

Short communication

Plasticity in response to soil texture affects the relationships between a shoot and root trait and responses vary by population

Alicia J. Foxx^{1*}, Siobhán T. Wojcik²

¹Genomics and Bioinformatics Research Unit; United States Department of Agriculture, Agricultural Research Service, 1600 SW 23rd Drive Gainesville, FL 32608, USA

²Lake Forest College, 555 N. Sheridan Rd., Lake Forest IL, 60045, USA

Abstract

FOXX, A.J., WOJCIK, S.T., 2021. Plasticity in response to soil texture affects the relationships between a shoot and root trait and responses vary by population. *Folia Oecologica*, 48 (2): 199–204.

The relationships between shoot and root traits can inform plant selection for restoration, forestry, and agriculture and help to identify relationships that inform plant productivity and enhance their performance. But the strength of coordination between above- and belowground morphological and physiological traits varies due to differences in edaphic properties and population variation. More assessments are needed to determine what conditions influence these relationships. So, we tested whether plant population and soil texture affect the relationship between shoot and root traits which have important ecological ramifications for competition and resource capture: shoot height and root tip production. We grew seedlings of two populations of *Bromus tectorum* due to its fast growing nature in a growth chamber in loam soil, sand, and clay. We found variation in height by plant population and the substrate used ($R^2 = 0.44$, $p < 0.0001$), and variation in root tip production by the substrate used ($R^2 = 0.33$, $p < 0.0001$). Importantly, we found that relationships between shoot height and root tip production varied by soil texture and population ($R^2 = 0.54$, $p < 0.0001$), and growth in sand produced the strongest relationship and was the most water deficient substrate ($R^2 = 0.32$). This shows that screening populations under several environments influences appropriate plant selection.

Keywords

population variation, root tips, soil texture, trait relationships, water stress

Introduction

The relationships between shoot and root traits make it possible to assess potential coupling between above- and belowground traits. Knowledge of these trait relationships are important for assessments in many fields such as agriculture for phenotyping studies aimed at crop improvement to increase aboveground yield (McGRAIL et al., 2020) and restoration, for matching optimal traits to environments that improve plant performance (LEGER and BAUGHMAN, 2015). Shoot-root trait relationships are also used to characterize ecological strategies and whether shoots and roots have coordinated responses to

resources (FRESCHET et al., 2010; SHEN et al., 2019; ABBASI et al., 2021). These relationships are also used to determine whether shoot traits can be good predictors of root traits to reduce time and labor-intensive field root excavation. However, while growth and functioning of both organs are connected via morphological and physiological processes, such as translocation of photoassimilates and water, root and shoots experience direct and indirect interactions with the abiotic and biotic environment that interfere with the strength of the relationships between their traits (KEMBEL and CAHILL, 2011). More research is needed to identify the conditions that impact the relationships of shoots and roots.

*Corresponding author:

e-mail: alicia.foxx@usda.gov

© 2021 Authors. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>)

Here we assess the relationship between one shoot and one root trait: plant height and root tip production as a component of root system architecture. Plant height is an important trait that influences light capture for photosynthesis and plays an important role in ecological strategy (WESTOBY, 1998), and taller plants are better able to pre-empt light from neighbors (LIU et al., 2009; CRAINE and DYBZINSKI, 2013). Plant height is also plastic in response to the abiotic and biotic environment, for example, in response to competitors and water stress (LIU et al., 2009; BOUTRAA et al., 2010). Root tips, hidden in the soil, are ecologically important for different plant growth forms, from herbaceous species to tree species. Root tips are responsible for most of the nitrate and water uptake from the soil (LAZOF et al., 1992; VARNEY and CANNY, 1993). Root tip production by plants is highly plastic. For instance, *Lolium perenne* increased lateral root proliferation eightfold under water stress (JUPP and NEWMAN, 1987) to increase resource capture. Greater root tip proliferation also aids resource capture indirectly through increased sites for mycorrhizal associations (OLÁH et al., 2005) and improves survival in dry and competitive conditions (STEVANATO et al., 2011; ATWATER et al., 2015; FOXX and KRAMER, 2020a, 2020b). Determining the number of the root tips is labor- and time-intensive, and coordination with an easy to measure aboveground trait of plant –height –would aid in trait extrapolation. However, research has shown coordinated and decoupled responses of shoot and root traits to environmental stressors (FOXX and FORT, 2019), thus, how plasticity affects shoot-root relationships requires integration in research. The spatial and temporal variation in resource availability and physical properties of soils (CHAPMAN et al., 2012) have importance to plant plastic responses. Different soil textures provide the plant with different physical and nutrient environments. For example, the bulk flow movement of water and nutrients to the roots, accounts for most nutrient capture for plants (CASPER and JACKSON, 1997) and varies by soil texture (CHAPMAN et al., 2012). Bulk flow in sand decreases significantly as the soil dries out (CHAPMAN et al., 2012), and clay is negatively charged, causing ammonia to bind to it (NYE and TINKER, 1977) and thus is not readily available to the plant. Loam soil is heterogeneous and has greater nutrient and water holding capacity which improves growth conditions for the plant. Few studies have assessed the influence of plant plasticity on shoot-root relationships with different soil textures. Additionally, traits, such as

