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RESPONSE OF *AMORPHA FRUTICOSA* SEEDLINGS TO DROUGHT AND REWATERING IN ARID AND SEMI-ARID ENVIRONMENT

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Abstract

Amorpha fruticosa is widely planted in arid and semi-arid areas of northern China as the pioneer species for vegetation restoration. To determine the response of *A. fruticosa* to drought and rewatering, a greenhouse experiment was conducted maintaining desired soil water content following weighing method. Results showed that compensation effects occurred at different growth stages of *A. fruticosa* after rewatering, when the soil relative water content was ≥70%. Post-drought rewatering significantly triggered the compensatory improvement in plant height (19.49% and 7.23%), basal diameter (49.81% and 9.09%), leaf area (7.82% and 8.16%), root length (1.67% and 0.94%), root volume (10.86% and 11.67%) and dry matter content (26.32% and 12.29%) over control at initial and fast growth stages, respectively,under soil relative water content of 87.84%. Whereas, post-drought rewatering did not significantly affect the recovery of *A. fruticosa* at late growth stage, but 70% was the ideal soil relative water content for dry matter accumulation as compared to control. Thirty (30) days of drought at initial growth stage and 15 days of drought at fast and late growth stages were relatively ideal for biomass yield. The responses of seedlings to drought stress and rewatering suggest that it could significantly contribute to effective irrigation management of *A. fruticosa* in arid and semi-arid environment.

Key words: Drought stress, *Amorpha fruticosa*, Compensation effect, Root morphology, Growth stage.

Introduction

Water deficit is the most serious problem for plant growth and development in arid and semi-arid environment, where rainfall is the only source of soil water (Huxman *et al*., 2004). In these regions, drought has emerged as a persistent event in recent decades due to changes in climatic conditions (Yan *et al*., 2017), and severe drought stress have significantly reduced the growth and net biomass yield of different forest tree species in large-scale plantation (Breshears *et al*., 2009; Allen *et al*., 2010; Hicke & Zeppel, 2013). To solve this problem, controlled irrigation in arid and semi-arid regions has emerged as effective means for reducing agricultural water use (Ayana, 2011). Previous research results demonstrated that plants can adapt to environmental abiotic stress (Walter *et al*., 2011) by altering their morphology (Aubin-Horth & Renn, 2009). However, the effects of water stress are not the same for all species (Karkanis *et al*., 2011). Plants often minimize the impact of drought stress by adjusting the growth and development performance. For example, changes in plant height, leaf area, root characterization, biomass yield, photosynthetic performance, antioxidant enzyme activities and osmotic regulation (Li *et al*., 2008; Zhang *et al*., 2016). Chaves *et al*., (2003) indicated that shoot development showed more sensitivity to water stress than root development, and the mechanisms responsible for a sustained root growth under drought conditions include adjustment of osmotic pressure and enhancement in the loosening capacity of cell wall. Wu *et al*., (2011) also reported decreased plant growth and net biomass yield with reduction in precipitation amount. Mathobo *et al*., (2017) observed that drought stress caused significant reduction in dry biomass production of dry beans (*Phaseolus vulgaris*) in South Africa. Ahmad *et al*., (2007) also reported reduced dry biomass yield in wheat under water stress conditions.

In recent years, with the gradually increasing crisis of water and resultant frequent drought events, development of water-saving technologies in agroforestry has received great concern (Wang *et al*., 2016). The Loess Plateau in China is characterized by a dry climate and gullied topography that cause severe soil erosion (Zhang *et al*., 2008), which is a major challenge for environmental restoration for plant growth. For establishing sustainable vegetation and production in agroforestry, drought intensity and duration are considered the most critical ecological limiting factors. But rapid precipitation after a period of drought can alter soil moisture level, and even a little precipitation may increase plant growth and biomass yield in a desert ecosystem (Reynolds *et al*., 2004). Previous reports suggested that many plants can recover the effect of drought during rehydration (Gallé *et al*., 2007), and the recovery of plant growth and development after post-drought rewatering is a long and complex process (Chen *et al*., 2016). *Amorpha fruticosa* is commonly grown in the Loess Plateau as a pioneer species for vegetation restoration because of its strong adaptability to drought stress, fast growth, and rich fodder value. However, the ecological adaptability of *A. fruticosa* seedlings in these regions under soil drought and rewatering is not well understood at different growth stages. On this basis, the common deciduous shrub *A. fruticosa* was selected to evaluate the response of plant growth, morphology, root characterization and biomass accumulation to soil drying and rewatering conditions in the arid and semi-arid Loess Plateau for the irrigation management and rational utilization of the typical woody plant seedlings.

