Root Biomass and Distribution Patterns in a Semi-Arid Mesquite Savanna: Responses to Long-Term Rainfall Manipulation

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Abstract

Expansion of woody plants in North American grasslands and savannas is facilitated in part by root system adaptation to climatic extremes. Climatic extremes are predicted to become more common with global climate change and, as such, may accelerate woody expansion and/or infilling rates. We quantified root biomass and distribution patterns of the invasive woody legume, honey mesquite (*Prosopis glandulosa*), and associated grasses following a long-term rainfall manipulation experiment in a mixed grass savanna in the southern Great Plains (United States). Root systems of mature trees were containerized with vertical barriers installed to a depth of 270 cm, and soil moisture was manipulated with irrigation (Irrigated) or rainout shelters (Rainout). Other treatments included containerized, precipitation-only (Control) and noncontainerized, precipitation-only (Natural) trees. After 4 yr of treatment, soil cores to 270 cm depth were obtained, and mesquite root length density (RLD) and root mass, and grass root mass were quantified. Mesquite in the Rainout treatment increased coarse-root (>2 mm diameter) RLD and root mass at soil depths between 90 cm and 270 cm. In contrast, mesquite in the Irrigated treatment increased fine-root (<2 mm diameter) RLD and root mass between 30 cm and 270 cm depths, but did not increase total root mass (fine+coarse) compared to the Control. Mesquite root-to-shoot mass ratio was 2.8 to 4.6 times greater in Rainout than the other treatments. Leaf water stress was greatest in the Rainout treatment in the first year, but not in subsequent years, possibly the result of increased root growth. Leaf water use efficiency was lowest in the Irrigated treatment. The increase in coarse root growth during extended drought substantially increased mesquite belowground biomass and suggests an important mechanism by which woody plant encroachment into grasslands may alter below ground carbon stocks under climate change scenarios predicted for this region.

Key Words: carbon isotope ratio, carbon sequestration, climate change, leaf water potential, root-to-shoot ratio, woody plant encroachment

INTRODUCTION

Woody plant encroachment into grass-dominated systems has been among the most important global land cover changes over the past two centuries (van Vegten 1983; Scholes and Archer 1997; Van Auken 2000, 2009; Archer et al. 2001; Tape et al. 2006; Maestre et al. 2009). This dramatic and geographically widespread vegetation change appears to be driven primarily by land uses including reduced fire frequency and livestock grazing, but may also be a response to environmental changes such as increased atmospheric CO_2, increased atmospheric deposition, and climate change (Archer et al. 1995; Kramp et al. 1998; Bond and Midgley 2000; Asner et al. 2004; Wigley et al. 2010). Although this vegetation change is well-documented and widely reported, the causes and potential consequences at ecosystem to global scales remain poorly understood.

In the southern Great Plains region of North America, the leguminous tree/shrub honey mesquite (*Prosopis glandulosa* Torr. var. *glandulosa*) has increased dramatically in abundance during the past 150 yr, and now covers $>20\%$ of the land surface in large portions of this region (Shelford 1963; Johnson and Mayeux 1990). This deep-rooted, nitrogen-fixing woody species has significantly altered above- and belowground primary productivity, biogeochemistry, and hydrologic processes at ecosystem to regional scales (Schlesinger et al. 1990; Boutton et al. 1999, 2009; Archer et al. 2001; Asner et al. 2003; Zou et al. 2005; Dai et al. 2006; Hughes et al. 2006; Boutton and Laio 2010).

A key biological attribute that has likely enabled mesquite to expand its range and dominance in this region is a dimorphic root system comprised of shallow lateral roots that can extend well beyond the canopy drip line, as well as a deep taproot (Heitschmidt et al. 1988; Ansley et al. 1990; Gile et al. 1997; Gibbens and Lenz 2001). The taproot accesses deeper water during drought; however, on sites with limited deep water, mesquite can also adjust leaf water potential, stomatal conductance, and whole plant leaf area during droughts (Ansley et al. 1992, 1998). While many studies have documented point-in-time root distribution of perennial shrubs in arid and semi-arid (i.e., "dryland") ecosystems (Castellanos et al. 1991; Jackson et al. 1996; Gibbens and Lenz 2001;

Schenk and Jackson 2002b; McCulley et al. 2004), little is known regarding the plasticity of shrub root growth and allocation patterns in response to extended periods of drought or wetness (Hodgkinson et al. 1978; Reynolds et al. 1999). Data are especially lacking for mature shrubs and trees growing in situ.

Some studies have suggested that responses of semi-arid shrubs to short-term droughts may first involve increased fine root growth from an existing coarse root macro-structure (Fernandez and Caldwell 1975; Wilcox et al. 2004), and responses to longer term droughts may involve modifications to coarse-root system architecture for more distant soil exploration (Belsky 1994; Ogle and Reynolds 2004; Schwinning and Sala 2004) or loss of root growth in upper soil layers (Reynolds et al. 1999). Responses to long-term wet periods are mostly unknown for semi-arid rangeland shrub species. Some studies have demonstrated increases in fine root growth in shallow soil layers of shrub and tree species following irrigation pulses (Richards and Cockroft 1975; Hodgkinson et al. 1978), but there is no information regarding differential responses of root size classes to extended soil moisture changes. Currently, there is not sufficient information in the literature to hypothesize anything other than an equal allocation of growth to fine and coarse roots in response to long-term soil moisture changes.

How will rooting patterns of this regionally dominant tree species respond to climate changes predicted for this region? Although precipitation increased by approximately 10% to 30% in the southern Great Plains region during the past 100 yr (National Assessment Synthesis Team 2001; Parmesan and Galbreath 2004; Karl et al. 2009), most climate models are projecting 10% to 20% decreases in rainfall amounts for this same area during the next 100 yr (Karl et al. 2009). A deeper or laterally more extensive root system may confer a competitive advantage to mesquite over grasses during extended droughts or wet periods and contribute significantly to their encroachment on grasslands (Canadell et al. 1996; Dawson and Pate 1996; Schenk and Jackson 2002a; Padilla and Pugnaire 2007). Under extended drought, the two-layer distribution of grass and woody plant roots described by Walter (1954) may become more pronounced if woody plants are able to extend roots to deeper depths (Schenk and Jackson 2002a). Therefore, recent predictions of increasing climatic extremes in the southern Great Plains and southwestern United States (Seager et al. 2007; Karl et al. 2009) may increasingly favor woody plants over grasses (Volder et al. 2010) and markedly affect belowground C storage (Boutton et al. 2009; Bai et al. 2010).

Our objectives were to determine the long-term (i.e., multiple year) effects of soil drought or wetness on 1) root distribution and biomass allocation, 2) fine vs. coarse root allocation, and 3) leaf moisture stress and water use efficiency (WUE) in mature (height > 3 m) mesquite. Our study was designed to address six hypotheses: 1) mesquite exposed to prolonged soil drought would increase root growth in deeper soil layers; 2) mesquite exposed to prolonged soil wetness would increase root growth in shallow soil layers and proportionally shift overall root distribution toward shallow layers; 3) the proportion of fine to coarse root mass would not change in response to long-term changes in soil moisture; 4) a more pronounced two-layer root distribution arrangement between mesquite and grass roots would develop under extended drought; 5) the root-to-shoot (R:S) mass ratios would increase in drought-stressed trees and decrease in well-watered trees; and 6) leaf moisture stress and WUE would increase under extended drought and decrease under prolonged soil wetness.

