

Alessandra Fravolini
Kevin R. Hultine
Dan F. Koepke
David G. Williams

Role of Soil Texture on Mesquite Water Relations and Response to Summer Precipitation

Abstract: In the arid Southwest United States, monsoon precipitation plays a key role in ecosystem water balance and productivity. The sensitivity of deeply rooted plants to pulses of summer precipitation is, in part, controlled by the interaction between soil texture, precipitation intensity, and plant rooting depth and activity. In this study we evaluated the water relations of a leguminous tree species *Prosopis velutina* Woot. (velvet mesquite) occurring across three different aged soils varying in soil texture during two consecutive summers that substantially differed in the amount of monsoonal precipitation (1999 and 2000). We predicted that mesquite trees occurring on different textured geomorphic surfaces would be exposed to different levels of premonsoon water deficit and would not respond equally to summer precipitation. During both years, predawn and midday leaf water potentials were more negative on coarse textured soils than on medium and fine textured soils before the onset of the monsoon, indicating that plant water status is less favorable during drought on coarse-textured soils. However, leaf water potentials recovered rapidly on coarse-textured soils in response to monsoonal precipitation. These results suggest that mesquite sensitivity to future changes in winter and summer precipitation may not be uniform across the landscape, and that the interaction between precipitation and soil-plant hydraulic properties need to be better understood to realistically predict impacts of land cover change on ecosystem carbon and water balance.

Acknowledgments: The valuable help of Nathan English and Rico Gazal in reviewing this manuscript is gratefully acknowledged. Precipitation data sets were provided by the Santa Rita Experimental Range Digital Database. The study was funded by the National Science Foundation.

Introduction

According to the two-layer hypothesis, different plant life forms extract water from varying soil depths, such that deeply rooted woody plants extract water from winter precipitation that percolates deep into the soil profile while shallowly rooted grasses and herbaceous plants rely mostly on growing season precipitation (Walter 1974). However, some studies have shown a consistent overlap in water use between different functional types having different rooting depths (Lin and others 1996; Reynolds and others 1999; Schulze and others 1996; Yoder and Nowak 1999), suggesting that in a water-limited ecosystem the two layer hypothesis may be an oversimplification.

Alessandra Fravolini is a Ph.D. Candidate in the Department of Renewable Natural Resources at the University of Arizona, Tucson; e-mail: alefravo@u.arizona.edu. She completed a Laurea degree in biology with an emphasis in ecology at the University La Sapienza of Rome, Italy. Kevin R. Hultine is a Ph.D. Candidate in the Department of Renewable Natural Resources at the University of Arizona, Tucson. He completed a B.S. degree in forest resources at the University of Idaho, and an M.S. degree in the Department of Renewable Natural Resources at the University of Arizona. Dan F. Koepke is a Research Technician in the Department of Renewable Natural Resources at the University of Arizona, Tucson. He completed a B.S. degree in watershed management in the Department of Renewable Natural Resources at the University of Arizona. David G. Williams is an Associate Professor in the Departments of Renewable Resources and Botany, University of Wyoming. Director of the University of Wyoming Stable Isotope Laboratory, and Adjunct Associate Professor in the School of Renewable Resources, University of Arizona. He completed a B.A. degree in botany at the University of Texas, Austin, an M.S. degree in range science at Texas A&M University, and a Ph.D. degree in botany at Washington State University.

In: McClaran, Mitchel P.; Ffolliott, Peter F.; Edminster, Carleton B., tech. coords. Santa Rita Experimental Range: 100 years (1903 to 2003) of accomplishments and contributions; conference proceedings; 2003 October 30–November 1; Tucson, AZ. Proc. RMRS-P-30. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Changes in precipitation are likely to be the dominant factor affecting future shifts in vegetation structure and ecosystem processes in arid and semiarid regions. In southeastern Arizona, interannual variations, more than long-term variations, are typically the dominant component in the total variance of summer precipitation and are of greatest importance in terms of increasing pressures on limited resources such as water and mineral nutrients (Adams and Comrie 1997). The pattern of summer precipitation in semiarid regions is characterized by the occurrence of numerous small pulses (approximately 10 to 15 events smaller than 10 mm) and by occasional large pulses (1 to 4 events greater than 20 mm). In most arid and semiarid regions, only the large pulses significantly affect the water balance and productivity of deeply rooted plants (Noy-Meir, 1973).

