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Clonal integration facilitates the invasion of two root-suckering plants (Rorippa amphibia and Rorippa sylvestris) in a water-heterogeneous environment

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Abstract

Environmental heterogeneity is common in nature. Clonal integration is an important trait that allows clonal plants to grow in resource-heterogeneous environments. The aim of this work was to study the effects of clonal integration on the growth and propagation of two root-suckering plant species under water-heterogeneous conditions and to elucidate their adaptive strategy to water stress. Two root-suckering plants of the genus Brassicaceae, *Rorippa amphibia* and *Rorippa sylvestris*, have invaded Liaoning Province, China. The greenhouse pot experiments were performed in the research center of the Shenyang Agricultural University. Mother and daughter fragments collected from these two plants were grown under either well-watered or water-limited conditions to mimic the homogeneous and heterogeneous water condition. Morphological traits (root-shoot ratio, the number of new shoots, etc.) and the biomass of mother and daughter fragments were measured. The results showed that clonal integration did not occur under water-homogeneous conditions. However, under water-heterogeneous conditions, clonal integration transported the resources from resource-rich environments to resource-defficient environments. When the resources were re-allocated, clonal integration increased the root-shoot ratio and the number of new shoots on daughter fragments, which facilitated the spread of the plants. At low water availability, *R. sylvestris* had higher root-shoot ratios and more new shoots on daughter fragments than *R. amphibia*, suggesting that *R. sylvestris* had higher invasibility than *R. amphibia*. The findings enhanced our understanding of how clonal integration facilitates the invasion of root-suckering plants in resource-heterogeneous environments and provided insights into management measures for invasive alien species.

Introduction

It is well known that biological invasion has become a serious global problem which causes great damage to native ecosystems (Callaway and Aschehoug, 2000; Rejmánek and Marcel, 2015; Richardson et al., 2000; Van Kleunen et al., 2010, Van Kleunen et al., 2015). Clonal plants play an important role in biological invasion. Among 2670 invasive plant species originating from Central Europe, 66.5% (about 2000 plant species) have clonal life-history traits (Klimes et al., 1997). In China, 196 out of 515 recorded invasive plant species are clonal plants (Wang et al., 2016a), and 49.2% of 315 plant species distributed in Northeast China are clonal plants (Song and Dong, 2002; Song et al., 2001). In general, the most important trait associated with clonal growth is clonal integration, which is an ability of clonal plants to transport the substances and/or signals between connected ramets to adjust and adapt to various environmental stress (Dong and Yu, 2007). Clonal integration can increase the growth and propagation of connected ramets, either individually or as a whole, and promote the spread of clonal ramets from original habitats where the seeds are planted (Alpert, 1999; Hartnett and Bazzaz, 1983; Roiloa and Retuerto, 2006; Slade and Hutchings, 1987; Saitoh et al., 2002). Since clonal integration might be associated with the adaptability of invasive plants to the environment, it is of great importance to elucidate the relationship between clonal integration and adaptability of invasive plants in the early stage of invasion.

To successfully invade new habitats, clonal plants have to cope with the heterogeneity in environmental resources such as light, nutrients, water, etc. (You et al., 2016; Wang et al., 2017; Chen et al., 2018). The adaptive strategy of clonal plants to environmental heterogeneity has always been one of the hot topics in the field of biological invasion. Clonal integration could enable clonal plants to share the products of photosynthesis, mineral nutrient, or water between ramets, thereby increasing the survival and growth of individual ramets when they experience different conditions (Alpert, 1996; Hutchings & Wijesinghe, 1997; Dong et al., 2015; Lyu et al., 2016; Shi et al., 2021). For example, when some ramets are damaged or restricted by regional environmental stress, unaffected ramets could help these ramets survive or escape from adverse habitats through translocation of resources among connected ramets (Hellström et al., 2006; Wang et al., 2009; Lyu et al., 2016). In heterogeneous environments, clonal integration can improve the performance of mother and daughter ramets in *Wedelia trilobata*, a typical invasive clonal plant, to facilitate their invasion into waterlogged areas (Saptiningsih et al.,2018). In homogeneous environments, however, clonal integration has different effects on the growth of clonal plants. For example, clonal integration enhances the growth of the aboveground parts of connected ramets of a clonal weed *Alternanthera philoxeroides* and increase their resistance to pathogenic fungi (Qi et al., 2017), but it does not affect the growth of the other invasive plant *Phalaris arundinacea* treated with homogeneous simulated herbivory (Yu et al., 2018). Therefore, it is necessary to understand the adaptive strategy of invasive clonal plants in either homogeneous or heterogeneous environments.

In China, the most dangerous invasive plants are clonal plants, such as *Mikania micrantha*, *Alternanthera philoxeroides*, *Spartina alterniflora*, *Eupatorium adenophora*, and so on. Recent studies mainly focus on clonal plants with rhizomes and stolons, but little is known about clonal plants with root suckers. In clonal plants with root suckers, adventitious buds on the roots of parent plants may grow and spread to form new colonies (Alpert, 1996; Li et al., 2011; Peng et al., 2014). As for clonal plants with root suckers, the number of ramets that can produce aboveground shoots from adventitious buds on the roots is a key factor for clonal growth, distribution pattern and population size of new ramets (Zheng et al., 2019). The current knowledge about clonal integration in plants with rhizomes and stolons is not sufficient to completely elucidate the mechanisms underlying the invasion of clonal plants with root suckers.

R. amphibia and *R. sylvestris*, belonging to the family *Brassicaceae Burnett* (*Cruciferae*), are perennial herbaceous plants, which propagate primarily by root suckering. These two plants prefer a humid environment and are tolerant to waterlogging. In Liaoning province, they are first found in lawns, probably introduced via the horticulture trade. These plants have spread rapidly in recent years, formed patchy distributions and become the dominant plant species in lawns, which creates challenges for the maintenance and management of lawns (Zhang et al., 2009; Wang et al., 2016b; Miao et al., 2019). At the same time, improper irrigation might lead to the spatial heterogeneity of soil moisture in lawns. Therefore, understanding the mechanism by which clonal integration influences the spread of clonal plants with root suckers in water-heterogeneous environment is necessary.