root tip production can vary by plant source population and have important influences on plant survival and competition (FOXX and KRAMER, 2020a, 2020b). HAJEK et al. (2013) showed intraspecific variation in aspen demes for nine root and shoot traits and varying strength of shoot-root trait relationships. Taken together, considering how shoot and root traits and their relationships vary by source population and in response to soil textures is important to fully understand how well traits can be used to infer about either organ.

To assess the impact of soil texture and source population on trait plasticity and on the relationship between a shoot and a root trait, we used a growth chamber study with *Bromus tectorum* growing in three granulometrically different substrates: clayey, loamy, and sandy textures. We hypothesize that 1) plant height and root tip production will vary by soil texture and source population, and 2) that the relationships between height and root tip production will differ by soil texture and source population.

Material and methods

We used the annual grass *Bromus tectorum* L., which is invasive, particularly in arid regions of the United States (CHAMBERS et al., 2007; YOUNG and CLEMENTS, 2007). We selected it due to its quick growth and high rate of germination (FOXX and KRAMER, 2020a). Seeds were haphazardly wild collected from two plant populations, one located near Moab, UT, USA (The Bonderman Field Station at Rio Mesa, hereafter, Rio Mesa, Table 1) and one from Kanab, UT, USA (Johnson Creek, Table 1) in June 2013. Seeds were stored at 15% humidity and at 15 °C for two years prior to the experiment. We surface sterilized 150 seeds of both populations with 8% bleach solution for 30 seconds followed by a deionized water rinse for one minute. Next, we placed seeds of each population on separate 90 mm diameter petri dishes filled with 1.5% solidified agar for cold moist stratification at 3 °C in a refrigerator at the Chicago Botanic Garden (Glencoe, IL, USA) until we observed germination indicated by radicle emergence (1mm). Cold-moist stratification began on 21 October 2015, and seeds were moved to the growth chamber on 31 October 2015 for warm stratification at 25.5 °C/15 °C and 15%/6% relative humidity on a 12-h day/night cycle.

Table 1. *Bromus tectorum* population location information for wild seed collections and sample size for each substrate type

Seed collection location	Geographical coordinates	Substrate used	Sample size
Rio Mesa (UT, USA)	38.793°N, 109.191°W	Clay	13
		Loam	12
		Sand	14
Johnson Creek (UT, USA)	37.0475°N, 112.5263°W	Clay	10
		Loam	15
		Sand	14

One germinant was planted in each cone-tainer (Stuewe and Sons, Tangent, OR USA) filled with one of three substrate types: commercial fine sand, loam (Fafard germination mix, Sungro horticulture, Agawam, MA, USA), and clay pellets. Germinants were planted in the substrates on 4 November 2015. We applied Murashige-Skoog (Sigma Aldrich, MO, USA) half strength nutrients (4g L^{-1}) after four days of growth. Plants were watered twice weekly. We measured plant height after seven days of growth, and we mounted the plants on labeled paper following harvesting with gentle root washing after 14 days of growth to measure root tip production. Root tip production is the sum of the parent root tips and all of their branches. Lastly, we measured the substrate moisture content using a standard volume of substrate in filled, plant-free cone-tainers using a soil moisture probe following uniform wetting of the soil samples with water. We used ten samples per substrate type.