Large (greater than or equal to 20 mm) but not small (less than or equal to 10 mm) summer rainfall events from two weather stations adjacent to the Santa Rita Experimental Range: Tumacacori, 31°34'N and 111°03'W (from 1980 to 2000) and Green Valley, 31°54'N and 111°00'W (from 1990 to 2000) were correlated with total summer precipitation (fig. 1). Apparently the occurrence of wet summers is generated by a few large rainfall events. From these data, we predict that the response of deeply rooted plants to

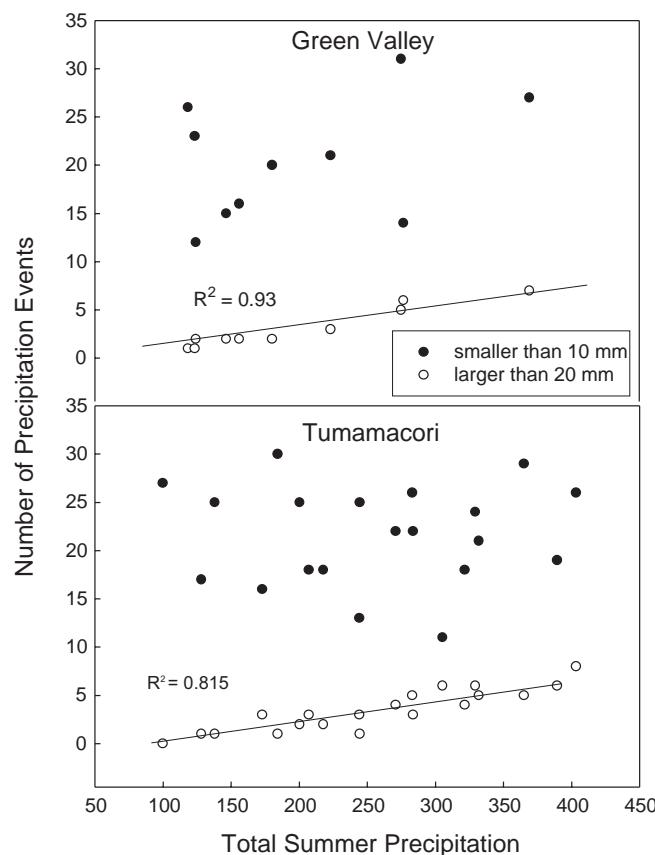


Figure 1—Correlation between total summer precipitation and numbers of events smaller than 10 mm (filled circles) or larger than 20 mm (open circles) at the Tumacacori and Green Valley weather stations in southeastern Arizona.

summer precipitation is strongly dependent on the occurrence of large rain events (more than 20 mm) that are sufficient to percolate below the rooting depth of grasses and annuals herbaceous plants.

Although patterns of precipitation are strongly linked to primary productivity in arid and semiarid regions (Eamus 2003), they cannot entirely explain vegetation dynamics without considering the influence of edaphic factors on plant water availability. Soil texture is a major factor controlling plant distribution and abundance by affecting moisture availability to plants (Bristow and others 1984; Smith and others 1995; Sperry and others 1998). For example, coarse, sandy soils lose moisture much more easily than fine textured soils because of the weaker capillary forces in the large pore spaces. Plants therefore growing in sandy soils potentially exhaust their water supplies more rapidly than plants in a finer textured soil, resulting in greater water stress, lower productivity, and more allocation of resources to the roots compared to plants in fine textured soils (Sperry and others 2002).

In this study we assessed the sensitivity of leaf water potential, a measure of plant water status, in *Prosopis velutina* Woot. (velvet mesquite) to summer precipitation across a soil texture gradient during the 1999 and 2000 growing seasons on the Santa Rita Experimental Range in Southeastern Arizona. This investigation was part of a larger study to assess the extent to which soil morphology and summer precipitation mediates the water balance and productivity of mesquite on the Santa Rita Experimental Range. Information from this study and future studies will substantially aid our ability to predict spatial and temporal patterns of woody plant encroachment and establishment in arid and semiarid rangelands.

