Original Research

Plant water variables and reproductive traits are influenced by seasonal climatic variables in *Prosopis burkartii* (Fabaceae) at Northern Chile

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ABSTRACT

Prosopis burkartii is a critically endangered phreatophyte legume endemic to the Atacama Desert of northern Chile where only 50 individuals remain. We studied seasonal water variables and flower parameters in a population of 15 *P. burkartii* individuals. For each tree, xylem water potential (Ψ) was estimated by measuring two twigs with a Scholander pressure bomb. Each month, we made 3 measurements of xylem Ψ in each tree: pre-dawn (Ψ_{pd}), midday (Ψ_{md}), and late-afternoon (Ψ_{la}). We also measured pre-dawn hydraulic conductivity (K) and the percent loss of hydraulic conductivity (PLC) on the same trees. Flower parameters were estimated using tagged twigs. The total number of flowers produced by each plant, the number of pods per plants, number of fertile pods and the percentage of abortion of flowers and pods were estimated. Values of Ψ ranged from -2.7 ± 0.1 (July) to -0.8 ± 0.2 MPa (September). On a daily basis, individuals had maximal Ψ at pre-dawn and minimal Ψ at midday, with a recovery of Ψ during the late-afternoon likely due to the low evaporative demand at that time. Furthermore, the native conductance of the stems (Ki) had inverse trends in comparison with PLC data. Number of flowers per plant was strongly correlated with Ψ_{md} estimated during October. During the study period, we observed that Ψ_{md} had higher values during the spring and at the beginning of summer, indicating maintenance of a favorable plant water status during the season of flowering at the time of day when thermal stress is greatest. The differences in PLC suggest that individuals of *P. burkartii* can maintain functional xylem conduits during summer droughts and extract water from the soil while maintaining high values of midday Ψ, the period of the day with the greatest stress.

1. Introduction

Xylem water potential (Ψ) is one of the most important physiological parameters for the assessment of plants in hyper-arid zones because it indicates the level of drought stress experienced by a plant. For example, seasonal analyses of Ψ and plant water use efficiency in xeric ecosystems are used to investigate the role of abiotic parameters, such as winter frosts and summer droughts (Nilsen et al., 1986; Skelton et al., 2015). In addition, in habitats with significant drought stress, some conservation plans use measurements of midday xylem Ψ to determine when to start irrigation (Moriana et al., 2012). Moreover, Ψ in species of arid climates correlates strongly with other physiological variables such as transpiration rate (Wan and Sosebee, 1991; McDowell, 2011), seedling growth

(Villagra and Cavagnaro, 2006), and photosynthetic rate (Delatorre et al., 2008). Furthermore, Ψ and soil moisture play an important role for monitoring vitality in vegetation. Nevertheless, another potential use of both traits in plants seems to be predictive, in reproductive output terms. For example, in evergreen trees it has been documented that lowest xylem water potential and increase of percent loss of conductivity (PLC) during summer months limited reproduction parameters in *Quercus ilex* stands during the next autumn (Alejano et al., 2008). Similarly in semiarid habitats, Haukos and Smith (2006) found a strong relationship between soil moisture and number and biomass of seeds of *Polygonum pensylvanicum*. Nevertheless, little is known about the effects of natural climatic conditions on the seasonal changes in plant water relations and the reproduction parameters of arid and hyperarid vegetation.

Similarly, studies of other plant water parameters related to hydraulic conductivity suggest that seasonal changes in PLC are associated with environmental conditions such as temperature, humidity, and photosynthetically active radiation (PAR) (Cruziat

et al., 2002). Interestingly, desert species seem to have varying responses to seasonal droughts and stressful periods. For example, when *Prosopis chilensis* is under severe drought stress (−4 MPa), it has a PLC of approximately 80% in the stems (López et al., 2013); in contrast, when *Prosopis velutina* is under the same severe drought stress, the percent of embolism in this species is close to 65% (Pockman and Sperry, 2000).

Flowering processes are influenced by numerous physiological (carbohydrate reserves, hormonal content) and climate factors (temperature, rainfall, relative humidity, photoperiod and water availability) (Villagra et al., 2010). In this context, *Prosopis* species of semiarid habitats produce abundant flowers at a predictable time of the year, and temperature seems to be the most predictable weather parameter correlated with reproduction variables in non-phreatophyte *Prosopis* species (Risio et al., 2016). Nonetheless, this hypothesis has not been widely tested on phreatophyte species of the *Prosopis* genus.

Mesquite trees (genus *Prosopis*, family *Fabaceae*) are widely distributed in several natural ecosystems of South and North America. These species are important components of desert lands in northern Chile and southern Peru, although they are classified as invasive species in other arid regions (Yasuda et al., 2014). Their fruits are used in the cattle and gastronomy industries, and natural populations provide habitats for fauna, serve as carbon sinks, and enrich the soil by nitrogen fixation (Razanamandranto et al., 2004; Valdivia and Romero, 2013). *Prosopis burkartii* is a critically endangered phreatophyte species endemic to northern Chile, where only 50 individuals remain (Ministerio de Medio Ambiente, 2011; Carevic, 2014). Despite the urgent need for its conservation, our understanding of physiological and reproduction parameters that limit its abundance lags far behind that of other *Prosopis* species (Mooney et al., 1980; Delatorre et al., 2008). An examination of seasonal variations of drought stress and its underlying causes may help to identify key drivers of changes in xylem Ψ and hydraulic conductivity in *P. burkartii*, and thereby guide conservation efforts that aim to preserve this culturally important plant. We examine the hypothesis that seasonal changes in plant water variables of the plant–soil system and flower sprout traits are related to changes in climatic variables, especially the critical periods of frost and drought.

