Increasing CO2: Comparative Responses of the C4 Grass Schizachyrium and Grassland Invader Prosopis

H. Wayne Polley; Hyrum B. Johnson; Herman S. Mayeux

Ecology, Volume 75, Issue 4 (Jun., 1994), 976-988.

Stable URL:
http://links.jstor.org/sici?sici=0012-9658%28199406%2975%3A4%3C976%3AICCROT%3E2.0.CO%3B2-J

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at http://www.jstor.org/about/terms.html. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

Ecology is published by The Ecological Society of America. Please contact the publisher for further permissions regarding the use of this work. Publisher contact information may be obtained at http://www.jstor.org/journals/esa.html.

Ecology
©1994 The Ecological Society of America

JSTOR and the JSTOR logo are trademarks of JSTOR, and are Registered in the U.S. Patent and Trademark Office. For more information on JSTOR contact jstor-info@umich.edu.

©2003 JSTOR

http://www.jstor.org/
Wed May 14 13:53:52 2003

Ecology, 75(4), 1994, pp. 976–988
© 1994 by the Ecological Society of America

INCREASING CO_2: COMPARATIVE RESPONSES OF THE C_4 GRASS *SCHIZACHYRIUM* AND GRASSLAND INVADER *PROSOPIS*[1]

H. WAYNE POLLEY, HYRUM B. JOHNSON, AND HERMAN S. MAYEUX
Grassland, Soil and Water Research Laboratory, U.S. Department of Agriculture, Agricultural Research Service, Temple, Texas 76502 USA

Abstract. The woody C_3 *Prosopis glandulosa* (honey mesquite) and C_4 perennial grass *Schizachyrium scoparium* (little bluestem) were grown along a gradient of daytime carbon dioxide concentrations from near 340 to 200 μmol/mol air in a 38 m long controlled environment chamber. We sought to determine effects of historical and prehistorical increases in atmospheric CO_2 concentration on growth, resource use, and competitive interactions of a species representative of C_4-dominated grasslands in the southwestern United States and the invasive legume *P. glandulosa*. Increasing CO_2 concentration stimulated N_2 fixation by individually grown *P. glandulosa* and elicited in C_3 seedlings a similar relative increase in leaf intercellular CO_2 concentration, net assimilation rate, and intrinsic water use efficiency (leaf net assimilation rate/stomatal conductance). Aboveground biomass of *P. glandulosa* was not altered by CO_2 concentration, but belowground biomass and whole-plant water and nitrogen use efficiencies increased linearly with CO_2 concentration in seedlings that were grown alone. Biomass produced by *P. glandulosa* that was grown with *S. scoparium* was not affected by CO_2 concentration. Stomatal conductance declined and leaf assimilation rates of *S. scoparium* at near maximum incident light increased at higher CO_2 concentration, but there was no effect of CO_2 concentration on biomass production or whole-plant water use efficiency of the C_4 grass. Rising CO_2 concentration, especially the 27% increase since the beginning of the 19th century, may have contributed to more abundant *P. glandulosa* on C_4 grasslands by stimulating the shrub's growth or reducing the amount of resources that the C_3 required. Much of the potential response of *P. glandulosa* to CO_2 concentration, however, appears to be contingent on the shrub's escaping competition with neighboring grasses.

Key words: biomass production; carbon isotopes; little bluestem; mesquite; ^{15}N; N_2 fixation; nitrogen use efficiency; photosynthesis; water use efficiency; southwestern U.S.

INTRODUCTION

Density and abundance of the woody C_3 *Prosopis* (mesquite; *P. glandulosa* Torr. var. *glandulosa*, *P. glandulosa* var. *torreyana* (L. Benson) M. C. Johnst., *P. velutina* Woot.) increased substantially on C_4 grasslands in the southwestern United States during the past 150 yr (Glendening 1952, Johnston 1963, Buffington and Herbel 1965). *Prosopis* possesses characteristics of an aggressive invader, including production of abundant, long-lived seed that germinate over a wide range of temperatures and edaphic conditions (Glendening and Paulsen 1955), rapid root growth, and potential for N_2 fixation (Shearer et al. 1983, Johnson and Mayeux 1990). Yet, these leguminous shrubs may only recently have expanded onto upland grasslands (Buffington and Herbel 1965, Archer 1989) from mesic drainages or rocky slopes (Bogusch 1950) occupied perhaps through the Holocene (Smeins 1983).

The increased abundance of *Prosopis* has been variously attributed to rather site-specific changes, which increased seedling recruitment or reduced size-dependent plant mortality. These include suppression of grassland fires that selectively kill seedling shrubs (Glendening and Paulsen 1955, Wright et al. 1976), possible changes in rodent populations (Brown and Heske 1990) and in rodent-mediated seedling mortality (Paulsen 1950), changes in the seasonality (Neilson 1986), intensity, and effectiveness of precipitation that favored *Prosopis* over resident grasses (Hastings and Turner 1965), and various effects of the large number of livestock introduced in the latter 19th century. Most notable among these are ingestion and dissemination of *Prosopis* seed (Glendening and Paulsen 1955, Brown and Archer 1987, Archer 1989) and overgrazing that reduced competition from resident grasses for required resources (Scifres et al. 1971, Van Auken and Bush 1989, 1990) and increased spatial heterogeneity of soil nitrogen (N) and water (Schlesinger et al. 1990).

Each of these contributed to enhance *Prosopis* growth in some circumstances, but a consensus as to which are most important is lacking. York and Dick-Peddie (1969), for example, concluded that lightly grazed desert grasslands supported less woody cover than heavily grazed areas in southern New Mexico, USA. Glendening (1952), Smith and Schmutz (1975), Meyer and Bovey (1982), and Brown and Archer (1989), however, provide experimental evidence that *Prosopis* establish-

[1] Manuscript received 28 January 1993; revised 10 September 1993; accepted 15 September 1993.

es (and thus may increase) on grasslands across grazing intensities (but see Bush and Van Auken 1990). Several have proposed that open C_4 grasslands were maintained by fire (e.g., Johnston 1963), but fire presumably was infrequent in portions of the arid and semiarid regions of *Prosopis*' range and may not kill plants beyond the seedling stage (Glendening and Paulsen 1955). It is thus unlikely that any of the conventionally cited agents provides a definitive explanation for the apparently explosive increase in *Prosopis* over the geographically, edaphically, and climatically diverse regions involved. Some combination of these (Smeins 1983) or other variables likely contributed.

Accompanying the increased density of *Prosopis* on grasslands was a 27% rise in atmospheric carbon dioxide concentration from ≈275 μmol/mol air at the beginning of the 19th century (Neftel et al. 1985, Raynaud and Barnola 1985) to the current level near 350 μmol/mol (Keeling et al. 1989). The historical increase in CO_2 concentration, like the ≈95 μmol/mol rise from a glacial minimum to the 1800 level (Delmas et al. 1980, Neftel et al. 1988), may greatly have increased production of some plants (LaMarche et al. 1984, Hari and Arovaara 1988, Baker et al. 1990, Allen et al. 1991, Polley et al. 1992*a*). Responses to CO_2 concentration vary among species, however, and particularly between plants with C_3 and C_4 photosynthetic metabolisms (Bazzaz and Carlson 1984, Patterson and Flint 1990, Johnson et al. 1993). Because leaf photosynthetic rates often are more sensitive to CO_2 concentration in C_3 than C_4 species, rising CO_2 concentration may preferentially have enhanced growth of C_3 shrubs relative to the C_4 species that dominated grasslands in the southwestern U.S. at the beginning of the 19th century (Mayeux et al. 1991, Johnson et al. 1993). There are numerous other potential benefits of higher CO_2 concentration to plant growth, including greater N_2 fixation by C_3 legumes and higher water and nitrogen use efficiencies (Idso 1989). Some of these changes may have a greater impact on grassland vegetation, which appears generally to be limited by water (Sala et al. 1988) or nitrogen availabilities (Seastedt et al. 1991) than the influence of CO_2 concentration on leaf photosynthesis.

In the present study, monospecific (monocultures) and mixed plantings (mixtures) of the woody legume *P. glandulosa* Torr. var. *glandulosa* (honey mesquite) and the perennial C_4 grass *Schizachyrium scoparium* (Michx.) Nash. (little bluestem) were maintained for two growing seasons at one of two water treatments (well watered and periodically droughted) along a daytime gradient from near 340 to 200 μmol/mol CO_2. The C_4, *S. scoparium*, is a codominate of the mixedgrass and tallgrass prairies in the U.S. (Risser et al. 1981). Leaf gas exchange and related parameters calculated from stable carbon (C) isotope ratios ($^{13}C/^{12}C$) of whole leaves, evapotranspiration, plant biomass production and N yields, legume N_2 fixation, and plant water and nitrogen use efficiencies were assessed to test the prediction that rising CO_2 concentration has increased growth and competitive ability of *P. glandulosa* relative to *S. scoparium*. Results provide an initial test of potential effects of increasing CO_2 concentration on the balance of woody plants and C_4 grasses on perennial grasslands in the southwestern U.S.

