

NOTE TO USERS

This reproduction is the best copy available.

UMI[®]

WATER UPTAKE BY *PROSOPIS VELUTINA*: THE ROLE OF SOIL
HYDRAULIC LIMITS AND ROOT FUNCTION

by

Kevin Richard Hultine

A Thesis Submitted to the Faculty of the
SCHOOL OF NATURAL RESOURCES

In Partial Fulfillment of the Requirements
For the Degree of

DOCTOR OF PHILOSOPHY
WITH A MAJOR IN NATURAL RESOURCES STUDIES

In the Graduate College
THE UNIVERSITY OF ARIZONA

2004

UMI Number: 3145076

INFORMATION TO USERS

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleed-through, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

UMI[®]

UMI Microform 3145076

Copyright 2004 by ProQuest Information and Learning Company.

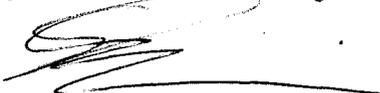
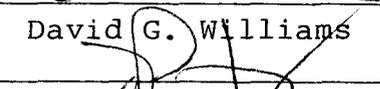
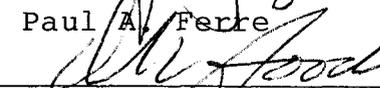
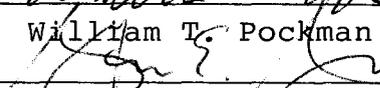
All rights reserved. This microform edition is protected against unauthorized copying under Title 17, United States Code.

ProQuest Information and Learning Company
300 North Zeeb Road
P.O. Box 1346
Ann Arbor, MI 48106-1346

THE UNIVERSITY OF ARIZONA ®
GRADUATE COLLEGE

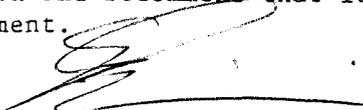
As members of the Final Examination Committee, we certify that we have read the dissertation prepared by Kevin Richard Hultine entitled Water use by Prosopis velutina: the role of soil hydraulic limits and root function

and recommend that it be accepted as fulfilling the dissertation requirement for the Degree of Doctor of Philosophy

	<u>March 17, 2004</u>
David G. Williams	Date
	<u>June 16, 2004</u>
Paul A. Ferre	Date
	<u>June 3, 2004</u>
David C. Goodrich	Date
	<u>May 3, 2004</u>
William T. Pockman	Date
	<u>June 16, 2004</u>
Steven E. Smith	Date

Final approval and acceptance of this dissertation is contingent upon the candidate's submission of the final copy of the dissertation to the Graduate College.

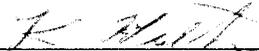
I hereby certify that I have read this dissertation prepared under my direction and recommend that it be accepted as fulfilling the dissertation requirement.

	<u>March 17, 2004</u>
Dissertation Director	Date
David G. Williams	

STATEMENT BY AUTHOR

This dissertation has been submitted as partial fulfillment of requirements for an advanced degree at the University of Arizona and is deposited in the University Library to be made available to borrowers under the rules of the library

Brief quotations from the dissertation are allowable without special permission, provided that accurate acknowledgement of source is made. Requests for permission for extended quotation from or reproduction of this manuscript in whole or in part may be granted by the head of the major department or Dean of the Graduate College when in his or her judgment the proposed use of the material is in the interest of scholarship. In all other instances, however, permission must be obtained from the author.

SIGNED: 

ACKNOWLEDGEMENTS

Many thanks to my research advisor, Dr. David Williams for his continued support, encouragement, and intellect in the field of ecophysiology. I am grateful to my other committee members: Paul “Ty” Ferré, David Goodrich, William Pockman, and Steve Smith for their support and input throughout my graduate program.

I am extremely grateful for the time, input and technical support from the following people in the Williams’ lab: Nathan English, Patrick Ellsworth, Alessandra Fravolini, Rico Gazol, Dan Potts, Brittney Schmidt, Alea Trafton, and Enrico Yopez-Gonzalez. Special thanks to Bill Cable and Dan Koepke. Without their time and input, many sections of this dissertation would not be possible.

I would also like to thank Tim Keifer, Carl Unkrich, and Russ Scott from the USDA-ARS Southwest Watershed Research Center, along with Steve Burgess and Anna Tyler for their technical support.

Thanks to Jill Gibson and Terrie Thompson of SAHRA for managing research funds and academic issues of my dissertation.

Special thanks to Hana Blumenfeld, Mark Brewer, Darryl Brown, Steve Jandreau, Cindy Salo, and Keirith Snyder for their support, encouragement, and insight. I am very grateful for the support and encouragement from Joan Powers, John Belt, and Richard and Mary Hultine.

Financial support for this research was provided by the NSF Science in Technology Center for Sustainability of semi-Arid Hydrology and Riparian Areas, and by the Upper San Pedro Partnership. Additional support was provided by a William G. McGinnies Scholarship in Arid Land Studies and a grant provided by the Water Resource Research Council at the University of Arizona.

TABLE OF CONTENTS

LIST OF FIGURES	6
LIST OF TABLES.....	7
ABSTRACT.....	8
INTRODUCTION	10
PRESENT STUDY	18
LITERATURE CITED	22
APPENDIX A: Summer pulse utilization by a dominant Chihuahuan desert phreatophyte with respect to soil texture: implications from experimental irrigation.....	35
Abstract	36
Introduction.....	38
Materials and methods	41
Results.....	49
Discussion	52
Literature Cited	58
Tables and figures	63
APPENDIX B: Influence of soil texture on water use in a dominant warm-desert phreatophyte.....	72
Abstract	73
Introduction.....	75
Material and methods.....	78
Results.....	86
Discussion	89
Literature cited	96
Tables and figures	101
APPENDIX C: hydraulic redistribution by a dominant warm-desert phreatophyte: seasonal patterns and response to precipitation pulses	110
Abstract	111
Introduction.....	113
Materials and methods	116
Results.....	124
Discussion	128
Literature cited	135

LIST OF FIGURES

APPENDIX A

FIGURE 1, Volumetric soil water content	67
FIGURE 2, Predawn and midday water potentials.....	68
FIGURE 3, Sap flow in response to irrigation.....	69
FIGURE 4, Sap flow and gravimetric water loss of single tree.....	70
FIGURE 5, Correlation between HRM and gravimetric water loss	71

APPENDIX B

FIGURE 1, Root and stem vulnerability curves	106
FIGURE 2, E_{crit} at several over a range of root to leaf area ratios.....	107
FIGURE 3, Extraction limit over a range of root to leaf area ratios.....	108
FIGURE 4, Correlation between wood density and vulnerability to xylem cavitation..	109

APPENDIX C

FIGURE 1, Minimum dormant season soil temperatures.....	143
FIGURE 2, Root sap flow in Tree 1 during dormant season.....	144
FIGURE 3, Root sap flow in Tree 2 during dormant season.....	145
FIGURE 4, 24 hour sap flow patterns in root and stems during dormancy.....	146
FIGURE 5, Root sap flow in Tree3 during growing season.....	147
FIGURE 6, Volumetric soil water content of vadose zone	148

LIST OF TABLES

APPENDIX A

TABLE 1, Soil texture of study sites at SRER.....	65
TABLE 2, Sapwood and leaf area of trees measures for sap flow	66

APPENDIX B

TABLE 1, Characteristics of study sites.....	103
TABLE 2, Leaf water potentials and xylem conductance	104
TABLE 3, Xylem cavitation and conduit diameters.....	105

APPENDIX C

TABLE 1, Sapwood area of stems and roots measured for sap flow	142
--	-----

ABSTRACT

The encroachment of deeply rooted woody plants into grasslands throughout the world has the potential to alter local, regional, and global water balance. The consequence of encroachment by woody plants on ecosystem water balance is, in part, related to the sensitivity of these plants to summer and winter precipitation pulses. This dissertation addresses the primary question: does pulse sensitivity of a dominant warm-desert woody plant, velvet mesquite (*Prosopis velutina* Woot.) vary across soil texture and water availability gradients? To address this question, sap flow and xylem anatomy and function were evaluated in mature velvet mesquite trees at two upland sites varying in soil texture at the Santa Rita Experimental Range (SRER), and one floodplain site along the San Pedro River National Conservation Area (SPRNCA). Experimental irrigation was used to assess the sensitivity of mesquite plants to small and large precipitation pulses. There was a moderate response to both small (10 mm) and large (35 mm) irrigation inputs by trees on sandy-loam soil, while trees on loamy-clay soil were only responsive to the large pulse. The differential response between sites was associated with differences in infiltration of the experimental pulses between the two soil types. Model predictions of the critical transpiration rate (E_{crit}) - above which hydraulic conductivity through the soil-plant continuum falls to zero - showed that trees at the sandy-loam site operated well below their maximum transpiration rate before the onset of the monsoon. Conversely, plants on loamy-clay soils likely operate closer to their maximum permissible transpiration rates throughout the growing season. Hydraulic

redistribution was observed and rates were tightly coupled to growing season and dormant season precipitation inputs. Hydraulic redistribution could enhance pulse sensitivity by transferring soil water to regions of the root zone that are otherwise dry, thereby allowing a greater proportion of the root system to participate in the extraction of pulse water during transpiration. Results from this research suggest that patterns of mesquite water relations are strongly mediated by soil texture. Nevertheless, once established, mesquite plants substantially modify ecosystem water balance, due to their responsiveness to growing season precipitation pulses, and their ability to withstand severe water deficits between precipitation pulses.

INTRODUCTION

Arid and semiarid regions are characterized by a high degree of spatial and temporal heterogeneity in plant water supply. Ecosystem hydrology, productivity, and biogeochemical cycling in these regions are tightly linked to growing season precipitation pulses (Noy-Mier 1973, Ehleringer et al. 1991). However, the degree to which ecosystem productivity and function are coupled to summer moisture inputs is highly variable depending on the proportion of deep-rooted woody plants and shallow-rooted grasses and herbaceous plants present within the community. Woody plants have a large effect on ET and water yield primarily due to their ability to access and transpire water that may otherwise recharge deep soil layers, groundwater, and/or streams (Jarvis and McNaughton 1986, Huxman et al. In Press). In riparian zones, deep-rooted plants have access to an essentially unlimited supply of groundwater for a significant part of the year. Where deep roots are directly accessing groundwater adjacent to stream channels, the potential exists for decreases in streamflow (Scott et al. 2000, Scott et al. 2003). In contrast, woody plants in arid and semi-arid upland ecosystems may not have a direct impact on groundwater recharge or stream flow. Nevertheless, they may enhance ecosystem ET, due in part, to their expansive root systems that can access moisture in deep soil layers, otherwise beyond the reach of shallow grass and herbaceous roots. Moreover, the establishment of woody plants in arid and semi-arid grasslands often leads to the development of “islands of fertility” (Brown and Archer 1989, Schlesinger et al. 1990). Once these islands establish, vegetation cover may become heterogeneous across

the landscape and the potential for runoff and erosion following precipitation is enhanced significantly.

In order to quantify the relative differences in root functioning between shallow-rooted grasses and more deeply rooted woody plants, we must first identify phenotypic differences that characterize the water use and below ground activity of the separate life forms. Grasses tend to have small root area:shoot area ratios, high leaf conductance that is relatively insensitive to plant water potential, and are relatively intolerant of declining soil moisture content in the rhizosphere (Schwinning and Ehleringer 2001). Grasses in arid and semi-arid regions are predominantly C_4 and rely heavily on summer pulses of precipitation (Ehleringer 1985). Woody plants in xeric environments tend to have large root area:shoot area ratios, deep roots, have a high potential for hydraulic redistribution, and are moderately to highly tolerant of declining soil moisture content. Woody plants that possess comparatively deep roots are less responsive to small pulses and rely heavily on subsurface water and large pulse events that percolate beyond the depth of shallow grass roots (Snyder and Williams 2000, Schwinning and Ehleringer 2001). Juvenile woody plants tend to rely primarily on water in shallow soil layers, directly competing with grasses and herbs until their roots systems can extend to deeper soil layers with stable water supplies (Weltzin and McPherson 1997).

The dynamics of water use by woody plants, and their propensity to alter ecosystem and hydrologic processes, may be highly dependent on soil texture and availability of groundwater. In dry climates, coarse-textured soils are associated with more extensive vegetation cover, possibly as a result of more available water and higher

Ψ_s in these soils (Kinraide 1984; Sperry et al. 1998; Sperry and Hacke 2002). The relatively high saturated hydraulic conductivity (K_s) in coarse soils allows for greater infiltration to deep soil layers, opposed to running off or ponding. Further, dry zones tend to form during drought near the surface of coarse soils due to their large pore spaces. Dry zones inhibit the movement of deep water to the surface, reducing evaporative loss and allowing the soil to retain a larger proportion of its stored water (Campbell and Norman 1998). Likewise, plants occurring on these soils can differ greatly in their potential for water extraction as determined by their xylem hydraulic conductance (k_x), cavitation resistance, and their root area to leaf area ratios ($A_r:A_l$) (Sperry et al. 1998, 2002). The rate of transpiration depends, in part, on the hydraulic conductance of the xylem per unit leaf area. Xylem elements differ substantially in their ability to sustain negative pressure without cavitation and subsequent loss in hydraulic conductivity (Tyree and Sperry 1988). Resistance to cavitation is correlated with the range of water potentials experienced by the plant. Plants growing in coarse-textured soils generally operate under consistently higher water potentials than plants in fine-textured soil (Sperry et al. 1998, Hacke et al. 2000), and have xylem that is less resistant to cavitation.

The influence of soil water availability on plant hydraulic characteristics is generally more pronounced in roots than in stems. For example, *Acer grandidentatum* not only have roots that were more vulnerable than stems, but the safety margin at which they operate (the difference between the minimum water potential observed in the field and the critical water potential that induces runaway cavitation) were smaller than in stems (Alder et al. 1996). Differences in cavitation vulnerability are linked to differences

in xylem anatomy; roots tend to have larger and longer xylem conduits (Pate et al. 1995, Jackson et al. 2000). Consequently, roots generally have a greater maximum hydraulic conductivity than stems, but larger vessels may allow for easier air entry which induces cavitation (Alder et al. 1996, Linton et al. 1998, Kolb and Sperry 1999). Likewise, roots growing in coarse soils often have a greater hydraulic conductance than roots in fine-textured soils, but are more vulnerable to catastrophic xylem cavitation (Ψ_{crit}) (Hacke et al. 2000). The higher potential for root hydraulic failure in coarse soil could be offset by having greater rooting depths, and or greater $A_r:A_l$ than plants in fine-textured soils (Sperry et al. 1998, 2002). Previous investigations have reported both trends across soil texture gradients (Hacke et al. 2000, Schenk and Jackson 2002). Increased rooting depths, and high $A_r:A_l$ could shift the potential for hydraulic failure from the rhizosphere to the plant (particularly the roots) and maximize water extraction in arid environments (Sperry et al. 1998).

In much of the arid southwest, growing season precipitation accounts for 50 to 75% of annual precipitation, requiring plants in these regions to efficiently utilize growing season precipitation pulses, that often do not percolate into the vadose zone. During a large pulse event, the saturated hydraulic conductivity is quickly achieved in coarse-textured soil as soil water potential (Ψ_s) approaches zero. However, coarse soils show a much more abrupt decline in K_s with Ψ_s during periods of soil drying. Consequently, plants occurring on these soils tend to optimize their utilization of short duration pulses by increasing their $A_r:A_l$, show a greater vertical rooting distribution, and have a greater maximum k_x relative to plants in fine-textured soil (Sperry et al. 2002).

During a small pulse, the larger air spaces in coarse soil do not fill enough to enhance K_s to the extent that mesquite plants can utilize the pulse. During large events, soil Ψ approaches zero and K_s is established regardless of soil texture. During these conditions plants occurring on coarse soil are initially more efficient at using the pulse since soil K_s and $A_r:A_l$ are greater in sand. However, as soils dry, water in coarse soils is quickly drained from the large pore spaces and the pulse is quickly exhausted relative to fine-textured soils.

If soils dry between pulses, then root hydraulic conductance may be substantially reduced from cavitation, particularly small roots that are generally more vulnerable than large roots (Zimmerman 1983, Hacke et al. 2000). Hydraulic failure in small, shallow roots could localize failure to relatively cheap replaceable tissues compared to taproots, stems, or branches. In coarse soils, hydraulic failure in small lateral roots could direct uptake during drought to deeper soil layers without substantially disrupting the transport stream (Jackson et al. 2000). During pulse events, conductance could be restored in the shallow root systems by refilling cavitated vessels or re-growing fine roots. Between pulses, hydraulic redistribution could mitigate soil drying, and prolong fine root activity by keeping the roots hydrated.

Hydraulic redistribution, the transfer of water from moist to dry soil layers through root systems, occurs when reduced transpiration (usually at night) allows xylem water potential to exceed water potential in the dry soil. The phenomenon is common among plants with dimorphic root systems that extend from shallow to deep soil layers (Caldwell et al. 1998). The linkage between hydraulic redistribution and hydrological

processes at the ecosystem scale is still not fully understood. Its impact on ecosystem processes should be related to the vertical direction in which water is transferred. The upward transfer of water (hydraulic lift) has been observed in several species and life forms, and across varying environments (Richards and Caldwell 1987, Caldwell and Richards 1989, Dawson 1993, 1996, Hultine et al. 2003a). Hydraulic lift potentially facilitates transpiration and nutrient uptake of not only the redistributing plant, but also the co-occurring shallowly rooted plants.

More recent investigations have focused on the downward transfer of water (hydraulic descent) after surface soils are wetted by precipitation (Burgess et al. 1998, 2001, Schultze et al. 1998, Hultine et al. 2003b). Downward hydraulic redistribution is difficult to gauge because monitoring subtle changes in water content of deep soil layers is logistically complex. Nevertheless, measurements of root sap flow coupled with capacitance probe measurements of soil water content have provided strong evidence of the phenomenon (Burgess et al. 2001). Hydraulic descent may occur with both growing season and dormant season moisture pulses. The downward transfer of water during the growing season may reduce evapotranspiration since water is diverted from shallowly rooted competitors and soil evaporation processes, and thereby extend and enhance pulse utilization. During the dormant season k_x of roots is likely substantially lower than during the growing season, considering that few, if any live absorptive roots are maintained (Hendrick and Pregitzer 1992). However, hydraulic descent should still be present since cavitation from freezing is unlikely below the soil surface and water loss

from roots can still occur at junctions within highly branched fine root systems (Caldwell et al. 1998).

The focus of this research was to 1) determine the water use patterns of mature velvet mesquite plants (*Prosopis velutina* Woot.) occurring on coarse and fine-textured soils in response to small and large precipitation pulses, 2) assess the combined importance of xylem function and rhizosphere conductance to seasonal patterns of mesquite water use on coarse- and fine-textured soils, and 3) determine the seasonal patterns of hydraulic redistribution in mesquite roots occurring within a floodplain ecosystem. The goal of this research was to shed light on the development of mesquite hydraulic architecture and function in response to spatial and temporal changes in soil water availability, and develop a clearer understanding of the mechanisms by which woody plants potentially alter the ecology and hydrology of ecosystems previously dominated by grasses. Specific questions include: 1) is the sensitivity of mesquite plants to large and small pulses of growing season precipitation controlled by soil texture and available water? 2) To what extent does soil texture influence seasonal water use patterns of mesquite plants? 3) Does the pattern of hydraulic redistribution correspond to growing season and dormant season precipitation pulse inputs? This research is presented in article format in accordance with the *Renewable Natural Resource Studies* graduate program guidelines, and contains three manuscripts submitted, or intended to be submitted to peer review journals.

Field work was conducted at two locations at the Santa Rita Experimental Range (SRER) in Santa Cruz County Arizona, varying in soil texture, and at a perennial stream

site along the San Pedro River near Boquillas Ranch in Cochise County Arizona. Patterns of plant water use before and after small and large irrigation events were measured on mature mesquite trees at both sites at the SRER. Results from this experiment are presented in Appendix A, and will be submitted for publication as part of a larger investigation on carbon and water balance of mesquite plants following irrigation. Measurements of xylem cavitation vulnerability, maximum conductance, and anatomy were measured on shallow roots, and secondary stems of mature mesquite trees from both SRER field sites. Results from this investigation are presented in Appendix B and will be submitted for publication in *Oecologia*. Seasonal patterns of sap flux were measured on lateral and taproots of three mature velvet mesquite trees along the San Pedro River. Irrigation was applied to two of the trees in early spring to assess root responses to precipitation pulses during periods of dormancy. This investigation is presented in Appendix C, and has been accepted for publication in *Functional Ecology*.

PRESENT STUDY

The encroachment of mesquite (*Prosopis* spp.) into historic upland and floodplain grasslands has had dramatic impacts on ecosystem water balance, productivity, and biogeochemical cycling. The propensity of mesquite plants to alter ecosystem function is, in part due to its extensive root system, coupled with its ability to cope with severe water limitations. In this dissertation, the influence of mesquite encroachment on ecosystem water balance was assessed by considering three important questions related to mesquite water relations. First, does the sensitivity to small (<10 mm) and large (>20 mm) summer precipitation pulses vary between mesquite plants on sandy-loam and loamy-clay soils? Second, is pulse sensitivity related to soil and xylem hydraulic limits? Third, what are the seasonal patterns (if any) of hydraulic redistribution in mesquite plants in response to precipitation pulses. The methods, results, and conclusions of these investigations are presented in the papers appended to this dissertation.

We used experimental irrigation to assess the sensitivity of mature mesquite plants at the Santa Rita Experimental Range to summertime precipitation pulses. Transpiration in this species occurring on loamy-clay soils increased 50% over a two week period following a large (35 mm) irrigation event, whereas transpiration increased only 8% following the same irrigation at a sandy-loam site. Conversely, there was no apparent response at the loamy-clay site to a small (10 mm) irrigation event, while transpiration was measurably higher at the sandy-loam site following the 10-mm irrigation. The greater sensitivity of mesquite plants on sandy-loam soil to small

irrigation inputs may explain why they occur at the SRER at much higher densities than on loamy-clay soils. In southeastern Arizona, small (<10 mm) growing season precipitation pulses are far more frequent than large (>20 mm) pulses (Fravolini et al. 2003). Moreover, total annual growing season precipitation is strongly correlated with infrequent, large precipitation pulses (>20 mm), while there is no correlation between total annual monsoon precipitation and frequently occurring small rainfall events (<10 mm). The large response between transpiration in mesquite plants growing on loamy-clay soil and large irrigation suggests that predicted changes in annual growing season precipitation (Houghton et al. 1996) could have a dramatic impact on the hydrology and productivity of upland ecosystems dominated by fine-textured soils.

Contrary to similar studies (Lin et al. 1996, Williams and Ehleringer 2000), mesquite plants at the SRER demonstrated a near immediate response to irrigation at both sites, despite the absence of precipitation in the previous weeks before irrigation. This may have been facilitated by highly resistant xylem to drought-induced cavitation. In the present study, mesquite roots and stems at both sites at the SRER were highly resistant to xylem cavitation, and operated with a wide safety margin (the difference between Ψ observed in the field and the critical Ψ that induces hydraulic failure). There was no apparent tradeoff between cavitation resistance and maximum hydraulic conductivity, in either roots or stems across the three sites. The combined importance of rhizosphere and xylem constraints to transpiration was considered for both sites at the SRER using a transport model that gauged the resistances of rhizosphere, root, and stem xylem in series. At the sandy-loam site, low rhizosphere conductance during drought sharply reduced the

permissible rate of transpiration without hydraulic failure along the soil-plant continuum. Conversely, rhizosphere conductance at the loamy-clay site was far less limiting to mesquite transpiration during drought. Results suggest that, despite similarities in xylem function, mesquite transpiration fluxes on sandy-loam soils are highly sensitive to growing season precipitation pulses, whereas fluxes on loamy-clay soils may be better coupled to inter-annual changes in precipitation.

