Mesquite Root Distribution and Water Use Efficiency in Response to Long-term Soil Moisture Manipulations

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Abstract: This study quantified honey mesquite (*Prosopis glandulosa*) root growth and water use efficiency following chronic soil drought or wetness on a clay loam site in north Texas. Root systems of mature trees were containerized with barriers inserted into the soil. Soil moisture within containers was manipulated with irrigation (Irrigated) or rain sheltering (Rainout). Other treatments included containerized precipitation-only (Control) and non-containerized precipitation-only (Natural) with three trees per treatment. After four years of treatment, soil cores to 2.7 m depth were obtained beneath each tree canopy. Mesquite and grass roots were extracted, separated into size classes, and weighed. Root length density (m m^{-3}) was quantified for mesquite roots. Averaged over the entire sample depth, Irrigated trees doubled root length density of small (< 2 mm diam.) roots compared to Control trees (232 vs 105 m m^{-3}). Below 90 cm depth, root length density of large (2 to 10 mm diameter) roots was five times greater in Rainout (36 m m^{-3}) than Control trees (7 m m^{-3}). Over all depths, root biomass was greatest in Rainout trees and root:shoot (biomass) ratio was three times greater in Rainout than Control or Irrigated trees. Mesquite leaf carbon isotope ratio ($\delta^{13}C$) was lower (more negative) in Irrigated trees than other treatments, suggesting these trees had lower water use efficiency. Leaf $\delta^{13}C$ was not different between Rainout and Control trees. Mesquite adapted to chronic wet or drought cycles through increased root growth but patterns of distribution differed as Irrigated trees emphasized growth of small roots throughout the profile and Rainout trees grew large roots into deeper soil layers.

Introduction

Encroachment of woody plants into arid and semi-arid grasslands has occurred on a world-wide scale (van Vegten 1983; Smeins 1983; Ansley and others 2001; Archer and others 2001). Causal factors include reduced fire frequency, livestock overgrazing, increased seed distribution via livestock consumption and fecal deposition, and possibly increased CO_2 levels that favors growth of C_3 shrubs over C_4 grasses (Archer and others 1995; Kramp and others 1998). Success of woody plants is also attributed to an ability to grow deeper roots than grasses and thus better withstand droughts (Hinckley and others 1983; Hesla and others 1985; Gibbons and Lenz 2001).

In the southern Great Plains and southwestern USA, adaptation of honey mesquite (*Prosopis glandulosa* Torr.) to a variety of environments may be related to a plasticity of root system distribution (Gile and others 1997). When available, mesquite will exploit sources of deep water by growing a taproot (Phillips 1963; Mooney and others 1977; Nilsen and others 1981). Mesquite can also persist on sites that have little or no ground water by growing lengthy shallow lateral roots (Heitschmidt and others 1988; Ansley and others 1990). Mesquite in north Texas have been termed "facultative phreatophytes" that function as phreatophytes if unlimited water is available, but are capable of surviving on sites with limited soil water (Wan and Sosebee 1991).

Few studies have observed the influence of extended droughts or wet periods on water relations and rooting behavior of woody perennials such as mesquite, yet prolonged climatic trends may confer competitive advantage to woody perennials such as mesquite and contribute significantly to their encroachment on grasslands (Kummerow 1980; Ansley and others 1992; Archer and others 1995). Our objective was to determine the effect of chronic drought or wetness on distribution and quantity of mesquite roots. A second objective was to quantify the isotopic carbon signature of mesquite foliage as an indicator of water use efficiency response to extended droughts or wet periods. We hypothesized that (1) mesquite exposed to chronic drought would grow deeper roots in search of other water sources and (2) mesquite exposed to chronic wetness would emphasize root growth in shallow layers and possibly sacrifice some deeper roots. Finally, because the site where we were conducting the study had little or no available soil moisture below about 2 m depth (from Ansley and others 1990, 1992), we hypothesized that trees exposed to chronic drought would eventually die.

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Materials and Methods

Site Description and Treatments

The study was conducted within a dense stand of mature mesquite trees in the northern Rolling Plains ecological area of Texas, south of Vernon (33°52'N, 99°17'W; elevation 368 m). Average annual precipitation is 665 mm. Primary grass species are Texas wintergrass (*Nassella leucotricha*) and buffalograss (*Buchloe dactyloides*). Soils are Typic Paleustolls of the Deandale and Kamay series (Koos and others 1962). Both series have clay loam surfaces underlain by a sandstone and shale parent material beginning at 1 m depth. Soil moisture measurements to 8 m depth indicated that there was little available moisture below 2 m depth.