METHODS

Site Description

The study was conducted on a native mesquite savanna site in north Texas (lat 33°52′N, long 99°17′W; elevation 368 m). Average annual precipitation is 665 mm, which occurs in a bimodal pattern with peak periods in May (119 mm) and October (77 mm; National Oceanic and Atmospheric Administration 2002). The herbaceous layer consists of a mixture of C_3 and C_4 perennial grasses. The dominant perennial C_3 grass is Texas wintergrass (*Nassella leucotricha* [Trin. & Rupr.] Pohl). Primary C_4 grasses include buffalograss (*Bouteloua dactyloides* [Nutt.] J.T. Columbus), vine mesquite (*Panicum obtusum* Kunth), and several dropseeds (*Sporobolus* spp.). Soils are fine, smectitic, thermic Typic Paleustalfs of the Kamay series with clay loam textures underlain by fractured sandstone/shale parent material at 2 m to 3 m depth (US Department of Agriculture–Natural Resource Conservation Service 2010).

Treatments

Twelve large, multistemmed mesquite trees (mean height: 3.4 ± 0.1 m; canopy diameter 5.1 ∀0.2 m; number of basal stems 5.8 ± 0.4) occurring within a 1.5-ha area were randomly selected for the study. Three trees (as replicates) were randomly assigned to each of four treatments: Control (CT), which had the root system of each tree containerized and received precipitation only; Rainout (RO), which had the root system containerized and precipitation blocked; Irrigated (IR), which had the root system containerized and received precipitation plus irrigation; and Natural (NA), which did not have root systems containerized trees and received precipitation only. The root containers were necessary to maintain the integrity of the treatment manipulations, both to ensure that RO trees did not extend lateral roots beyond the rain shelters and to block other trees from extending roots into the root zone of the IR trees. They were also needed to contain water flow in the IR treatment to the intended area. The NA treatment was included to ascertain the effects of the containers themselves. One month prior to treatment establishment, aboveground portions of neighboring mesquite trees that occurred within 20 m of each experimental tree were removed, and remaining stumps were killed with diesel oil.

Root system containers were installed during the dormant season (January–February 1986) and consisted of a 2.7-m deep vertical trench cut in a hexagonal shape around each tree, with each side 4.06 m long and each point of the hexagon 4.1 m from tree center. The soil wall was wrapped with a sheet metal and plastic barrier before re-filling the trench. The root container isolated the soil around each tree in the horizontal plane with a soil surface area within each containerized area of 42.4 m². The bottom of each container was open; however, soil

moisture measurements to 10 m depth on the site indicated that there was little soil moisture from 2.5 to 10 m depth.

The rain shelters (RO treatment only) consisted of a wood frame covered with wire netting and clear 6-mil plastic that was suspended beneath the foliage of each tree (Jacoby et al. 1988). Shelters were 0.8 m high along a middle ridge through the tree center and each half extended with a slight downward slope away from the ridge to 0.5 m height at 1 m beyond the root container wall. The wire netting and plastic cover was built to within 1 cm around each support stem and thus prevented most rainfall from falling on the soil surface within the containerized area while allowing tree foliage to be continually exposed to sunlight. The shelters did not stop stem flow water from draining along bark channels and to the soil at the immediate base of the tree. Shelters were established on 28–29 May 1986 and remained in place through 1989 with the exception of a 4.5-month period from December 1986 to April 1987 when heavy storms in September and October damaged the shelters and the plastic covering was replaced.

The IR treatment consisted of water obtained from a municipally approved drinking water system, trucked to the site and applied via a drip system with 50 emitters (rated 3.8 liters $\cdot$ hr^{-1}) at 0.3 m spacing within the containerized area (Jacoby et al. 1988; Ansley et al. 1992). About seven to nine irrigations (each 25–50 mm) were applied between May and August each year from 1986 to 1988 that increased annual precipitation by ~40–50% above the 30-yr average. Three irrigations were applied in June and early July 1989; irrigation was discontinued after mid-July to observe responses of trees in the IR treatment to drying conditions.

Measurements

Volumetric soil moisture was measured at 2- to 3-wk intervals during the 1986–1989 growing seasons (April–August) using a neutron probe (Troxler Laboratories, Research Triangle Park, NC). Measurements were made at four locations around each tree, each at 2 m lateral distance from tree center (within containers of containerized trees), and at 30-cm increments from 30 cm to 180 cm soil depth. Three measurement periods in April–May 1986 served as pretreatment data. Soil moisture was measured in the NA treatment only in 1989.

Root sampling was conducted from November 1989 to May 1990. Three 10-cm diameter soil cores to 270-cm depth were obtained near the canopy drip line of each tree (within containers of containerized trees) using a soil-coring device (Giddings Inc, Ft. Collins, CO). Each core was divided into 10-cm segments between 0 cm and 90 cm depth, and 30-cm segments from 90 cm to 270 cm. Sampling was stratified so that one soil core was taken from each replicate tree before the second core was taken, etc.

Roots were separated from soil for each root segment with a hydro-pneumatic elutriation system (Gillison's Variety Fabrication, Inc, Benzonia, MI) and separated into size classes during 1990 and 1991. Mesquite roots were divided into fine (< 2 mm diameter) and coarse (> 2 mm diameter) size classes (Castellanos et al. 1991; Jackson et al. 1997; Wilcox et al. 2004). All roots < 0.5 mm diameter were separated into grass vs. mesquite roots on the basis of color. Mesquite root length density (RLD; m $\cdot$ m^{-2}) was quantified using an automated

image analyzer (Decagon Devices, Inc, Pullman, WA; Bohm 1979; Harris and Campbell 1989). Mesquite and grass root mass densities (g $\cdot$ m^{-2}) were then determined for each segment after oven drying at 60°C for 72 h. In addition to reporting actual RLD and root mass values at these depths, fine-to-coarse RLD ratios, fine-to-coarse root mass ratios, and percent of total RLD and root mass were calculated within each of four pooled soil depths (0–60, 60–120, 120–180, and 180–270 cm) for each tree.

Canopy volume $\cdot$ tree^{-1} was determined at pretreatment in 1985 and at the end of 1988 by measuring height, canopy diameter, and tree base diameter and determining canopy volume based on a conic frustum shape using the equation:

$$V = (\pi h/3)(a^2 + ab + b^2) \qquad [1]$$

Where h=canopy height, a=radius of canopy, and b=radius of tree base. Percent change in volume from 1985 to 1988 was determined for each tree.

Root-to-shoot (R:S) mass ratios were calculated for each tree by dividing root mass by canopy mass. Canopy mass $\cdot$ tree^{-1} (kg) was determined by measuring the diameters of all basal stems, determining dry mass of each stem using a stem diameter/stem mass equation developed for the study area by Ansley et al. (2010) and summing stem masses. Root mass $\cdot$ tree^{-1} (kg) was determined by multiplying the total (fine+coarse) root mass density (g $\cdot$ m^{-2}) from 0 cm to 270 cm depth by the container surface area (42.4 m^2). The same surface area was used for the NA treatment.

Predawn leaf water potential (Ψ) was used as an indicator of plant moisture stress (as per Ansley et al. 1992) and was measured on containerized trees three to four times during the 1986–1988 growing seasons, and on tree in all four treatments during 1989. Two leaves were excised at 1- to 2-m height in the center of each canopy before sunrise, and Ψ was determined using a Scholander pressure bomb (Turner 1981). Mesquite leaf carbon isotope ratios (δ^{13}C) were determined on leaf samples from each tree collected at 2- to 3-wk intervals during the 1988 and 1989 growing seasons. Leaves were oven-dried for 48 h at 60°C then pulverized in a centrifugal mill (Angstrom, Inc, Belleville, MI). Leaves were analyzed for δ^{13}C with a dual inlet, triple collector isotope ratio mass spectrometer (Micromass 903, VG Isogas, Middlewich, United Kingdom; Boutton 1991). Carbon isotope ratios are presented in δ notation:

$$\delta = [(R_{\text{SAMPLE}} - R_{\text{STD}})/R_{\text{STD}}] \times 10^3 \qquad [2]$$

where R_{SAMPLE} is the ^{13}C/^{12}C ratio of the sample and R_{STD} is the ^{13}C/^{12}C ratio of the V-PDB standard (Coplen 1996). Precision of duplicate measurements was $\pm$ 0.1%.