Materials and Methods

Materials and environmental conditions: The soil and one-year-old seedlings were collected from the Yangling District of Shaanxi Province in Northwest China. The soil water holding capacity was 22.3%. Collected soil was manually crushed, properly homogenized, air-dried and sieved to >5 mm for pot experiment. All pots were placed in a greenhouse under natural light condition in Northwest Agriculture & Forestry University, Shaanxi Province (34°16′N, 108°4′E). The average annual rainfall at the study site was 650 mm which mostly occurs between July and September. The mean day and night temperatures were between 27°C and -15°C, and relative humidity ranged from 35% to 70%.

Experimental design: The plant growing period after starting drought stress (6 months) was divided into three growth stages: initial growth stage (from mid-April to mid-June), fast growth stage (from mid-June to mid-August), and late growth stage (from mid-August to mid-October). Soil relative water contents at five levels, i.e., 100% (Control, 87.84%, 70%, 52.16%, and 40%, and four drought stress durations, i.e., 15, 30, 45, and 60 days were applied during each growth stage of *A. fruticosa*. The used soil moisture contents were determined in accordance with the D-optimum designs of Kiefer *et al*., (1959). Pots were prepared in three batches to determine the response to soil drying and rewatering during the three growth stages.

Plant management: Each pot (32×27×30 cm) was filled with 10 kg of air-dried soil. Two seedlings of *A. fruticosa* were transplanted into each pot. Three replicates were maintained for each treatment and pots were arranged following the randomized complete block design. The surfaces of pots were covered with 1.2 kg of grits to prevent soil water evaporation. To induce seedling recovery from transplantation, sufficient water was provided to all pots for 1 month before starting the drought stress. All plants were grown for 6 months to investigate the impact of drought stress and rewatering at three growth stages. Moreover, 100% soil relative water content was maintained in all pots other than that wherein the period of drought stress was performed. To maintain the desired soil relative water content, all pots were weighed every day and added the lost amount of water.

Measurement: After six months of plant growth all the seedlings from each treatment were harvested, washed carefully, and separated into leaves, stems, and roots. Plant height and basal diameter of each plant was recorded. The leaf area of *A. fruticosa* was measured according to crisscross method (Liu *et al*., 2014). Root morphological parameters such as total length, surface, volume, and average diameter were scanned using the automated image analysis software package WinRHIZO 2013 (Regent Instruments Quebec, Canada). The stem, leaf, and root samples were oven-dried at 80°C (Xu *et al*., 2015) until the constant weight reached. Subsequently, the dry mass (leaves, stems, and roots) of each plant was recorded.

Statistical analysis: Statistical analysis of experimental data was conducted using Excel 2010 and SPSS 22.0. One-way ANOVA using least significant difference test (LSD) at 0.05 level was performed to check the significance of treatment effects for each parameter. All graphical work was conducted using OriginPro 8.5 software (Originlab Corporation, Northampton, MA, USA).

Results

Plant height and basal diameter: Fig. 1 presents the changes in plant height and basal diameter under rewatering after drought. Rewatering compensated plant height and basal diameter but did not totally eliminate the impact of drought on *A. fruticosa* growth (Fig. 1A and B). At initial and fast growth stages, plant height and basal diameter gradually decreased with the decrease in soil relative water content from 87.84% to 40%, whereas at late growth stage, they initially increased and then decreased. When soil relative water content was 87.84%, rewatering triggered evident compensation effects of drought on plant height and basal diameter at initial and fast growth stages compared with control plants. Particularly at initial growth stage after rewatering at 87.84% soil relative water content treatment, plant height and basal diameter increased by 19.49% and 49.81% as compared to the control plants, respectively. At fast growth stage after rewatering at 87.84% soil relative water content treatment, plant height and basal diameter increased by 7.23% and 9.09% as compared to the control plants, respectively. At late growth stage after rewatering, plant height and basal diameter did not recover to the control levels due to pre-drought effect (40% and 52.16% soil relative water content), and at 40% soil relative water content, the plant height and basal diameter decreased by 15.88% and 29.43%, respectively over control. In response to water stress duration, rewatering compensated plant height and basal diameter, and significant difference was not observed between treated and control plants at initial and fast growth stages (Fig. 1C and D). Contrarily, plant height and basal diameter significantly decreased at late growth stage (except in plant height for 15 days drought) and did not recover to the control level.