Materials and Methods

Study Site

The study site was located on the Santa Rita Experimental Range (SRER) 35 km south of Tucson, AZ. Mean annual precipitation (average of the last 30 years) on the SRER ranges from about 250 to 500 mm, depending on elevation. Greater than 50 percent of the mean annual precipitation occurs during the summer monsoon (July to September) with high interannual variation. Mean daytime air temperature is 32 °C during summer, while mean nighttime temperature during winter is 5 °C. The plant communities on the SRER have been altered dramatically over the last 100 years by the encroachment of velvet mesquite trees into former grasslands. The geomorphology on the SRER varies from mesic sandy uplands that originated during the Holocene to clay rich Pleistocene alluvial fans (Medina 1996).

Experimental Design and Data Collection

Three sites representing young Holocene (4,000 to 8,000 ybp), late Pleistocene (75,000 to 130,000 ybp), and mid-Pleistocene (200,000 to 300,000 ybp) geomorphic surfaces were selected on the SRER. The percentage of sand, silt, and clay for each selected surface is reported in table 1. At each site, a single plot between 0.25 and 0.5 ha was established,

Table 1—Texture fractions of soils collected on Holocene, late and early Pleistocene geomorphic surfaces in the Santa Rita Experimental Range.

Surface origin	Soil depth	Sand fraction	Silt fraction	Clay fraction
- cm -				
Holocene	5	85.1	8.9	6.1
	10	85.1	7.9	7.0
	30	80.0	10.2	9.8
	60	78.7	12.4	8.9
Late Pleistocene	5	81.3	11.1	7.7
	10	77.4	12.4	10.2
	30	77.4	12.0	10.5
	60	77.4	12.4	10.2
Mid-Pleistocene	5	74.8	12.1	13.1
	10	76.1	11.2	12.7
	30	62.0	12.7	25.3
	60	45.6	15.6	38.8

and all mesquite plants were identified and placed within one of three height classes; less than 1 m, 1 to 2 m, and greater than 2 m. Three to five individuals of each size class were randomly selected at each site for leaf water potential measurement. Leaf water potential measured just before dawn yields an approximation of the soil water potential in the rooting zone, given the assumption that during the evening leaf water comes into equilibrium with soil water (Davis and Mooney 1986; Donovan and Ehleringer 1994). Midday leaf water potential is measured to gauge the minimum water potential a plant can tolerate. Predawn leaf water potential (Ψ_{pd}) was measured between 2 a.m. and 5 a.m. approximately once every 4 weeks throughout the growing seasons (May through September) of 1999 and 2000 using a Scholander-type pressure chamber (PMS Instruments, Corvallis, OR, U.S.A.). Midday leaf water potential (Ψ_{md}) was measured between 1000 and 1300 hours every 4 weeks throughout the 2000 growing season.

Statistical Analysis

Multivariate analysis for repeated measures (MANOVA) was performed on untransformed data to test the effect of geomorphic surface, precipitation, and their interaction on predawn and midday leaf water potential. In order to identify the specific differences in leaf water potential across geomorphic surfaces that were statistically meaningful, a least significant difference (LSD) contrast analysis was performed within the MANOVA framework. Results are discussed only at the highest level of significance ($P \leq 0.05$) and are reported within the result and discussion section. JMP 4 software for IBM (SAS Institute Inc.) was used to perform all statistical analysis.

Results and Discussion

Total summer precipitation on the Holocene in 1999 was 395 mm, while in 2000, total growing season precipitation was 302 mm. Precipitation data for the other two sites was

unavailable. Total monthly precipitation at the Holocene from November 1998 through September 2000 is presented in fig. 2. Winter and spring precipitation was relatively light before the 1999 and 2000 growing seasons, likely resulting in dry soil conditions before the onset of monsoon precipitation.

