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Deepening Rooting Depths Improve Plant Water and Carbon Status of a Xeric Tree during Summer Drought

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Abstract: Exploring the effects of drought on trees of different sizes is an important research topic because the size-dependent mortality pattern of the major dominant species significantly affects the structure and function of plant communities. Here we studied the physiological performance and non-structural carbohydrates (NSCs) dynamics of a small xeric tree species, *Haloxylon ammodendron* (C.A.Mey.) of different tree size with varying rooting depth, during summer drought. We measured predawn (Ψ_{pd}) and midday (Ψ_m) leaf water potential, osmotic potential at saturated turgor (π_{100}), and turgor lost point (Ψ_{tlp}), stomatal conductance (g_s) at noon, maximum photochemical efficiency of photosystem II (Fv/Fm) in the morning, and NSCs concentration, from June–September. Our results demonstrated that the summer drought reduces the overall performance of physiological traits of the small young trees more than the larger adult trees. Ψ_{pd}, g_s and Fv/Fm dropped larger in the small-diameter groups than the larger diameter groups. Substantial osmotic adjustments were observed in small size individuals (with lower π_{100} and Ψ_{tlp}) to cope with summer drought. Furthermore, mean concentration of NSCs for the leaf and shoot were higher in September than in July in every basal stem diameter classes suggested the leaf and shoot acted as reserve for NSC. However the root NSCs concentrations within each basal stem diameter class exhibited less increase in September than in the July. At the same time, the small young tress had lower root NSCs concentrations than the larger adult tree in both July and September. The contrasting root NSC concentrations across the basal stem diameter classes indicated that the roots of smaller trees may be more vulnerable to carbon starvation under non-lethal summer drought. The significant positive relationship between rooting depth and physiological traits & root NSCs concentration emphasize the importance of rooting depth in determining the seasonal variation of water status, gas exchange and NSCs.

Keywords: drought; tree size; leaf water potential; root depth; non-structural carbohydrates

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1. Introduction

Climate change has increased the frequency and severity of drought over global terrestrial ecosystems [1]. Drought-induced tree deaths have been reported in various forest ecosystems [2–4]. The size-dependent mortality pattern is an important aspect of plant population dynamics and has important influence on the structure and composition of forest, which can be very sensitive to climatic change [5]. The size related contrasting physiological response to drought and their hydraulic traits performance may explain the frequently observed size-dependent mortality pattern [6,7], which make the interactions between drought and tree ontogenetic composition and remains a research field previously studied [8,9]. However, most of the research on the plant physiological response to climate and drought focus on different trees species, and quantitative data about the response of same tree with different size groups was relatively insufficient [10].

As trees grow up, their size and structural complexity increase [11], trees with contrasting size may response differently to external environmental change [12,13], finally inducing different physiological responses to variation in resource availability [10]. Commonly, the competition for above-ground resource is robustly size-asymmetric. For instance, light resource is supplied from top to bottom for tree growth and forestalled by larger trees [14,15]. However, the competition for underground resource is usually considered to be size-symmetric [5,16]. Under these circumstances, the quantity of available resources enhances proportionally with individual dimension [10], which means that biomass allocation changed with tree dimension may have a fundamental impact on size-dependent tree mortality patterns. Therefore, the belowground biomass allocation and thus the dimensions of the root systems were the key in determining the scope of the resource that plants foraging and thus the species competitive advantage [17,18].

In a water deficient habitat, the sizes and shapes of plants root systems are determinate factor on the availability of water to individual plants [19–21]. Widespread root systems with a large surface area allows extraction of water from a larger soil volume, thus facilitating greater soil water uptake and deeper roots permit plants to switch water capture to deeper layers during drought and avoid hydraulic failure [22–24]. Species often have dual or dimorphic root systems with upper lateral roots that make use of small rainfall events that penetrate into limited soil depths, and deep roots that exploit deep water sources [25]. However, dual root systems develop fully only after the plants grow up, and seedlings usually have incomplete lateral root development from xeric habitats [25,26]. Therefore, for the xerophytes, rooting depth plays a critical role for the seedlings to survive the drought [24].

Haloxylon ammodendron (C.A.Mey.) is a sub-tree xerophilous plant, which is widely distributed in desert regions of central Asia with average annual rainfall between 30 and 200 mm [27]. At the Southern fringe of the Gurbantonggut desert, *H. ammodendron* trees were naturally growing as a dominant species in the inter sand-dune lowland. This hinter-land is a representative cold desert in central Asian desert regions with stable snow cover in winter, rather occasional and disconnected precipitation in summer [28]. From March—May, the soil moisture was relatively high owing to snowmelt, but soil moisture is quickly exhausted due to the high vapor pressure deficit and temperature [29]. As a result, vegetation in this desert often suffers water deficits in summer, and the herbaceous layer flourishes only in the spring.

For this xeric tree species, the drought-resistance strategy is to give priority to underground biomass allocation in order to promote water exploring. For the seedling and juvenile, the drought-resistance strategy is not fully developed, and hydraulic failure is the main cause of plant death during lethal drought. For the larger and older trees, too much belowground investment (for the water capture) at the cost of leaf area may cause carbon starvation during extended drought [30]. For the desert xerophytic tree species, all these may be attributed to the rooting depth. Based on this hypothesis, the aim of the current study was to investigate the physiological performance and non-structural carbohydrates (NSCs) dynamics of different rooting depth groups of this small xeric tree during the growing season. Here we address how summer drought affect the physiological traits and NSCs of *H. ammodendron* and relate the physiological traits and NSCs to rooting depth in a field experiment. Specifically, our aims were to test the hypothesis that deepening root depth not only improve plant water status, but also help maintain better NSCs status during summer drought.