Resistance to cavitation may also facilitate hydraulic redistribution of water by deep root systems (Caldwell et al. 1998). Hydraulic lift (the upward transfer of soil water) occurs in mesquite roots during extended periods of drought, and immediately reverses direction (i.e. hydraulic descent) in response to moderate rain events. Mesquite roots apparently redistribute significant amounts of soil water during the growing season, but also during periods of crown dormancy in winter. In arid regions, dormant season hydraulic descent may buffer plants from water deficits during initial stages of the growing season by transferring soil water derived from winter precipitation to deep soil layers and away from zones of evaporation in surface layers.

Vegetation cover change has important implications for the transport of water, nutrients, and energy at landscape scales. It is clear that the encroachment and establishment of deeply rooted woody plants, coupled with changes in regional climate will play a considerable role in the hydrology and productivity of arid and semi-arid ecosystems. Understanding the mechanisms that underlie the functional attributes of woody vegetation across soil texture and water availability gradients will allow us to

develop a conceptual framework to predict the diverse avenues that woody plants can affect ecosystem hydrology and productivity across the landscape.

LITERATURE CITED

- Alder, N.N, Sperry, J.S. and Pockman, W.T. 1996. Root and stem xylem embolism, stomatal conductance, and leaf turgor in *Acer grandidentatum* populations along a soil moisture gradient. *Oecologia* **105**: 293-301
- Alumbaugh, D., Chang, P.Y., Paprocki, L., Brainard, J.R., Glass, R.J., & Rautman, C.A. 2002. Estimating moisture contents in the vadose zone using cross-borehole ground penetrating radar: A study of accuracy and repeatability, *Water Resources Research* **38**: 1309, doi:10.1029/2001 WR000754.
- Archer, S.A. 1995. Tree-grass dynamics in a *Prosopis*-thornscrub savanna parkland: reconstruction of the past and predicting the future. *Ecoscience* **2**: 83-99
- Barrett, D.J., Hatton, T.J., Ash, J.E., Ball, M.C. 1995. Evaluation of the heat pulse velocity technique for measurement of sap flow in rainforest and eucalypt forest species of south-eastern Australia. *Plant, Cell and Environment* **18**: 463-469
- Becker, P., and Edwards, W.R.N. 1999. Corrected heat capacity of wood for sap flow calculations. *Tree Physiology* **19**: 767-768
- Brooks, J.R., Meinzer, F.C., Coulombe, R., & Gregg, J. 2002. Hydraulic redistribution of soil water during summer drought in two contrasting Pacific Northwest coniferous forests. *Tree Physiology* **22**: 1107-1117
- Brown, J.R., and Archer S.A. 1989. Woody plant invasion of grasslands: establishment of honey mesquite (*Prosopis glandulosa* var. *glandulosa*) on sites differing in herbaceous biomass and grazing history. *Oecologia* **80**: 19-26.

- Burgess, S.S.O., Adams, M.A., Turner N.C., and Ong, C.K. 1998. The redistribution of soil water by tree root systems. *Oecologia* **115**: 306-311
- Burgess, S.S.O., Pate, J.S. Adams, M.A., & Dawson, T.E. 2000. Seasonal water acquisition and redistribution in the Australian woody phreatophyte, *Banksia prionotes*. *Annals of Botany* **85**: 215-224
- Burgess, S.S.O., Adams, M.A., Turner, N.C., White D.A., & Ong, C.K. 2001a. Tree roots: conduits for deep recharge of soil water. *Oecologia* **126**:158-165
- Burgess, S.S.O., Adams, M.A., Turner, N.C., Beverly, C.R., Ong, C.K., Khan, A.A.H., and Bleby, T.M. 2001b. An improved heat pulse method to measure slow and reverse flow in woody plants. *Tree Physiology* **21**: 589-598
- Burton, A.J., Pregitzer, K.S., Ruess, R.W., Hendrick, R.L., & Allen., M.F. 2002. Root respiration in North American forests: effects of nitrogen concentration and temperature across biomes. *Oecologia* **131**: 559-568
- Caldwell, M.M. & Richards, J.H. 1989. Hydraulic lift: water efflux from upper roots improves effectiveness of water uptake by deep roots. *Oecologia* **79**:1-5
- Caldwell, M.M., Dawson, T.E., and Richards J.H. 1998. Hydraulic lift: consequences of water efflux from the roots of plants. *Oecologia* **113**:151-161
- Campbell, G.S. 1985. *Soil physics with Basic*. Elsevier Science Publishing., Amsterdam.
- Campbell, G.S. 1986. *An Introduction to Soil Physics*. Springer Verlag., Berlin
- Campbell, G.S., and Norman, J.N. 1998. *An Introduction to Environmental Biophysics*. And Springer, New York

- Cochard, H., & Tyree, T.E. 1990. Xylem dysfunction in *Quercus*: vessel sizes, tyloses, cavitation, and seasonal changes in embolism. *Tree Physiology* **6**: 393-407
- Dawson, T.E. 1993. Hydraulic lift and water use by plants: implications for water balance, performance and plant-plant interactions. *Oecologia* **95**: 565-574
- Dawson, T.E. 1996. Determining water use trees and forests from isotopic, energy balance and transpiration analysis: the roles of tree size and hydraulic lift. *Tree Physiology* **16**: 263-272
- Ehleringer, J.R. 1985. Annuals and perennials of warm deserts. In: Physiological ecology of North American plant communities, eds Chabot, B.F., Mooney, H.A., Chapman and Hall, New York, pp 162-180
- Ehleringer, J.R., Phillips, S.L., Schuster, W.S.F., and Sandquist, D.R. 1991. Differential utilization of summer rains by desert plants. *Oecologia* **88**: 430-434
- Emerman, S.H. 1996. Towards a theory of hydraulic lift in trees and shrubs. *Sixteenth American Geophysical Union hydrology days*. (ed H.J. Morel-Seytoux), pp147-157. Hydrology Days Publication, Atherton, California
- Eppstein, M.J., & Dougherty, D.E. 1998. Efficient three-dimensional data inversion: soil characterization and moisture monitoring from cross-well ground penetrating radar at the Vermont test site. *Water Resources Research* **34**: 1889-1900
- Fravolini, A., Hultine K.R., Koepke, D.F., and Williams, D.G. 2003. Role of soil texture on mesquite water relations and response to summer precipitation. In: McLaran, M., Ffoliott, P.F., Edminster, C.B. Santa Rita Experimental Range: one hundred years (1903 to 2003) in accomplishments and contributions; conference

proceedings; 2003 October 30-November 1; Tucson, AZ, USDA Forest Service
proceedings RMRS-P-00

Glinski, J. and Lipiec, J. 1990. *Soil Physical Conditions and Plant Roots*. CRC Press,
Boca Raton

Golluscio, R.A., Sala, O.E., and Lauenroth, W.K. 1998. Differential use of large rainfall
events by shrubs and grasses: a manipulative experiment in the Patagonian steppe.
Oecologia **115**: 17-25

Goodrich D.C., Williams D., Unkrich C L., Scott R.L., Hultine K.R., Pool D., Coes A.L.,
Hogan J.F., and Millar S. 2003. Ephemeral channel recharge and
evapotranspiration from near-channel vegetation. In, Recharge and Vadose Zone
Processes: Alluvial Basins of the Southwestern United States, eds. F.M. Phillips,
J.F. Hogan, and B. Scanlon, Water Resources Monograph series, Washington DC,
American Geophysical Union

Hacke, U.G., and Sauter, J.J. 1995. Vulnerability to xylem embolism in relation to leaf
water potential and stomatal conductance in *Fagus sylvatica*, *F. Purpurea*, and
Populus balsamifera. *Journal of Experimental Botany* **46**: 1177-1183

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

- Hacke, U.G., Sperry, J.S., and Pitterman, J. 2000b. Drought experience and cavitation resistance in six shrubs from the Great Basin, Utah. *Basic and Applied Ecology* **1**, 31-41
- Hacke, U.G., Sperry, J.S., Pockman, W.T., Davis, S.D., and McCulloh K.A. 2001. trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* **126**: 457-461
- Hendrick, R.L., and Pregitzer, K.S. 1992. The demography of fine roots in a northern hardwood forest. *Ecology* **73**: 1094-1104
- Hillel, D. 1982. *An Introduction to Soil Physics*. Academic Press. San Diego, CA, USA.
- Houghton, J.T., Miera, G., Filho, B., Callander, B.A., Harris, N., Kattenberg, A., and Maskell, K. 1996. *Climate Change 1995: The Science of Climate Change*. Cambridge University Press, Cambridge, UK
- Hultine, K.H., Williams, D.G., Burgess, S.S.O., and Keefer, T.O. 2003a. Contrasting patterns of hydraulic redistribution in three desert phreatophytes. *Oecologia* **135**: 167-175
- Hultine, K.R., Cable, W.L., Burgess, S.S.O., and Williams, D.G. 2003b. Hydraulic redistribution by deep roots of a Chihuahuan Desert phreatophyte. *Tree Physiology* **23**: 353-360
- Hultine, K.R., Scott, R.L., Cable, W.L., Williams, D.G., and Goodrich, D.C. In Press. Hydraulic redistribution by a dominant warm-desert phreatophyte: seasonal patterns and response to precipitation pulses. *Functional Ecology*

- Huxman, T.E., Wilcox B.P., Scott R., Snyder K., Breshears D., Small E., Hultine K., Pockman W., and Jackson R. In Press. Woody plant encroachment and the water cycle: an ecohydrological framework. *Ecology*
- Jackson, R.B., Canadell, J., Ehleringer, J.R., Mooney, H.A., Sala, O.E., & Schulze, E.D. 1996. A global analysis of root distributions for terrestrial biomes. *Oecologia* **108**: 389-411
- Jackson, R.B., Sperry, J.S., and Dawson, T.E. 2000. Root water uptake and transport: using physiological processes in global predictions. *Trends in Plant Science* **5**: 482-488
- Jaquish, L.L. and Ewers, F.E. 2001. Seasonal conductivity and embolism in the roots and stems of two-clonal ring-porous trees, *Sassafras albidum* (Lauraceae) and *Rhus typhina* (Anacardiaceae). *American Journal of Botany* **88**: 206-212
- Jarvis, P.G., and McNaughton, K.G. 1986. Stomatal control of transpiration: scaling up from leaf to region. *Advances in Ecological Research* **15**: 1-49
- Jury, W.A., Gardner, W.R., and Gardner, W.H. 1991. *Soil Physics*. John Wiley, New York
- Kinraide., T.B. 1984. The influence of soil texture on the vegetation of a grazed short-grass prairie in Colorado. *Southwestern Naturalist* **29**: 277-287
- Kolb, K.J., and Sperry, J.S. 1999. Transport constraints on water use by the Great Basin shrub, *Artemisia tridentata*. *Plant, Cell and Environment* **22**: 925-936
- Lin, G., Phillips, S.L., Ehleringer, J.R. 1996. Monsoonal precipitation responses of shrubs in a cold desert community on the Colorado Plateau. *Oecologia* **106**: 8-17

- Linton, M.J., Sperry, J.S., and Williams, D.G. 1998. Limits to water transport in *Juniperous osteosperma* and *Pinus edulus*: implications for drought tolerance and regulation of transpiration. *Functional Ecology* **12**: 906-911
- Marshall, D.C. 1958. Measurement of sap flow in conifers by heat transport. *Plant Physiology* **33**: 385-396
- McElrone, A.J., Pockman, W.T., Martinez-Viltalta, J., and Jackson R.B. In Review. Xylem structure and function in stems and roots of trees to 20 m depth. *New Phytologist*
- Návar, J., & Bryan, R.B. 1994. Fitting the analytical model of rainfall interception of Gash to individual shrubs of semi-desert vegetation in northeastern Mexico. *Agricultural and Forest Metereorology* **68**: 133-143
- Nobel, P.S. 1994. Root-soil responses to water pulses in dry environments. In *Exploitation of Environmental Heterogeneity by Plants* (eds. M.M. Caldwell and R.W. Pearcy), pp. 285-304. Academic Press, San Diego, CA
- North, G.B., and Nobel, P.S. 1995. Hydraulic conductivity of concentric root tissues of *Agave deserti* Engelm. Under wet and drying conditions. *New Phytologist* **130**: 47-57
- Noy-Meir, E. 1973. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* **4**: 23-51

- Paltineanu, I.C., & Starr, J.L. 1997. Real-time soil water dynamics using multisensor capacitance probes: laboratory calibration. *Soil Science Society of America Journal* **61**: 1576-1585
- Pate, J.S., Jeschke, D.W., Aylward, M.J. 1995. Hydraulic architecture and xylem structure of the dimorphic root systems of South-West Australian species of Proteaceae. *Journal of Experimental Botany* **46**: 907-915
- Pockman, W.T., Sperry, J.S., and O'Leary, W.J. 1995. Sustained and significant negative water pressure in xylem. *Nature* **378**: 715-716
- Pockman, W.T., & Sperry, J.S. 1997. Freezing-induced xylem cavitation and the northern limit of *Larrea tridentata*. *Oecologia* **109**: 19-27
- Pockman, W.T., and Sperry, J.S. 2000. Vulnerability to xylem cavitation and the distribution of Sonoran Desert vegetation. *American Journal of Botany* **87**: 1287-1299
- Rendig V.V., and Taylor, H.M. 1989. *Principles of Soil-Plant Interrelationships*. McGraw Hill, New York
- Richards, J.H. & Caldwell, M.M. 1987. Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. *Oecologia* **73**: 486-489
- Sala, O.E., Lauenroth, W.K., and Parton, W.J. 1992. Long-term soil water dynamics in the shortgrass steppe. *Ecology* **73**: 1175-1181

- Scott R.L., Shuttleworth, W.J., Keefer, T.O., & Warrick, A.W. 2000. Modeling multiyear observations of soil moisture recharge in the semiarid American southwest. *Water Resources Research* **36**: 2233-2247
- Scott, R.L., Watts, C., Garatuza Payan, J., Edwards, E., Goodrich, D.C., Williams, D., and Shuttleworth, J.W. 2003. The understory and overstory partitioning of energy and water fluxes in an open canopy, semiarid woodland. *Agricultural and Forest Meteorology* **114**: 127-139
- Scott, R. L., Edwards, E.A., Shuttleworth, J.W., Huxman, T.E., Watts, C. and Goodrich, D.C. In Press. Interannual and seasonal variation in fluxes of water and carbon dioxide from a riparian woodland ecosystem. *Journal of Agricultural and Forest Meteorology*
- Schenk, H.J., and Jackson, R.B. 2002. The global biogeography of roots. *Ecological Monographs* **72**: 311-328
- Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrell, W.M., Virginia, R.A., and Whitford, W.G. 1990. Biological feedbacks in global desertification. *Science* **247**: 1043-1047
- Schultze, E.D., Caldwell, M.M., Canedell, J., Mooney, H.A., Jackson, R.B., Parson, D., Scholes, R., Sala, O.E., Trimborn, P. 1998. Downward flux of water through roots (i.e. inverse hydraulic lift) in dry Kalahari sands. *Oecologia* **115**: 460-462
- Schwinning, S., and Ehleringer, J.R. 2001. Water use trade-offs and optimal adaptations to pulse-driven arid ecosystems. *Journal of Ecology* **89**: 464-480

- Smith, D.M., Jackson, N.A., Roberts, J.M., & Ong, C.K. (1999) Reverse flow in tree roots and downward siphoning of water by *Grevillea robusta*. *Functional Ecology* **13**:256-264
- Snyder, K.A., and Williams, D.G. 2000. Water sources used by riparian trees varies among stream types on the San Pedro River, Arizona. *Agricultural and Forest Meteorology* **105**: 227-240
- Soil Science Society of America. 1997. Glossary of soil science terms. *Soil Science Society of America*, Madison, WI
- Sorensen, R.B., Jones, T.L., Campbell, G.S., and Montes-Helu, M. 1999. Heat pulse needles to measure pecan tree transpiration. *Applied Engineering in Agriculture* **15**: 651-657
- Sperry, J.S., and Tyree, M.T. 1988. Mechanism of water stressed-induced xylem embolism. *Plant Physiology* **88**: 581-587
- Sperry, J.S., Donnelly, J.R., and Tyree, M.T. 1988. A method for measuring hydraulic conductivity and embolism in xylem. *Plant, Cell and Environment* **11**: 35-40
- Sperry, J.S. 1993. Winter embolism and spring recovery of *Betula cordifolia*, *Fagus grandifolia*, and *Acer rubens*. *Water transport in plants under water stress* (ed. A. Raschi, M. Borghetti, & J. Grace). Cambridge University Press, Cambridge, UK.
- Sperry, J.S., and Saliendra, N.Z. 1994. Intra-and inter-plant variation in xylem cavitation in *Betula occidentalis*. *Plant, Cell and Environment* **17**: 1233-1241
- Sperry, J.S., Nichols, K.L., Sullivan, J.E.M., and Eastlick, S.E. 1994. Xylem embolism

- in ring-porous, diffuse porous, and coniferous trees of northern Utah and interior Alaska. *Ecology* **75**: 1736-1752
- Sperry, J.S. 1995. Limitations on stem water transport and their consequences. In Gartner, B.L.(ed) *Plant stems: physiology and functional morphology*. Academic Press, San Diego, pp 105-124
- Sperry, J.S., Adler, F.R., Campbell, G.S., and Comstock, J.P. 1998. Limitation of plant water use by rhizosphere and xylem conductance: results from a model. *Plant, Cell and Environment* **21**: 347-359
- Sperry, J.S., and Hacke, U.G. 2002. Desert shrub water relations with respect to soil characteristics and plant functional type. *Functional Ecology* **16**: 367-378
- Sperry, J.S., Hacke, U.G., Oren, R., and Comstock, J.P. 2002. Water deficits and hydraulic limits to leaf water supply. *Plant, Cell and Environment* **25**: 251-263
- Swanson, R.H. 1983. Numerical and experimental analyses of implanted-probe heat pulse velocity theory. Ph.D. Thesis, University of Alberta, Edmonton, Alta
- Swanson, R.H., and Whitfield, D.W.A. 1981. A numerical analysis of heat pulse velocity and theory. *Journal of Experimental Botany* **32**: 221-239
- Swanson, R.H. 1994. Significant historical developments in thermal methods for measuring sap flow in trees. *Agricultural and Forest Meteorology* **72**: 113-132
- Topp, G.C., Davis, J.L., and Annan, A.P. 1980. Electromagnetic determination of soil water content: measurements in coaxial transmission lines. *Water Resources Research* **16**: 574-582
- Tyree, M.T., and Sperry, J.S. 1988. Do woody plants operate near the point of

- catastrophic xylem dysfunction caused by dynamic water stress? Answers from a model. *Plant Physiology* **88**: 574-580
- Tyree, M.T., Davis, S.D., and Cochard, H. 1994. Biophysical perspectives of xylem evolution: is there a tradeoff of hydraulic efficiency for vulnerability to dysfunction. *International Association of Wood Anatomists Journal* **14**: 335-360
- Tyree, M.T., Velez, V., and Dalling, J.W. 1998. Root and shoot hydraulic growth dynamics in five neotropical seedlings of different light requirements: scaling to show ecotype differences. *Oecologia* **114**: 293-298
- Walter, H. and Stadelmann, E. 1974. A new approach to the water relations of desert plants. *Desert Biology* **2**: 213-310
- Weltzin, J.F., and McPherson, G.R. 1997. Spatial and temporal soil moisture resource partitioning by leaves and grasses in a temperate savanna, Arizona, USA. *Oecologia* **112**: 156-164
- Widen B., & Majdi, H. (2001) Soil CO² efflux and root respiration at three sites in a mixed pine and spruce forest: seasonal and diurnal variation. *Canadian Journal of Forest Research* **31**: 786-796
- Williams, D.G. and Ehleringer, J.R. 2000. Intra- and interspecific variation for summer precipitation use in pinyon-juniper woodlands. *Ecological Monographs* **70**:517-537
- Williams, D.G. and K.A. Snyder. 2003. Response of woody plants to heterogeneity of

soil water in arid and semi-arid environments. Pages 28-46. In J. Weltzin and G. McPherson (eds.). *Precipitation in terrestrial ecosystems*. University of Arizona Press, Tucson.

Weltzin, J.F., Loik, M.E., Schwinning, S., Williams, D.G., Fay P.A., Haddad, B.M., Harte, J., Huxman, T.E., Knapp, A.K., Lin, G., Pockman, W.T., Shaw, M.R., Small, E.E., Smith, M.D., Smith, S.D., Tissue, D.T., Zak, J.C. 2003. Assessing the response of terrestrial ecosystems to potential changes in precipitation. *BioScience* **53**: 941-952

Zimmermann, M.H., and Jeje, A.A. 1981. Vessel-length distribution in some American woody plants. *Canadian Journal of Botany*. **59**: 1882-1892

Zimmermann, M.H. 1983. *Xylem structure and the ascent of sap*. Springer, Heidelberg, Berlin, New York

SUMMER PRECIPITATION PULSE USE BY A DOMINANT
CHIHUAHUAN DESERT PHREATOPHYTE WITH RESPECT TO SOIL
TEXTURE: IMPLICATIONS FROM EXPERIMENTAL IRRIGATION

Kevin R. Hultine

School of Natural Resources, University of Arizona, Tucson, AZ, 85721, USA

ABSTRACT

Soil texture plays an important role in the distribution and productivity of woody vegetation, and their subsequent impact on ecosystem hydrology. In arid and semi-arid environments, coarse-textured soils are associated with more diverse and extensive woody vegetation cover, possibly as a result of greater infiltration of ephemeral growing season precipitation pulses. In this investigation, we assessed the sensitivity of a dominant Sonoran Desert tree species, velvet mesquite (*Prosopis velutina* Woot.) occurring on sandy-loam (Holocene) and loamy-clay (Pleistocene) soils to large (35 mm) and small (10 mm) growing season moisture inputs. Large and small experimental irrigation pulses were delivered to mature mesquite plants on sandy-loam and loamy-clay soils in June, 2002. Volumetric soil water content (θ), predawn (Ψ_{pd}) and midday (Ψ_{md}) leaf water potential, and tree sap flux were measured immediately prior to, and continuously for two weeks following irrigation. As expected, infiltration of irrigation water to deep soil layers was much greater on the Holocene surface, regardless of pulse size. In fact, there was no measurable infiltration of the small irrigation pulse on the loamy-clay soil. Mesquite plants on the loamy-clay soil that received 10-mm irrigation inputs showed no change in Ψ_{pd} or Ψ_{md} , compared to control plots, indicating there was no utilization of irrigation water. Conversely, mean daily sap flux in mesquite plants on loamy-clay soil that received the large irrigation treatment increased by an average of 50% relative to control trees, and attained a maximum increase of 90% on day three following irrigation. The relative change in daily sap flux was much smaller on the

sandy-loam than on the loamy-clay soil; average increases relative to the control trees were 8 and 1% in large and small irrigation inputs respectively on the Holocene surface, with maximum increases reaching 40, and 26% in large and small irrigation treatments respectively. Results from this investigation demonstrate that mesquite plants on coarse- and fine-textured soils respond differently to small and large growing season precipitation pulses. Differences in pulse use by mesquite plants may play a considerable role in their distribution and productivity across various soil textures given that the annual frequency of small and large precipitation pulses is highly variable and will likely follow predicted changes in global and regional precipitation patterns.

