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Influence of mesquite (*Prosopis glandulosa*) on soil nitrogen and carbon development: Implications for global carbon sequestration

Dieter Geesing, Peter Felker* & Ralph L. Bingham

Center for Semi-Arid Forest Resources, Caesar Kleberg Wildlife Institute, Campus Box 218, Texas A & M University, Kingsville, TX 78363 U.S.A.

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The genus *Prosopis* contains many N-fixing species throughout the world's semi-arid regions. Previous work with *Prosopis glandulosa* found that small young trees obtained most of their N from N-fixation, while mature trees that had accumulated 1.3 Mg N ha^{-1} in the soil beneath their canopy derived a much smaller percentage of their N from N-fixation. This work examined the percentage of nitrogen derived from nitrogen-fixation (%Ndfa) and soil development as a function of tree size on seven Texas sites. The tree basal diameters ranged from 3.2 cm to 76.4 cm. Leaf and trunk core samples were taken from trees to determine N, P, and natural abundance ratios of $^{15}\text{N}/^{14}\text{N}$. Soil samples were taken 75 cm from the trunk and outside the influence of the tree canopy. Soil values for organic C, available P, pH, NO_3 , NH_4 and $^{15}\text{N}/^{14}\text{N}$ were measured. A comparison of $^{15}\text{N}/^{14}\text{N}$ from background soil parent material and the leaves or trunk was used to estimate the percentage of N derived from N fixation. Increases under canopy over background in soil C, N, and P were significantly correlated with trunk diameter and had maximum values of 17.7 Mg ha^{-1} for C, 4.4 Mg ha^{-1} for N and 13 kg ha^{-1} for available P. The soil C/N ratio was negatively correlated with trunk diameter. Leaf concentrations of N and P increased with trunk diameter. The soil N was significantly correlated with leaf N and P, the soil P was significantly correlated with leaf P. The $^{15}\text{N}/^{14}\text{N}$ ratios of the soil were highly correlated with the $^{15}\text{N}/^{14}\text{N}$ of the leaves, but were not correlated with the $^{15}\text{N}/^{14}\text{N}$ ratios of trunk wood. The trunk wood had a much higher % Ndfa (75%) than the leaves (25%). This difference was to be expected, since the trunk represents the oldest tissues (when the trees obtained most of its N from fixation) while the leaves represent the current years growth and is coupled with soil $^{15}\text{N}/^{14}\text{N}$ values. The %Ndfa of the leaves declined significantly with soil nitrate levels as would be expected since the N-fixation process is strongly inhibited by available N. If an increase of 2 Mg ha^{-1} soil C could be achieved on the subtropical, semi-arid areas to which *Prosopis* and *Acacia* are adapted, $6.2 \times 10^9 \text{ Mg}$ of carbon would be sequestered. As projected 2010 carbon emissions are $8.5 \times 10^9 \text{ Mg}$ of carbon, management of tree legumes in arid regions has significant potential to positively impact global C sequestration.

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Keywords: natural abundance $^{15}\text{N}/^{14}\text{N}$; agroforestry; nitrogen fixation; semi-arid; algarrobo; sustainable agriculture

*Current address: Peter Felker, Facultad de Agronomía y Agroindustrias, Secretaría de Producción y Medio Ambiente, 514 La Plata, (4200) Santiago del Estero, Argentina. E-mail: Peter_Felker@hotmail.com

Introduction

The 25% of the earth's surface that is subtropical and semi-arid is often dominated by nitrogen-fixing trees of the genera *Acacia* and *Prosopis*. The soils of these ecosystems typically range from 0.2 to 0.6 g N per kg soil and from 2 to 7 g C per kg soil (Virginia & Jarrell, 1983; Rundel *et al.*, 1982; Tiedemann & Klemmedson, 1973; Shankar *et al.*, 1976; East & Felker, 1993) and have the lowest organic C and N contents of any soil ecosystem (Jenny, 1944). There has been considerable controversy concerning the management of these arid ecosystems, with some suggesting that woody legumes must be eliminated to pave the way for herbaceous vegetation for livestock grazing (Fisher *et al.*, 1977), while others have suggested possibilities of arid forestry for lumber or silvopastoral systems to provide trees for livestock browse and soil improvement (Felker, 1998). Part of the management problems of arid woody vegetation and soils stems from the intense human and animal pressure on these ecosystems for fuelwood and forage. Sene (1996) estimates that 500 million people live in these drylands and are among the world's poorest communities lacking the basic necessities of food security, inadequate access to drinking water and inadequate sanitation.

While water was deemed to be the unquestioned limit to productivity of arid ecosystems by some workers (Hadley & Szarek, 1981), more comprehensive analyses have suggested that N may be more limiting to sustainable productivity than water (Woodmansee, 1978; Felker, 1998). Due to the importance of organic matter on cation exchange capacity, water infiltration rates, soil bulk density and porosity, it is possible that soil organic carbon may be more important to sustainable plant productivity than water or nitrogen. Charreau & Vidal (1965) and Dancette & Poulain (1969) have stressed that the positive effect of *Faidherbia albida* on soil fertility in the African Sahel is probably more attributable to improvements in organic carbon than any other feature. Breman & Kessler (1997) concur with this basic premise stating '[The] extremely poor soil fertility, the extreme aridity of a long dry season causing fragility of perennial plant communities and rapid turnover of organic matter are more important constraints to rural development than water scarcity [in the Sahel]'.

Not only is soil organic carbon important for rural economic development, but the sequestration of organic carbon on such extensive areas of the world's semi-arid regions could be significant in the world carbon budget and global warming. Recent analyses of carbon storage in forestry (Alig *et al.*, 1997; Swisher, 1997) for use in Global Environment Facility assessment of world carbon stocks have not considered carbon storage from forestry of arid lands.

Build up of soil organic carbon is only possible with additions of both organic matter and nitrogen. Nitrogen additions are essential to decrease the C/N ratio and facilitate the decomposition of high C/N containing dry matter such as grasses. As soil organic matter degradation is much more rapid above 35°C than at lower temperatures (Jenny, 1944), and as savanna trees decrease soil temperatures by 5–12°C (Belsky *et al.*, 1993), the shading effect of trees helps build soil organic matter.

There has been controversy in the literature regarding the cause of the islands of fertility surrounding nitrogen fixing trees in arid regions (Scholes & Archer, 1997; Belsky *et al.*, 1993; Weltzin & Coughenour, 1990). Despite the fact that trees such as *Prosopis* can fix N, some workers (Garcia-Moya & McKell, 1970; Barth & Klemmedson, 1982) have suggested that the increased nutrients under the canopies is simply a redistribution of nutrients from deeper in the profile and outside the canopy.

However, Rundel *et al.* (1982) conclusively demonstrated that *Prosopis glandulosa* in the California desert fixed about 30 kg N ha⁻¹ year⁻¹ which is about 15 times the annual deposition of N in west Texas (Loftis & Kurtz, 1980). Johnson & Mayeux (1990) found nodules on 19 mesquites at five locations in the eastern portions of mesquite's range. Despite the fact that they did not detect nodules on the five more western sites, seedlings grown on soils from the western sites nodulated, indicating the presence of *Prosopis*

rhizobia. Johnson & Mayeux (1990) concluded 'that honey mesquite must be a significant contributor to the nitrogen budget of range ecosystems in south-western United States and Mexico and the genus *Prosopis* is likely to play an important role on a global scale'.

In a study to identify whether factors such as thinning, pruning, or P fertilization influenced N-fixation at the stand level of mature *Prosopis* trees, Villagra & Felker (1997) made the serendipitous discovery that the percent of N derived from nitrogen-fixation in the entire tree was inversely proportional to tree size. Since the larger trees had accumulated 1200 kg ha⁻¹ more N than soils outside their canopy (East & Felker, 1993) and since N-fixation is repressed by available N, this suggested that young trees just colonizing an infertile site obtained most of their N from fixation, while mature trees that had accumulated large quantities of N obtained most of their N from the soil. A similar inhibition of nitrogen-fixation by available N has also been reported by Dommergues (1995).