2. Materials and Methods

2.1. Plant Material and Experimental Design

Our research work was carried out at the Fukang Station of Desert Ecology, Chinese Academy of Sciences (44°17′ N, 87°56′ E, 475 m asl), which was located at the Southern fringe of the Gurbantonggut Desert. The study area is a typical continental arid temperate climate. The minimum air temperature in winter is −42.2 °C and the maximum air temperature in summer is 44.2 °C. Annual mean precipitation is between 70 and 180 mm, of which 25% is snowfall. The annual pan evaporation is much higher than its annual precipitation [31]. An automatic weather station installed in 2005 near our study area was used to obtain meteorological data (Campbell Scientific, Logan, UT, USA). For the physiological traits performance during growing season (June–September), we conducted a field experiment in 2014. According to our field survey, *H. ammodendron* population was divided into five rooting depth groups depending on basal stem diameter. Five individual trees of each diameter group were selected and marked with labels. The height, crown width, and basal stem diameter of *H. ammodendron* were recorded with diameter tape and tapeline. Crown width was the average of the major and minor axis length of each respective crown. The rooting depth of every tree was estimated based on the relationship between aboveground stem diameter and previous excavation-measured rooting depth [30]. The basic information of the studied tree was shown in Table 1.

Table 1. Basic information of the measured trees for each diameter class. Data are mean ± 1 SE.

Diameter Class (cm)	Basal Stem Diameter (cm)	Rooting Depth (m)	Height (m)	Crown Width (m)
0–1	0.82 ± 0.10	1.65 ± 0.10	0.45 ± 0.08	0.26 ± 0.03
1–2	1.60 ± 0.09	2.64 ± 0.12	0.64 ± 0.04	0.55 ± 0.07
2–4	2.97 ± 0.26	4.68 ± 0.38	1.12 ± 0.09	0.97 ± 0.12
4–8	5.59 ± 0.39	6.82 ± 0.15	1.46 ± 0.31	1.65 ± 0.21
>8	12.12 ± 1.04	7.29 ± 0.00	1.94 ± 0.25	2.23 ± 0.28

2.2. Determination of Water Potential

The predawn ($\Psi_{pd)}$ and midday (Ψ_m) leaf water potential determination were carried out during the middle of each month from June—September. On each experimental day, two leaves per tree from the marked 25 trees were cut for Ψ_{pd} and Ψ_m measurement respectively. In total, 50 leaves were used to measure Ψ_{pd} and Ψ_m on each experimental day. Hence there were five replicates per rooting depth group. The leaf water potential was determined with a Model 1000 pressure chamber (PMS Instrument Co., Albany, NY, US). Details on this procedure are described in Xu et al. 2016 [30].

2.3. Maximum Photochemical Efficiency and Gas Exchange

Chlorophyll fluorescence emission was determined on the health leaves with 5 replicates in each rooting depth group before the sun rose (in the early morning, 05:00–05:30 h, local time), using a portable plant efficiency analyzer (Pocket PEA, Hansatech, King's Lynn, UK). After 20 min of dark adaptation by using leaf chips, the value of maximum photochemical efficiency of photosystem II (Fv/Fm) was measured. For most plants, the near optimal values of Fv/Fm were between 0.79 and 0.84. Under drought stress, the values of Fv/Fm decreases for many plants [32,33]. Stomatal conductance was measured with five repetitions within each rooting depth group on leaves from selected trees between 08:00 and 10:00 h local time with a leaf porometer on clear days (Model SC-1, Decagon).

2.4. Water Relation Parameters

The leaf water relations of the 5 rooting depth groups of *H. ammodendron* were determined by pressure-volume (PV) curves. PV curve parameters were determined on the marked 5 trees of every group at the end of July and at the beginning of the August. Also, 6–8 PV curves were done in each rooting depth group by using the bench drying method [34,35]. The leaves were scissored at pre-dawn

(04:00–05:00 h), recut and next rehydrated in 100 mL centrifuge tubes filled with deionized water for at least 4 h, with only the green leaves come out of the water. Following rehydration, leaves were taken out from the tubes, and the water of the leaves surface was rapid removed with paper towel. The weight of the leaves was done before leaf water potential determined. Only the re-hydrated leaves that had a water potential greater than −0.5 MPa were used to make PV curves. The water potential and weight of the leaves were then determined repeatedly at different dry time. Detailed measurement of PV curves and calculation of osmotic potential at turgor loss point (Ψ_{tlp}), and full turgor (π_{100}) referred to the approach of Schulte and Hinckley [36].

2.5. Non-Structural Carbohydrates Concentrations

NSCs we determined include free, low molecular weight sugars (glucose, fructose and sucrose) and starch. To avoid the influence of phenological phase on NSC fluctuation such as the growths of leaves and shoots, we collected samples at the mid July and mid-September. Two groups of 25 trees with 5 plants at each basal stem diameters were marked. Sampling for NSC on lateral root (diameters of 1–10 mm), shoot and leaf were done on July 23th and 24th at the beginning of the drought period, and on September 22th and 23th after physiological measurement finished. About 20 g fresh sample of each organ in every tree were oven dried at 65 °C. The Detailed sample handling and determination process was described in Xu et al. 2016 [30]. The extraction of NSC referred to Anderegg and the literature they cited [37]. After digestion of sucrose and starch, the concentrations of the two ingredients were measured colorimetrically using the phenol–sulfuric acid method and a Cary 60 spectrophotometer Agilent (Cernusco, Milan, Italy).

2.6. Data Analysis and Statistics

The average values and standard errors of each data set were computed by descriptive statistical methods. The significance in difference among leaf water potential, maximum photochemical efficiency of photosystem II, stomatal conductance, turgor lost traits and NSCs concentrations for rooting depth groups was tested by using one-way analysis of variance (ANOVA). A sigmoidal model was established based on our previous research and was used to predict the rooting depth of current target species. Linear regression and sigmoidal model was adopted to fit the data between rooting depth and physiological traits and among physiological traits. Charting was processed using the software Origin 9.0 (Origin Lab Corp., Northampton, MA, USA). These data handling were conducted using statistical software SPSS 16.0 (SPSS Inc., Chicago, IL, USA).