Materials and Methods

Controlled environment chamber

P. glandulosa and *S. scoparium* were grown in a ventilated glasshouse within a 38 m long controlled environment chamber. The chamber, described in detail by Mayeux et al. (1993), consists of five, ≈7.6 m lengths of a 0.76 m deep and 0.45 m wide soil container. Lengths are arranged parallel to one another. The plastic-lined soil containers are partitioned into contiguous 0.6 m long, water-tight compartments. Aerial growth of plants was enclosed in a tunnel-shaped transparent polyethylene cover. The cover was attached to the top of the soil container, and covers of adjacent 7.6 m lengths were connected by ducts to form a continuous 38 m chamber. Air was moved one direction through the chamber with a blower.

Photosynthesis by enclosed plants progressively depleted the CO_2 concentration and increased the $^{13}C/^{12}C$ of air as it moved the 38 m from the air intake to the outlet of the chamber. A continuous and stable CO_2 concentration gradient from near 340 to 200 μmol/mol was maintained during daylight (9–10 h daily) by automatically varying the rate of air flow (range = 1–5 m^3/min) through the chamber in response to changes in incident photosynthetic photon flux density (PPFD) and CO_2 depletion by enclosed plants. The CO_2 concentration was measured each minute with an infrared gas analyzer (Inficon Binos, Leybold–Heraeus GmbH, Germany) in air drawn from the chamber outlet and sequentially from the beginning of each of the five, 7.6 m lengths. Blower speed was increased each night to exhaust respired CO_2 from the chamber.

Air drybulb and dewpoint temperatures were reset each 7.6 m along the chamber to those within the ventilated glasshouse with chilled-water cooling coils and resistance heating elements. Gradients in temperature and vapor pressure deficit of air (VPD) within each 7.6 m length were calculated from measurements taken with fine-wire thermocouples and DEW-10 chilled-mirror hygrometers (General Eastern Instruments, Maine, USA) at extremes of 7.6 m lengths. Data from occasional days on which CO_2 concentration regulation was manually interrupted, temperature sensors malfunctioned, or records were incomplete were deleted before CO_2 concentration and environmental variables were compiled.

Species and culture

Forty-three of the 64 contiguous 0.6 m long compartments along the soil container were planted 17 May

1989 with "experimental" plants of *P. glandulosa* and *S. scoparium*. The C_3 oats (*Avena sativa* L.) and C_4 grasses *Cenchrus incertus* (M. A. Curtis) and *Digitaria ciliaris* (Retz.) Koel. were grown in compartments at extremes of each 7.6 m chamber length as photosynthetic "sinks" to improve regulation of the CO_2 concentration gradient. Oats were grown from February through April 1990. The C_4 grasses were grown as sinks for the remainder of the experiment. Remaining compartments were seeded on 11 May 1990 with 'Gaspe' yellow flint *Zea mays*. The stable C isotope composition of *Z. mays* served as a proxy for the $^{13}C/^{12}C$ of chamber air (Marino and McElroy 1991).

Thirty-six of the experimental soil compartments were planted with *P. glandulosa* and *S. scoparium* monocultures separated by 1:4 *P. glandulosa/S. scoparium* mixtures. Two additional compartments were planted to *P. glandulosa* monocultures and five other compartments were planted to species mixtures. Species monocultures contained either a single individual of *P. glandulosa* grown from seed or four individuals of *S. scoparium*, two grown from ramets and two from seed. Species mixtures contained four plants of *S. scoparium* and one of *P. glandulosa*. Ramets randomly chosen from one of six *S. scoparium* genets were transplanted to opposite ends of compartments that contained the grass. Seeds of *S. scoparium* were planted on opposite sides of these compartments. *P. glandulosa* was grown in the center of compartments. Planting densities and arrangements in species mixtures were chosen to approximate those encountered by *P. glandulosa* seedlings during establishment in C_4 grasslands.

Soil N was labeled by adding solution containing 0.23 g ^{15}N as $K^{15}NO_3$ to the fine sandy loam field soil (classified as Udic Paleustalfs; Huckabee et al. 1977) in each compartment before planting. The $^{15}N/^{14}N$ of seedlings from *S. scoparium* monocultures was used as a proxy for the $^{15}N/^{14}N$ of soil N available to *P. glandulosa* in determining N_2 fixation by the shrub (Shearer and Kohl 1986).

Two watering regimes were imposed with the initial intent to examine possible interactive effects of CO_2 concentration and water availability on plant performance. Because plants subjected to the two watering treatments were harvested at different times, it was not possible to distinguish effects of water availability on plant response to CO_2 concentration from those of plant age and season of growth. Most of the variables measured in this experiment, however, apparently were little affected by the different watering regimes.

Soil water in a total of 24 compartments located near the ends or air exits of the five chamber lengths was restored weekly to "field capacity" (well-watered treatment, ≈20% volumetric water content). The remaining 19 compartments at the beginning or air entrance of chamber lengths were kept near field capacity during the first growing season from planting until 11 August 1989 and during the second growing season from 1 March 1990, when established plants broke dormancy, until 17 May 1990. At other times (August to December 1989 and May to October 1990), water was added to these compartments only after it had declined to ≈65% of the volumetric content at field capacity (periodically droughted treatment). Plants exposed to the two watering regimes were located in opposite halves (near the air entrance or air exit) of each 7.6 m length along the chamber to minimize differences in air temperatures and VPD to which plants within each watering regime were exposed. Soil water content in each of the closed 0.6 m long soil compartments was measured weekly through the sides of the wooden soil containers with a TROXLER 3218 surface moisture gauge (Troxler Electronics, North Carolina, USA). An empirically determined relationship between the volume of water lost per compartment and the decline in gauge reading from field capacity was used to calculate water additions.

CO_2 concentration and environmental variables

A continuous gradient from a mean (± 1 SE) 341.8 ± 0.8 to 204.3 ± 0.7 μmol/mol CO_2 (n = 156 d) was maintained from 1 August 1989 until most plants were dormant, 29 November 1989, and from 1 March 1990, when plants began to grow, until final harvest on 9 October 1990. The mean daytime CO_2 concentration to which plants in each 0.6 m long soil compartment were exposed was estimated from the linear regression of CO_2 concentration at the six locations routinely sampled on distance from the air intake (r^2 = 0.96). Chamber CO_2 concentration increased at night from a mean 360 μmol/mol at the air intake to 390 μmol/mol at the chamber outlet.

The mean drybulb temperature of air that was introduced during daylight to the five lengths of chamber did not vary consistently with time from mid-September to December 1989 ($\bar{X}$ = 23.1°C, n = 57 d). The drybulb temperature of air introduced to chamber lengths increased linearly in 1990 from a mean 19.8°C on 1 March to 25.4°C at harvest on 9 October and varied by a mean 2.8°C (n = 108 d) among lengths. The VPD of air introduced to successive lengths of chamber did not change systematically through 1989 ($\bar{X}$ = 1.64 kPa, n = 40) or 1990 ($\bar{X}$ = 1.18 kPa, n = 48). Drybulb temperatures rose between the beginnings and ends of chamber lengths. That rise decreased in 1989 from a daytime mean of 6.3°C in August and September to 4.2°C from October to December (n = 88 d) and increased linearly with time in 1990 from 4.5°C on 1 March to 9.5°C on 9 October (n = 108 d) when experimental plants were confined to one-half of each chamber length only. The VPD increased a mean 0.5 kPa from the beginnings to ends of 7.6 m lengths in each year. Temperatures at night decreased linearly in 1989 from a mean 22.7°C in August to 15.9°C in December (n = 88 d). Nighttime temperatures increased from March to ≈1 June 1990, but subsequently

varied little across chamber lengths ($\bar{X}$ = 20.3°C, n = 56 d).

The PPFD incident on plants in the chamber was calculated as the product of quantum flux measured by 1-m line quantum sensors (191SB, LI-COR, Nebraska, USA) mounted above the chamber and transmission by the polyethylene cover (90%). Incident PPFD exceeded 1300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at midday under clear skies. The daily integral of PPFD incident on plants in the chamber was ≈55% of that above the glasshouse.

Leaf gas exchange and C isotopes

Net CO_2 assimilation (A) and stomatal conductance to water vapor (g) were measured on recent fully expanded leaves with a LCA-2 infrared gas analyzer (Analytical Development Company, Hertfordshire, England). Gas exchange was determined in May 1990 when all plants were well watered. Measurements were taken on clear days with near maximum incident PPFD at the CO_2 concentration at which plants were grown.

Air temperatures inside the leaf cuvette typically were 1°–4°C above those to which leaves were exposed before measurements. Single leaves per plant were measured at mean leaf temperatures of 31.6° ± 0.5° and 33.2° ± 0.8°C, incident PPFD of 1391 ± 38 and 1394 ± 51 $\mu mol \cdot m^{-2} \cdot s^{-1}$, and leaf-to-air vapor pressure differences of 0.62 ± 0.02 and 0.55 ± 0.08 kPa (all mean ± 1 SE) for *S. scoparium* (n = 20) and *P. glandulosa* (n = 17), respectively. Boundary layer conductances of leaves were estimated with filter paper replicas (Parkinson 1985), and instantaneous gas exchange parameters, including the ratio of leaf intercellular CO_2 concentration (c_i) to ambient CO_2 concentration (c_a) and intrinsic water use efficiency (A/g), were calculated using one-sided leaf area (von Caemmerer and Farquhar 1981).

