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ORIGINAL ARTICLE

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Habitat-specific responses of seed germination and seedling establishment to soil water condition in two *Rheum* species in the high Sino-Himalayas

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Abstract Knowledge of how germination and seedling establishment respond to soil water condition is crucial for plant conservation under global warming and land-use changes. We tested the flooding and drought tolerance of two plant species with different occurrences along a soil water gradient by assessing seed germination, seedling survival, seedling growth, and root characteristics. In the high Sino-Himalayas, *Rheum alexandrae* typically occurs in wetlands, *R. nobile* in scree or open slope with well-drained soils. Seeds and seedlings of the two species were subjected to different soil water conditions in controlled greenhouse experiments. Seed germination in both species was inhibited by high soil water content; however, seeds of *R. alexandrae* were more tolerant to flooding, especially to submergence. Seedling survival, biomass accumulation, root diameter, and root porosity of *R. alexandrae* increased significantly with increased soil water content, but submergence was lethal for seedlings. Seedling survival, biomass accumulation, and root length of *R. nobile* increased significantly in response to reduced soil water content. These results indicate that in the two species, seed germination and seedling establishment in response to different soil water condition are habitat-specific. Because both species are susceptible to moderate changes in soil water condition, their species-specific requirements with respect to this factor should be a consideration when planning their conservation.

Keywords Drought · Flooding · Stress tolerance · Seed germination · Seedling establishment

Introduction

Plant distribution and abundance may be determined largely by the seed germination and seedling establishment of a species (Harper 1977; Reader 1993; Kellogg et al. 2003). It is therefore critical to determine how seed germination and seedling establishment are controlled by environmental factors (Reader 1993). Soil water condition is one of the most important environmental factors determining seed germination and seedling establishment, and thus determining plant distribution (Otsus and Zobel 2004; Li et al. 2011; Wang et al. 2012). On one hand, flooding reduces oxygen availability and redox potential in the soil (Armstrong and Drew 2002; Van Eck et al. 2006; Iwanaga and Yamamoto 2008), limiting seed germination and seedling growth, and may even cause seedling death (Visser et al. 2000). Furthermore, nutrient uptake in flooding habitat is usually limited, resulting in restricted seedling growth (Luo et al. 2008). On the other hand, drought can affect the metabolism of many plants as a result of an increase in the production of superoxides or hydrogen peroxide (Hsiao and Xu 2000; Chaves et al. 2003; Taylor et al. 2004; Pagter et al. 2005), thus limiting the germination and establishment of plant species (Otsus and Zobel 2004; Wang et al. 2012).

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Generally, plants can resist fluctuation in soil water condition through a number of ways, including anatomical, morphological, or physiological responses. Through higher amylase activity and anaerobic respiration, seeds of flood-tolerant species are capable of germination under flooded conditions (Ismail et al. 2009), while seeds of drought-tolerant species can accumulate proline and soluble sugars to cope with drought stress (Li et al. 2013). Adjustment of root characteristics, such as diameter, length, and porosity, is one of the most important acclimations of seedling to fluctuating soil water condition (Sorrell et al. 2000; Colmer 2003). For example, plants growing in regular or permanently flooded soil develop unbranched roots with well-developed aerenchyma, while plants growing in drought-prone soil develop a deep root system with much branched adventitious roots (Visser et al. 2000). However, in plants, a trade-off usually exists between tolerance to flooding and tolerance to drought. Luo et al. (2008) found that plants with the highest tolerance to flooding had the lowest tolerance to drought and vice versa. Thus, changes in soil water condition inevitably influence the distribution and abundance of species dependent on their particular water requirements (Wang et al. 2012). Because global warming and land-use changes affect soil water condition, knowledge of how seed germination and seedling establishment relate to changes in soil water condition is vital in predicting local plant population dynamics and formulating species-specific conservation and management strategies (Froend and Mccomb 1994), especially for rare and endemic plants. Recently, many studies explored the effect of soil water condition on seed germination and seedling establishment, respectively (Casanova and Brock 2000; Visser et al. 2000; Luo et al. 2008; Leyer and Pross 2009; Richards and Cao 2012). However, there is little research quantifying the effect of soil water condition on seed germination and seedling establishment in a species simultaneously, even though the requirements for germination may differ from the requirements for seedling establishment in many plants (Deegan et al. 2007). Furthermore, the responses of seed germination and seedling establishment to soil water condition are inconsistent between different plant taxa (Webb et al. 2012).

