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Soil moisture influences the root characteristics of a herbaceous riparian plant along a regulated river

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Abstract

River ecosystems of regulated rivers are threatened by water extraction and flow regime alteration in the context of climate change and increasing human populations. Riparian plant root growth is important to sustain plant health and provide functions including bank stabilization. The root systems of riparian plants on regulated rivers may suffer from lower soil moisture due to lack of natural flow variability. This study aimed to evaluate how soil moisture influences the root system of a herbaceous riparian plant. Plants of *Juncus amabilis* were dug out along a soil moisture gradient, corresponding with positions close to or distant from the water margin and low or high relative bank elevation. Root depth, belowground space occupation, root mass fraction and mean fractal dimension were used to evaluate root structural dynamics in relation to bank position and soil moisture. The ratio between root and aboveground dry weights of sampled plants was constant over the elevation range sampled. Plant root systems tended to grow deeper, occupy more belowground space, and have fewer branches as soil moisture declined. These findings indicate that lower soil moisture levels and reduced river flows may significantly influence herbaceous riparian plant growth and survival. Riparian plant health and function will likely be promoted by flow regimes that provide adequate and timely water delivery.

Introduction

Many river ecosystems are threatened by river regulation, such as high water extraction and flow regime alteration, which impact the health of native riparian flora and fauna (Kingsford 2000). In the context of climate change and increasing human populations, these threats may be exacerbated (Arthington et al. 2010; Head et al. 2013). In regulated rivers, environmental flows are commonly provided to promote ecosystem health and service provision (Poff et al. 2010). The management of environmental flows has been refined over recent years as flow-ecology relationships are further understood (Riis et al. 2020; Zhang et al. 2018), but there remain uncertainties around balancing benefits and damages to riparian plants (Shenton et al. 2012). To determine the flows required for maintaining riverine ecosystems, it is necessary to better understand how riparian plants respond to water availability (Merritt et al. 2010). In particular, the relationship between environmental flows and soil moisture provision to sustain plant growth, linked to root characteristics, is poorly understood (Doody et al. 2015).

The root system is an important indicator of the ecological functions of riparian plants (Liu, et al. 2020). The aboveground parts of a plant depend on the root system for fixed support and absorbing necessary nutrients and water for growth (Guo et al. 2022). For water and soil conservation, interweaving root systems result in network consolidation and root-soil binding, which can help control slope erosion and improve soil quality (Xu et al. 2021). Moreover, the root system of riparian plants can influence the hydrologic and hydraulic properties of the river and can reduce river pollution (Pollen-Bankhead and Simon 2010; Tron and Perona, et al. 2015; Yang et al. 2018).

The characteristics of herbaceous riparian plant root systems are complex because of the highly variable environmental conditions and diversity of plant species in riparian zones. Apart from the belowground

water table and infiltration from rainfall, which are major soil moisture sources (Wang et al. 2019), soil moisture resources available to riparian plants occur from the infiltration to the bank from river channel flows, which are highly variable (Fig. 1). The root system of some herbaceous riparian plants may be sensitive to soil moisture changes and have great plasticity (Larson and Funk 2016; Tron and Perona et al. 2015), such that roots of the same species may grow differently in different environments (e.g., Abdul-Jabbar et al. 1982). Moreover, unlike woody plants, which can reach a deeper water table, herbaceous plants may have to change root architecture and biomass to survive droughts (Tufekcioglu et al. 1999).

Managers of regulated rivers must decide the timing, magnitude, and duration of individual flows within flow regimes to best achieve desired outcomes within the system constraints. For vegetation, these outcomes often relate to provision of flows to support plant health (Tonkin et al. 2020). Healthy plants require adequate soil moisture at particular times of the year and at different soil depths depending on the growth stage of the plant, with herbaceous plants being more vulnerable to soil moisture variation than deeper-rooted plants (Wang et al. 2019). To achieve better outcomes from environmental flows, a better understanding of riparian plants' root systems and their interactions with soil moisture and other factors is needed. Furthermore, there is little research on the root systems of herbaceous riparian plants, with most studies focusing on agricultural plants (e.g., Tufekcioglu et al. 2001) or woody plants (e.g., Argus et al. 2015). Thus, field-based studies are required to better understand how herbaceous riparian plant root system characteristics change with different soil moisture dynamics.

This study aims to investigate how soil moisture influences the root system of a herbaceous riparian plant, *Juncus amabilis*. Firstly, this study examines whether soil moisture affects its root system characteristics, including the root mass fraction, root depth, belowground space occupation, and mean fractal dimension. Finally, we consider the implications of these relationships for environmental flow management to benefit riparian vegetation.