Key words- tree sap flow, plant-soil interactions, *Prosopis velutina*, climate change, woody plant encroachment

INTRODUCTION

Arid and semiarid regions are characterized by a high degree of spatial and temporal heterogeneity in plant water supply. In much of the southwestern United States, vegetation productivity is tightly linked to pulses of summertime precipitation (Noy Meir 1973, Schwinning and Ehleringer 2001). However, the degree of coupling between summer “monsoon” precipitation and ecosystem productivity depends on the seasonal distribution of small and large precipitation pulses and the abundance of shallowly rooted grasses and herbaceous plants and deeply rooted trees and shrubs. Grasses are highly sensitive to small and large pulses of summertime precipitation (Sala et al. 1992, Golluscio et al. 1998). Conversely, mature woody plants that possess comparatively deeper roots are less responsive to small pulses and rely heavily on subsurface water and infrequent large pulse events that percolate beyond the depth of shallow grass roots (Walter and Stadelmann 1974, Snyder and Williams 2000, Schwinning and Ehleringer 2001).

The differential response to pulse size between grasses and woody plants is key to understanding future patterns of ecosystem productivity and hydrology given that climate fluctuations that produce changes in the amount of summertime precipitation are controlled primarily by the frequency of large, rather than small rain events (Sala et al. 1992, Fravolini et al. 2003). Climate models predict that changes in precipitation in the southwestern United States will be significant over the next 100 years (Houghton et al. 1996, Weltzin et al. 2003). Regional changes in climate coupled with shifts in the

relative abundance of grasses and woody plants across the landscape promises to have dramatic implications on ecosystem productivity, hydrology, and biogeochemical cycling.

Superimposed on regional patterns of climate are the effects of soil texture on plant water availability and productivity. In dry climates, coarse-textured soils are associated with more extensive vegetation cover, possibly as a result of less evaporation and greater infiltration (Kinraide 1984; Sperry et al. 1998; Sperry and Hacke 2002). The relatively high saturated hydraulic conductivity of coarse soils allows for greater infiltration to deep soil layers, opposed to running off or ponding. Coarse-textured soils lose more moisture and conductivity at higher soil water potentials (Ψ_s) than fine-textured soils because of the weaker capillary forces retaining water in the larger pore spaces. Dry zones, therefore, tend to form during drought near the surface of coarse soils. Although root water uptake in dry zones may be substantially reduced, they inhibit the movement of deep water to the surface, reducing evaporative loss and allowing the soil to retain a larger proportion of its stored water (Campbell and Norman 1998).

The differences in soil moisture retention favors divergent rooting behaviors between plants on coarse and fine-textured soils suggest that plants occurring on coarse-textured soils will have deeper roots than plants on fine-textured soils (Jackson et al. 2000, Hacke et al. 2000, Sperry and Hacke 2002). The high Ψ_s needed for plant water uptake from coarse soils requires that the roots be in relatively wet soil, and hence grow deep. Vertical root growth may also be enhanced by the ease of penetration through sandy soils. Conversely, the mechanical difficulty of penetrating fine soils, coupled with

the shallower wetting depth, even during wet winters, may create less demand for deep roots in fine-textured soils. Therefore, the sensitivity of mature woody plants to small and large precipitation pulses may not be equal across soil textures.

In this investigation, we measured leaf water potential and used the heat ratio method (HRM) to measure sap flow to assess the response of the leguminous tree species, velvet mesquite (*Prosopis velutina* Woot.) to small (10 mm) and large (35 mm) irrigation treatments at two sites varying in soil texture on the Santa Rita Experimental Range in southeastern Arizona, USA. One site was on a young Holocene (4000 to 8000 ybp) geomorphic surface characterized by sandy-loam soils. The other site was on a mid-Pleistocene geomorphic surface characterized by loamy-clay soils. The goal of this investigation was to assess whether the interaction between soil texture and precipitation event size mediates patterns of water use in mature mesquite trees at an upland site where groundwater is likely unavailable. We predicted that 1) mesquite plants at the loamy-clay site would be less responsive to a small pulse event than mesquite plants at the sandy-loam site due to the lower infiltration rates that occur in loamy-clay soils, and 2) mesquite plants on loamy-clay soils would demonstrate a greater relative response to a large pulse event due to a larger root biomass in the zone of infiltration. In a separate study, we used a weighing lysimeter to determine potential offsets and non-linearity between transpiration rates estimated with HRM and measured gravimetric water loss in a potted mesquite. Data from this investigation was used to assess the potential pitfalls of using an invasive sap flow technique in ring-porous wood.

MATERIALS AND METHODS

Site description

The study was conducted at two sites located on the Santa Rita Experimental Range (SRER) in southeastern Arizona, USA. Two upland sites, one representing a young Holocene (4,000 to 8,000 ybp) geomorphic surface, and one site representing a mid-Pleistocene (200,000 to 300,000 ybp) geomorphic surface were selected on the SRER. The Holocene surface (31° 47'N, 110° 50' W, 1190 m elevation) was characterized by sandy-loam soils (sand, silt, and clay fractions are presented in Table 1) with relatively high saturated hydraulic conductivity. The overstory was dominated by a mixed-age stand of *Prosopis velutina* Woot. The understory was dominated by *Eragrostis lehmanniana* Nees. intermixed with other grasses. The mid-Pleistocene (31° 47'N, 110° 54' 1090 m elevation) site was located 5 km from the Holocene site and had loamy-clay soils (Table 1) with comparatively low saturated hydraulic conductivity. The overstory was dominated by a mixed age stand of *P. velutina*, however, the number of stems per hectare was substantially lower on the Pleistocene than on the Holocene site (60 and 540 stems ha⁻¹, respectively). The understory vegetation on the Pleistocene surface was much more sparse than on the Holocene and was dominated by *E. lehmanniana*. Mean annual precipitation at both sites is about 400 mm with approximately 56% falling during the summer monsoon (July-September). Mean annual air temperature on the SRER is 32 °C during summer, while mean nighttime temperature during winter is 5 °C.

Irrigation treatment

Eighteen mature velvet mesquite trees were selected at each site and six replicates were randomly assigned to large (35 mm), small (10 mm), or no irrigation (control) treatments. Five-meter radius watering plots were established around each tree assigned to an irrigation treatment. The perimeter of each plot was trenched to a depth of five cm to prevent runoff from the plot, and a steel fence was erected around all experimental plots to prevent trampling by cattle. Water was delivered to the plots using a gas powered pump on the evening (to reduce surface evaporation) of June 24, 2002.

Volumetric soil water content measurements

Volumetric soil water content (θ) was measured to trace the movement of irrigation water through the soil profile. Three, one by three-meter plots were trenched to a depth of one meter at each site. Calibrated time domain reflectometry (TDR) sensors were installed in each trench in a vertical profile at 10-, 20-, 30-, 40-, and 50-cm depths (one sensor per depth). Installation was accomplished by gently tapping the sensors into the side-walls of each trench. 10-cm long pilot holes were drilled to assist installation in the loamy-clay soil on the Pleistocene surface. TDR sensors were constructed of dual 3-mm diameter, 17.5-cm long stainless steel welding rods. The rods were molded in a fiberglass resin epoxy (TAP Plastics, Dublin, CA, USA) with a rod separation of 2 cm. Electromagnetic waveforms were measured from each sensor the day before irrigation and on days 1, 2, 4, 6, 8, 11, and 14 following irrigation, using a Rg 58/U co-axial cable

connected to a Campbell TDR 100 (Campbell Scientific, Logan, UT, USA). Volumetric soil water content was calculated using the Topp Equation (Topp et al. 1980).

Sap flow experiments

Nine trees representing three replicates of each irrigation treatment were selected at each site for sap flow measurements. Mean basal diameters, sapwood area (A_s), leaf area (A_l), and sapwood area to leaf area ratios ($A_s:A_l$) of trees at both sites are presented in Table 2. We chose the heat ratio method (HRM, Burgess et al. 1998, 2001) to measure sap flux because of its accuracy at low fluxes relative to other methods Burgess et al. 2001). A single heat ratio probe set was inserted into the xylem of the main stem of each tree. A stainless steel drill guide was placed over an exposed section of sapwood to ensure accurate placement of the probe sets. The probe sets were constructed by Thermal Logic (Pullman WA, USA) and consisted of three 35-mm long stainless steel probes spaced 6 mm apart. The center probe contained an Evanohm 44- Ω line heater, while the two outside probes contained three chromel-constantan thermocouple sensors spaced 5, 10, and 20 mm from the base of the probe. After probe installation, the stems were covered with aluminum foil to prevent radiant heating by direct sunlight. Measurements were recorded continuously every half-hour for three weeks starting June 22, 2002 (two days before irrigation), except for trees that received the small pulse plots at the Pleistocene, where all the probe sets were mechanically destroyed by cattle six days into the experiment. Measurements were recorded with Campbell Scientific CR10X data loggers and control systems (Campbell Scientific, Logan UT, USA). A 6-second heat

pulse was produced to heat the sapwood and temperatures were recorded during the period in which the ratios of the down- and upstream temperatures were most constant (between 40 and 80 s after the heat pulse). The heat pulse velocity (V_h ; cm s^{-1}) was calculated according to Burgess et al. (1998):

$$(1) \quad V_h = \frac{k}{x} \ln\left(\frac{v_1}{v_2}\right)$$

where k is the thermal diffusivity of wet wood, x is the distance between the line heater and the thermocouple sensors, and v_1 and v_2 are the increases in temperature at equidistant points downstream and upstream, respectively, x cm from the heater. Errors arising from small inaccuracies in probe placement were corrected at the conclusion of the study by severing the roots to stop all sap flow. Probe spacing error was determined according to Burgess et al. (2001):

$$(2) \quad 4kt \ln\left(\frac{v_1}{v_2}\right) = (x_1^2) - (x_2^2) + 2V_h(x_1 - x_2)$$

where x_1 and x_2 are distances in cm of the down- and upstream probes, respectively, and t is the median measurement time (in this case, 60 s) after the release of the heat pulse (Marshall 1958). At $V_h = 0$, Eq. 2 yields:

$$(3) \quad x_2 = \sqrt{4kt \ln\left(\frac{v_1}{v_2}\right) + x_1^2}$$

where x_2 is designated the incorrectly spaced probe, and x_1 is assumed to be correctly spaced at 6 mm. Because it is unknown which probe is incorrectly spaced, or whether both probes are incorrectly spaced, Eq. 3 was solved for x_1 and x_2 and the two solutions

were averaged to generate an intermediate solution for both probes (Burgess et al. 1998). The thermal diffusivity of wet wood (k) was calculated empirically from Marshall (1958):

$$(4) \quad k = \frac{k_{gw}}{\rho c} 10000$$

where k_{gw} is the thermal conductivity ($\text{J m}^{-1} \text{s}^{-1} \text{°C}^{-1}$), ρ is the density (kg m^{-3}) (cf. Burgess et al. 2001) and c is the specific heat capacity ($\text{J kg}^{-1} \text{°C}^{-1}$) of fresh sapwood. We calculated k_{gw} from:

$$(5) \quad k_{gw} = k_w m_c \frac{\rho_b}{\rho_w} + k_{dw} (1 - m_c \frac{\rho_b}{\rho_w})$$

where k_w and k_{dw} are the thermal conductivities of water ($6.025 \times 10^{-1} \text{J m}^{-1} \text{s}^{-1} \text{°C}^{-1}$) and dry wood respectively, m_c is the moisture fraction of fresh wood (kg kg^{-1}), ρ_b is the *basic* density (dry weight/ fresh volume) of sapwood, and ρ_w is the density of water (Swanson 1983, Burgess et al. 2001).

Drilling holes and inserting probes inevitably causes extensive mechanical damage to xylem tissues. We corrected for wounding using a “finite-element” numerical model generated by Burgess et al. (2001):

$$(6) \quad V_c = aV_h + bV_h^2 + cV_h^3$$

where the coefficients a , b , and c , are derived from numerical analysis of the effect of wounding on V_h for varying wound widths. (Note that for negative values of V_h , the form $V_c = aV_h - bV_h^2 - cV_h^3$ should be used.) Coefficients in Eq. 6 were derived over the measurement time of $t = 40\text{-}80$ s after the release of the heat pulse. We estimated the wound width by measuring the discoloration of sapwood from the formation of tyloses around the probe insertion points. Wound diameters ranged from 0.19 cm to 0.30 cm.

Corrected values of heat pulse velocity (V_c) were converted to sap velocity (V_s) (cm hr^{-1}) according to Barrett et al. (1995):

$$(7) \quad V_s = \frac{V_c \rho_b (c_w + m_e c_s)}{\rho_s c_s}$$

where c_w and c_s are the specific heat of dry wood ($1200 \text{ J kg}^{-1} \text{ }^\circ\text{C}^{-1}$ at $20 \text{ }^\circ\text{C}$, Becker and Edwards 1999), and sap (assumed to equal that of water, $4182 \text{ J kg}^{-1} \text{ }^\circ\text{C}^{-1}$ at $20 \text{ }^\circ\text{C}$), and ρ_s is the density of sap (assumed to equal that of water, 998 kg m^{-3} at $20 \text{ }^\circ\text{C}$). Sap flow (kg d^{-1}) was calculated by multiplying the cross sectional sapwood area under the bark (πr^2) by V_s . Because invasive methods such as HRM often underestimate sap flow rates in ring-porous species (Swanson 1994), we reported the percent difference between control and irrigated trees before and after irrigation calculated from:

$$(8) \quad \left(\frac{V_{s,n}}{V_{s,0}} - \frac{V_{s,n\text{control}}}{V_{s,\text{control}0}} \right) * 100$$

where the subscripts n , 0 , and control represent the mean sap velocity on the n th day following irrigation, the mean sap velocity measured prior to irrigation, and the mean sap velocity of trees that received no irrigation, respectively.

HRM estimates of sap flow were compared with gravimetric water loss using a weighing lysimeter in a separate greenhouse study to test for potential inaccuracies in sapflow. A single potted mesquite having a basal diameter of 5-cm was placed on an electronic weighing lysimeter (Pennsylvania 6400, Pennsylvania Scale Co., Lancaster PA, USA). The tree was watered every 48 hours to field saturation, and the 60 cm diameter pot was covered with a thick plastic to prevent soil evaporation. The tree was

instrumented with a single HRM sensor at its base, and sap flow was measured using the protocol described above. Sap flow and gravimetric water loss were measured concurrently using a Campbell CR10x data logger and control system. Measurements were taken during three, 72- to 90-hour intervals over a 30-day period to test whether inaccuracies in sap flow estimates changed over time.

Leaf water potential measurements

Predawn Ψ_{pd} and midday Ψ_{md} leaf xylem water potentials were measured on all experimental trees on the day prior to irrigation, and on days 1, 2, 4, 6, 8, 11, and 14 following irrigation. A single shoot tip from each tree was cut with a sharp razor blade and measured at predawn between 0200 and 0400 hours, and at midday between 1100 and 1300 hours. A Scholander-type pressure chamber (PMS Instruments, Corvallis, OR, USA) was used for all measurements.

Statistical analysis

The field experiment consisted of a randomized 2 by 3 factorial design with two sites, three treatments, and three to four replicates for each site by treatment combination. Regression analysis was performed to determine the mean response of sap flow against irrigation treatment, followed by regression analysis to relate site differences in sap flow responses to irrigation. Within, and between site differences were determined using analysis of covariance. Due to mechanical damage to the sap flow probes, analysis did not include data from the small irrigation treatment on the loamy-clay soil. Regression

analysis was also performed to correlate sap flow with gravimetric water loss.

Multivariate analysis for repeated measures (MANOVA) was used to test the effect of site, treatment, time, and their interactions on Ψ_{pd} and Ψ_{md} . A least significant difference (LSD) test was performed within the MANOVA framework to identify specific differences in treatment effects across sites. JMP 4.0 for Windows (SAS Institute) was used for all statistical analyses.

RESULTS

As expected, there was a much larger relative change in volumetric water content on the Holocene surface than on the Pleistocene surface in response to the small (10 mm) and large (35 mm) irrigation pulses (Figure 1a-d). Moreover, the wetting front advanced to deeper soils at the Holocene surface than at the Pleistocene surface (Figure 1a-d).

Changes in θ were small at the sandy-loam site in response to the 10-mm pulse.

However, the wetting front reached 50 cm on day 14 following irrigation (Figure 1a).

Within the first 24 hours, θ in sandy-loam soils increased dramatically in the upper 30 cm in response to the large pulse. Increases in θ were less significant but present at 50 cm (Figure 1b). Patterns of infiltration were substantially different in loamy-clay soils following irrigation. In fact, we detected no infiltration at 10 cm in response to the small pulse (Figure 1c). Small increases in θ were detected following the large pulse; at 10 cm, θ increased from 1.6 to 3.3% eight days after the release of the pulse. The wetting front advanced to 30 cm by day 14, as θ increased slightly from an initial value of 7.6% to 8.1% (Figure 1d).

Initial predawn and midday leaf xylem water potentials were substantially higher at the loamy-clay site than at the sandy-loam site. Mean predawn water potentials increased dramatically at both sites in response to the large pulse and achieved a maximum Ψ_{pd} four days after the release of the pulse (Figure 2a and c, Fravolini, unpublished data). There were no apparent site differences in response to the large irrigation ($F_{1,18} = 0.51$, $P = 0.48$, from a linear contrast). Trees that received the 10-mm

pulse also achieved maximum mean Ψ_{pd} on day four after the pulse. However, unlike the large pulse, there were significant site differences in response to the small pulse ($F_{1,18} = 19.09$, $P = 0.0004$, from a linear contrast). The change in Ψ_{pd} on the loamy-clay surface was barely detectable, suggesting that 10 mm of irrigation did little to enhance the water balance of mesquite plants on these soils (Figure 2c).

Patterns of Ψ_{md} were similar to patterns of Ψ_{pd} . Again there were no apparent site differences in response to the large pulse ($F_{1,18} = 0.03$, $P = 0.91$, from a linear contrast, Fravolini, unpublished data), and trees that received the large pulse achieved maximum midday water potentials on day eight at the sandy-loam site and day two at the loamy-clay site following the pulse (Figure 2b and d). Conversely, trees at the sandy-loam site showed a greater response to the small pulse than trees at the loamy-clay site ($F_{1,18} = 5.80$, $P = 0.027$, from a linear contrast). Changes in mean Ψ_{md} of mesquite plants on sandy-loam soils that received the 10-mm pulse were relatively small and mirrored changes in Ψ_{md} of mesquite plants that received no water (Figure 2b). Midday Ψ of trees on loamy-clay soils mesquite plants showed little or no change over time in response to the 10-mm pulse (Figure 2d).

Although, within treatment variability was high, we were able to detect a response to the 35-, and 10-mm irrigation treatments. Maximum sap flow was achieved in all treatments three days after the release of the experimental pulse (Figure 3a and b). Regardless of treatment or soil type, mean sap flow rates never rose above 0.85 kg day^{-1} . We suspect that these data represent a significant underestimation of tree sap flow due to the uncertainties of mechanical wounding that occurs in ring-porous wood during probe

installation, and/or the spacing of the thermocouples within the inserted needles did not capture the most conductive region of the wood matrix (see below). Trees on the loamy-clay soil showed a greater response to the 35-mm pulse than trees given the same 35-mm pulse on sandy-loam soil ($F_{3,80} = 37.09$, $P < 0.0001$, from ANCOVA, Figure 3c). At the loamy-clay site, sap flow in trees that received 35 mm of irrigation increased 90% three days following irrigation, and averaged 50% over the 14-day study period relative to trees that received no irrigation. At the sandy-loam site, sap flow in trees that received large and small irrigation treatments respectively, increased by 40 and 26% by day three, and averaged 8 and 1% over the course of the study relative to the control trees (Figure 3c). There was a moderate difference in the relative change in sap flow between the two irrigation treatments ($F_{3,80} = 3.91$, $P = 0.0514$, from ANCOVA, Figure 3c).

In a separate study, we set out to test for potential offsets between measured rates of sap flow using HRM and actual rates of transpiration by measuring gravimetric water loss in a potted mesquite tree having a similar basal diameter as trees measured at the SRER. Rates of sap flow in the potted mesquite were comparable to rates measured at the SRER. However, we found that sap flow was grossly underestimated using HRM in the potted mesquite (Figure 4). An analysis of the slope revealed that the relationship of the offset was linear (Est. = $0.105 + 0.022 * \text{Meas}$, $R = 0.33$, $F_{684} = 336$, $P < 0.0001$, Figure 5), suggesting that measured changes in relative sap flow between watering treatments at the SRER were not an artifact of errors in sap flow techniques.

DISCUSSION

The productivity and distribution of vegetation in arid and semi-arid environments is primarily limited by water availability. In most arid regions, inputs of growing season precipitation are characterized by ephemeral pulses that are highly variable in timing, duration, and intensity. Plants, therefore, must be adapted to utilize precipitation that is highly unpredictable. In this investigation, we set out to test the sensitivity of the leguminous tree species velvet mesquite (*Prosopis velutina* Woot.) occurring on sandy-loam and loamy-clay soils to small and large precipitation events. Mesquite trees on loamy-clay soils showed a greater response to a large pulse (35 mm) compared to those on sandy-loam soils (Figure 3c). However, mesquite plants on loamy-clay soils appeared insensitive to small pulses (10 mm), whereas mesquite plants on sandy-loam soils were somewhat sensitive to a 10-mm pulse (Figure 3c).

Soil texture plays a key role in plant-water relations. In dry climates, coarse soils are associated with more extensive vegetation cover, possibly due to greater availability of water in these soils. Coarse-textured soils hold water at relatively high Ψ_s due to the large pore spaces associated with coarse soils (Jury et al. 1991). Conversely, the smaller pore spaces in finely textured soils hold more water at lower Ψ_s . Moreover, water in coarse soils percolates to deeper layers in the soil profile, and is less exposed to evaporative processes at the soil surface compared to that in fine-textured soils. This may, in part, explain why mesquite trees at the SRER occur at much higher densities on coarse-textured Holocene surfaces than on fine-textured Pleistocene surfaces.

Plants typically grow more extensive and deeper root systems in coarse-textured soils than in fine-textured soils (Jackson et al. 2000, Hacke et al. 2000, Sperry and Hacke 2002). Such trends have been shown in mature loblolly pine trees in the southeastern United States (Hacke et al. 2000), and in Great Basin Desert shrubs (Sperry and Hacke 2002). It is plausible that mesquite trees on the loamy-clay surface had a substantially greater proportion of their roots in the upper 30 cm of the soil profile compared to trees on the Holocene surface. A larger proportional root area near the surface would facilitate a greater response to large precipitation events, assuming that other physiological factors such as root hydraulic characteristics and stomatal sensitivity remain fairly constant across sites. In the present study, infiltration following the large experimental pulse barely reached 30 cm on the Pleistocene surface, whereas the wetting front on the Holocene surface was easily detectable at 50 cm following irrigation. Nevertheless, mesquite trees on the loamy-clay soil were substantially more sensitive to irrigation than trees on the sandy-loam soil, suggesting that they maintain a greater proportion of their root systems in shallow soil layers. In systems where mesquite plants have access to deep water (i.e. groundwater) transpiration remains fairly constant during rain-drought cycles (Scott et al. 2003), although the trees may shift water sources when shallow soil water becomes available (Snyder and Williams 2000).

Conversely, mesquite plants on sandy-loam soils appeared more sensitive to the 10-mm pulse than mesquite plants on loamy-clay soils. In fact, although our sap flow estimates were circumvented by mechanical damage to the sensors, trees on the loamy-clay surface apparently did not utilize the small pulse at all. Predawn and midday leaf

water potentials at the loamy-clay site did not change in response to the irrigation treatment, indicating that water balance was unaffected by the small pulse. Further, a deuterium spike added to the irrigation water was barely present in the xylem water of mesquite plants on loamy-clay soils following the small pulse (Fravolini et al., unpublished data). Finally, there was no measurable infiltration of the pulse at 10 cm or below, whereas, on the Holocene surface, the wetting front from the small pulse reached 50 cm. Mesquite roots rarely occur at either site above 10 cm (personal observation), possibly due to high soil temperatures that occur in shallow soils during summer. Thus, it appears likely that mesquite plants at the loamy-clay site rely exclusively on winter moisture or on large pulses of summertime precipitation.