Both *Rheum alexandrae* and *R. nobile* are rare perennial monocarpic herbs endemic to the high eastern Himalayas and are used in traditional Tibetan medicine (Byg et al. 2010; Song et al. 2013a). Even though they are related (Sun et al. 2012) and similar in many respects (e.g., morphology, life history; Song et al. unpublished), they have clearly different distributions, associated with the soil water condition. *R. alexandrae* is mainly found in alpine wetlands, including marsh, swampy meadows, and lake shores (Fig. S1a; Chen 1993), while *R. nobile*, the sympatric species, usually occurs on alpine scree and occasionally in the open patches of alpine meadow, i.e., in well-drained habitats (Fig. S1b; Song et al. 2013b). In this study, we aimed to examine how *R. alexandrae* and *R. nobile* respond to soil water conditions. Since the responses of plants to environmental conditions may vary depending on their habitats (Kudo and Hirao 2006; Necajeva and Levinsh 2008; Kudo et al. 2010; Engels et al. 2011), we hypothesized that the responses of seed germination and seedling establishment of the two species to soil water condition are habitat-specific, i.e., *R. alexandrae* is more tolerant to flooding than *R. nobile*, while *R. nobile* is more tolerant to drought than *R. alexandrae*. To test this hypothesis, we determined (1) the effect of soil water condition on seed germination and seedling establishment in the two species, and (2) seed germination and seedling survival of the two species after short-term submergence. Furthermore, in order to understand the specific mechanisms of seedling establishment, we determined the effect of soil water condition on root characteristics (length, diameter, and porosity) in the two species.

Materials and methods

Species description and seed collection

Both *Rheum nobile* and *R. alexandrae* are giant perennial herbs that are endemic to the eastern high Himalayas, growing at altitudes of 4,000 to 6,000 m a.s.l. (Li and Gao 1998; Chowdhery and Agrawala 2009). They reproduce exclusively from seed and flower between early June and early July after growing for 5–7 years and produce a stout conical compound raceme concealed by translucent bracts (Fig. S1), which persist until the seeds have ripened (Song et al. 2013a). Each plant produces up to 7,000 samara fruits and 800 samara fruits for *R. nobile* and *R. alexandrae*, respectively (Song et al. 2013a). Each fruit of these two species contains only one seed. The fruits mature between late August and late September, and seeds germinate between late May and early June.

Seeds of both species were collected in 2011, from Huluhai Lake (28°31′N–99°57′E, 4,450 m a.s.l.) and Yongjiongyi (28°24′N, 99°55′E, 4,490 m a.s.l.), in Shangri-la County, Yunnan Province, SW China. In each population, seeds were collected from at least ten individuals. The annual precipitation recorded from 1982 to 1984 at the nearest meteorological station (28°23′N, 99°01′E, 4,290 m a.s.l.) was 680–790 mm. The annual average air temperature was −1.0 °C (Wang 2006). In the laboratory, after being air-dried, collected seeds were kept under −20 °C for 1 month to break dormancy (Wang et al. 2010). Experiments were conducted in a greenhouse at the Kunming Institute of Botany, The Chinese Academy of Sciences (25°8′N and 102°44′E, 1,788 m a.s.l.). During the experiment, the temperature was kept at 25 ± 2 °C in the day and 15 ± 2 °C at night.

Seed germination

In order to test the effect of soil water condition on seed germination, 15 seeds of each species were sown in pots

(15 cm in diameter and 15 cm in height) containing a 1:1 mixture of sand and clay; there were 25 pots for each species. The pots of each species were randomly distributed in five groups and each group of both species was placed into a large container (80 cm in length, 60 cm in width, and 50 cm in height). Therefore, each container contained ten pots (five per species). Five soil water treatments were applied: 5, 0, −5, −10 cm, and drought. The former four treatments consisted of different water levels relative to the soil surface and were created by filling the containers with water at different depths; while the "drought" treatment meant that there was no water in the container. For the former four treatments, tap water was supplied daily to maintain the water level; for the drought treatment, pots were watered every fourth day. These treatments were intended to simulate different soil water conditions in the field. Emerged seedlings were counted every day until there was no increase in seedling number for 15 consecutive days.