Twelve multi-stemmed mesquite (3.5 ± 0.3 m height; 5.1 ± 0.2 cm diameter, 6.1 ± 0.7 basal stems) were selected for the study on the basis of uniform canopy size. All trees occurred within a 1.3 ha area. During December 1985 through February 1986, aerial portions of neighboring woody vegetation occurring within 20 m of each experimental tree were removed and remaining stumps killed with diesel oil. A 0.5 m wide and 2.5 m deep trench was dug and a sheet metal and plastic barrier was placed vertically around each of nine trees before re-filling the trench (Ansley and others 1988). Each barrier wall was hexagon shaped with each point of the hexagon 4.1 m from tree center. Trees with root barriers were called "containerized" trees, although bottoms of the containers were unsealed; however, soils were dry below 2 m depth. Surface area and soil volume within each container was 42.4 m^2 and 106 m^3 (2.5 m x 42.4 m^2), respectively. Each container wall extended 10 cm above ground to prevent flooding onto the container surface. The three non-containerized trees were termed Natural trees.

Three containerized trees, termed Control trees, had no manipulations other than the root container. Control and Natural trees received rainfall only. Three containerized trees, termed Irrigated trees, received precipitation plus periodic irrigation at about 35 mm each month during the growing season. The irrigation system was supplied via underground polyvinyl chloride (PVC) tubing connected to a 23,000 L tank and electric pump powered by a generator. Water from a municipally approved drinking system was supplied to the tank. Three other containerized trees, termed Rainout trees, received a reduced soil moisture level after installation of a "sub-canopy" rain shelter beneath the foliage of each tree that prevented water from falling on the surface of the container but allowed foliage to be exposed to sunlight. Rain shelters consisted of a wood frame suspended 1 m above ground that was covered with wire netting and glasshouse grade 6-mil plastic (Jacoby and others 1988). The frame and covering were built around the base stems of each tree and extended beyond the root container edge with a slight slope away from tree center. The shelters did not exclude stem flow. Plastic sheets were applied to shelters 29 May 1986. Shelters remained in place from May 1986 through July 1989, except for an eight month period from September 1986 to April 1987 for repairs. Irrigation treatments were also discontinued at the end of July 1989.

Measurements

Four 5-cm diameter aluminum tubes were installed within each root container to 2.2 m depth at 2 m laterally from tree center for soil moisture measurement. Volumetric soil moisture was measured every two weeks and at 30 cm increments to 180 cm depth during each growing season (April-September) using a neutron probe (Greacen 1981). Measurements were calibrated to field-collected samples.

For root measurements, three 10-cm diameter soil cores were taken to 270-m depth near the drip line of each tree during the fall 1989 to spring 1990 using a soil coring device (Giddings Inc., Ft. Collins, CO). Each core was divided into 10-cm segments from 0 to 90 cm, and 30-cm segments from 90 to 270 cm. Soil was separated from all roots in each segment with a hydro-pneumatic elutriation system (Smucker and others 1982). Mesquite roots were separated from roots of other species using a dissecting scope and were divided into two size classes, small (0 to 2 mm diameter) and large (2 to 10 mm diameter). Total root length within each soil segment and root size class was quantified using an automated image analyzer (Harris and Campbell 1989). Values for root length were expressed as root length density (RLD; m root length m^{-3} of soil) (Bohm 1979). Following RLD determination root samples were oven dried and weighed.

Leaf samples were collected from each tree at two week intervals during the 1988 and 1989 growing seasons. Samples were oven dried and ground and isotopic carbon ratio ($\delta^{13}C$), percent N and percent C was determined using methods described by Boutton (1991). Leaf samples were also collected in late August and September 1989, one month following termination of irrigation July 1989 to determine the effect of dry down within root containers following chronic wetness on leaf $\delta^{13}C$.

Canopy height of each tree was measured each year. Canopy biomass in each treatment was estimated from a height-to-mass relationship determined by harvesting over 20 trees (height range: 2-5 m) near the study site as part of another study (Ansley, unpublished data). Root:shoot (R:S) ratios were calculated for containerized trees using these derived canopy mass values and root mass data that were scaled to the volume of the root containers.