To what extent are the observed patterns caused by genetic variation? To our knowledge velvet mesquite plants at the SRER have not undergone rigorous testing of the genetic variation in traits such as root distribution and function. It is plausible that mesquite seeds have been readily dispersed between the two study sites given the small distance (approximately 5 km) and lack of significant geologic barriers between sites. Nevertheless, selective pressures caused primarily by differences in soil hydraulic properties may have generated substantial genetic variation across the two study sites. Future work involving common garden studies would greatly improve our ability to predict water use patterns by mesquite plants and their subsequent impact on the hydrologic cycle at large scales.

Differences in the utilization of growing season precipitation pulses across soil textures may have important implications for the encroachment and establishment of

woody plants at the landscape level (Huxman et al. In Press). The amount of summertime precipitation in semi-arid environments is strongly coupled to the frequency of large pulses of precipitation (Sala et al. 1992, Golluscio et al. 1998). In southeastern Arizona, for example, total annual monsoon precipitation is strongly correlated with infrequent, large precipitation pulses (>20 mm), while there is no correlation between total annual monsoon precipitation and frequently occurring small rainfall events (<10 mm) (Fravolini et al. 2003). Therefore, predicted changes in the precipitation amount that falls in the southwestern United States over the next century (Houghton et al. 1996) may have a dramatic impact on the encroachment, establishment, and productivity of woody plants in southwestern ecosystems. On fine-textured soils, reduced monsoonal precipitation may have a significant negative impact on woody plants that rely on large precipitation events. Conversely, decreases in monsoonal precipitation could favor woody plants on coarse-textured soils if reduced precipitation inhibits the establishment of co-occurring grasses and herbaceous plants that could utilize moisture that would otherwise percolate to deeper soils layers.

The near immediate response of mesquite plants to experimental irrigation was somewhat unexpected given that there had been no appreciable precipitation over the last several weeks before the experiment. Plants are often unresponsive to growing season precipitation that immediately follows extended periods of drought (Lin et al. 1996, Williams and Ehleringer 2000, Hultine et al. 2003). Responses to precipitation after extended drought requires plants to either develop “rain” roots as water becomes available (Nobel 1994), or remain hydraulically conductive (Tyree and Sperry 1988,

Jackson et al. 2000). Shallow roots of velvet mesquite at the SRER are highly resistant to cavitation, and they operate with a wide safety margin (the difference between Ψ observed in the field and the critical Ψ that induces hydraulic failure via cavitation)(Hultine et al. unpublished data). Thus, it is plausible that mesquite roots were fairly conductive prior to the pulse experiment, thereby allowing the immediate uptake of the irrigation water.

Mesquite sap flow measured at the SRER was likely grossly underestimated by the HRM approach. Sap flow estimates in ring porous species (i.e. mesquite) are often inaccurate when measured with invasive methods, such as HRM (Swanson 1994, Sorensen et al. 1999, Goodrich et al. 2004). One possible explanation for these inaccuracies is the effect of wounding during the insertion of sap flow needles. Finite element numerical models have proven successful for compensating for wound effect in diffuse porous species (Swanson and Whitfield 1981, Burgess et al 2001). However, such models have not proven successful for use with ring-porous wood. This may be due to excessive wounding of the large, highly conductive xylem elements that characterize ring-porous wood. Another possible explanation is that the spacing of the paired thermocouples within the inserted needles may not capture the most conductive region of the wood matrix. Almost all sap movement in ring-porous wood occurs in a very narrow band, usually the outermost growth ring. Therefore it is possible, even likely, that even the outermost thermocouple junction (in this case, 5 mm) was not centered within the most conductive xylem.

In the present study, HRM measurements of sap flow were more than an order of magnitude below the actual rate of tree water loss. Surface mounted sap flow gauges (at the possible expense of reduced sensitivity to low rates of sap flow) may prove more accurate in ring porous wood relative to invasive techniques. Nevertheless, the linear offset between HRM estimates of transpiration and actual transpiration strongly suggests that measured changes in sap flow observed at the SRER were not an artifact of measurement error. Clearly, more work is needed to improve the accuracy of invasive sap flow techniques in ring-porous species.

We observed considerable differences in pulse utilization by velvet mesquite plants occurring on sandy-loam and loamy-clay soils. Mesquite plants on the loamy-clay surface were substantially more responsive to the large irrigation (35 mm) treatment, whereas, mesquite plants on the sandy-loam surface were more responsive to the small irrigation (10 mm) treatment. In fact, mesquite plants on the loamy-clay surface showed no sensitivity to the small irrigation treatment. Although it is unclear whether different pulse utilization strategies translate to differences in fitness, productivity and resource allocation, results from this investigation show that soil texture could play a considerable role in patterns of ET on many scales.

LITERATURE CITED

- Barrett, D.J., Hatton, T.J., Ash, J.E., Ball, M.C. 1995. Evaluation of the heat pulse velocity technique for measurement of sap flow in rainforest and eucalypt forest species of south-eastern Australia. *Plant, Cell and Environment* **18**: 463-469
- Becker, P., and Edwards, W.R.N. 1999. Corrected heat capacity of wood for sap flow calculations. *Tree Physiology* **19**: 767-768
- Burgess, S.S.O., Adams, M.A., Turner N.C., and Ong, C.K. 1998. The redistribution of soil water by tree root systems. *Oecologia* **115**: 306-311
- Burgess, S.S.O., Adams, M.A., Turner, N.C., Beverly, C.R., Ong, C.K., Khan, A.A.H., and Bleby, T.M. 2001 An improved heat pulse method to measure slow and reverse flow in woody plants. *Tree Physiology* **21**: 589-598
- Campbell, G.S., and Norman, J.N. 1998. *An Introduction to Environmental Biophysics*. And Springer, New York
- Fravolini, A., Hultine K.R., Koepke, D.F., and Williams, D.G. 2003. Role of soil texture on mesquite water relations and response to summer precipitation. In: McLaran, M., Ffoliott, P.F., Edminster, C.B. Santa Rita Experimental Range: one hundred years (1903 to 2003) in accomplishments and contributions; conference proceedings; 2003 October 30-November 1; Tucson, AZ, USDA Forest Service proceedings RMRS-P-00
- Golluscio, R.A., Sala, O.E., and Lauenroth, W.K. 1998. Differential use of large rainfall

events by shrubs and grasses: a manipulative experiment in the Patagonian steppe.

Oecologia **115**: 17-25

Goodrich D.C., Williams D., Unkrich C L., Scott R.L., Hultine K.R., Pool D., Coes A.L., Hogan J.F., and Millar S. 2004. Ephemeral channel recharge and evapotranspiration from near-channel vegetation. In, Recharge and Vadose Zone Processes: Alluvial Basins of the Southwestern United States, ed. F.M. Phillips, J.F. Hogan, and B. Scanlon, Water Resources Monograph series, Washington DC, American Geophysical Union

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

Houghton, J.T., Miera, G., Filho, B., Callander, B.A., Harris, N., Katttenberg, A., and Maskell, K. 1996. Climate Change 1995: The Science of Climate Change. Cambridge University Press, Cambridge, UK

Hultine, K.R., Cable, W.L., Burgess, S.S.O., and Williams, D.G. 2003. Hydraulic redistribution by deep roots of a Chihuahuan Desert phreatophyte. *Tree Physiology* **23**: 353-360

Huxman, T.E., Wilcox B.P., Scott R., Snyder K., Breshears D., Small E., Hultine K., Pockman W., and Jackson R. (In Press) Woody plant encroachment and the water cycle: an ecohydrological framework. *Ecology*

Jackson, R.B., Sperry, J.S., and Dawson, T.E. 2000. Root water uptake and transport:

- using physiological processes in global predictions. *Trends in Plant Science* **5**: 482-488
- Jury, W.A., Gardner, W.R., and Gardner, W.H. 1991. *Soil Physics*. John Wiley, New York
- Kinraide., T.B. 1984. The influence of soil texture on the vegetation of a grazed short-grass prairie in Colorado. *Southwestern Naturalist* **29**: 277-287
- Lin, G., Phillips, S.L., Ehleringer, J.R. 1996. Monosoonal precipitation responses of shrubs in a cold desert community on the Colorado Plateau. *Oecologia* **106**: 8-17
- Marshall, D.C. 1958. Measurement of sap flow in conifers by heat transport. *Plant Physiology* **33**: 385-396
- Nobel, P.S. 1994. Root-soil responses to water pulses in dry environments. In *Exploitation of Environmental Heterogeneity by Plants* (eds. M.M. Caldwell and R.W. Pearcy), pp. 285-304. Academic Press, San Diego, CA
- Noy-Meir, E. 1973. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* **4**: 23-51
- Sala, O.E., Lauenroth, W.K., and Parton, W.J. 1992. Long-term soil water dynamics in the shortgrass steppe. *Ecology* **73**: 1175-1181
- Scott, R.L., Watts, C., Garatuza Payan, J., Edwards, E., Goodrich, D.C., Williams, D., and Shuttleworth, J.W. 2003. The understory and overstory partitioning of energy and water fluxes in an open canopy, semiarid woodland. *Agricultural and Forest Meteorology* **114**: 127-139
- Schwinning, S., and Ehleringer, J.R. 2001. Water use trade-offs and optimal adaptations

- to pulse-driven arid ecosystems. *Journal of Ecology* **89**: 464-480
- Snyder, K.A., and Williams, D.G. 2000. Water sources used by riparian trees varies among stream types on the San Pedro River, Arizona. *Agricultural and Forest Meteorology* **105**: 227-240
- Sorensen, R.B., Jones, T.L., Campbell, G.S., and Montes-Helu, M. 1999. Heat pulse needles to measure pecan tree transpiration. *Applied Engineering in Agriculture* **15**: 651-657
- Sperry, J.S., Adler, F.R., Campbell, G.S., and Comstock, J.P. 1998. Limitation of plant water use by rhizosphere and xylem conductance: results from a model. *Plant, Cell and Environment* **21**: 347-359
- Sperry, J.S., and Hacke, U.G. 2002. Desert shrub water relations with respect to soil characteristics and plant functional type. *Functional Ecology* **16**: 367-378
- Swanson, R.H. 1983. Numerical and experimental analyses of implanted-probe heat pulse velocity theory. Ph.D. Thesis, University of Alberta, Edmonton, Alta
- Swanson, R.H., and Whitfield, D.W.A. 1981. A numerical analysis of heat pulse velocity and theory. *Journal of Experimental Botany* **32**: 221-239
- Swanson, R.H. 1994. Significant historical developments in thermal methods for measuring sap flow in trees. *Agricultural and Forest Meteorology* **72**: 113-132
- Topp, G.C., Davis, J.L., and Annan, A.P. 1980. Electromagnetic determination of soil water content: measurements in coaxial transmission lines. *Water Resources Research* **16**: 574-582
- Tyree, M.T., and Sperry, J.S. 1988. Do woody plants operate near the point of

catastrophic xylem dysfunction caused by dynamic water stress? Answers from a model. *Plant Physiology* **88**: 574-580

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

Williams, D.G. and Ehleringer, J.R. 2000. Intra- and interspecific variation for summer precipitation use in pinyon-juniper woodlands. *Ecological Monographs* **70**: 517-537

Weltzin, J.F., Loik, M.E., Schwinning, S., Williams, D.G., Fay P.A., Haddad, B.M., Harte, J., Huxman, T.E., Knapp, A.K., Lin, G., Pockman, W.T., Shaw, M.R., Small, E.E., Smith, M.D., Smith, S.D., Tissue, D.T., Zak, J.C. 2003. Assessing the response of terrestrial ecosystems to potential changes in precipitation. *BioScience* **53**: 941-952

FIGURE CAPTIONS

Figure 1 – Volumetric soil water content (θ) of Pleistocene and Holocene surfaces at the Santa Rita Experimental Range measured with time domain reflectometry in late June and early July, 2002. Measurements were taken at 10, 20, 30, 40, and 50 cm depths the day prior to the release of an experimental pulse (Day 0), and on days 1, 4, 8, and 14 after the release of the pulse. a. Volumetric water content in response to a 10-mm pulse on a sandy-loam, Holocene surface, b. θ in response to a 35-mm pulse on a sandy-loam, Holocene surface, and c. θ in response to a 10-mm pulse on a loamy-clay, Pleistocene surface, d. θ in response to a 35-mm pulses on a sandy-loam Holocene surface.

Figure 2 – Mean predawn and midday leaf xylem water potential (Ψ_x) measured on velvet mesquite trees at the Santa Rita Experimental Range in late June and early July, 2002 (Fravolini, unpublished data). Measurements were taken on trees assigned to either 10-mm irrigation, 35-mm irrigation, or control treatments (no irrigation). The X axis represents the number of days after the irrigation (Day 0 is the day prior to irrigation). a. Predawn Ψ_x on Holocene surfaces, b. midday Ψ_x on Holocene surfaces, c. predawn Ψ_x on Pleistocene surfaces, d. midday Ψ_x on Pleistocene surfaces. Error bars represent the standard error of the mean.

Figure 3 – Mean daily rates of sap flow in velvet mesquite trees at the Santa Rita Experimental Range in response to experimental irrigation. Trees received either, 35

mm, 10 mm, or no irrigation. Mean sap flow values (kg day⁻¹) were summed from measurements conducted every 0.5 hours between 0600 and 2030 hours. The X axis represents the number of days after the irrigation (Day 0 is the day prior to irrigation). Error bars represent the standard error of the mean. a. Sap velocity measured on mesquite plants in sandy-loam (Holocene) soils, b. Sap velocity measured on mesquite plants in loamy-clay (Pleistocene) soils, c. Relative difference in mean tree sap velocity between watered velvet mesquite plants and un-watered mesquite plants on loamy-clay and sandy-loam soils.

Figure 4 – Example of the relationship between basal transpiration measured on a mesquite tree using the heat ratio method (HRM), and gravimetric water loss measured in the same tree with a weighing lysimeter.

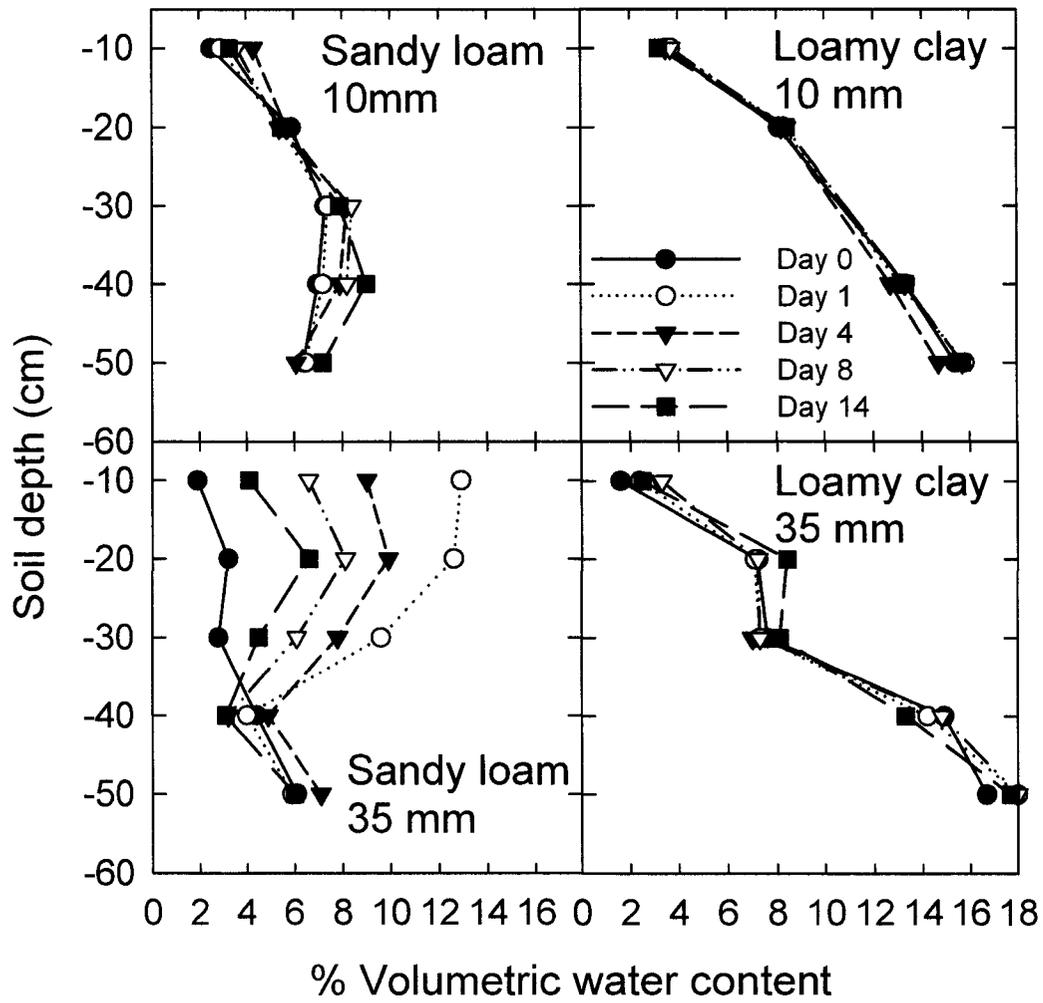
Figure 5 – Correlation between estimated transpiration and measured gravimetric water loss on a single mesquite tree (Est. = $0.105 + 0.022 * \text{Meas}$, $R = 0.57$, $F_{684} = 336$, $P < 0.0001$). Transpiration was estimated from measurements of basal sap flow using the heat ratio method (HRM). Gravimetric water loss was measured with a weighing lysimeter.

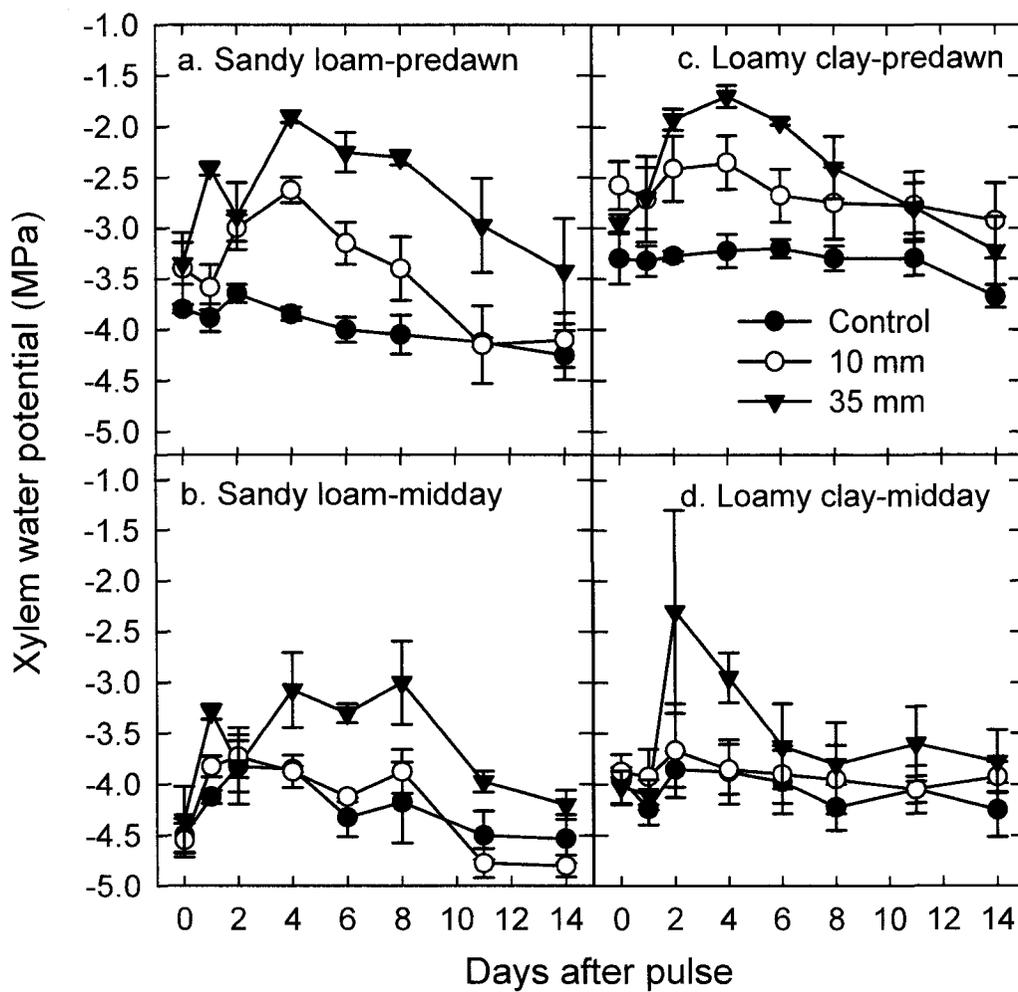
Table 1 - Texture fractions of soils on Holocene and Pleistocene geomorphic surfaces at the Santa Rita Experimental Range in southeastern Arizona, USA (Fravolini, unpublished data).

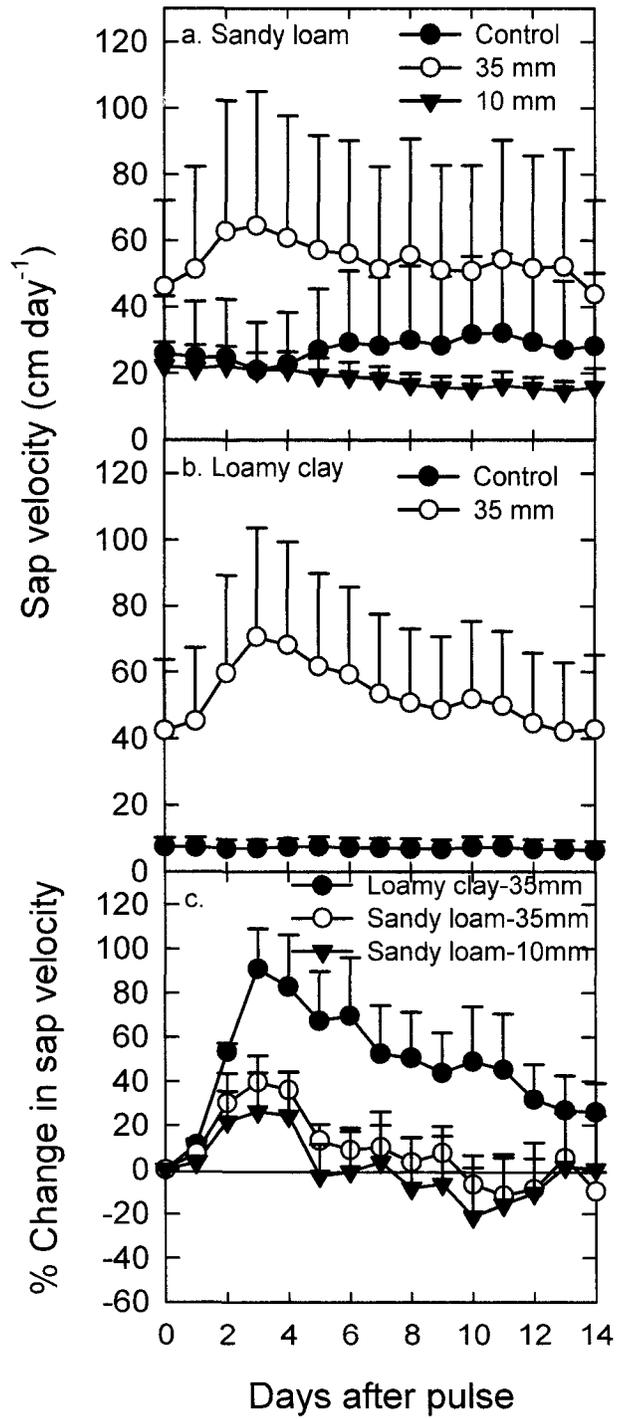
Location	Soil depth	Sand fraction	Silt fraction	Clay fraction
	<i>cm</i>	-----	<i>percent</i>	-----
Holocene	10	85.0	7.9	7.0
	30	80.0	10.2	9.8
	60	78.7	12.4	8.9
Pleistocene	10	76.1	11.2	12.7
	30	62.0	12.7	25.3
	60	45.6	15.6	38.8

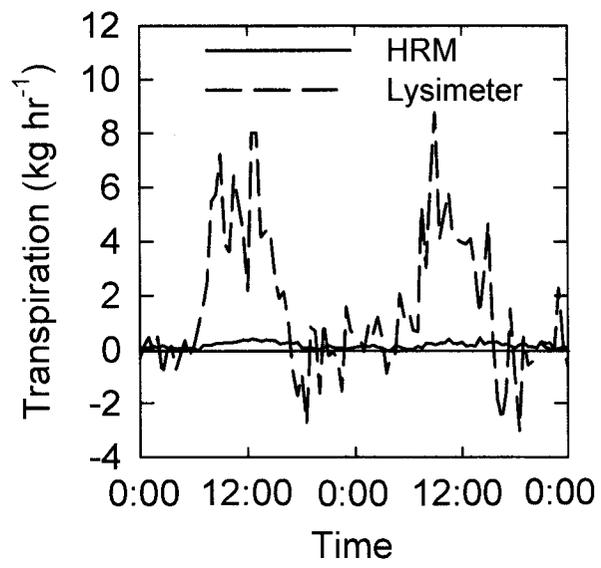
Table 2 - Basal diameter, sapwood area (A_s), leaf area (A_l), and sapwood area to leaf area ratio ($A_s:A_l$) of velvet mesquite trees at the Santa Rita Experimental Range measured for sap flow. Numbers in parenthesis represent standard errors of the mean ($n = 9$ trees per site).