Materials And Methods

Collection and cultivation of fragments of two plants

In late April of 2019, the ramets of *R. amphibia and R. sylvestris* (500 ramets per species) were collected from green belts on the campus of Shenyang Agricultural University, and the subsequent experiments were conducted in the greenhouse of the Department of Biology at Shenyang Agricultural University. Each ramet had 4–5 leaves. All roots of each ramet were removed, and only the leaves and the base of the root remained. The ramets were planted in plastic pots (13 cm in diameter and 12 cm in height) filled with sandy loam soil purchased from a local market. After 40 days of culture, the length of the adventitious roots was about 20 cm, and there were still no new ramets on adventitious roots. The fragments with similar-sized roots were selected for the subsequent experiments. Root fragments at 10 cm from the base of the ramet were used as mother fragments, and the remaining fragments of 10–20 cm in length were used as daughter fragments. Mother and daughter fragments were separately planted in plastic pots (16 cm in diameter and 16 cm in height) containing 1 kg sandy loam soil, one fragment per pot.

Experimental design

The experimental design is schematically illustrated in Fig. 1. In this study, a total of 48 pairs of mother and daughter fragments were planted, and they were divided into 6 groups, 8 pairs per group. Among them, 16 pairs in two groups were severed to prevent the occurrence of clonal integration between mother and daughter fragments, and others remained connected. After planting, all pots were watered once with 400 ml of water per pot for recovery. After 1 week of recovery growth, daughter and mother fragments were subjected to either high water availability or low water availability. At high water availability, each pot was watered with 200 mL water every 2 days, and at low water availability, each pot was watered with 100 mL water every 4 days. So, 6 groups of paired mother and daughter fragments were grown under either homogeneous or heterogeneous water conditions, including: connected daughter fragments at low water availability and mother fragments at high water availability (LH), connected daughter and mother fragments at low water availability (L1, 1: connected), disconnected daughter and mother fragments at low water availability (L0, 0: disconnected), connected daughter fragments at high water availability and mother fragments at low water availability (HL), connected daughter and mother fragments at high water availability (H1, 1: connected), and disconnected daughter and mother fragments at high water availability (H0, 0: disconnected). In addition, hand weeding and pest control were conducted throughout the whole experiment.

Characterization of morphological traits and biomass allocation

At the end of the treatment, morphological traits of mother and daughter fragments, including plant height, the number of new shoots, were measured. The above- and below-ground biomass of the fragments were separately collected, dried (60°C, 60 hours), and weighed. The total biomass and root-shoot ratio were also calculated.

Statistical analysis

All data are presented as mean ± standard deviation (SD, n = 8). Data were analyzed using SPSS version 22.0 (SPSS, Inc., Chicago, IL, USA). Significant differences among groups were analyzed using a one-way ANOVA followed by Tukey's multiple comparison test. Differences were considered statistically different when a P value was less than 0.05.

Results

Effects of clonal integration on the biomass of mother and daughter fragments

Under homogeneous conditions, clonal integration did not affect the total biomass of daughter and mother fragments in both *R. amphibia* and *R. sylvestris*. When daughter and mother fragments were grown under homogeneous condition, no differences in total biomass were found between daughter fragments connected to and severed from mother fragments (Fig. 2a and 2b). Similarly, no differences in total biomass were found between mother fragments connected to and severed from daughter fragments (Fig. 2c and 2d). By contrast, under water-heterogeneous conditions, clonal integration could remarkably increase the total mass of both plants grown at low water availability. When mother fragments were grown at high water availability, the total biomass was significantly higher in connected daughter fragments than disconnected daughter fragments which were grown at low water availability (Fig. 2a and 2b). Similarly, when daughter fragments were grown at high water availability, the total biomass was significantly higher in connected mother fragments than disconnected mother fragments grown at low water availability (Fig. 2c and 2d). In addition, the increase in total biomass of daughter or mother fragments at low water availability had no impact on total biomass of connected mother or daughter fragments (Fig. 2). The results suggest that, under the water-heterogeneous condition, clonal integration did not affect the total mass of fragments grown at high water availability but could increase the total biomass of fragments grown at low water availability; the resources were always transported from the resource-rich environment to the resource-deficient environment.

Effects of clonal integration on biomass allocation (root-shoot ratio) of mother and daughter fragments

Under the water-homogeneous condition, clonal integration had no effect on the root-shoot ratio of mother and daughter fragments grown at low water availability in both *R. amphibia* and *R. sylvestris*.

At low water availability, there were no differences in the root-shoot ratio between daughter fragments connected to and severed from mother fragments (Fig. 3a and 3b). At high water availability, the root-shoot ratio differed between mother fragments connected to and severed from daughter fragments in *R. amphibia*, but no difference was found in *R. sylvestris* (Fig. 3c and 3d). Under the water-heterogeneous condition, clonal integration significantly affected the root-shoot ratio in both *R. amphibia* and *R. sylvestris.* When daughter fragments were grown at low water availability and mother fragments were grown at high water availability, the root-shoot ratio of connected daughter fragments was significantly higher than that of disconnected daughter fragments (Fig. 3a and 3b). The results suggest that clonal integration could facilitate the allocation of the biomass in the root of daughter fragments in both plants.

Effects of clonal integration on the number of new shoots on mother and daughter fragments

Under the water-homogeneous condition, clonal integration had a significant impact on the number of new shoots on daughter fragments grown at low water availability in both plants, as well as mother fragments grown at high water availability. At low water availability, the number of new shoots was significantly higher in daughter fragments connected to mother fragments than those severed with mother fragments in both plants (Fig. 4a). Similarly, at high water availability, the number of new shoots was significantly higher in daughter fragments connected to mother fragments than those severed with mother fragments in both plants (Fig. 4b). However, at high water availability, the number of new shoots was significantly lower in mother fragments connected to daughter fragments than those severed with daughter fragments in *R. sylvestris* (Fig. 4d). Under the water-heterogeneous condition, clonal integration significantly affected the number of new shoots on mother and daughter fragments in both plants. When daughter fragments were grown at low water availability and mother fragments were grown at high water availability, the number of new shoots on connected daughter fragments was significantly higher than that of disconnected daughter fragments (Fig. 4a and 4b).