In order to test the germination ability after short-term submergence, 200 seeds of each species were put in glass vials and submerged at a depth of 5 cm. Two weeks later, 75 ungerminated seeds of each species were selected randomly and transferred to pots exposed to similar drought treatment as above. There were 15 seeds in each pot and five replicates for each species. Emerged seedlings were counted every day until there was no increase in seedling number for 15 consecutive days.

At the end of each germination experiment, ungerminated seeds were evaluated for viability followed by Braga et al. (2003). Viable ungerminated seeds were regarded as dormant.

Seedling establishment and root characteristics

Twenty seeds of each species were germinated in each of 100 pots (15 cm in diameter and 15 cm in height) containing a 1:1 mixture of sand and clay; the emerging seedlings served for the experiments described below. Tap water was supplied daily according to the plants' growth. After 30 days, only six seedlings (of similar sizes, ca. 4 cm in height) were retained in each pot.

In order to test the effect of soil water condition on seedling establishment, we used again five soil water treatments: 5, 0, −5, −10 cm, and drought (as described for the seed germination experiment). Each treatment was replicated five times, and in total there were 25 pots (with six seedlings in each pot) for each species. Seedling survival was checked at 8 weeks after the start of the experiment. The surviving seedlings were harvested at the end of the experiment. Roots were cleaned with tap water, and the length and diameter of the main root were measured using a Vernier caliper and microscope with an ocular micrometer (Xie et al. 2005). The plants were then dried at 75 °C for 48 h and weighed.

In order to test seedling survival ability after short-term submergence, 32 pots (with six seedlings in each pot) of each species were submerged at a depth of 5 cm. Subsequently, four pots of each species were transferred to containers without water (i.e., drought condition) every day for evaluating survival.

In order to test the capacity of the lacunar system to deliver oxygen to below-ground tissues, the porosity of the main root was determined using the pycnometer method (Jensen et al. 1969; Van Noordwijk and Brouwer 1988). Fifteen pots (with six seedlings in each pot) of each species were distributed evenly amongst the five soil water treatments: 5, 0, −5, −10 cm, and drought (as described for the seed germination experiment). Eight weeks later, the main roots of plants from different treatments were cut into 2–3-mm segments and their porosity was determined using a 5-ml pycnometer. Each measurement was replicated three times.

Data analysis

In this study, individual pots are considered as the experimental units and, accordingly, the measured variables are averaged for each pot. For example, when considering biomass of seedlings with different soil water treatments, the measure for all plants in a given pot were averaged prior to analysis. For comparing differences in seed germination, seedling survival, biomass accumulation, and length, diameter and porosity of the main root, two-way ANOVA was used in which species and treatment were considered as fixed factors. When a significant interaction effect was detected between species and treatment, multiple-comparisons test was performed in each species. Tukey test ($p < 0.05$) was used for multiple comparisons among means. Data were $\log_{10}$-transformed or square root-arcsine-transformed if necessary to achieve variance homogeneity, and homogeneity was tested by using Levene's test. All statistical analyses were carried out with SPSS (18.0). Measurements are reported as means ± 1SE.

Results

Seed germination

At the end of each germination experiment, all ungerminated seeds of both species had rotted. Species type had no significant effect on seed germination ($F_{1,\ 48} = 0.06$, $p = 0.80$), but treatment did ($F_{5,\ 48} = 141.7$, $p < 0.001$), and there was significant interaction between these factors ($F_{5,\ 48} = 10.79$, $p < 0.001$). The highest seed germination of both species occurred in the drought and the −10-cm-soil-water treatments (Fig. 1): 80.0 ± 4.7 and 76.0 ± 4.5 %, respectively, for *R. alexandrae* and 94.7 ± 2.5 and 90.7 ± 4.0 % for *R. nobile*. Unlike *R. nobile*, for which no seeds germinated, 5.3 ± 3.9 % of the seeds of *R. alexandrae* germinated when submerged in 5 cm of water depth. When ungerminated seeds of *R. alexandrae* were transferred from