Statistical Analysis

Root length density and root mass data were analyzed within each root size and soil depth segment using a one-way ANOVA with treatment (Irrigated, Rainout, Control, Natural) as the main effect (three replicates per treatment) (SAS 1988). Non-normal data were square-root transformed prior to analysis. Means were separated using LSD ($P < 0.05$). Soil moisture values were pooled over all depths and sample dates within each year prior to analysis and analyzed with a

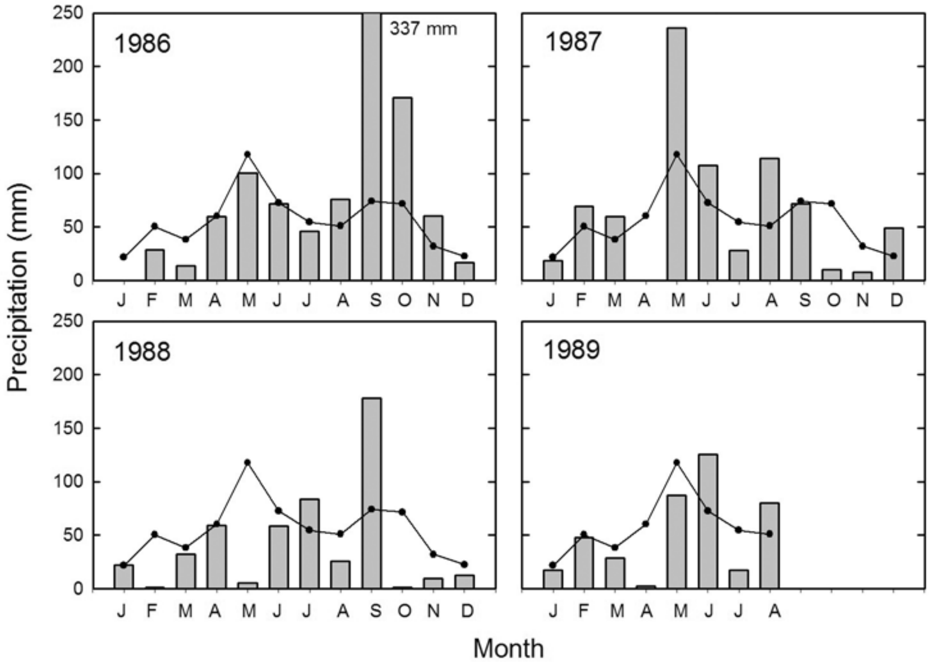

Figure 1. Monthly precipitation at the research site from 1986 until August 1989. Line indicates 30-yr average precipitation for each month.

two-way repeated measures GLM with treatment and year as main effects.

Results

Precipitation and Soil Moisture

Precipitation was near average for every month in 1986 except for extremely high amounts in September and October (fig. 1). Precipitation was above normal in 1987, below normal in 1988 and slightly below normal in 1989 prior to termination of soil manipulations in July 1989.

For the duration of the study (June 1986 through July 1989), total incoming water (precipitation or irrigation) was 2,438, 2,629, 3,455, and 1,021 mm for Natural, Control, Irrigated, and Rainout trees, respectively (table 1). Average annual incoming moisture was 1,037 mm (41 in.) for Irrigated and 306 mm (12 in.) for Rainout trees with Control and natural trees near the normal 665 mm (26 in.). Small differences in incoming water between Control and Natural trees were the result of periodic irrigations of Control and/or Rainout trees as part of other studies (Ansley and others 1992). The largest influx of water to Rainout trees occurred from September 1986 to April 1987 when rain shelters were removed for repairs and rainfall was well above normal.

At study initiation, all containerized trees had similar soil moisture when averaged over all depths (fig. 2). Soil moisture was greatest in Irrigated and lowest in Rainout treatments throughout the study. Soil moisture in the Control treatment was between Irrigated and Rainout trees. Abundant rainfall during the fall of 1986 and the 1987 growing season increased soil moisture substantially in the Irrigated and Control treatments in 1987. Soil moisture also increased slightly in the Rainout treatment due to removal of shelters from September 1986 to April 1987. Soil moisture near Natural trees was

Table 1. Incoming water for each treatment during the 40-month period from 29 May 1986 through 05 September 1989. NA = Natural, CT = Control, IR = Irrigated, RO = Rainout.