All analyses were performed using R (R CORE TEAM, 2021, version 4.1.0). Plant height was square root transformed to meet assumptions of normality. To evaluate whether root tip production and shoot height varied by the source population and the substrate used, we used a generalized linear model for count data with a Poisson distribution and a linear model, respectively. To assess if the relationship between plant height and root tip production varied by the source population and the substrate used, we used a generalized linear model to compare the relationships. For all models, the source population and substrate used were included as additive terms in the most complicated model, and we used stepwise backwards elimination of nonsignificant variables ($p \geq 0.05$) to select the minimally adequate model (CRAWLEY, 2005). Data are available online (FOXX and WOJCIK, 2020).

Results

Sand and clay had similar moisture content and had a greater water deficit than loam, both with up to 60% less water (Fig. 1). Plant height significantly differed between different populations and substrate textures ($R^2 = 0.44$; $p < 0.0001$; Fig. 2a). Growth in the clay substrate resulted

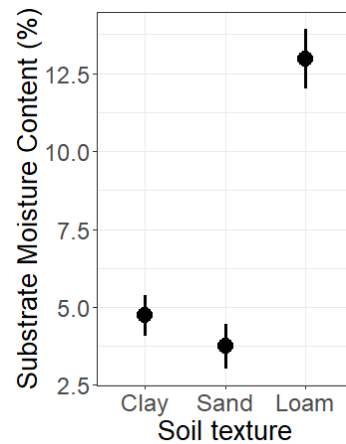


Fig. 1. Mean and standard error of moisture content in samples of clay, sand, and loam substrates.

in the shortest plants for both populations, whereas plants were taller in sand than clay, and loam resulted in the tallest plants. Root tip production differed by soil texture, but not by population ($R^2 = 0.32$, $p < 0.0001$, Fig. 2b). Plants had greater root tip production in sand and similar and lower root tip production in clay and loam, respectively.

The relationship between the root tip production and shoot height significantly differed by soil texture and marginally by plant population ($R^2 = 0.54$, $p < 0.0001$, Fig. 3). There was a generally positive relationship between root tip production and plant height. Sand and clay had larger slopes, which indicated stronger relationships between the traits. Greater root tip production positively influenced plant height the most in sand, followed by clay, and the least in loam. In the case of sand and loam substrates, the Johnson Creek plant population increased root tip production more in relationship to an increase in plant height than did the Rio Mesa population, and the opposite relationship was observed in clay (Fig. 3).

Discussion

We show that shoot and root traits and their relationships are affected by soil texture and this differs by plant

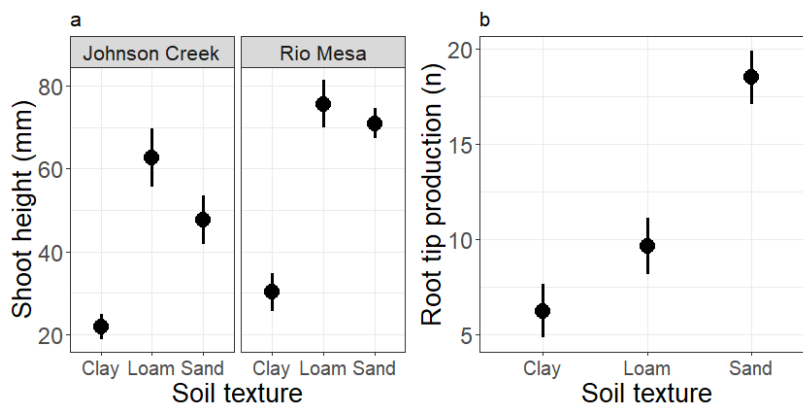


Fig. 2. Mean and standard error of *Bromus tectorum* seedlings for shoot height (a) and the production root tips (b) for two source populations grown in clay, sand, and loam substrates.