The transition of active N-fixation in young trees to significantly less N-fixation in older trees observed by Villagra & Felker (1997) was only obtained on one site. Thus, this study sought to confirm this finding on diverse sites in Texas. In addition, this study aimed to find out what threshold levels of soil variables might be related with declines in N-fixation of mature trees and if soil threshold levels would be correlated with leaf and stem nutrient levels.

A second important component of this study was to estimate what increases in soil P and organic N and C could be related to the development of mature nitrogen-fixing trees such as *Prosopis*. Using estimates of soil C sequestration per tree, percent canopy cover and estimates of land area to which semi-arid tree legumes are adapted, it is possible to estimate the total global C sequestration from tree legumes in semi-arid regions. This estimated total C sequestration will be compared with the targeted C reductions to decrease global warming.

Methods

This study examined correlations between concentrations of N, P, organic C and natural abundance ¹⁵N/¹⁴N ratios in the soil and N, P, ¹⁵N/¹⁴N ratios in the trunk and leaves of small (< 7 cm basal diameter), medium (7 to 38 cm basal diameter) and large *Prosopis glandulosa* trees (> 38 cm diameter). Seven sites were chosen in South Texas whose soil families, location and mean annual rainfall are summarized in Table 1. At each site three small, three medium and three large trees were selected. The co-ordinates for the sites were obtained from the Texas Department of Transportation (1994). Soil maps for the sites in Frio, Atascosa and Jim Wells counties were obtained from their respective soil surveys (USDA, 1979, 1980, 1992). The soil description for the Gonzales county site was obtained by oral communication (Wain Fairchild, 1998, pers. comm.) and for the other sites from soil maps available at the Natural Resource Conservation Service (USDA 1977, 1991). The rainfall data were obtained from the Southern Regional Climate Center (1998).

In May 1997, a 20-cm deep soil subsample was taken 75 cm from the trunk of each tree in all four cardinal directions. A mature leaf subsample was taken below the growing tips from all four cardinal directions, as recommended for forest trees by Weetmann & Wells (1990). For each tree, the subsamples were then bulked to form a single sample per tree.

To reduce the cost of the natural abundance ¹⁵N/¹⁴N analyses some pooling of samples was necessary. All soil samples were pooled for the largest trees of similar sizes at each site, as were plant samples. Samples were pooled likewise for all three small trees at each site. In contrast, the samples for the three medium-size trees at each site were not pooled in order to be able to test for site differences. The range of diameters for the three medium-size trees at any site did not exceed 9 cm. Thus, 11 sets (soil, leaf and

Table 1. Background site characteristics for *Prosopis* field plots in South Texas (May 1997)

Site (Country)	Soil	Rainfall 30-year mean (1961–90) (mm)	Rainfall (05/1996– 04/1997) (mm)
Frio 98°55'W 28°50'N	Fine-loamy, mixed, hyperthermic Aridic Haplustalfs; Fine, montmorillonitic, hyper- thermic Aridic Paleustalfs	645	568
Live Oak 98°05'W 28°30'N	Fine-loamy, mixed, hyperthermic Typic Calcisustolls	701	737
Atascosa (West) 98°25'W 28°45'N	Fine, mixed, hyperthermic Pachic and Udic Paleustalfs	698	579
Atascosa (East) 98°20'W 28°55'N	Fine, mixed, hyperthermic Pachic and Udic Paleustalfs	698	579
Gonzales 97°45'W 29°20'N	Fine smectitic thermic Oxyaquic Vertic Paleustalfs	850	929
Kleberg 97°55'W 27°20'N	Fine-loamy, mixed, hyperthermic Aquic Paleustalfs; loamy, mixed, hyperthermic Arenic Paleustalfs	701	647
Jim Wells 98°08'W 27°32'N	Fine-loamy, mixed, hyperthermic Mollic Albaqualfs; fine-loamy, mixed, hyperthermic Typic Arguistolls	706	525

wood) of samples for large trees, seven sets for small trees and 21 sets for medium trees were obtained and a total of 39 sets of tree and soil data was used for regression analyses to investigate correlations between soil and tree parameters.

Villagra & Felker (1997) found that total tree biomass was correlated with weighted tree $\delta^{15}\text{N}$ ($\delta^{15}\text{N} = {}^{15}\text{N}/{}^{14}\text{N}$ ratio expressed as parts per thousand; weighted tree $\delta^{15}\text{N}$ is the sum of the $\delta^{15}\text{N}$ of branches, stems, leaves and trunk multiplied by their respective percentage of the total tree biomass). Furthermore, trunk $\delta^{15}\text{N}$ had the greatest correlation of all factors measured with the whole tree $\delta^{15}\text{N}$. Thus, we used a core of the trunk as a surrogate of weighted $\delta^{15}\text{N}$ per tree. To ensure there was no effect of $\delta^{15}\text{N}$ or % N as a function of stem cross section, we examined the $\delta^{15}\text{N}$ of samples taken at the centre and just inside the bark of a 40 cm trunk section. No significant differences were observed between the two locations (df. = 6, $t = -1.93$, $p = 0.103$). To minimize possible age $\delta^{15}\text{N}$ and % N tree ring effects, a 12-mm diameter hand drill was used to obtain a wood sample from just inside the bark to the centre in the trunk.

We used the natural $\delta^{15}\text{N}$ method pioneered by Shearer & Kohl (1986) to estimate the percentage of nitrogen derived from the atmosphere. However, this technique often

suffers from the ability to choose a suitable non-fixing reference plant. Villagra & Felker (1997) observed high variability in $\delta^{15}\text{N}$ values of the reference plants but low variability in $\delta^{15}\text{N}$ values of the soils of their study area. Thus, in our study we used soil $\delta^{15}\text{N}$ reference samples for the calculation of percent nitrogen derived from atmosphere (%Nd_{fa}). The reference soil samples were taken from outside the influence of mesquite canopy, but on the same soil parent material, in compliance with the suggestions made by Villagra & Felker (1997).

The percentage of %Nd_{fa} was estimated by using the expression (Shearer & Kohl, 1986):

$$\frac{\delta^{15}\text{N}_r - \delta^{15}\text{N}_p}{\delta^{15}\text{N}_r - \delta^{15}\text{N}_a} \times 100 = \% \text{Nd}_{fa}$$

where $\delta^{15}\text{N}_r$ is for the reference soil material, $\delta^{15}\text{N}_p$ is for the fixing plant, and $\delta^{15}\text{N}_a$ is the $\delta^{15}\text{N}$ value of leaves of young *Prosopis glandulosa* grown hydroponically with N-free medium over 2 years. This value was estimated to be -1.7‰ . The natural abundance $\delta^{15}\text{N}$ analyses were done through contract with the Stable Isotope Ratio Facility for Environmental Research at the University of Utah in Salt Lake City.

Wood and leaf samples were dried for 8 days at 43.3°C and then ground on a Wiley Mill to pass a 40-mesh sieve (Jones & Case, 1990). Soil samples were air-dried for 12 days at room temperature, then ground to pass a 0.5-mm sieve. Leaf and wood phosphorus were measured using the colorimetric method of Murphy & Riley (1962) at 714 nm. For the digestion 0.2 g leaf material or 0.5 g wood material was used in 10 ml concentrated nitric acid in accordance with the method of Havlin & Soltanpour (1980). To accommodate the low N and P concentrations in the wood, the wood digest was only brought up to 35 ml volume with distilled water while the leaf samples were brought up to 50 ml volume. For the same reason 8.0 ml of this dilution was taken for wood analysis while 3.0 ml was taken for leaf analysis.

Sodium bicarbonate extractable soil P was determined colorimetrically at 714 nm using the method of Olsen & Sommers (1982). Due to low soil P concentrations, the ratio of soil to extracting solution was increased from 5g:100 ml to 7.5g:50 ml and the volume of the aliquot taken for analysis was increased from 5.0 to 10.0 ml.

