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Intraspecific competition in honey mesquite: Leaf and whole plant responses

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Abstract

Leaf and whole plant responses of honey mesquite *(Prosopis glandulosa* Torr.) to intraspecific competition were compared under low (LD) or high (HD) stand density in a semi-arid region of north Texas. The HD trees occurred within a stand of 300 trees ha^{-1}. The LD trees occurred in areas of the dense stand that were thinned to 80 trees ha^{-1} with no neighbors within 10 m of study trees. Tree size was similar in each treatment at study initiation. Five years after thinning, tree height, canopy volume, basal stem diameter, leaf area, and leaf area index were significantly greater in LD than HD trees. No differences in leaf predawn water potential, stomatal conductance, and photosynthesis were found between LD and HD trees during growing seasons 4 or 6 years after study initiation. Results indicate resources necessary for growth of individual mesquite plants were limiting under increased stand density and suggest the occurrence of intraspecific competition. Limitations were manifest at the whole plant level via modification of tree size and leaf area per tree, and not through adjustment of leaf physiological processes. The limiting factor appeared to be soil water. Daily water loss tree^{-1} was 2.5 to 4 times greater in LD than HD trees, and ranged from 119 to 205 kg and 46 to 59 kg in LD and HD trees, respectively. Projected daily water loss by mesquite at the stand level was similar between treatments, however, and ranged from 9,500 to 17,700 kg ha^{-1}.

Key Words: leaf area, photosynthesis, stomatal conductance, water potential, water relations, soil moisture

Honey mesquite (*Prosopis glandulosa* Torr.) inhabits a variety of arid and semiarid environments in the southwestern USA and Mexico and can occur in either savannas or as dense woodland thickets. It has been hypothesized that mesquite avoids drought because of an ability to grow a deep root system (Mooney et al. 1977, Levitt 1980). However, several studies have shown that mesquite adjusts leaf stomatal conductance and/or modifies leaf area in response to drought (Nilsen et al. 1981, Nilsen et al. 1983, Nilsen et al. 1987, Wan and Sosebee 1990). Ansley et al. (1990a, 1991) found that severing of lateral roots reduced mesquite leaf transpiration by as much as 50% on a semi-arid site in Texas, and that dependence on lateral roots was site-specific. This implies that, on some sites, water in shallow soil layers may be critical to mesquite physiological activity, and that lateral roots of neighboring mesquite might affect water availability via intraspecific competition.

Assuming intraspecific competition occurs at some level of mesquite density, a further question exists as to what strategy mesquite plants would employ to respond to resource limitations. While it seems logical that the first responses to stress would be those that were readily recoverable, such as stomatal closure, Bradford and Hsaio (1982; p 310) noted that, "it is therefore surprising that a nearly irreversible restriction of canopy size is one of the most sensitive responses to water stress for many species". Since most studies of woody plant water relations have been based on measurements of the individual leaf, quantification of whole plant responses to increasing competition is needed (Schulze et al. 1982, Ehleringer 1984, Meinzer et al. 1988). Leaf responses may not parallel whole plant responses under all conditions (Schulze et al. 1985, Hinckley and Ceulemans 1989).

We selected a site in north Texas, where mesquite dependence on shallow lateral roots has been documented (Ansley et al. 1991), to quantify intraspecific competition in this species. We measured the consequences of neighbor removal on physiological activity and growth of mesquite, to identify the organizational level (leaf or whole plant) most responsive to intraspecific competition.

Materials and Methods

Research was conducted on an area of native rangeland 30 km south of Vernon, Tex. (33°52', 99°17'W, elevation 368 m). Average annual precipitation is 665 mm with peak rainfall periods in May (119 mm) and October (77 mm). Average last spring frost is in mid-April and first fall-frost is in mid-November. Soils are Typic Paleustolls of the Deandale series (fine, mixed, thermic) and Typic Paleustalfs of the Kamay series (fine, mixed, thermic) (Koos et al. 1962). Dominant herbaceous understory species are buffalograss (*Buchloe dactyloides* [Nutt.] Engelm.), a warm-season shortgrass, and Texas wintergrass (*Nasella leurotricha* [Trin. and Rupr. Pohl], a cool-season midgrass.

The study occurred within a 4-ha stand of multistemmed mesquite that averaged 300 trees ha^{-1} (6 basal stems tree^{-1}; 1,800

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stems ha $^{-1}$; 40% canopy cover). Tree density and canopy cover were determined by direct measurement from 1:2500-scale infrared aerial photographs. In January 1986, four 0.25-ha areas within this stand were randomly selected and converted to a low density (LD) treatment (80 trees ha^{-1}; 5 basal stems tree^{-1}; 400 stems ha^{-1}; 12% canopy cover) by removing above ground portions of about 75% of the trees, and applying diesel fuel to stem bases to kill the plants. Four replicate areas of high density (HD) mesquite were identified adjacent to each thinned area. The HD areas were selected at random from a pool of 8 HD candidates that were located on the aerial photographs.

Herbaceous standing crop was estimated in LD and HD treatments during 1991 by clipping to 2–3 cm height, one 0.25 m^2 quadrat per treatment replicate. Sampling was conducted in interspaces between mesquite, although in the HD treatment, this was often within 1 m of a tree canopy. Standing crop was not quantified at study initiation in 1985. Standing crop values were estimated on a kg ha^{-1} basis from the 0.25 m^2 values. Livestock grazing was excluded from the site during the study.