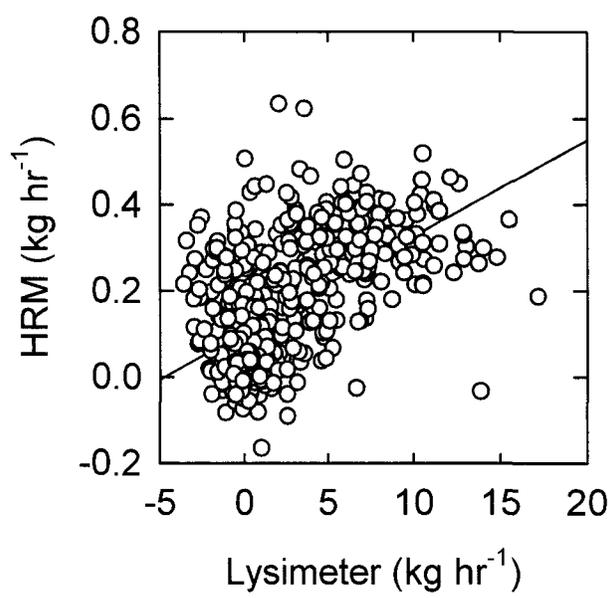
Site	Basal dia cm	A_s cm^2	A_l cm^2	$A_s:A_l$ $\text{cm}^2 \text{ m}^{-2}$
Holocene	6.95 (0.50)	10.39 (0.45)	1.45 (0.15)	7.75 (0.75)
Pleistocene	7.37 (0.64)	10.18 (0.64)	1.90 (0.24)	5.78 (0.53)











INFLUENCE OF SOIL TEXTURE ON WATER USE IN A DOMINANT
WARM-DESERT PHREATOPHYTE

Kevin R. Hultine

School of Natural Resources, University of Arizona, Tucson, AZ, 85721, USA

ABSTRACT

We investigated hydraulic constraints on water uptake by velvet mesquite (*Prosopis velutina* Woot.) at two sites in southeastern Arizona, USA; one with sandy-loam soils and the second with loamy-clay soils. We expected trees on sandy-loam soil to have less negative plant and soil water potentials during drought, have a lower resistance to xylem cavitation, and reach E_{crit} (the maximum permissible steady state transpiration rate without hydraulic failure) at higher soil water potentials than trees on loamy-clay soil. Surprisingly, minimum predawn leaf xylem water potentials (Ψ_{pd}) measured during the height of summer drought were significantly lower at the sandy-loam site (-3.5 ± 0.1 MPa; all errors are 95% confidence limits) than at the loamy-clay site (-2.9 ± 0.1 MPa). Minimum midday water potentials (Ψ_{min}) also were lower at the sandy-loam site (-4.5 ± 0.1 MPa) than at the loamy-clay site (-4.0 ± 0.1 MPa). Despite the different leaf water potentials, there were no significant differences in either root or stem xylem embolism, mean cavitation pressure, or Ψ_{100} (Ψ_x causing 100% cavitation) between trees at the sandy-loam and loamy-clay sites. Model predictions of E_{crit} showed considerable differences between sites; E_{crit} on sandy-loam soil approached zero at substantially higher (less negative) Ψ_s than on loamy-clay soil. Differences in E_{crit} between sites were attributed to large differences in rhizosphere conductance at progressively lower bulk soil water potentials (Ψ_s). Predicted values of E_{crit} at estimated values of Ψ_s (estimated from measured values of Ψ_{pd}) suggests that trees at the sandy-loam site, even with substantial adjustment in absorbing root area to leaf area ratios,

operated well below their maximum transpiration rate before the onset of the monsoon. Transpiration rates likely recovered to near maximum in response to precipitation, suggesting that seasonal transpiration fluxes at the sandy-loam site is highly dependent on growing season precipitation pulses. Conversely, predicted values of E_{crit} at measured Ψ_{pd} suggest that plants on loamy-clay soil operated at or near maximum permissible transpiration rates throughout the growing season, demonstrating that fluxes on loamy-clay soils may be better coupled to inter-annual changes in precipitation. Information on the combined importance of xylem and rhizosphere constraints to leaf water supply across soil texture gradients provides insight into processes controlling water balance at the landscape scale.

Key words: xylem cavitation, plant water relations, *Prosopis velutina*, Chihuahuan desert, plant-soil interactions

INTRODUCTION

Plants play an important role in the water cycle because they transport water from the soil to the atmosphere via transpiration. The encroachment of woody plants into ecosystems formerly dominated by grasses has the potential to alter ecosystem water balance by increasing rooting depth and changing the depth from which plants extract water for transpiration. Regardless of rooting depth, hydraulic limitations on water uptake and transport play an important role in the regulation of transpiration over a range of environmental conditions. Limitations imposed by soil and plant hydraulic characteristics determine how invasion of woody plants into grasslands affect key aspects of the hydrologic cycle. This paper reports a study designed to assess the differences in these hydraulic limits in woody shrubs on two different soil surfaces.

Soil texture greatly influences infiltration and moisture retention (Jury et al. 1991), and thus strongly influences plant water availability and productivity (Sperry et al. 1998, Hacke et al. 2000a, Sperry and Hacke 2002). In arid regions, productivity and above ground biomass are often higher on coarse-textured than on fine-textured soils (Kinraide 1984, Smith et al. 1997). This may be due to the relatively higher saturated hydraulic conductivity in coarse-textured soils that allows for greater infiltration to deep soil layers, opposed to running off or ponding (Campbell and Norman 1998). However, in more mesic environments, coarse-textured soils may induce greater hydraulic limits to plant water uptake compared to fine-textured soils because coarse-textured soils lose more moisture and conductivity at higher water potentials than fine-textured soils.

Therefore, plants that grow in coarse-textured soils require less negative water potentials to exhaust their water supply than do plants in fine-textured soils. Plants may overcome the effects of steeply declining soil hydraulic conductivity (K_s) at high Ψ_s by developing higher root to leaf area ratios ($A_r:A_l$), thereby reducing rates of water uptake per root surface area (rhizosphere flux density), or by extending roots to deeper soil layers where soil water may be more plentiful.

Regardless of climate or soil type, xylem cavitation resistance should correlate with the range of water potentials experienced by the plant, given that excessive costs (i.e. carbon allocation and/or reduced hydraulic efficiency) may be associated with overly resistant xylem (Sperry 1995, Alder et al. 1996, Hacke et al. 2001). Therefore, plants occurring on coarse-textured soils that typically operate at higher Ψ_s may be more vulnerable to cavitation than plants on fine-textured soils (Sperry et al. 1998, 2002; Hacke et al. 2000a). This trend may be particularly apparent in roots that tend to operate with a much narrower safety margin (the difference between the minimum Ψ observed in the field and xylem water potential (Ψ_x) causing 100% cavitation) and demonstrate a greater plasticity than stems across moisture gradients (Alder et al. 1996; Hacke et al. 2000a; Jackson et al. 2000).

Over the last 100 years, the deeply-rooted leguminous tree/shrub *Prosopis* spp. has encroached and established in upland and floodplain grasslands throughout the southwestern United States and northern Mexico (Brown and Archer 1989, Archer 1995). The encroachment of mesquite has the potential to dramatically alter hydrologic processes in these systems, due in part to their ability to cope with water limitations

during early life stages, followed by exploitive use of stable water sources during maturity (Brown and Archer 1989). However, the dynamics of mesquite water use and the interaction between plant and soil hydraulic limits of this deeply rooted taxon may be highly variable across soil texture gradients. We assessed the relationship between xylem cavitation vulnerability, xylem anatomy and soil texture in two populations of velvet mesquite (*Prosopis velutina* Woot.) in southeastern Arizona, USA. One population was within a seasonally dry site with sandy-loam soils that have a relatively high saturated K_s that declines steeply at high Ψ_s . The second population was within an adjacent seasonally dry site with loamy-clay soils that have comparably lower saturated K_s that declines more slowly at high Ψ_s . We predicted that plants on sandy-loam soils would operate at higher soil water potentials and have xylem that is less resistant to cavitation (particularly in the roots).

Data on plant and soil hydraulic characteristics were used to parameterize a transport model (Sperry et al. 1998) to identify differences in E_{crit} (the maximum steady state transpiration rate, above which hydraulic conductance falls to zero) between the two sites. We predicted that plants on sandy-loam soils would approach E_{crit} at substantially higher Ψ_s than plants on loamy-clay soils given the steep K_s (Ψ_s) function and potentially greater vulnerability to xylem cavitation on sandy-loam soils.

MATERIALS AND METHODS

Research sites

The study was conducted at two sites within the Santa Rita Experimental Range (SRER) in southeastern Arizona, USA. One site was on a young Holocene (4,000 to 8,000 ybp) geomorphic surface and one site was on a mid-Pleistocene (200,000 to 300,000 ybp) geomorphic surface. The site on the Holocene surface was characterized by sandy-loam soils with relatively high saturated hydraulic conductivity (Table 1). The vegetation overstory at this site was dominated by a mixed-aged stand of *Prosopis velutina* Woot. The understory was dominated by *Eragrostis lehmanniana* Nees. intermixed with other grasses. Mean annual precipitation is about 394 mm with approximately 56% falling during the summer monsoon (July-September). The site on the mid-Pleistocene surface was located 5 km from the Holocene site and was characterized as having loamy-clay soils with a substantially lower saturated hydraulic conductivity than soils on the sandy-loam surface (Table 1). The overstory was dominated by a mixed-age stand of *P. velutina*, however, the number of stems per hectare was substantially lower on the Pleistocene than on the Holocene surface (Table 1). The understory vegetation on the Pleistocene surface was much more sparse than on the Holocene surface and was also dominated by *E. lehmanniana*. Mean annual precipitation at the Pleistocene site is about 430 mm with 56 % falling during the summer monsoon. Mean annual air temperature on the SRER is 32 °C during summer, while mean nighttime temperature during winter is 5 °C.

Xylem water potential

Six individual mesquite plants were randomly selected at each site for water potential measurements. Leaf xylem water potential was measured using a Scholander-type pressure chamber (PMS Instruments, Corvallis, OR, USA) during the 2003 growing season in June, before the onset of the monsoon, and once in mid-August at the peak of the monsoon. A single shoot tip from each of the six trees were cut with a sharp razor blade and measured at predawn (Ψ_{pd}) between 0200 and 0400 h, and at midday (Ψ_{min}) between 1100 and 1300 h.

Vulnerability curves

Vulnerability curves were estimated in root and stem segments using the air-injection, or “air-seeding” method (Sperry and Saliendra 1994). According to the air seeding theory (Zimmermann 1983), the negative xylem water potential (Ψ_x) required to pull air into a xylem conduit (i.e. the air-entry potential) and cause cavitation is equal to the opposite positive pressure required to push air into the conduit when Ψ_x is equal to atmospheric pressure. The air injection method produces results that are comparable with other methods used to study vulnerability curves, including the dehydration (Alder et al. 1996, Pockman and Sperry 2000) and centrifugal methods (Pockman et al. 1995).

Vulnerability curves were measured on 5 to 6 trees per site during the 2003 growing season. Roots occurring between 20 – 50 cm depths were carefully excavated near the base of the tree. Stems and roots were cut underwater, and were transported to

the laboratory in sealed plastic bags with moist paper towels. All collected stems and roots had an approximate inside bark diameter of 5 mm and were cut longer than the estimated maximum vessel lengths to prevent air from being artificially introduced into the xylem vessels. Maximum vessel lengths were measured on roots ($175 \text{ cm} \pm 23.5$, $n = 6$) and stems ($66.7 \text{ cm} \pm 3.6$, $n = 20$) using methods previously described by Zimmermann and Jeje (1981). In the laboratory, segments were re-cut underwater to prevent the introduction of additional emboli. The segment ends were trimmed with a sharp razor blade to eliminate flow restrictions introduced when the stem and root segments were cut in the field. Prior to determination of the vulnerability curve, the segments were flushed with deionized water at 100 kPa to insure that the vulnerability curve included all potentially functional xylem. Flushed segments were inserted through a double-ended pressure sleeve previously described by Pockman and Sperry (2000). One end of the segment was fitted with rubber gaskets and was installed in a tubing manifold filled with filtered deionized water. Each segment was measured individually by applying gravity-induced pressure of 10 to 20 kPa depending on the length of the segment, and xylem hydraulic conductivity ($k_x = \text{mass flow per pressure gradient}$) was determined by collecting the flow from the segment in tared vials filled with cotton. After flushing, pressure inside the chamber was raised to 0.1 MPa and maintained for 20 minutes to exclude all open vessels (if present) from the k_l measurements. The pressure was then returned to atmosphere and the segment was allowed to equilibrate for 10 minutes before making initial measurements of k_x . Previous studies have measured k_x while pressure was held at 0.1 MPa in the pressure sleeve to avoid the leakage of xylem

inside the chamber. However, we found that measurements were less variable after the pressure inside the chamber was returned to atmosphere. After the initial measurement the process was repeated at progressively higher pressures at 1.0 MPa increments until embolism reached 95% or greater. The percentage loss of k_x was plotted as the conductivity at each pressure ($k_{x, p}$) against the initial measure of conductivity at 0.1 ($k_{x, 0.1}$): $PLC = 100 * (1 - k_{x, p} / k_{x, 0.1})$.

The vulnerability curves were used to calculate mean cavitation pressure and Ψ_{100} . The mean cavitation pressure was determined by first considering the vulnerability curve as a cumulative distribution of loss of conductance with pressure, then replotting the curve as a frequency distribution over the same pressure or “pressure classes” (Sperry and Saliendra 1994). The mean cavitation pressure for the distribution was calculated using the mid-points of each pressure class. Mean cavitation pressure was determined for the entire vulnerability curve for comparison with conduit diameter and maximum k_x . The critical cavitation pressure (Ψ_{100}) was estimated as Ψ_x at 100% cavitation using a third-order polynomial fitted to each vulnerability curve.

Specific conductance, leaf specific conductance, and sapwood area / leaf area ratios

Specific conductance (k_s) yields a direct measure of hydraulic efficiency independent of conducting area. The k_s ($\text{kg s}^{-1} \text{m}^{-1} \text{MPa}^{-1}$) was calculated by dividing the maximum k_x by the mean cross-sectional conducting area of each root and stem segment. The cross-sectional conducting area was considered all the area beneath the root cortex or

bark, unless heartwood was visually present. Cross-sectional area was measured with digital calipers.

Leaf-specific conductance (k_l) was calculated by dividing projected leaf area of each stem segment by maximum k_x . The ratio between mean cross sectional sapwood area and projected leaf area ($A_s:A_l$) was also calculated. Projected leaf area was determined by analyzing computer scans of individual leaflets using NIH Image.

Model Application

We used a transport model (previously described by Sperry et al. 1998, and Hacke et al. 2000) to estimate E_{crit} (above which k_l goes to zero and hydraulic failure occurs) based on soil hydraulic properties and xylem vulnerability curves. The model is capable of predicting the steady state transpiration rate (E), however, such predictions require knowledge of rooting depth and $A_r:A_l$ ratios, which are nearly impossible to assess given the deeply rooted nature of mesquite plants (Phillips 1963). The model divided the soil-plant continuum into three components in series: rhizosphere (region between bulk soil and root surface), root system, and shoot system. An initial saturated k_l representing the maximum conducting capacity k_l^* was assigned to each component. The initial saturated rhizosphere conductance was calculated from K_s ($\text{mmol s}^{-1} \text{MPa}^{-1} \text{m}^{-1}$) assuming a cylindrical rhizosphere sheath of 5 mm thickness from bulk soil to root surface. The K_s was determined from measured soil texture fractions according to Campbell (1985). The rhizosphere conductance could not be directly converted to a leaf area basis because estimates of $A_r:A_l$ were lacking in this system. Instead the model was run over a range of

$A_r:A_l$ from 0.1 to 30 to assess the sensitivity of the $A_r:A_l$ on the soil-plant continuum. For both sites, root and shoot systems were divided into lateral and axial components. For the root systems, lateral root components were divided into five soil layers centered on five depths from 0.05 to 2 m (0.4 m increments). Relative change in root surface area with depth was estimated from mesquite root distribution patterns reported from the La Copita Research Area in southern Texas, USA (Watts and Archer, unpublished). Initial soil water content was assumed equal across all soil layers. Root axial lengths were determined by relative depths of the midpoint of each soil layer. The initial saturated root and stem leaf specific conductance was assigned from:

$$(1) \quad k_l = E/(\Psi_s - \Psi_{\min})$$

where Ψ_s is the initial soil water potential, assumed to equal Ψ_{pd} . Values of Ψ_s and Ψ_{\min} were from leaf water potential measurements taken in June 2003 (See above). Because we had no reliable estimates of E , the model was run with an initial value of one $\text{mmol s}^{-1} \text{m}^{-2}$ leaf area. The root and shoot components were assumed to constitute 50% each of the total hydraulic resistance of the plant (Hacke et al. 2000). The pressure dependent decrease in k_l for root and shoot components was calculated from a Weibull function fit to vulnerability curve data:

$$(2) \quad k_l = k_l^* e^{-(\Psi/d)^c}$$

where d and c are curve fitting parameters. We used the same fitting parameters for axial and lateral components for both roots and shoots. The Ψ_s -dependent decrease in rhizosphere conductance was calculated as:

$$(3) \quad k_l = K_s X (\Psi_e / \Psi_s)^{(2+3/b)}$$

where X is a factor that converts soil conductivity to leaf-specific conductivity based on cylindrical geometry of the rhizosphere and the $A_r:A_l$ ratio (Sperry et al. 1998), ψ_c is the air entry potential, and b is a soil fitting parameter (Campbell 1985).

Xylem anatomy and wood density

conduit diameters were measured on a minimum of four roots and stems per site used to establish vulnerability curves. Transverse sections were cut using a rotary microtome (Model 820, American Optical, Buffalo, New York, USA). The sections were stained with toluidine blue (0.05%) to improve contrast and were mounted in glycerol. The slides were photographed at 100x with a digital camera (Nikon Coolpix, Nikon, Tokyo, Japan) mounted to a Nikon compound microscope (Nikon Eclipse E400, Nikon). Two to six randomly selected radial sections were photographed on each root and stem segment. The lumens of all xylem conduits were analyzed within each section using the software application NIH image (version 1.62 for Macintosh). A minimum of 203 conduits were analyzed per site. Mean conduit diameter (d) was calculated from the cross-sectional area of each conduit measured by the imaging software. We also calculated the mean hydraulic diameter (d_h), which yields the estimated percentage of total conductance contributed by each conduit. The mean of the hydraulically weighted distribution is given by: $\Sigma d^5 / \Sigma d^4$ (Sperry et al. 1994).

Wood density (D_t) was measured on stems and roots using the method described by Hacke et al. (2000b). Five to 13 root and stem samples were measured per site, including roots and stems measured for cavitation vulnerability. Segments of 2.5 to 3 cm

lengths were cut out of roots and stems and the cortex and bark were removed from each organ respectively. Wood volume was determined by Archimedes' principle. The segments were immersed in a water-filled beaker that was placed on a balance. Displacement weight was measured to the nearest 0.01 g and was converted to sample volume by the formula: displacement weight / 0.998 (g cm⁻³), where 0.998 g cm⁻³ is the density of water at 20 °C. Segments were then oven-dried at 90 °C for 48 hours, and their dry weight was measured. Wood density was calculated as the ratio of dry weight per volume.

RESULTS

Minimum values of predawn and midday water potentials occurred in June at both sites during the 2003 growing season. June predawn and midday water potentials were significantly lower at the sandy-loam site than at the loamy-clay site (Table 2), and averaged $-3.5 \text{ MPa} \pm 0.1$, $n = 6$, and $-2.9 \text{ MPa} \pm 0.1$, $n = 6$, respectively ($P = 0.0079$). The lower Ψ_{pd} suggests that mesquite plants on sandy-loam soils sustained more water stress than plants on loamy-clay soils before the onset of the monsoon (assuming there is no disequilibrium between rhizosphere and leaf Ψ at either site). Midday Ψ_{min} was also lower on sandy-loam soils than on loamy-clay soils and averaged $-4.5 \text{ MPa} \pm 0.1$, $n = 6$, and $-4.0 \pm 0.1 \text{ MPa}$, $n = 6$, respectively ($P = 0.0029$). After the onset of the monsoon, predawn and midday Ψ_x converged at both sites near -1 MPa and -3 MPa respectively (data not shown). There were no significant site differences in either root or stem maximum specific hydraulic conductance (Table 2), however leaf specific conductance and sapwood to leaf area ratios ($A_s:A_l$) were higher at the sandy-loam site (Table 2).

Surprisingly, roots appeared only slightly more vulnerable to cavitation than stems; roots became completely embolized at pressures only one to two MPa higher than that observed in stems at both sites. Mesquite stems at the sandy-loam site were slightly more vulnerable than stems at the loamy-clay site down to -7.0 MPa (Figure 1). Mean cavitation pressure and Ψ_{crit} were similar between sites for both roots and stems (Table 3). Mean cavitation pressure in roots ranged from -5.5 MPa on sandy-loam soils to -5.7 MPa on loamy-clay soils ($P = 0.86$), while mean cavitation pressure in stems ranged from

–5.5 MPa on sandy loam to –6.3 on loamy clay ($P = 0.61$). Critical xylem pressure in roots ranged from –6.5 MPa on sandy loam to –6.6 MPa on loamy clay ($P = 0.97$), while Ψ_{crit} in stems ranged from –7.0 MPa in stems to –8.3 MPa on loamy clay ($P = 0.33$).