Soil, wood and leaf N was determined using a modification of the salicylate-dichloroisocyanurate colorimetric method at 660 nm (Felker, 1977; Cline *et al.*, 1986) after Kjeldahl digestion in general accordance with the recommendations by Fleck & Munro (1965). For soil, 1.5 g material was digested in 12 ml H₂SO₄ with preformulated Kjeldahl catalyst (K₂SO₄/CuSO₄·5H₂O/Se) at 375°C for 90 min. Leaf (0.2 g) and wood material (0.4g) were digested in the same mixture at 420°C for 50 min. Soil pH was measured using 0.01 M CaCl₂ (McLean, 1982).

Soil nitrate-nitrogen (NO₃⁻-N) and ammonia-nitrogen (NH₄⁺-N) were determined by the Texas A&M University College Station Plant and Soils laboratory after 0.5 M NaCl extraction using an autoanalyser (Markus *et al.*, 1985). Soil organic carbon was analysed using the Walkley-Black titration method (Nelson & Sommers, 1982).

The data were statistically analysed using SAS (1988). A correlation matrix was calculated to identify the variables with the greatest correlation. For the most significant correlations, linear and quadratic regressions were obtained and figures developed.

Fresh biomass estimates were obtained using the equation (El Fadl *et al.*, 1989):

$$\log_{10} (\text{fresh biomass kg}) = 3.827 + 1.052 \times \log_{10} (\text{basal area m}^2).$$

Results

The soil families, location, 30-year mean annual rainfall and 1997 annual rainfall for the sites are presented in Table 1. The texture of soils for four of the seven sites was fine-loamy. The sites ranged 2° (220 km) in latitude and 1°10' (128 km) in longitude. The

Table 2. Soil characteristics under (listed by average diameter of canopy tree) and outside *Prosopis* canopy for seven field plots in South Texas (May 1997). At each site, the samples of small trees (< 7 cm diameter) and of large trees (> 38 cm) were, respectively, pooled. Medium trees (7 to 38 cm) were not pooled. Their values are means

Site Average diameter (cm) per number of observations	C g kg ⁻¹	N g kg ⁻¹	C/N	P mg kg ⁻¹	delta ¹⁵ N ‰	pH	NO ₃ -N mg kg ⁻¹	NH ₄ -N mg kg ⁻¹
Jim Wells								
42.0/1 (3 pooled)	15.7	1.69	9.3	5.2	5.2	7.5	4	8
24.3/3	15.0	1.39	10.9	2.9	7.5	6.5	4	7
5.5/1 (3 pooled)	11.4	1.00	11.4	1.9	5.4	7.1	2	9
outside canopy/1	11.1	0.93	11.9	2.7	6.8	7.5	1	6
Live Oak								
76.4/1 (2 pooled)	13.9	2.21	6.3	7.6	5.1	7.3	2	8
49.3/1	12.9	1.87	6.9	6.6	3.3	8.0	1	5
26.1/3	11.9	1.67	7.2	11.1	6.5	6.0	1	7
5.1/1 (3 pooled)	7.5	1.05	7.1	7.2	7.3	7.8	1	6
outside canopy/1	9.9	0.79	12.5	7.5	4.5	5.9	40	15
Atascosa (West)								
58.5/1 (2 pooled)	12.4	1.79	6.9	21.4	9.8	5.0	11	7
40.4/1	11.1	1.71	6.5	19.9	10.0	4.9	9	10
24.5/3	7.7	0.76	10.4	12.2	6.1	4.7	1	5
6.0/1 (3 pooled)	7.4	0.98	7.6	9.5	7.6	5.7	1	6
outside canopy/1	7.0	0.57	12.3	8.5	3.8	6.0	1	5
Frio								
72.8/1	11.8	1.51	7.8	12.4	8.6	5.8	8	8
42.8/1 (2 pooled)	10.7	1.38	7.8	6.6	8.7	5.9	5	8
31.0/3	8.7	1.07	8.2	3.2	5.9	6.3	1	6
6.23/1 (3 pooled)	8.2	0.89	9.2	2.7	6.0	6.2	1	7
outside canopy/1	8.3	0.99	8.4	2.9	8.5	6.5	1	14

Gonzales								
61-3/1 (3 pooled)	14.9	1.61	9.3	3.2	2.7	4.9	1	12
29-3/3	11.3	1.42	8.0	3.5	5.9	4.9	1	7
3-2/1 (3 pooled)	12.7	1.04	12.2	2.0	4.2	7.7	1	9
outside canopy/1	12.1	0.99	12.2	1.3	5.8	7.8	1	9
Kleberg								
41-2/1 (3 pooled)	12.1	1.59	7.6	13.6	6.2	6.3	1	9
27-2/3	10.3	1.29	8.2	5.0	9.2	5.9	1	6
6-23/1 (3 pooled)	12.5	1.24	10.1	3.5	4.9	7.9	1	5
outside canopy/1	7.2	0.66	10.9	2.9	6.5	5.8	1	5
Atascosa (East)								
59/1	11.4	1.58	7.2	9.4	6.0	5.4	1	14
39-2/1 (2 pooled)	13.9	1.75	7.9	10.9	4.9	5.4	1	17
24-4/3	11.6	1.48	7.8	12.4	6.6	5.2	2	8
3-7/1 (3 pooled)	7.9	0.86	9.2	9.9	5.9	5.1	1	11
outside canopy/1	8.2	0.83	9.9	6.6	8.9	5.5	1	4

Table 3. *Prosopis* plant characteristics listed by average diameter for seven field plots in South Texas (May 1997). The values are derived from pooled samples for small diameter trees (< 7 cm) and from pooled samples for large trees (> 38 cm) of similar size. Samples of medium trees (7 to 38 cm) were not pooled. Their values are means

Site	Leaf N	Leaf P	Leaf $\delta^{15}\text{N}$	Leaf Ndffa	Wood N	Wood P	Wood $\delta^{15}\text{N}$	Wood Ndffa
Average diameter (cm)	%	%	‰	%	%	%	‰	%
number of observations								
Jim Wells								
42.0/1 (3 pooled)	3.44	0.31	3.9	34.1	0.42	0.0091	1.2	65.9
24.3/3	3.08	0.22	3.8	35.7	0.30	0.0060	1.1	67.5
5.5/1 (3 pooled)	2.55	0.22	2.4	51.8	0.31	0.0089	0.2	77.6
Live Oak								
76.4/1 (2 pooled)	3.87	0.27	3.2	21.0	0.35	0.0057	- 3.0	121.1
49.3/1	3.62	0.24	3.1	22.6	0.32	0.0088	- 0.7	83.9
26.1/3	3.06	0.21	3.6	14.5	0.29	0.0067	- 0.3	77.4
5.1/1 (3 pooled)	2.89	0.16	4.0	8.1	0.29	0.0108	1.1	54.8
Atascosa (West)								
58.5/1 (2 pooled)	3.70	0.50	8.3	- 81.8	0.42	0.0081	4.9	- 20.0
40.4/1	3.68	0.31	8.6	- 87.3	0.30	0.0076	2.5	23.6
24.5/3	3.11	0.20	3.6	3.0	0.32	0.0070	0.1	67.9
6.0/1 (3 pooled)	3.22	0.41	4.4	- 10.9	0.32	0.0065	2.5	23.6
Frio								
72.8/1	3.11	0.24	7.3	11.8	0.28	0.0048	- 0.4	87.3
42.8/1 (2 pooled)	3.52	0.26	6.8	16.7	0.32	0.0103	2.7	56.9
31.0/3	2.90	0.15	2.8	56.2	0.30	0.0034	0.6	77.1
6.2/1 (3 pooled)	3.30	0.18	2.4	59.8	0.29	0.0030	- 1.4	97.1

Gonzales

61-3/1 (3 pooled)	3.43	0.23	2.0	50.7	0.33	0.0045	4.4	18.7
29-3/3	3.41	0.27	2.4	45.3	0.29	0.0033	- 0.5	84.4
3-2/1 (3 pooled)	3.06	0.21	5.4	5.3	0.38	0.0125	- 0.9	89.3

Kleberg

41-2/1 (pooled)	3.94	0.23	3.5	36.6	0.32	0.0119	- 1.7	100.0
27-2/3	3.30	0.20	4.8	20.3	0.28	0.0074	- 0.7	87.8
6-23/1 (3 pooled)	3.37	0.22	2.4	50.0	0.27	0.0085	- 1.3	95.1

Atascosa (East)

59/1	3.60	0.27	3.3	52.8	0.28	0.0038	- 0.1	84.9
39-2/1 (2 pooled)	3.37	0.26	3.0	55.7	0.28	0.0059	- 1.2	95.3
24-4/3	3.27	0.22	3.2	53.8	0.27	0.0034	- 0.6	89.6
3-7/1 (3 pooled)	3.56	0.21	2.3	62.3	0.29	0.0090	- 0.3	86.8

mean annual rainfall ranged from a low of 645 mm for the Frio site to 850 mm for the Gonzalez site during 1961–90. On five of the seven sites, the last year's rainfall before sampling was below their mean annual rainfall for 1961–90.