We hypothesized that the root system of *J. amabilis* is likely to be shallower when adjacent to the river because of the opportunities and limitations imposed by the higher water table (Fig. 1). The root biomass and the mean fractal dimension may be high because the abundant water resources can support abundant plant biomass, as well as the need for high root density anchor plants to the soil during high river flows. Conversely, a plant's root system is likely to be deeper and occupy more belowground space (with low root density) when elevated from the water because of the lower soil moisture from reduced inputs from groundwater or high river flows.

Method

Study site

Our study site was located at Doaks Reserve on the Campaspe River, downstream of Lake Eppalock (-36.816384, 144.519085). The Campaspe River is a tributary of the River Murray located in south-eastern Australia and is highly regulated to supply water for agriculture. Since regulation via damming, high

winter flows are captured and slowly released later for summer irrigation, meaning natural peak flows in winter-spring are greatly reduced and summer flows are artificially elevated, resulting in a relatively flat flow regime (Humphries et al. 2002).

The study area has a mean annual precipitation of around 500 mm, and mean annual temperature of 22 ℃ (Cartwright and Miller 2021). The surface soil of the study site is sandy loam with areas of gravel in scoured stream beds (Tonkin et al. 2020). The study area occurs within an agricultural region (livestock pasture and dryland cropping) but with public river frontages maintaining a narrow band of natural woodland. The riparian vegetation is river red gum (*Eucalyptus camaldulensis*) woodland, with graminoids being the dominant understory vegetation. The understory herbaceous vegetation along the river channel comprises both native and exotic species, including sedges (e.g., *Cyperus eragrostis*), rushes (e.g., *Juncus amabilis* and *J. usitatus*), and grass species (e.g., *Poa labillardierei*, and many exotic pasture species).

Study species

The plant species chosen for this study was *J. amabilis*, which is widespread along waterways in the state of Victoria. It is a shortly-rhizomatous (underground stem that forms roots and shoots) perennial tufted graminoid. *J. amabilis* flowers between austral November and December and sets seeds usually between December and April (Albrecht 1994). The growth of *Juncus* species plants' root systems may be greatly influenced by changes in soil moisture (Kaczmarek-Derda et al. 2019).

Study design

In the study area, soil moisture decreases as the distance from the river and the relative elevation from the water level increases (Tonkin et al. 2020). This feature of soil moisture distribution was used to simplify our study design. In this study, we collected plants at positions from low relative elevation to high relative elevation to explore how selected root systems characteristics varied from high to low soil moisture. To reduce the influence of differing bank slopes, the sample locations selected were on similar gently sloped riverbank geomorphic features.

Sample collection

Plant samples were collected randomly along the soil moisture gradient, including sample positions both close to and distant from the river, from low and high elevations relative to the river toe. Mature plants of different ages that were shorter than 1 m were selected. Plants on steep slopes or in densely treed areas were avoided to minimize the potential influences of these environmental factors.

Firstly, we recorded plant location details such as GPS coordinates, distance along the bank contour from the river (the nearest stream edge), and relative elevation from the water level. Secondly, we excavated the selected plants. When removing the root system, a soil cylinder of approximately 40 cm in diameter and a depth of approximately 25 cm was collected. The root system at the top 25 cm of the soil is generally the most active part of a riparian herbaceous plant and comprises most of the root biomass (Tufekcioglu et al. 1999). Lastly, we gently removed excess soil. The soil removed in this step was refilled to reduce

impacts on the local environment. Collected plants were placed in plastic bags and then in plastic tubs for transporting back to the nursery. Thirty-three plants in total were collected.

Sample processing

Plant samples were cleaned in the nursery using a water spray gun to remove all soil. The cleaning was conducted carefully (mainly using the “shower” setting on the hose) to reduce the loss of fine roots, young leaves and decayed stems.

Then we measured the characteristics of the root system, including root length, root depth and crown root angle. Plant size, including the plant height (the length of the longest, second longest and third longest stem) and the circumference at the base of the plant, were also measured. After drip-drying, photos of the root system were taken using an SLR camera. Finally, each sample was separated into roots and aboveground plant parts (i.e., stems and leaves). These were put in separate paper bags and dried in an oven at 80 ℃ for five days. An electric balance (accurate to ± 0.01 g) was then used to weigh the dry weight of the roots and the aboveground parts.

Data analysis

The software Root Estimator for Shovelomics Traits (REST) (downloaded from https://sourceforge.net/projects/rest4roots/) (Colombi et al. 2015) was used for processing photos of the root system to obtain detailed root system architecture data. This software can identify the roots by choosing the 90% region of interest (ROI). Based on the 90% ROI, this software was used to calculate the mean fractal dimension, the standard deviation of the regression from the box-count algorithm (this box-count algorithm is used to calculate the mean fractal dimension), and other traits related to root architecture.