Two trees of similar size (2–3 m height) were identified within each treatment replicate (16 total) and referred to as low density (LD) or high density (HD) trees. All neighboring mesquite within 10 m of experimental LD trees were killed. Canopy height, width and volume were measured on these trees in October 1985 prior to standing thinning and again in 1990. Canopy volume was calculated as follows:

$$\text{Volume} = V_{top} + V_{bot}, \text{ where}$$
$$V_{top} = [4/3\pi(a/2)(b/2)((h/2)]/2; \text{ and}$$
$$V_{bot} = [1/3(h/2)]\ [\pi(a/2)(b/2)) + ([\pi(c/d)(d/2)) + \sqrt{}(\pi(a/2)(b/2))(\pi(c/2)(d/2)]];$$

where h = canopy height, a = width of canopy along the north-south axis, b = width of canopy along the east-west axis, c = width of base of canopy along the north-south axis, and d = width of base of canopy along the east-west axis (Ansley et al. 1990b). These trees were not destructively sampled and were referred to as "nonharvest" trees.

In 1989, 8 additional trees (1 per treatment replicate) were selected for leaf physiological and leaf area measurements. These trees were referred to as the "physiology" trees. The LD physiology trees were included in the original population of trees in the thinned blocks in 1986. Leaf stomatal conductance (g; mmol m^{-2} s^{-1}), apparent net photosynthesis (A; µmol m^{-2} s^{-1}), transpiration (E; mmol m^{-2} s^{-1}), and water use efficiency (WUE; µmol A/mmol E) were measured using a Li-Cor LI-6200 closed chamber system (LiCor Inc., Lincoln, Neb.). Measurements were made at 6 hour (1989) or 2-hour (1991) intervals from 0800 to 1400 (CST) on 3 leaves on the sunlit aspect of each canopy about 1.5 to 2 m above ground. Different leaves were selected during each sample period. Approximately 5–9 cm^2 leaf area (1 leaf surface) was enclosed in the chamber and harvested after each measurement to determine leaf area. Duration of each measurement was 30–40 sec and chamber air flow was varied to maintain relative humidity (RH) near ambient. Photosynthetically active radiation (PAR, 400 to 700 nm) was determined at the position where g and A were measured using a quantum sensor which was mounted to the leaf chamber. Sampling was conducted on clear or mostly clear days. Some branches were removed from trees adjacent to the HD trees so that light conditions would approximate that of the LD trees. Reported values for leaf g, E, and A were based on the area of 1 leaf surface. Leaf E data from 1989 was lost during data processing.

Predawn leaf petiole xylem water potential (predawn leaf ψ) was measured on each 1991 physiology sample date. Two leaves were excised from the center of each canopy and predawn leaf ψ was measured immediately with a Scholander pressure bomb (Turner 1981). Subcanopy soil moisture was measured in 1991 with a neutron probe at 30-cm increments to 90 cm depth (Greacen 1981). Two aluminum access tubes were inserted at 2-m lateral distance from the base of each physiology tree within the canopy drip line during 1990. Soil moisture was not measured prior to 1991. Precipitation was recorded on the site with a rain gauge.

Six 15-mm diameter (± 3 mm) branches were removed from each of the 8 physiology trees in early September 1991 prior to any fall abscission. All leaves were harvested and total leaf area (both surfaces) per branch was determined with an area meter. Whole plant leaf area (WPLA) of each tree was estimated by counting the number of 15-mm diameter branches supporting foliage, and multiplying that by the leaf area per branch (Ansley et al. 1991, 1994). Plant leaf area (WPLA) was assumed to be proportional to the leaf area supported by individual twigs (Comstock et al. 1988). Per tree leaf area density (m^2 m^{-3} canopy volume) was determined by dividing WPLA by canopy volume. Per tree leaf area index (LAI) was determined by dividing WPLA by the measured ground surface area covered by each tree canopy (i.e., canopy cover). Canopy size, number, and diameter of basal stems tree^{-1} (i.e. stems occurring within 20 cm of the ground), and number of 15-mm diameter branches supported by each basal stem were determined prior to leaf harvesting in 1991. Canopy size was not measured on the physiology trees in 1985.

Average distance of physiology trees to nearest neighbors was determined from the aerial photographs taken after establishment of LD areas using a variation of the point-centered quarter method (after Cook and Stubbendieck 1986). Ground area around each tree was divided into 4 quadrats along cardinal directions and distance (tree center to tree center) from the experimental tree to the 3 nearest neighbors within each quadrant was measured on the photograph and averaged. Nearest neighbor distance was also measured directly at the site using the same quadrat sampling procedure that was used on the aerial photographs.

Water use tree^{-1} day^{-1} was calculated by multiplying mean daily leaf E (1 leaf surface) by WPLA of each tree (including both leaf surfaces) and correcting for reduction in E by shading within the canopy. Another study on similar-sized mesquite determined empirically that E was reduced in each of 4 equal-width canopy layers (from most sunlit to most shaded) by 0, 17, 26, and 38% (Ansley et al. 1991). These E extinction percentages were used for the current study. Leaf distribution was assumed to be equal within each canopy layer. A "day" was defined as the 8-hour period of maximum sunlight (0800–1600 CST) when most transpiration in this species occurs (Cuomo et al. 1992). Daily water use tree^{-1} was then scaled to the stand level based on trees ha $^{-1}$ within LD and HD areas. A t-test was used to evaluate stand density as the source of variation for each response variable.

Results

Mean distance of nearest neighbors to the "nonharvest" trees was 6.6 m (s.e. = 0.4 m; n = 8) and 18.5 m (s.e. = 1.4 m; n = 8) in the HD and LD treatments, respectively. Mean distance of nearest neighbors to the "physiology" trees was 5.9 m (s.e. = 0.7 m; n =

4) and 18.0 m (s.e. = 1.7 m; n = 4) by photograph estimate and 7.1 m (s.e. = 0.9 m) and 17.3 m (s.e. = 1.3 m) by ground measurement in the HD and LD treatments, respectively. Distance of nearest neighbors within each treatment was similar among the nonharvest and physiology trees.

