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Responses of different physiological parameter thresholds to soil water availability in four plant species during prolonged drought

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ABSTRACT

Large-scale vegetation restoration on the Loess Plateau in China has been performed by the central government in recent decades; however, the planting of incompatible vegetation during these efforts has resulted in serious environmental problems, such as dry soil layers, that are widespread and difficult to ameliorate. To determine the proper evaluation indices for plant available soil water content (PASWC) in commonly reforested plants and crops, we examined the physiological responses of *Robinia pseudoacacia* (tree), *Amorpha fruticosa* (shrub), *Medicago sativa* (perennial leguminous herb) and *Zea mays* (crop) to prolonged drought; these plants were planted widely in the semiarid Loess Plateau region of China. Leaf water status, gas exchange and fluorescence parameters did not show marked changes at the beginning of the prolonged drought but changed rapidly as PASWC continued to decrease. These data were fitted with a sigmoid function ($P < 0.0001$). In addition, different physiological parameters showed different PASWC thresholds; the fluorescence parameters exhibited the lowest PASWC threshold among the four species, with an upper threshold that was less than 50% of the PASWC for all but *Z. mays*. In this study, the photosynthesis rate was a better indicator of the PASWC, and the upper and lower thresholds of PASWC of the normalized photosynthesis rate were 64.1% and 47.6%, 83.0% and 44.1%, 82.7% and 35.2%, 82.9% and 39.3% for *R. pseudoacacia*, *A. fruticosa*, *M. sativa* and *Z. mays*, respectively. The current study also suggests that *R. pseudoacacia* is a suitable afforestation species in areas with higher levels of rainfall. These results provide important information for determining the PASWC and the supply capacity of soil water on the Loess Plateau.

1. Introduction

Water availability is one of the principal factors limiting plant growth and development in ecosystems (Huxman et al., 2004), especially in semi-arid and arid areas, where precipitation is the main source of soil water due to climate changes (Hoerling and Kumar, 2003; Huxman et al., 2004). Severe drought could result in significant declines in net primary productivity and large-scale tree mortality events (Allen et al., 2010; Breshears et al., 2005; Hicke and Zeppel, 2013), which have received extensive attention from agroforestry and ecological researchers in recent years (Lacape et al., 1998; Lagergren and Lindroth, 2002; Sadras and Milroy, 1996; Sinclair et al., 2005).

Modeling plant responses to prolonged drought requires not only an understanding of but also quantitative relationships between soil water content and plant physiological traits (Sadras and Milroy, 1996; Soltani et al., 2000). To date, several physiological strategies of plants have been documented in response to drought, including the closure of leaf stomata, decrease in water potential and changes in fluorescence (Bresson et al., 2015; Rouhi et al., 2007; Yan et al., 2016). The closure of leaf stomata may help to maintain a favorable leaf water level during drought, although this depends on the severity and duration of the stress and would reduce the movement of CO_2 and water vapor (Bresson et al., 2015). Therefore, the effects of a drought become evident in the stomata, which reduce their aperture to prevent desiccation (Flexas and Medrano, 2002). The photosynthesis rate is then affected by internal water deficiency following stomatal closure, and net photosynthesis is unavoidably reduced due to decreased CO_2 availability at the chloroplast level (Gallé et al., 2007). The decreases in mesophyll photosynthesis capacity and carboxylation efficiency also contribute to the decrease in photosynthesis under severe drought conditions (Galmés et al., 2007). Therefore, gas exchange responses to drought were used to determine drought conditions; a few studies have addressed the different thresholds of gas exchange response in different plants, under different experimental conditions and using different

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evaluation methods (Casadebaig et al., 2008; Sadras and Milroy, 1996; Sinclair et al., 2005; Soltani et al., 2000). Previous studies typically used single indicators to evaluate plant available soil water content (PASWC) based on type of plant; however, multi-index comprehensive research into different plants is rare.

Chlorophyll fluorescence has become a ubiquitous and powerful parameter used to track changes in the photosynthetic capacity of plants in response to abiotic factors (Bresson et al., 2015; Maxwell and Johnson, 2000). The closure of stomata promotes an imbalance between the photochemical activity of photosystem II (PSII) and the electron requirement for carbon fixation, leading to over-excitations and subsequent photoinhibitory damage to the PSII reaction centers under dry soil conditions (Bresson et al., 2015). Consequently, a substantial decline in the maximum quantum efficiency of PSII (Fv/Fm) in response to drought is observed in various plant species (Baker and Rosenqvist, 2004) and is closely related to decreased leaf water status (Woo et al., 2008), which could be used as an indicator of plant performance under drought conditions because chlorophyll fluorescence data is intuitive and easily comprehensible and could provide useful information on plant status (Calatayud et al., 2006). However, whether this parameter could be used to characterize and quantify the PASWC requires further research.