Firstly, we calculated is the root mass fraction using the formula:

$$Root\ mass\ fraction = \frac{Root\ dry\ weight\ (g)}{Root\ dry\ weight\ (g) + Aboveground\ dry\ weight(g)} \qquad \text{(Eqn. 1)}$$

For analyses, we then used elevation relative to the water level to represent the soil moisture gradient. Soil moisture is known to be higher where the relative elevation is low, and soil moisture decreases as the relative elevation increases. Firstly, we calculated the corrected root depth. As larger plants may have deeper roots, the corrected root depth is standardized by the formula:

$$Corrected\ root\ depth\ (cm/g) = \frac{Root\ depth\ (cm)}{Root\ dry\ weight\ (g) + Aboveground\ dry\ weight\ (g)} \qquad \text{(Eqn. 2)}$$

For each plant, we also calculated the belowground space. The belowground space represents the volume of the most active part of the root system. It was calculated as a cylinder, based on the maximal

crown root width (the width of the 90% ROI), and root depth (the height of the 90% ROI) of each plant sampled.

$$Belowground\ space\ (cm^3) = \frac{Maximal\ root\ width^2\ (cm^2) \times \pi \times Height\ of\ 90\%\ ROI\ (cm)}{4} \quad \text{(Eqn. 3)}$$

The belowground space was standardized using the formula:

$$Belowground\ space\ factor\ (cm^3/g) = \frac{Maximal\ root\ width^2\ (cm^2) \times \pi \times Height\ of\ 90\%\ ROI\ (cm)}{4 \times (Root\ dry\ weight\ (g) + Aboveground\ dry\ weight\ (g))} \quad \text{(Eqn. 4)}$$

We then investigated how the root depth, belowground space occupation, mean fractal dimension and the standard deviation of the regression (the latter two are provided by the REST software) vary as relative elevation increases. This was done initially for individual variables via paired plots and trends. Trend lines were calculated using linear regression to explore whether the relationships between the plant root variables and relative elevation were positively or negatively correlated. Trends were documented via their equation, R^2 and p-value. Linear regression models were then expanded by adding a second predictor variable of total plant dry biomass to account for plant size influences on root characteristics. Plant samples whose total dry weight was lower than 3.5 g were excluded, as the REST software had difficulties appropriately characterizing the roots or these samples (see Limitations section of the Discussion). This resulted in the removal of 7 samples from the analyses and final sample size of 26 plants. A summary of outputs with all plant samples (n = 33) is provided in the Supplementary Information. R (version 4.2.2, R Core Team 2022) was used to conduct all plots and statistical analysis.

Results

Root mass fraction

Plant root and aboveground dry weights were positively correlated (Fig. 2a). In fact, the linear correlation was surprisingly close ($R^2 = 0.86$, $p < 0.001$), given the variation in plant size. As the value of y-intercept (-1.8) is very low when compared with the average aboveground dry weight (25.73 g), the ratio between the aboveground dry weight and the root dry weight is closely approximated by the coefficient of x (in this case, 9.6). Therefore, the aboveground dry weight was approximately 10 times greater than the root dry mass, regardless of plant size or bank elevation position (Table 1). This also means that the corresponding root mass fraction is relatively constant regardless of plant size. From Eq. 1, the root mass fraction can be estimated as 0.094. When comparing root mass fraction against relative elevation, there was no correlation (Fig. 2b).

Root depth

As the relative elevation from the water level increases, the corrected root depth tended to increase (Fig. 3a). In expanded regressions, the total plant dry weight and relative elevation are statistically significant predictors of plant root depth (Table 1). Thus, for plants with the same dry weight, a plant that grows in lower soil moisture tends to have a deeper root system. Some plants' root systems at low relative elevations tended to grow sideways rather than deeper (Fig. 4). However, there was considerable variation in the data, with several plants at relatively low elevations having deeper root depths than samples at high elevations (Fig. 3a), which is accounted for at least partially by plant size (Table 1).

Belowground space of the root system

There is a positive correlation between belowground space factor and relative elevation (Fig. 3b), which means that a plant that grows in lower soil moisture occupies more belowground space relative to its weight. However, the relative elevation had no significant effect when biomass was accounted for (Table 1). Belowground space was instead significantly larger in plants with more biomass (Table 1). Root systems at higher elevations have more dispersed roots at lower densities, presumably seeking areas of higher soil moisture (Fig. 4).

Mean fractal dimension and standard deviation of regression

As the relative elevation between a plant and the river increases, the mean fractal dimension of its roots Declines significantly (Fig. 3c, Table 1). The mean fractal dimension is related to the complexity of the root system architecture (Nielsen et al. 1997). The mean fractal dimension is lower when a root system has fewer branches or lateral roots and a lower number of axis roots (Fitter and Stickland 1992). The standard deviation of the regression tended to increase as relative elevation increased but this correlation was not significant with or without incorporating biomass (Fig. 3d, Table 1). Total plant dry weight didn't have a clear influence on the mean fractal dimension (Table 1).