Discrimination by *P. glandulosa* against $^{13}CO_2$ (Δ) was determined from $\delta^{13}C$ values of air and upper-canopy leaves of the C_3 shrub. Temporally integrated values of leaf c_i/c_a (Farquhar et al. 1982) and A/g (Polley et al. 1993) then were calculated for *P. glandulosa* assuming 29‰ as discrimination by ribulose-1,5-bisphosphate carboxylase against ^{13}C during CO_2 fixation (Roeske and O'Leary 1984).

The $\delta^{13}C$ of air was measured at midday on 22 April and 9 July 1990 at six locations spaced evenly across the CO_2 concentration gradient. Discrimination by the C_4 *Z. mays* was calculated from the measured relationship of $\delta^{13}C$ of air to CO_2 concentration (9 July 1990) with the $\delta^{13}C$ of whole leaves harvested 28 June 1990 and did not vary significantly with growth CO_2 concentration ($\bar{X}$ = 3.13‰, n = 9) (Polley et al. 1993). We used a Δ of 3.1‰ and the linear relationship between the $\delta^{13}C$ of *Z. mays* leaves harvested 20 September 1990 and mean daytime CO_2 concentration to calculate the $\delta^{13}C$ of air to which the *P. glandulosa* plants harvested in October 1990 were exposed. The c_i/c_a, and related A/g, of *P. glandulosa* leaves that were harvested in May and October 1990 were calculated from the measured (April) or derived (September) linear relationships of $\delta^{13}C$ of air to CO_2 concentration, respectively.

Harvests and analyses

Senescent material, leaves of *P. glandulosa* and aboveground tissues of *S. scoparium*, were collected at the end of the first growing season (12 December 1989) from plants forced into dormancy by cold temperatures. Well-watered and periodically droughted plants subsequently were harvested at different times. Aboveground tissues were harvested from well-watered plants in 24 soil compartments between 16 and 30 May 1990. The *S. scoparium* in these compartments was allowed to regrow to provide a photosynthetic "sink" for CO_2. Leaves, attached and fallen, and aboveground stems of *P. glandulosa* and aboveground material and crowns of *S. scoparium* in the remaining 19 compartments (periodically droughted treatment) were harvested on 9 October 1990. Four soil cores, each 45 mm in diameter, then were composited per 0.6 m long soil compartment. Fine roots were hand separated from oven-dried (60°C) soils. Remaining tap and lateral roots of *P. glandulosa* were completely excavated. All plant material was dried at 60°C and weighed.

The consistent differences in $\delta^{13}C$ between the C_3 *P. glandulosa* and C_4 *S. scoparium* were used to calculate the root biomass of each species present in soil cores recovered from *P. glandulosa/S. scoparium* mixtures (Polley et al. 1992*b*). The mass of ^{13}C in roots extracted from mixtures is the sum of the products of the ratio of ^{13}C to total C (derived from $\delta^{13}C$ values) and root C mass (biomass × percentage of C composition) of the individual species. All components in the algebraic expression, except biomass of *S. scoparium* and *P. glandulosa* roots, were determined from measurements on roots recovered from cores, surface roots attached to crowns of clonal *S. scoparium*, and tap roots of *P. glandulosa* from each species mixture. The equation then was solved for root biomass of *S. scoparium* by setting biomass of *P. glandulosa* equal to the difference between measured total biomass and that of *S. scoparium* roots.

Kjeldahl N was measured on plant components of *P. glandulosa* from each harvest and on tissue harvested from *S. scoparium* that grew until October 1990. Nitrogen mass of *S. scoparium* roots in species mixtures was the product of the N concentration of roots attached to crowns and biomass determined with C isotopes. The difference between the total N mass of fine roots in each *P. glandulosa/S. scoparium* mixture and calculated N of *S. scoparium* roots gave the N mass of fine roots of *P. glandulosa*.

Biomass and N masses of aboveground material produced over the experiment, including those of senescent tissues collected at the end of the first growing

season (December 1989), were summed to give aboveground biomass and N accretion per species (= clonal + seedling plants for *S. scoparium*) in each 0.6 m long soil compartment. Aboveground biomass and N masses of plants harvested on 9 October 1990 were added to those of belowground (roots plus crowns) material present at harvest to derive cumulative or total biomass production and N accretion per species and soil compartment. Instantaneous ratios of belowground to aboveground biomass and N were calculated from standing crops on 9 October 1990. Apparent water use efficiency in biomass production (WUE) was cumulative biomass harvested per species monoculture divided by water lost to evapotranspiration. Nitrogen use efficiency (NUE) per species was calculated as the ratio of total biomass production to both cumulative leaf (*P. glandulosa*) and total N accretion (*P. glandulosa, S. scoparium*). The former value is an index of the efficiency with which *P. glandulosa* used the N invested in photosynthetic tissues to acquire carbon. The latter value of NUE reflects the amount of biomass that plants produced per unit of N acquired. The ratio of N mass in standing crop at harvest to cumulative N yield provided a measure of N turnover.

The fraction of total N in *P. glandulosa* that was derived from N_2 fixation was estimated from plant ^{15}N abundances (Shearer and Kohl 1986). The $^{15}N/^{14}N$ signature of leaf blades from seedlings of *S. scoparium* grown in grass monocultures across the CO_2 concentration gradient was used as an estimate of the ^{15}N of soil N available to the legume. Leaf ^{15}N of *P. glandulosa* that depended entirely on atmospheric N_2 as a N source was assumed equal to -1.3 $\delta^{15}N$ or 0.3658% ^{15}N (Shearer et al. 1983).

Relationships of leaf gas exchange to CO_2 concentration during measurements and of leaf $\delta^{13}C$ values and plant yield parameters to daytime CO_2 concentration were fit with polynomial regression equations (Weisberg 1980). Separate linear regressions by species were fit to yield components from monocultures and mixtures. Regressions for monocultures and mixtures were compared (*F* test) to determine effects of interspecific competition.

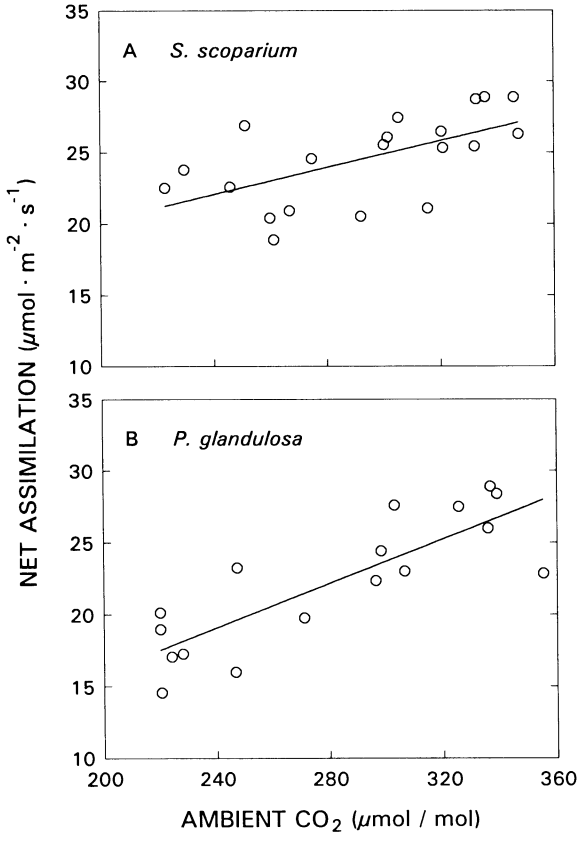

FIG. 1. Net assimilation rates of leaves of (A) the C_4 *Schizachyrium scoparium* and (B) C_3 *Prosopis glandulosa* as a function of the CO_2 concentration at which plants were grown along a daytime gradient of subambient CO_2 concentration. Lines are linear regressions of single measurements for *S. scoparium* ($r^2 = 0.36$, $P = .005$, $n = 20$) and *P. glandulosa* plants ($r^2 = 0.69$, $P < .0001$, $n = 17$) in May 1990 vs. CO_2 concentration.

RESULTS

Leaf gas exchange

Stomatal conductance (*g*) of *S. scoparium* decreased 34%, from 0.29 to 0.19 $mol \cdot m^{-2} \cdot s^{-1}$ (not shown), and *A* increased 26% in May 1990, from 21.4 to 27.0 $\mu mol \cdot m^{-2} \cdot s^{-1}$, with the 53% rise in daytime CO_2 concentration from 225 to 345 μmol/mol (Fig. 1A). Conversely, *g* of *P. glandulosa* was not significantly ($P > .05$) related to CO_2 concentration or c_i (not shown). A fractional increase in CO_2 concentration elicited nearly the same relative increase in *A* (Fig. 1B), however, and leaf c_i of well-watered *P. glandulosa* remained an almost constant fraction of CO_2 concentration (0.65). The slopes of linear regressions of *A* on CO_2 concentration did not differ significantly between species (*F* test, $P = .14$). Still, *A* was ≈20% greater on average for *S. scoparium* than *P. glandulosa* at 225 μmol/mol CO_2, while CO_2 assimilation rates were comparable for the two species at 345 μmol/mol CO_2 (near 27 $\mu mol \cdot m^{-2} \cdot s^{-1}$).