Statistical Analysis

The soil moisture data set was very large, and initial analyses using a two-way general linear model (GLM) mixed model with treatment and sample date as main effects showed significant ($P \leq 0.05$) treatment by date interactions in all years of the study. For this article, we intend only to use soil moisture as a background reference to establish yearly average differences in soil moisture for each treatment at each measured soil depth. Therefore, soil moisture data were pooled over all sample dates each year and analyzed within each depth using a

one-way analysis of variance (ANOVA) with treatment as the main effect and three replicates per treatment (SAS 2003).

Mesquite RLD and mesquite and grass root mass density data were pooled into 10 soil depth segments (0–10, 10–30, and 30 cm segments from 30 cm to 270 cm) and analyzed within each root size class and depth segment using a one-way ANOVA with treatment as the main effect ($n=3$). A one-way ANOVA was used to analyze differences in fine-to-coarse RLD and root mass ratios in the four pooled soil depths, percent of total RLD and root mass in the four pooled soil depths, canopy volume, percent change in canopy volume, total mesquite and grass root mass density (0–270 m depth), aboveground mesquite canopy mass, and mesquite R:S mass ratios. Mesquite leaf data (predawn leaf Ψ, $\delta^{13}C$) were analyzed using a GLM repeated measures analysis with treatment (CT, RO, and IR only) as the whole plot and date as the split plot (three replicates per treatment). We used the replicate×treatment mean square as the error term to test effects of treatment, and the pooled error to test effects of date and treatment×date interactions (SAS 2003). Nonnormal data were square-root transformed prior to analysis. All means were separated by LSD ($P \leq 0.05$).

## RESULTS

Precipitation and Irrigation Amounts

Precipitation was normal or above normal for most months in 1986, well above normal in September and October 1986, above normal for five of the first 8 mo in 1987, and normal or below normal during the first half of 1988 and 1989 (Fig. 1). Total incoming water from precipitation or irrigation during the 41-mo study period was greatest in the IR treatment and least in the RO treatment, with the CT and NA treatments intermediate (Table 1). Total water input for the 41-mo period was 39% greater in the IR than the CT and NA treatments. The RO treatment received 164 mm precipitation from December 1986 to April 1987 when rain shelters were removed for repairs after the September and October storms.

Soil Moisture

Soil moisture was maintained at a greater level in the IR than the RO treatment at most soil depths from 1986 to 1988, with moisture in the CT usually intermediate between the other treatments (Fig. 2). Differences between treatments were greatest in 1987 and 1988. Pretreatment measurements indicated no differences between treatments at any depths. Differences in soil moisture between the IR treatment and other treatments disappeared at the 30 and 60 cm depths when irrigation was discontinued in July 1989. However, some treatment differences were still apparent at lower depths. Soil moisture in the NA treatment appeared to be drier than the CT treatment at depths below 90 cm in 1989, but differences were not statistically significant.

Root and Canopy Growth

Mesquite fine-root RLD was greater in the IR than the CT treatment at 4 of the 10 pooled soil depth segments (Fig. 3A). There were few differences in fine-root RLD between CT, RO,
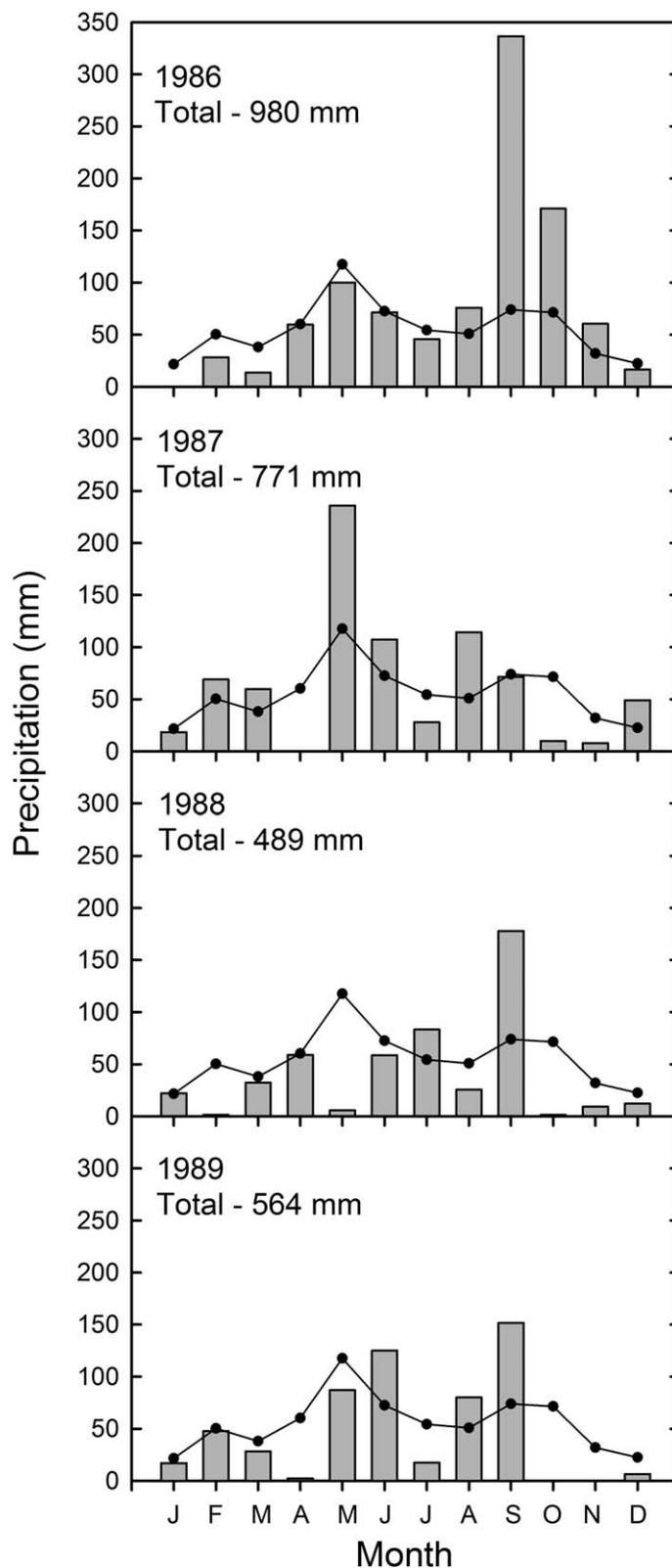
Figure 1. Monthly precipitation from 1986 to August 1989 (bars). Line is 30-yr mean for each month (National Oceanic and Atmospheric Administration 2002).

Table 1. Water input from precipitation and irrigation for each treatment from 1 June 1986 through 31 October 1989.

| Interval | Months | Precipitation (mm) | | Irrigation (mm)[2] | Precipitation + Irrigation (mm) | | | |
		IR, CT, and NA[1]	RO	IR	IR	CT	NA	RO
1 June 1986–30 November 1986	6	761	0	283	1 044	761	761	0
1 December 1986–17 April 1987	4.5	164	164	0	164	164	164	164
18 April 1987–31 August 1987	5.5	557	0	325	882	557	557	0
1 September 1987–31 March 1988	6	123	0	0	123	123	123	0
1 April 1988–31 July 1988	4	207	0	350	557	207	207	0
1 August 1988–31 May 1989	10	409	0	0	409	409	409	0
1 June 1989–31 October 1989	5	374	0	61	435	374	374	0
Totals	41	2 595	164	1 019	3 614	2 595	2 595	164
Average/Month (mm)		63.3 [3]			88.1	63.3	63.3	4.0

[1]IR indicates Irrigated; CT, Control; NA, Natural; RO, Rainout.
[2]Irrigation values are precipitation equivalent in millimeters over the surface area of each root container.
[3]Normal average per month is 56.6 mm (based on normal 2 319 mm over this 41-mo period).

and NA treatments at any depth. Coarse-root RLD was greater in the RO than the other treatments at 90 cm to 120 cm depth and the four depth segments below 120 cm to 150 cm (Fig. 3B). Similar relationships between treatments were seen with the root mass responses (Figs. 3C and 3D). Both the CT and NA treatments had greatest coarse-root RLD and coarse-root mass at the 30–60 and/or 60–90 cm depths.