Table 1
The outputs of analyzing the relationship between root characteristics and several predictors by using a linear regression model

Individual root variable models						
Model attributes		Root mass fraction	Root depth	Belowground space	Mean fractal dimension	Standard error of regression
Intercept	Estimated value	0.1324	10.9128	546.5040	1.7615	0.1616
	p-value	< 0.0001	< 0.0001	0.2680	< 0.0001	< 0.0001
Relative elevation	Estimated value	-0.0055	1.2391	169.8800	-0.0146	0.0084
	p-value	0.4950	0.0070	0.3210	0.0086	0.0836
Total biomass	Estimated value	-0.0004	1.3655	64.1910	0.0006	< 0.0001
	p-value	0.3400	< 0.0001	< 0.0001	0.0481	0.8789
Multiple R-squared		0.04723	0.5503	0.6689	0.4299	0.1290
Adjusted R-squared		-0.0356	0.5112	0.6401	0.3803	0.0533
Degrees of freedom		23	23	23	23	23
p-value		0.5733	0.0003	< 0.0001	0.0016	0.2043

Discussion

Our results suggest that reduced soil moisture changes the root architecture rather than the root mass fraction of *J. amabilis* plants. *J. amabilis* plants tend to root deeper, occupy more belowground space reduce root branching under low soil moisture conditions (Figs. 3 and 4).

Root mass fraction

The root mass fraction (the ratio between the root dry weight and the aboveground dry weight) describes the biomass allocated to the root system and can help explain how soil moisture influences the root system of plants. Many studies suggest plants may change their biomass allocation under limited soil moisture (Padilla et al. 2009). According to Larson and Funk (2016), it is a common strategy for herbaceous plants to increase root mass fraction in response to droughts. This increasing biomass investment in the root system during water stress may contribute to some invasive species' survival and spread (Cowie et al. 2020). However, other studies support the idea that plants do not change their root mass fraction, although a higher root mass fraction can help plants to behave better in water deficit

conditions (Farrell et al. 2013). In this study, the root mass fraction of the sampled plants did not change across the soil moisture gradient surveyed; also lighter plants have the same root mass fraction as heavy plants (Fig. 2), which indicates that plant size or age may not influence a plants' root mass fraction in this species. Therefore, variation of root architecture, rather than root dry weight, is more likely to reflect how the root system of *J. amabilis* changes under different soil moisture conditions.

Root depth

The root system of *J. amabilis* plants tends to be deeper as elevation increases and soil moisture decreases. Generally speaking, a deeper root system enables increased water uptake from the soil because there is commonly higher water content in deeper soils (Colombi et al. 2018). Also, as the anaerobic conditions below the groundwater table can inhibit root growth, high groundwater levels can stop plants adjacent to the river from rooting deeper and may cause a shallower root system (Ebrahimi-Mollabashi et al. 2019). However, rooting depth is unlikely to increase without limit as relative elevation increases and soil moisture decreases. At some point, root depth increases will cease, and plant health will decline if adequate water resources are not reached. This is particularly true for low soil moisture conditions where interruption of soil capillary continuity can make longer roots uptake less soil water than shorter roots (Tron and Bodner, et al. 2015). This means that the environmental conditions distant from the river are likely to become unsuitable for herbaceous riparian plants where the water table is far below the surface, or the root depth capacity is insufficient. For young plants that germinate at moderate bank elevations within reach of deeper water resources, the provision of occasional shallow soil moisture resources from rainfall or river flows may be essential for survival until deeper roots are developed.

It should be noted that some plants at low elevations had relatively deep roots. One potential reason for this is that *Juncus* species develop aerenchyma allowing them to transport oxygen from the air to their roots, enabling roots to grow under high soil moisture and even saturated soil conditions (Voesenek et al. 2006). Furthermore, there are other potential benefits of rooting deeper for plants adjacent to the river, such as increasing mechanical anchoring and survival during high-flow events (Pollen-Bankhead and Simon 2010) and competing with shrubs or trees in riparian zones (Groeneveld and Or 1994). So, in some circumstances, it is possible that herbaceous plants adjacent to the river may have deep roots, which may account for the variability in root depth we observed at low elevations.