Effects of clonal integration on the height of daughter and mother fragments

Under the water-homogeneous condition, clonal integration did not affect the height of daughter and mother fragments in both *R. sylvestris* and *R. amphibia*. There was no difference in height between daughter fragments connected to mother fragments and those severed with mother fragments in both plants, as well as between mother fragments connected to daughter fragments and those severed with daughter fragments (Fig. 5). Under the water-heterogeneous condition, clonal integration significantly decreased the height of daughter fragments grown at high water availability in *R. sylvestris*, but significantly increased the height of mother fragments grown at low water availability in *R. amphibia.* The height of connected daughter fragments grown at high water availability was significantly lower than that of severed daughter fragments grown at low water availability in *R. sylvestris* (Fig. 5a), and the height of connected mother fragments grown at low water availability was significantly higher than that of severed mother fragments grown at high water availability in *R. amphibia* (Fig. 5d).

Under the water-heterogeneous condition, clonal integration significantly increased the biomass of clonal segments at low water availability and facilitated the allocation of accumulated biomass toward the root in daughter fragments at both high and low water availability. The results suggested that clonal integration could improve the growth of both plants under the water-heterogeneous condition. When daughter fragments connected to mother fragments, in *R. sylvestris*, the total biomass, root-shoot ratio and the number of new shoots on daughter fragments grown at low water availability, the total biomass and root-shoot ratio of daughter fragments grown at high water availability, the total biomass and root-shoot ratio of mother fragments grown at low water availability, the root-shoot ratio of mother fragments grown at high water availability, were significantly higher than those in *R. amphibia*. These results suggested that *R, sylvestris* had higher adaptability to the water-heterogeneous condition than *R. amphibian*.

Discussion

Recent studies have shown that the positive effects of clonal integration on the growth and propagation of clonal plants were highly influenced by the direction of resource translocation within clonal fragments (You et al., 2016; Zhu et al., 2017; Mao et al., 2009). In the water-heterogeneous environment, well-watered ramets could translocate water to water-stressed ramets for resource sharing (Mao et al.,2009). In the water-homogeneous environment, however, water was seldom transferred between the ramets (Pauliukonis & Gough, 2004). Our results are consistent with these reports above. When daughter and mother fragments were grown under the water-homogeneous condition, clonal integration did not affect the total biomass. However, when daughter and mother fragments were grown under the water-heterogeneous condition, the total biomass of clonal segments at low water availability increased significantly, possibly due to the translocation of resources from the fragments with high-level resources to those with low-level resources through the connection between fragments. This indicated the occurrence of clonal integration which allocated resources from clonal segments with high-level resources to those with low-level resources. This result was consistent with the previous reports (Song et al., 2013; Wang et al., 2017). On the other hand, slightly different from the report by Wang (Wang et al., 2017), clonal integration did not significantly increase the total biomass of the fragments grown at high resource availability which connected to the fragments grown at low resource availability, possibly because that, only when the growth of clonal segments in both plants at high resource availability was not affected, resources could be translocated to clonal segments at low resource availability through clonal integration.

In heterogeneous habitats, clonal integration could remarkably affect biomass allocation of clonal plants (Wang et al., 2008; Yu et al., 2009; You et al., 2014; Huang et al., 2018). In this study, under the water-heterogeneous condition, clonal integration increased the root-shoot ratio of daughter fragments in both plants, decreased the root-shoot ratio of mother fragments in *R. sylvestris* at high water availability, but had no effect on the root-shoot ratio of mother fragments in *R. amphibia* at high water availability. The change in biomass allocation of daughter fragments in both plants is different from that found in *Alternanthera philoxeroides*, a stoloniferous clonal plant (You et al., 2016). The difference might be related to their different clonal forms. Both *R. amphibia and R. sylvestris* propagate through root suckers, but *Alternanthera philoxeroides* propagates through stolons. Root suckering could increase the belowground biomass of the fragments by allocating more biomass to the parts with more resources, and it is a manifestation of functional specialization for abundant resource in clonal plants (Dong and Yu, 2007). The results suggest that a specialized resource-acquiring structure for absorbing water has been developed in daughter fragments, which could improve their growth and propagation to generate more new ramets (Zheng et al.,2019;Sun et al., 2019). The number of new shoots generated by daughter and mother fragments is a direct indicator of their reproductivity. Clonal integration could enhance the sprout of new fragments in both root-sucking plants. Under low resource conditions, daughter fragments generated more new shoots, which is really an adaptive strategy for plants in an adverse environment to increase the ratio of propagule in order to reduce the risk of population extinction. Under high resource condition, daughter fragments had more resources, and an increase in the number of new shoots could

achieve the goal of propagation and spread. Mother fragments were not significantly affected by clonal integration. Moreover, under the normal condition without water stress, clonal integration even decreased the number of new shoots produced by mother fragments in *R. amphibia*, possible because daughter and mother fragments in both plants played different roles in the process of clonal integration, and daughter fragments allocated more biomass in the root to produce more new shoots.

Clonal integration could facilitate daughter fragments of two clonal plants to increase the number of new shoots in a resource-deficient environment, which is one of the adaptive strategies of clonal plants experiencing unfavorable environments to reduce the risk of population extinction. At the same time, in a resource-rich environment, daughter fragments could utilize more resources to increase the number of new shoots to propagate and spread. On the other hand, we found that clonal integration had no significant effects on mother fragments of two plants, and even reduced the number of new shoots on mother fragments in *R. sylvestris* under the well-watered condition. The possible reason is that, when clonal integration occurs, daughter and mother fragments in these two root-suckering plants showed the division of labor in response to local growing conditions, and daughter fragments allocate more biomass to the roots to produce more new shoots.

Plant height is one of the important traits of plant growth. Under the water-heterogeneous condition, clonal integration could increase the plant height of daughter fragments in *R. amphibia* and mother fragments in *R. sylvestris* when clonal segments of two plants were exposed to water stress. Under the water stress condition, daughter fragments in *R. amphibia* transported the resources not only to the belowground parts but also to the aboveground parts, which improved the growth of the aboveground parts, thereby improving the growth of the whole clonal segment. This mechanism could also explain the reason for the increase in plant height of mother fragments in *R. sylvestris*.