The basic soil characteristics from under and from outside (background) the canopy and the plant characteristics are summarized in Tables 2 and 3, respectively. The range in soil C (7 to 12.1 g kg⁻¹) and N (0.57 to 0.93 g kg⁻¹) for the background soils was greater than for other *Prosopis* sites in Arizona of 2.7 g C kg⁻¹ and 0.24 g N kg⁻¹ (Tiedemann & Klemmedson, 1986) and India of 1.9 g C kg⁻¹ and 0.42 g N kg⁻¹ (Shankar *et al.*, 1976). The C/N ratios were less variable than the absolute values of N and C and the C/N ratios were well within the range of reported C/N ratios for many soils.

Half of the background available soil P values were less than 3 mg kg⁻¹ which put them in agreement with other values of 2.9 mg kg⁻¹ (East & Felker, 1993) and 1.2 to 2.1 mg kg⁻¹ available P (Wightman & Felker, 1990) for other Texas range sites. These values are considerably lower than values of 12 mg kg⁻¹ that are generally considered limiting for annual crops (Olsen & Sommers, 1982). A considerable range in pH of the background soils of 5.5 to 7.8 was observed that should help to generalize the results of this study.

The background soil nitrate-nitrogen (all but one <1 mg kg⁻¹) and ammonium-nitrogen values (4–15 mg kg⁻¹) were low for normal agricultural and forest soils. The mean soil $\delta^{15}\text{N}$ under and outside the canopies were virtually identical and were not significantly ($p = 0.8570$) different. The mean leaf N value of 3.27 ± 0.3 (standard deviation), which is about 20% protein, was high for many arid plants and in contrast to leaf P (mean 0.23 ± 0.68) did not exhibit much variation among sites. The wood N was about 10 times lower than the leaf N, but the wood P was about 36 times lower than the leaf P.

To test for site differences, an analysis of variance was performed using data for the three medium trees at each of the seven sites. Sites were different for the variables diameter ($p = 0.05$), soil N ($p = 0.004$), soil C ($p = 0.0001$), soil C/N ($p = 0.01$), soil P ($p = 0.0005$), soil $\delta^{15}\text{N}$ ($p = 0.0001$), leaf N ($p = 0.04$), leaf P ($p = 0.01$), leaf $\delta^{15}\text{N}$ ($p = 0.005$) and wood P ($p = 0.02$). Surprisingly none of the sites were different for wood N related values [wood N ($p = 0.66$), wood $\delta^{15}\text{N}$ ($p = 0.31$) and wood Ndfa ($p = 0.304$)]. The significant differences among sites for the soil variables should help to generalize the results of this study.

The %Ndfa of the wood and leaves were highly correlated ($r = 0.64024$, $p = 0.0001$). However, paired *t*-tests showed significant differences between the %Ndfa of wood and leaves within each diameter class (large trees: 12.1% Ndfa leaves, 65.2% Ndfa wood, $p = 0.0139$, $n = 11$; medium trees: 32.7% Ndfa leaves, 78.8% Ndfa wood, $p = 0.0001$, $n = 21$; small trees: 32.3% Ndfa leaves, 74.9% Ndfa wood, $p = 0.0166$, $n = 7$). The tendency for decreased %Ndfa in the largest tree size is reminiscent of the work of Villagra & Felker (1997).

Of all correlations examined, those between tree diameter and increase over soil background in soil N, soil C and soil P were the most significant. The linear relationship between these variables is illustrated in Fig. 1. The increase in soil C was also correlated with increase in soil N ($r = 0.70195$, $p = 0.0001$) and P ($r = 0.34776$, $p = 0.0301$). Soil nitrate-nitrogen level was also significantly correlated with tree diameter ($r = 0.362$, $p = 0.02$), but soil ammonium-nitrogen level was not ($r = 0.275$, $p = 0.090$). The fact that these soil values tended to increase with trunk diameter is evidence that the trees did not fortuitously come to occupy an island of fertility. The maximum observed increase under vs. outside the canopy of 17.7 Mg ha⁻¹ for C, 4.4 Mg ha⁻¹ for N and 13.0 kg ha⁻¹ for P (for 20 cm topsoil and assuming a soil bulk density of 1.55) are very significant in economic terms.

The decrease in soil C/N ratio with increasing diameter ($p = 0.0052$) is illustrated in Fig. 2. The decreasing C/N ratio from smaller to larger trees is an indicator of improved soil fertility since small C/N ratios are generally associated with soils of high biological

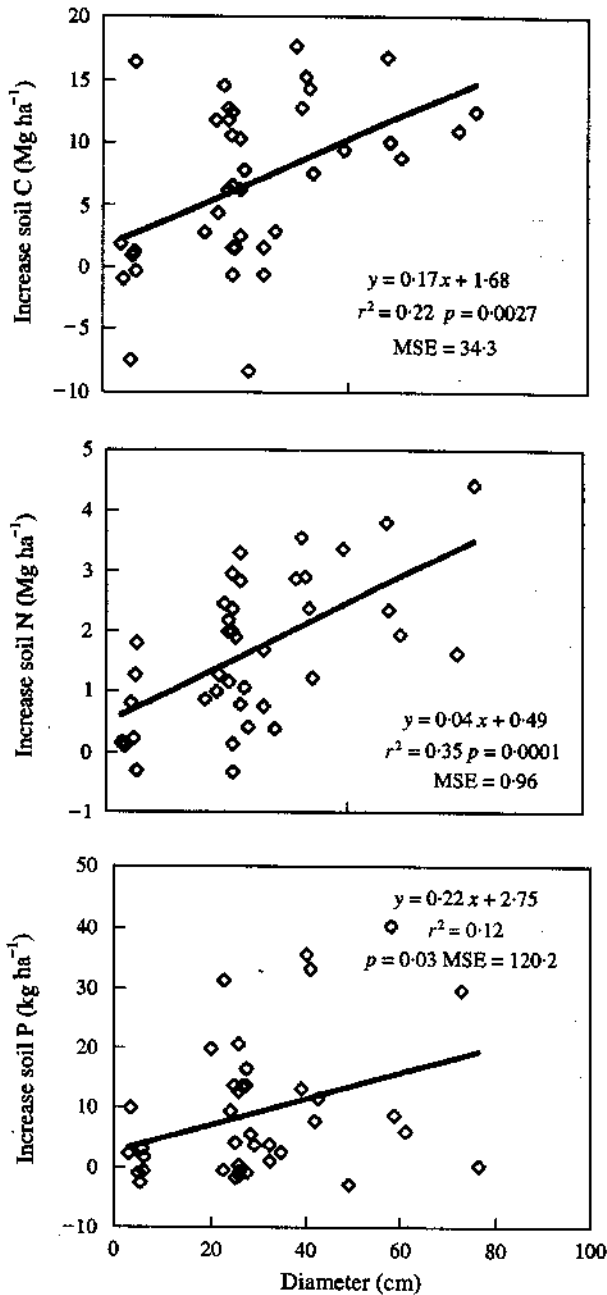


Figure 1. Estimated linear relationship ($n = 39$) between increase per hectare in soil C, soil N and soil P vs. *Prosopis* tree diameter across seven sites in South Texas (May 1997). The increase is the difference between values under and outside (background) tree canopy for a soil depth of 20 cm and assuming a bulk density of 1.55 g cm^{-3} .