	Precip. (mm)		Irrigation (mm)[1]			Precip.+ Irrigation (mm)			
Interval	NA CT IR	RO	IR	CT[2]	RO[2]	NA	CT	IR	RO
29 May 86 to 31 Aug 86	193	0	283	73	73	193	266	476	73
01 Sep 86 to 30 Apr 87	731	731	0	0	99	731	731	731	830
01 May 87 to 31 Aug 87	485	0	325	92	92	485	577	810	92
01 Sep 87 to 30 Apr 88	253	0	0	0	0	253	253	253	0
01 May 88 to 05 Sep 89	776	0	409	26	26	776	802	1185	26
Totals (mm)	2438	731	1017	191	290	2438	2629	3455	1021
Average per year (mm)						732	788	1037	306

[1] Irrigation values are precipitation equivalent in mm over the surface area of each root container.
[2] CT and RO trees were irrigated occasionally FROM 1986 to1988 as part of other study objectives not specific to this paper.

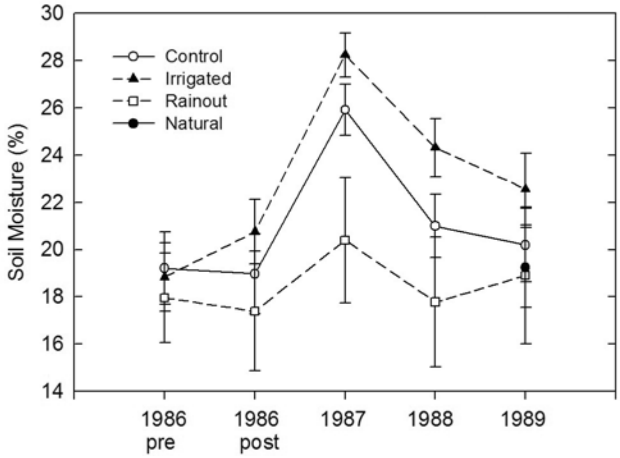

Figure 2. Soil moisture when averaged over all depths and dates in each growing season. Vertical bars indicate ±1 S. E. (n = 3). Data for NA treatment were not available, 1986-88.

not measured until 1989 and was similar to the Rainout and Control treatments.

Grass cover was > 50 percent in all treatments at study initiation and remained at 50 to 80 percent in Natural, Control, and Irrigated treatments throughout the study. Grass cover declined in the Rainout treatment such that, by 1989, most of the area beneath the rain shelters was bare ground.

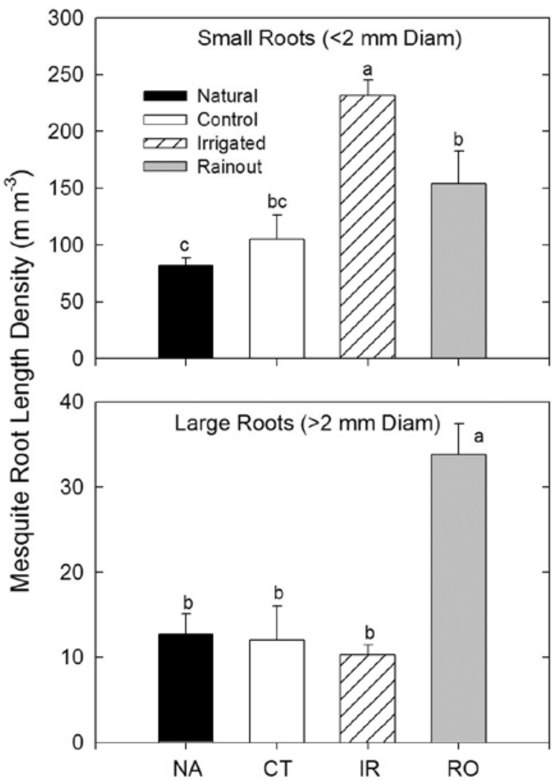

Figure 3. Root length density of small and large mesquite roots averaged over all soil depth segments (0-270 cm depth). Error bars indicate ± 1 S. E. (n = 3). Means with similar letters are not significant at P < 0.05.