The *A/g* of *S. scoparium* and *P. glandulosa* increased 89 and 65%, respectively, from 225 to 345 μmol/mol CO_2 in May 1990 (Fig. 2). Higher *A* (Fig. 1B) accounted for the CO_2-induced increase in *A/g* of *P. glandulosa*. Both an increase in *A* and decline in *g* contributed to higher *A/g* in *S. scoparium*.

Carbon isotopes

The $\delta^{13}C$ of chamber air measured on 22 April 1990 (Fig. 3A) and of *Z. mays* leaves harvested in September 1990 (Fig. 3B), a proxy for the $\delta^{13}C$ of chamber air, increased linearly (became more enriched in ^{13}C) as plant photosynthesis depleted CO_2 concentration from near 340 to 200 μmol/mol. Leaf $\delta^{13}C$ values of *P. glan-*

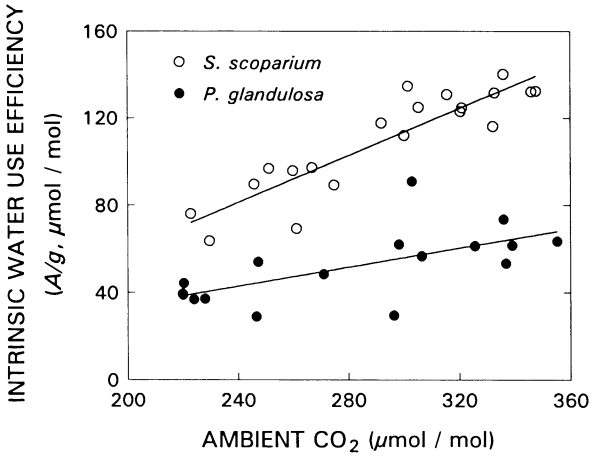

FIG. 2. Intrinsic water use efficiency (leaf net assimilation, A, divided by stomatal conductance to water, g) of the C_4 *S. scoparium* and C_3 *P. glandulosa* as a function of the daytime CO_2 concentration at which plants were grown. Lines are linear regressions of single gas exchange measurements for *S. scoparium* ($r^2 = 0.81$, $P < .0001$, $n = 20$) and *P. glandulosa* plants ($r^2 = 0.42$, $P = .005$, $n = 17$) vs. CO_2 concentration.

dulosa increased linearly in well-watered (Fig. 3A) and periodically droughted plants as CO_2 concentration declined (Fig. 3B). At neither harvest did regressions of $\delta^{13}C$ on CO_2 concentration differ between plants grown in monocultures and mixtures (F test, $P > .50$).

Inferences from gas exchange measurements were supported by C isotope analyses. The c_i calculated from leaf $\delta^{13}C$ values of *P. glandulosa* increased linearly with daytime CO_2 concentration in both well-watered and periodically droughted plants (Fig. 4). The intercepts of extrapolated regressions of c_i on CO_2 concentration did not differ significantly from zero in either group of plants (t test, $P = .46$ and .14 for well-watered and periodically droughted plants, respectively). The ratio of c_i to c_a calculated from $\delta^{13}C$ values thus was nearly constant across CO_2 concentration in *P. glandulosa* from both the well-watered and periodically droughted treatments ($\bar{X} = 0.60$ and 0.53, respectively) and, for well-watered plants, was similar to the c_i/c_a calculated from gas exchange measurements. The c_i/c_a was lower, however, in the droughted and older plants harvested in October. Calculated A/g of *P. glandulosa*, like that measured instantaneously (Fig. 2), increased by the same relative amount as CO_2 concentration.

Biomass, N, and N_2 fixation: well-watered plants

Aboveground biomass produced by *S. scoparium* monocultures ($n = 6$) and both aboveground biomass production and N accretion of well-watered *P. glandulosa* monocultures ($n = 8$) harvested May 1990 did not change consistently with CO_2 concentration (Table 1). Aboveground biomass of *S. scoparium* and *P. glandulosa* in mixtures also did not vary significantly with CO_2 concentration, but effects of competition were evident in the reduced yield of *P. glandulosa* in mixtures compared to monocultures. Averaged across CO_2 concentration, aboveground biomass production and N accretion of mixture-grown *P. glandulosa* were both ≈53% of those in *P. glandulosa* monocultures. Conversely, mean biomass production of *S. scoparium* in mixtures ($n = 10$) was virtually identical to that in monocultures across CO_2 concentration.

The $^{15}N/^{14}N$ signature of *S. scoparium* that was grown from seed in monocultures decreased a mean 0.3% ^{15}N from December 1989 to May 1990 across CO_2 concentration, and, in May, increased linearly from ≈1.2 to 1.4% ^{15}N as CO_2 concentration declined ($n = 5$ plants). We used the relationship of *S. scoparium* ^{15}N to CO_2 concentration to estimate the percentage of ^{15}N

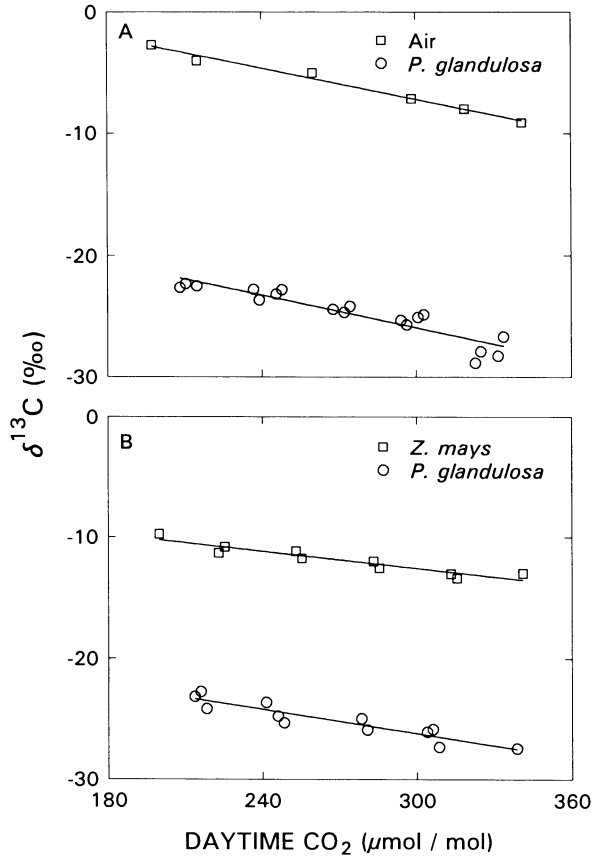

FIG. 3. The stable C isotope composition ($\delta^{13}C$) of air and upper leaves from C_3 *P. glandulosa* and C_4 *Z. mays* plants along a daytime gradient of subambient CO_2 concentration. Lines are linear regressions of $\delta^{13}C$ on instantaneous (air) or mean daytime CO_2 concentration [CO_2] (plant leaves) in (A) April (air; $\delta^{13}C = 5.60 - 0.04[CO_2]$, $r^2 = 0.99$, $P < .0001$, $n = 6$) and May (*P. glandulosa*; $\delta^{13}C = -12.57 - 0.04[CO_2]$, $r^2 = 0.85$, $P < .0001$, $n = 18$ well-watered plants) and (B) September (*Z. mays*; $\delta^{13}C = -5.59 - 0.02[CO_2]$, $r^2 = 0.89$, $P < .0001$, $n = 10$ plants) and October 1990 (*P. glandulosa*; $\delta^{13}C = -16.24 - 0.03[CO_2]$, $r^2 = 0.86$, $P < .0001$, $n = 12$ droughted plants).

TABLE 1. Mean biomass production and N accretion of well-watered and periodically droughted *P. glandulosa* and *S. scoparium* plants that were harvested in May and October 1990 from monocultures and 1:4 *P. glandulosa*/*S. scoparium* mixtures grown across a daytime gradient from near 340 to 200 μmol/mol CO_2.†

Variable	*P. glandulosa*		*S. scoparium*	
	Monoculture	Mixture	Monoculture	Mixture
		Well-watered (May)		
Aboveground biomass production (g)	122.0	64.8	137.9	138.4
Aboveground N accretion (g)	2.5	1.3	...	...
		Periodically droughted (October)		
Aboveground biomass production (g)	298.1	120.4	404.0	345.6
Belowground biomass (g)	148.0*	69.7	182.6	140.0
Total biomass production (g)	446.1*	190.1	586.6	485.6
Aboveground N accretion (g)	5.1	2.1	2.7	2.2
Belowground N (g)	1.9	0.8	1.2	1.0
Total N accretion (g)	7.0	2.9	3.9	3.2

* Variables that were statistically related to [CO_2] are designated by * (see Fig. 6).

† Soils were watered to field capacity weekly (well-watered) or only after soil water had declined to 65% of the volumetric content at field capacity (periodically droughted). Belowground biomass and N were measured in October only. Biomasses and N masses of leaves collected at the end of the first growing season, December 1989, were added to those of aboveground material at harvest to give aboveground biomass production and N accretion per species. Nitrogen was not measured for *S. scoparium* harvested in May.

of soil N available to *P. glandulosa* harvested in May 1990. The fraction of plant N that *P. glandulosa* in monocultures derived from N_2 fixation generally increased at higher CO_2 concentration (Fig. 5). Estimates of N_2 fixation by *P. glandulosa* grown in C_3/C_4 mixtures (0–20% of plant N) were not related to growth CO_2 concentration (not shown).