Leaf area: As illustrated in Fig. 2A, under drought stress and rewatering conditions, leaf area of *A. fruticosa* gradually decreased with the decrease in soil relative water content from 87.84% to 40%, whereas significant reduction in leaf area was observed at 40% and 52.16% soil relative water content treatments. Although rewatering did not completely eliminate the effects of drought stress on leaf area, 70% and 87.84% soil relative water contents triggered the compensation effects in leaf area after rewatering at initial and fast growth stages but not at late growth stage. In the treatment with 87.84% soil relative water content, in comparison to the control, leaf area had evident compensation effect at initial and fast growth stages after rewatering, and its values increased by 7.82% and 8.16%, respectively. Regarding the response to drought duration, rewatering did not effectively eliminate the effects of drought on the leaf area of *A. fruticosa* at all three growth stages, and leaf area did not recover to the control levels (Fig. 2B). Moreover, no significant difference was observed among all drought duration treatments at all three growth stages.

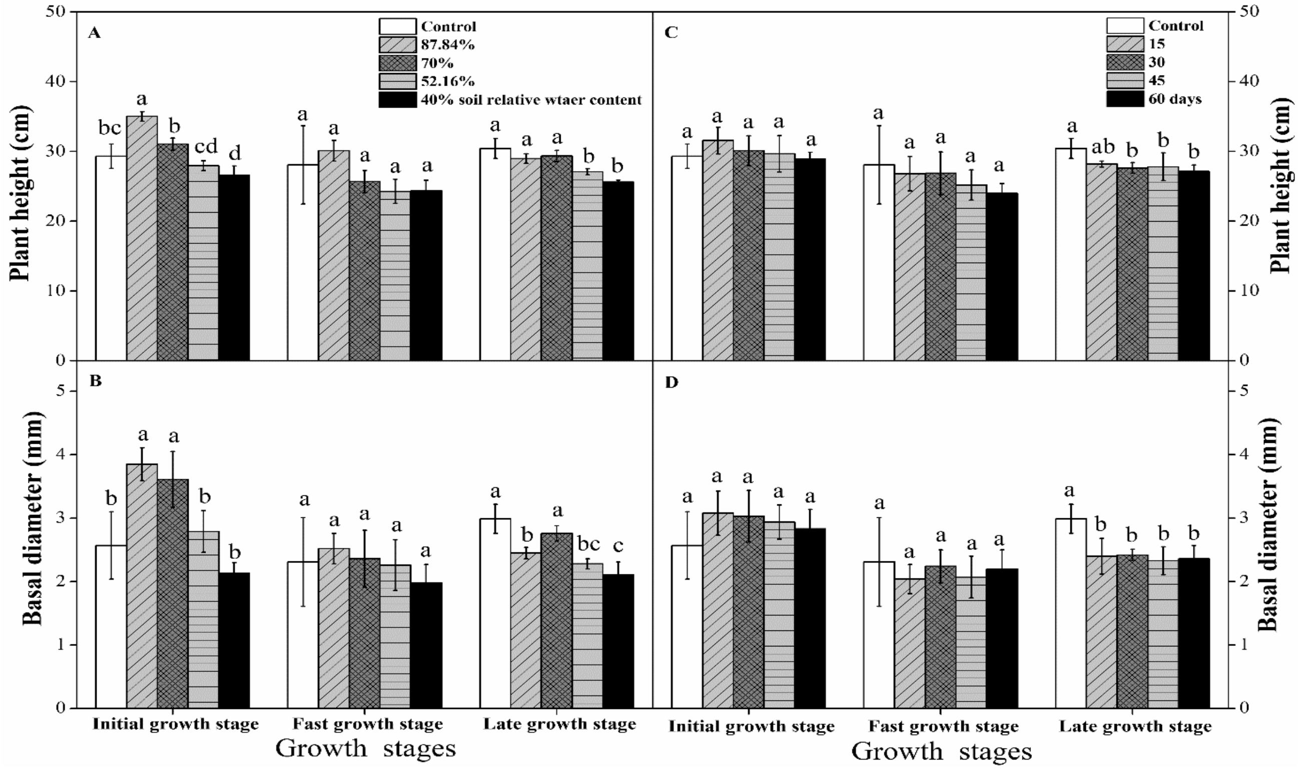

Fig. 1. Changes in mean plant height and mean basal diameter of *A. fruticosa* after rewatering under different soil moisture levels as relative water content (A and B) and drought durations as days) (C and D). Different letters refer significant differences among different soil relative water content treatments and drought duration treatments at 0.05 level.

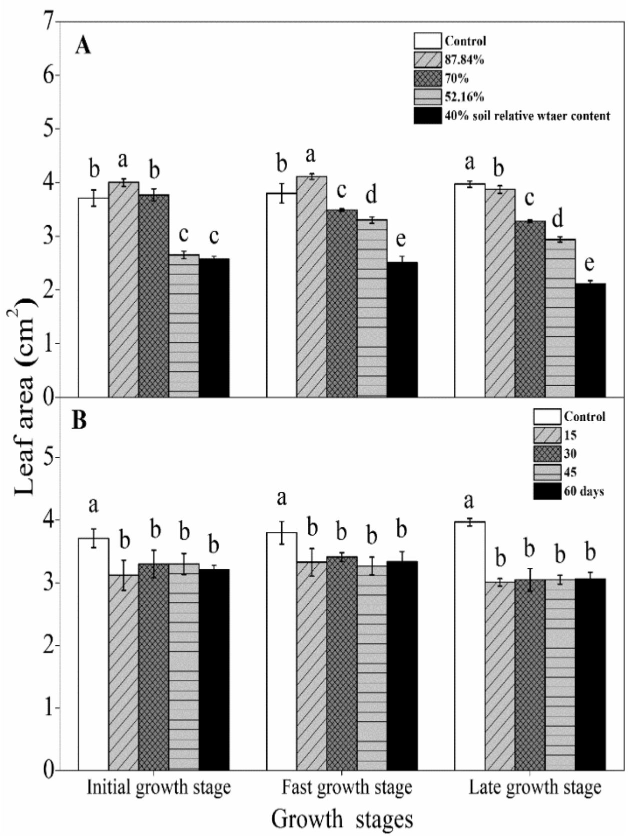

Fig. 2. Changes in mean leaf area of *A. fruticosa* after rewatering under different soil moisture levels as relative water content (A) and drought durations as days) (B). Different letters refer significant differences among different soil relative water content treatments and drought duration treatments at 0.05 level.