Annual precipitation was above average from 1985 to 1991 except during 1988 and 1989 when it was below the 30-year mean (Fig. 1). Thus, the trees did not experience an extended drought during the 7 years. Precipitation was 8% above normal (464 vs. 430 mm) and 83% above normal (785 vs. 430) during the 1989 and 1991 growing seasons (April–September), respectively.

Nonharvest Tree and Herbaceous Understory Growth

There was no difference ($P < 0.05$) in canopy height or volume between LD and HD trees when measured at study initiation in 1985 (Fig. 2). Canopy width (diameter) was slightly greater in LD trees. By the end of the 1990 growing season, mean canopy height and width were significantly greater in LD than in HD trees. Mean canopy volume of LD trees was nearly 3 times that of HD trees (55.4 vs 20.1 m^3) by the end of 1990.

There was no apparent difference in herbaceous understory standing crop between treatments at study initiation in 1985 (no data). All treatment replicates were dominated by buffalograss in

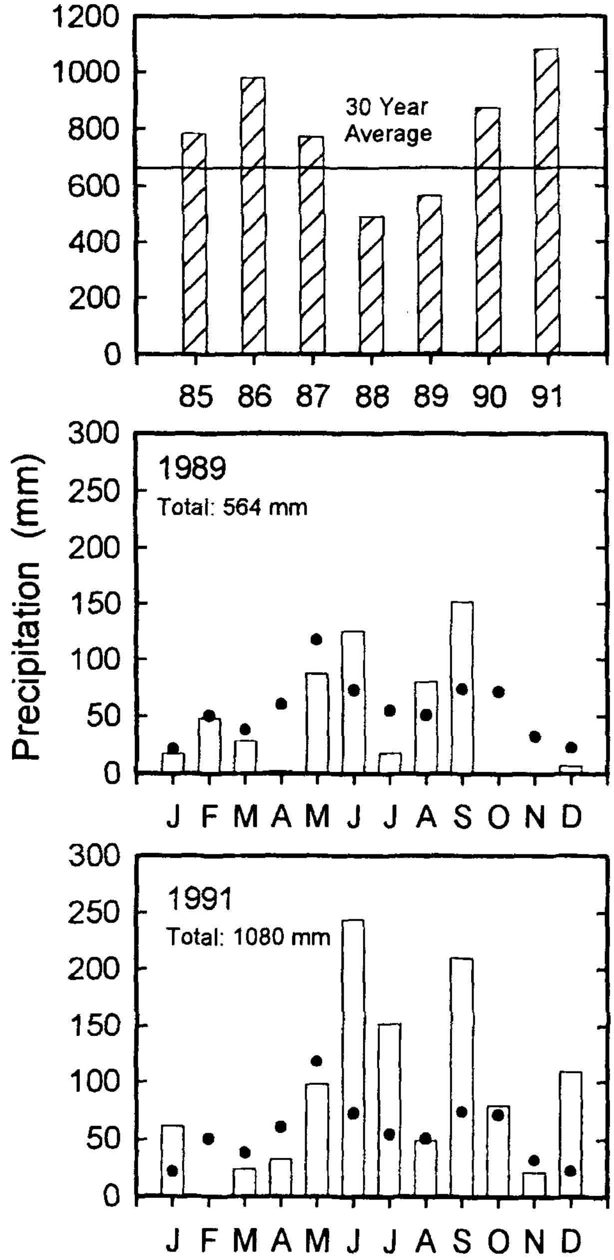

Fig. 1. Annual precipitation 1985 to 1991 compared to the 30-yr average (top), and monthly precipitation totals in 1989 (middle) and 1991 (bottom). Solid circles are 30-yr averages for each month.

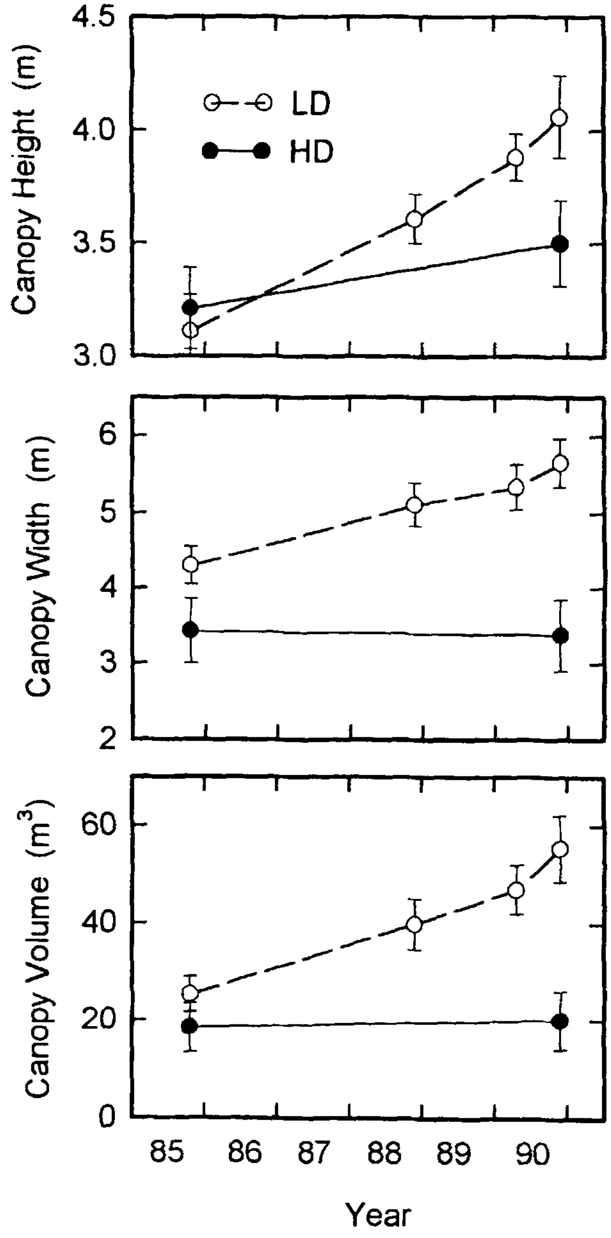

Fig. 2. Canopy height, width and volume of nonharvest mesquite trees in low (LD) and high (HD) density treatments. Vertical bars are ± 1 s.e. (n = 8). HD trees were not measured in 1988 or early 1990.