Conclusions

In terms of three indicators (total biomass, root-shoot ratio, and plant height), the present results confirmed the first hypothesis that clonal integration occurred between daughter and mother fragments under the water-heterogeneous condition, rather than the water-homogeneous condition. Furthermore, the results also supported the second hypothesis that, under the water-heterogeneous condition, the biomass was allocated from the fragments with rich resources to those with deficient resources, thereby increasing the total biomass of daughter and mother fragments grown under resource-deficient condition. Under water-heterogeneous conditions, clonal integration could allocate more total biomass to the roots of daughter fragments in both plants. The possible mechanism is that clonal plants with root-suckers could generate many adventitious shoots on the roots, which increased the probability of producing new shoots, eventually facilitating the propagation and spread of plant communities. Two plants had differential ability to adapt to the water-heterogeneous environment, and *R. sylvestris* was more invasive than *R. amphibia* in heterogeneous environments.

Declarations

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Data availability If the manuscript is accepted, the supporting data will be archived in an appropriate public repository (e.g., Figshare)

Conflict of interest The authors declare that they no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Authors' Contribution M. Shao: Investigation, Supervision, Methodology, Formal analysis, Writing-review & editing; Q. Wang: Investigation, Supervision, Methodology, Formal analysis, Writing-original draft; B. Yan, Y. Xu, Y. Ma and S. Xu: Supervision, Methodology, Formal analysis; B. Qu: Conceptualization, Methodogy, Investigation, Supervision, Formal analysis, Writing-review & editing.

References

1. Alpert P (1999) Clonal integration in Fragaria chiloensis differs between populations: ramets from grassland are selfish. Oecologia 120:69–76. https://doi.org/10.1007/s004420050834
2. Alpert P (1996) Nutrient sharing in natural clonal Fragments of Fragaria chiloensis. Journal of Ecology 84:395–406. https://doi.org/10.2307/2261201
3. Callaway RM, Aschehoug ET (2000) Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. Science 290:521–523. https://doi.org/10.1126/science.290.5491.521
4. Chen BM, Su JQ, Liao HJ, *et al*. (2018) A greater foraging scale, not a higher foraging precision, may facilitate invasion by exotic plants in nutrient-heterogeneous conditions. Annals of Botany 121:561–569. https://doi.org/10.1093/aob/mcx172
5. Dong BC, Zhang Q, Alpert P, *et al*. (2015) Clonal integration in homogeneous environments increases performance of Alternanthera philoxeroides. Oecologia 179:393–403. https://doi.org/10.1007/s00442-015-3338-y
6. Dong M, Yu FH (2007) Cloning plant ecology terms and concepts. Journal of Plant Ecology 31:689–694. https://doi.org/10.17521/cjpe.2007.0089
7. Hartnett DC, Bazzaz FA (1983) Physiological integration among intraclonal ramets in Solidago canadensis. Ecology 64:779–788. https://doi.org/10.2307/1937201
8. Hellström K, Kytöviita MM, Tuomi J, et al. (2006) Plasticity of clonal integration in the perennial herb Linaria vulgaris after damage. Functional Ecology 20:413–420. https://doi.org/10.1111/j.1365-2435.2006.01115.x

9. Hutchings MJ, Wijesinghe DK (1997) Patchy habitats, division of labour and growth dividends in clonal plants. Trends in Ecology Evolution 12: 390–394. https://doi.org/10.1016/s0169-5347(97)87382-x
10. Kleunen MV, Dawson W, Essl F, *et al*. (2015) Global exchange and accumulation of non-native plants. Nature 525:100–103. https://doi.org/10.1038/nature14910
11. Kleunen MV, Weber E, Fischer M (2010) A Meta-analysis of trait differences between invasive and non-invasive plants species. Ecology Letters 13:235–245. https://doi.org/10.1111/j.1461-0248.2009.01418.x
12. Klimes L, Klimesova J, Hendriks R, Groenendael J (1997) Clonal plant architectures: a comparative analysis of form and function. In H. de Kroon and J. van Groenendael (eds). *The ecology and evolution of clonal plants*. Leiden, Backhuys Publishers, 1–29. https://www.researchgate.net/publication/309373277
13. Li ZJ, Jiao PP, Zhou ZL, *et al*. (2011) Anatomic characteristics of transverse lateral roots and adventitious buds of Populus euphratica. Journal of Beijing Forestry University 33:42–48. https://doi.org/10.13332/j.1000-1522.2011.05.020
14. Lyu XQ, Zhang YL, You WH (2016) Growth and physiological responses of Eichhornia crassipes to clonal integration under experimental defoliation. Aquat Ecol 50:153–162. https://doi.org/10.1007/s10452-015-9557-9
15. Mao SY, Jiang CD, Zhang WH, *et al*. (2009) Water translocation between ramets of strawberry during soil drying and its effects on photosynthetic performance. Physiologia Plantarum 137:225–234. https://doi.org/10.1111/j.1399-3054.2009.01275.x
16. Miao Q, Wang QL, Niu Z, *et al*. (2019) Occurrence and damage of new regional invasive plant—Rorippa sylvestris(L.) Besser in Shenyang. Plant Quarantine 33:69–72. https://doi.org/10.19662/j.cnki.issn1005-2755.2019.00.057
17. Huang QQ, Li XX, Huang FF, *et al*. (2018) Nutrient addition increases the capacity for division of labor and the benefits of clonal integration in an invasive plant. Science of The Total Environment 643:1232–1238. https://doi.org/10.1016/j.scitotenv.2018.06.294
18. Pauliukonis N, Gough L (2004) Effects of the loss of clonal integration on four sedges that differ in ramet aggregation. Plant Ecology 173:1–15. https://doi.org/10.1023/B:VEGE.0000026342.25767.17
19. Peng G, Zhao CY, Li J, *et al*. (2014) Water Source of root suckers of populus euphratica in the Tarim River Basin, Xinjiang. Arid Zone Research 31:1093–1099. https://doi.org/10.13866/j.azr.2014.06.17
20. Qi SS, Wu J, Chen Q, *et al*. (2017) Effects of clonal integration on the resistance of Alternanthera philoxeroides to fungi pathogen. Ecology and Environmental *Sciences* 26:729–734. https://doi.org/10.16258/j.cnki.1674-5906.2017.05.001
21. Rejmánek, Marcel (2015) Ecology: Global trends in plant naturalization. Nature 525:39–40. https://doi.org/10.1038/nature15206
22. Richardson DM, Pyek P, Marcel Rejmánek, *et al*. (2000) Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions 6:93–107. https://doi.org/10.1046/j.1472-