Root morphology: Fig. 3 shows the effects of rewatering after drought stress on root morphological characteristics. Rewatering after drought stress partially compensated the root length, surface area, and volume of *A. fruticosa* (Fig. 3A to D). When soil relative water content was ≥70%, compensation effects were found at initial and fast growth stages. After rewatering, treatments with 87.84% soil relative water content had the maximum values in root morphological parameters at initial and fast growth stages (except for root surface area at initial growth stage). At late growth stage, rewatering did not effectively induce compensation effects on root morphological parameters, compared with the control. But these parameters of *A. fruticosa* had no significant difference between the treatment with 70% soil relative water content and the control. Moreover, values of all the root morphological indexes of *A. fruticosa* were lower than those of the control levels after rewatering under 52.16% and 40% soil relative water content treatments at all three growth stages. In terms of root average diameter, no significant difference was recorded between treated and control plants (except for 40% soil relative water content treatment at fast growth stage). In response to drought duration, after rewatering, root morphological parameters were the same between drought stress and control treatments at initial and fast growth stages (except for root surface area at fast growth stage). At late growth stage, root length and root surface area had significant differences between drought stress and control treatments (except for root length with 45 days drought), whereas root volume and root average diameter had no significant differences between drought stress and control treatments after rewatering. Under post-drought rewatering conditions, root morphological parameters did not fully recover to the control levels at all three growth stages (Fig. 3E to H).