The transport model revealed that despite similarities in xylem function, patterns of E_{crit} varied substantially between sites. E_{crit} at the sandy-loam site fell below the modeled maximum rate of transpiration (horizontal line in Figure 2) at the minimum mean bulk soil water potential measured in June (solid vertical line in Figure 2) over a range of $A_r:A_l$ from 1 to 20 (Figure 2a). This suggests that actual water use at the sandy-loam site was severely limited before the onset of the monsoon in mid-July. After the onset of the monsoon, the E_{crit} curve fell above the maximum transpiration line at mean Ψ_s measured in August (dashed vertical line in Figure 2) when the $A_r:A_l$ ratio was 5 and above, indicating that patterns of mesquite water use at this site are highly sensitive to seasonal inputs of precipitation. Conversely, maximum transpiration rates fell within the water use envelope at minimum mean bulk water potentials in June regardless of the $A_r:A_l$ ratio (Figure 2b), suggesting that water use at the loamy-clay site was never severely limited throughout the growing season. The model predicted that hydraulic failure would occur in the rhizosphere and not in the xylem at the sandy-loam site across a range of $A_r:A_l$ of 0.1 to 30 (filled circles, Figure 3). In fact, rhizosphere failure occurred at –2 MPa or higher regardless of $A_r:A_l$. Hydraulic failure was limited to the rhizosphere, in part because of the greater than expected xylem cavitation resistance, although the model predicted some loss in root and stem conductivity at –2 MPa. However, we cannot rule out the possibility that fine roots much smaller in diameter than

those we measured are substantially more vulnerable to cavitation, thereby potentially shifting rhizosphere failure to the xylem. Hydraulic failure at the loamy-clay site was sensitive to the $A_r:A_l$ function; hydraulic failure shifted from the rhizosphere to the xylem at an $A_r:A_l$ ratio between 3 and 4 (open circles, Figure 3).

Hydraulically weighted mean conduit diameter was larger in mesquite stems at the loamy-clay site than at the sandy-loam site ($78.2 \pm 7.5 \mu\text{m}$ and $59.0 \pm 7.6 \mu\text{m}$, respectively, $P = 0.0727$, Table 3). Likewise d_h in roots was slightly higher at the loamy-clay site than at the sandy-loam site ($177.2 \pm 25.7 \mu\text{m}$ and 159.2 ± 22.7 , respectively), however, differences were not significant ($P = 0.56$, Table 3). Despite having stems with larger conduits, mesquite trees at the loamy-clay site were no more vulnerable to cavitation than trees at the sandy-loam site, suggesting that there is no tradeoff between xylem hydraulic efficiency and cavitation vulnerability in velvet mesquite plants as reported with other species (Tyree et al. 1994, Alder et al. 1996, Pockman and Sperry 2000, Hacke et al. 2001).

Wood density did not vary across sites in either roots or stems ($P = 0.98$ for roots, and $P = 0.52$ for stems, Table 3). Mean wood density of roots ranged from 0.52 g cm^{-3} on sandy loam to 0.53 on loamy clay, while in the stems, wood density ranged from 0.67 on sandy loam to 0.69 on loamy clay. There was a significant linear increase in mean cavitation pressure with increasing D_l across all the samples (Mean cav = $0.21 - 8.32 * D_l$, $R^2 = 0.39$, $P = 0.0052$, $n = 18$, Figure 4), suggesting that wood density may be related to xylem support and cavitation resistance.

DISCUSSION

This investigation revealed significant differences in soil hydraulic limits to water use by velvet mesquite trees in sandy-loam versus loamy-clay soils. Surprisingly, these differences did not translate into substantial phenotypic adjustments in xylem hydraulic properties across the two soil textures. Nevertheless, soil and plant hydraulic limitations on water uptake and transport play an important role in the regulation of seasonal patterns of transpiration over a range of environmental conditions. The dependence of plant water use on soil and plant hydraulic characteristics suggests that the influence of woody plant invasion on the hydrologic cycle of ecosystems formerly dominated by grasses may be uneven across landscapes with different soil textures.

According to the model, the combined affects of soil and xylem hydraulic limits to leaf water supply were far more significant throughout much of the growing season at the sandy-loam site than at the loamy-clay site. Given that xylem resistances were fairly similar between sites, differences in hydraulic limits were likely caused by sharp contrasts in rhizosphere conductance. Coarse-textured soils lose more moisture at high Ψ_s than do fine-textured soils because of the weaker capillary forces that retain water in the larger pore spaces (Campbell 1985). Therefore, plants growing in sandy-loam soil likely require less negative soil water potentials to exhaust the water supply in the rhizosphere than do plants growing in loamy-clay soil, resulting in greater hydraulic limits during drought. The lower k_1 and higher sapwood area to leaf area ratio ratios at the sandy-loam site supports the model output showing that drought stress was more

significant on sandy-loam than on loamy-clay soil throughout much of the growing season.

Plants on coarse-textured soils may reduce hydraulic limits in the rhizosphere by reducing the rate of water uptake per unit surface area (rhizosphere flux density) through the development of high root conducting surface area to leaf area ratios ($A_r:A_l$). Within a species, plants on coarse soils often have higher $A_r:A_l$ ratios than plants on fine-textured soils (Glinski and Lipiec 1990, Hacke et al. 2000a). In fact, $A_r:A_l$ in 15-year old *Pinus taeda* stands in North Carolina, USA were six times higher in sand than in loam soils, thereby sharply reducing the rhizosphere flux density at the sand site (Hacke et al. 2000a). In theory, plants would operate near the $A_r:A_l$ threshold where xylem is most limiting, unless nutrient rather than water limitations require an excess $A_r:A_l$ ratio (Sperry et al. 1998). However, in the current study, rhizosphere failure in sandy-loam soil occurred before xylem failure at modeled $A_r:A_l$ ratios that were well above values that have been previously reported in other species (Rendig and Taylor 1989, Tyree et al. 1998, Hacke et al. 2000), due in part to the higher than expected cavitation resistance of roots and stems at this site. Conversely, according to the model, hydraulic failure in loamy-clay soils would shift from the rhizosphere to the xylem at a $A_r:A_l$ between 3 and 4, well within the range of $A_r:A_l$ ratios reported in other species in fine-textured soils (Tyree et al. 1998, Hacke et al. 2000a). Data of mesquite root density and distribution patterns would greatly improve model parameterization. Unfortunately, given the extremely expansive root systems of mesquite plants – rooting depths have been reported

below 50 m (Phillips 1963) – data of root distributions were unobtainable for this investigation.

Woody plants occurring on coarse-textured soils are often more vulnerable to xylem cavitation than the same species on finer soils, suggesting that resistance to cavitation parallels the range of Ψ_s in which water is physically extractable from the rhizosphere. (Sperry et al. 1998, Hacke et al. 2000a, Sperry and Hacke 2002). This is because costs, in terms of hydraulic efficiency (Tyree et al. 1994) and carbon investment (Wagner et al. 1998, Hacke et al. 2001) may be associated with cavitation resistance. In the present study, differences in soil texture did not translate into significant differences in xylem cavitation resistance between sites in either the roots or stems, to the extent that xylem in mesquite plants at the sandy-loam site was far more resistant to cavitation than would appear necessary. One consideration is that despite having substantially greater maximum conductance and mean hydraulic conduit diameter, mesquite roots at both sites were only slightly more vulnerable to cavitation than stems, suggesting that there may not be an inherent tradeoff within individual mesquite plants between cavitation resistance and hydraulic efficiency as shown in some species (Sperry and Saliendra 1994), but not others (Alder et al. 1996). Alternatively, xylem cavitation resistance may be associated with wood density. The construction of progressively denser wood, at the cost of greater carbon investment and slower rates of growth, may prevent the implosion of xylem elements from increasingly negative pressures that occur in the xylem as Ψ_s decreases and/or leaf water demand increases (Hacke et al. 2001). In the present study, cavitation resistance increased with increasing wood density suggesting that high cavitation

resistance in mesquite plants is associated with greater carbon investment to woody tissues.

There may be advantages for having overly resistant xylem in these systems. For example, the relatively high cavitation resistance in shallow roots may facilitate mesquite utilization of summer rain that generally occurs in low-frequency intense pulses. The higher the percent loss of conductivity of shallow roots prior to pulse events, the less uptake would be expected to occur following the event unless the cavitation was rapidly reversed. Re-filling of embolized conduits has been previously reported in diffuse-porous species, but not in ring-porous species such as velvet mesquite (Jaquish and Ewers 2001). Mesquite plants have been shown to respond immediately to simulated rain after extensive drought on both sandy-loam and loamy-clay soils (Fravolini et al. in prep), strongly suggesting that mesquite plants immediately develop new rain roots in response to precipitation (North and Nobel 1995) or the root system remains conductive during drought.

Resistance to cavitation may also facilitate hydraulic redistribution of water by deep root systems (Caldwell et al. 1998, Sperry and Hacke 2002, Hultine et al. 2003). Hydraulic lift occurs in mesquite roots during extended periods of drought (Hultine et al. 2004), and immediately reverses direction (i.e. hydraulic descent) in response to moderate rain events. These patterns of hydraulic redistribution suggest that a large portion of the root systems remains in hydraulic contact with the soil during drought by virtue of high cavitation resistance.

Our study estimated cavitation resistance in shallow roots of limited diameter range, leaving a large portion of the root xylem uncharacterized. There is likely substantial variation in cavitation resistance within the expansive root systems of mature mesquite plants that span well beyond the soil depths at which we are able to sample. Deep roots may be less resistant to cavitation than shallow roots (McElrone et al. in review). Likewise, large roots tend to be more resistant than smaller roots (Hacke et al. 2000a) to the extent that fine roots, which have the greatest surface area and hence the greatest potential for water uptake, may be substantially more vulnerable than the larger roots that were measured in this study.

We predicted that mesquite trees occurring on sandy-loam soils with high saturated K_s would have a higher Ψ_{\min} than trees on the loamy-clay surface that has a substantially lower K_s . Our results indicated that Ψ_{\min} during peak drought was in fact lower in sandy-loam than in loamy-clay soil. Below average precipitation over the previous 24 months at both sites greatly reduced infiltration to the rooting zone. However, because mesquite plants occur at much greater densities on the sandy-loam surface than on the loamy-clay surface, it may be that the total extraction of bulk soil water by roots was much greater during the previous 24 months, thereby exhausting the available water in the bulk soil to the extent that Ψ_{\min} was lower on the sandy-loam soil than on the loamy-clay soil. Patterns of pre-monsoon predawn and midday Ψ_x in 2003 at both sites paralleled patterns reported from other years on the SRER with below average winter and spring moisture including 1999 and 2000 (Fravolini et al. 2003).

Growing season precipitation pulses play a major role in ecosystem water balance in much of the southwestern United States. However, small growing season precipitation pulses (< 10 mm) that frequently occur during the summer monsoon apparently do not penetrate to the rooting zone at the loamy-clay site because of the low K_s in these soils (Fravolini et al. in prep). Therefore, trees on loamy clay apparently only respond to larger precipitation pulses that occur much less frequently than smaller events. Conversely mesquite trees on sandy-loam soils are highly sensitive to small precipitation pulses in terms of pulse water uptake and carbon gain (Fravolini et al. in prep). Given that mesquite transpiration at the sandy-loam site was severely limited by low rhizosphere conductance before the monsoon, it is likely that carbon and water fluxes are well coupled to precipitation inputs during the summer monsoon whereas fluxes at the loamy-clay site are likely better coupled to inter-annual changes in precipitation. Climate change is expected to bring substantial variations in inter- and intra-annual summer precipitation patterns in the arid southwestern United States (Houghton et al. 1996, Weltzin 2003). Changes in precipitation patterns coupled with differences in soil hydraulic limits across the landscape will likely lead to subsequent differences in plant water use that may have important consequences to future patterns of plant community structure and ecosystem water balance.

The prediction of water use by plants during and after drought requires information on the hydraulic limits that occur as a result of soil drying and xylem cavitation. Lack of information greatly reduces our understanding of how the invasion of woody plants into arid and semi-arid grasslands may influence the water cycle at large

scales. Information of hydraulic limits also provides a mechanistic understanding behind plant processes such as response to precipitation pulses, foliar dieback, and carbon exchange.

LITERATURE CITED

- Alder, N.N., Sperry, J.S. and Pockman, W.T. 1996. Root and stem xylem embolism, stomatal conductance, and leaf turgor in *Acer grandidentatum* populations along a soil moisture gradient. *Oecologia* **105**: 293-301
- Archer, S.A. 1995. Tree-grass dynamics in a *Prosopis*-thornscrub savanna parkland: reconstruction of the past and predicting the future. *Ecoscience* **2**: 83-99
- Brown, J.R., and Archer S.A. 1989. Woody plant invasion of grasslands: establishment of honey mesquite (*Prosopis glandulosa* var. *glandulosa*) on sites differing in herbaceous biomass and grazing history. *Oecologia* **80**: 19-26.
- Caldwell, M.M., Dawson, T.E., and Richards J.H. 1998. Hydraulic lift: consequences of water efflux from the roots of plants. *Oecologia* **113**: 151-161
- Campbell, G.S., and Norman, J.N. 1998. *An Introduction to Environmental Biophysics*. And Springer, New York
- Fravolini, A., Hultine K.R., Koepke, D.F., and Williams, D.G. 2003. Role of soil texture on mesquite water relations and response to summer precipitation. In: McLaran, M., Ffoliott, P.F., Edminster, C.B. Santa Rita Experimental Range: one hundred years (1903 to 2003) in accomplishments and contributions; conference proceedings; 2003 October 30-November 1; Tucson, AZ, USDA Forest Service proceedings RMRS-P-00
- Glinski, J. and Lipiec, J. 1990. *Soil Physical Conditions and Plant Roots*. CRC Press, Boca Raton
- Hacke, U.G., Sperry, J.S., Ewers, B.E., Ellsworth, D.S., Schafer, K.V.R., and Oren R.

- 2000*a*. Influence of soil porosity on water use in *Pinus taeda*. *Oecologia* **124**: 495-505
- Hacke, U.G., Sperry, J.S., and Pitterman, J. 2000*b*. Drought experience and cavitation resistance in six shrubs from the Great Basin, Utah. *Basic and Applied Ecology* **1**, 31-41
- Hacke, U.G., Sperry, J.S., Pockman, W.T., Davis, S.D., and McCulloh K.A. 2001. trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* **126**: 457-461
- Houghton, J.T., Miera, G., Filho, B., Callander, B.A., Harris, N., Kattenberg, A., and Maskell, K. 1996. *Climate Change 1995: The Science of Climate Change*. Cambridge University Press, Cambridge, UK
- Hultine, K.R., Cable, W.L., Burgess, S.S.O., and Williams, D.G. 2003. Hydraulic redistribution by deep roots of a Chihuahuan Desert phreatophyte. *Tree Physiology* **23**: 353-360
- Hultine, K.R., Scott, R.L., Cable, W.L., and Williams, D.G. 2004. Hydraulic redistribution by a dominant warm-desert phreatophyte: seasonal patterns and response to precipitation pulses. *Functional Ecology* In Press
- Jackson, R.B., Sperry, J.S., and Dawson, T.E. 2000. Root water uptake and transport: using physiological processes in global predictions. *Trends in Plant Science* **5**: 482-488
- Jaquish, L.L. and Ewers, F.E. 2001. Seasonal conductivity and embolism in the roots and

- stems of two-clonal ring-porous trees, *Sassafras albidum* (Lauraceae) and *Rhus typhina* (Anacardiaceae). *American Journal of Botany* **88**: 206-212
- Jury, W.A., Gardner, W.R., and Gardner, W.H. 1991. *Soil Physics*. John Wiley, New York
- Kinraide, T.B. 1984. The influence of soil texture on the vegetation of a grazed short-grass prairie in Colorado. *Southwestern Naturalist* **29**: 277-287
- McElrone, A.J., Pockman, W.T., Martinez-Vilalta, J., and Jackson R.B. In Review. Xylem structure and function in stems and roots of trees to 20 m depth. *New Phytologist*
- North, G.B., and Nobel, P.S. 1995. Hydraulic conductivity of concentric root tissues of *Agave deserti* Engelm. Under wet and drying conditions. *New Phytologist* **130**: 47-57
- Pockman, W.T., Sperry, J.S., and O'Leary, W.J. 1995. Sustained and significant negative water pressure in xylem. *Nature* **378**: 715-716
- Pockman, W.T., and Sperry, J.S. 2000. Vulnerability to xylem cavitation and the distribution of Sonoran Desert vegetation. *American Journal of Botany* **87**: 1287-1299
- Rendig V.V., and Taylor, H.M. 1989. *Principles of Soil-Plant Interrelationships*. McGraw Hill, New York
- Smith, S.D., Monson, R.K., and Anderson, J.E. 1997. *Physiological Ecology of North American Desert Plants*. Springer Verlag, Berlin
- Sperry, J.S., and Tyree, M.T. 1988. Mechanism of water stressed-induced xylem

- embolism. *Plant Physiology* **88**, 581-587
- Sperry, J.S., and Saliendra, N.Z. 1994. Intra-and inter-plant variation in xylem cavitation in *Betula occidentalis*. *Plant, Cell and Environment* **17**: 1233-1241
- Sperry, J.S., Nichols, K.L., Sullivan, J.E.M., and Eastlick, S.E. 1994. Xylem embolism in ring-porous, diffuse porous, and coniferous trees of northern Utah and interior Alaska. *Ecology* **75**: 1736-1752
- Sperry, J.S. 1995. Limitations on stem water transport and their consequences. In Gartner, B.L. (ed) *Plant stems: physiology and functional morphology*. Academic Press, San Diego, pp 105-124
- Sperry, J.S., Adler, F.R., Campbell, G.S., and Comstock, J.P. 1998. Limitation of plant water use by rhizosphere and xylem conductance: results from a model. *Plant, Cell and Environment* **21**, 347-359
- Sperry, J.S., and Hacke, U.G. 2002. Desert shrub water relations with respect to soil characteristics and plant functional type. *Functional Ecology* **16**: 367-378
- Sperry, J.S., Hacke, U.G., Oren, R., and Comstock, J.P. 2002. Water deficits and hydraulic limits to leaf water supply. *Plant, Cell and Environment* **25**: 251-263
- Tyree, M.T., and Sperry, J.S. 1988. Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? Answers from a model. *Plant Physiology* **88**: 574-580
- Tyree, M.T., Davis, S.D., and Cochard, H. 1994. Biophysical perspectives of xylem evolution: is there a tradeoff of hydraulic efficiency for vulnerability to dysfunction. *International Association of Wood Anatomists Journal* **14**: 335-360

- Tyree, M.T., Velez, V., and Dalling, J.W. 1998. Root and shoot hydraulic growth dynamics in five neotropical seedlings of different light requirements: scaling to show ecotype differences. *Oecologia*
- Wagner, K.R., Ewers, F.W., and Davis, S.D. 1998. Tradeoffs between hydraulic efficiency and mechanical strength in the stems of four co-occurring species of chaparral shrubs. *Oecologia* **117**: 53-62
- Weltzin, J.F., Loik, M.E., Schwinning, S., Williams, D.G., Fay P.A., Haddad, B.M., Harte, J., Huxman, T.E., Knapp, A.K., Lin, G., Pockman, W.T., Shaw, M.R., Small, E.E., Smith, M.D., Smith, S.D., Tissue, D.T., Zak, J.C. 2003. Assessing the response of terrestrial ecosystems to potential changes in precipitation. *BioScience* **53**: 941-952
- Zimmermann, M.H., and Jeje, A.A. 1981. Vessel-length distribution in some American woody plants. *Canadian Journal of Botany*. 59: 1882-1892
- Zimmermann, M.H. 1983. *Xylem structure and the ascent of sap*. Springer, Heidelberg, Berlin, New York

FIGURE CAPTIONS

Figure 1 – Estimated Ψ_x causing cavitation in (a) roots and (b) stems of *Prosopis velutina* trees occurring on sandy-loam and loamy-clay soils in southeastern Arizona, as measured with air injection. Vulnerability curves are shown as mean percentage loss of maximum hydraulic conductance at each pressure applied. Error bars are the standard error of the means ($N = 5$ or 6).

Figure 2 – The effect of soil texture on E_{crit} for *Prosopis velutina* trees occurring on sandy-loam and loamy-clay soils in southeastern Arizona, USA. **a.** Water use envelopes on sandy-loam soils at $A_r:A_l$ ratios of 1, 5, 10, and 20. **b.** Water use envelopes on loamy-clay soils at $A_r:A_l$ ratios of 1, 5, 10, and 20. The horizontal lines represent the maximum transpiration rate used in the model, in absence of actual transpiration rates. The solid vertical lines represent the minimum predawn water potentials measured during the 2003 growing season (-3.52 MPa on sandy loam and -2.94 on loamy clay, Table 2), while the dashed lines represent the predawn water potentials measured in August, after the onset of the monsoon. Predicted E_{crit} values assumed equal ψ_s throughout the soil profile.

Figure 3 – Modeled extraction limits (bulk soil Ψ at E_{crit}) versus root to leaf area ratios ($A_r:A_l$). The dashed curves for sandy-loam and loamy-clay soils assume that the rhizosphere alone limits water extraction (i.e. no xylem cavitation). Horizontal lines represent the xylem pressure causing 100 % cavitation of *Prosopis velutina* trees

occurring on sandy-loam and loamy-clay soils. The extraction limit for a soil plus xylem cavitation is found by crossing over from the soil curve to the xylem line as $A_r:A_l$ increases. The line does not cross over for *Prosopis* plants on sandy-loam soils, suggesting that rhizosphere K rather than xylem K limits soil water extraction at this site regardless of the $A_r:A_l$ ratio.

Figure 4 – Relationship between mean cavitation pressure and wood density in mesquite roots and stems at the Santa Rita Experimental Range in southeastern Arizona, USA.

Mean cavitation pressure = $0.21 - 8.32 * D_t$ ($R^2 = 0.39$, $F = 10.43$, $P = 0.0052$, $n = 18$).

Table 1 - Mean annual precipitation, location, elevation, stand density, soil texture, and saturated soil hydraulic conductivity (K_s) at two sites used to study water relations of *Prosopis velutina* trees at the Santa Rita Experimental Range in southeastern Arizona, USA. Precipitation values in paranthesis represent mean annual precipitation during the summer months (July - September). K_s was calculated from silt and clay fractions according to Campbell (1985).