Mesquite fine-to-coarse-RLD ratio was much greater in the IR treatment than the other treatments at 60–120 and 120–180 cm depths, and was 10-fold greater in the IR than the RO treatment at the 180–270 cm depth (Table 2). The fine-to-coarse-root mass ratio was much greater in the IR treatment than the other treatments at 120–180 and 180–270 cm depths, and was greater in the IR than the RO treatment at the 60–120 cm depth.

The percent of total RLD and total root mass allocated to each of four pooled depths is shown in Figure 4. There was a greater allocation of fine-root RLD at lower depths in the IR (120–180 cm depth) and the RO (180–270 cm depth) treatments than in the CT and NA treatments. For coarse roots and fine+coarse roots, there was a greater allocation of RLD at the lowest depth segment (180–270 cm) in the RO treatment than in the other treatments. Trends were similar for percent root mass allocation, with one main exception: the greater allocation of coarse-root RLD in the IR than the RO treatment at 0–60 cm depth was not found for coarse root mass.

Grass root mass was concentrated in the upper 30 cm of soil in all treatments and was lower in the RO treatment than the other treatments at 0–10 cm depth (Fig. 5). The percentage of total grass root mass in the upper 60 cm was between 87% and 92% in all treatments.

Tree canopy volume did not differ between treatments on either sample date. However, the percent increase in volume from 1985 to 1988 was greater in the IR than the other treatments (Fig. 6).

When calculated over the entire profile (0–270 cm depth), mesquite fine root mass density was greater in the IR than the CT or NA treatments (Table 3). Coarse and fine+coarse root mass density was greater in the RO than the other treatments. Grass root mass density was lower in the RO than the other treatments. When calculated on a per tree basis, mesquite

fine+coarse root mass · tree^{-1} was 2.6 to 3.3 times greater in the RO than the other treatments, while aboveground mass · tree^{-1} was similar among treatments. The R:S mass ratio was 2.8 to 4.6 times greater in the RO than the other treatments. The CT and NA treatments had similar values for all variables shown in Table 3.

### Mesquite Predawn Leaf and Carbon Isotope Ratios
Mesquite predawn leaf Ψ was much lower in the RO than the IR or CT treatments, and was lower in the CT than the IR treatment in 1986 (Fig. 7). Predawn leaf Ψ increased in all treatments in 1987 due to large rainfall in late 1986 and was initially lowest in the RO treatment but declined more rapidly in the CT than the other treatments as the 1987 growing season progressed. In 1988, predawn leaf Ψ was lowest in the CT initially and declined more rapidly in the CT than the other treatments from July to August after a late-June wet period that increased predawn leaf Ψ in the CT. This trend was also observed in 1989. From late 1987 through 1989, predawn leaf Ψ was not different between the IR and RO treatments. The IR treatment had lower leaf $\delta^{13}C$ than the other treatments in 1988 and early 1989 (Fig. 8). After irrigation was discontinued in mid-July 1989, leaf $\delta^{13}C$ increased in the IR treatment relative to the CT in August and September.

DISCUSSION

Mesquite Root Distribution
Exposure to prolonged soil drought stimulated growth of coarse and fine roots into deeper soil layers. Both RLD and root mass responses showed this pattern. These results support our first hypothesis and are similar to a New Mexico study by Reynolds et al. (1999) who found that experimentally water-stressed mesquite increased root growth in lower depths (the lowest depth measured in their study was 108 cm). They also found that drought-stressed mesquite decreased root growth at shallow depths (0–36 cm); we did not observe this trend.

Some studies have suggested that responses of semi-arid shrubs to short-term droughts may first involve increased fine root growth from the existing coarse root macro-structure to access nearby water sources (Fernandez and Caldwell 1975;
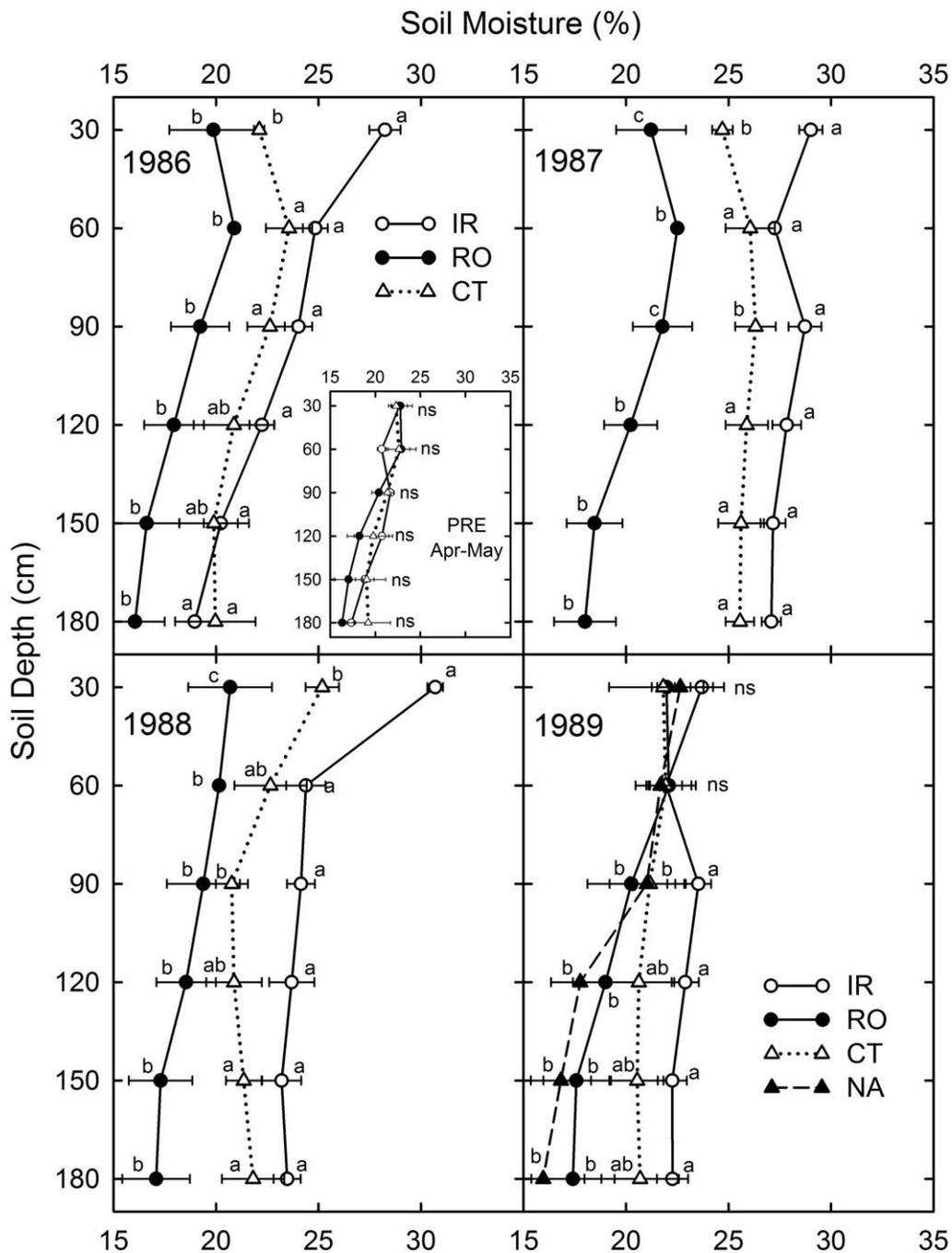
Figure 2. Soil moisture from 30 cm to 180 cm depth averaged over all growing season sample periods in Irrigated (IR), Rainout (RO), and Control (CT) treatments, 1986–1989, and the Natural (NA) treatment, 1989. Pretreatment values are shown in the inset panel (PRE). Error bars are ± 1 standard error (*n*=3). Means with similar letters are not significantly different at *P* ≤ 0.05. NS indicates no significant differences.