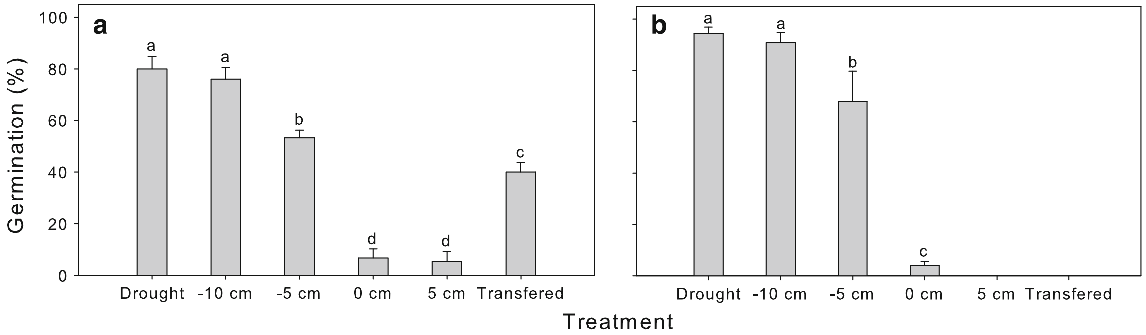

Fig. 1 Percentage seed germination (mean ± SE, $n = 5$) of *Rheum alexandrae* (**a**) and *R. nobile* (**b**) in the drought treatment (watered every fourth day), −10-, −5-, 0- and 5-cm water level relative to the soil surface, and when transferred to drought treatment after being submerged in water to a depth of 5 cm for 2 weeks. *Different letters* indicate significant differences between treatments at $p < 0.05$

the 5-cm water depth to the drought treatment, the percentage of germination (40 ± 3.65 %) was significantly higher than that in the 0 or 5 cm water treatments, but lower than in the other three treatments. However, no seeds germinated when ungerminated seeds of *R. nobile* were transferred from 5 cm water depth to the drought treatment (Fig. 1).

Seedling establishment

No seedlings of either species survived in the 5-cm soil water treatment at 8 weeks after the start of the experiment, so this treatment was excluded from subsequent analyses. Both species type ($F_{1,\ 32} = 1.24$, $p = 0.27$) and treatment ($F_{3,\ 32} = 0.09$, $p = 0.96$) had no significant effects on seedling survival, but there was significant interaction between these two factors ($F_{3,\ 32} = 30.27$, $p < 0.001$). Seedling survival for *R. alexandrae* was reduced significantly with the reduction in soil water content (Fig. 2): the percentage survival at water treatments of 0 cm (96.7 ± 3.3 %) and −5 cm (90.0 ± 6.7 %) were 2.9–2.7 times higher than in the drought treatment (33.3 ± 7.5 %). In contrast, seedling survival in *R. nobile* significantly increased with the reduction in soil water content (Fig. 2): the percentage survival in the drought treatment (100 %) was 2.7 times higher than in the 0-cm-water treatment (36.5 ± 9.6 %).

The ability of *R. alexandrae* seedlings to tolerate short-term submergence was greater than that of *R. nobile* (Fig. 3): 3 days after being submerged in water, 91.7 ± 4.8 % of the seedlings of *R. alexandrae* had survived, whereas the equivalent rate was close to zero (4.2 ± 4.2 %) for *R. nobile*. Furthermore, all seedlings of *R. alexandrae* died at 7 days after being submerged in water, while 4 days for *R. nobile*.

Species type had no significant effect on seedling growth ($F_{1,\ 32} = 0.17$, $p = 0.69$), but treatment did ($F_{3,\ 32} = 5.14$, $p < 0.01$), and there was significant interaction between these factors ($F_{3,\ 32} = 90.35$, $p < 0.001$). Growth of seedlings in *R. alexandrae* decreased significantly with the reduction in soil water content (Fig. 4): biomass of seedlings at 0-cm water treatment (38.1 ± 1.9 mg) was 2.0 times higher than in the drought treatment (19.0 ± 1.2 mg). The opposite result was found in *R. nobile*, for which biomass of seedlings