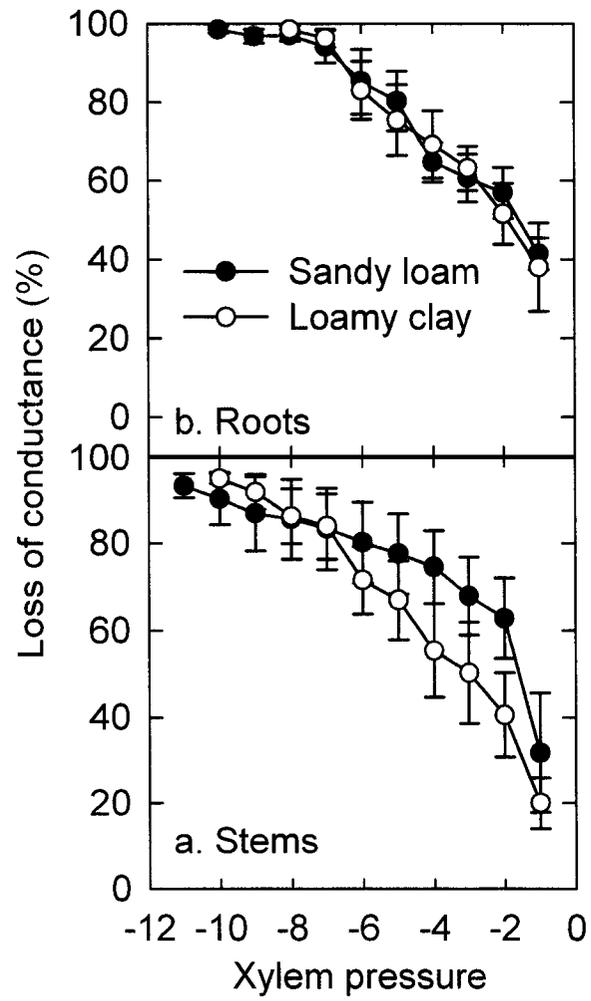
	Sandy loam	Loamy clay
Annual precipitation (mm)	394 (220)	430 (241)
Location	31° 47'N, 110° 50'W	31° 47'N, 110° 54'W
Elevation (m)	1190	1090
Stand density (stems ha ⁻¹)	540	60
Soil texture (30-60 cm):		
Pecent sand	79	54
Percent silt	11	14
Percent clay	9	32
K_s (mol s ⁻¹ MPa ⁻¹ m ⁻¹)	29.72	8.68

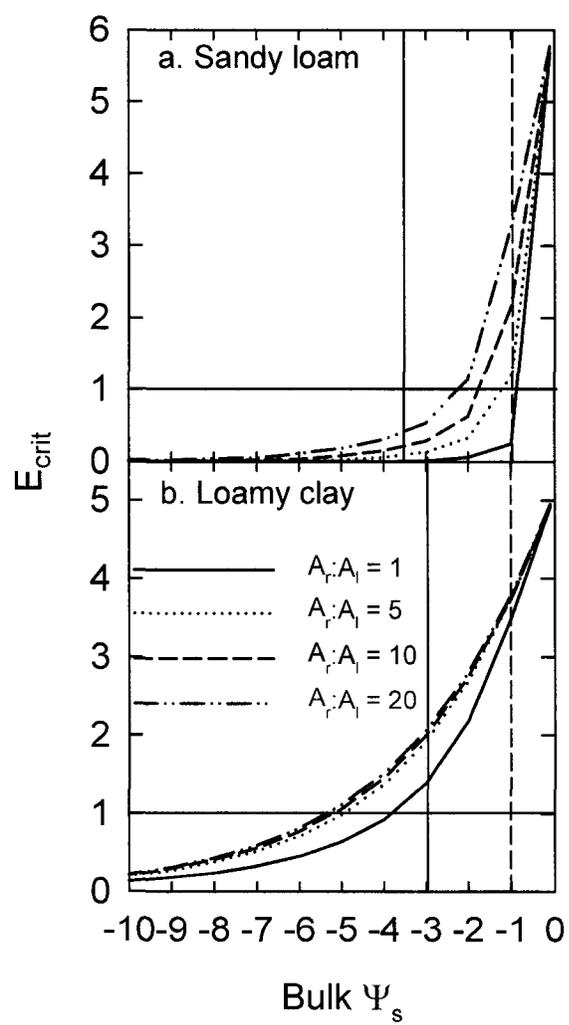
Table 2 - Minimum predawn (Ψ_{pd}) and midday leaf water potentials (Ψ_{min}), root (k_r), stem (k_s), and leaf (k_l) specific conductivities, and sapwood to leaf area ratios ($A_s:A_l$) of *Prosopis velutina* trees on sandy-loam and loamy-clay soils at the Santa Rita Experimental Range, in southeastern Arizona, USA.

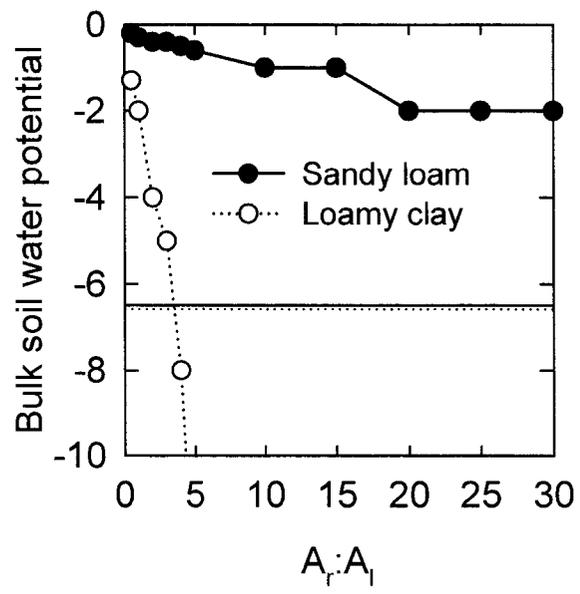
	Sandy loam	Loamy clay	<i>P</i>
Ψ_{pd} (MPa)	-3.52 ± 0.14	-2.94 ± 0.14	0.0079
Ψ_{min} (MPa)	-4.47 ± 0.12	-3.95 ± 0.09	0.0029
k_r ($\text{kg s}^{-1} \text{m}^{-1} \text{MPa}^{-1}$)	22.47 ± 6.78	31.13 ± 11.11	0.53
k_s ($\text{kg s}^{-1} \text{m}^{-1} \text{MPa}^{-1}$)	0.39 ± 0.10	0.36 ± 0.04	0.79
k_l ($\text{kg s}^{-1} \text{m}^{-1} \text{MPa}^{-1}$)	$7.1 \cdot 10^{-4} \pm 2.2 \cdot 10^{-4}$	$2.5 \cdot 10^{-4} \pm 7.1 \cdot 10^{-5}$	0.0808
$A_s:A_l$ ($\text{m}^2 \text{m}^{-2}$)	$7.8 \cdot 10^{-4} \pm 7.5 \cdot 10^{-5}$	$5.8 \cdot 10^{-4} \pm 5.3 \cdot 10^{-5}$	0.0484

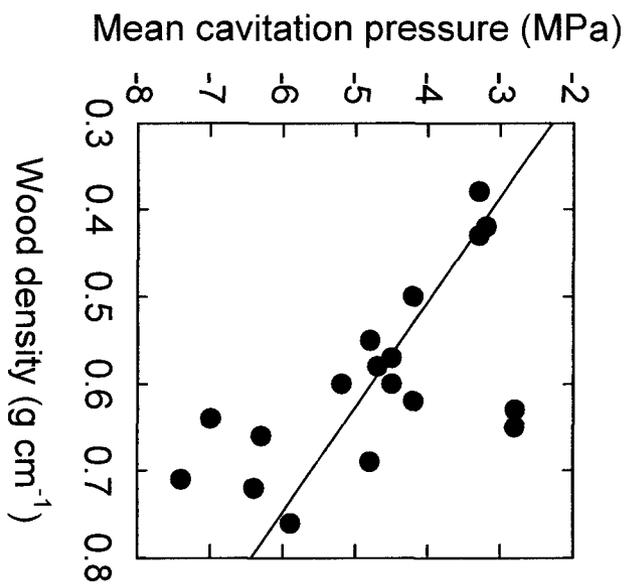
Table 3 - Mean cavitation pressure, pressure causing 100 percent loss of conductance (Ψ_{100}), mean conduit diameter (d), hydraulically weighted conduit diameter (d_h), and wood density (D_t) of roots and stems of *Prosopis velutina* trees on sandy-loam and loamy-clay soils at the Santa Rita Experimental Range in southeastern Arizona, USA. Numbers in parentheses are the standard error of the means

	Sandy loam	Loamy clay	<i>P</i>	Sandy loam	Loamy clay	<i>P</i>
	Roots			Stems		
Mean cav	-5.45 (0.91)	-5.66 (0.69)	0.86	-5.51 (1.28)	-6.33 (0.95)	0.61
Ψ_{100}	-6.50 (1.1)	-6.55 (0.67)	0.97	-7.03 (1.19)	-8.34 (0.44)	0.33
d (μm)	71.5 (3.0)	86.5 (4.0)	0.0018	35.9 (1.0)	47.2 (1.2)	<0.0001
d_h (μm)	159.0 (22.7)	177.2 (25.7)	0.56	78.2 (7.5)	59.0 (7.6)	0.0727
D_t (g cm^{-3})	0.52 (0.04)	0.53 (0.04)	0.98	0.67 (0.02)	0.69 (0.02)	0.52









HYDRAULIC REDISTRIBUTION BY A DOMINANT, WARM-DESERT
PHREATOPHYTE: SEASONAL PATTERNS AND RESPONSE TO
PRECIPITATION PULSES

Kevin R. Hultine

School of Natural Resources, University of Arizona, Tucson, AZ, 85721, USA

ABSTRACT

1. Hydraulic redistribution may have important consequences to ecosystem water balance where plant root systems span large gradients in soil water potential. To assess seasonal patterns of hydraulic redistribution, we measured the direction and rate of sap flow in taproots, lateral roots, and main stems of three mature *Prosopis velutina* Woot. trees occurring on a floodplain terrace in semi-arid southeastern Arizona, USA. Sap flow measurements on two of the trees were initiated before the end of the winter dormancy period, prior to leaf flush.
2. Despite the absence of crown transpiration during the dormant season, sap flow was detected in lateral and taproots of *P. velutina*. Reverse flow (i.e., flow away from the stem) in the lateral root and positive flow (i.e., flow towards the stem) in the taproot was observed in one tree, indicating the presence of hydraulic lift. Conversely, reverse flow in the taproot and positive flow in the lateral root was observed in the second tree, indicating hydraulic descent.
3. Hydraulic descent was induced in the roots of the former tree by wetting the rooting zone in the upper 70 cm of the soil surface with 50 mm of irrigation.
4. Patterns and rates of nocturnal sap flow in roots of a third tree measured during the growing season were similar to that observed during the dormant season. Nocturnal reverse flow in the lateral root and positive flow in the taproot was observed prior to the onset of the summer monsoon. Hydraulic descent commenced immediately following the first large monsoon rain event, and continued after subsequent rain events. After

adjusting for differences in sapwood area, maximum diurnal rates of hydraulic descent in the taproots of trees instrumented during the dormant season were 73, and 69% of the maximum nighttime rate of hydraulic descent observed during the growing season.

5. Despite very limited potential for direct infiltration, volumetric soil moisture levels in deep soil layers (1.5-9.5 m) increased 2 to 8% ($\text{cm}^3 \text{ cm}^{-3}$) by the end of the monsoon (late September) indicating that plant roots were redistributing non-trivial amounts of water to deep soil layers.

6. Roots of *Prosopis velutina* apparently redistribute significant amounts of soil water during the growing season, but also during periods of crown dormancy in winter. In arid regions, dormant- season hydraulic descent may buffer plants from water and nutrient deficits during initial stages of the growing season by transferring soil water derived from winter precipitation to deep soil layers and away from zones of evaporation in surface layers and shallow-rooted herbaceous plants.

Key-words: hydraulic descent, hydraulic lift, root sap flow, *Prosopis velutina*, soil moisture redistribution

INTRODUCTION:

Plant roots capture, store and transport soil water, and in doing so alter ecosystem water, energy, and nutrient balance. One potentially important process facilitated by roots is the passive redistribution of water from moist to dry soil layers. Hydraulic redistribution (*sensu* Burgess et al. 1998) occurs during periods of low crown transpiration (e.g., nocturnal periods) when water potential of the root xylem rises to values intermediate between root-occupied moist and dry soil layers. Under these circumstances, roots act as conduits for passive transport between soil layers. Hydraulic redistribution has been detected in a wide variety of plant life forms including grasses (Caldwell & Richards 1989) and succulents (Caldwell et al. 1998), but appears most common in deep-rooted trees and shrubs that can forage for stable water sources across multiple soil layers. The importance of hydraulic redistribution for ecosystem water balance depends largely on its vertical direction, magnitude, duration, and seasonality.

Initiation of reverse sap flow in plant roots (i.e., flow away from the stem and into surrounding soil) corresponds with measurable changes in soil moisture within the rooting zone (Burgess et al. 2000; Brooks et al. 2002), establishing a clear connection between reverse flow and hydraulic redistribution. Evidence of hydraulic redistribution from soil moisture data has typically focused on the upward transfer of soil water (hydraulic lift), since soil moisture measurements of subsurface soils are logistically difficult to obtain. However, advancement in soil moisture instrumentation including frequency domain capacitance probes (Paltineanu & Starr 1997), and cross-borehole

ground penetrating radar (GPR) (Eppstein & Dougherty 1998; Alumbaugh et al. 2002) can measure very slight changes in diel and seasonal water content in deep soil layers.

Because hydraulic redistribution does not require metabolic energy, plants potentially could redistribute water during periods of dormancy, as long as their roots maintain axial (xylem) and radial conductivity, and physical contact with the surrounding soil. Hydraulic redistribution throughout extended periods of the dormant season may have important ecological and hydrological consequences. During wet winters, deep-rooted plants could redistribute water from moist surface soils to deep soil layers (hydraulic descent), and away from shallow-rooted competitors and soil evaporative processes. The “banking” of soil water during dormancy for future use may be particularly beneficial for plants occurring in arid and semiarid regions that are typically warm and dry during the early stages of the growing season, such as in the southwestern United States where rainfall is scarce in late spring. Conversely, dry winter years could produce patterns of hydraulic lift if there is sufficient water storage in the deep soil layers of the rooting zone. Dormant season hydraulic lift may enhance shallow root longevity and activity of not only the deep-rooted “lifter”, but also co-occurring shallow-rooted plants (Richards and Caldwell 1987; Dawson 1993) as long as a significant amount of the hydraulically lifted water is not lost to soil evaporation.

We monitored seasonal patterns of root and stem sap flow, and seasonal fluctuations in soil water content of subsurface soil layers in a mature stand of velvet mesquite (*Prosopis velutina* Woot.) on a floodplain terrace of the San Pedro River in southeastern Arizona, USA. Our goal was to determine if mesquite roots were capable of

redistributing soil water during periods of plant dormancy, and if so, how the magnitudes and patterns of dormant season redistribution compared to that during the growing season.

MATERIALS AND METHODS

Site description

The site was located on an alluvial floodplain terrace near the San Pedro River in southeastern Arizona, USA (31°40'N, 111°11'W; 1190 m elevation). Depth to groundwater ranged from 7 to 11 m. The overstory vegetation was a mixed-age stand dominated by the leguminous tree *Prosopis velutina* Woot. *P. velutina* stem diameters ranged from just a few cm to over 75 cm, and average leaf area index was about 1.6 m²/m² (Scott et al. 2003). The shallow groundwater table was the primary source of transpiration by overstory vegetation (Scott et al. 2003). The understory vegetation was dominated by the perennial bunchgrass *Sporobolus wrightii* Munro. intermixed with annual herbaceous dicots. The alluvial soils were comprised mostly of sandy loams interspersed with layers of gravels and clays.

Climate in the upper San Pedro valley is semi-arid with temperatures ranging from a mean maximum of 24.8°C to a mean minimum temperature of 9.9°C. Nighttime temperatures within the riparian corridor are typically 2 to 8°C lower than the surrounding valley due to cold air drainage (Scott et al. in press). Air temperature was measured 6 m above the soil surface (mid-canopy height) using a temperature/relative humidity probe (Vaisala, Woburn, MA). Soil temperature was measured at 5- and 15-cm depths with soil thermocouples. Precipitation is bimodal with roughly 60% of the 350 mm mean annual distribution of precipitation falling during the summer monsoon

(July through September) and about 23% falling during the winter months (December through March). Precipitation at the site was measured with a tipping bucket rain gauge.

Sap flow measurements

We used the heat ratio method (HRM) in this investigation to measure xylem sap flow. The HRM has been described previously in detail (Burgess et al. 2001*a*, 2001*b*, Hultine et al. 2003*a*). Briefly, the HRM employs temperature probes at equal distances up- and downstream from a pulsed heat source. The difference in heat carried up- and downstream is proportional to the magnitude of sap flux, and the sign of the difference indicates the flux direction. We measured sap flow in the stems, tap roots, and main lateral roots of three *P. velutina* trees in the Spring, Summer, and early fall of 2002. Two trees were selected in early March approximately 30 m from the river channel to measure root and stem sap flow during periods before and during leaf flush (Tree 1 and Tree 2, Table 1). An additional tree (Tree 3) was selected roughly 400 m from the river in early July for growing season measurements of sap flow. The close proximity of Trees 1 and 2 to the river allowed for easy extraction of river water to irrigate the trees during the experiment (described below). Soil around the trees was carefully excavated to expose large roots at the base of the trees. The taproot, and one main lateral root were selected on each tree for sensor installation. A single sap flow sensor was inserted into the xylem of the lateral root, while two sensors were inserted into the larger taproot on each tree. A single sensor was also inserted into the main stem of each tree. After sensor installation, the roots were covered with a tarpaulin to thermally insulate the exposed roots from

nighttime freezing and to minimize radiant heating during the day by direct sunlight. The sap flow sensors (Thermal Logic, Pullman, WA, USA) consisted of three 35 mm long stainless steel probes spaced 6 mm apart. The central probe contained an Evanohm 44- Ω line heater, while the outside probes contained three-paired thermocouple junctions spaced to measure heat pulse velocity at 5, 10, and 20 mm radial depths.

After correcting for wounding effect (Burgess et al. 2001*b*), heat pulse velocity (V_h) was converted to sap velocity (V_s) (cm / hour) according to Barrett et al. (1995):

$$(1) \quad V_s = \frac{V_h \rho_b (c_w + m_c c_s)}{\rho_s c_s}$$

where c_w and c_s are the specific heat of dry wood (1200 J kg⁻¹ °C⁻¹ at 20 °C, Becker and Edwards 1999) and sap (assumed to equal that of water, 4182 J kg⁻¹ °C⁻¹ at 20 °C), and ρ_s is the density of sap (assumed to equal that of water, 998 kg m⁻³ at 20 °C), ρ_b is the density of wood, and m_c is the moisture content of wood. Volumetric sap flow (L day⁻¹) was calculated after first subtracting the bark thickness from the radius of the stem or root. The heartwood radius was subtracted from gross wood area after it was identified by visual observation of the dark color associated with heartwood. The sapwood area was then divided into concentric bands coinciding with the depth of each thermocouple junction within the probes. Thus, estimates of sap flow were weighted by the amount of conducting sapwood of each band.

Because HRM measurements of sap flow are very sensitive to spacing between the temperature probes and the central heating probe, the true spacing between probes

must be validated. To validate a zero flow we severed the roots and stem at the conclusion of the study to stop all flow. Spacing between probes was calculated according to Burgess et al. (1998):

$$(2) \quad x_2 = \sqrt{4kt \ln\left(\frac{v_1}{v_2}\right) + x_1^2}$$

where x_2 (mm) is designated the incorrectly spaced probe, x_1 is assumed to be correctly spaced at 6 mm, k is the thermal diffusivity of fresh wood (measured from cores of the individual roots and stems), v_1 and v_2 are the increases in temperature at equidistant points downstream and upstream respectively, and t is the median measurement time after the release of the heat pulse (in this case 60 s). Since it is unknown which probe is incorrectly spaced, or whether both probes are incorrectly spaced, Eq. 1 was solved for x_1 and x_2 and the two solutions were averaged.

In some cases, we were unable to obtain a zero measurement to correct for probe mis-alignment. In these cases, X-ray radiographs were taken of the inserted probes from the side and top to obtain a three dimensional view inside the root segment (Diagnostic X-Ray Laboratory, University of Arizona Medical Center). This approach previously has shown comparable results with the traditional *in situ* method for probe spacing corrections (Hultine et al. 2003b). Distances between probes were measured from the X-ray image using the software application NIH Image (version 1.62 for Macintosh), and the protocol described in Hultine et al. (2003b).

Irrigation experiment

Eleven days after sap flow measurements were initiated during the dormant winter period, we applied 50 mm of irrigation to Trees 1 and 2 to assess the potential response of sap flow in deep and shallow roots to pulses of dormant season precipitation. The ground surface within a 5-m radius around each tree was cleared, and a gas-powered pump was used to deliver river water to the cleared area (78.53 m²) of each tree at a rate of 20 L minute⁻¹. Runoff from the plots was absent due to the relatively low application rate coupled with the high infiltration rate of the coarse sandy loam soil. Care was taken to avoid applying water near the base of the trees where the roots were instrumented with sap flow sensors. Water content reflectometers (CS615, Campbell Scientific Inc., Logan, Utah) were installed in a vertical profile in one of the irrigation plots at 10-, 20-, 30-, 50-, 70-, and 90-cm depths to assess the rate and depth of infiltration after irrigation. Two WCR probes were installed at each depth except at 70 and 90 cm where single probes were installed.

Vadose zone soil moisture measurements

Volumetric soil water content (θ) of deep soil layers (1.5-9.5 m depths) was estimated periodically near Tree 3 using cross-borehole ground penetrating radar (see Alumbaugh et al. (2002) for details). Briefly, cross-borehole ground penetrating radar yielded the travel time of the direct wave from the source to the receiver using a center frequency of 50 MHz along a 0.25-m incremental-depth-sampling interval. The travel times in combination with the known separation between two adjacent, PVC-lined,

boreholes (1.72 m and 2.13 m) were used to estimate profiles of the dielectric constant. Profiles of volumetric water content were computed using the dielectric values via a well-known empirical relationship (Topp et al. 1980).

In addition, soil hydraulic properties were estimated to assess the importance of capillary rise from groundwater, and infiltration during the monsoon season to vadose zone θ . Capillary rise (h) was calculated by combining measurements of groundwater depth with estimates of soil pore size distribution and a general capillary rise equation:

$$(3) \quad h = \frac{2\sigma \cos \gamma}{\rho_w g r}$$

where σ is the surface tension of water, ρ_w is the density of water, γ is the contact angle (assume to equal zero), g is the acceleration due to gravity (9.81 m/s^2), and r is the pore radius. The temperature-dependent variables σ and ρ_w were calculated by estimating the mean annual soil temperature at 1.5 m (top of the GPR profile). Soil temperature (T) at this depth was calculated according to Campbell (1986):

$$(4) \quad T = T_s + A(0)e^{-z/D} \sin(\omega t - z/D)$$

where T_s ($^{\circ}\text{C}$) is the temperature at the soil surface, $A(0)$ is the amplitude of the surface temperature fluctuation, ω is the angular frequency of the of the oscillation given by $2\pi/\tau$, where τ is the period of oscillation (365 days), D is the damping depth (m), and z is the soil depth (1.5 m). Damping depth was determined as:

$$(5) \quad D = \left(\frac{2k}{\omega}\right)^{1/2}$$

where κ is the thermal diffusivity of the soil, estimated to be $0.2 \text{ mm}^2 \text{ s}^{-1}$ according to the soil texture and volumetric soil water content (Campbell 1986). Pore radius distribution was estimated from soil texture analysis (determined for various soils within the vertical profile) by calculating the relationship between θ and soil matric potential (Ψ_m) using coefficients reported by Campbell (1985), and by rearranging Equation 3 to solve for r , where Ψ_m is assumed to equal h (Hillel 1982). Fluctuations in groundwater depth were measured with a water level transducer (MiniTROLL in situ Inc, Laramie, WY, USA) installed in a pre-existing well piezometer.

The flux of surface moisture into the GPR profile was calculated by estimating the amount of soil water storage that infiltrated below 1.5 m. Soil water storage (S) was calculated as:

$$(6) \quad S = P - ET_u - I_c$$

Where P is the total amount of precipitation that fell on the site during the experiment (248 mm), ET_u (mm) is the total evapotranspiration of the understory (understory vegetation plus soil evaporation), and I_c (mm) is the estimated canopy interception.

Runoff was assumed to be negligible due to the shallow slope and high saturated conductivity of the coarse shallow soil layers. Total ET_u was calculated by multiplying mean daily ET_u by the length of the monsoon season (July 8 to September 25). We used a previously published value of 1.5 mm day^{-1} for mean daily ET_u at the site (Scott et al. 2003). Canopy interception was estimated using coefficients reported by Návar and Bryan (1994) for individual *Prosopis* canopies multiplied by the total overstory canopy cover at our field site (70%, Scott et al. 2003).

Infiltration of S into the GPR profile was calculated by estimating the amount of water transmitted via capillary descent (i.e. Eq. 3), and the volume fraction of macropores, where during ponding, water may move rapidly through the profile without interacting with the soil matrix. Macropores were defined according to the Soil Science Society of America (1997) as all pores having a diameter greater than $75\ \mu\text{m}$. Infiltration via macropore flow was calculated as the volume fraction of macropore space (V_m), estimated from pore radius distribution, multiplied by S .

Statistical analysis

Linear regression analysis (ANOVA) was used to test whether patterns of root sap flow varied with time following experimental irrigation. Linear regression was also performed to test the relationship in the direction and magnitude of sap flow between the taproot and lateral root of each tree. Statistical analysis was performed using JMP 4.0 (SAS Institute Inc.)