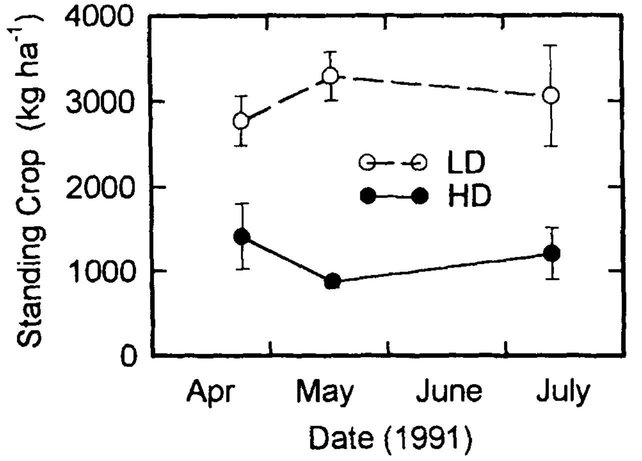

Fig. 3. Herbaceous standing crop in LD and HD treatments during 1991. Vertical bars are ± 1 s.e. (n = 4). Treatment differences are significant ($P \leq 0.05$).

interspaces and Texas wintergrass beneath canopies. During the 1991 growing season, herbaceous standing crop was near 3,000 kg ha^{-1} in LD areas and 1,100 kg ha^{-1} in HD areas (Fig. 3).

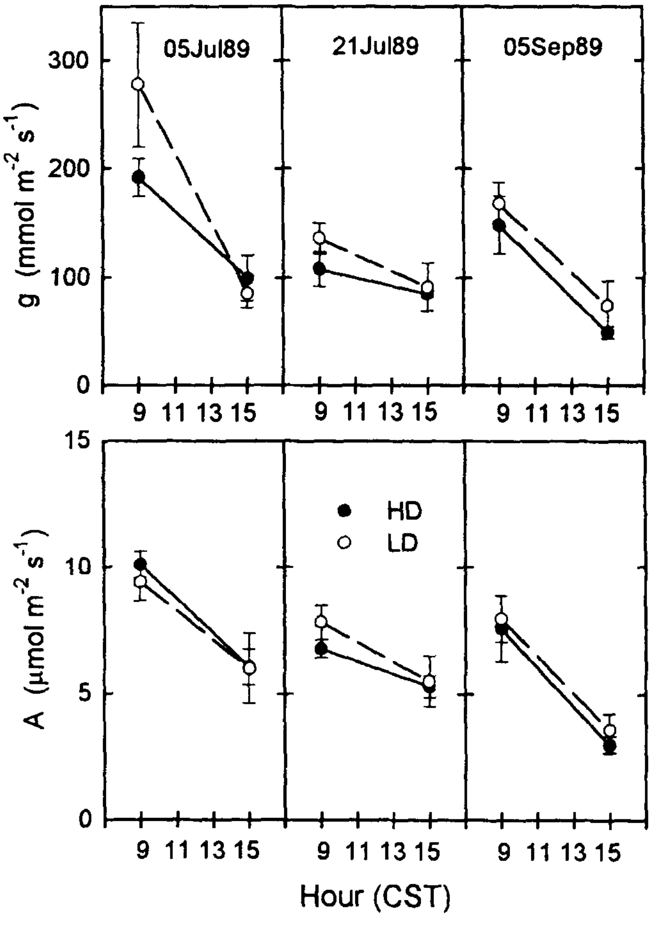

Fig. 4. Leaf stomatal conductance (g) and photosynthesis (A) in LD and HD physiology trees on 3 dates in 1989. Vertical bars are ± 1 s.e. (n = 4)

Leaf Responses of Physiology Trees

Photosynthetically active radiation (PAR) was similar between treatments during the 8-hour period when leaf measurements were made in both years (data not shown). Leaf stomatal conductance (g) ranged from 45 to 290 mmol m^{-2} sec^{-1}, and leaf photosynthesis (A) ranged from 3 to 13 μmol m^{-2} sec^{-1} across both treatments and sample years (Figs. 4 and 5). These values are comparable to those previously found for mesquite (Wan and Sosebee 1990, Ansley et al. 1990a, 1991) and for oak (*Quercus virginiana*) and ashe juniper (*Juniperus ashii*) in southern Texas (Owens and Schreiber 1992).

During all 1989 and 1991 sample days, leaf A declined during the day from peak morning levels ranging from 8 to 13 μmol m^{-2} sec^{-1} to 3 to 9 μmol m^{-2} sec^{-1} in afternoons. The same diurnal trend was observed for leaf g, except on 25 June 1991 when g remained relatively constant for both treatments, and on 26 August 1991 when g did not decline until after 1300 CST (Fig. 5). Responses of g on these 2 dates were influenced by precipitation events which occurred a few days before measurement. Diurnal leaf g and A did not differ between LD and HD treatments during 1989 (Fig. 4) or 1991 (Fig. 5).