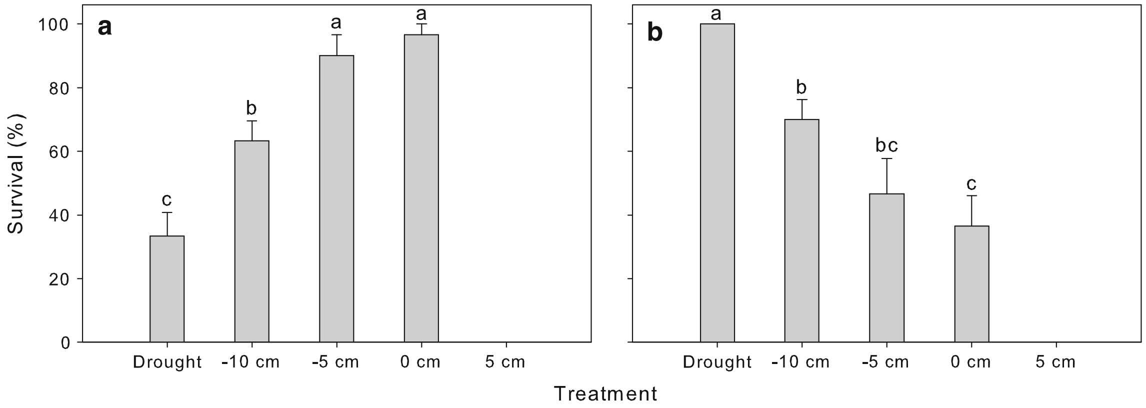

Fig. 2 Percentage survival (mean ± SE, $n = 5$) of *Rheum alexandrae* (**a**) and *R. nobile* (**b**) seedlings in the drought treatment (watered every fourth day) and −10-, −5-, 0-, and 5-cm water level relative to the soil surface. *Different letters* indicate significant differences between treatments at $p < 0.05$

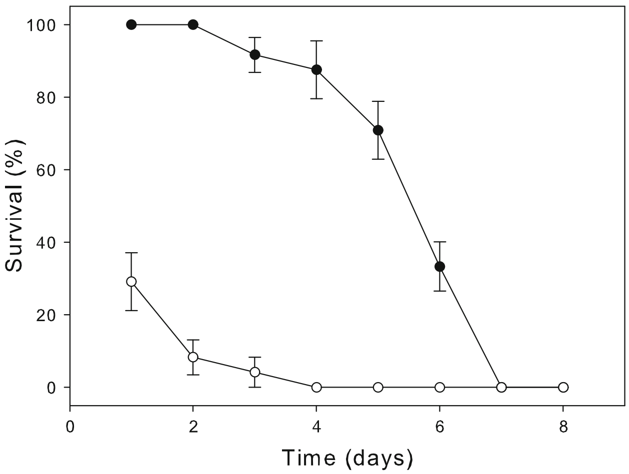

Fig. 3 Percentage survival (mean ± SE, $n = 4$) of *Rheum alexandrae* (*filled circle*) and *R. nobile* (*open circle*) seedlings submerged in water for different numbers of days

increased significantly with the reduction in soil water content (Fig. 4): biomass of seedlings in the drought treatment (42.2 ± 1.5 mg) was 2.7 times higher than in the 0 cm water treatment (15.9 ± 1.4 mg).

Root characteristics

Both, species type ($F_{1,\ 32} = 162.03$, $p < 0.001$) and treatment ($F_{3,\ 32} = 19.55$, $p < 0.001$) had significant effects on root length, and a significant interaction between these two factors was detected ($F_{3,\ 32} = 18.72$, $p < 0.001$). On average, the root length of *R. alexandrae* was 30.85 ± 0.86 mm, whereas for *R. nobile* it was 54.36 ± 3.53 mm. In *R. alexandrae*, no significant difference in root length was found between treatments (Fig. 5); but for *R. nobile*, root length increased significantly with the reduction in soil water content (Fig. 5): root length in the drought treatment (73.7 ± 3.6 mm) was 1.9 times higher than in the 0-cm water treatment (38.0 ± 3.5 mm).

Both species type ($F_{1,\ 32} = 55.3$, $p < 0.001$) and treatment ($F_{3,\ 32} = 31.07$, $p < 0.001$) had significant effects on root diameter, and a significant interaction between these two factors was detected ($F_{3,\ 32} = 36.37$, $p < 0.001$). On average, the root diameter of *R. alexandrae* was 1.03 ± 0.03 mm whereas for *R. nobile* it was 0.92 ± 0.01 mm. In *R. alexandrae*, root diameter increased significantly with increasing soil water content (Fig. 5): roots formed in the 0-cm water treatment had a greater diameter (1.26 ± 0.02 mm) than those in the drought treatment (0.87 ± 0.02 mm). In contrast, the diameter of the roots of *R. nobile* did not respond to soil water condition (Fig. 5).