activity (Schachtschabel *et al.*, 1984). The increase in both leaf N ($p = 0.0015$) and leaf P ($p = 0.0373$) with increasing diameter (Fig. 3) is indicative of the general increase in soil fertility created by the trees with increasing age. Villagra & Felker (1997) found that the percent Ndfa declined with tree size, which they surmised was due to increased

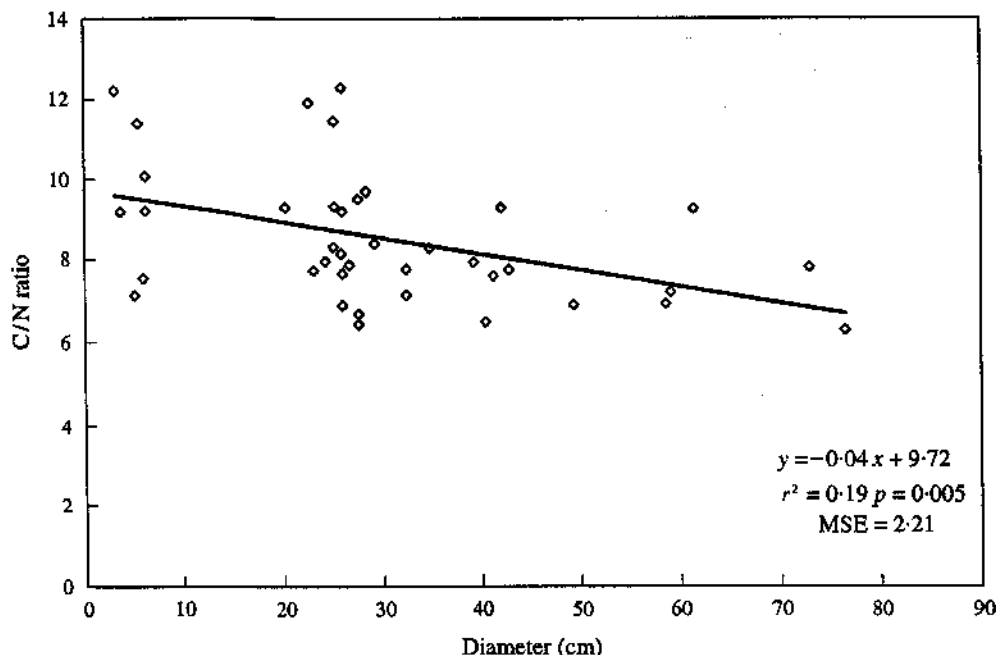


Figure 2. Estimated linear relationship ($n = 39$) between soil C/N ratio under canopy versus *Prosopis* tree diameter across seven sites in South Texas (May 1997).

N availability in the older trees. Our data did not indicate that the %Ndfa declined with increasing diameter for either leaf ($p = 0.2481$) or wood tissues ($p = 0.5394$). However, the increase of leaf $\delta^{15}\text{N}$ with tree diameter was nearly significant ($p = 0.0676$) and is included for comparative purposes (Fig. 4).

The observed increase of leaf N with leaf P ($p = 0.0034$) is common in N-fixing legumes due to the strong phosphorus requirement in nitrogen-fixation (Sanginga *et al.*, 1995) (Fig. 5). A similar relationship was observed by Cline *et al.*, (1986) for *P. glandulosa* in greenhouse pot studies. A change in leaf P from 0.1 to 0.5% represents a change in leaf crude protein from about 18.7 to 23.4% and illustrates the significant influence of P on crude protein production in nitrogen-fixing legumes.

The estimated linear relationship between total soil N and both leaf N and P concentrations is presented in Figs 6 and 7 and illustrates the coupling between these important soil and leaf nutrients. Not only were the concentrations of N in the soil and leaves highly correlated ($r = 0.542$, $p = 0.0004$, $n = 39$), but the isotopic composition of $\delta^{15}\text{N}$ in the soils and leaves were also very highly correlated ($r = 0.696$, $p = 0.0001$, $n = 39$). In contrast the correlation between the $\delta^{15}\text{N}$ in the soils and the $\delta^{15}\text{N}$ of the wood was not significant ($r = 0.258$, $p = 0.113$, $n = 39$). This illustrates a tighter coupling in N transfer between leaves and soils than between soil and wood.

Figure 8 shows the estimated linear relationship between soil and leaf P indicating the possibility of using either soil or leaf P values to assess the P status of *Prosopis* stands.

A comparison of soil nitrate-nitrogen and soil ammonium-nitrogen levels reveals that soil ammonium-nitrogen was more highly correlated with soil C ($r = 0.316$, $p = 0.050$, $n = 39$) than nitrate-nitrogen ($r = 0.258$, $p = 0.113$, $n = 39$) and more correlated with leaf N ($r = 0.320$, $p = 0.0465$, $n = 39$) than nitrate-nitrogen ($r = 0.218$, $p = 0.182$, $n = 39$). In contrast, nitrate-nitrogen was more highly correlated with soil N ($r = 0.323$, $p = 0.0445$, $n = 39$) than ammonium-nitrogen ($r = 0.288$, $p = 0.0746$, $n = 39$) and soil P ($r = 0.412$, $p = 0.0091$, $n = 39$) than ammonium-nitrogen ($r = 0.115$, $p = 0.50$, $n = 39$).