There was no relationship between tree height and leaf water potential at any of the sites for either year, thus, data for all size classes were pooled. Predawn leaf water potentials differed between the 1999 and 2000 growing seasons and across geomorphic surfaces (significant year-by-surface effect $F_{3,666} = 44.44$, $P < 0.001$ from MANOVA), particularly during the early monsoon and postmonsoon periods (fig. 3a and b). Seasonal values of Ψ_{pd} were more similar between years on the mid-Pleistocene surface compared to either of the other surfaces; mean Ψ_{pd} values on the mid-Pleistocene surface ranged from near -1 to -2 MPa during both years (fig. 3a and b). Predawn water potential on the Holocene surface was lower before the 1999 and 2000 monsoon seasons, and after the 2000 monsoon than on the other two surfaces, indicating a much greater water deficit on the Holocene surface during these periods. Conversely, Ψ_{pd} was significantly higher on the Holocene and late Pleistocene surfaces relative to the mid Pleistocene during the 1999 monsoon. Mean Ψ_{pd} on the Holocene surface ranged from less than -4 MPa before both monsoon seasons to greater than -1 MPa during the 1999 monsoon and late monsoon of 2000. Early monsoon values of mean Ψ_{pd} in 2000 were significantly lower than in 1999 on the Holocene and late Pleistocene surfaces due to the lower rainfall in 2000 during the early monsoon period.

The seasonal pattern of Ψ_{md} was similar to that of Ψ_{pd} in 2000. Again, the lowest values at all sites were observed before the onset of the monsoon. Mean Ψ_{md} was lowest before and after the monsoon on the Holocene surface, followed by the late Pleistocene and mid-Pleistocene surfaces, respectively (fig. 4). The mesquite plants on the mid-Pleistocene surface showed little change in Ψ_{md} after the onset of the monsoon, and differed by less than 1 MPa throughout the year.

Pulses of monsoon precipitation can be extremely heterogeneous both spatially and temporally. We therefore can not discount the possibility that there were differences in the amount of monsoon precipitation among the three sites in a given year. However, winter precipitation is much less variable at this spatial scale such that differences in premonsoon Ψ_{pd} among the sites were likely related to differences in the hydraulic properties of the three geomorphic surfaces. As soils dry, air spreads through irregular pore spaces, and soil water potential (Ψ_s) declines causing a reduction in soil hydraulic conductivity (k_s). The lower that k_s becomes, the ability for plant roots to extract water from soil pores decreases. The relationship between Ψ_s and k_s is not constant across soil textures; coarse soils with large pore spaces have high saturated k_s , but demonstrate a much more abrupt decline in k_s with Ψ_s than finer textured soils (Jury and others 1991). The relatively sandy soil textures on the late Pleistocene and particularly on the Holocene surface suggests that plants at these sites will exhaust their water supplies much more quickly than plants on the mid-Pleistocene surface, and will become water stressed more rapidly as soils dry between precipitation pulses compared to plants