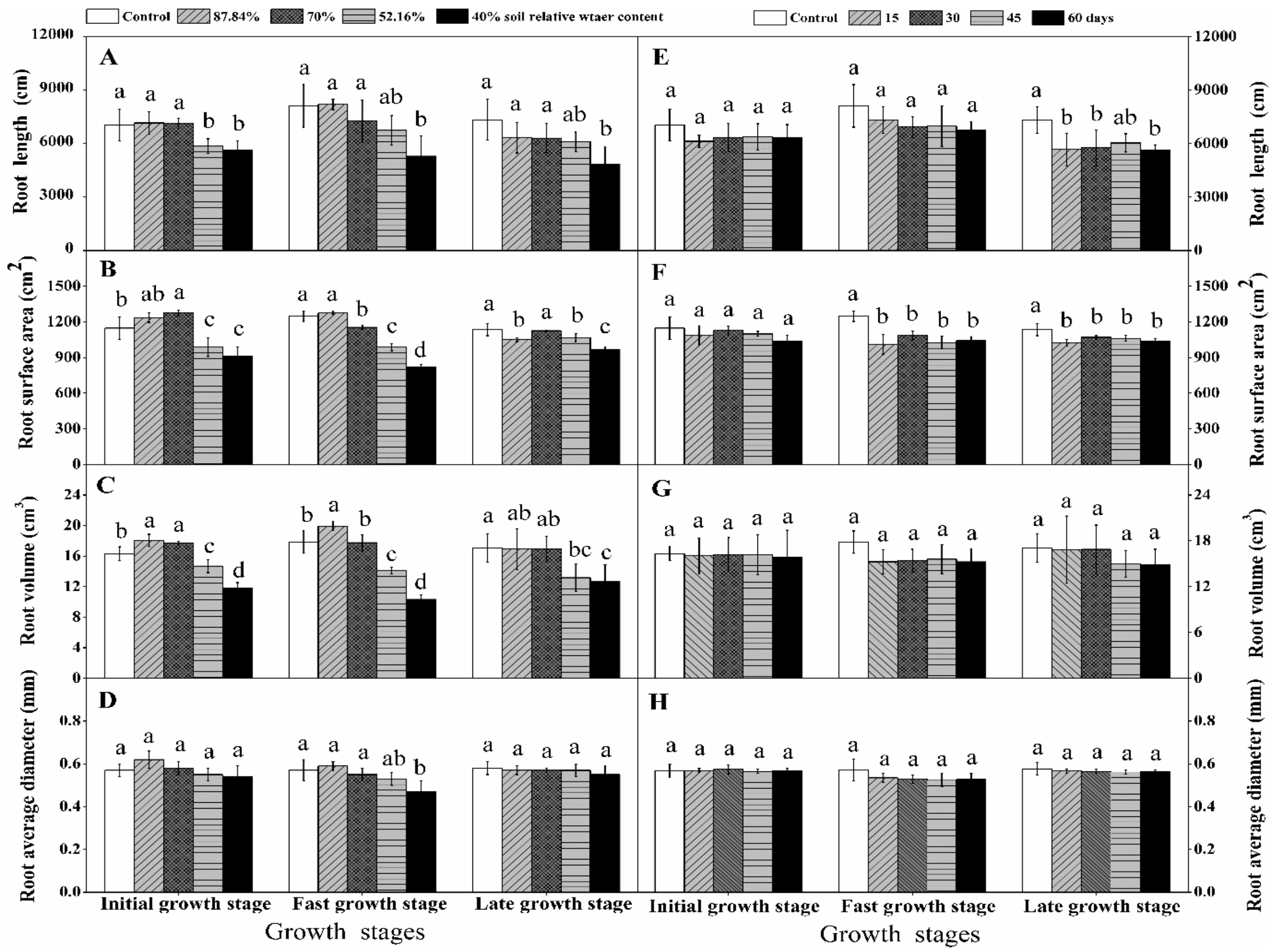

Fig. 3. Changes in mean root morphological parameters of *A. fruticosa* after rewatering under different soil moisture levels as relative water content (A, B, C, and D) and drought durations as days) (E, F, G, and H). Different letters refer significant differences among different soil relative water content treatments and drought duration treatments at 0.05 level.