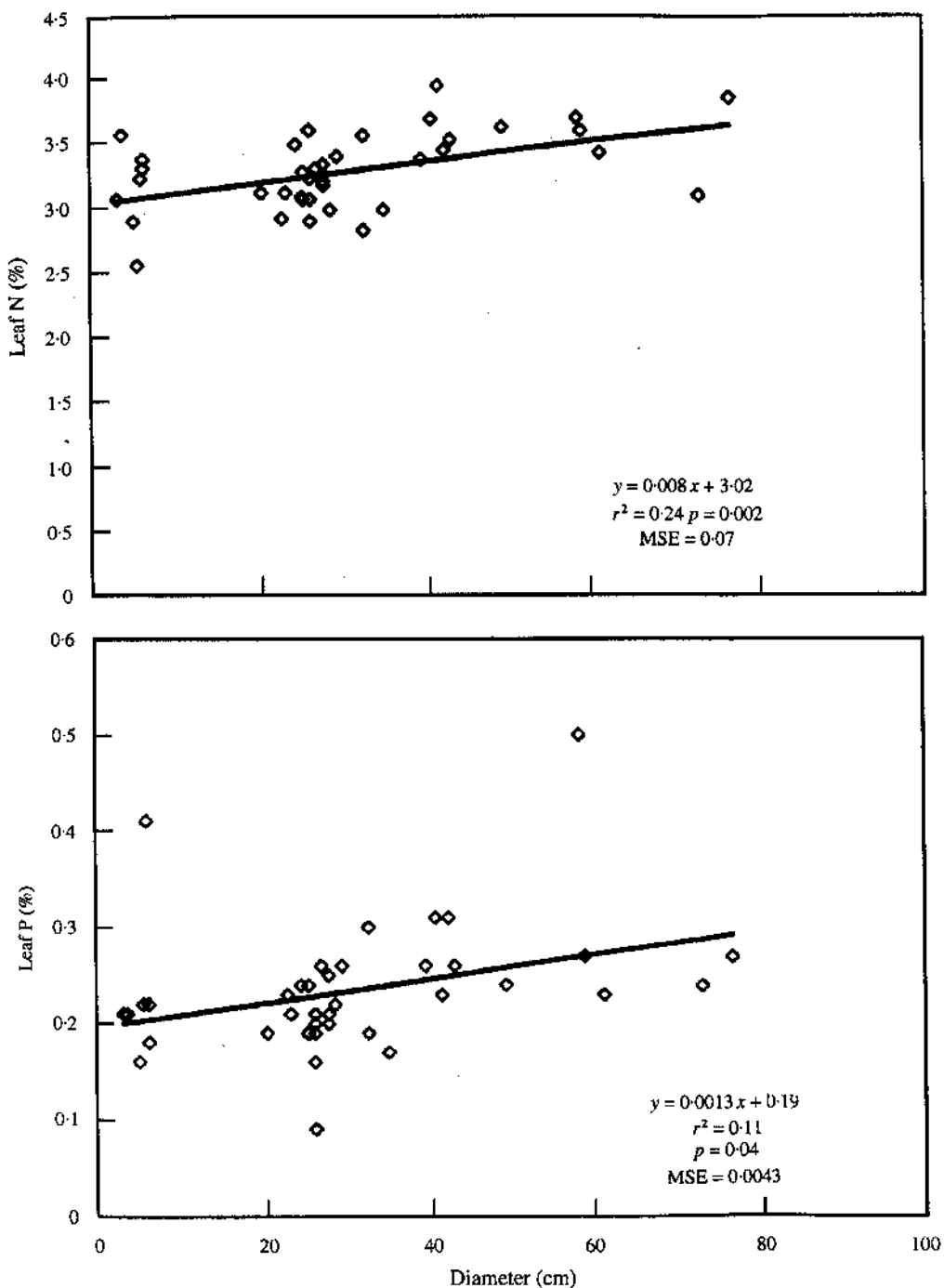


Figure 3. Estimated linear relationship ($n = 39$) between *Prosopis* leaf N (%) and leaf P (%) vs. tree diameter across seven site in South Texas (May 1997).

Perhaps the most striking of the correlations is the very highly significant negative linear relationship between soil nitrate-nitrogen level and the percent of N derived from nitrogen fixation in both the leaves and the wood (Fig. 9). Ammonium-nitrogen was not

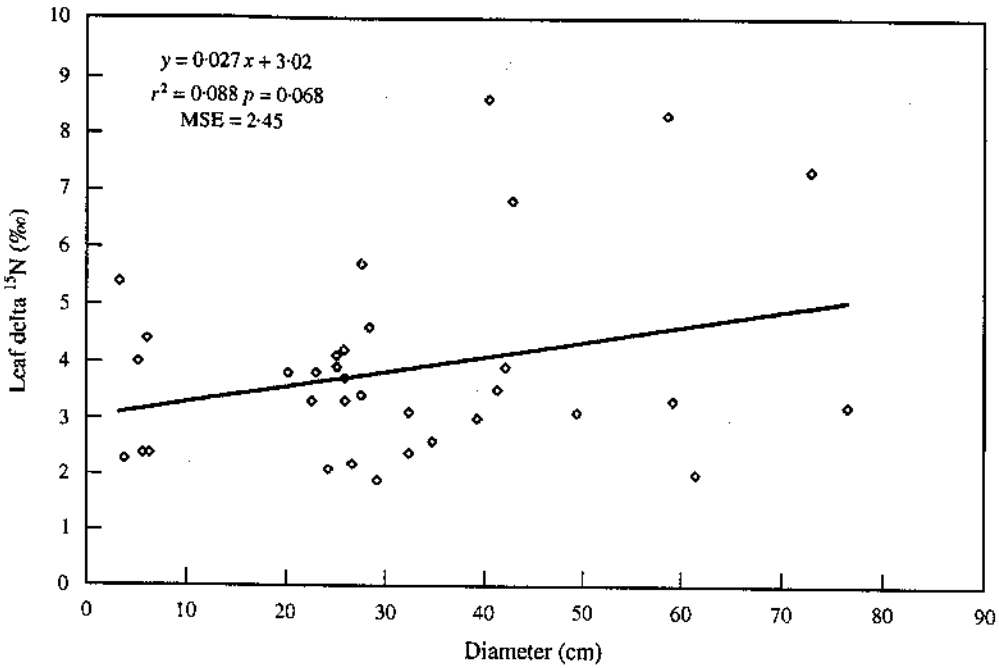


Figure 4. Estimated linear relationship ($n = 39$) between *Prosopis* leaf $\delta^{15}\text{N}$ (‰) vs. tree diameter across seven sites in South Texas (May 1997).

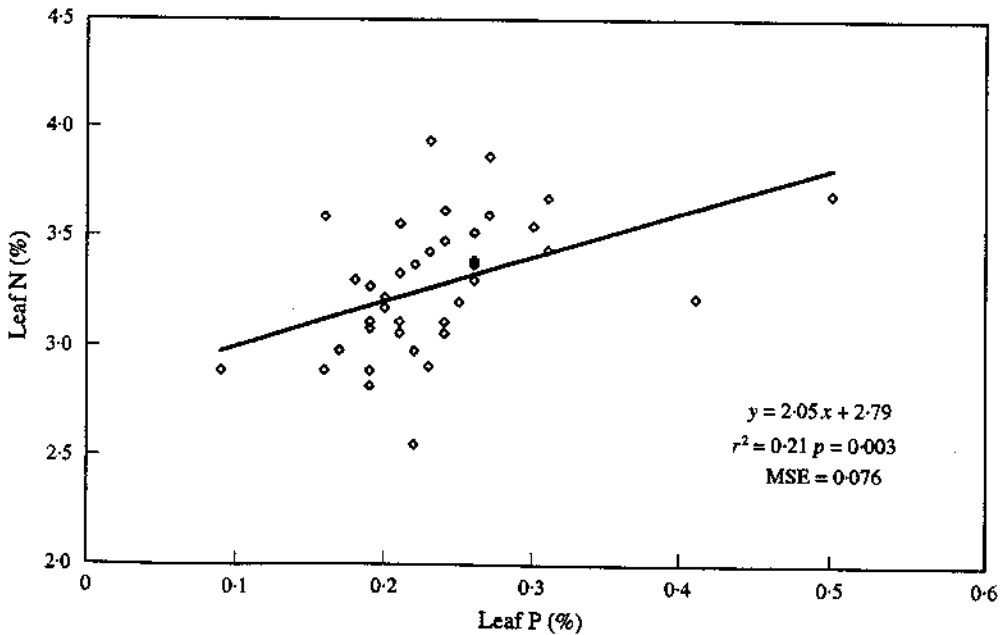


Figure 5. Estimated linear relationship ($n = 39$) between *Prosopis* leaf N (‰) vs. leaf P (%) across seven sites in South Texas (May 1997).

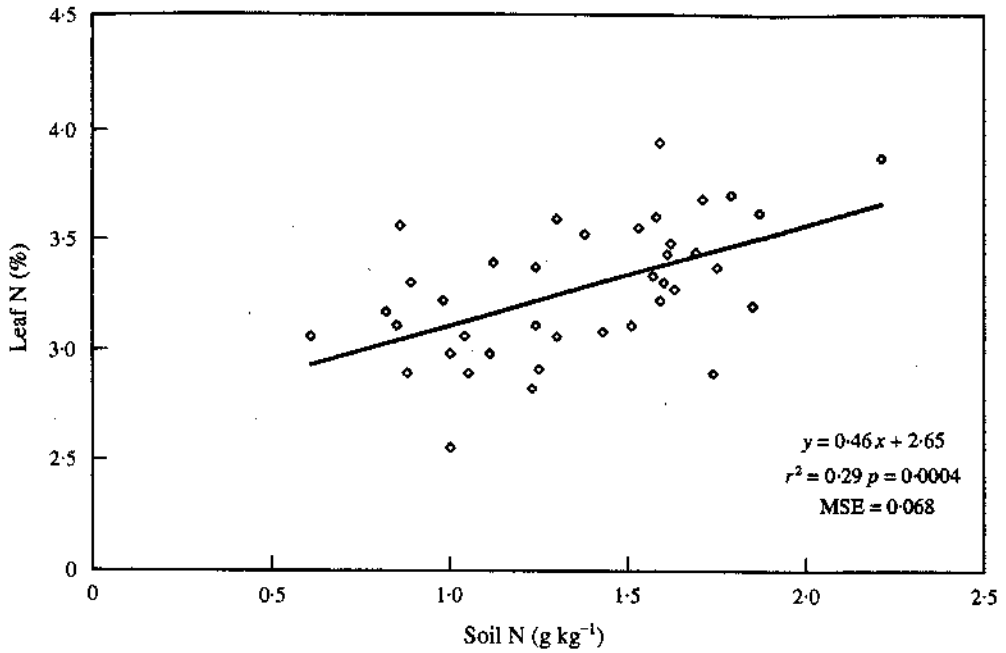


Figure 6. Estimated linear relationship ($n = 39$) between *Prosopis* leaf N (%) vs. total soil N (g kg^{-1}) under canopy across seven sites in South Texas (May 1997).