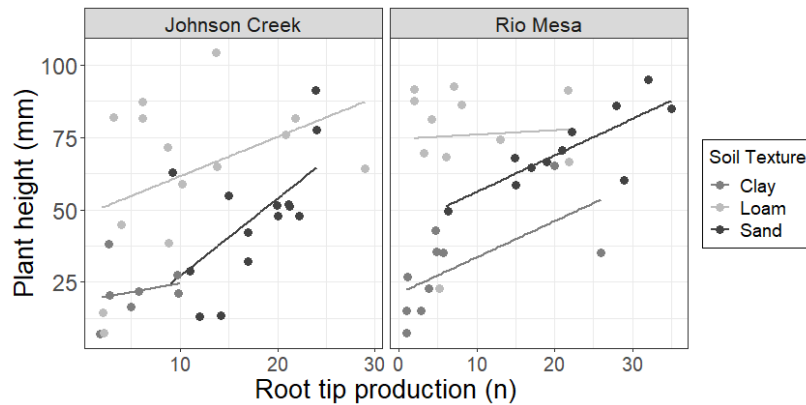


Fig 3. Relationships between the root tip production and shoot height of seedlings of two *B. tectorum* populations growing in clay, sand, and loam substrate.

source population. Furthermore, soil texture influenced plastic responses of root tip production and soil texture and source population of plants influenced plant height. To our knowledge, no study simultaneously addresses plant populations and their plasticity induced by granulometrically different substrates and their effects on the relationships of traits. Notably, sand had the strongest effect on shoot-root linkage, followed by clay. Both sand and clay had greater water deficit and produced the most root tips, while clay pellets suppressed aboveground growth the most. These findings suggest that the resulting physical properties of the substrates and source plant population play an important role in the strength of shoot-root trait relationships and affect the possibility to derive traits of a plant organ from the traits of another.

Dry sand increased root tip production, and this agrees with findings in the literature (JUPP and NEWMAN, 1987; PLACIDO et al., 2020). Because the sand substrate had the lowest moisture content, coupled with comparable shoot height with loam substrate with nearly 60% greater moisture content, this indicates that greater root tip production in sand likely improved water uptake (SHARMA and GHIDYAL, 1977; SHARP and DAVIES, 1979) and supported aboveground growth. This is surprising given evidence that shoot growth decreases with water stress (SILVA et al., 2012), however measuring other aboveground traits in this study revealed different patterns. The Rio Mesa population had greater shoot height than the Johnson Creek, but we lack information about the population and site that could help explain these trait patterns in response to the substrate used. Loam substrate produced the tallest plants with the fewest root tips and this is likely due to the greater water and nutrient availability in loam due to organic matter - which does not warrant a number of plastic responses due to abundant resources (e.g., SORGONÀ et al., 2007). Both shoot height and root tip production were lowest in the clay substrate, and the particle size of the pellets and large pore space between the pellets likely influenced this relationship due to low moisture content. Hydraulic conductivity increases with particle size (CHAPMAN et al., 2012) as do infiltration and percolation through the substrate, which reduce moisture content. The resulting

water loss due to substrate properties likely suppressed root and shoot growth and this was similarly found in soil with higher content of rock fragments (large particle size) which negatively impacted leaf growth (MARTRE et al., 2002); though SASSE (2020) showed variable trends in root tip production in response to particle size.

Shoot-root trait relationship

The relationship between shoot height and root tip production was strongest in the case of sand substrate and weakest in the case of the loam substrate (Fig. 2). This coincides with stronger relationships between shoots and roots under greater water stress. The process that underlies these patterns may lie in the responses of the individual traits to the moisture content and in the physical properties of the substrates described above. In sand, the greater root tip production likely improved uptake of soil water and supported plant height, which accounts for the stronger linkage. Similarly, the weaker shoot-root linkage in the case of the loam substrate is due to the opposing responses of root tip production compared to shoot height and a study by WANG and TAUB (2010) showed reduced root plasticity in high nutrient content and under greater water availability. SHEN et al. (2019) tested the role of two abiotic factors, soil fertility and light gradients, on the relationship between plant shoot and root traits in species of a subtropical rainforest. The authors found shoot traits to be good predictors of root traits, at varied resource availability. The trait and substrate results parallel our findings even though the rainforest habitat differs from the arid environment that *B. tectorum* of this study was collected from.