As before, both, species type ($F_{1,\ 16} = 486.0$, $p < 0.001$) and treatment ($F_{3,\ 16} = 9.16$, $p = 0.001$) had significant effects on root porosity, and a significant interaction between these two factors was detected ($F_{3,\ 16} = 5.17$, $p < 0.05$). The porosity of the roots of *R. alexandrae* was 11.7 ± 0.5 % whereas for *R. nobile* it was 4.5 ± 0.2 %. In *R. alexandrae*, root porosity increased significantly with increasing soil water content (Fig. 5): the porosity of the roots increased from 10.1 ± 0.8 % (drought) to 13.9 ± 0.4 % (0 cm). However, there was no significant difference in the porosity of roots of *R. nobile* between the treatments (Fig. 5).

Discussion

Seed germination

Despite that it mainly grows in wetlands, *R. alexandrae*, like *R. nobile*, exhibited the highest germination rate in the treatment with low soil water content (corresponding to well-drained soil; Fig. 1), indicating that plant distribution patterns along specific environmental gradient

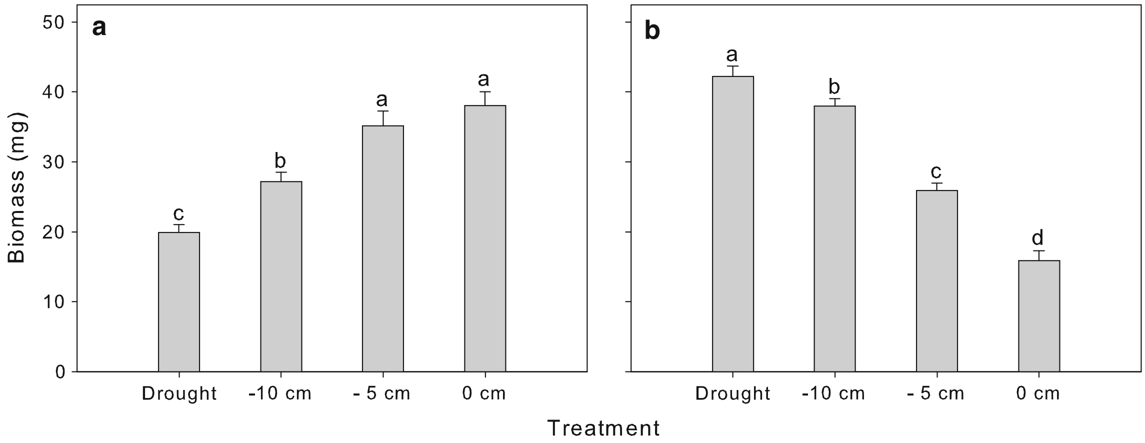

Fig. 4 Biomass (mean ± SE, $n = 5$) of *Rheum alexandrae* (**a**) and *R. nobile* (**b**) seedlings in the drought treatment (watered every fourth day) and −10-, −5-, and 0-cm water level relative to the soil surface after 8 weeks. *Different letters* indicate significant differences between treatments at $p < 0.05$