Belowground space

The root system of *J. amabilis* plants occupies larger belowground space when soil moisture is lower, but this relationship was strongly influenced by plant biomass. Less belowground space occupied by plants adjacent to the river may be caused by increases in root tissue density. To survive inundation during high-flow events, *Juncus* plants may change their root tissue density, such as by establishing a lateral diffusion barrier, to reduce radial oxygen loss during oxygen transportation (Sauter 2013). Such changes can increase the root tissue density and root diameter, causing a decrease in the specific root length and the belowground space occupied by the roots. When soil moisture decreases, some studies suggest that the proportion of fine roots increases to improve the ability for water uptake, which may cause an

increased specific root length (Tron and Bodner, et al. 2015). However, other studies suggest that the specific root length may remain the same in different soil moisture conditions for some species, implying that the root diameter and root tissue density are unlikely to change (Thorne and Frank 2008). So, there are multiple potential mechanisms causing the root system of *J. amabilis* to extend further and occupy more belowground space in response to low soil moisture conditions. However, it should be noted that the increase in belowground space occupation is closely associated with plant weight. This is because the root mass fraction is roughly a constant, as discussed previously, which determines the total root biomass used for increasing belowground space occupation. So, smaller plants occupy less belowground space under the limits of biomass.

Root mean fractal dimension

Soil moisture can also influence the fractal dimension of roots, an important trait of root architecture. The fractal dimension is related to the interactions between the root system and the soil and, specifically, soil water uptake in drier conditions (Dannowski and Block 2005; Tron and Bodner et al. 2015). In this study, the mean fractal dimension was used as a measure of the branching of the root system, which indicates root system complexity (Fitter and Stickland 1992). According to our findings, *J. amabilis* plants growing in lower soil moisture conditions have fewer root branches when compared with plants in higher soil moisture. Some studies corroborate this finding, indicating lower mean fractal dimensions can protect plants against water deficit conditions (Alados and El Aich 2008; Yang et al. 2014). The reasons why root fractal dimension changes like this are complex. One potential reason is that the proportion of coarse roots increases under drought stress (Larson and Funk 2016). This can increase the average root diameter. Furthermore, as indicated above, the root length increases as the root system extends deeper and occupies more space in drier conditions in search of water. The longer average root length and increased average root diameter can lead to a decline in the total number of branches and mean fractal dimension of the root system.

Despite an apparent visible trend, we found that *J. amabilis* plants have no significant trend in developmental errors (standard deviation of the regression) when the soil moisture decreases. These developmental errors are generally caused by environmental factors (Alados et al. 1998). One reason for this may be related to soil moisture variation. Compared with the soil moisture at positions close to the river, the soil moisture of the positions more distant from the river, which may vary from very dry (long duration with no rain) to very wet (heavy rain or floods), is more variable (Tonkin et al. 2020). Such variation in soil moisture may cause metabolic changes and increase the developmental instability of the root system (Freeman et al. 2003).

Limitations

There are multiple limitations of this study. For example, the root system traits measured are based on 2D methods, not 3D, which can analyze the root systems better. But we don’t expect that the use of 3D models would greatly change the presence or direction of relationships observed in our study. The slight plant destruction during sample excavation and cleaning can result in root attribute inaccuracies, such as

reduced root length/depth and biomass values. We assumed that the issues impacted the plants consistently, so that there was minimal impact on broader relationships.

The REST software used in our study to characterize root systems faced the risk of lower accuracy when samples were small. One reason for this is that the belowground space occupation estimation considers root systems as cylinders, which may misestimate the volume of root systems. This is because the root systems are unlikely to be symmetrical under natural conditions (Hawkes and Casper 2002). For larger plants, some studies examine the rotational symmetry of their root systems and conclude that the deviation from rotational symmetry is small (e.g., Colombi et al. 2015). For smaller plants, the standard deviations of lateral root spread are larger when plant size gets smaller, causing reduced root symmetry (Berger et al. 2006; Tumber et al. 2022). Besides, smaller plants usually have lower root density and cannot fill their surrounding space completely. So, the REST software, which includes many parameters for overlapped roots, such as the root thickness, tends to overestimate the belowground space occupation, especially when plants are small. The REST software may not be suitable for small plants, as it was originally designed for maize after flowering (Colombi et al. 2015). Moreover, the root characteristics of smaller plants may not vary significantly, with soil moisture changes not having sufficient time to adapt to them.

Management implications

Along rivers, soil moisture is closely associated with river discharge and can significantly influence the root system of riparian plants. For *J. amabilis*, low soil moisture can cause deeper root depth, potentially more belowground space occupation, less root branching and other root system architecture changes. This demonstrates how the root architecture of a plant can adapt to lower soil moisture. However, such adaptations have limits, as indicated previously. So, it can be expected that lower soil moisture will lead to fewer *J. amabilis* plants in the riparian zone and plants located at relatively high elevations may not survive if the soil moisture conditions decrease (Wang et al. 2019).

The negative impacts of low soil moisture on *J. amabilis* and other herbaceous species are likely to be greater for seedlings and young plants. These young or shallow-rooted plants are not able to reach soil moisture provided through the water table unless they are at low bank elevations. The survival of these plants may be dependent on surface water provision through rainfall or elevated river flows, particularly in drier seasons (Fig. 1). If managers desire herbaceous riparian plants (such as *J. amabilis*) to occur at higher elevations, or for those plants at higher elevations to have larger aboveground biomass, soil moisture provision through brief elevated flows may be needed in drier periods. However, any increase in the depth or frequency of flows should carefully consider the negative effects of herbaceous plant inundation, particularly in summer (Vivian et al. 2020).