We detected population-level differences in this shoot-root trait relationship which indicates that aspects of the population's biology influenced the trait responses, though we lack information about the populations to draw parallels to plant traits. Interestingly, root tip production responded significantly to soil texture while height did not, suggesting an overriding importance of edaphic characteristics, but other studies have shown variability among populations in other grass species (ROWE and LEGER, 2011; ATWATER et

al., 2015; FOX and KRAMER, 2020a, 2020b). No study to our knowledge simultaneously tests source population and plasticity in response to different soil textures.

Future work and study limitations

Our results generally suggest that conclusions about root traits based on shoot traits (or vice versa) must be based on the results of testing different abiotic environments and consider population variation (ADU, 2020). We used *B. tectorum* to test this principle because it grows quickly. It is an invasive species, and its invasiveness is linked to capabilities of its fibrous root system. These findings may differ in non-invasive species, and more work on multiple populations of non-invasive species is needed. The fact that the plant height was recorded after seven days of growth and the root tip production was recorded after 14 days of growth raises the possibility that the relationships could have been different with synchronized trait recordings. However, the relationships here were still strong and significant (Fig. 2), and sufficient to draw conclusions. The two traits studied here are of ecological significance, though assessing multiple root and shoot traits would enhance future research that tests various substrates. Finally, future research should focus on heterogeneity of substrates including particle size and pore size distribution to link the findings more strongly to natural conditions in the field.

Conclusions

Our results indicate that the substrate used, and potentially the water content and pore size affect a shoot-root trait relationship and the strength of inference for shoot height from root tip production and vice versa. Greater water stress and stressful physical attributes of the soil, which reduce moisture content, led to a closer coordination of shoot height to the root tip production than did the substrate with greater moisture content. Researchers wishing to draw inference on root or shoot traits using traits of the other organ must consider substrate properties and plant population effects on these outcomes.

Acknowledgements

We thank Dr. Andrea Kramer for collecting and providing seeds of the Johnson Creek population used in this study and for providing helpful feedback on this manuscript. We extend gratitude to the Program in Plant Biology and Conservation and the Chicago Botanic Garden for use of the facilities and resources. We thank Dr. Lynn Westley for the Lake Forest College internship for which STW was supported and Dr. Jeremie Fant for program coordination.

References

ABBASI, U.A., YOU, W.H., YAN, E.R., 2021. Correlations between leaf economics, hydraulic, and shade-tolerance

traits among co-occurring individual trees. *Acta Oecologica*, 110: 103673. <https://doi.org/10.1016/j.actao.2020.103673>

- ADU, M.O., 2020. Causal shoot and root system traits to variability and plasticity in juvenile cassava (*Manihot esculenta* Crantz) plants in response to reduced soil moisture. *Physiology and Molecular Biology of Plants*, 26: 1799–1814. <https://doi.org/10.1007/s12298-020-00865-4>
- ATWATER, D.Z., JAMES, J.J., LEGER, E.A., 2015. Seedling root traits strongly influence field survival and performance of a common bunchgrass. *Basic and Applied Ecology*, 16: 128–140. <https://doi.org/10.1016/j.baae.2014.12.004>
- BOUTRAA, T., AKHKHA, A., AL-SHOABI, A.A., ALHEJELI, A.M., 2010. Effect of water stress on growth and water use efficiency (WUE) of some wheat cultivars (*Triticum durum*) grown in Saudi Arabia. *Journal of Taibah University for Science*, 3: 39–48. [https://doi.org/10.1016/S1658-3655\(12\)60019-3](https://doi.org/10.1016/S1658-3655(12)60019-3)
- CASPER, B.B., JACKSON, R.B., 1997. Plant competition underground. *Annual Review of Ecology and Systematics*, 28: 545–570. <https://doi.org/10.1146/annurev.ecolsys.28.1.545>
- CHAMBERS, J.C., ROUNDY, B.A., BLANK, R.R., MEYER, S.E., WHITTAKER, A., 2007. What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? *Ecological Monographs*, 77: 117–145.
- CHAPMAN, N., MILLER, A.J., LINDSEY, K., WHALLEY, W.R., 2012. Roots, water, and nutrient acquisition: let's get physical. *Trends in Plant Science*, 17: 701–710. <https://doi.org/10.1016/j.tplants.2012.08.001>
- CRAINE, J. M., DYBZINSKI, R., 2013. Mechanisms of plant competition for nutrients, water and light. *Functional Ecology*, 27: 833–840. <https://doi.org/10.1111/1365-2435.12081>
- CRAWLEY, M.J., 2005 *Statistics: an introduction using R*. Chichester: John Wiley & Sons Ltd. 376 p.
- FOX, A.J., FORT, F., 2019. Root and shoot competition lead to contrasting competitive outcomes under water stress: a systematic review and meta-analysis. *PLoS ONE*, 14: 1–17. <https://doi.org/10.1371/journal.pone.0220674>
- FOX, A.J., KRAMER, A.T., 2020a. Variation in number of root tips influences survival in competition with an invasive grass. *Journal of Arid Environments*, 179: 104189. <https://doi.org/10.1016/j.jaridenv.2020.104189>
- FOX, A.J., KRAMER, A.T., 2020b. Hidden variation: cultivars and wild plants differ in trait variation with surprising root trait outcomes. *Restoration Ecology*: 1–8. <https://doi.org/10.1111/rec.13336>
- FOX, A., WOJCIK, S., 2020. *Bromus tectorum* population root and shoot trait responses to differing substrate types. *Arch: Northwestern University Institutional Repository*. <https://doi.org/10.21985/n2-kt71-ye45>.
- FRESCHET, G.T., CORNELISSEN, J.H.C., VAN LOGTESTIJN, R.S.P., AERTS, R., 2010. Evidence of the “plant economics spectrum” in a subarctic flora. *Journal of Ecology*, 98: 362–373. <https://doi.org/10.1111/j.1365-2745.2009.01615.x>
- HAJEK, P., HERTEL, D., LEUSCHNER, C., 2013. Intraspecific variation in root and leaf traits and leaf-root trait