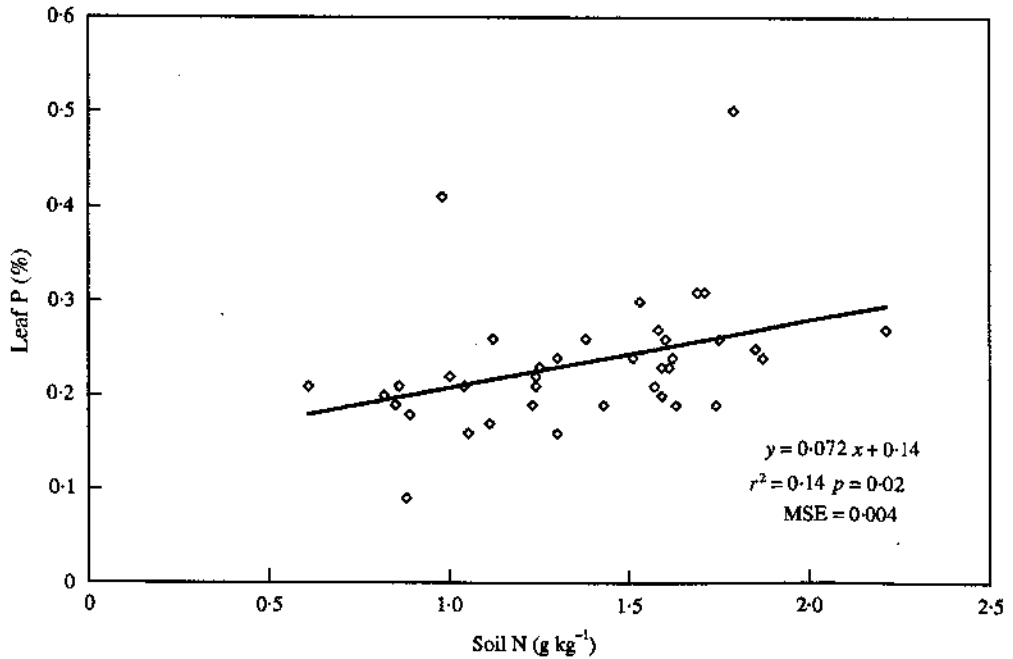


Figure 7. Estimated linear relationship ($n = 39$) between *Prosopis* leaf P (%) vs. total soil N (g kg^{-1}) under canopy across seven sites in South Texas (May 1997).

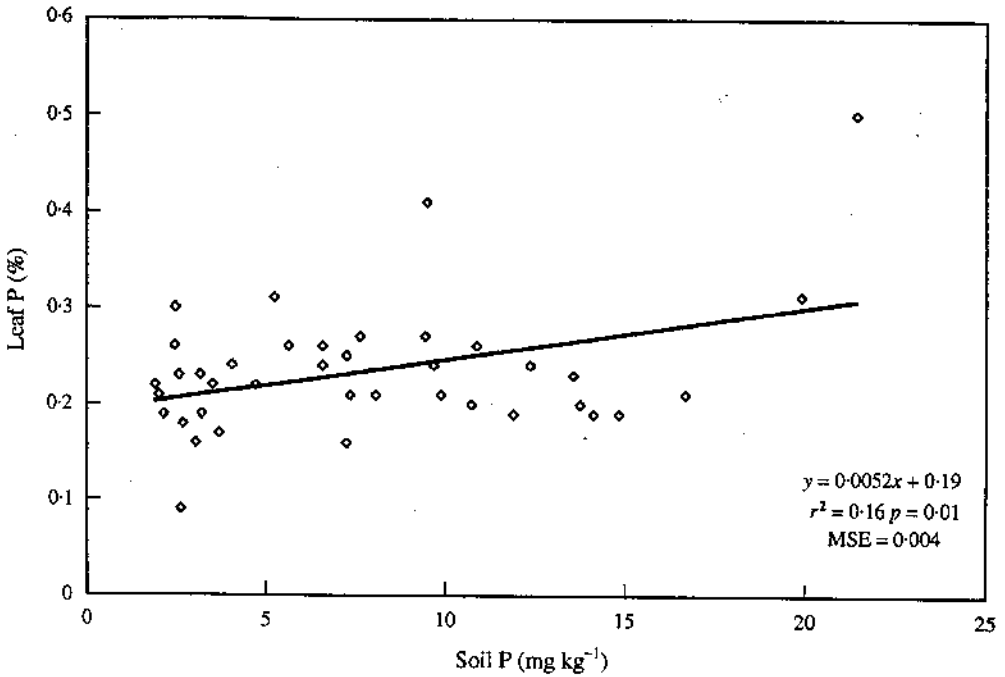


Figure 8. Estimated linear relationship ($n = 39$) between *Prosopis* leaf P (%) vs. soil P (mg kg⁻¹) under canopy across seven sites in South Texas (May 1997).

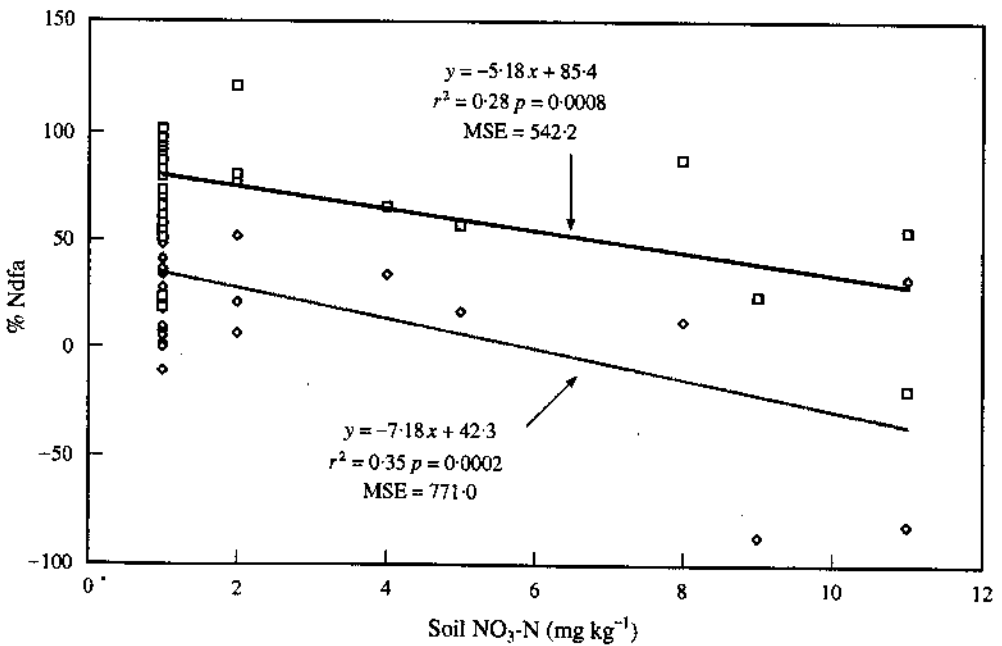


Figure 9. Estimated linear relationship ($n = 39$) between percent nitrogen derived from atmosphere (%Ndfa) in *Prosopis* leaves and trunk wood vs. soil nitrate-nitrogen (mg kg⁻¹) under canopy across seven sites in South Texas (May 1997): \diamond = %Ndfa leaf; \square = %Ndfa wood; — = %Ndfa wood; — = %Ndfa leaf.