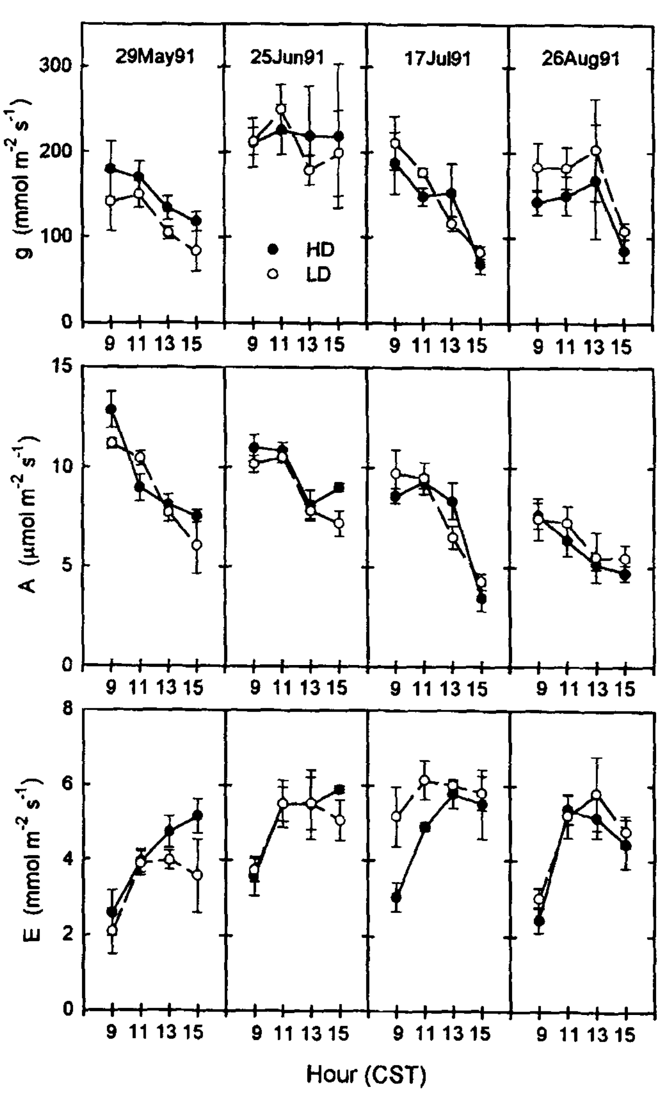

Fig. 5. Leaf stomatal conductance (g), photosynthesis (A) and transpiration (E) in LD and HD physiology trees in 1991. Vertical bars are ± 1 s.e. (n = 4).

Leaf E tended to increase during the morning hours and declined slightly in afternoons during 1991. Leaf E was greater in LD than in HD trees during the morning of 17 July 1991, but did not differ between treatments during other sample periods.

When diurnal leaf measurements were pooled into daily values, average daily g and A declined slightly from July to September 1989 with no differences between density treatments (data not shown). In 1991, average daily leaf g and A peaked in both treatments during June and declined after June (Fig. 6). Peak average daily E occurred in June in HD trees and in July in LD trees. Peak average daily WUE occurred in May in both treatments. There were no differences in average daily g, A, E, or WUE between treatments during 1991, except during July when E was greater in LD than in HD trees. Predawn leaf ψ declined after June 1991, with no significant differences between treatments during 1991.

Subcanopy soil moisture at 30 and 60 cm depths peaked during late June following over 200 mm of rain that fell in early June 1991 (Fig. 7). Soil moisture did not differ between LD and HD treatments at any depth measured during 1991.

Physiology Tree Growth and Structure

Tree height, canopy width and volume, and basal stem diameter were significantly greater in LD than in HD physiology trees in 1991 (Table 1). Average number of basal stems tree^{-1} was similar between treatments in 1991, supporting the assumption that the physiology trees were of similar size at study initiation in 1985. There were nearly twice as many 15-mm diameter branches in LD than in HD physiology trees by September 1991. Mean diameter and oven dry weight of twigs supported by 15-mm branches did not differ between treatments. Diameters of the harvested 15-mm branches did not differ between treatments. Diameters of the harvested 15-mm branches (6 tree^{-1}; 24 treatment^{-1}) ranged from 14.3 to 15.9 mm. Oven dry weight of twigs supported by each 15-mm branch ranged from 58 to 190 g.

There was a positive relation (r^2 = 0.84) between basal stem diameter and number of 15-mm branches supported by each basal stem (Fig. 8). This relationship was independent of LD/HD treatment effect and was curvilinear, indicating that slight increases in basal stem diameter supported an increasingly greater number of 15-mm branches.

Table 1. Structural and leaf area comparisons between low and high desnity physiology trees, September 1991.

Variable	Low Density Trees (LD)	High Density Trees (HD)
Tree Height (m)	4.2 a[1]	3.5 b
Canopy Width (m)	5.7 a	4.7 b
Canopy Volume (m^3)	56.2 a	32.5 b
Basal Stem Diameter (m)	0.10 a	0.07 b
Number of Basal Stems Tree^{-1}	5.0 a	5.5 a
Number of 15-mm Branches Tree^{-1}	87 a	45 b
15-mm Branch Diameter (mm)	15.1 a	15.1 a
O.D. Twig Weight 15-mm Branch^{-1} (g)	129.9 a	121.6 a
Leaf Area 15-mm Branch^{-1} (m^2)	0.81 a[2]	0.50 b
Leaf Area Tree^{-1} (WPLA) (m^2)	69.7 a	23.1 b
Leaf Area Density (m^2 m^{-3} canopy volume)	1.29 a	0.71 b
Canopy Ground Cover Tree^{-1} (m^2)	25.3 a	17.6 b
Leaf Area Index Tree^{-1}	2.91 a	1.35 b

[1] Means within a row followed by different letters are significantly different at $P \leq 0.05$ (n = 4).