3. Results

3.1. Summer Drought and Root Depth

Temperature and precipitation in 2014 were shown in Figure 1. Compare with annual mean precipitation 140.8 mm (averaged from 2005–2015), the annual precipitation was lower in 2014 (with the value of 113.1 mm). April and May were relatively wet, with the value of 31.7 mm and 21.6 mm respectively, equaled 74% and 123% of the 10 years average. July and August there only had 9.3 and 3.2 mm precipitation respectively, equaled 55% and 16% of the 10 years average (Figure 1), which implies a relatively dry summer. The logarithm equation between basal stem diameter and rooting depth was established based on our previous investigation [30] and was used to calculate the rooting depth of the measured trees (Figure 2). According to the calculation results, the rooting depth groups were 1.31–1.84 m, 2.3–3.00 m, 3.39–5.54 m, 6.3–7.11 m, 7.28–7.29 m. For convenience of presentation and discussion, we define the small young trees: With average rooting depth of 165 ± 0.10 m and 2.64 ± 0.12 m in the basal stem diameter classes of 0–1 cm and 1–2 cm respectively; intermediate-sized trees: With average rooting depth of 4.68 ± 0.38 m in the basal stem diameter class of 2–4 cm; and the large adult trees: With average rooting depth of 6.82 ± 0.15 m and 7.29 ± 0.00 m in the basal stem diameter classes of 4–8 cm and >8 cm, respectively.

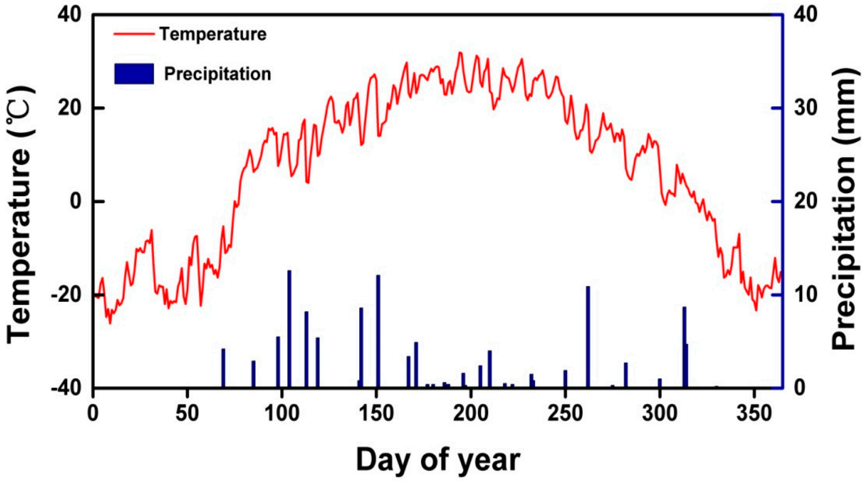

Figure 1. Daily precipitation (mm) and temperature (°C) of 2014.

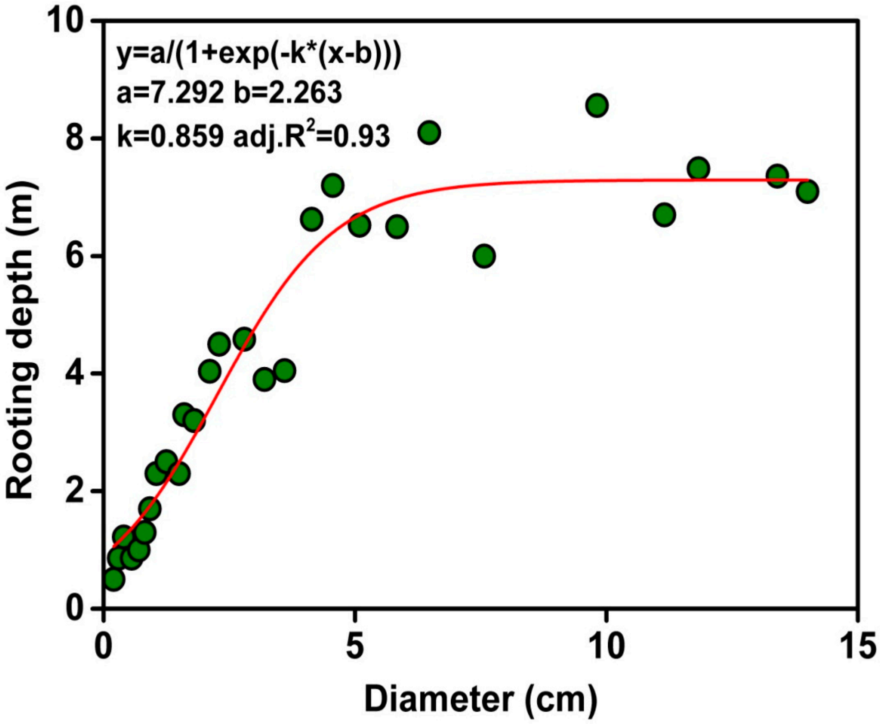

Figure 2. The relationship between rooting depth and basal stem diameter. Data were repotted from previous study by Xu et al. (2016). A sigmoildal model was used to fit the data.

3.2. Physiological Performance During the Growing Season

Physiological traits varied significantly during the period of our experiment (Figure 3). During the summer drought period, the predawn leaf water potential (Ψ_{pd}) get more negative as the drought progressed for all 5 rooting depth groups with different basal stem diameter range. For the shallowest rooting depth group in small young trees with diameter 0–1 cm, the predawn leaf water potential (Ψ_{pd}) dropped down larger (the fall was −2.87 MPa) than deepest rooting depth group in adult trees with diameter >8 cm (the fall was −1.90 MPa) indicated that small plants suffered a stronger water stress than adult trees in the summer (Figure 3a).