4642.2000.00083.x

23. Roiloa SR, Rubén Retuerto (2006) Physiological integration ameliorates effects of serpentine soils in the clonal herb Fragaria vesca. Physiologia Plantarum 128:662–676. https://doi.org/10.1111/j.1399-3054.2006.00790.x
24. Saitoh T, Seiwa K, Nishiwaki (2002) Importance of physiological integration of dwarf bamboo to persistence in forest understorey: a field experiment. Journal of ecology 90:78–85. https://doi.org/10.1046/j.0022-0477.2001.00631.x
25. Saptiningsih E, Dewi K, Santosa, *et al*. (2019) Clonal integration of the invasive plant Wedelia trilobata (L.) Hitch in stress of flooding type combination. International Journal of Plant Biology 10:1–18. https://doi.org/10.4081/pb.2018.7526
26. Shi XP, Bai YF, Song P, *et al*. (2021) Clonal integration and phosphorus management under light heterogeneity facilitate the growth and diversity of understory vegetation and soil fungal communities. Science of The Total Environment 767:144322. https://doi.org/10.1016/j.scitotenv.2020.144322
27. Slade AJ, Hutchings MJ (1987) An analysis of the costs and benefits of physiological integration between ramets in the clonal perennial herb Glechoma hederacea. Oecologia 73:425–431. https://doi.org/10.1007/BF00385260
28. Song MH, Dong M, Jiang GM, *et al*. (2001) Clonal plants along NECT and relation of their importance to environmental conditions. Acta Ecologica Sinica 21:1095–1103.
29. Song MH, Dong M (2002) Importance of clonal plants in community. Acta Ecologica Sinica 22:1960–1967.
30. Song YB, Yu FH, Keser LH, *et al*. (2013) United we stand, divided we fall: a meta-analysis of experiments on clonal integration and its relationship to invasiveness. Oecologia 171: 317–327.https://doi.org/10.1007/s00442-012-2430-9
31. Sun JQ, Wang SC, Liu YF, *et al*. (2019) Clonality and ecological function of ferns. Journal of West China Forestry Science 48:110–115. https://doi.org/10.16473/j.cnki.xblykx1972.2019.03.017
32. Wang N, Li WF, Zhou B, *et al*. (2016a) Invasiveness, clonal form and geographical origin of invasive clonal plant species in China. Biodiversity Science 24:12–19.
33. Wang N, Yu FH, Li PX, *et al*. (2008) Clonal integration affects growth, photosynthetic efficiency and biomass allocation, but not the competitive ability, of the alien invasive Alternanthera philoxeroides under severe stress. Annals of Botany 101:671–678. https://doi.org/10.1093/aob/mcn005
34. Wang N, Yu FH, Li PX, *et al*. (2009) Clonal integration supports the expansion from terrestrial to aquatic environments of the amphibious stoloniferous herb Alternanthera philoxeroides. Plant Biology 11:483–489. https://doi.org/10.1111/j.1438-8677.2008.00133.x
35. Wang Y, Shi Y, Dai BQ (2016b) Turf-weed study in autumn in Shenyang Normal University campus. Journal of Shenyang Normal University. Natural Science Edition 34:300–304.
36. Wang YJ, Müller-Schärer H, Kleunen MV, *et al*. (2017) Invasive alien plants benefit more from clonal integration in heterogeneous environments than natives. New Phytologist 216:1072–1078.

https://doi.org/10.1111/nph.14820

37. You WH, Fan SF, Yu D, *et al*. (2014) An invasive clonal plant benefits from clonal integration more than a co-occurring native plant in nutrient-patchy and competitive environments. Plos One 9:e97246. https://doi.org/10.1371/journal.pone.0097246
38. You WH, Han CM, Liu CH, *et al*. (2016) Effects of clonal integration on the invasive clonal plant Alternanthera philoxeroides under heterogeneous and homogeneous water availability. Science Reports 6:29767. https://doi.org/10.1038/srep29767
39. Yu FH, Wang N, Alpert P, *et al*. (2009) Physiological integration in an introduced, invasive plant increases its spread into experimental communities and modifies their structure. American Journal of Botany 96:1983–1989. https://www.jstor.org/stable/20621977
40. Yu HP, Wang TT, Jian MF, *et al*. (2018) Effects of clonal integration on the growth and physiology of Phalaris arundinacea under simulated herbivory. Chinese Journal of Applied and Environmental Biology 24:434–440. https://doi.org/10.19675/j.cnki.1006-687x.2017.12006
41. Zhang SM, Li ZX, Wang Q, *et al*. (2009) A Newly Recorded Species Rorippa amphibia (L.) Besser from China. Journal of Tropical and Subtropical Botany 17:176–178.
42. Zheng YQ, Zhai JT, Chen JL, *et al*. (2019) Seasonal variations of clonal propagation characteristics of Populus pruinosa schrenk, organ nutrient and soil fertility, and their coupling associations in the forest and forest edges. Bulletin of Botanical Research 39:347–357.
43. Zhu CG, Li WH, Ma JX, et al. (2017) Clonal water integration characteristics and ecological significance of Populus euphratica Oliv. in hyper-arid habitats. Plant Science Journal 35:344–3