[2] All leaf areas and LAI calculations include both leaf surfaces.

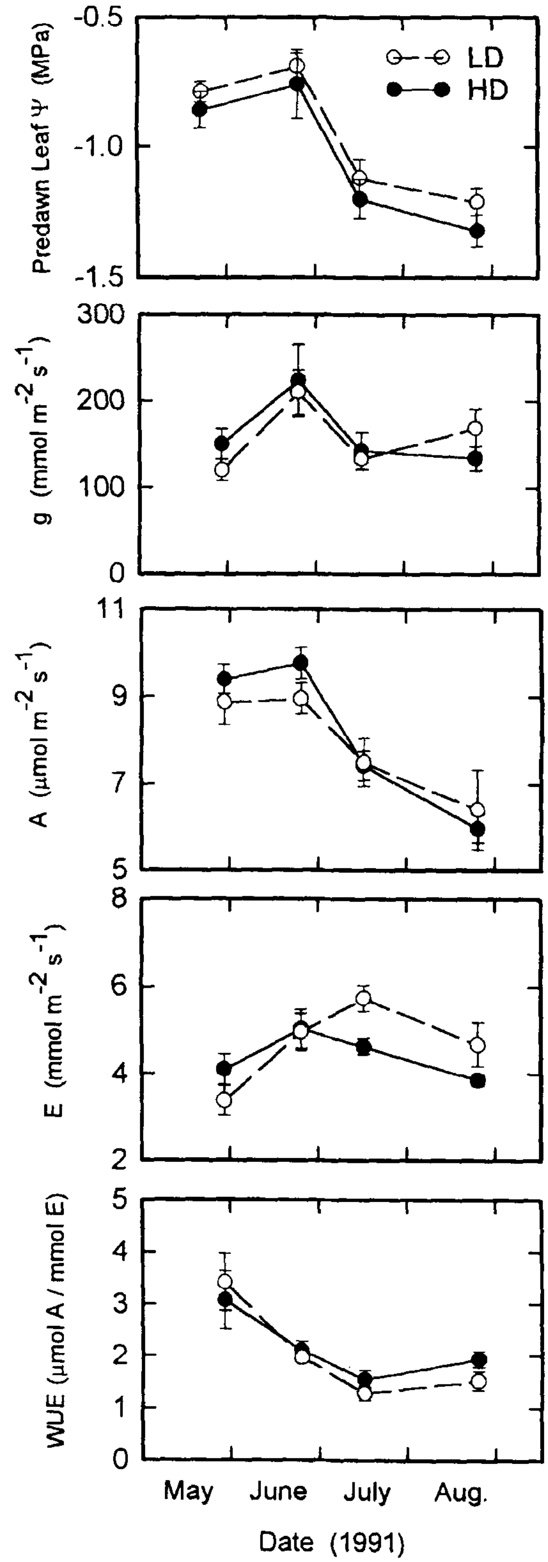

Fig. 6. Predawn leaf water potential (predawn leaf ψ) and average daily means of leaf stomatal conductance (g), photosynthesis (A), transpiration (E), and water use efficiency (WUE) in LD and HD physiology trees in 1991. Verticial bars are ± 1 s.e. (n = 4).

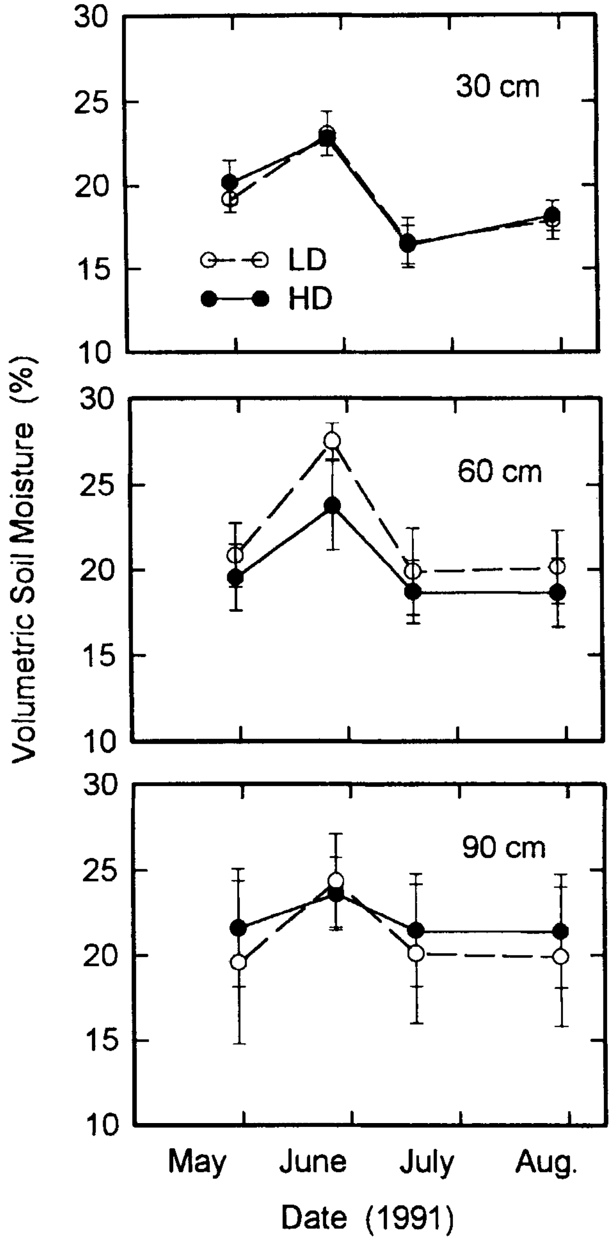

Fig. 7. Volumetric soil moisture at 3 depths beneath LD and HD trees during 1991. Vertical bars ± 1 s.e. (n = 4).