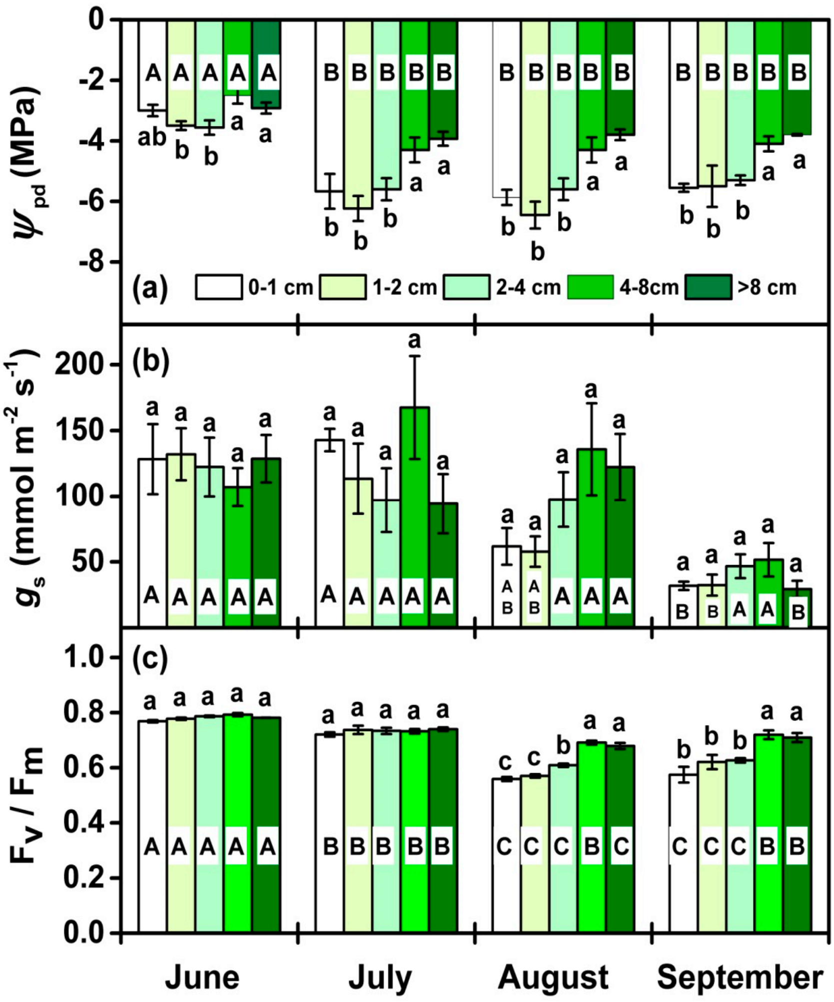

Figure 3. Predawn leaf water potential (Ψ_{pd}, **a**), stomatal conductance (g_s, **b**) and maximum photochemical efficiency (Fv/Fm, **c**) variation of *H. ammodendron* across basal stem diameter class during the growing season (means ± SE). The capital letter showed the significance difference of the same diameter groups across the growing season from June–September, and the lowercase letter showed the significance difference among the diameter groups at the same trial day (All *p*-values < 0.05). Data are mean ± 1 SE ($n = 5$).

The stomatal conductance at noon (g_s) showed greater variability for the same diameter class during the growing season and across the diameter class on the same trial days. For the small young trees in the diameter group of 0–1 cm and 1–2 cm showed down adjustment of stomatal conductance in August and September (Figure 3b). The maximum photochemical efficiency (Fv/Fm) dropped down in every basal stem diameter class as the drought progressed in July, August and September (Figure 3c). Fv/Fm dropped larger in the small diameter groups (the fall was 0.20 and 0.16 for 0–1 cm and 1–2 cm classes respectively) than the larger diameter groups (the fall was 0.07 and 0.10 on 4–8 cm and >8 cm diameter class respectively). The small young trees showed lower maximum photochemical efficiency than larger adult trees across diameter classes on the same trial day in August and September.

3.3. Relationship between Rooting Depth and Physiological Traits

Rooting depths were significant related to Ψ_{pd}, in August and September in which the highest Ψ_{pd} occurred in the deepest root depth at the largest basal stem diameter group (Figure 4a,b). The rooting depths were also close related to the maximum photochemical efficiency (Fv/Fm) in August and September with the lowest (Fv/Fm) in the shallowest rooting depth (Figure 4c,d). The PV curve parameters (Ψ_{TLP} and π_{100}) determined at the end of June and at the beginning of August were also closely related to rooting depth (Figure 4e,f). A tendency of increasing water potential at full turgor (π_{100}) along the increased basal stem diameter group was observed (Figure 4e); π_{100} ranged between −3.81 MPa and −2.90 MPa. Values of osmotic potential at the turgor loss point (Ψ_{TLP}) displayed an analogous trend (Figure 4f); Ψ_{TLP} ranged between −5.96 MPa and −4.35 MPa, as recorded in the diameter class of 0–1 cm and >8 cm respectively. The Ψ_{pd} were also closely related to Fv/Fm, Ψ_{TLP} and π_{100} in August and September (Figure 5). The correlations between stomatal conductance (g_s) and rooting depth, & Ψ_{pd} were most pronounced in August with the lowest g_s in the shallowest rooting depth (Figure 6).