Biomass, N, and N_2 fixation: periodically droughted plants

There was a linear, marginally significant ($P = .09$) increase with higher CO_2 concentration in total biomass produced by periodically droughted *P. glandulosa* monocultures ($n = 6$ plants) that resulted largely from a significant ($P = .05$) linear increase in root biomass (Fig. 6). A linear increase in the amount of aboveground biomass produced at higher CO_2 concentration was not significant ($P = .18$). Total biomass produced by *P. glandulosa* in monoculture increased 57%, and the ratio of belowground to aboveground biomass increased from 0.41 to 0.80 with the 55% increase in CO_2 concentration from 220 to 340 μmol/mol.

Both aboveground and belowground biomass produced by *P. glandulosa* were lower in mixtures than in monocultures (Table 1), and biomass of shrubs in mixtures was not influenced by CO_2 concentration. The difference in biomass produced between *P. glandulosa* in monocultures and adjacent mixtures along the CO_2 concentration gradient cannot directly be compared to assess effects of competition from *S. scoparium* because total water supplied and thus potentially available to plants in monocultures and mixtures differed. Soil in compartments with species mixtures typically dried quickly, and mixtures received a mean 24 and 18% more water than monocultures with *P. glandulosa* and

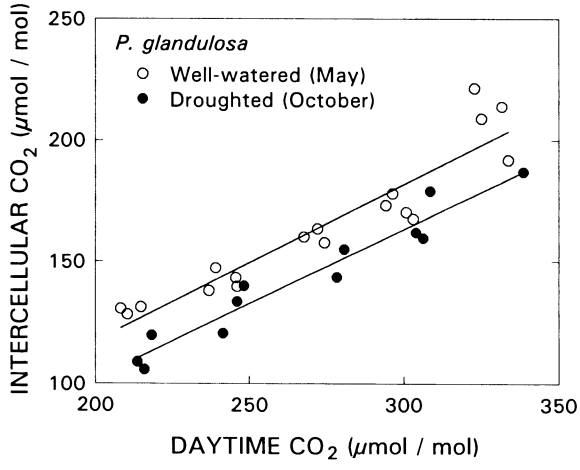

FIG. 4. Leaf intercellular CO_2 concentration of *P. glandulosa* calculated from the $\delta^{13}C$ of leaves and the mean daytime CO_2 concentration at which plants were grown. Lines are linear regressions of single measurements for continuously well-watered and periodically droughted plants that were harvested in May ($r^2 = 0.88$, $P < .0001$, $n = 18$) and October 1990 ($r^2 = 0.94$, $P < .0001$, $n = 12$), respectively, on CO_2 concentrations. The $\delta^{13}C$ of air used to calculate intercellular CO_2 concentration at the October harvest was determined from the $\delta^{13}C$ of *Z. mays* plants grown across the CO_2 concentration gradient assuming a constant discrimination relative to air of 3.1‰.

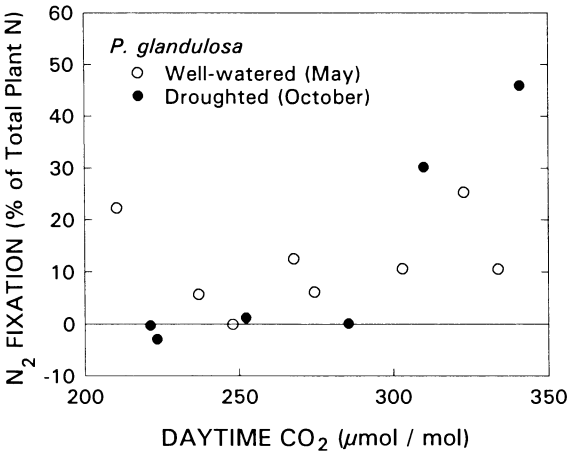

FIG. 5. Estimates of the percentage of plant nitrogen (N) that was derived from N_2 fixation by *P. glandulosa* from well-watered and periodically droughted monocultures harvested in May and October 1990, respectively, as a function of daytime CO_2 concentration at which plants were grown. Soils were watered to field capacity weekly (May) or after soil water had declined to ≈65% of the volumetric content at field capacity (October). The $^{15}N/^{14}N$ signature of soil N accumulated and metabolized by *P. glandulosa* was estimated from the $^{15}N/^{14}N$ signature of leaf blades taken from monocultures of *S. scoparium* grown across the same CO_2 concentration gradient and with the same watering regime.

S. scoparium, respectively. Total water added to compartments containing *P. glandulosa/S. scoparium* mixtures differed by a maximum of 30%. Under these conditions, the contribution of *P. glandulosa* to total biomass production and N accretion in species mixtures did not vary with CO_2 concentration ($\bar{X}$ = 42% for N and 28% for biomass, n = 7). Ratios of *P. glandulosa* belowground to aboveground biomass in mixtures were not obviously related to CO_2 concentration or to total or root biomass or N yield of *S. scoparium* neighbors, but were on average 1.5 times greater in five of six mixtures than in adjacent *P. glandulosa* monocultures across the CO_2 concentration gradient.

There was no consistent relationship of CO_2 concentration to the $^{15}N/^{14}N$ signature of seedling *S. scoparium* in monocultures in October 1990 ($\bar{X}$ = 1.13%, n = 6), but percentage of ^{15}N values were ≈0.2% greater below 255 μmol/mol CO_2. We thus used the ^{15}N signature of the *S. scoparium* monoculture nearest each *P. glandulosa* plant as a proxy for the percentage of ^{15}N of available soil N. Estimates of N_2 fixation in *P. glandulosa* monocultures declined from 45.9% of plant N at 340 μmol/mol to near zero at 285 μmol/mol CO_2 (Fig. 5). The $^{15}N/^{14}N$ signature was greater in *P. glandulosa* than *S. scoparium* in species mixtures at lowest CO_2 concentration, but percentage of ^{15}N was a mean 0.06% lower in the shrub above 240 μmol/mol CO_2 as would be expected if *P. glandulosa* fixed N_2.

Mean N accretion of *P. glandulosa,* like biomass production, was lower in mixtures than in monocultures, but aboveground, belowground, and total N accretion per *P. glandulosa* individual did not vary with CO_2 concentration in either monocultures or mixtures (Table 1). A single linear equation described the relationship between plant N mass at harvest on 9 October 1990 and root biomass of *P. glandulosa* grown in both monocultures (excluding those that fixed N_2) and mixtures across CO_2 concentration (Fig. 7), suggesting that *S. scoparium* reduced N accretion of *P. glandulosa* primarily by restricting root growth rather than N accretion per unit root biomass.

The N concentration of crowns plus roots from *P. glandulosa* grown in monocultures decreased linearly with increasing CO_2 concentration (r^2 = 0.98, P = .0001, n = 6), but stem and leaf N concentrations were not altered. As a result, the NUE of *P. glandulosa* monocultures, calculated as the ratio of biomass production to both total plant (Fig. 8) and leaf N accretion, increased by 40% from 220 to 340 μmol/mol CO_2. Nitrogen turnover, the ratio of N mass present at final harvest to cumulative N accretion per plant, did not differ with CO_2 concentration or between *P. glandulosa* grown in monocultures and mixtures ($\bar{X}$ = 0.9).

Biomass production and N accretion by periodically droughted *S. scoparium* (clonal + seedling plants) were lower in mixtures (n = 7) than monocultures (n = 6), but did not vary significantly with CO_2 concentration (Table 1). Ratios of *S. scoparium* belowground to aboveground biomass decreased marginally (P = .13, n = 6) in monocultures as CO_2 concentration rose, but were positively correlated in mixtures across CO_2 concentration to total biomass of neighboring *P. glandu-*

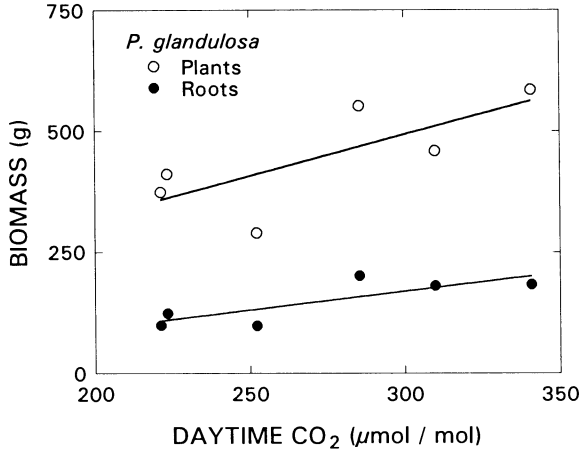

FIG. 6. Whole-plant biomass production and root biomass of individual *P. glandulosa* seedlings (n = 6) that were grown across a daytime CO_2 concentration gradient. Soils were watered to field capacity after soil water had declined to ≈65% of the volumetric content at field capacity. Root biomass was measured at final harvest, October 1990, only. Plant production is cumulative aboveground biomass plus root biomass at harvest. Lines are linear regressions of whole-plant (r^2 = 0.55, P = .09) and root biomass on CO_2 concentration (r^2 = 0.66, P = .05).