Figures

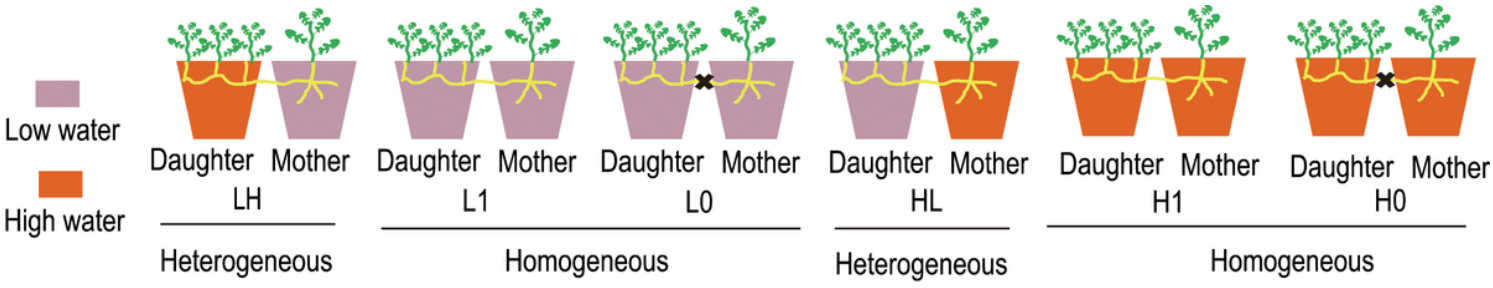

Figure 1

Schematic diagram of the experimental design. Six groups of paired mother and daughter fragments were grown under either homogeneous or heterogeneous water conditions, including: connected daughter fragments at low water availability and mother fragments at high water availability (LH), connected daughter and mother fragments at low water availability (L1, 1: connected), disconnected daughter and mother fragments at low water availability (L0, 0: disconnected), connected daughter fragments at high water availability and mother fragments at low water availability (HL), connected daughter and mother

fragments at high water availability (H1, 1: connected), and disconnected daughter and mother fragments at high water availability (H0, 0: disconnected)

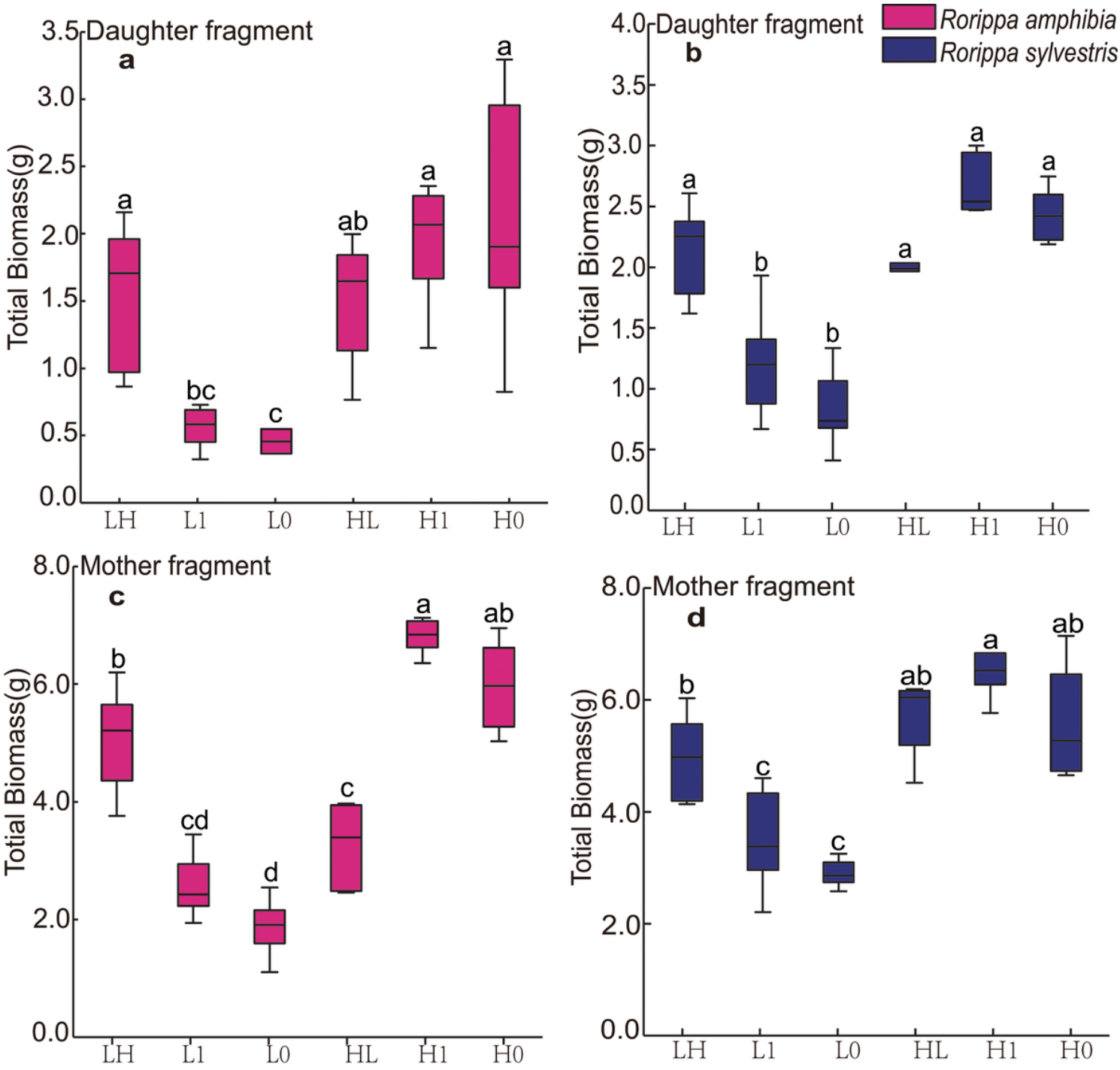

Figure 2

Comparison of the total biomass of the ramets in two plants at high or low water availability. (a): daughter fragments of R. amphibia; (b): daughter fragments of R. sylvestris; (c): mother fragments of R. amphibia; and (d): mother fragments of R. sylvestris. Different lowercase letters indicate a significant difference between treatments ($P < 0.05$)