Wilcox et al. 2004). Responses to longer term droughts may involve modifications to coarse-root system architecture for more distant soil exploration (Ogle and Reynolds 2004; Schwinning and Sala 2004). Our results indicate that under a multiyear drought, mesquite substantially modified coarse root macro-structure through an investment in coarse root growth to explore deeper soil depths.

Regarding our second hypothesis, when exposed to prolonged above-normal moisture conditions via irrigations, mesquite increased fine root (but not coarse root) growth throughout the profile. We reject our second hypothesis

because, while fine root growth did increase in the IR treatment, it was not limited to upper soil layers as we had hypothesized. Our results support the findings of Collins and Bras (2007) who estimated in a root growth model that short and frequent summer storms favored deeper rooting, although no distinction was made between fine and coarse root growth. In an African field study, Belsky (1994) found that *Acacia tortilis* roots were greater in the first meter of soil on a wet site compared to a dry site, but this may have been related to soil differences as much as moisture conditions.
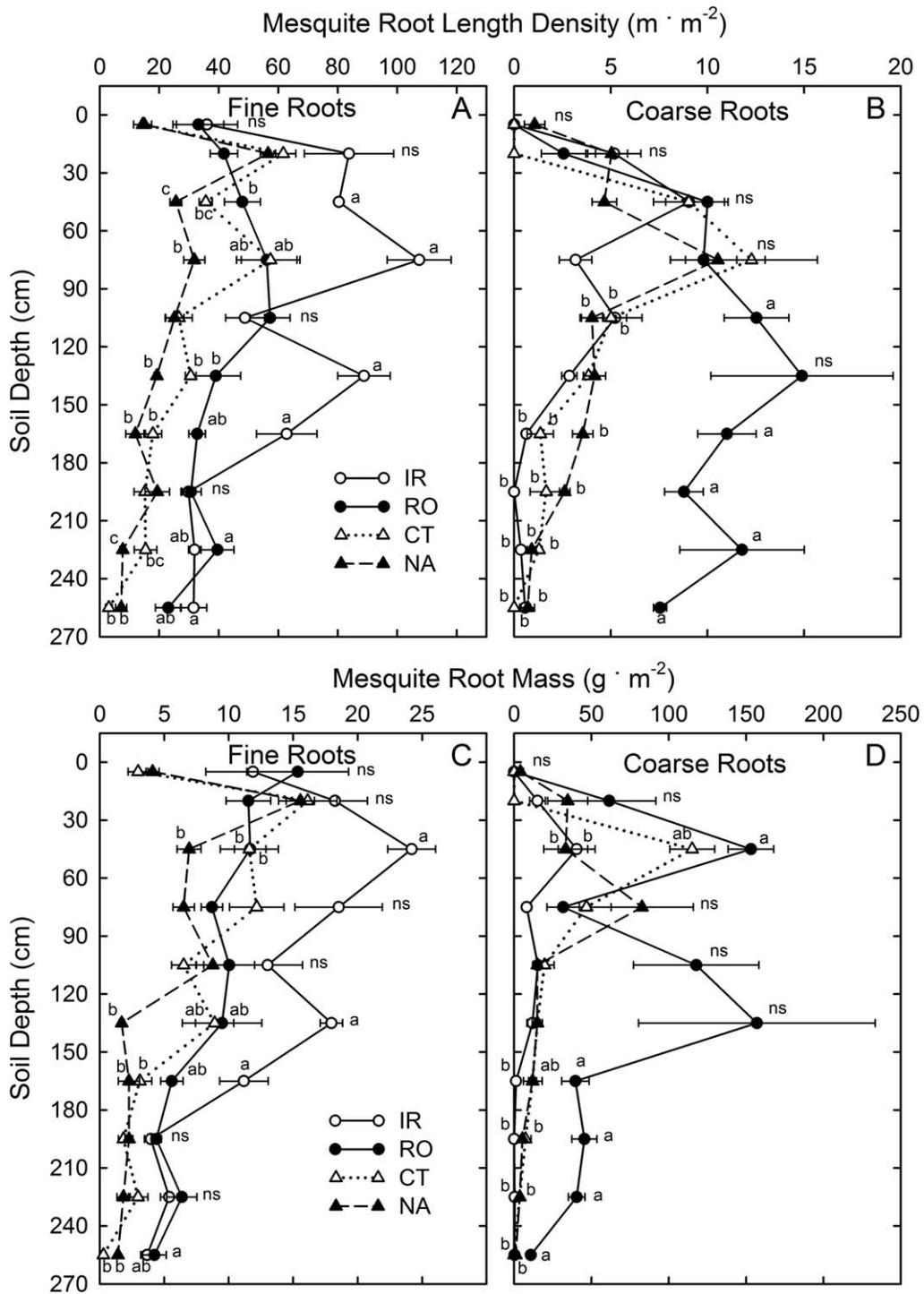
Figure 3. Root length density (RLD) and root mass of fine and coarse mesquite roots within 10 soil depth segments in each treatment (IR, Irrigated; RO, Rainout; CT, Control; NA, Natural). Values displayed are for 0–10 cm, 10–30 cm, and 30-cm increments below 30 cm. Error bars are ± 1/2 standard error ($n = 3$). RLD means with similar letters are not significantly different at $P \leq 0.05$. NS indicates no significant differences.

Regarding our third hypothesis, the growth of fine and coarse roots was not proportionally similar in all treatments; thus, we reject this hypothesis. Both the fine-to-coarse RLD ratios and fine-to-coarse root mass ratios were considerably greater in the IR treatment compared to the other treatments at lower soil depths.

Mesquite vs. Grass Root Distribution

When soil moisture was not manipulated (CT and NA treatments), mesquite fine-root mass was greatest at 10–30 cm soil depths, and coarse-root mass was greatest at 30–90 cm depths (Figs. 3C and 3D). These results are similar to that found on a site near the current study site (McCulley et al. 2004). Grass root mass in our study was concentrated in the

Table 2. Fine-to-coarse ratios for mesquite root length density (RLD) and root mass in four pooled soil depths in each treatment (Mean ± SE; $n = 3$). Means within a row with similar letters are not different at $P \leq 0.05$.

Depth (cm)	Irrigated	Rainout	Control	Natural
(Fine-to-Coarse RLD Ratio)				
0–60	14.8 ± 4.4 a	9.8 ± 1.5 a	15.6 ± 6.2 a	10.0 ± 2.1 a
60–120	18.1 ± 2.5 a	6.1 ± 2.2 b	6.9 ± 2.3 b	5.8 ± 2.5 b
120–180	44.0 ± 8.3 a	3.3 ± 0.6 b	10.7 ± 2.3 b	5.4 ± 2.7 b
180–270	43.6 ± 18.4 a	3.8 ± 0.9 b	17.8 ± 11.5 ab	8.6 ± 3.0 ab
(Fine-to-Coarse Root Mass Ratio)				
0–60	1.22 ± 0.4 a	0.23 ± 0.1 a	0.28 ± 0.04 a	0.78 ± 0.51 a
60–120	1.28 ± 0.13 a	0.38 ± 0.29 b	0.50 ± 0.27 ab	0.55 ± 0.33 ab
120–180	3.22 ± 0.99 a	0.35 ± 0.26 b	0.57 ± 0.19 b	0.64 ± 0.57 b
180–270	13.56 ± 4.68 a	0.16 ± 0.02 b	0.89 ± 0.43 b	0.59 ± 0.16 b

upper 10 cm in all treatments, similar to findings of many other studies (Yoder et al. 1995; Snyman 2009). Thus, in nonmanipulated situations, grass and mesquite root systems were distributed in a two-layer pattern as found elsewhere (Walter 1954; Lee and Lauenroth 1994; Le Roux et al. 1995).