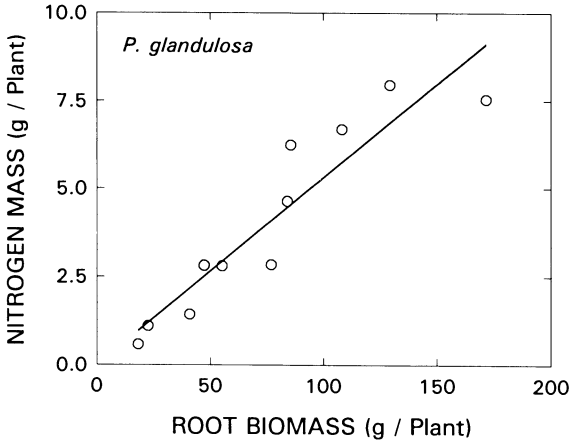

FIG. 7. The relationship between root biomass and whole-plant nitrogen mass at harvest (October 1990) for *P. glandulosa* seedlings grown in monocultures ($n = 4$) and mixtures with *S. scoparium* ($n = 7$) across a daytime CO_2 concentration gradient. *P. glandulosa* that fixed N_2 were excluded ($n = 2$). The line is a linear regression of nitrogen mass on root biomass ($r^2 = 0.86$, $P < .0001$).

losa ($r^2 = 0.63$, $P = .03$, $n = 7$). The NUE of *S. scoparium* increased linearly across monocultures and mixtures (Fig. 8) by the same amount per unit increase in CO_2 concentration as did NUE of *P. glandulosa* ($P = .88$). Nitrogen mass at harvest was a mean 81% of cumulative N accretion over the experiment for *S. scoparium* grown in monocultures and mixtures.

Water use and water use efficiency

Apparent transpiration per unit leaf mass of well-watered *P. glandulosa*, the ratio of soil water loss (evapotranspiration) from monocultures from 18 April to 15 May 1990 to leaf biomass at harvest on 16 May 1990, declined by 31% from 210 to 334 μmol/mol CO_2 (Fig. 9A). This decline in apparent transpiration per unit leaf mass, however, primarily reflected a decrease at higher CO_2 concentration in specific leaf area (leaf area per unit biomass) (Fig. 9B). Transpiration per leaf area of *P. glandulosa* did not vary with CO_2 concentration (not shown).

Apparent WUE in biomass production of *P. glandulosa* from periodically droughted monocultures increased on average from $\approx$1.46 to 2.44 g/L H_2O at daytime CO_2 concentrations of 220 and 340 μmol/mol air, respectively (Fig. 10). The biomass produced by droughted *S. scoparium* monocultures per unit evapotranspiration did not vary consistently with CO_2 concentration.

DISCUSSION

Most of the factors that are thought to have contributed to greater abundance of *Prosopis* on C_4 grasslands either reduced mortality of woody seedlings or promoted recruitment of *Prosopis* by increasing the availability of resources to seedlings. Once well established in grassland, *Prosopis* is relatively insensitive to fire (Glendening and Paulsen 1955) and drought (Archer 1989). The 27% rise in CO_2 concentration since the beginning of the 19th century may similarly have contributed to more abundant *Prosopis* by stimulating seedling growth rates or reducing the amount of resources that the legume required to grow until seedlings were largely uncoupled from competition with neighboring grasses and the primary causes of mortality. The effect of rising CO_2 concentration on *P. glandulosa* on C_4 grasslands may have been particularly great if benefits to plant growth were expressed preferentially in the C_3 species.

Nitrogen dynamics

Higher CO_2 concentration generally stimulated N_2 fixation of individually grown *P. glandulosa*, but the trend was particulary strong in older, periodically droughted plants (Fig. 5). We assumed in estimating N_2 fixation by *P. glandulosa* that the $^{15}N/^{14}N$ signature of *S. scoparium* from monocultures was representative of soil N accumulated and metabolized by the legume (Shearer and Kohl 1986). That assumption may have been compromised by temporal variation in $^{15}N/^{14}N$ signature of available soil N (indicated by the 0.3% ^{15}N change of *S. scoparium* from 1989 to 1990) and relative uptake of N by the two species (suggested by the higher percentage of ^{15}N of *P. glandulosa* than *S. scoparium* in several mixtures). It seems unlikely, however, that any resulting bias in our estimates was systematically related to CO_2 concentration or would negate the generally positive effect of higher CO_2 concentration on N_2 fixation by *P. glandulosa*.

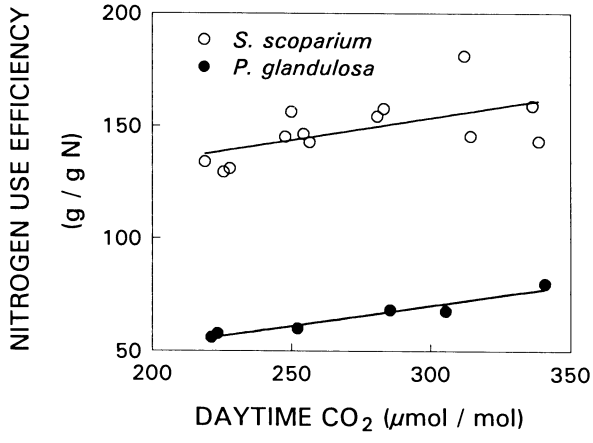

FIG. 8. Plant nitrogen use efficiency (the ratio of cumulative biomass production to total nitrogen accretion) of periodically droughted plants of *Schizachyrium scoparium* grown in monocultures ($n = 6$) and mixtures with *Prosopis glandulosa* ($n = 7$) and individually grown *P. glandulosa* ($n = 6$) across a daytime CO_2 concentration gradient. Lines are linear regressions of nitrogen use efficiency for *S. scoparium* ($r^2 = 0.35$, $P = .03$) and *P. glandulosa* ($r^2 = 0.94$, $P = .001$) on CO_2 concentration.

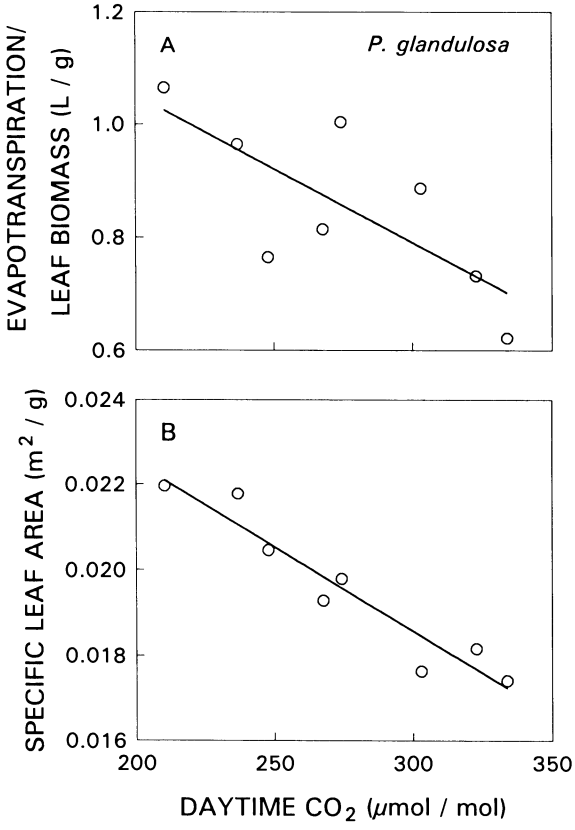

FIG. 9. (A) Apparent transpiration per unit leaf biomass (the ratio of evapotranspiration from 18 April to 15 May 1990 to leaf biomass on 16 May 1990), and (B) specific leaf area in May 1990 of individuals of *P. glandulosa* from monospecific plantings (n = 8 plants) grown across a daytime CO_2 concentration gradient. Water was added weekly to restore soils to field capacity. Lines are linear regression equations (A, $r^2 = 0.56$, $P = .03$; B, $r^2 = 0.91$, $P = .002$).

Higher CO_2 concentration also reduced the amount of plant N that *P. glandulosa* required per unit of growth in monoculture, but increasing CO_2 concentration had a similar absolute effect on NUE of the C_4 *S. scoparium* (Fig. 8). The efficiency with which N is used to produce biomass is a function of photosynthesis or biomass accumulation per unit leaf N, the fraction of plant N incorporated in leaves, and N loss to turnover (e.g., Berendse and Elberse 1990). In *P. glandulosa,* NUE increased because higher CO_2 concentration increased biomass gain per unit leaf N. Biomass produced per leaf N accretion is one measure of the N cost of C assimilation that incorporates effects of leaf N turnover. By this index, NUE of periodically droughted *P. glandulosa* in monocultures increased 40% with the 55% increase in CO_2 concentration from 220 to 340 μmol/mol. Similar relative changes in A and CO_2 concentration (Fig. 1B) and the absence of changes in leaf N per unit area in well-watered *P. glandulosa* also are indicative of a near proportional increase in C gain per unit leaf N and CO_2 concentration. The fraction of plant N invested in leaves and aboveground N turnover of *P. glandulosa* were not altered by CO_2 concentration, so the ratio of biomass production to cumulative N accretion, a measure of whole-plant NUE that integrates production per unit plant N and N turnover, also increased 40% in *P. glandulosa* monocultures from 220 to 340 μmol/mol CO_2 (Fig. 8).