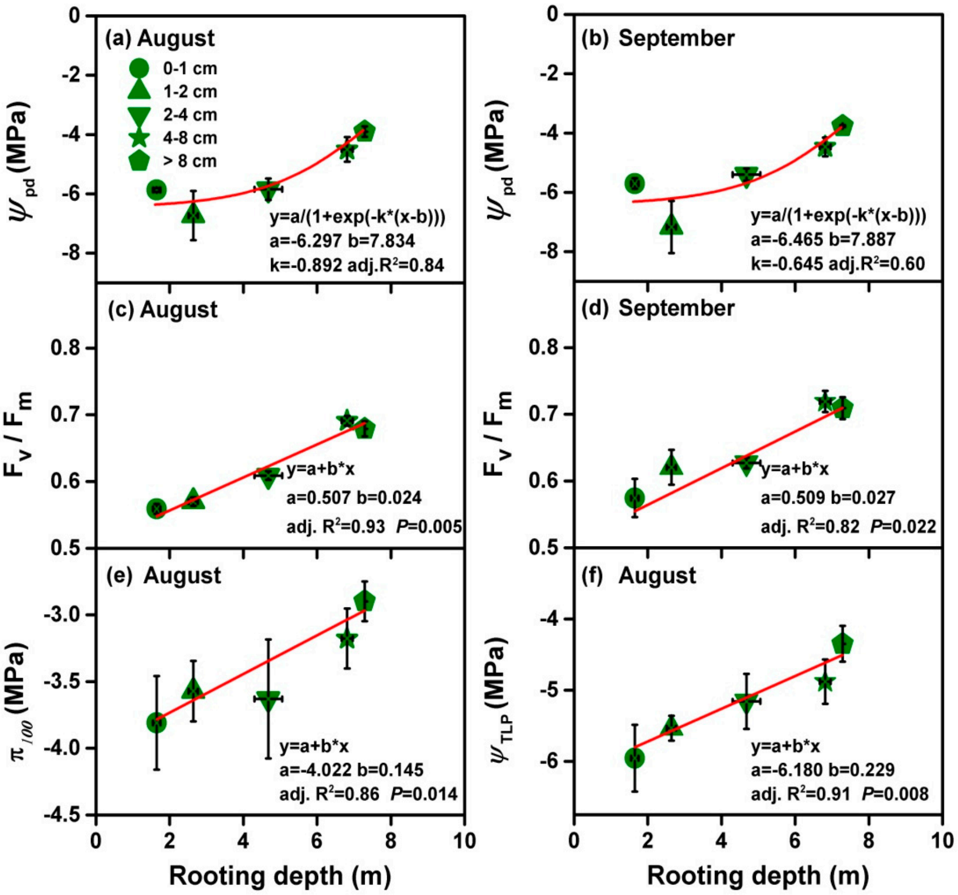

Figure 4. Predawn leaf water potential (Ψ_{pd}, **a**,**b**), the maximum photochemical efficiency of photosystem II (Fv/Fm, **c**,**d**), osmotic potential at full turgor (π_{100}, **e**) and osmotic potential at turgor lost point (Ψ_{TLP}, **f**) in relation to rooting depth. Data are mean ± 1 SE (n = 5).

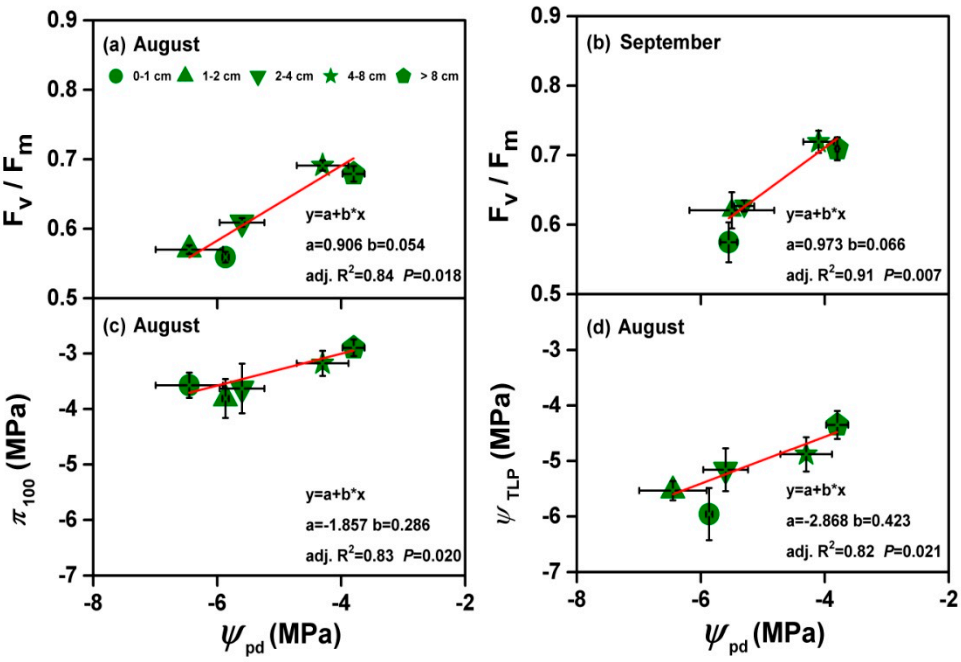

Figure 5. The maximum photochemical efficiency of photosystem II (Fv/Fm, **a**,**b**), osmotic potential at full turgor (π_{100}, **c**) and osmotic potential at turgor lost point (Ψ_{TLP}, **d**) in relation to predawn leaf water potential (Ψ_{pd}). Data are mean ± 1 SE (n = 5).

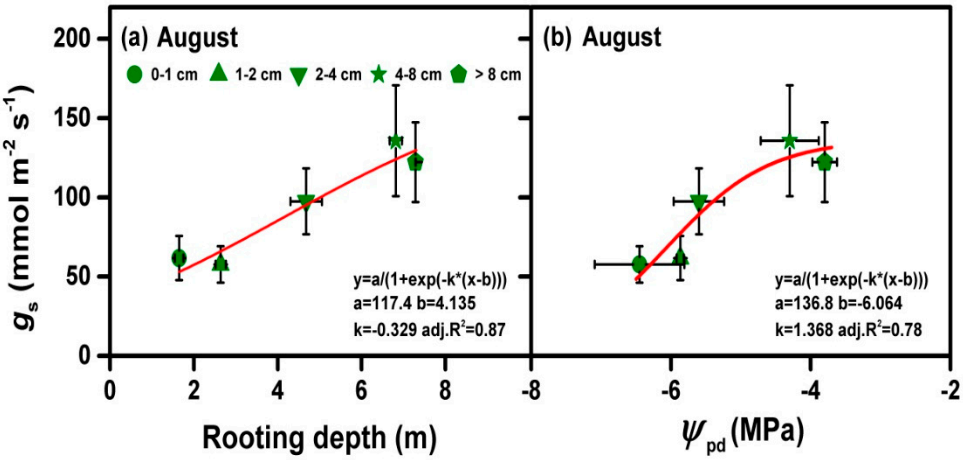

Figure 6. Stomatal conductance (g_s) in relation to rooting depth (**a**) and predawn leaf water potential (Ψ_{pd}, **b**). Data are presented as mean ± 1 SE (n = 5).