The differences in vertical distribution between mesquite and grass roots became more pronounced in both the RO and IR treatments, thus supporting our fourth hypothesis, although we only anticipated this to occur in the RO treatment. In both these treatments, grass roots remained greatest in the 0–10 cm layer (although considerably reduced in the RO treatment), but mesquite root growth increased in deeper soil layers without any increase in upper (0–10 and 10–30 cm) soil layers compared to the CT. In the RO treatment in particular, the mesquite rooting depth shifted to what could be described as a "deep" classification, defined by Schenk and Jackson (2005) as when more than 5% of the total root mass is located below 2 m. We did not divide our soil core sampling exactly at the 2-m point, but our results would appear to support Schenk and Jackson (2005) as the percent allocation of total (fine+coarse) root mass below 1.8 m was 5.0% and 7.3%, respectively, in the CT and NA treatments, but was 16.9% in the RO treatment (Fig. 4). These results suggest that mesquite and grasses would develop a more pronounced two-layer root distribution arrangement under long-term periods of drought.

R:S Mass Ratios

Regarding our fifth hypothesis, the increased mesquite R:S mass ratio in the RO treatment was due to increased root growth, but not reduced canopy growth, as canopy growth rates were similar to the CT. The reason why the increase in R:S ratio in the RO treatment was substantial was because much of the increased root growth was from the heavier coarse roots. In contrast, even though fine root growth increased in the IR treatment to double that of the CT, the R:S mass ratio remained similar to the CT for two reasons. First, even though the canopy volume growth rate was greater in the IR treatment, the canopy mass at study end was not different between the IR and CT treatments. Second, there was a decrease in coarse root mass in the IR treatment to half of that in the CT that was not statistically different from the CT, but offset the increase in fine

root mass such that total root mass (fine+coarse) was not different between IR and CT treatments.

The R:S ratios were similar between the CT and NA treatments. However, we note that the soil volume within the root containers was used to convert root mass density to root mass·tree^{-1} in the NA treatment even though trees in this treatment surely had lateral roots that extended beyond the soil volume defined by the containers, and consequently, the R:S ratio was very likely higher than what our data show. Thus, our results support a portion of our fifth hypothesis—that R:S ratio would increase in drought-stressed trees—however, the R:S ratio was not reduced in well-watered trees, as was expected.

Chew and Chew (1965) and Ludwig (1977) found that R:S mass ratios of mature *Larrea tridentata* in Arizona and New Mexico ranged from 0.2 to 0.9. Castellanos et al. (1991) found a R:S mass ratio of 0.42 in a dry deciduous tropical forest in Mexico. Compared to these nonmanipulated systems, trees in the RO treatment in our study were at the high end of the range of R:S mass ratios. We know of no studies that have quantified R:S ratio responses of mature shrub species to long-term drought or wetness. In a seedling study in containers, Padilla et al. (2009) found that drought increased R:S ratios in several Mediterranean shrub species. While our results appear to be compatible with some of the R:S ratios found for similar species in the literature, we recognize that these results are based on a relatively few number of soil cores and as such are at risk of being in error.

The total (fine+coarse) root mass density of 745 g·m^{-2} found in the RO treatment (0–270 m depth) was considerably lower than the approximately 21 000 g·m^{-2} root mass reported for all species (woody+herbaceous) within a 0–150 cm depth in a mixed-woody grove in south Texas that was dominated by mature mesquite trees (Midwood et al. 1998). About 82% of the total root mass in Midwood et al.'s study was in the upper 60 cm, most of which was probably from grasses. In our study, the percent of total mesquite root mass in the upper 60 cm ranged from 42% to 52% in the four treatments. Over 87% of the grass root mass was in the upper 60 cm in all treatments. Our lower values may relate to the heavy clay loam soil texture or to lower overall biomass due to a more northern latitude and shorter growing season.
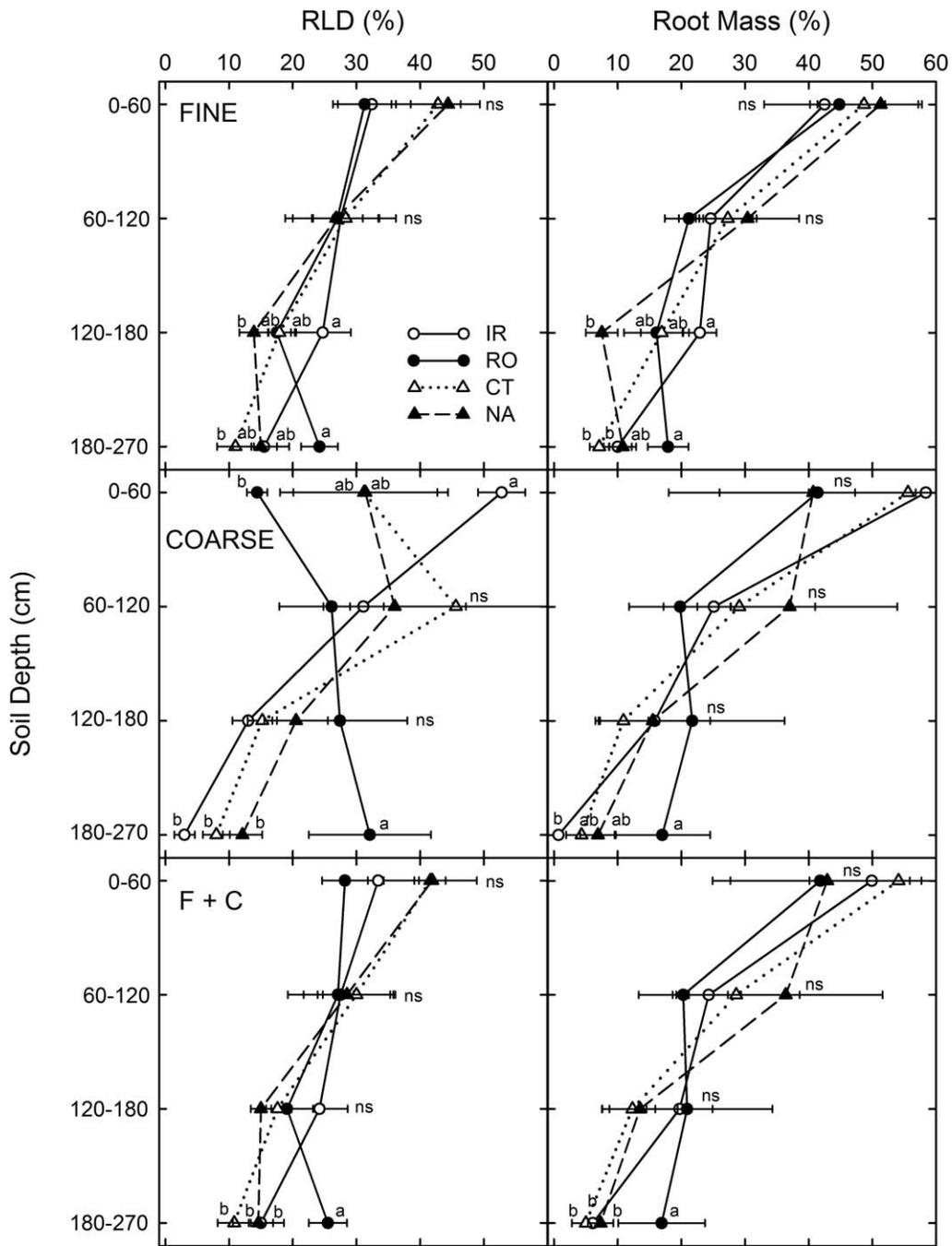
Figure 4. Percent of mesquite total root length density (RLD) and total root mass within four pooled depths in each root size class and treatment (Mean ± SE; *n* = 3). Means with similar letters within a depth in each panel are not different at *P* ≤ 0.05.