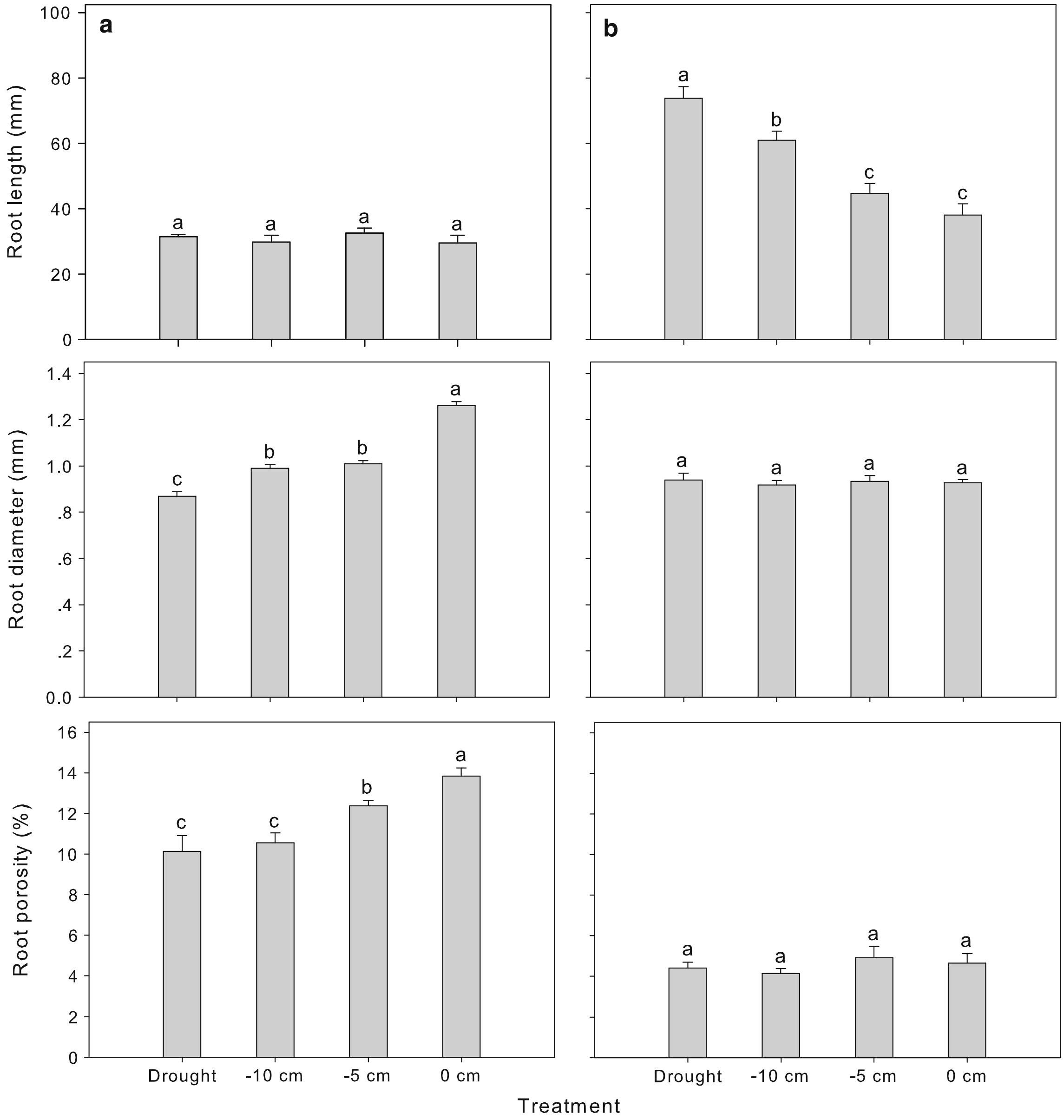

Fig. 5 Root length, root diameter, and root porosity (mean ± SE, $n = 5$, $n = 5$, $n = 3$) of *Rheum alexandrae* (**a**) and *R. nobile* (**b**) seedlings in the drought treatment (watered every fourth day) and −10-, −5-, and 0-cm water level relative to the soil surface. *Different letters* indicate significant differences between treatments at $p < 0.05$

cannot solely be explained by germination pattern. Similar results have been reported from other studies: germination of many wetland plants is inhibited by flooding (Ungar 1978; Galinato and Van der Valk 1986; McKee and Mendelssohn 1989; Crain et al. 2004; Engels et al. 2011), probably because the metabolism of seeds is inhibited by oxygen deficit in flooded soils during germination (Corbineau and Côme 1995; Bradford et al. 2007). The germination characteristic of *R. alexandrae* may be an adaptation to the soil water condition in its natural habitats during the time in the year when germination is occurring. Germination of *R. alexandrae* commences in late May, when the snow at higher elevations has not yet melted and the rainy season has not begun, so the natural water level at this time of the year is very low, especially in seasonal wetlands (Wang 2006; Wang et al. 2007). For example, in late May, the water level of Huluhai Lake, where many *R. alexandrae* plants grow, is almost 40 cm lower than in mid-June. Seeds of most wetland plants can regulate the timing of germination through controlling dormancy to avoid germination in unfavorable conditions (Britton and Brock 1994; Webb et al. 2012), and specific environmental conditions, such as fluctuating temperature or chilling, may function to trigger germination at the most propitious time (Meyer and Kitchen 1994). However, in our study, all ungerminated seeds for both species had no viability, indicating they are non-dormant. It therefore seems unlikely that low germination in flooding treatment was induced by dormancy.