Water use efficiency

Effects of higher CO_2 concentration on plant WUE were preferentially expressed in the C_3 *P. glandulosa.* Stomatal conductance of *S. scoparium* declined proportionally less and instantaneous measurements of intrinsic WUE (A/g) increased proportionally more than CO_2 concentration (Fig. 2), but whole-plant WUE of the C_4 grass did not respond to CO_2 concentration (Fig. 10). Both leaf gas exchange and C isotope analyses indicated that leaf c_i/c_a of well-watered and periodically droughted *P. glandulosa* was conservative across subambient CO_2 concentration, as it is in other C_3 species (Polley et al. 1993). Leaf A/g of the shrub thus increased by the same relative fraction as CO_2 concentration whether grown in monoculture or mixture with the C_4 grass (Fig. 2). The ratio of biomass produced by *P. glandulosa* in monoculture to evapotranspiration, a measure of whole-plant WUE, increased by a similar fraction (67%) as CO_2 concentration from 220 to 340 μmol/mol (Fig. 10).

Higher WUE may have benefited establishing *Prosopis* seedlings in arid areas by rendering the shrub better able to survive periods of water deprivation. There is correlative evidence that higher WUE is positively associated within and across species with growth or survival in dry habitats (Ehleringer and Cooper 1988). DeLucia and Heckathorn (1989) and DeLucia and Schlesinger (1991), however, questioned the impor-

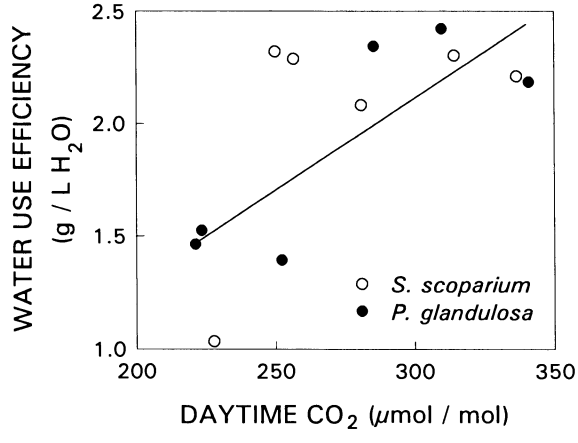

FIG. 10. Apparent water use efficiency (cumulative biomass divided by water lost to evapotranspiration) of *S. scoparium* (n = 6) and *P. glandulosa* (n = 6) monocultures across a daytime CO_2 concentration gradient. The line is a linear regression of water use efficiency for *P. glandulosa* ($r^2 = 0.69$, $P = .04$) on CO_2 concentration.

tance of high WUE to plant growth in arid environments by arguing that traits associated with a higher WUE (at a given CO_2 concentration) entail costs that are otherwise disadvantageous in competitive, water-limited environments. Further, plant success in arid environments partially depends on traits that are not necessarily associated with WUE, including the ability to capture soil water or maintain high turgor pressures as tissue water contents decline.

There are important differences, however, between an increase in WUE at higher CO_2 concentration and the higher WUE that typically occurs at a single CO_2 concentration when soil or atmospheric water content declines. In the latter case, higher WUE often is associated with reduced stomatal conductance, c_i, and A (Fischer and Turner 1978, DeLucia and Schlesinger 1991). But the increase in C_3 WUE at higher CO_2 concentration may result largely or, as in *P. glandulosa,* almost totally from an increase in c_i and photosynthesis with a minimal reduction in stomatal conductance and transpiration per unit leaf area. At higher CO_2 concentration, the increase in WUE thus may be positively correlated with growth. To the extent that increased growth permits greater exploration of soil for water and more effective osmotic regulation, the CO_2 concentration driven increase in WUE will be associated with increased water uptake, greater total transpiration, and a slower decline in leaf water potentials. Leaf water potentials generally decline more slowly and to less negative values in plants grown at elevated than current CO_2 concentration (Sionit et al. 1981, Paez et al. 1983, Rogers et al. 1984). There also is evidence that some plants grown at elevated CO_2 concentration maintain higher turgor pressures during drought (Sionit et al. 1981).

CO_2 concentration and competition

Competitive effects of *S. scoparium* on *P. glandulosa* were evident in both well-watered and periodically droughted treatments as lower biomass production and N accretion by mixture- than monoculture-grown *P. glandulosa* (Table 1). The C_4 grass also reduced or eliminated in competing *P. glandulosa* the increase in N_2 fixation, NUE, and belowground biomass that occurred at higher CO_2 concentration in individually grown seedlings of the C_3 shrub. Others have found that the response of individual species to CO_2 concentration is sensitive to the presence and traits of neighboring plants (Bazzaz and McConnaughay 1992). Results from studies in controlled environments are thus difficult to extrapolate to the field where environmental conditions and the identities, sizes, growth rates, and other traits of competing plants may vary.

In this experiment, *S. scoparium* and *P. glandulosa* were planted simultaneously, watered to maintain soil moisture within a limited range, and grown in a limited rooting volume (210 L) for a short time. In the field, there are fewer restrictions on rooting volume or depth, water and N availabilities vary spatially and temporally, and the spatial and temporal patterns of resource capture by woody plants and grasses may differ. Here, more deeply rooted, potentially taller, N_2-fixing seedlings of *P. glandulosa* sometimes rapidly escape competition with neighboring grasses (Brown and Archer 1989). Environmental and other variables that affected the growth of C_4 grasses thus likely influenced competitive interactions between grasses and *P. glandulosa* and the rapidity and extent to which establishing seedlings of *P. glandulosa* responded to rising CO_2 concentration. Possible shifts in the genetic composition of *P. glandulosa* populations during the last 150 yr may also have affected the species' response to CO_2 concentration. The global increase in atmospheric CO_2 concentration to present, however, is one factor that across landscapes and physiographic regions potentially favored a greater increase in growth of *Prosopis* than C_4 grasses.

Acknowledgments

Mark Dumesnil and Anne Gibson assisted in data collection and processing and in figure preparation. Rod Bovey supplied mesquite seed, and B. B. McInteer of Isotope Services analyzed C and N isotopes in plants. R. J. Ansley, R. W. Bovey, K. Owens, D. Pantone, and O. W. Van Auken provided helpful reviews of the manuscript.

Literature Cited

Allen, L. H., Jr., E. C. Bisbal, K. J. Boote, and P. H. Jones. 1991. Soybean dry matter allocation under subambient and superambient levels of carbon dioxide. Agronomy Journal **83**:875–883.

Archer, S. 1989. Have southern Texas savannas been converted to woodlands in recent history? American Naturalist **134**:545–561.

Baker, J. T., L. H. Allen, Jr., and K. J. Boote. 1990. Growth and yield responses of rice to carbon dioxide concentration. Journal of Agricultural Science, Cambridge **115**:313–320.

Bazzaz, F. A., and R. W. Carlson. 1984. The response of plants to elevated CO_2. I. Competition among an assemblage of annuals at two levels of soil moisture. Oecologia (Berlin) **62**:196–198.

Bazzaz, F. A., and K. D. M. McConnaughay. 1992. Plant–plant interactions in elevated CO_2 environments. Australian Journal of Botany **40**:547–563.

Berendse, F., and W. T. Elberse. 1990. Competition and nutrient availability in heathland and grassland ecosystems. Pages 93–116 *in* J. B. Grace and D. Tilman, editors. Perspectives on plant competition. Academic Press, San Diego, California, USA.

Bogusch, E. R. 1952. Brush invasion in the Rio Grande plain of Texas. Texas Journal of Science **4**:85–91.

Brown, J. H., and E. J. Heske. 1990. Control of a desert–grassland transition by a keystone rodent guild. Science **250**: 1705–1707.

Brown, J. R., and S. Archer. 1987. Woody plant seed dispersal and gap formation in a North American subtropical savanna woodland: the role of domestic herbivores. Vegetatio **73**:73–80.

Brown, J. R., and S. Archer. 1989. Woody plant invasion of grasslands: establishment of honey mesquite (*Prosopis glandulosa* var. *glandulosa*) on sites differing in herbaceous biomass and grazing history. Oecologia (Berlin) **80**:19–26.

Buffington, L. C., and C. H. Herbel. 1965. Vegetational changes on a semidesert grassland range from 1858 to 1963. Ecological Monographs **35**:139–164.

Bush, J. K., and O. W. Van Auken. 1990. Growth and survival of *Prosopis glandulosa* seedlings associated with shade and herbaceous competition. Botanical Gazette **151**: 234–239.

Delmas, R. J., J.-M. Ascencio, and M. Legrand. 1980. Polar ice evidence that atmospheric CO_2 20,000 yr BP was 50% of present. Nature **284**:155–157.

DeLucia, E. H., and S. A. Heckathorn. 1989. The effect of soil drought on water-use efficiency in a contrasting Great Basin desert and Sierran Montane species. Plant, Cell and Environment **12**:935–940.

DeLucia, E. H., and W. H. Schlesinger. 1991. Resource-use efficiency and drought tolerance in adjacent Great Basin and Sierran plants. Ecology **72**:51–58.

Ehleringer, J. R., and T. A. Cooper. 1988. Correlations between carbon isotope ratio and microhabitat in desert plants. Oecologia (Berlin) **76**:562–566.