The Loess Plateau in China is well known for its severe soil erosion (Zhang et al., 2008), where features a dry climate and gullied topography and poses a major challenge for environmental restoration because of the aridity and severe soil erosion. Unfortunately, evapotranspiration is projected to increase in the future (Li et al., 2012). To improve the environmental quality and reduce water and soil losses in this region, the government has implemented vegetation restoration practices that include planting trees, shrubs and herbs; however, many of the selected plants were not ideal for extensive plant restoration, particularly given the limited soil water; this region often experiences low soil water potential for a majority of the year due to low annual precipitation, which is mostly concentrated in the months of July-September (Zhang et al., 2015). The planting of incompatible vegetation has led to some serious issues, such as stunted, old trees and dry soil layers, which are widespread and difficult to ameliorate on the Loess Plateau (Yan et al., 2015). Thus, there is an urgent need to better understand the thresholds for significant changes in the physiological properties of commonly used species in the region in response to low soil water, which could provide useful information for determining the soil water supply capacity, the sustainable utilization of soil reservoirs and the recovery of vegetation on the Loess Plateau.

To the best of our knowledge, the PASWC thresholds for physiological responses in the species planted in this area have not been studied. Thus, in this study, we characterize the response patterns of leaf water status, gas exchange and fluorescence parameters to prolonged drought in four species, including three large-scale vegetative restoration species, *Robinia pseudoacacia* L. (tree), *Amorpha fruticosa* L. (shrub), and *Medicago sativa* L. (herbage), and one crop (*Zea mays* L.), which is widely planted in this region. The primary aim of this study is to quantify how the leaf water status, gas exchange and fluorescence parameters depend on PASWC and to propose a robust methodology to characterize and quantify PASWC in the four different species. The results may assist in determining the PASWC and may provide information for the selection and management of reforestation species on the Loess Plateau.

2. Materials and methods

2.1. Plant material and growth conditions

The experiment was undertaken in an open-sided greenhouse with a glass roof at the Institute of Soil and Water Conservation in the Northwest A & F University in Yangling, Shaanxi (34°17′56″N, 108°04′07″E). The experimental site has a temperate, semi-humid climate with a mean annual temperature of 13 °C and a mean annual precipitation of 632 mm, of which approximately 60% falls from July–September.

Table 1
Physical and chemical properties of the soil used in this study.

Property	Value
Taxonomy	Udic Haplustalf
Texture	
2000–50 μm (g kg^{-1})	64
50–2 μm (g kg^{-1})	694
< 2 μm (g kg^{-1})	342
Bulk density (g cm^{-3})	1.27
pH (H_2O)	8.30
Water-holding capacity (%)	22.8
Soil organic carbon (g kg^{-1})	7.45
Soil total nitrogen (g kg^{-1})	0.84
Soil total phosphorus (g kg^{-1})	0.69

The plants chosen in this study include two deciduous woody legume species (2-year-old seedlings), *R. pseudoacacia* and *A. fruticosa*, one perennial leguminous herb (*M. sativa*) and one crop (*Z. mays*). These plants have been planted widely on the Loess Plateau. Ninety days before the start of the experiment, *R. pseudoacacia* (40–60 cm tall and 3–5 mm in diameter at the stem base) and *A. fruticosa* (30–50 cm tall and 3–5 mm in diameter at the stem base) were transplanted from the field to pots; ninety and forty days before the experiment, the alfalfa and maize were planted as seeds, respectively. The pots were 400 L (980 × 760 × 680 cm, length × width × height) each; this size was chosen to ensure the reliability of the experimental results because small pots may change the experimental results and undermine the purpose of the experiment (Poorter et al., 2012). Four *A. fruticosa* and *R. pseudoacacia* plants, 30 alfalfa plants or 6 maize plants were planted in each pot. The soil used in the study was collected from the 0 to 20 cm soil layer; the physical and chemical properties of the soil are presented in Table 1.

The plants were subjected to two different treatments: well-watered (control saplings) and not watered (stressed saplings). These were arranged in a completely randomized design. The stressed and control saplings were identical during the drought. All plants were well irrigated until the onset of the experiments; the control plants were then continuously watered throughout the experimental period, while drought stress in the stressed saplings was induced by withholding water. Throughout the experiment, the predawn leaf water potential (PLWP), leaf relative water content (RWC), gas exchange and chlorophyll fluorescence were determined using sunny leaves from the upper crown of the selected plants in each treatment. A total of three duplicates per treatment were measured, and at least four measurements per duplicate were taken.

2.2. Measurements

Spot PLWP measurements from both the control and stressed plants were performed between 05:00 and 06:00 h using a PMS 600 pressure chamber (PMS Instruments Company, Albany, USA), with two repetitions for every plant. Gas exchange traits were measured in at least two leaves per plant selected from 09:00 to 11:00 h using the Li-Cor model 6400 system (Lincoln, NE, USA). Fully expanded, mature leaves from the upper crowns were selected and marked for the gas exchange measurements on each sunny day or the second day after each rainy day during the experimental period, and adjacent leaves were selected for the PLWP measurements. The environmental conditions in the leaf chamber consisted of a saturating photosynthetic photon flux density between 1000 and 1500 μmol m^{-2} s^{-1} during the measurement periods; the temperature and relative humidity inside the leaf cuvette were always close to ambient air values.

Chlorophyll fluorescence was recorded with a portable pulse