Mesquite Leaf Moisture Stress and WUE

Trees in all containerized treatments were moisture-stressed (predawn leaf $\Psi < -1$ Megapascal) during the first growing season, but trees in the RO treatment were more stressed than those in the other treatments. The increase in predawn leaf Ψ in all treatments in the second year was due to recovery from root severing (Ansley et al. 1990) and the large amount of rainfall in late 1986 and in May–June 1987. The RO treatment received some rainfall when the shelters were off for repairs and this increased predawn leaf Ψ and soil moisture, but both of these variables remained lower in this treatment than the others at

the beginning of the 1987 growing season. However, during 1987, a transition occurred in which soil moisture remained lower in the RO treatment compared to the other treatments but predawn leaf Ψ did not. This may have been the time when enhanced root growth in the RO treatment began to have an impact, and the additional water uptake increased predawn leaf Ψ to levels similar to the IR treatment.

During 1988 and 1989, when precipitation was lower than the previous 2 yr, trees in the RO treatment clearly showed that they had adapted to the rain sheltered conditions, likely via new root growth, and actually became less moisture-stressed
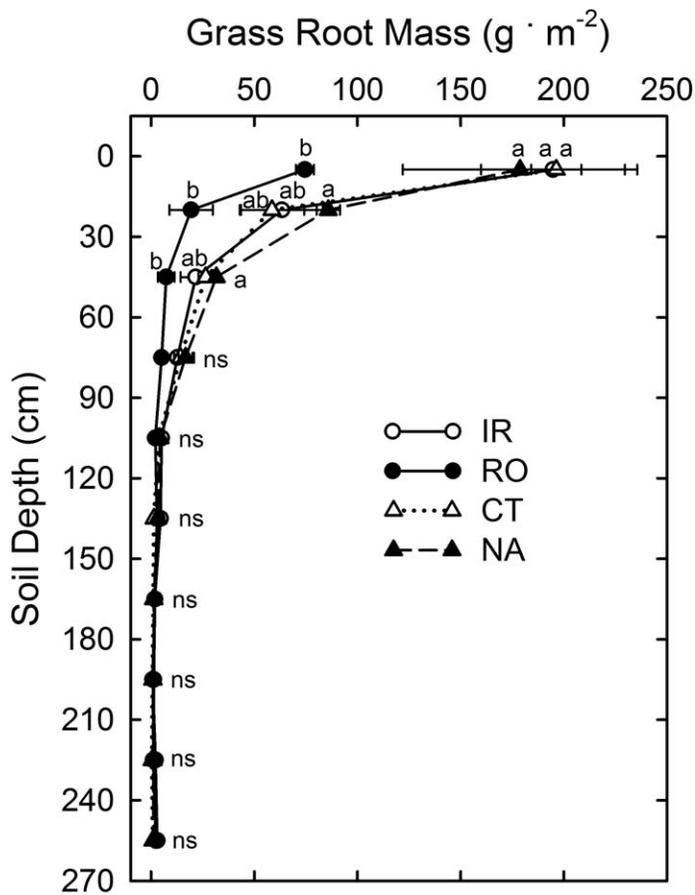
Figure 5. Grass root mass within 10 soil depth segments and when averaged over all depths in each treatment. Error bars are ± 1 standard error (*n*=3). Means with similar letters are not significantly different at $P \leq 0.05$.

(e.g., had higher predawn leaf Ψ) than trees in the CT treatment by July 1989. In the fourth year when irrigation was discontinued, predawn leaf Ψ declined in the IR treatment, but it was still not lower than the other treatments.

Interpretation of leaf $\delta^{13}C$ responses is hindered by the lack of data in the first 2 yr of the study. However, the observation that there was no difference in leaf $\delta^{13}C$ between the RO and CT treatment in 1988 and 1989 reinforces the suggestion that trees in the RO treatment were able to capture sufficient soil moisture through increased root growth and did not adjust WUE. For this reason, we reject our sixth hypothesis that leaf moisture stress and WUE would increase under extended drought.

A lower leaf $\delta^{13}C$ in the IR treatment than the CT and RO treatments in 1988 and early 1989 implies a lower WUE in the IR treatment (Ehleringer 1988). This supports the latter portion of our sixth hypothesis that WUE would decrease under prolonged soil wetness. The rapid increase in leaf $\delta^{13}C$ in the IR treatment in the latter part of the 1989 growing season after irrigation was discontinued may indicate that moisture-stress in this treatment became severe enough to cause an increase in leaf $\delta^{13}C$ and WUE. Indeed predawn leaf Ψ in the IR treatment was lower in late 1989 than at any time since the first year. The soil moisture reduction in the 30 and 60 cm depths of the IR treatment in 1989 after irrigation was stopped is an indication of rapid moisture use and possible depletion in this treatment.

MANAGEMENT IMPLICATIONS

Our study demonstrated that root systems of mature honey mesquite exhibit a great deal of plasticity by modifying architecture in response to long-term deviations in soil moisture levels and afford this species a competitive advantage over grasses not only during drought, but also during extended
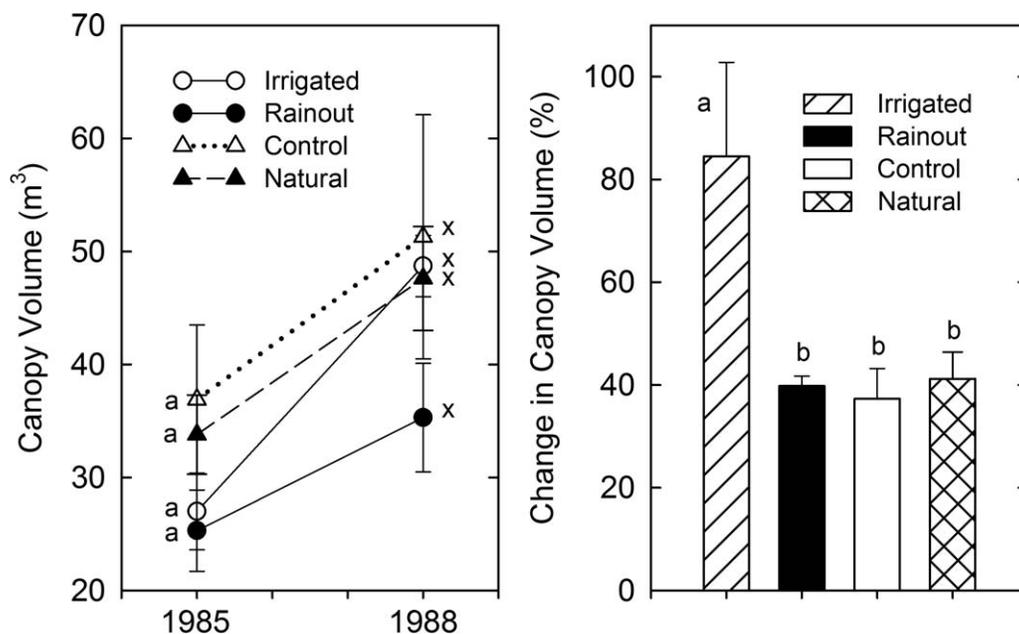
Figure 6. Mesquite canopy volume in each treatment at pretreatment (1985) and at study end (1988; left), and the percent change in volume during that period (right). Means with similar letters (right panel) or within each date (left panel) are not significantly different at $P \leq 0.05$.

