., 2016). As a consequence, the higher the RLD, the greater the ability of plants to obtain water and nutrients, which likely explains the positive correlation between RLD and aboveground biomass we observed.

However, SRL-fine root exhibited a positive correlation with RLD, whereas SRL-coarse root exhibited a negative relationship with RLD (Figure 6). In addition, SRL-fine root was positively correlated with leaf area and aboveground biomass, whereas SRL-coarse root was largely negatively correlated with leaf area and aboveground biomass. This suggests that in order to produce longer roots to pursue deeper underground water, an energetic trade-off occurred at the expense of aboveground biomass allocation. These data also suggest different construction costs between fine and coarse roots for *P. communis*, as longer and thinner fine roots harbor less costs than coarse roots with respect to soil water and/or nutrient uptake for plant growth (Reich, 2014). We thus posit that producing fine roots with high SRL should be more efficient than coarse roots in exploration of water for a given soil volume (Bauhus & Messier, 1999).

5 | CONCLUSIONS

In summary, we found that under increasingly deeper soil watertables, plant function tends to initially respond positively as watertable depth increases yet then negatively at the deepest depths. The most important traits for aboveground biomass responses appear to be leaf area, SRL-fine root, and height, whereas for root biomass, the most important traits were leaf area, SRL-

coarse root, and RLD. Further, *P. communis* altered the ratio of coarse and fine roots to optimally utilize available soil moisture from different soil layers and appeared to alter leaf area to enhance whole-plant photosynthetic capacity. For root architectural responses under continuous increases in underground water table, *P. communis* produced longer and thinner coarse roots to reach deeper soil layers, while also producing more fine roots to allow efficient water absorption within the topsoil and the deepest soil depths. We suggest interactions between leaf area and the energetic and spatial allocation of coarse and fine roots drive biomass responses to increasing watertable depths. In addition, as *P. communis* is a key driver of ecosystem functioning and health; the plasticity of this dominant species to watertable depth may partially alleviate the negative impacts of increasing groundwater use and depletion within the Inner Mongolia region of China, yet that limitations on this plasticity will be realized at the deepest water table depths.

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