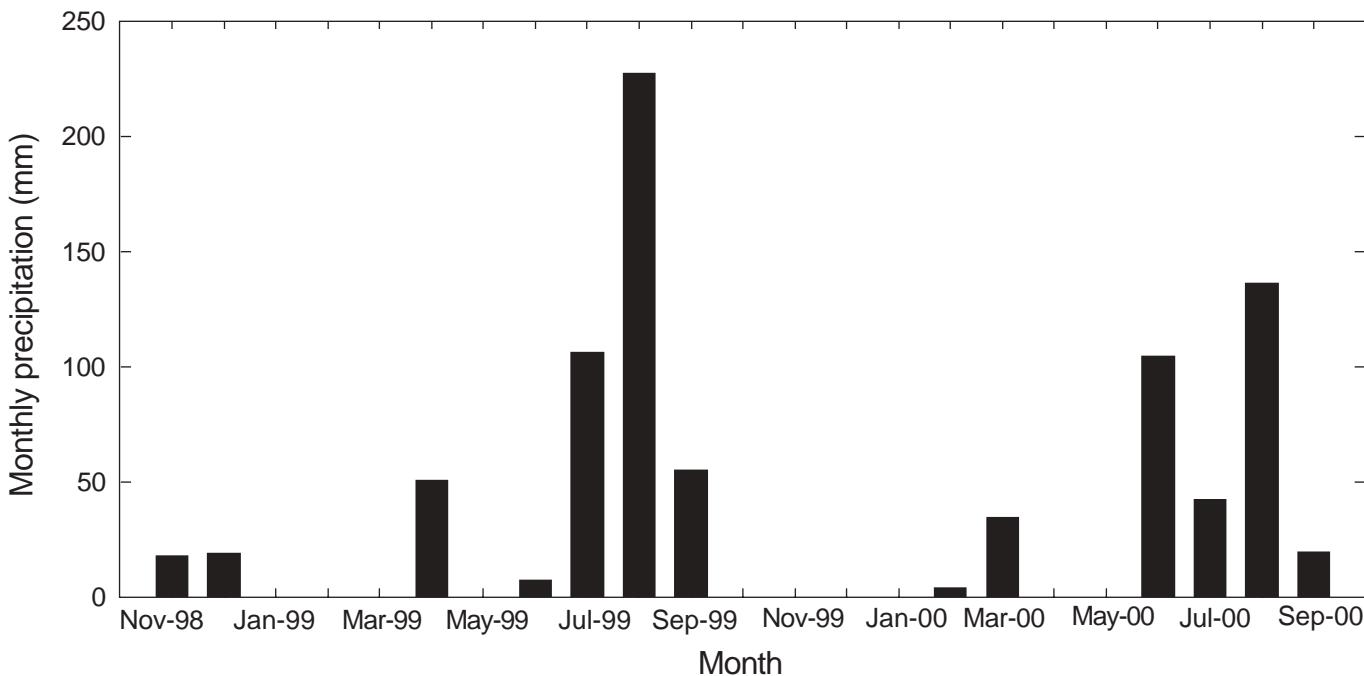


Figure 2—Total monthly precipitation measured at the Santa Rita Experimental Range between November 1998 and September 2000.

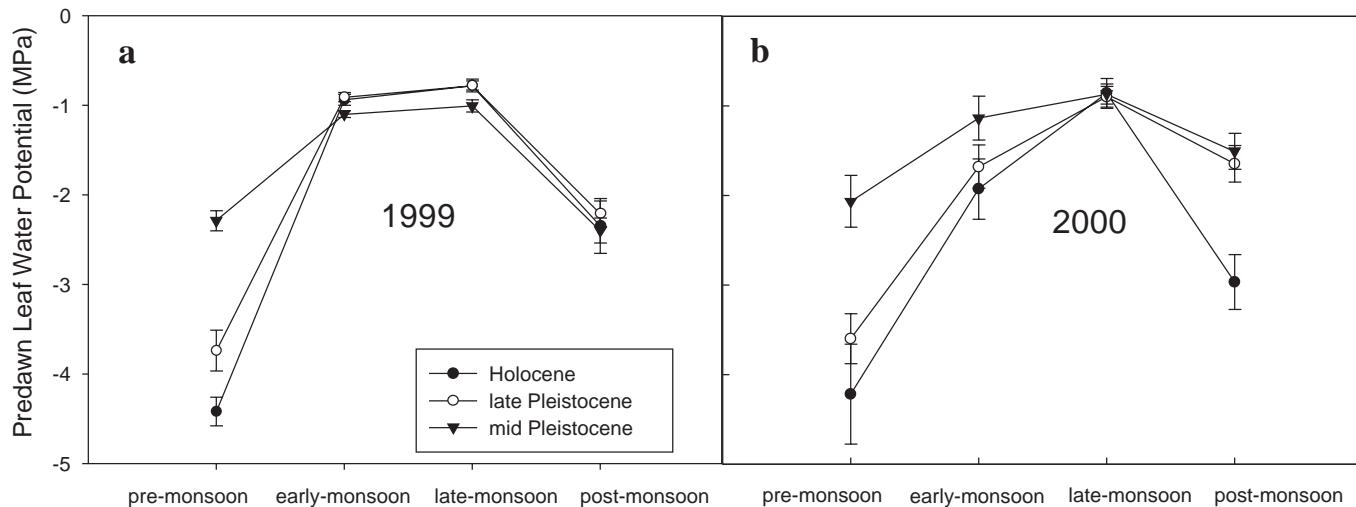


Figure 3—The time course of predawn leaf water potential Ψ_{pd} of mesquite trees across three different aged soils during the wetter monsoon season 1999 (a) and the drier 2000 (b) on the SRER. Error bars indicate \pm one standard error.