Even though seed germination of both species was inhibited by flooding, *R. alexandrae* exhibited better germination in submerged condition and germination recovery was also better after short-term submergence than for *R. nobile* (Fig. 1), indicating that seed germination of *R. alexandrae* is more tolerant to flooding stress than *R. nobile*. This is consistent with results presented by Necajeva and Levinsh (2008) and Engels et al. (2011): the seeds of plants periodically exposed to a certain stress are more tolerant of the stress than those of plants less exposed to that stress. Consequently, the different abilities to tolerate flooding may explain, in part, why *R. alexandrae* is able to occur in wetland habitats, while *R. nobile* is not, since successful germination is the first requirement for plants to occupy a new site and develop a persistent population, especially species that rely entirely on seeds for regeneration (Ceccon et al. 2006; Song et al. 2013b). Unfortunately, we could not compare tolerance of seed germination to drought stress between *R. alexandrae* and *R. nobile*, since seed germination of *R. alexandrae*, like in *R. nobile*, was not inhibited by the applied drought stress (Fig. 1), probably because drought stress was not strong enough with watering every fourth day.

Seedling establishment and root characteristics

It can be argued that seedling survival and growth are the most important events following seed germination for the recruitment of new individuals to a population and in determining plant distribution (Fenner 1987; Ungar 1995). In this study, seedling survival and growth in *R. nobile* were reduced with increasing soil water content, which suggests that well-drained soils are best for early seedling survival and growth in this species. The result also suggests that *R. nobile* is tolerant to drought. Drought-tolerant plants possess special features to cope with a lack of water. For example, they develop longer roots (Luo et al. 2008), what we also found in the current study. Root length of *R. nobile* increased significantly when soil water content was low: long roots help plants to absorb water by enhancing the root–soil contact and allowing them to reach deeper soil layers (Luo et al. 2008). However, long roots are harmful to plants in flooded soil because more oxygen is consumed by large root systems (Justin and Armstrong 1987; Bell and Sultan 1999). Moreover, oxygen concentration is reduced with increasing soil depth (Norsworthy and Oliveira 2006). Thus, root characteristics of *R. nobile* that can be considered as an adaptation to drought stress necessarily result in its intolerance to flooding.

Response of *R. alexandrae* to increased soil water content exhibited inconsistent trend: the highest seedling survival and biomass accumulation occurred in waterlogging condition (−5 cm and 0 cm), but no seedling survived was found in submerged condition (5 cm). This is consistent with many studies on wetland plants (Webb et al. 2012). Our results indicate that young seedlings of *R. alexandrae* are very sensitive to flooding resulting from snow melt and heavy rain, a common occurrence in the summer in alpine wetlands (Deegan et al. 2007; Wang et al. 2007). Nevertheless, even though like in *R. nobile*, no seedlings survived in submerged condition by the end of the experiment, *R. alexandrae* was more tolerant to flooding than *R. nobile*, especially for the ability to tolerate short-term submergence. In flooding environment, oxygen deficit is the key factor limiting plant establishment. Plants growing in wetlands can alleviate anoxic stresses through morphological and physiological adjustments, such as shallow root systems (Blom 1999; Xie et al. 2008), increased root diameter (Visser et al. 2000), and well-developed aerenchyma (Laan and Blom 1990); our results indicate that the roots of *R. alexandrae* are characterized by such features. However, such characteristics, in combination with the non-responsive root length to reduced soil water content (Fig. 5), is not helpful for plants to absorb water in drought conditions (Fraser and Karnezis 2005; Luo et al. 2008), and thus make *R. alexandrae* sensitive to drought (lower seedling survival and growth in drought conditions), as is the case for other wetland plants (Lentz and Dunson 1998; Luo et al. 2008).

Conclusions

It can be concluded that the responses of *R. alexandrae* and *R. nobile* to soil water condition were habitat-specific: the species inhabiting wetlands is more tolerant to flooding stress than the species inhabiting well-drained habitats, while the species inhabiting well-drained habitats is more tolerant to drought stress than the species inhabiting wetland, which might be an important reason accounting for their different distribution in relation to soil water condition in the high Sino-Himalayas. Our results indicate that germination and seedling establishment of both species are susceptible to moderate changes in soil water condition. With increasing global warming and more human activities (agricultural production, mineral exploitation, and etc.), soil hydrological conditions have changed dramatically in alpine areas in recent years. For example, in the region around the source of the Yangtze River alone, wetland area has decreased by 29 % in the last 40 years (Wang et al. 2007). Consequently, creating appropriate hydrological conditions will be necessary in order to conserve both species, *R. alexandrae* in particular because the extent of wetlands is shrinking. The species-specific requirements with respect to soil water condition should be considered in conservation efforts of the two species.

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