Leaf area supported by each 15-mm branch ranged from 0.18 to 0.64 m^2 in HD, and from 0.48 to 1.2 m^2 in LD trees, respectively. Mean leaf area supported by each 15-mm branch was 65% greater in LD (0.81 m^2, s.e. = 0.05) than HD (0.49 m^2; s.e. = 0.01) trees (Table 1). Within-treatment variation of leaf area per 15-mm branch was low (LD: cv = 23%; HD: cv = 12%), suggesting that estimation of whole plant leaf area by determining leaf area of a few 15-mm branches and counting all 15-mm branches $tree^{-1}$ was reasonably accurate. Leaf area $tree^{-1}$ (WPLA), leaf area density, canopy ground cover $tree^{-1}$ and leaf area index were significantly greater in LD than HD trees.

Tree and Stand-Level Transpiration

The LD trees transpired 2.5 to 4 times more water $tree^{-1}$ than HD trees. When pooled across treatment, daily E $tree^{-1}$ ranged from 46 to 59 kg in HD trees and 119 to 205 kg in LD trees during the 1991 growing season (Table 2). Projected daily transpiration by mesquite at the stand level ranged from 9,557 to 17,756 kg ha^{-1}. Mesquite transpiration ha^{-1} was only slightly greater in HD than LD areas in May and June, and did not differ from LD areas during July and August 1991. Equalization in stand transpiration between treatments was due to greater daily E $tree^{-1}$ in the LD treatment being offset by a greater number of trees $stand^{-1}$ in the HD treatment.

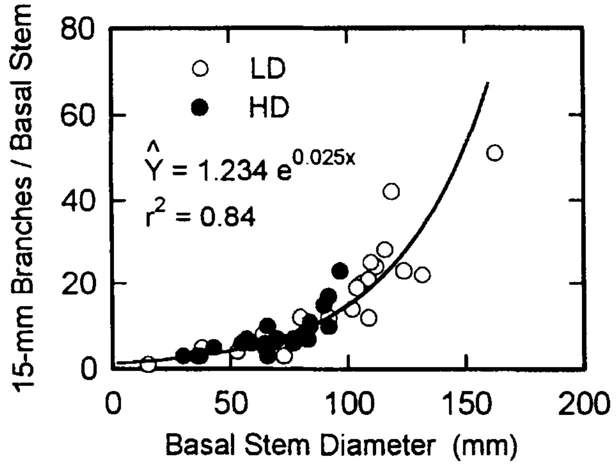

Fig. 8. Relation between basal stem diameter and number of 15-mm diameter branches supported by each basal stem in LD and HD physiology trees (4 trees $treatment^{-1}$; n = 42).

Table 2. Projected daily transpiration per tree and per stand (1 hectare) under different levels of mesquite density[1].

Date	Treatment	Transpiration Per Tree ($kg\ tree^{-1}\ day^{-1}$)	Transpiration Per Stand ($kg\ ha^{-1}\ day^{-1}$)
29 May 91	HD	47 a[2]	13,975 a
	LD	119 b	9,557 b
25Jun91	HD	59 a	17,756 a
	LD	172 b	13,793 a
17Jul91	HD	54 a	16,241 a
	LD	205 b	16,365 a
26Aug91	HD	46 a	13,761 a
	LD	166 b	13,274 a

[1] Based on a density of 300 and 80 trees ha^{-1} in HD and LD treatments, respectively.
[2] Means within a column on a particular date followed by different letters are significantly different at $P \leq 0.05$ (n = 4).

Discussion

This study demonstrated that intraspecific competition exists in adult mesquite. We hypothesize that competition occurred among lateral roots in interspaces between trees, and that the limiting resource was likely water. Daily water use by mesquite trees in HD areas (46–59 kg $tree^{-1}$ day^{-1}) was similar to the 30–75 kg $tree^{-1}$ day^{-1} reported for mesquite under similar intraspecific conditions on a site 60 km from the current study area (Ansley et al. 1991). Water use by LD trees (119–205 kg $tree^{-1}$ day^{-1}) was somewhat greater than the 108 kg tree^{-1} day^{-1} reported by Ansley et al. (1994) on different LD trees on the same study site. The fact that mesquite water use at the stand level was the same in HD and LD areas for much of the growing season implies that (1) there was a limited pool of water available to mesquite, and (2) mesquite density in the HD areas had reached or exceeded the point of resource limitation. As mesquite density increased on this site, so did competition for water, and individuals responded by conserving water loss.

We did not measure soil water in interspaces between mesquite. However, the finding that differences in mesquite growth occurred even though there were no differences in subcanopy soil moisture between treatments, indirectly supports the hypothesis that intraspecifc competition occurred among lateral roots in interspaces. The finding that mesquite thinning increased grass growth in interspaces also suggests that mesquite intraspecific competition occurred among lateral roots. When tree density was reduced, some of the newly available water in interspaces apparently was absorbed by lateral roots of remaining trees, and another portion went to increased grass growth. In support of this hypothesis, several studies in semi-arid regions of Texas have documented increases in herbaceous growth in interspaces between mesquite (where canopy shading is not a factor) following mesquite reduction treatments (Dahl et al. 1978, McDaniel et al. 1982). While root studies near the study site indicate that mesquite lateral roots in interspaces generally occur between 0.5 to 1 m below the soil surface, which is below where most grass roots occur (Fisher et al. 1973, Heitschmidt et al. 1988), they apparently negatively affect water availability to grasses. Nutrient release from killed mesquite roots in the LD treatment areas may also have affected responses of remaining mesquite and grasses.