Root Growth and Distribution

Mesquite root length density (RLD) of small (< 0.2 mm diameter) roots, when averaged over all soil segments (0 to 270 cm depth), was significantly greater in Irrigated trees than Natural or Control trees, with Rainout tree RLD intermediate trees in the other treatments (fig. 3). Mesquite RLD of large roots (> 0.2 mm diameter) was significantly greater in Rainout trees than in all other treatments when averaged over all soil segments. Large root RLD was similar among Natural, Control, and Irrigated trees.

Small root RLD, when averaged within 10 soil segments, was greater in Irrigated trees than Control or Natural trees in half of the soil segments (fig. 4). Most of these differences occurred within 30 to 180 cm depths. Small root RLD of Rainout trees fell between that of Irrigated and Control trees in most segments. At 0 to 10 cm, small root RLD showed a trend of being greater in Rainout and Irrigated than Control or Natural trees, but this was not significant at the 5 percent significance level.

Distribution of large root RLD was similar in Natural, Control, and Irrigated trees with greatest values between 30 to 90 cm and a sharp decline below 60 or 90 cm depth (fig. 4). In contrast, large root RLD of Rainout trees was three to eight

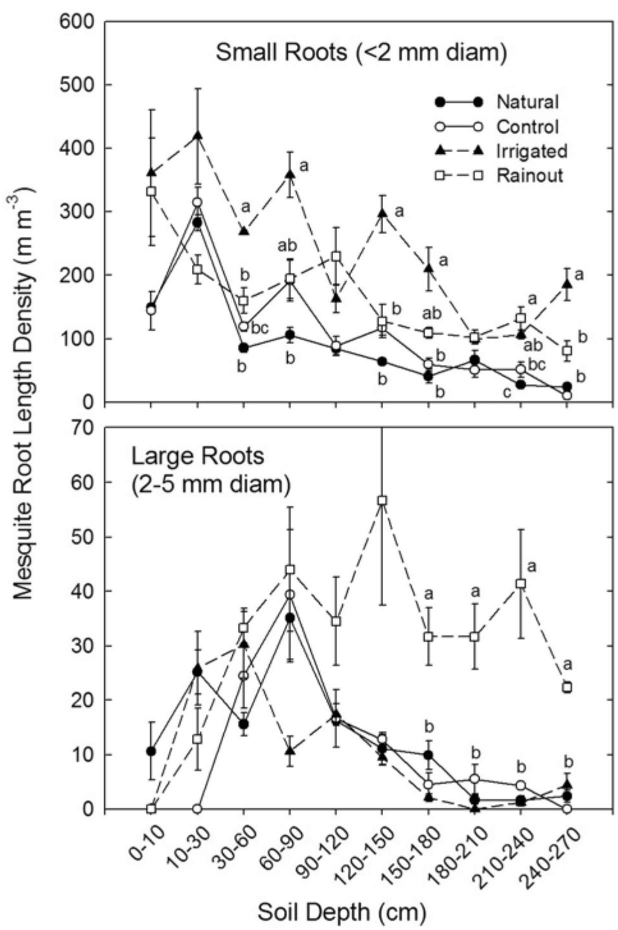

Figure 4. Root length density of small and large mesquite roots within 10 soil depth segments. Error bars indicate ± 0.5 S. E. (n = 3). Means with similar letters are not significant at P < 0.05.

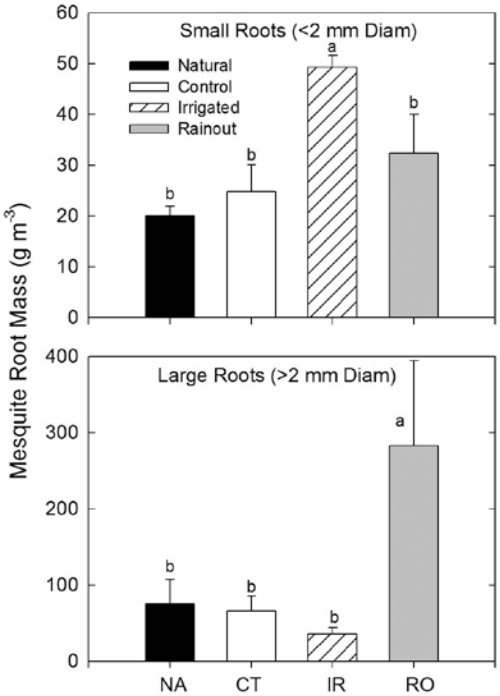

Figure 5. Root mass of small and large mesquite roots averaged over all soil depth segments (0-270 cm depth). Error bars indicate ± 1 S. E. (n = 3). Means with similar letters are not significant at P < 0.05.