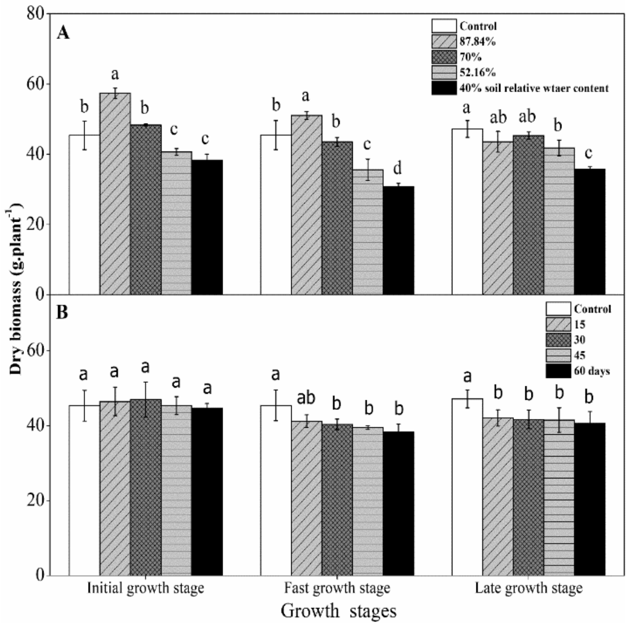

Fig. 4. Changes in mean dry matter accumulation of *A. fruticosa* after rewatering under different soil moisture levels as relative water content (A) and drought durations as days) (B). Different letters refer significant differences among different soil relative water content treatments and drought duration treatments at 0.05 level.

Dry matter: As summarized in Fig. 4, post-drought rewatering compensated the dry matter of *A. fruticosa*. Results indicated that rewatering partially eliminated the effect of water stress on the dry matter content of *A. fruticosa* at inital, fast, and late growth stages (Fig. 4A). Dry biomass yield under drought stress and rewatering conditions was compensated in the following order: initial, fast, and late growth stages. In the treatments with 87.84% soil relative water content, plant dry matter increased by 26.32% at initial growth stage after rewatering as compared to control. Similarly, in treatment with 87.84% soil relative water content, significant compensation to dry matter content (12.29%) at fast growth stage was determined after rewatering than control. At late growth stage, dry matter was lower than that of control levels, but in the treatments with 70% and 87.84% soil relative water contents, dry matter had no significant difference compared with the control. Dry matter reduced by 3.98% with 70% soil relative water content treatment after rewatering. Drought stress (40% and 52.16% soil relative water content) significantly decreased the dry matter of *A. fruticosa* and did not recover to the control levels after rehydration. In response to drought duration, rewatering eliminated the influence of drought duration on production of dry matter at initial growth stage but not at fast growth stage (except for 15 days drought at fast growth stage) and late growth stage (Fig. 4B).

Discussion

Plant growth is a comprehensive manifestation of plant metabolic process in morphology, which is affected by many factors. Water deficit is one of the significant environmental factors that retards the plant growth and development process (Liao *et al*., 2012). Availability of soil water and rainfall have a great influence on plant growth parameters such as plant height, basal diameter, stem volume, number of leaves, and leaf area (Achten *et al*., 2010; February *et al*., 2013). Our experiment results showed that the compensatory growth of *A. fruticosa* was observed after rewatering at 70% and 87.84% soil relative water content treatments at initial and fast growth stages, respectively. In contrast, we did not observe a similar trend for the compensation effects of *A. fruticosa* in late growth stage under rewatering conditions. When soil relative water content was ≥70% at initial growth stage, post-drought rewatering increased the plant height, basal diameter, and leaf area of *A. fruticosa.* At fast growth stage, a similar response was observed under a soil relative water content ≥87.84%. For the two lowest soil water contents (52.16% and 40% soil relative water contents), post-drought rewatering did not effectively eliminate the impact of water stress on three traits (plant height, basal diameter, and leaf area) of *A. fruticosa* at the three growth stages. Compensatory growth did not occur probably due to drought effects. Wang *et al*., (2018) observed a significant increase in seedling height in the plots with increased precipitation than in the control (ambient precipitation) plants. Similar results were obtained by Bunker and Carson (2005), who reported increased seedling height with water addition during the dry season. In consistent with this view, plants always reduced their leaf area to minimize drought effect (Li *et al*., 2008). In agreement, drought stress treatment significantly decreased the leaf area of *Quercus variabilis* and *Quercus mongolica* seedlings (Xu *et al*., 2015). Similarly, our findings were in accordance with the results of Han *et al*., (2015), who reported that leaf area was significantly reduced under drought stress treatment.