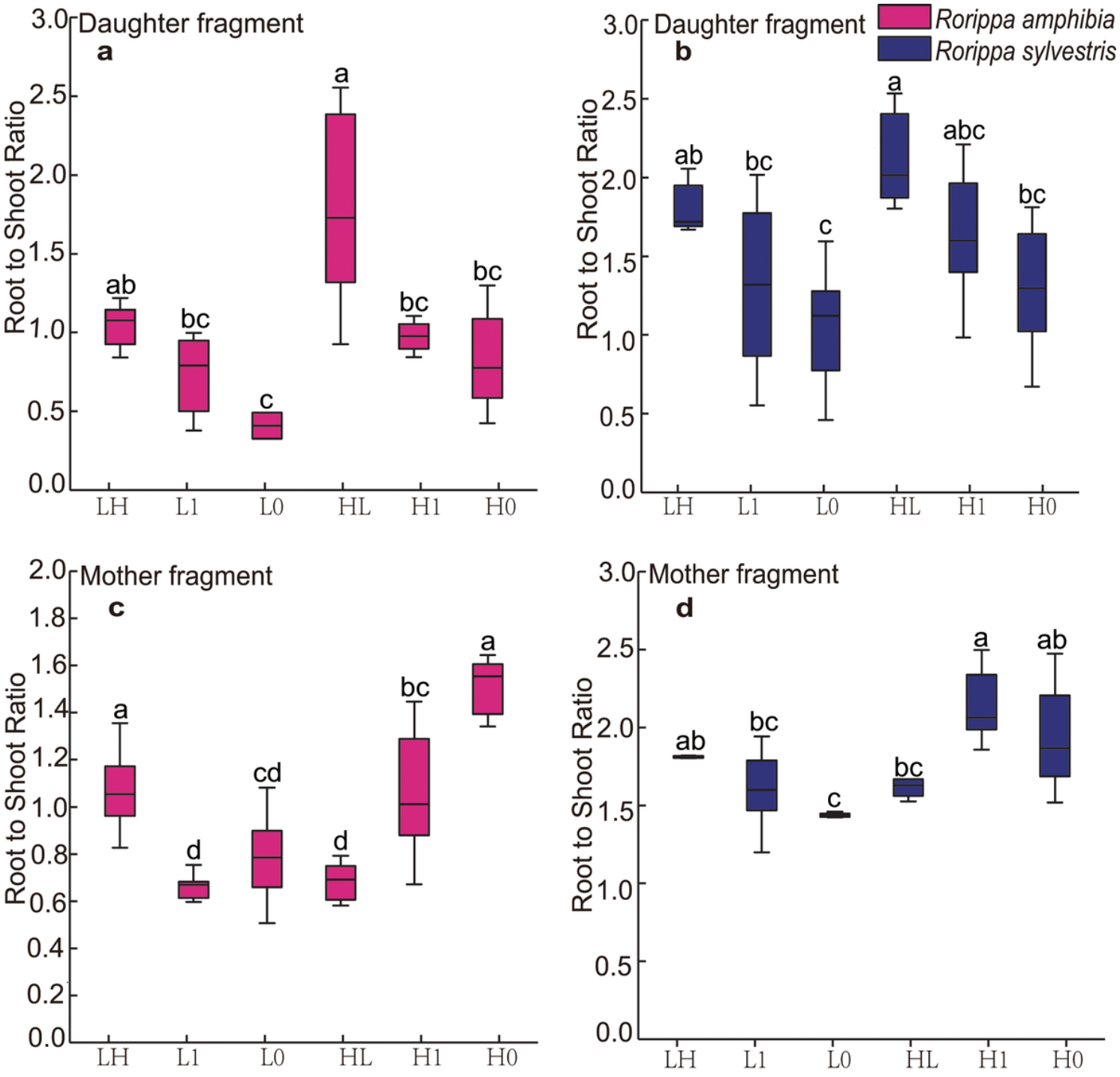

Figure 3

Comparison of root-shoot ratios in two plants under different levels of water availability. (a): daughter fragments of *R. amphibia*; (b): daughter fragments of *R. sylvestris*; (c): mother fragments of *R. amphibia*; and (d): mother fragments of *R. sylvestris.* Different lowercase letters indicate a significant difference between treatments ($P < 0.05$)