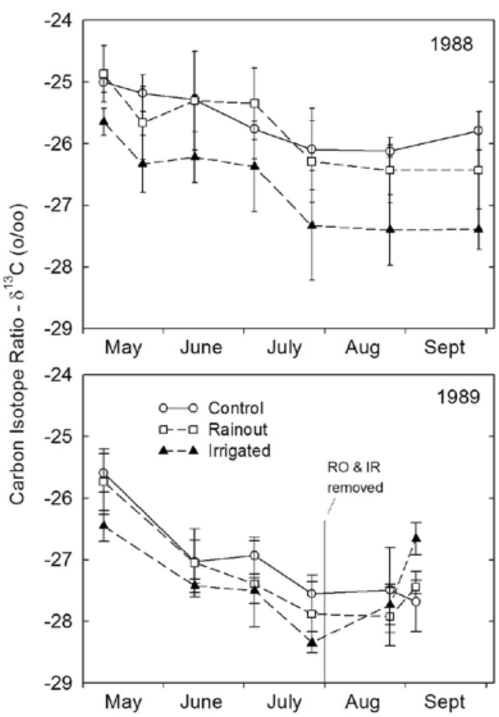

Figure 6. Carbon isotope ratios of mesquite leaf tissue in each treatment during 1988 and 1989. Error bars indicate ± 1 S. E. (n = 3).

times greater than the other treatments in segments below 90 cm. Averaging the six segments below 90 cm depth, RLD of large roots was 36.4, 7.3, 7.1, and 5.8 m m^{-3} in Rainout, Control, Natural, and Irrigated trees, respectively.

Irrigated trees exhibited greater small root mass than trees in the other treatments when averaged over all soil segments (fig. 5). Rainout trees exhibited greater large root mass than trees in other treatments but variability was high. Large root mass was similar in Control, Natural, and Irrigated trees.

Carbon Isotope Ratios and Canopy Growth

Leaf $\delta^{13}C$ declined in all treatments during each growing season (fig. 6). Irrigated trees tended to have lower $\delta^{13}C$ values than other treatments throughout 1988 and 1989, although differences between treatments were greater in 1988. After rain sheltering and irrigation treatments were discontinued at the end of July 1989, $\delta^{13}C$ increased sharply in Irrigated trees. Leaf C/N ratio was slightly lower in Irrigated trees (14.6 ± 0.3) than Control (15.4 ± 0.6) or Rainout (15.2 ± 0.5) trees throughout 1988, the result of a combination of slightly higher N and lower C in these trees than in the other treatments. There were no differences in leaf N, C, or C/N ratios between treatments in 1989.

Mesquite canopy height increased in all treatments by 0.5 m over the course of the study to about 4 m, with no difference between treatments (table 2). The root:shoot ratio was 0.3 for Control and Irrigated trees and 1.2 for Rainout trees.

Discussion

Survival of mesquite after 4 years of nearly continuous rain-sheltering reinforces the suggestion by Gile and others (1997) and other studies that root system plasticity affords this species a competitive advantage during extended droughts. When moisture was not manipulated (Natural and Control treatments), most mesquite roots were concentrated at 10 to 90 cm soil depth (fig. 4). Grass roots in these treatments were concentrated in the upper 10 cm (data not shown). Thus, grass and mesquite root systems were distributed in the classic "two-layer" pattern proposed by Walter (1954) and Walker and Noy Meir (1982) in which grasses occupy the upper soil layer and woody plant roots occur beneath the grass roots.

Exposed to chronic soil drought, Rainout mesquite explored deeper soil layers by investing energy into growth of larger "feeder" roots from which smaller roots extended. Caldwell (1976) emphasized that continued root extension into regions of soil in which the plant already has a well-established root system is a means for evading drought. Other studies have shown there can be considerable space between roots of woody plants (Chew and Chew 1965; Ludwig 1977), including mesquite (Heitschmidt and others 1988), that may be exploited during droughts.

We hypothesized that rain-sheltered mesquite would eventually die within a few years because the study site had little or no soil moisture below 2 m depth. Because the root containers

Table 2. Root mass (g m-3), root mass within each container, canopy height, projected canopy biomass, and root: shoot biomass ratios for containerized trees at study end, 1989.