The soil moisture conditions in spring and summer may be of particular concern. In temperate climates, evaporation starts to exceed precipitation rates in spring which can lead to reduced plant growth and stress. So, briefly increasing river discharge in spring and summer, i.e., via environmental flows, to inundate banks and increase shallow soil moisture levels may be important for plant health, particularly

in drier years. Furthermore, higher river discharge during spring and summer can reduce the abundance of exotic terrestrial species (Greet et al. 2015), which may also benefit the growth and recruitment of native riparian plants such as *J. amabilis* through reduced competition for resources. However, this management strategy is likely to face some challenges. One is drought, especially prolonged droughts, such as the Millennium Drought (Doody et al. 2015) which reduces rainfall inputs to soil moisture, as well as reducing river flows and environmental water allocations. These impacts are also expected to be exacerbated by climate change due to predictions of locally reduced inflows in the coming decades (Adamson et al. 2009). It may be difficult to balance water usage between the requirements for the environment and human needs, such as irrigation, during dry times (Kirby et al. 2014).

Conclusion

Soil moisture along rivers is closely related to streamflow dynamics and can influence multiple root system characteristics of herbaceous riparian plants such as our study species, *J. amabilis*. As the soil moisture decreases, the root system of *J. amabilis* tends to grow deeper, potentially occupy more underground space (with low density), have fewer branches, and have more developmental instability. However, these characteristic changes for adapting to water deficit conditions are limited because of other environmental factors and the basic needs for plants to grow and reproduce. Increased soil moisture levels at certain times of the year are likely essential to maintain health of *J. amabilis* plants at higher bank elevations. River managers should consider actions, such as releasing environmental flows in spring and briefly in summer, to avoid long periods of low soil moisture conditions to promote herbaceous riparian vegetation health in regulated rivers.

Declarations

Conflict of Interest

All authors have been fully engaged in this study. The authors have no relevant financial or non-financial interests to disclose. This manuscript has not been published elsewhere. The authors declare no competing interests. The data and R code will be shared in a public repository upon acceptance.

Ethical Approval

There are no ethical approval requirements, and as all sites were on Crown land, no access permission was required. Fieldwork was conducted under a Flora and Fauna Guarantee Act 1988 research permit, number 10009567.

Informed Consent

All authors agree to get this manuscript published.