2. Material and methods

2.1. Study area

We studied a natural population of 15 mature trees of *Prosopis burkartii* Muñoz (Muñoz, 1971) at the Universidad Arturo Prat Estación Experimental Canchones (EEC), Tarapaca region (UTM zone 19, 444080 m E, 7,739,311 m S, 1050 m a.s.l.). This population has a density of 0.03 ind m^{-2} and has been shown to regenerate through its roots. The average height of individuals in this population is 2.14 ± 0.99 m (mean ± se). The climate of the study area is extremely arid, with an average annual precipitation of 0.6 mm and an average annual temperature of 20.9 °C (1970–2015). Historical records of mean temperature during growing season (September to November) show an average of 24 °C. Historical records indicate that the frost period is from June to August (mean temperature of 15.4 °C) with a mean of 30–35 frost days per year, although some years had only 9 days of frost (Arenas, 2013). The vegetation is scarce, but there is a natural forest with several species of *Prosopis* (*P. tamarugo*, *P. burkartii*, and *P. alba*), salt grass (*Distichlis spicata*), and cachiyuyo (*Atriplex atacamensis*).

2.2. Environmental and soil moisture variables

Meteorological data were obtained from a local weather station that recorded precipitation, relative humidity, air temperature, and wind speed during the study period on an hourly basis (Table 1). The weather station was 0.3 km from the study site. Soil moisture digital probes (ECHO$^{®}$) were installed next to each measured tree, with a probe monitoring the mean soil water content from 5 to 15 cm depth and another probe from 15 to 40 cm depth.

2.3. Plant water variables

For each tree (n = 15), xylem Ψ was estimated each month from January to December 2014, using standard methodology with a Scholander pressure bomb. Each month, we performed 3 measurements of xylem Ψ per tree: pre-dawn (Ψ_{pd}), midday (Ψ_{md}), and late-afternoon (Ψ_{la}). On each sampling date, two twigs per tree, each with 4–5 healthy leaves, were cut from the perimeter of the middle area of the crown, at the east and west positions, no later than 1.0–1.5 h before dawn (predawn), no later than 1.0 h after midday (midday) and no later than 1.0 h after 17:00 h (late-afternoon). Hydraulic conductivity (K) was measured on twigs (35–40 millimeters long) from the same trees, and the percent loss of hydraulic conductivity (PLC, %) was determined as described by Melcher et al. (2012) and Carevic et al. (2014) using a Hydraulic Conductance Flow Meter (HCFM-XP, 180 Dynamax Inc., Houston, TX, USA). To determine hydraulic variables, twigs were cut off under water, no later than 1 h after sunrise (to have enough light operate in the forest, i.e., between 07:00 and 08:00 h) and transported to the EEC laboratory in an isotherm bag to prevent embolism. The mean of 4–6 approximately constant values were taken as the native flow rate and used to calculate the native conductance of the stem (Ki) in terms of m × P, where m is the mass flow through a stem segment and P is the pressure applied, driving the flow, expressed in kg H$_2$O s^{-1} MPa^{-1}. The maximum hydraulic conductance (Kmax) was measured after perfusing stems repeatedly for 20 min, until flow ceased to increase. This procedure aimed to remove xylem embolism. K was expressed as the ratio of Ki to the cross section of the debarked stem segment (measured in meters). The percent loss of hydraulic conductance (PLC) of twigs was then calculated as: PLC(%) = (1 − Ki/Kmax) × 100.

2.4. Flower sprouts and pod tagging

The reproductive success of flowers was assessed in different weeks from October 2014 to April 2015 (the period of flower sprouts in *P. burkartii*) by tagging flowers appearing during an entire week with a thread of a particular color. A different color thread was used for each week so that at harvest flower production as well as pod and seed production could be followed on a weekly basis. This tagging procedure provided the total number of flowers produced by each plant (total number of tags per plant), the number of pods per plant (number of tags with a date of podding), the number of fertile pods (number of fruits per pod and plant, counted at harvest of mature fruits), and the calculation of the percentage of abortion of flowers and pods (Vadez et al., 2012). Harvest of mature fruits was determined following Greenberg and Parresol (2002). To achieve this, four plastic containers per tree were fixed to the ground with long nails. The upper part of each container had a diameter of 0.45 m. The containers were placed under the crown of the trees and faced northwards, southwards, eastwards, and westwards, at a distance of 3/4 of the crown radius in each direction. Mature fruits were collected from January to April 2015 and were taken to the laboratory in polyethylene bags (one per tree and direction) to be counted.