Table 3. Mesquite and grass root mass density (0–270 cm depth), mesquite root mass · tree^{-1}, mesquite aboveground mass · tree^{-1}, and mesquite R:S mass ratio in each treatment (Mean ± SE; $n=3$). We used the same soil volume for trees in the Natural treatment as with the containerized trees. Means within a row with similar letters are not different at $P \leq 0.05$.
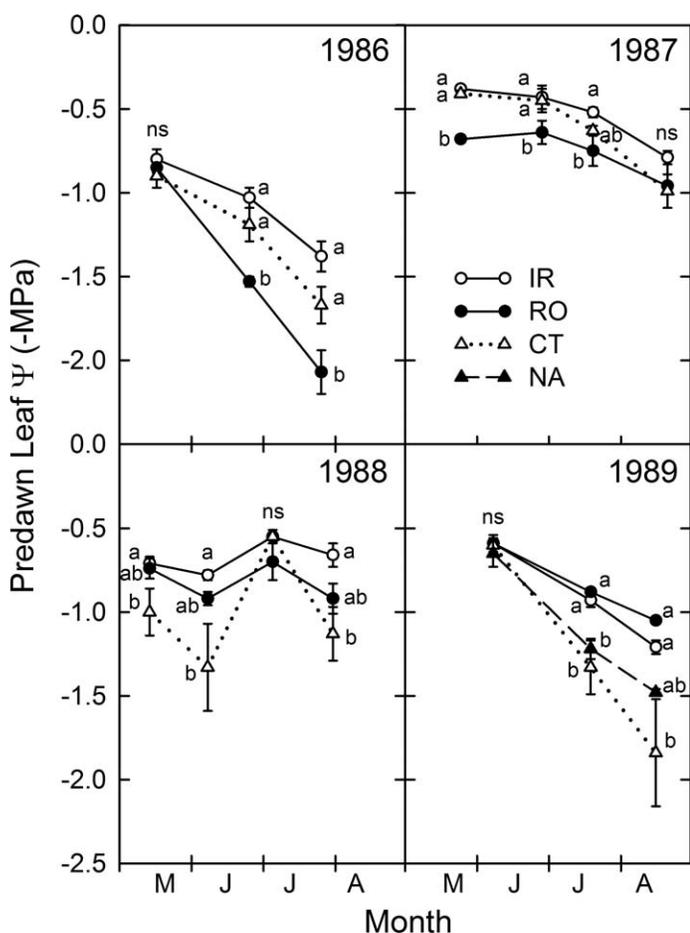
	Treatment			
Variable	Irrigated	Rainout	Control	Natural
Mesquite fine root mass density (g · m^{-2})	128.0 ± 3.8 a	87.4 ± 21.1 ab	66.5 ± 13.8 b	51.4 ± 2.1 b
Mesquite coarse root mass density (g · m^{-2})	93.1 ± 19.7 b	657.7 ± 197.4 a	219.7 ± 39.3 b	207.1 ± 86.7 b
Mesquite total root mass density (g · m^{-2})	221.1 ± 22.4 b	745.1 ± 214.5 a	286.2 ± 53.0 b	258.5 ± 85.6 b
Grass root mass density (g · m^{-2})	309.7 ± 48.7 a	117.6 ± 24.7 b	303.9 ± 20.3 a	325.4 ± 58.5 a
Mesquite + grass root mass density (g · m^{-2})	530.8 ± 54.0 a	862.6 ± 201.1 a	590.1 ± 72.5 a	583.8 ± 137.4 a
Mesquite fine + coarse root mass · tree^{-1} (kg)[1]	9.4 ± 0.9 b	31.6 ± 9.1 a	12.1 ± 2.2 b	11.0 ± 3.6 b
Mesquite aboveground mass · tree^{-1} (kg)	47.6 ± 1.2 a	34.7 ± 1.9 a	40.1 ± 8.5 a	39.6 ± 10.4 a
Mesquite R:S mass ratio	0.20 ± 0.02 b	0.91 ± 0.27 a	0.32 ± 0.08 b	0.27 ± 0.03 b

[1]Root mass tree^{-1} (kg) = [root mass density (g · m^{-2})] × [surface area of container (42.4 m^2)]/1 000.

periods of wetness. The strategy employed by this species for coping with extended drought is to increase root growth, including coarse macro-structure roots, in order to maintain a canopy growth rate similar to that during nondrought conditions rather than to transition physiologically to some reduced metabolic level. Under prolonged wetness, the increase

in canopy growth rate was supported by an increase in fine root growth, but not in coarse root growth.

Mesquite root growth responses to soil moisture manipulations provide an indication of potential responses of this and similar woody species to predicted climate change increases in

Figure 7. Mesquite predawn leaf Ψ in each treatment from May to August, 1986–1989. Error bars are ± 1 standard error ($n=3$). Means with similar letters are not significantly different at $P \leq 0.05$. NS indicates no significant differences.
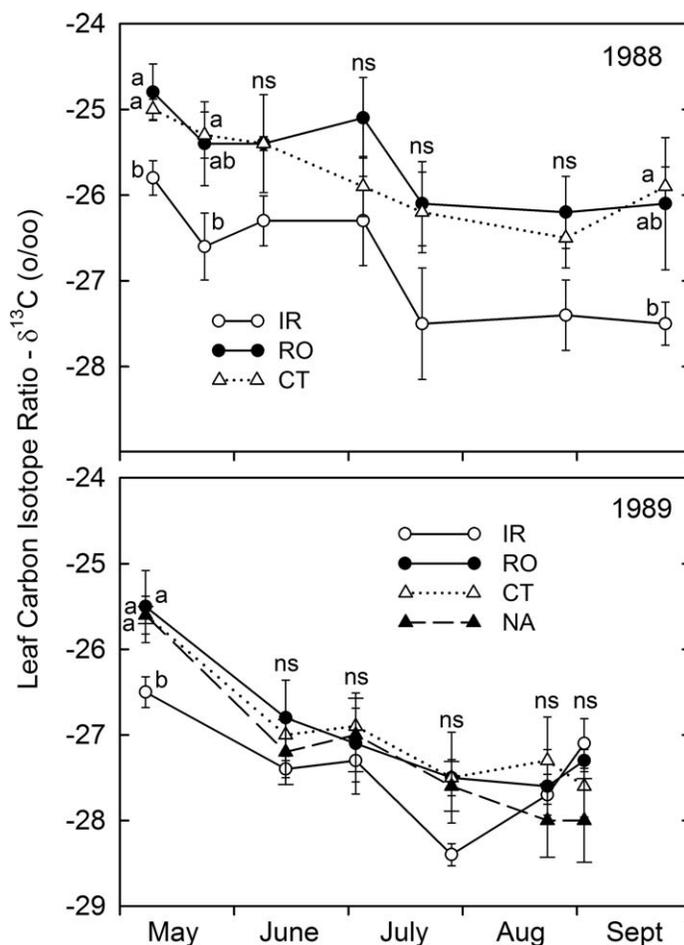
Figure 8. Mesquite leaf carbon isotope ratio in each treatment during the growing season, 1988 and 1989. Error bars are ± 1 standard error ($n=3$). Means with similar letters are not significantly different at $P \leq 0.05$. NS indicates no significant differences. An earlier version of some of these data was published in Ansley et al. (2007).

drought and temperatures in the southwestern United States (Seager et al. 2007; Karl et al. 2009). These responses could affect global predictions of root biomass and below ground carbon storage due to the extensive land areas that shrubs like mesquite occupy (Jackson et al. 1997; Schenk and Jackson 2005; Collins and Bras 2007; Robinson 2007). Our results suggest that mesquite would adapt to increasing soil drought from climate change through increases in root macro-structure resulting in substantial increases ($>100\%$) in belowground biomass and carbon sequestration. However, should climate change result in increased moisture, as has occurred in the southern Great Plains from 1958 to 2007 (Karl et al. 2009), then mesquite likely will adapt with increased fine root growth in mid to lower soil layers, although, as our data suggest, this would not necessarily lead to an increase in total root mass due to reduced coarse root mass.

ACKNOWLEDGMENTS

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