on the mid Pleistocene surface (Sperry and others 1998). On the other hand, the high k_s of coarse-textured soils may explain why Ψ_{pd} was slightly higher on the Holocene and Late Pleistocene surfaces relative to the mid-Pleistocene during the 1999 monsoon season. The above average rainfall during the 1999 monsoon likely included enough large events to saturate the soils within the rooting zone (fig. 1), thereby enhancing the water status of mesquite plants on the coarse-textured surfaces that have higher saturated

hydraulic conductivities (k_s) relative to that of the mid-Pleistocene surface. Regional climate change favoring greater precipitation would disproportionately favor the establishment and productivity of mesquite occurring on coarse-textured than on finer textured soils.

Plants in these regions must be adapted to sufficiently utilize short and infrequent pulses of growing season precipitation. During large pulse events, saturated k_s is quickly achieved in coarse-textured soils as Ψ_s approaches zero.

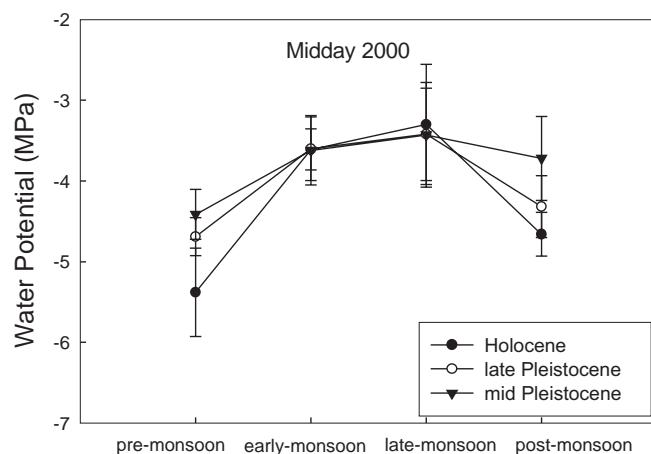


Figure 4—The time course of midday leaf water potential (Ψ_{md}) of mesquite trees measured during the 2000 (drier) monsoon season across three different aged soils in the SRER. Error bars indicate \pm one standard error.

However, as stated above, coarse-textured soils show a rapid decline in k_s with Ψ_s during periods of drought. Consequently, plants occurring on coarse soils tend to optimize their utilization of short-duration pulses by increasing their root area per leaf area ratio, show a greater vertical rooting distribution, and have a greater xylem hydraulic conductance relative to plants on finer textured soils (Sperry and others 2002). Having more root area to absorb water relative to leaf area reduces the rate of water uptake, and subsequent drop in k_s in the rooting zone, thereby delaying severe plant-water deficits that quickly occur in coarse-textured soils (Hacke and others 2000). Likewise, plants in drought-stressed environments tend to develop deep root systems to forage for water in deep soil layers (Cannadell and others 1998; Jackson and others 1996). Indeed, mesquite plants at the SRER do utilize water from deeper soil layers on the Holocene than on the mid-Pleistocene surface (Fravolini, unpublished data), strongly suggesting that this species develops and maintains deeper root systems on coarser textured soils.

Leaf water potential of mesquite on the SRER shows that soil morphology likely plays a key role in plant water status and may have important consequences for patterns of growth and productivity across the SRER. Current and future work on the SRER will address the impacts of soil texture and climate on the water status, recruitment, and productivity of mesquite plants.

References

Adams, D. K.; Comrie, A. C. 1997. The North American Monsoon. *Bulletin of American Meteorological Society*. 10: 2197–2213.