Mesquite develop extensive lateral roots on many sites in northwestern Texas. Seasonal water relations and plant leaf area of these mesquite are strongly influenced by precipitation patterns, suggesting that lateral roots contribute significantly to the plant's water supply (Ansley et al. 1991, Cuomo et al. 1992). Ansley et al. (1990a) determined that lateral roots extending beyond the canopy perimeter potentially can provide half the water supply of adult mesquite. Mesquite with extensive lateral roots may not have significant taproot development. Alternatively, taproots may exist but have an anchoring rather than a water absorption function. In a New Mexico study, actively absorbing roots were located beneath the canopies of small mesquite but, as the shrubs grew larger, subcanopy roots became inactive and served an anchoring function (Ho et al. 199x). The absorbing roots extended beyond the canopy perimeter. We hypothesize that rainfall patterns in northern Texas, which frequently wet the soil surface during the growing season, promote mesquite dependence on shallow lateral roots and thereby increase sensitivity to resource limitations caused by intraspecific competition.

In other regions of the continental USA, mesquite are less dependent on extensive lateral roots. At xeric sites in southern California and Arizona (annual precipitation 100–300 mm), mesquite are classified as phreatophytes because the plant depends on deep soil moisture (Phillips 1963, Mooney et al. 1977, Levitt 1980). Aboveground responses of these mesquite are decoupled from drought in shallow soil layers and include maintenance of relatively constant seasonal leaf transpiration and whole plant leaf area (Nilsen et al. 1983, 1987). These responses support the hypothesis that intraspecific competition is minimal in phreatophytic mesquite. Other research in xeric environments has demonstrated that intraspecific competition may not be as strong as interspecific competition. For example, in the Mojave Desert of southern California, interspecific competition between *Ambrosia dumosa* and *Larrea tridentata* was greater than intraspecific competition within each species (Fonteyn and Mahall 1978).

Mechanisms of Adjustment to Competition

Responses of mesquite to intraspecific competition were manifest at the whole plant level by modification of woody structure and leaf area per plant, and not through adjustment of leaf physiological processes. This agrees with observations of Bradford and Hsiao (1982) who noted that, for many species, the more sensitive response to water stress was restriction of canopy size rather than leaf physiological adjustments. In support of these findings, Meinzer et al. (1988) determined that leaf g and E were similar between irrigated and irrigated + nitrogen-treated *Larrea tridentata*, but the nitrogen-treated shrubs had greater plant leaf area. Conversely, Ehleringer (1984) found that reduced intraspecific competition increased leaf g and ψ in addition to whole plant leaf area in *Encelia farinosa* 2 years after thinning.

Responses of mesquite in the current study were measured several years after treatment when (we assume) responses of trees to the thinning treatment had stabilized. There is evidence that responses during the first year of treatment may differ substantially from subsequent years. Ansley et al. (1990a) found that mesquite responses to acute moisture stress (i.e., when lateral roots were severed) occurred at the leaf level during the first growing season after stress was imposed, but there were no differences in leaf responses between root-severed and control trees by the second growing season. Similarly, *Abies balsamea* and *Betula papyrifera* demonstrated differences in leaf ψ between thinned and control areas during the first growing season after thinning but not during the second year (Pothier and Margolis 1990). These authors suggested that alternate mechanisms such as morphological adaptation of leaves occurred in the second year to adjust to thinning.

Long-term responses to reduced moisture stress, as determined in the current study, involved adjustment of leaf area per plant by modification of structural attributes (number of branches tree^{-1}) as well as leaf area supported by each branch. Late-season, drought-induced abscission has been observed in mesquite (Ansley et al. 1992), and this process may have contributed to the lower whole plant leaf area found in HD than in LD trees. However, leaf litter did not appear to be greater beneath HD trees (unquantified) in September 1991 when branches were harvested. Moreover, precipitation was well above normal during June–September 1991.

Ecological and Management Implications

Significant increases in mesquite density have occurred in Texas in the last century. This has been due in part to increases in mesquite seed dispersal via livestock (cattle) feces (Archer 1995). Passage of consumed mesquite beans through the cattle digestive system enhances germination after fecal deposition (Brown and Archer 1989). Often as many as 20–30 mesquite seedlings can be found emerging from the same cattle fecal site.

There is little doubt that intraspecific competition occurs among mesquite seedlings emerging from a single fecal site. In northern Texas, Kramp et al. (199x) found that, of all cattle fecal sites initially observed to have emerging mesquite, either only 1 seedling per site became established, or all the seedlings at a site died. Interestingly, in Kramp et al.'s study, 42% of all cattle fecal sites that initially had emerging mesquite eventually yielded an established mesquite plant.

In another example of intraspecific competition, most mesquite seedlings that emerge beneath the canopy of an already established adult plant eventually die (Ruthven et al. 1993). It remains unknown whether young, even-aged mesquite that have established from different fecal sites experience intraspecific competition. It likely depends on stand density, as the current study demonstrated with adult mesquite. It is reasonable to assume, however, that young mesquite require a greater stand density (i.e., more individuals area^{-1}) than do older mesquite before intraspecific competition occurs. Phillips and McMahon (1981), and an abundance of other literature, indicate that competition among desert shrubs increases as plants grow.

The 2 mesquite densities used in the study represent a typical "woodland thicket" (300 trees ha^{-1}) and a more open 'savanna" (80 trees ha^{-1}). Management practices which reduce mesquite densities from thickets to savannas likely will increase grass growth as well as accelerate growth of remaining mesquite. Since much of the soil water that was released by reducing mesquite density was used by the remaining mesquite or by increased grass growth, thinning of mesquite stands may not increase off-site water yield on some sites.

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