RESULTS

Dormant-season hydraulic redistribution

Minimum air temperatures during the dormant season ranged from -15 to +15 °C at the study site (Fig. 1). Despite the freezing air temperatures, soil temperatures at 5 cm depths only briefly dropped below zero in late December, and again in early February. Soil temperatures at 15 cm depth never dropped below 1°C, suggesting that *P. velutina* roots were likely not subjected to freeze-thaw cycles that would induce xylem embolism.

Positive rates of sap flow (flow toward the stem) in the taproot of tree 1 ranged from 0.5-1.8 L Day⁻¹ (Figure 2a) prior to irrigation. Sap flow decreased slightly in this root between day-of-year (DOY) 64 and 74, however, the pattern was not significant ($P = 0.328$). After 50 mm of irrigation was applied, soil water content in the upper 30 cm of the profile increased within 12 hours, while infiltration at 50- and 70-cm depths took approximately 48, and 96 hours, respectively (Figure 2b). There was little or no infiltration at 90 cm. After irrigation, the direction of sap flow in the taproot immediately shifted from positive to reverse, and significantly increased in magnitude between the day of irrigation and day 92 by an average of 0.11 L Day⁻¹ ($R^2 = 0.91$, $P < 0.0001$, $n = 17$ days, from ANOVA). Reverse flow (flow away from the stem) leveled off at approximately 1.5 L Day⁻¹ after DOY 92. Sap flow in the smaller lateral root was much lower than in the taproot, but consistently flowed in the direction away from the stem prior to irrigation, the pattern expected with hydraulic lift. After irrigation, the direction of nocturnal sap flow in the lateral root shifted toward the stem, and remained positive throughout the

remainder of the experiment. Rates of sap flow in the lateral root and taproot were inversely correlated on a daily time-step, consistent with that expected during hydraulic redistribution ($R^2 = 0.59$, $P < 0.0001$, $n = 32$ days, from ANOVA).

The direction of sap flow in the roots of Tree 2 was different than that in Tree 1 prior to irrigation; reverse flow was detected in the taproot, while positive flow was detected in the lateral root (Figure 3a). After irrigation, rates of reverse sap flow in the taproot increased continuously from approximately 1.5 L Day^{-1} to 2.2 L Day^{-1} until DOY 80. Afterwards, reverse flow declined steadily until leaf flush on DOY 138. After leaf flush, sap flow in the taproot consistently increased until the amount of daytime positive sap flow equaled nocturnal reverse flow at the conclusion of the measurements. Response to irrigation in the lateral root was barely detectable. Nevertheless, daily sap flow rates in the lateral and taproots were weakly and inversely correlated between DOY 65 (beginning of the observations) and DOY 138 (beginning of leaf flush) ($R^2 = 0.20$, $P < 0.0001$, from ANOVA).

There was no consistent diurnal pattern of root or stem sap flow in either tree (Figure 4). Likewise, there was no consistent correlation between patterns of root and stem sap flow during the dormant season suggesting that flow patterns in the roots were not related to water loss from the stem.

Growing-season hydraulic redistribution

Growing season sap flow measurements were initiated before the onset of the monsoon. In fact, there had been no significant precipitation for 149 days prior to the

study. Thus, shallow soil layers were extremely dry at the beginning of the study.

Before the onset of the monsoon, nocturnal reverse flow was strongly evident in Tree 3's lateral root, and was accompanied by positive flow in the taproot (Figure 5a). After two moderate precipitation events on DOY 197 and 198, root sap flow patterns in Tree 3 shifted dramatically; nocturnal reverse flow commenced in the taproot, while nighttime positive flow was detected in the lateral root. This pattern was enhanced by large rain events on days 232 and 251 (Figure 5b), with maximum rates of reverse flow in the taproot approaching 9 L night^{-1} (Figure 5a). Rates of nocturnal sap flow in the taproot and lateral root were inversely correlated on a half-hourly time-step ($R^2 = 0.85$, $F = 9498$, $P < 0.0001$, from ANOVA).

Moisture of subsurface soil layers

Cross-borehole GPR measurements were made for the two adjacent vadose-zone profiles (-1.5 to 9.5 m) located near Tree 3 on 17 June (pre-monsoon, DOY 168), 15 August (mid-monsoon, DOY 227), 25 September (late-monsoon, DOY 267), and 20 November (post-monsoon, DOY 324) 2002. Soil moisture increased during the monsoon, particularly late monsoon where moisture in the deep soil layers was 2 to 8% higher than before the monsoon (Figure 6). In fact, total moisture within the vertical profile increased between June 17 and September 25 by 318 mm. Capillary rise over the same period could account for a net increase of only 25 mm, while infiltration modeled from capillary descent and macropore flow could account for only 20 mm. Soil moisture

decreased between late-monsoon and post-monsoon periods, but remained higher after the monsoon than before the monsoon (Figure 6).

DISCUSSION

Previous studies indicate when transpiration is reduced (usually at night) plant roots transport water from moist soil layers to drier regions of the soil profile (Richards & Caldwell 1987, Burgess et al. 1998, 2000, 2001, Smith et al. 1999, Hultine et al. 2003a,b). The phenomenon, termed hydraulic redistribution occurs in a wide range of ecosystems and plant life forms (Caldwell, Dawson, & Richards 1998). However, to our knowledge, no previous investigation has reported the phenomenon occurring during periods of plant dormancy. Our study shows that roots of the woody legume, *Prosopis velutina*, redistributed a significant amount of water in early spring prior to leaf flush (typically early November through mid-May), at rates comparable to that observed during the summer growing season.

After adjusting for differences in sapwood area among the taproots of the three trees, maximum rates of reverse flow ($L\ day^{-1}$) in the two trees instrumented during the dormant period were 71% of the maximum nightly rate of reverse flow observed in the taproot of a third tree during the summer, while nocturnal reverse flow in the taproot of the third tree was 25 to 50% of daytime positive flow during transpiration. Based on these observations, three to six days of reverse flow during the dormant season potentially could supply the taproot with enough moisture to meet the transpiration for one day during the growing season. We caution against strict conclusions based on a few individual trees. Nevertheless, given that crown dormancy in *P. velutina* at this site typically lasts about five months, hydraulic descent during wet winters could supply the

taproot with several days, or even several weeks of water for growing season consumption as long as a water potential gradient is maintained within the root zone.

The relative importance of hydraulic descent to plant water balance depends on the fate of shallow soil water if it is otherwise not redistributed by the root system. Soil water from winter precipitation apparently does not recharge deep soil layers along the alluvial river terrace (Scott et al., in press), nor at other upland sites in this region (Scott et al. 2000). Thus, much of the water that remains in shallow soil layers is either taken up early in the growing season by co-occurring shallow-rooted plants such as the perennial tussock grass *Sporobolus wrightii*, or is potentially lost to evaporation since potential evapotranspiration during the winter months and early spring remains relatively high in semi-arid climates. The ability to “bank” water during winter dormancy for later consumption presents a win-win scenario for deep-rooted plants, since there is a very small carbon investment to maintain the fine root systems that act as conduits for redistribution during winter dormancy (Widen & Majdi 2001; Burton et al. 2002). Nevertheless, the significance of hydraulic descent to water balance of mature mesquite plants in floodplain ecosystems is an open question since mature plants have access to groundwater throughout the growing season (Scott et al. 2003). Dormant-season hydraulic descent may play a much greater role in the water balance of mesquite growing in upland habitats where groundwater is not available within the rooting zone, or in young plants in the floodplain that have not yet grown roots into groundwater.

During years of little or no winter precipitation, the balance of redistribution is towards the upper soil layers (i.e., hydraulic lift). Hydraulic lift during extended periods

of the dormant season provides water storage in the upper soil layers that can be rapidly extracted during spring leaf flush since the upper soil layers generally contain the highest root length densities (Jackson et al. 1996). However much of the water that is deposited from deep soil layers to shallow soils may be lost to evapotranspiration before leaf flush or to other co-occurring plants. Further work is needed to establish a clear connection between dormant season hydraulic lift and whole plant water balance.

Regardless of its role in plant and ecosystem water balance, dormant-season hydraulic redistribution has several potentially important implications for plant nutrient balance (Richards & Caldwell 1987). Mineral nutrients are generally most abundant in the upper soil layers. However, the early growing season in most of the southwestern United States is characterized by warm daytime temperatures with little or no precipitation until the onset of the monsoon (usually mid July). For *P. velutina* trees at our field site, this represents between 80 and 120 days between spring leaf flush and the onset of the monsoon. Thus, the mobility of nutrients in the dry shallow soils is potentially low before the monsoon, and diffusion to roots is inhibited. Hydraulic lift during the dormant season can prolong the life span of fine roots and microorganisms and thereby enhance nutrient ion mobility and uptake during the dry periods of the growing season. Likewise, the dormant season transfer of mineral nutrients with hydraulic descent to deeper soil layers can potentially smooth the spatial heterogeneity of nutrients, and therefore, enhance plant nutrient uptake during the early growing season when water extraction is primarily from deep soils (Emerman 1996; Burgess et al. 2001).

In order for plant roots to redistribute water between soil layers, they must maintain axial (xylem) hydraulic conductivity (K_x). In many regions, xylem conduits in above ground tissues typically become dysfunctional during winter due to freeze-thaw cavitation (Cochard & Tyree 1990; Sperry 1993; Pockman & Sperry 1997). Conversely, xylem conduits in roots may not completely embolize where soils insulate roots from freezing temperatures. In the present study, *P. velutina* roots in the upper 50 cm of soil maintained 35% of maximum conductivity during winter, and 70% during summer before the onset of the monsoon (data unpublished). The relatively high xylem conductivities in winter are not surprising considering that soil temperatures at 15 cm never reached freezing despite that minimum air temperatures at mid-canopy reached $-15\text{ }^{\circ}\text{C}$ during the winter. *P. velutina* roots at the site are rarely found near the soil surface above 15 cm depth, particularly in the inter-canopy spaces where high temperatures in the upper top few centimeters of soil during the growing season are lethal to living root tissues.

Soil moisture levels in deep soil layers (-1.5 to -9.5 m) increased during the monsoon. We suspect that the observed soil moisture changes were due to hydraulic redistribution; moisture throughout the vertical transect increased 318 mm between June 17 and September 25, while capillary rise from groundwater fluctuations combined with infiltration could account for only 45 mm of moisture within the GPR profile. It is plausible that our estimates of infiltration are low for two reasons. First, our estimates of V_m , from texture analysis of the bulk soil may be low given the presence of root channels and cobbles. Second, the presence of macropores, according to our analysis, did not extend below -2.4 m. Depending on the continuity and connectivity of soil pores, it is

possible that the large pores supplied a significant amount of water below -2.4 m, that was not accounted for in our estimates. Nevertheless, precipitation between June 17, and September 25 totaled 248 mm. Therefore, even if all precipitation inputs were transferred below -1.5 m (highly unlikely), it would still not explain the observed change in moisture in the deep soil layers. Moreover, Scott et al. (in press), using profiles of soil moisture probes in the upper 1.0 m of soil at this site, report that infiltration of precipitation below 0.5 m rarely occurred during 2001 and 2002. Only one infiltration event was observed below 0.5 m, and this resulted in only a 2 % change in soil moisture content at 0.7 m.

The above argument requires reasonably accurate estimates of vadose zone θ . Although a site-specific calibration of apparent dielectric constant versus soil moisture content has not yet been established, Alumbaugh et al. (2002) argued that the precision error for this type of cross-borehole GPR measurement is ~ 0.5 % in moisture content estimation. If so, changes in vadose zone θ between June 17 and September 20 were between 290 to 350 mm. Therefore, the changes seen in the profile are arguably significant. Water content changes between $\sim 5.75 - 7.25$ m depth could not be estimated as there was too much attenuation of the waveform for an accurate estimation of the travel time. At this depth interval, well logs reveal a thick layer of clayey material.

After the onset of the monsoon, nocturnal reverse flow in the taproot was typically lower in magnitude than its daytime flow towards the stem, suggesting that the water content of deep soil layers should still be depleted (although at a lower rate) after precipitation wetted the upper soil layers. However, water content increased during the

monsoon in the deep soil layers despite the absence of direct recharge of precipitation below 1 m. It is likely that lateral roots, fine roots and root hairs extend from the taproot in relatively dry soil layers as well as the shallow groundwater table or capillary fringe. Thus, the bulk of daytime positive flow in the taproot was likely derived from the extraction of groundwater and that nocturnal reverse flow was a consequence of redistribution to the dry soil layers above the water table. Unfortunately, measurement of root sap flow alone can not detect the source nor the fate of water that moves through woody roots.

There were substantial differences in the pattern and direction of root sap flow during the dormant season between Trees 1 and 2 prior to irrigation. Sap in the taproot of Tree 1 flowed towards the stem, while sap in the lateral root flowed away from the stem. Before irrigation, we found reverse flow in the taproot, and positive flow in the lateral root of Tree 2. Differences in root sap flow between trees were likely caused by differences in the vertical distribution of roots within the various soil layers. Lateral roots of *P. velutina* at our site often extend vertically beyond the recharge zone (personal observation), and therefore unlike shallow lateral roots do not respond to pulses of moisture. In fact, sap flow patterns in the taproot of tree 2 suggest that some lateral roots were in deeper, wetter soil layers than the taproot. Hence, it is possible that the source of water supplied to Tree 2's taproot was from deep soil layers before irrigation, and from shallow (and possibly deep) soil layers after irrigation was applied.

We found evidence that plants redistribute a non-trivial amount of water during winter dormancy. The magnitude and vertical direction of redistribution likely depends

on the amount, and intensity of winter precipitation, and the vertical distribution and activity of fine roots. Potential benefits of redistribution include reducing water and nutrient deficits, particularly if the balance of redistribution over the dormant season occurs in the downward direction, and away from evaporative processes in the shallow soil layers. Hydraulic redistribution could play an important role in the ratio of ecosystem evaporation to transpiration on a diurnal, seasonal, and annual time step. Future work will focus on the relative impacts of hydraulic redistribution on soil hydraulic properties within the vadose zone, the water table, and stream discharge.

LITERATURE CITED

- Alumbaugh, D., Chang, P. Y., Paprocki, L., Brainard, J.R., Glass, R.J., & Rautman, C.A. 2002. Estimating moisture contents in the vadose zone using cross-borehole ground penetrating radar: A study of accuracy and repeatability, *Water Resources Research* **38**: 1309, doi:10.1029/2001 WR000754.
- Barrett, D.J., Hatton, T.J., Ash, J.E., & Ball, M.C. 1995. Evaluation of the heat pulse velocity technique for measurement of sap flow in rainforest and eucalypt forest species of south-eastern Australia. *Plant Cell and Environment* **18**: 463-469.
- Becker, P., and Edwards, W.R.N. 1999. Corrected heat capacity of wood for sap flow calculations. *Tree Physiology* **19**: 767-768.
- Brooks, J.R., Meinzer, F.C., Coulombe, R., & Gregg, J. 2002. Hydraulic redistribution of soil water during summer drought in two contrasting Pacific Northwest coniferous forests. *Tree Physiology* **22**: 1107-1117.
- Burgess, S.S.O., Adams, M.A., Turner N.C., & Ong C.K. 1998. The redistribution of soil

- water by tree root systems. *Oecologia* **115**: 306-311.
- Burgess., S.S.O., Pate, J.S. Adams, M.A., & Dawson, T.E. 2000. Seasonal water acquisition and redistribution in the Australian woody phreatophyte, *Banksia prionotes*. *Annals of Botany* **85**: 215-224.
- Burgess, S.S.O., Adams, M.A., Turner, N.C., White D.A., & Ong, C.K. 2001a. Tree roots: conduits for deep recharge of soil water. *Oecologia* **126**: 158-165.
- Burgess, S.S.O., Adams, M.A., Turner, N.C., Beverly, C.R., Ong, C.K., Khan, A.A.H., & Bleby, T.M. 2001b. An improved heat pulse method to measure slow and reverse flow in woody plants. *Tree Physiology* **21**: 589-598.
- Burton, A.J., Pregitzer, K.S., Ruess, R.W., Hendrick, R.L., & Allen., M.F. 2002. Root respiration in North American forests: effects of nitrogen concentration and temperature across biomes. *Oecologia* **131**: 559-568.
- Caldwell, M.M. & Richards, J.H. 1989. Hydraulic lift: water efflux from upper roots improves effectiveness of water uptake by deep roots. *Oecologia* **79**: 1-5.
- Caldwell, M.M., Dawson, T.E., & Richards, J.H. 1998. Hydraulic lift: consequences of water efflux from the roots of plants. *Oecologia* **113**: 151-161.
- Campbell, G.S. 1985. *Soil physics with Basic*. Elsevier Science Publishing., Amsterdam.
- Campbell, G.S. 1986. *An Introduction to Soil Physics*. Springer Verlag., Berlin
- Cochard, H., & Tyree, T.E. 1990. Xylem dysfunction in *Quercus*: vessel sizes, tyloses, cavitation, and seasonal changes in embolism. *Tree Physiology* **6**: 393-407.
- Dawson, T.E. 1993. Hydraulic lift and water use by plants: implications for water

- balance, performance and plant-plant interactions. *Oecologia* **95**: 565-574.
- Emerman, S.H. 1996. Towards a theory of hydraulic lift in trees and shrubs. *Sixteenth American Geophysical Union hydrology days*. (ed H.J. Morel-Seytoux), pp147-157. Hydrology Days Publication, Atherton, California.
- Eppstein, M.J., & Dougherty, D.E. 1998. Efficient three-dimensional data inversion: soil characterization and moisture monitoring from cross-well ground penetrating radar at the Vermont test site. *Water Resources Research* **34**: 1889-1900.
- Hillel, D. 1982. *An Introduction to Soil Physics*. Academic Press. San Diego, CA, USA.
- Hultine, K.H., Williams, D.G., Burgess, S.S.O., & Keefer, T.O. 2003a. Contrasting patterns of hydraulic redistribution in three desert phreatophytes. *Oecologia* **135**: 167-175.
- Hultine, K.H., Cable, W.L., Burgess, S.S.O., Williams, D.G. 2003b. Hydraulic redistribution by deep roots of a Chihuahuan Desert phreatophyte. *Tree Physiology* **23**: 353-360.
- Jackson, R.B., Canadell, J., Ehleringer, J.R., Mooney, H.A., Sala, O.E., & Schultze, E.D. 1996. A global analysis of root distributions for terrestrial biomes. *Oecologia* **108**: 389-411.
- Návar, J., & Bryan, R.B. 1994. Fitting the analytical model of rainfall interception of Gash to individual shrubs of semi-desert vegetation in northeastern Mexico. *Agricultural and Forest Meteorology* **68**: 133-143
- Paltineanu, I.C., & Starr, J.L. 1997. Real-time soil water dynamics using multisensor

- capacitance probes: laboratory calibration. *Soil Science Society of America Journal* **61**: 1576-1585.
- Pockman, W.T., & Sperry, J.S. 1997. Freezing-induced xylem cavitation and the northern limit of *Larrea tridentata*. *Oecologia* **109**: 19-27.
- Richards, J.H. & Caldwell, M.M. 1987. Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. *Oecologia* **73**: 486-489.
- Scott R.L., Shuttleworth, W.J., Keefer, T.O., & Warrick, A.W. 2000b. Modeling multiyear observations of soil moisture recharge in the semiarid American southwest. *Water Resources Research* **36**: 2233-2247.
- Scott, R.L., Watts, C., Garatuza Payan, J., Edwards, E., Goodrich, D.C., Williams, D., & Shuttleworth, J.W. 2003. The understory and overstory partitioning of energy and water fluxes in an open canopy, semiarid woodland. *Agricultural and Forest Meteorology* **114**: 127-139.
- Scott, R. L., Edwards, E.A., Shuttleworth, J.W., Huxman, T.E., Watts, C. & Goodrich, D.C. 2004. Interannual and seasonal variation in fluxes of water and carbon dioxide from a riparian woodland ecosystem. *Journal of Agricultural and Forest Meteorology*, in press.
- Smith, D.M., Jackson, N.A., Roberts, J.M., & Ong, C.K. 1999. Reverse flow in tree roots and downward siphoning of water by *Grevillea robusta*. *Functional Ecology* **13**: 256-264.
- Soil Science Society of America. 1997. Glossary of soil science terms. *Soil Science*

Society of America, Madison, WI

Sperry, J.S. 1993. Winter embolism and spring recovery of *Betula cordifolia*, *Fagus grandifolia*, and *Acer rubens*. *Water transport in plants under water stress* (ed. A. Raschi, M. Borghetti, & J. Grace). Cambridge University Press, Cambridge, UK.

Topp, G.C., Davis, J.L., & Annan, A.P. 1980. Electromagnetic determination of soil water content: Measurements in coaxial transmission lines. *Water Resources Research* **16**: 574-582

Widen B., & Majdi, H. 2001. Soil CO² efflux and root respiration at three sites in a mixed pine and spruce forest: seasonal and diurnal variation. *Canadian Journal of Forest Research* **31**: 786-796.

FIGURE LEGENDS

Figure 1 – Air temperature at 6 m above the soil surface and soil temperatures at 5-, and 15-cm depths during the dormant period between the 2001 and 2002 growing seasons.

Figure 2 – **a.** Total daily sap flow of the stem, taproot, and lateral root of a mature, single stemmed *Prosopis velutina* tree (Tree 1) measured from March 5 (DOY 64) to May 30 (DOY 95). Sap flow values were calculated from half hourly measurements from 0:00 hours to 23:30 hours. 50 mm of irrigation was applied on day 74. Negative values represent reverse flow (i.e. flow away from the crown). **b.** Percent soil water content measured by water content reflectometry probes at 10-, 20-, 30-, 50-, 70-, and 90-cm soil depths. 50 mm of irrigation was applied on day 74.

Figure 3 - Total daily sap flow of the stem, taproot, and lateral root of a mature, single stemmed *Prosopis velutina* tree (Tree 2) measured from March 5 (DOY 64) to May 30 (DOY 150). Sap flow values were calculated from half hourly measurements from 0:00 hours to 23:30 hours. 50 mm of irrigation was applied on day 74. Negative values represent reverse flow (i.e. flow away from the crown).

Figure 4 – An example of the 24 hour pattern of sap flow in the taproot, lateral root, and stem of Tree 1 during the dormant season. Measurements were recorded on DOY 65.

Figure 5 – **a.** Total daily nocturnal sap flow of the stem, taproot, and lateral root of tree 3, calculated from half hourly measurements from 20:00 hours to 05:30 hours during the 2002 growing season. Negative values represent reverse flow (i.e. flow away from the crown). **b.** Daily precipitation totals (mm day^{-1}) at the field site during the study.

Figure 6 – Relative change in soil water content after initial measurements on June 17, 2002. Measurements were conducted with cross-borehole ground penetrating radar. Values are the mean from two adjacent vertical transects. Water content changes between $\sim 5.75 - 7.25$ m depth could not be estimated as there was too much attenuation of the waveform for an accurate estimation of the travel time. At this depth interval, well logs reveal a thick layer of clayey material.

Table 1 - Outside diameter, sapwood thickness, and cross sectional sapwood area of *Prosopis velutina* stems, taproots, and lateral roots measured for sap flow in 2002 in southeastern Arizona, USA.

	Outside diameter (cm)	Sapwood thickness (cm)	Cross sectional sapwood area (cm ²)
<i>Tree 1</i>			
Stem	28.7	1.35	107
Taproot	6.80	1.75	22.5
Lateral root	6.70	1.60	21.5
<i>Tree 2</i>			
Stem	24.1	1.30	77.1
Taproot	9.85	1.25	28.6
Lateral root	3.95	1.35	7.5
<i>Tree 3</i>			
Stem	34.7	1.90	182.1
Taproot	19.1	1.90	86.8
Lateral root	8.35	1.20	21.6