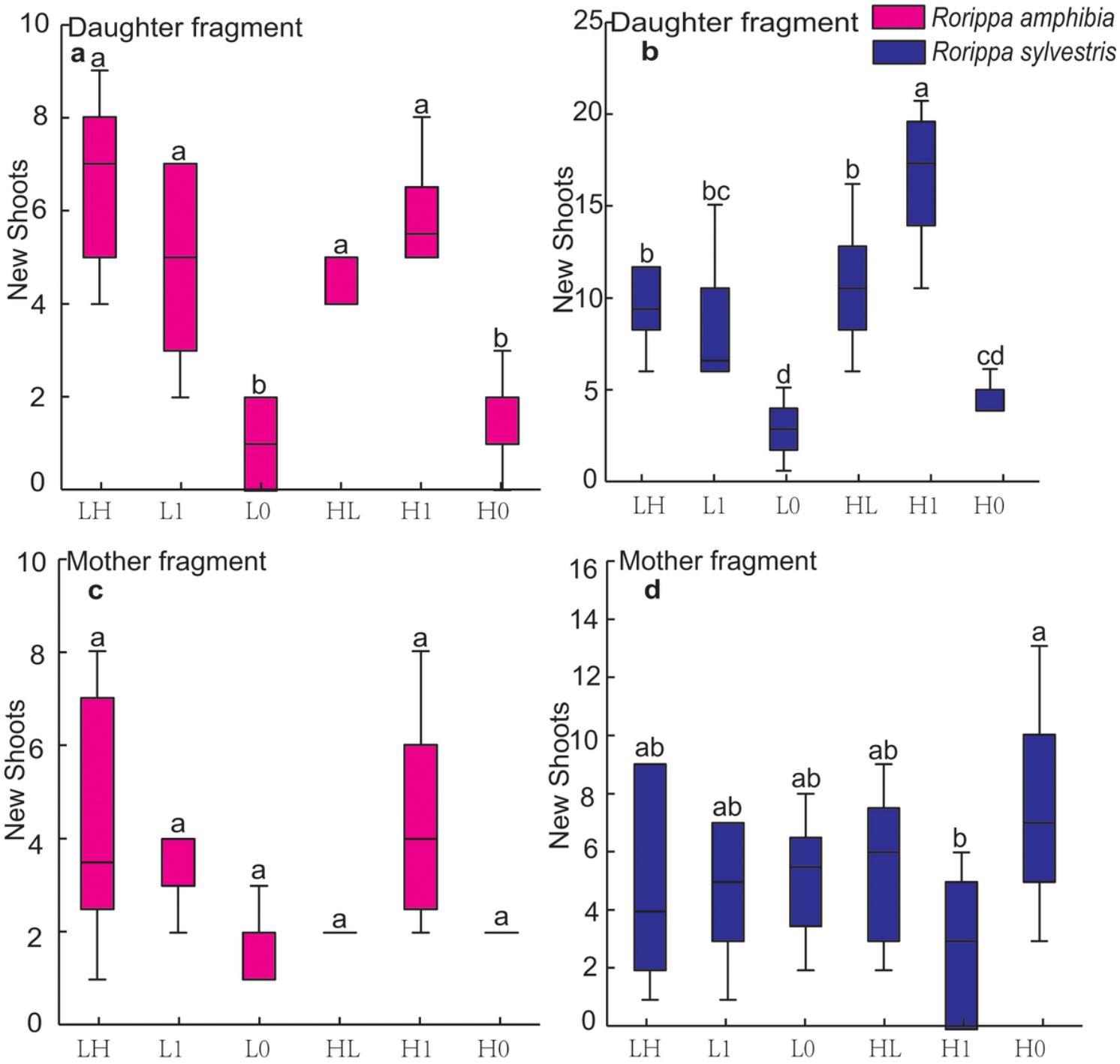

Figure 4

Comparison of the number of new fragments in two plants under different levels of water availability. (a): daughter fragments of R. amphibia; (b): daughter fragments of R. sylvestris; (c): mother fragments of R. amphibia; and (d): mother fragments of R. sylvestris. Different lowercase letters indicate a significant difference between treatments ($P < 0.05$)

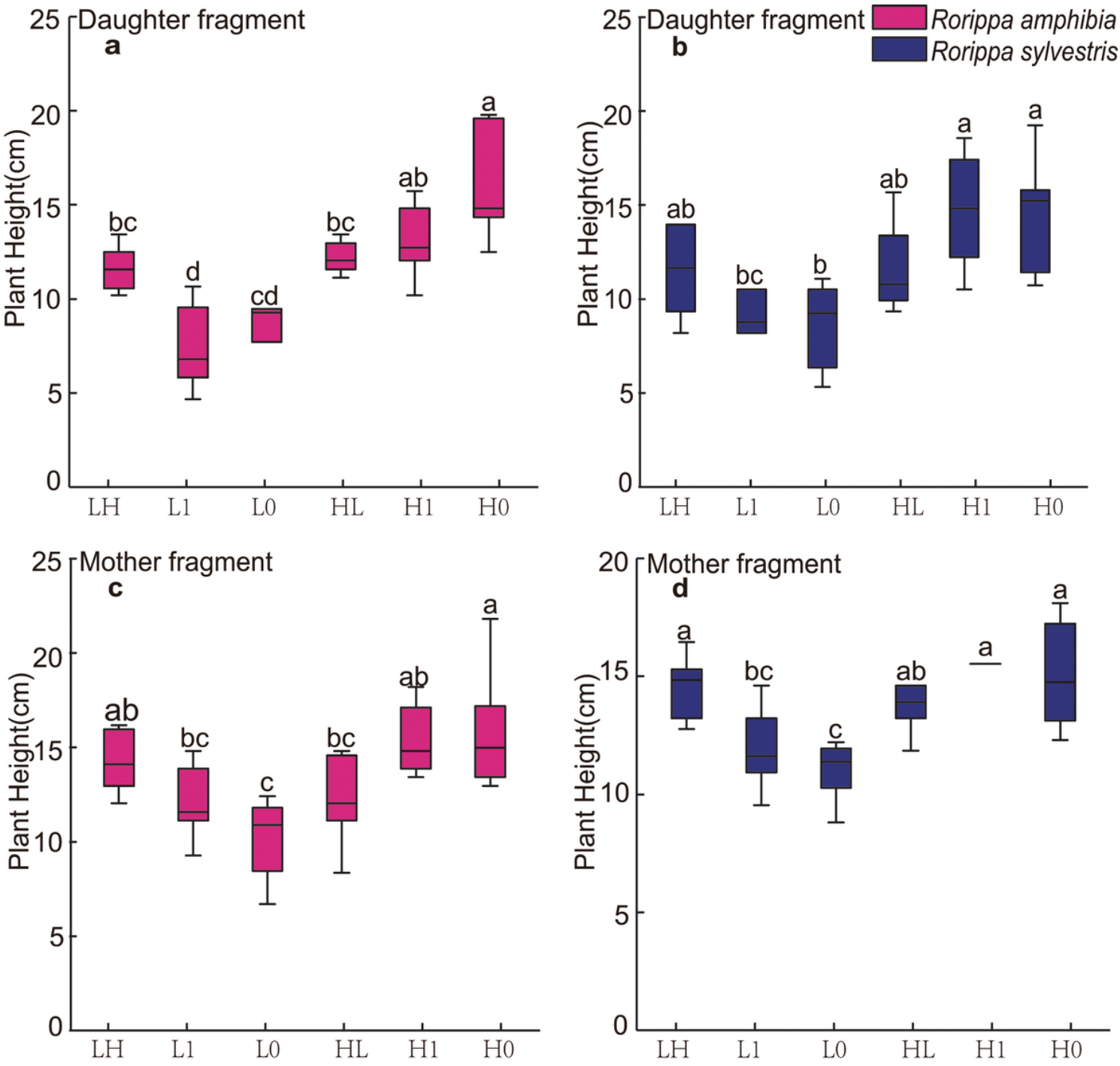

Figure 5

Comparison of the height of fragments in two plants under different levels of water availability. (a): daughter fragments of *R. amphibia*; (b): daughter fragments of *R. sylvestris*; (c): mother fragments of *R. amphibia*; and (d): mother fragments of *R. sylvestris.* Different lowercase letters indicate a significant difference between treatments ($P < 0.05$)