3.4. Non-Structural Carbohydrates Variation

Sugar is the major ingredient of NSCs in all organ types for each of the five rooting depth groups during the two sampling periods. NSCs concentrations were highest in foliage and then in roots, lowest in the shoot in July, but the lowest NSC concentrations were in the root in September (Figure 7). Root NSC between July and September within each rooting depth group (represented by basal stem diameter class) showed no significant differences (Figure 7a). However, the root NSC showed significant variation across the rooting depth groups. The small young trees in shallower rooting groups had lower total NSCs in roots than the larger adult trees in deeper rooting depth (Figure 7a). The lowest mean root NSC was found in the second shallowest rooting depth group with the value of 3.11 ± 0.17% and the highest mean root NSC was found in the deepest rooting depth group with the value of 9.14 ± 1.17%. The shoot and leaf NSC were significantly higher in September than July within every rooting depth groups (Figure 7b,c). The shoot and leaf NSC were lower in small young trees comparing with larger adult trees across the rooting depth group but only in July and no significant difference among leaf and shoot NSC across the rooting depth group in September (Figure 7b,c).

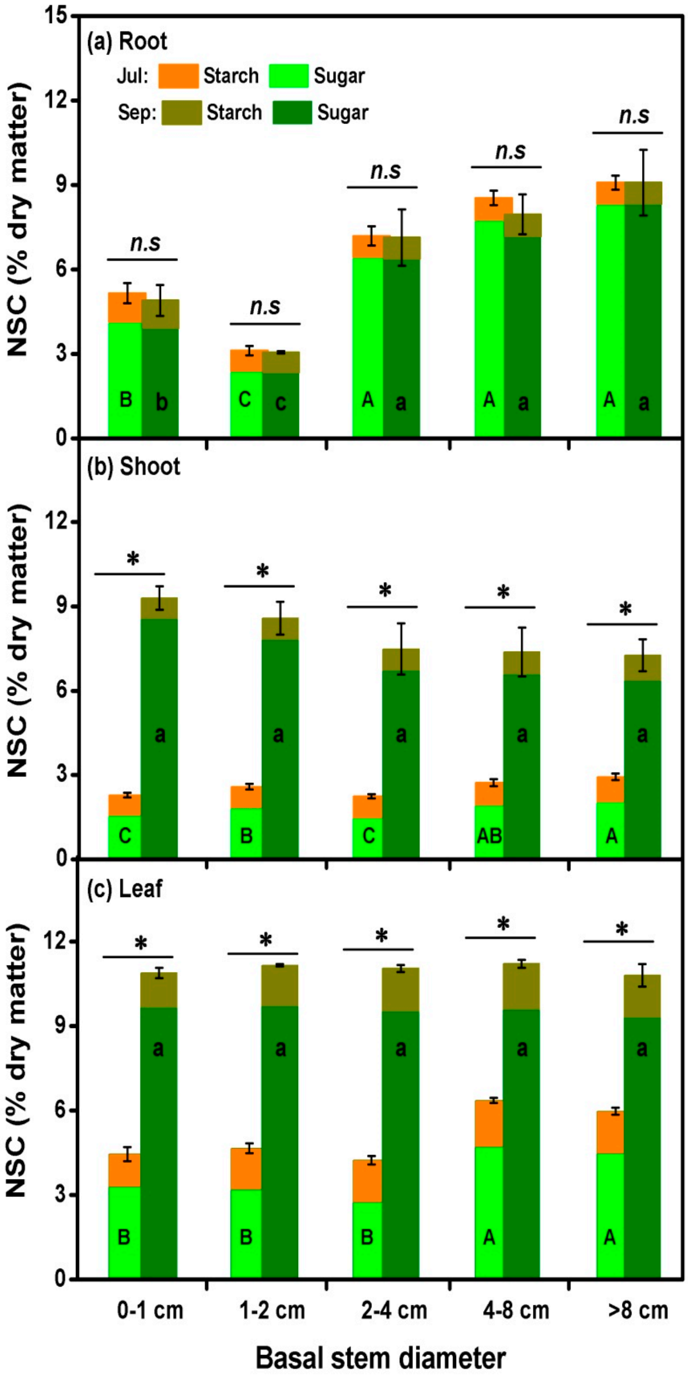

Figure 7. Mean root (**a**), shoot (**b**) and leaf (**c**) nonstructural carbohydrate (NSC) concentrations for *H. ammodendron* among rooting depth group as representation by different basal diameter classes. Data are mean ± 1 SE ($n = 5$). The different capital letters showed significant differences across basal stem diameter classes in July ($p < 0.05$); the different lowercase letters showed significant differences across basal stem diameter classes in September ($p < 0.05$); the asterisks indicate significant differences between July and September within each diameter class ($p < 0.05$). Error bars is the SE of the mean ($n = 5$).

NSCs concentration in roots characteristically went along a depth-related pattern in which the maximum concentrations occurred in the deepest rooting group and the minimum concentrations occurred in the lowest rooting depth group but such relationship were weak in September due to the summer drought (Figure 8a,b). Mean root NSCs concentrations raised with rooting depth by 0.9% m^{-1} in June ($p = 0.043$, Figure 8a). The roots NSCs were significantly correlated with Ψ_{pd} in June and September (Figure 8c,d) and with Ψ_m in June (Figure 8d,e).