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Figures

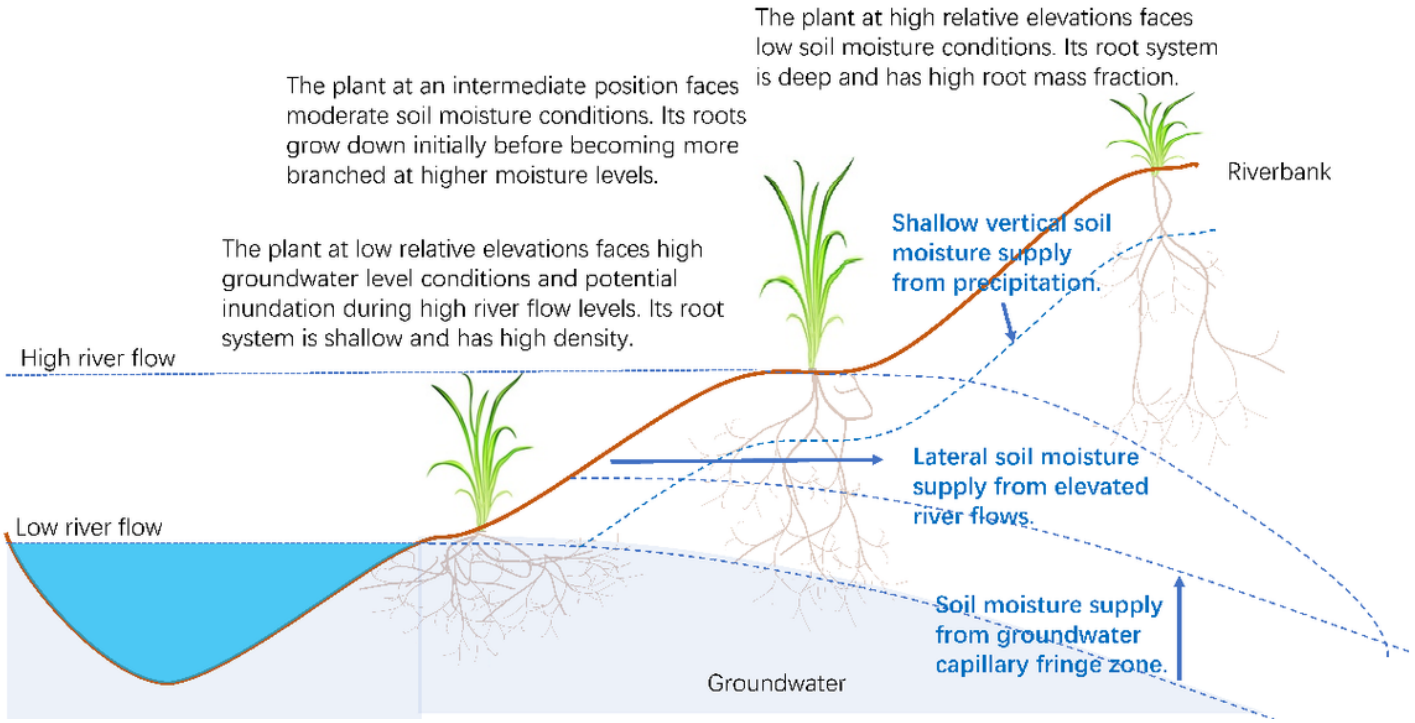


Figure 1

An illustration of a riverbank cross-section indicating the potential relationships between river flow, groundwater, rainfall precipitation, and the root system characteristics of a herbaceous riparian plant.

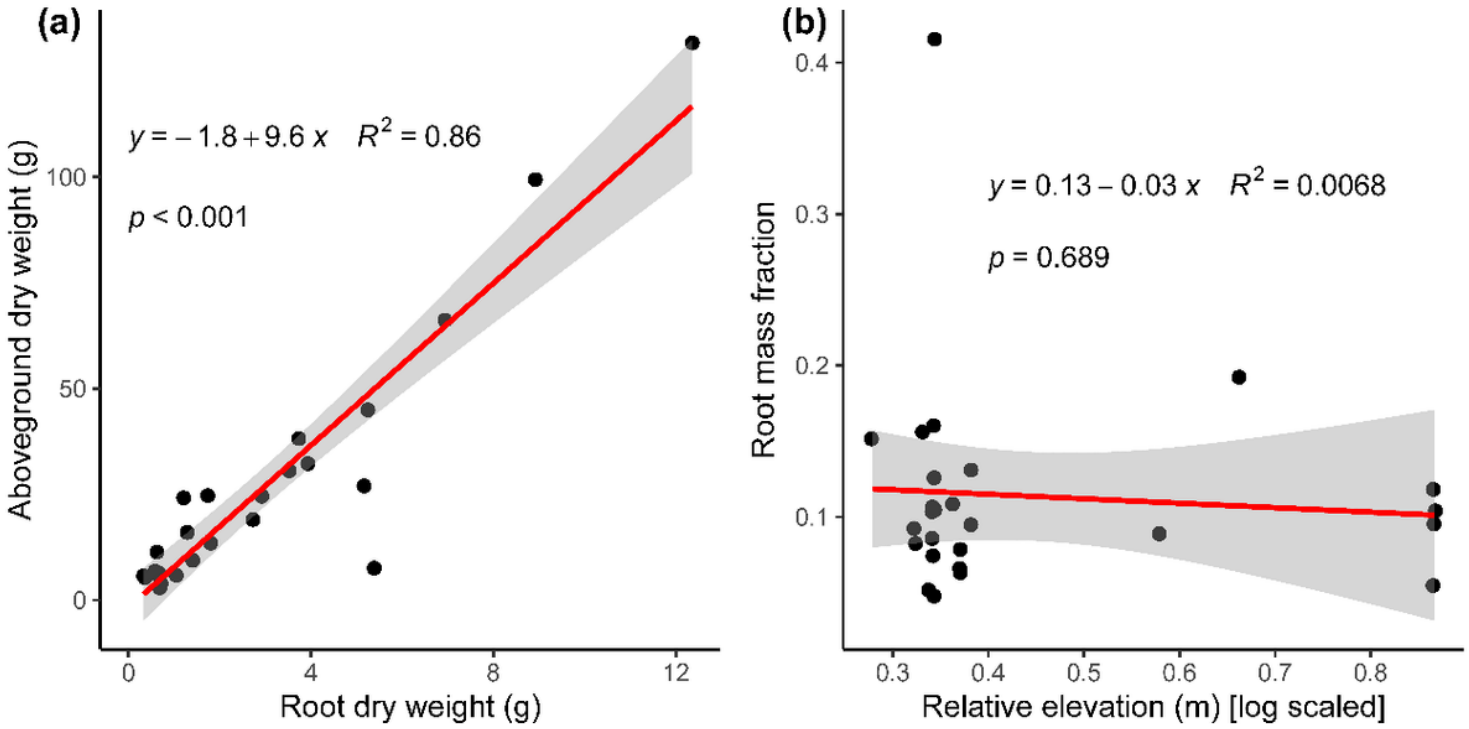


Figure 2

Relationship between the (a) root dry weight and the aboveground dry weight, and (b) root mass fraction and relative elevation. The red line is the trendline obtained using linear regression, the shaded area indicates the 95% confidence interval around the regression line