Root system is closely related to plant drought resistance. Plant roots are critical to plant growth as they play a vital role in water uptake, storage of organic substance, and absorption of inorganic nutrient (Wang *et al*., 2016). Root is the first part of the plant to experience changes under soil water stress because they are embedded in the soil. Plants can change their morphological characteristics under soil water availability (Padilla *et al*., 2007). For instance, plants can alter their root morphology to adapt with the changes in external environmental conditions (Valladares *et al*., 2007). Han *et al*., (2015) revealed that seminal roots undergo compensatory growth during rewatering. In the present experiment, results showed that rewatering triggered the compensation effects of water stress on the root morphology of *A. fruticosa* under a soil moisture content of not lower than 70% soil relative water content at initial and fast growth stage. Our findings agreed with the results of Xu *et al*., (2015), who suggested that the root volumes of *Q. variabilis* and *Q. mongolica* seedlings were significantly decreased under drought stress and smaller than those of well-watered (80% ± 10% field capacity) plants.

Seedling biomass is the best index for the productivity of forest ecosystems. In general, drought stress is the primary constraint to plant growth and productivity (Jain *et al*., 2013). Water stress significantly decreased the production of dry biomass of young Brazil nut (*Bertholletia excelsa*) (Schimpl *et al*., 2019). In this study, post-drought rewatering did not fully eliminate the effects of the two lowest soil water contents (40% and 52.16% soil relative water contents) on the dry matter production of *A. fruticosa* at all three growth stages. However, we found that upon post-drought, rewatering triggered the compensation impact of drought stress on the biomass accumulation of *A. fruticosa* at initial and fast growth stages under soil moisture of ≥ 70% relative water content. Then, significant compensation effects did not occur at late growth stage after post-drought rewatering, which may depend on the intensity of soil drought. Similar results were obtained on the leguminous shrub *Bauhinia faberi* var. *microphylla* (Li *et al*., 2008), *Zea mays* (Wang *et al*., 2016), *Cinnamomum burmannii* seedlings (Wang *et al*., 2018) and *B. excelsa* (Schimpl *et al*., 2019). In case of the drought duration for the dry matter production of *A. fruticosa*, rewatering eliminated the effects of water stress duration on biomass production at initial growth stage, and 30 days drought was suited for biomass accumulation. At fast growth stage, 15 days drought was ideal for biomass accumulation. A similar trend was observed at late growth stage, i.e., 15 days drought was relatively ideal for biomass accumulation.

Conclusion

Post-drought rewatering triggered the growth, root morphology, and dry matter production of *A. fruticosa* seedlings under soil relative water content of ≥ 70% at initial and fast growth stages, and the values of all parameters almost recovered to the control levels. In contrast, significant compensation effects did not occur at late growth stage of *A. fruticosa* after rewatering. From water saving point of view, 70% soil relative water content followed by rewatering was the relative optimum soil moisture used for *A. fruticosa* growth and development. Post-drought rewatering did not effectively eliminate the effects of the two lowest soil moisture contents (40% and 52.16% soil relative water contents) on the performance of *A. fruticosa* seedlings. Furthermore, 30 days drought at initial growth stage IGS and 15d days drought at fast and late growth stages were relatively ideal for the biomass accumulation of *A. fruticosa* in the arid and semi-arid environment of Northern China.

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