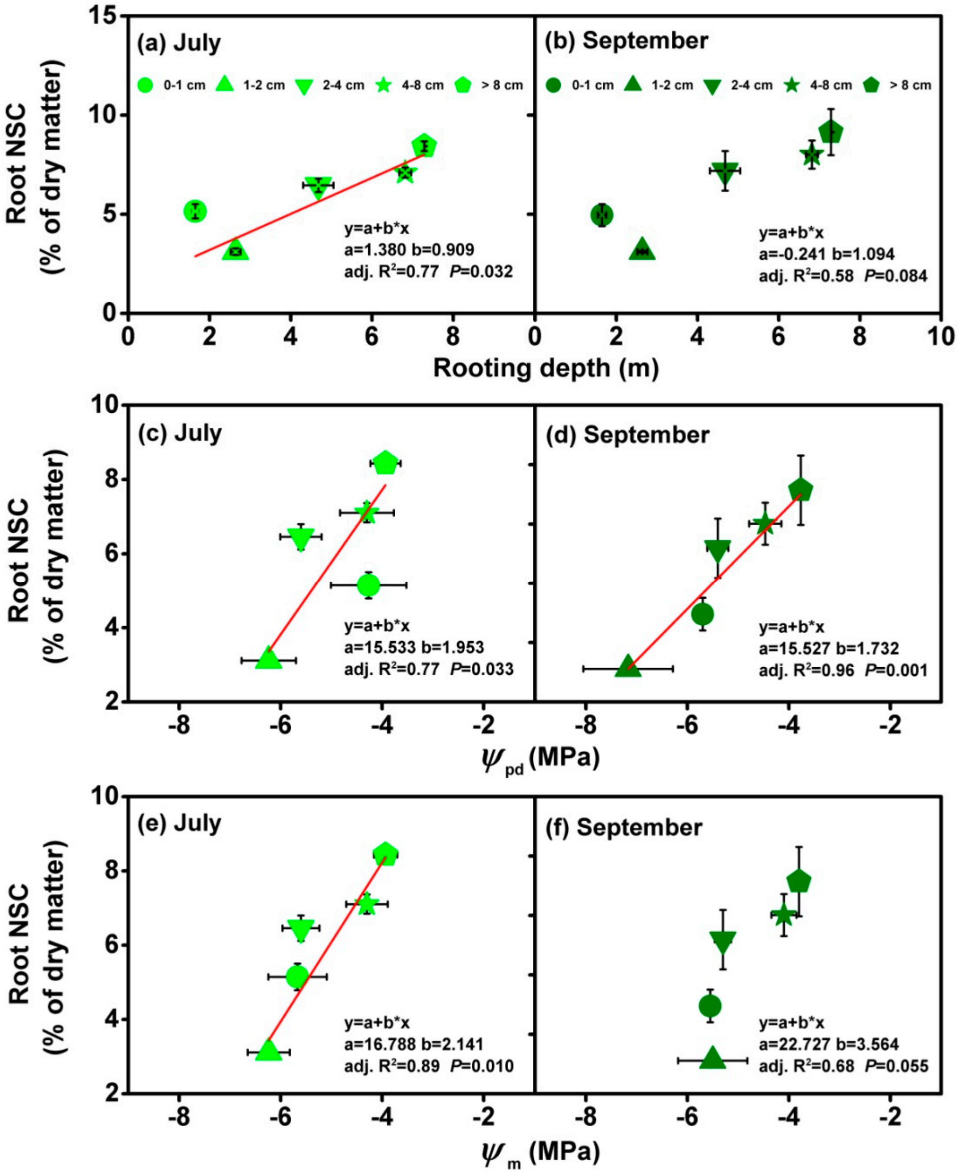

Figure 8. Percentage of dry matter in non-structural carbohydrates (NSC) of root drawn against rooting depth (**a**,**b**), predawn leaf water potential (Ψ_{pd}, **c**,**d**) and midday leaf water potential (Ψ_m, **e**,**f**) in mid-July of 2014 (**a**,**d**,**e**) and mid-September of 2014 (**b**,**d**,**f**). Data are mean ± 1SE ($n = 5$).

4. Discussion

Analysis based on different size of plant individuals in our current study displayed seasonal variations of plant water status, gas exchange rates, NSC content, which are evidently related to their discrepant access to water sources, according to our current estimation of rooting depth and previous analysis on water uptake pattern [31]. Our results verified the hypothesis that rooting depth is an important character in connecting water and carbon processes of plants underwent extremely dry conditions. Actually, for this xeric tree, individuals of different size underwent summer drought stress to different degree, as indicated by the pattern of leaf water potential decline from late spring to the end of summer. Especially, the larger adult tree maintained a more favorable water status and thus relative stable functional performance throughout the summer, while the small young tree in the diameter class of 0–1 and 1–2 cm, Ψ_{pd}, g_s, Fv/Fm, dropped to lower values at and after the dry summer. The contrasting traits performance among rooting depth group of this xeric tree are in consistent with the detected influence of the extreme summer drought on different plant species with contrasting rooting depth [38,39]. Our present results underscore the importance of rooting depth on seasonal changes of plant water status, gas exchange, and NSCs content.

4.1. Physiological Performance

Previous studies on other plants had demonstrated that physiological traits related to drought stress vary with individual ontogenetic stage [40–43], but the conclusions were not consistent [44]. A study on small oak trees revealed a weaker stomatal control on photosynthesis during drought period [10]. Other studies revealed a drop in water potential, stomatal conductance and photosynthetic capacity with aging on *Caragana korshinskii* [45] and *Quercus rubra* [46] under drought conditions. However, yet another study on *Cryptantha flava* (Boraginaceae) demonstrated that plants of different sizes dropped leaf water potential, stomata conductance, and water use efficiency equally under drought conditions [47].

In the current study, most of the physiological traits demonstrated significant changes including the leaf water potential at predawn (Ψ_{pd}), stomatal conductance between 08:00 and 10:00 h local time (g_s), maximum photochemical efficiency (Fv/Fm) across the growing season from the June–September in each of five rooting depth groups, except the g_s of the intermediate-sized trees (with average rooting depth of 4.68 ± 0.0.38 m, Figure 3b) and larger adult trees (with average rooting depth of 6.82 ± 0.15 m, Figure 3b). Most of the above-mentioned physiological traits were also significant different among the five rooting depth group in the same trial days in every month except Fv/Fm in June and July and g_s across growing season (Figure 3c). All these evidences suggested that, to a large extent, the summer drought reduces the overall performance of physiological traits of the smaller individuals more than the large individuals.

The values of maximum photochemical efficiency (Fv/Fm) measured after dark adaptation mirrored the potential quantum efficiency of PSII and were considered to be a sensitive index of plant photosynthetic implementation, with most favorable values of around 0.8 in health leaves [33]. In our current study, the value was between 0.77 ± 0.04 and 0.79 ± 0.01 in June across diameter classes. The value was then continuous dropped in July, August, and September and the small individual had consistent lower values than adult plants, which indicated that all size plants exposed to stress and the small trees suffered greater drought stress than adult trees (Figure 3c). The decline in turgor lost traits with decreasing tree size suggesting that increased tolerance to drought for the small trees which suffered greater water stress during summer (Figure 4e,f).