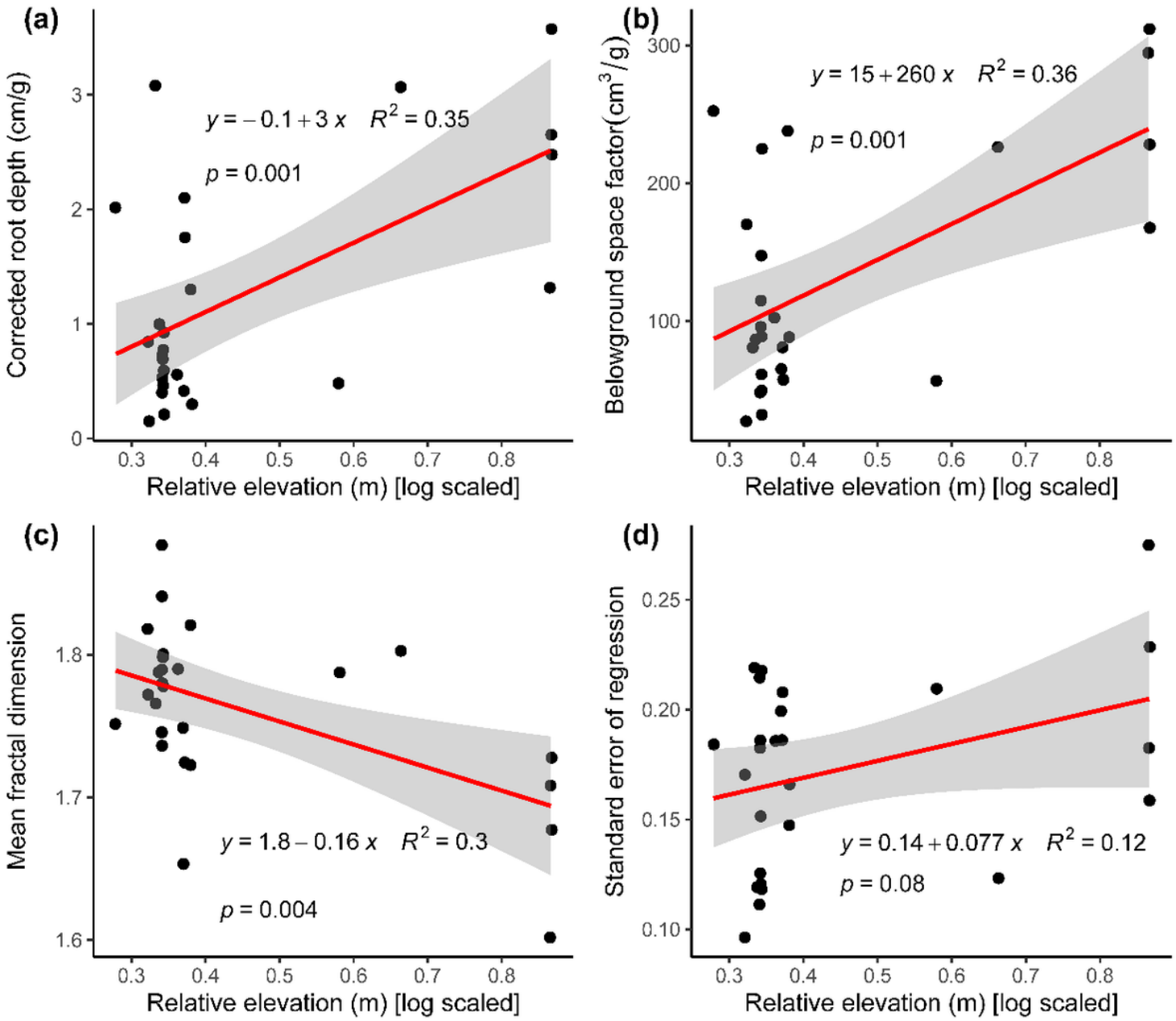


Figure 3

Relationships between the (a) corrected root depth, (b) belowground space occupation, (c) mean fractal dimension, and (d) the standard deviation of fractal dimension, and relative elevation. The red lines are the trendlines obtained using linear regression. The shaded areas indicate the 95% confidence interval around the regression lines



Figure 4

Photos of plant samples' root systems. The root system tends to be (a) shallower when the plant is at low relative elevation positions, or (b) deeper when the plant is at high relative elevation positions

Supplementary Files

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