Farquhar, G. D., M. H. O'Leary, and J. A. Berry. 1982. On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. Australian Journal of Plant Physiology **9**:121–137.

Fisher, R. A., and N. C. Turner. 1978. Plant productivity in the arid and semiarid zones. Annual Review of Plant Physiology **19**:277–317.

Glendening, G. E. 1952. Some quantitative data on the increase of mesquite and cactus on a desert range in southern Arizona. Ecology **33**:319–328.

Glendening, G. E., and H. A. Paulsen, Jr. 1955. Reproduction and establishment of velvet mesquite as related to invasion of semidesert grasslands. United States Department of Agriculture, Forest Service Technical Bulletin **1127**.

Hari, P., and H. Arovaara. 1988. Detecting CO_2 induced enhancement in the radial increment of trees. Evidence from northern timber line. Scandanavian Journal of Forest Research **3**:67–74.

Hastings, J. R., and R. M. Turner. 1965. The changing mile. University of Arizona Press, Tucson, Arizona, USA.

Huckabee, J. W., Jr., D. R. Thompson, J. C. Wyrick, and E. G. Paulat. 1977. Soil Survey Bell County Texas. United States Department of Agriculture, Soil Conservation Service, Washington, D.C., USA.

Idso, S. B. 1989. Carbon dioxide and global change: earth in transition. IBR, Tempe, Arizona, USA.

Johnson, H. B., and H. S. Mayeux, Jr. 1990. *Prosopis glandulosa* and the nitrogen balance of rangelands: extent and occurrence of nodulation. Oecologia (Berlin) **84**:176–185.

Johnson, H. B., H. W. Polley, and H. S. Mayeux. 1993. Increasing CO_2 and plant–plant interactions: effects on natural vegetation. Vegetatio **104/105**:157–170.

Johnston, M. C. 1963. Past and present grasslands of southern Texas and northeastern Mexico. Ecology **44**:456–466.

Keeling, C. D., R. B. Bacastow, A. F. Carter, S. C. Piper, T. P. Whorf, M. Heinmann, W. G. Mook, and H. Roeloffzen. 1989. A three-dimensional model of atmospheric CO_2 transport based on observed winds. 1. Analysis of observational data. Pages 165–236 *in* D. H. Peterson, editor. Aspects of climate variability in the Pacific and the western Americas. Geophysical Monograph 55. American Geophysical Union, Washington, D.C., USA.

LaMarche, V. C., Jr., D. A. Graybill, H. C. Fritts, and M. R. Rose. 1984. Increasing atmospheric carbon dioxide: tree ring evidence for growth enhancement in natural vegetation. Science **225**:1019–1021.

Marino, B. D., and M. B. McElroy. 1991. Isotopic composition of atmospheric CO_2 inferred from carbon in C_4 plant cellulose. Nature **349**:127–131.

Mayeux, H. S., H. B. Johnson, and H. W. Polley. 1991. Global change and vegetation dynamics. Pages 62–74 *in* L. F. James, J. O. Evans, M. H. Ralphs, and R. D. Child, editors. Noxious range weeds. Westview, Boulder, Colorado, USA.

Mayeux, H. S., H. B. Johnson, H. W. Polley, M. J. Dumesnil, and G. A. Spanel. 1993. A controlled environment chamber for growing plants across a subambient CO_2 gradient. Functional Ecology **7**:125–133.

Meyer, R. E., and R. W. Bovey. 1982. Establishment of honey mesquite and huisache on a native pasture. Journal of Range Management **35**:548–550.

Neftel, A., E. Moor, H. Oeschger, and B. Stauffer. 1985. Evidence from polar ice cores for the increase in atmospheric CO_2 in the past two centuries. Nature **315**:45–57.

Neftel, A., H. Oeschger, T. Staffelbach, and B. Stauffer. 1988. CO_2 record in the Byrd ice core 50,000 years BP. Nature **331**:609–611.

Neilson, R. P. 1986. High-resolution climatic analysis and southwest biogeography. Science **232**:27–34.

Paez, A., H. Hellmers, and B. R. Strain. 1983. CO_2 enrichment, drought stress and growth of Alaska pea plants (*Pisum sativum*). Physiologia Plantarum **58**:161–165.

Parkinson, K. J. 1985. A simple method for determining the boundary layer resistance in leaf cuvettes. Plant, Cell and Environment **8**:223–226.

Patterson, D. T., and E. P. Flint. 1990. Implications of increasing carbon dioxide and climate change for plant communities and competition in natural and managed ecosystems. Pages 83–110 *in* B. A. Kimball, editor. Impact of carbon dioxide, trace gases, and climate change on global agriculture. American Society of Agronomy, Madison, Wisconsin, USA.

Paulsen, H. A., Jr. 1950. Mortality of velvet mesquite seedlings. Journal of Range Management **3**:281–286.

Polley, H. W., H. B. Johnson, B. D. Marino, and H. S. Mayeux. 1993. Increase in C_3 plant water-use efficiency and biomass over glacial to present CO_2 concentrations. Nature **361**:61–64.

Polley, H. W., H. B. Johnson, and H. S. Mayeux. 1992*a*. Growth and gas exchange of oats (*Avena sativa*) and wild mustard (*Brassica kaber*) at subambient CO_2 concentrations. International Journal of Plant Sciences **153**:453–461.

Polley, H. W., H. B. Johnson, and H. S. Mayeux. 1992*b*. Determination of root biomasses of three species grown in a mixture using stable isotopes of carbon and nitrogen. Plant and Soil **142**:97–106.

Raynaud, D., and J. M. Barnola. 1985. An Antarctic ice core reveals atmospheric CO_2 variations over the past few centuries. Nature **315**:309–311.

Risser, P. G., E. C. Birney, H. C. Blocker, S. W. May, W. J. Parton, and J. A. Weins. 1981. The true prairie ecosystem. Hutchinson Ross, Stroudsburg, Pennsylvania, USA.

Roeske, C. A., and M. H. O'Leary. 1984. Carbon isotope effects on the enzyme-catalyzed carboxylation of ribulose bisphosphate. Biochemistry **23**:6275–6284.

Rogers, H. H., N. Sionit, J. D. Cure, J. M. Smith, and G. E. Bingham. 1984. Influence of elevated carbon dioxide on water relations of soybeans. Plant Physiology **74**:233–238.

Sala, O. E., W. J. Parton, L. A. Joyce, and W. K. Lauenroth. 1988. Primary production of the central grassland region of the United States. Ecology **69**:40–45.

Schlesinger, W. H., J. F. Reynolds, G. L. Cunningham, L. F. Huenneke, W. M. Jarrell, R. A. Virginia, and W. G. Whitford. 1990. Biological feedbacks in global desertification. Science **247**:1043–1048.

Scifres, C. J., J. H. Brock, and R. R. Hahn. 1971. Influence of secondary succession on honey mesquite invasion in north Texas. Journal of Range Management **24**:206–210.

Seastedt, T. R., J. M. Briggs, and D. J. Gibson. 1991. Controls of nitrogen limitation in tallgrass prairie. Oecologia (Berlin) **87**:72–79.

Shearer, G., and D. H. Kohl. 1986. N_2-fixation in field settings: estimations based on natural ^{15}N abundance. Australian Journal of Plant Physiology **13**:699–756.

Shearer, G., D. H. Kohl, R. A. Virginia, B. A. Bryan, J. L.

Skeeters, E. T. Nilsen, M. R. Sharifi, and P. W. Rundel. 1983. Estimates of N_2-fixation from variation in the natural abundance of ^{15}N in Sonoran desert ecosystems. Oecologia (Berlin) **56**:365–373.

Sionit, N., B. R. Strain, H. Hellmers, and P. J. Kramer. 1981. Effects of atmospheric CO_2 concentration and water stress on water relations of wheat. Botanical Gazette **142**:191–196.

Smeins, F. E. 1983. Origin of the brush problem—a geographical and ecological perspective of contemporary distributions. Pages 5–16 *in* Proceedings of the Brush Management Symposium. Texas Tech University Press, Lubbock, Texas, USA.

Smith, D. A., and E. M. Schmutz. 1975. Vegetation change on protected versus grazed desert grassland ranges in Arizona. Journal of Range Management **28**:453–458.

Van Auken, O. W., and J. K. Bush. 1989. *Prosopis glandulosa* growth: influence of nutrients and simulated grazing of *Bouteloua curtipendula*. Ecology **70**:512–516.

Van Auken, O. W., and J. K. Bush. 1990. Importance of grass density and time of planting on *Prosopis glandulosa* seedling growth. Southwestern Naturalist **35**:411–415.

von Caemmerer, S., and G. D. Farquhar. 1981. Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. Planta **153**:376–387.

Weisberg, S. 1980. Applied linear regression. John Wiley & Sons, New York, New York, USA.

Wright, H. A., S. C. Bunting, and L. F. Neuenschwander. 1976. Effect of fire on honey mesquite. Journal of Range Management **29**:467–471.

York, J. C., and W. A. Dick-Peddie. 1969. Vegetation changes in southern New Mexico during the past hundred years. Pages 157–166 *in* W. G. McGinnies and B. J. Goldman, editors. Arid lands in perspective. University of Arizona Press, Tucson, Arizona, USA.