Treatment	Root mass (g m-3)[1]	Root mass/cont. (kg)	Canopy height (m)	Canopy biomass (kg)[2]	Root:shoot ratio
Control	90.5	9.6	4.10	28.4	0.33
Irrigated	85.0	9.0	4.00	26.6	0.34
Rainout	315.3	33.4	4.13	28.9	1.15

[1] Data in left column taken from figure 5 (small + large roots).
[2] Canopy biomass (leaf + wood) was estimated via height-to-mass relationship derived from 23 harvested trees. Mass (y) to height (x) relationship was: $\hat{y} = 0.99 - 4.76\,x + 2.79\,x^2$; $r^2 = 0.76$.

prevented trees from growing extensive lateral roots that are critical to the water use patterns of mesquite on this site (Ansley and others 1990), we assumed that the combination of the root container and rain sheltering would result in tree mortality. However, mesquite not only survived 4 years of nearly continuous drought, but exhibited an aggressive strategy of increased root growth and continued canopy growth. Canopy growth was maintained levels similar to other less stressed treatments possibly because Rainout mesquite found new sources of soil moisture through increased root growth. In contrast, the grass understory in the Rainout treatment ultimately disappeared. These results imply that mesquite responses during drought were manifest through *increased* physiological activity and growth rather than by simply surviving drought at some reduced metabolic level.

Response to Prolonged Soil Wetness

One reason not often emphasized for the success of mesquite may be the ability to exploit wet periods through increased root growth. Irrigated mesquite in this study increased growth of small roots to a much greater degree than did trees in other treatments. This increase in small root growth was not concentrated in upper soil layers as we originally hypothesized; rather, it occurred throughout the profile. These smaller roots would theoretically be more efficient at absorbing soil moisture than would larger roots. High concentrations of fine roots would allow exploitation of frequent soil wettings. However, this did not translate into greater canopy height or biomass in this treatment. Perhaps Irrigated trees increased foliage density that we did not measure. Ansley and others (1998) found a similar response when intraspecific competition was removed from mesquite.

Lower carbon isotope ratio in Irrigated trees suggests a lower water use efficiency (WUE) in this treatment (Ehleringer 1988). In indirect support of this conclusion, the rapid increase in leaf $\delta^{13}C$ in this treatment in the latter part of the 1989 growing season when irrigation was terminated suggests leaf $\delta^{13}C$ values were closely linked to soil moisture conditions. We assume trees in this treatment, with their larger network of small roots, rapidly absorbed any excess soil moisture in the root containers following termination of irrigation and became sufficiently moisture stressed that it affected leaf isotopic ratio.

The lack of a difference in leaf $\delta^{13}C$ values between Rainout and Control trees suggests that Rainout trees were able to capture sufficient soil moisture through increased growth of large and small roots at least during the period of the study. Had the study continued, Rainout trees may have experienced sufficient moisture stress to have affected leaf water use efficiency and carbon isotope ratios.

Root:Shoot Ratios

The root:shoot (R:S) biomass ratios estimated for mesquite imply that mesquite adjusted root system mass to maintain a consistent canopy mass in response to soil drought. However, the increase in growth of small roots in Irrigated trees did not affect total root mass enough to change R:S ratio compared to the Control.

The R:S ratios estimated in this study were likely lower than actual R:S ratios because soil cores were obtained closer to the canopy dripline of each tree than directly beneath the center of the canopy where there was likely greater root mass per unit soil volume. The R:S ratio was not calculated for Natural trees because the root system in this treatment was not contained and roots were likely very extensive (Ludwig 1977; Heitschmidt and others 1988).

Summary and Implications

Root adaptation to prolonged climatic and edaphic changes is an important element for survival of adult mesquite. This study demonstrated that mesquite accelerated root growth during periods of drought and wetness and that major adjustments to root system architecture occurred within a few years. These results imply that mesquite has a natural competitive advantage during both wet and dry cycles. This inherent capability, coupled with any management practice, such as livestock grazing, that confers even a slight advantage to this species over other species during atypical climatic cycles will likely accelerate the process of ecosystem domination by mesquite. The tendency of managers to increase grazing during wet periods to “make up” for grazing losses during droughts will likely enhance the natural competitive advantage mesquite possesses via root system adaptation.

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