- linkages in eight aspen demes (*Populus tremula* and *P. tremuloides*). *Frontiers in Plant Science*, 4: 415. <https://doi.org/10.3389/fpls.2013.00415>
- JUPP, A., NEWMAN, I., 1987. Morphological and anatomical effects of severe drought on the roots of *Lolium perenne* L. *New Phytologist*, 105: 393–402. <https://doi.org/10.1111/j.1469-8137.1987.tb00876.x>
- KEMBEL, S.W., CAHILL, J., 2011. Independent evolution of leaf and root traits within and among temperate grassland plant communities. *PLoS ONE*, 6: 2–10. <https://doi.org/10.1371/journal.pone.0019992>
- LAZOF, D.B., RUFTY, T.W., REDINBAUGH, M.G., 1992. Localization of nitrate absorption and translocation within morphological regions of the corn root. *Plant Physiology*, 100: 1251–1258.
- LEGER, E.A., BAUGHMAN, O.W., 2015. What seeds to plant in the Great Basin? Comparing traits prioritized in native plant cultivars and releases with those that promote survival in the field. *Natural Areas Journal*, 35: 54–68. <https://doi.org/10.3375/043.035.0108>
- LIU, J.G., MAHONEY, K.J., SIKKEMA, P.H., SWANTON, C.J., 2009. The importance of light quality in crop-weed competition. *Weed Research*, 49: 217–224. <https://doi.org/10.1111/j.1365-3180.2008.00687.x>
- MARTRE, P., NORTH, G.B., BOBICH, E.G., NOBEL, P.S., 2002. Root deployment and shoot growth for two desert species in response to soil rockiness. *American Journal of Botany*, 89: 1933–1939. <https://doi.org/10.3732/ajb.89.12.1933>
- MCGRAIL, R.K., VAN SANFORD, D.A., MCNEAR, D.H., 2020. Trait-based root phenotyping as a necessary tool for crop selection and improvement. *Agronomy*, 10: 1–19. <https://doi.org/10.3390/agronomy10091328>
- NYE, P.H., TINKER, P.B., 1977. *Solute movement in the rhizosphere*. Oxford: Blackwell. 342 p.
- OLÁH, B., BRIÈRE, C., BÉCARD, G., DÉNARIÉ, J., GOUGH, C., 2005. Nod factors and a diffusible factor from arbuscular mycorrhizal fungi stimulate lateral root formation in *Medicago truncatula* via the DMI1/DMI2 signalling pathway. *Plant Journal*, 44: 195–207. <https://doi.org/10.1111/j.1365-313X.2005.02522.x>
- PLACIDO, D.F., SANDHU, J., SATO, S.J., NERSESIAN, N., QUACH, T., CLEMENTE, T.E., STASWICK, P.E., WALIA, H., 2020. The LATERAL ROOT DENSITY gene regulates root growth during water stress in wheat. *Plant Biotechnology Journal*, 18: 1955–1968. <https://doi.org/10.1111/pbi.13355>
- R CORE TEAM, 2021. *R: a language and environment for statistical computing*. Vienna, Austria: R Statistical Computing. [cit. 2021-05-19]. <https://www.R-project.org/>
- ROWE, C.L.J., LEGER, E., 2011. Competitive seedlings and inherited traits: a test of rapid evolution of *Elymus multisetus* (big squirreltail) in response to cheatgrass invasion. *Evolutionary Applications*, 4: 485–498. <https://doi.org/10.1111/j.1752-4571.2010.00162.x>