4.2. The Important of Rooting Depth

Under the condition of low habitat resources, rooting depth is vital for seedling establishment, water and nutrient absorption, and plant survival among different plant species [18,24,48]. The closely positive correlation between rooting depth and physiological parameters in our study on this small xeric tree disclosed that rooting depth play an important role for plants physiological performance during the prolonged extreme drought period in August. Size-dependent discrepancies in predawn leaf water potential were in accordance with rooting depths during the summer drought (Figure 4a,b). Predawn leaf water potential ranged from −6.45 ± 0.44 MPa for the small young trees with shallow rooting depth to −3.80 ± 0.18 MPa for the larger adult trees with deep rooting depth, indicating that the roots of the large and adult tree have gain access to relatively stable and plentiful soil moisture at groundwater capillary ascending zone [31,49], whereas small trees with shallow roots are adapted to use water deposited mainly by rainfall events.

During the severe drought period in August, stomatal aperture down-regulated to avoid further water loss in small young trees with the shallowest rooting depths, (Figure 6a). The positive correlation between rooting depth and g_s and π_{100} in August indicated that active osmotic adjustment and stomatal control did occur for the shallow-rooted small young trees (Figure 4e,f and Figure 6a). However the adjustments were not sufficient to achieve optimal physiological performance, as indicated by the dropdown in leaf water potential and Fv/Fm in August and September for the shallow-rooted young trees (Figure 4). The closely positive correlation between the size-specific physiological traits and Ψ_{pd} in August suggested that the water stress reduce physiological performance of the smaller size individual (Figure 5). We conclude that rooting depth finally dominates plant water status thus the physiological performance.

4.3. NSC Variation

Non-lethal drought reduces growth and increases C allocation to NSCs reserves, in accordance with sink limitation, in mature tropical shrubs, temperate mature pines and mature Mediterranean angiosperms [50]. Hardly any studies focused on reduced NSC, in accordance with source limitation, under non-lethal drought [51] but this did occur for mature trees, in leaves of several Mediterranean shrubs and trees, roots of subtropical and Mediterranean pines, and stems of semiarid pines [50]. In the natural environment, trees of different size may undergo different resources conditions, such as light,wind and water [12,13,30]. This, in combination with variable nature of the accessibility and requirement for mobile carbon by phenological events [52], make the size-depend NSCs concentration variation even more complex. For young trees under non-lethal drought condition, little data hold up source limitation [53] and even rises in NSCs reserves have been reported [54,55]. In our field study, the leaf and shoot NSCs concentration increased across all the basal stem diameter classes during the summer drought supported the previous conclusion of increased C allocation to NSCs reserves [52,56,57]. However, the root NSCs concentrations showed no significant increase between July and September within every diameter class (Figure 6). This may be due to the mobilization of photosynthate was constrained by phloem transport caused by summer drought [58–61]. In order to better elucidate the causes of low NSCs in roots, the future studies should give more attention on the capacity of phloem transport by using carbon isotope technique [62,63]. In addition to this, the influence of different development stage on NSC demand cannot be excluded. For example, small young tree may invest more energy for root growth. The contrasting root NSCs concentration across the basal stem diameter classes indicated that the roots of smaller trees may be more vulnerable to carbon starvation under non-lethal summer drought (Figure 7). It appeared that the root NSCs rather than shoot and leaf NSCs was more suitable for characterizing risk of carbon starvation for this desert plant species at different developmental stages.

Previous studies showed a positive correlation between concentration of NSCs and seasonal dry conditions [56], tree height [57], and water stress [52]. In tall trees with the long water transport path, action of gravity can cause greater water stress in the canopies [64]. Greater water stress may constraint canopy sink [64,65] and lead to NSCs concentrations to raise with tree height in canopy tissues [52]. However for xeric trees with small stature (1.7 m ± 0.2 in height) and thus short above ground vertical transport distance [66], this vertical trend may not exist. These different behaviors might be underlying the contrasting seasonal variation in NSCs content as demonstrated by previous researchers [38]. In this study, the NSCs concentration of all the organs (root, shoot and leaf) were positively related to rooting depth in July, and only the root NSCs concentration showed significant increasing trend with deep root (Figure 8a). Additionally the root NSCs concentrations were also strongly positive correlated to Ψ_{pd} and Ψ_m (Figure 8c–f). Therefore the summer drought influences the root NSCs variation. Our result implies that, for the small xeric tree, the rooting depth was also important in determining the root NSCs concentration through dominated plant water status. Rooting depth appeared to be a critical trait at the basis of tree resistance and resilience to extreme drought events and may be the most important traits defending trees with different size from drought-induced mortality. Further understanding of physiological mechanisms of the occurrence relationship between rooting depth, physiological traits and NSC is desired.

5. Conclusions

Our results demonstrated that the summer drought reduces the overall performance of physiological traits of the small young trees with basal stem diameter of 0–1 cm and 1–2 cm, more than the larger adult trees with basal stem diameter of 4–8 cm and >8 cm. Ψ_{pd}, g_s and Fv/Fm drops were larger in the small young trees than the large adult trees during the summer drought. Substantial osmotic adjustments were observed in small size individuals (with lower π_{100} and Ψ_{tlp}) to cope with summer drought. The contrasting root NSCs concentration across the basal stem diameter classes indicated that the roots of small young trees may be more vulnerable to carbon starvation under non-lethal summer drought. It appeared that the root NSCs rather than shoot and leaf NSCs was more suitable for characterizing risk of carbon starvation for this desert plant species at different developmental stages. The significant positive relationship between rooting depth and physiological traits and root NSCs concentration emphasize the importance of rooting depth in determining seasonal variation of water status, gas exchange and NSCs and may be the key trait defending trees from drought-induced mortality.

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