Bristow, K. L.; Campbell, G. S.; Calissendorf, C. 1984. The effects of texture on the resistance to water movement within the rhizosphere. *Journal of Soil Science Society of America*. 42: 657–659.

Canadell, J.; Jackson, R. B.; Ehleringer, J. R.; Mooney, H. A.; Sala, O. E.; Schulze, E. D. 1996. Maximum rooting depth of vegetation types at the global scale. *Oecologia*. 108: 583–595.

Davis, S. D.; Mooney, H. A. 1986. Water use patterns of four co-occurring shrubs. *Oecologia*. 70: 172–177.

Donovan, L. A.; Ehleringer, J. R. 1994. Water stress and use of summer precipitation in a Great Basin shrub community. *Functional Ecology*. 8: 289–297.

Eamus, D. 2002. How does ecosystem water balance affect net primary productivity of woody ecosystems. *Functional Plant Biology*. 30: 187–205.

Fravolini, A. 2000. Poster presented at the 3rd international conference on applications of stable isotope techniques to ecological studies; 2002 April/May; Flagstaff, AZ.

Hacke, U. E.; Sperry, J. S.; Ewers, B. E.; Ellsworth, D. S.; Schafer, K. V. R.; Oren, R. 2000. Influence of soil porosity on water use in *Pinus taeda*. *Oecologia*. 124: 495–505.

Jackson, R. B.; Canadell, J.; Ehleringer, J. R.; Mooney, H. A.; Sala, O. E.; Schulze, E. D. 1996. A global review of rooting patterns: root distribution by depth for terrestrial biomes. *Oecologia*. 108: 389–411.

Jury, W. A.; Gardner, W. R.; Gardner, W. H. 1991. *Soil physics*. New York: John Wiley and Sons.

Lin, G.; Phillips, E.; Ehleringer, J. R. 1996. Monsoonal precipitation responses of shrubs in a cold desert community on the Colorado Plateau. *Oecologia*. 125: 459–465.

Medina, A. L. 1996. The Santa Rita Experimental Range: history and annotated bibliography (1903–1988). Gen. Tech. Rep. RM-GTR-276. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Noy-Meir, E. 1973. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics*. 4: 23–51.

Reich, P. B.; Walters, M. B.; Ellsworth, D. S. 1997. From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences USA*. 94: 13730–13734.

Reynolds, J. F.; Virginia, R. A.; Kemp, P. R.; de Soyza, A. G.; Tremmel, D. C. 1999. Impact of drought on desert shrubs: effects of seasonality and degree of resource island development. *Ecological Monographs*. 69: 69–106.

Schulze, E. D.; Mooney, H. A.; Sala, O. E.; Jobbagy, E.; Buchmann, N.; Bauer, G.; Canadell, J.; Jackson, R. B.; Loret, J.; Osterheld, M.; Ehleringer, J. R. 1996. Rooting depth, water availability, and vegetation cover along an aridity gradient in Patagonia. *Oecologia*. 108: 389–411.

Smith, S. D.; Herr, C. A.; Leary, K. L.; Piorkowski, J. M. 1995. Soil plant water relations in a Mojave Desert mixed shrub community: a comparison of three geomorphic surfaces. *Journal of Arid Environments*. 29: 339–351.

Sperry, J. S.; Alder, F. R.; Campbell, G. S.; Comstock, J. C. 1998. Limitation of plant water use by rhizosphere and xylem conductances: results from a model. *Plant, Cell and Environment*. 21: 347–359.

Sperry, J. S.; Hacke, U. G.; Oren, R.; Comstock, J. P. 2002. Water deficits and hydraulic limits to leaf water supply. *Plant, Cell and Environment*. 25: 251–263.

Yoder, C. K.; Nowak, R. S. 1999. Soil moisture extraction by evergreen and drought-deciduous shrubs in the Mojave Desert during wet and dry years. *Journal of Arid Environments*. 42: 81–96.

Walter, H.; Stadelmann, E. 1974. A new approach to the water relations of desert plants. *Desert Biology*. 2: 213–310.