- SASSE, J., KOSINA, S.M., DE RAAD, M., JORDAN, J.S., WHITING, K., ZHALNINA, K., NORTHEN, T.R., 2020. Root morphology and exudate availability are shaped by particle size and chemistry in *Brachypodium distachyon* *Plant Direct*, 4: 1–14. <https://doi.org/10.1002/pld3.207>
- SHARMA, R.B., GHIDYAL, B.P., 1977. Soil water-root relations in wheat: water extraction rate of wheat roots that developed under dry and moist conditions. *Agronomy Journal*, 69: 231–233. <https://doi.org/10.2134/agronj1977.00021962006900020009x>
- SHARP, R.E., DAVIES, W.J., 1979. Solute regulation and growth by roots and shoots of water-stressed maize plants. *Planta*, 147: 43–49. <https://doi.org/10.1007/BF00384589>
- SHEN, Y., GILBERT, G.S., LI, W., FANG, M., LU, H., YU, S., 2019. Linking aboveground traits to root traits and local environment: implications of the plant economics spectrum. *Frontiers in Plant Science*, 10: 1–12. <https://doi.org/10.3389/fpls.2019.01412>
- SILVA, D.D., KANE, M.E., BEESON, R.C., 2012. Changes in root and shoot growth and biomass partition resulting from different irrigation intervals for *Ligustrum japonicum* Thunb. *Horticultural Science*, 47: 1634–1640. <https://doi.org/10.21273/HORTSCI.47.11.1634>
- SORGONÀ, A., ABENAVOLI, M.R., GRINGERI, P.G., CACCO, G., 2007. Comparing morphological plasticity of root orders in slow- and fast-growing citrus rootstocks supplied with different nitrate levels. *Annals of Botany*, 100: 1287–1296. <https://doi.org/10.1093/aob/mcm207>
- STEVANATO, P., TREBBI, D., BERTAGGIA, M., COLOMBO, M., BROCCANELLO, C., CONCHERI, G., SACCOMANI, M., 2011. Root traits and competitiveness against weeds in sugar beet. *International Sugar Journal*, 113: 24–28.
- VARNEY, G., CANNY, M., 1993. Rates of water uptake into the mature root systems of maize plants. *New Phytologist*, 123: 775–786. <https://doi.org/10.1111/j.1469-8137.1993.tb03789.x>
- WANG, X., TAUB, D.R., 2010. Interactive effects of elevated carbon dioxide and environmental stresses on root mass fraction in plants: a meta-analytical synthesis using pairwise techniques. *Oecologia*, 163: 1–11. <https://doi.org/10.1007/s00442-010-1572-x>
- WESTOBY, M., 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, 199: 213–227. <https://doi.org/10.1023/A:1004327224729>
- YOUNG, J., CLEMENTS, C., 2007. Cheatgrass rangelands by grazing. *Rangelands*, 29: 15–20. [https://doi.org/10.2111/1551-501X\(2007\)29\[15:CAGR\]2.0.CO;2](https://doi.org/10.2111/1551-501X(2007)29[15:CAGR]2.0.CO;2)

Received June 12, 2021
Accepted July 1, 2021