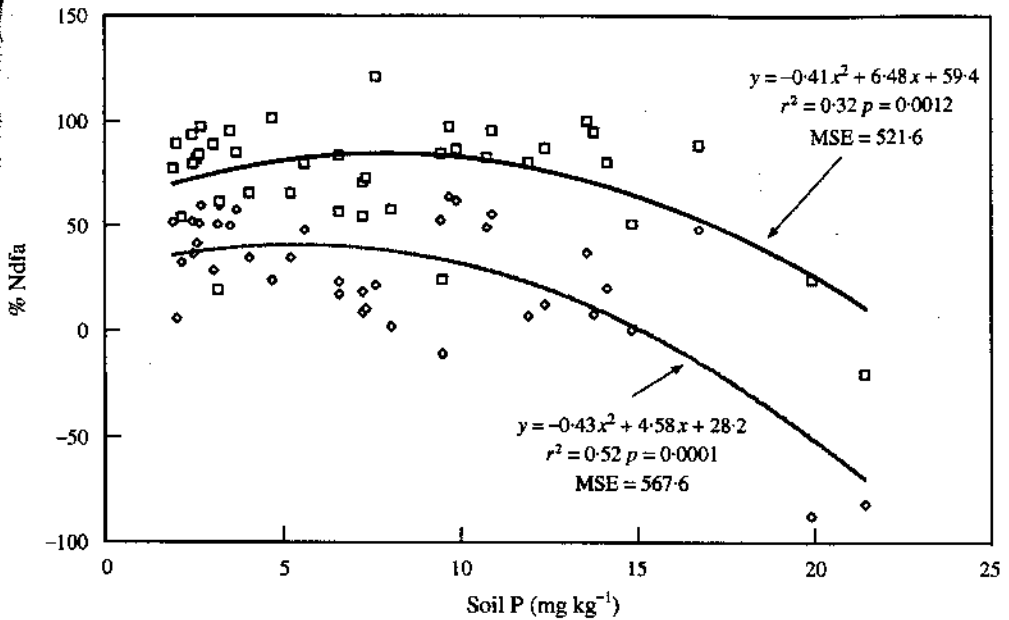


Figure 10. Estimated quadratic relationship ($n = 39$) in *Prosopis* leaves and trunk wood vs. soil phosphorus (mg kg^{-1}) under canopy across seven sites in South Texas (May 1997). The quadratic terms of both equations were significant at $p = 0.0023$: \diamond = % Ndfa leaf; \square = % Ndfa wood; — = % Ndfa leaf; — = % Ndfa wood.

significantly correlated with %Ndfa leaf ($r = 0.160$, $p = 0.329$, $n = 39$) or wood ($r = -0.045$, $p = 0.783$, $n = 39$). This suggests that as the soil nitrate accumulates under the trees as a result of the nitrogen-fixation, the nitrate represses the N-fixation process.

A process of decreasing %Ndfa in both leaves and wood with higher soil P values is indicated in Fig. 10. Since soil P was highly correlated with soil nitrate-nitrogen ($r = 0.414$, $p = 0.0091$, $n = 39$) and since increased P stimulates N-fixation, we suggest that it is probably the soil nitrate and not soil P that represses N-fixation. The %Ndfa in wood and leaf decreased with higher leaf P values (Fig. 11). In all four cases, the quadratic term of the polynomial model was significant.

We believe the consistently lower %Ndfa for the leaves than for the trunk is attributable to the fact that when the tree was young most of its N was obtained by N fixation (Villagra & Felker, 1997) which accumulated in the trunk. Thus, the trunk represents a much longer history of the plants N nutrition. In contrast, the leaves represent the newest growth, and as the soil N and leaf N are closely coupled (Fig. 6), the elevated $\delta^{15}\text{N}$ of the leaves with tree size (Fig. 4) represents the current status of the plants repression of N-fixation by accumulated soil N nutrients.

Discussion

The hypothesis that *Prosopis* selectively occurs on islands of fertility and that the increased fertility is not created by active N-fixation (Garcia-Moya & McKell, 1970; Barth & Klemmedson, 1982) must be rejected for two reasons. First, the %Ndfa of wood and leaves, that is based on the ratios of naturally occurring isotopes, firmly

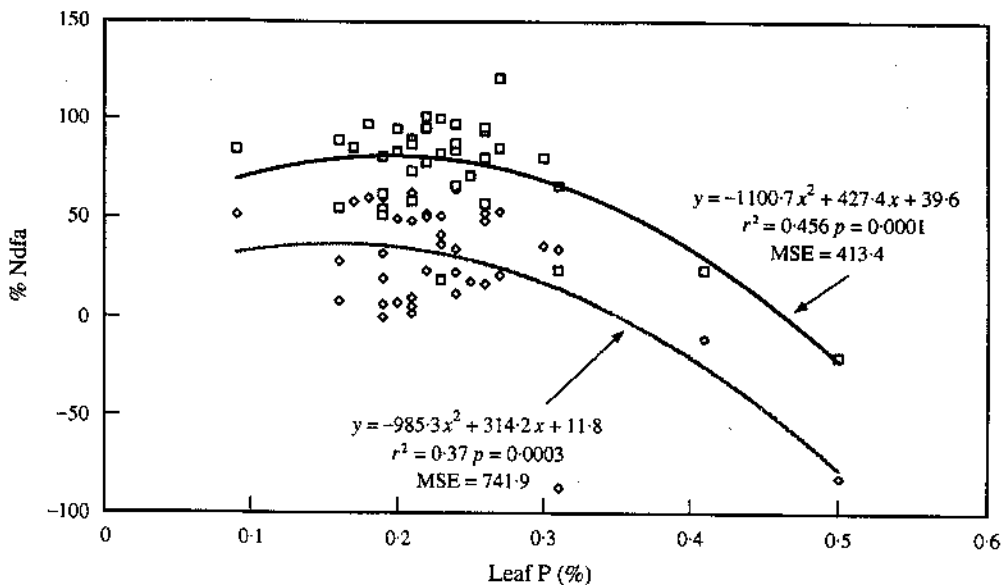


Figure 11. Estimated quadratic relationship ($n = 39$) between percent nitrogen derived from atmosphere (%Ndfa) in *Prosopis* leaves and trunk wood vs. leaf phosphorous (%) across seven sites in South Texas (May 1997). The quadratic terms were significant at $p = 0.003$ (wood) and at $p = 0.004$ (leaf): \diamond = %Ndfa leaf; \square = %Ndfa wood; — = %Ndfa leaf; - - - = %Ndfa wood.

indicate *Prosopis* is fixing N. Secondly, the nitrogen fixing process is behaving physiologically as expected in that as the trees became larger, there is an increase in soil nitrate that leads to a repression of the N fixing process and a lowering of %Ndfa in the leaves. In greenhouse studies, Shoushtari & Pepper (1985) found that acetylene production by nodules of *P. velutina* declined about 30% with a similar nitrate N concentration of about 10 mg l^{-1} .

We are aware of the extremely complex nature of naturally occurring nitrogen isotope transformation in forest soils and the difficulty in choosing reference plants to estimate N fixation using natural abundance nitrogen isotopes (Högberg, 1997). Perhaps the most compelling justification for this approach is the fact that the %Ndfa based on analyses of natural abundance nitrogen isotopes is consistent with expected physiological responses of nitrogen fixing plants. No doubt the use of many trees on multiple sites helped to overcome some of the limitations with this method.

The pumping of nutrients from deeper levels in the soil profile has been used to explain the increased soil fertility beneath the canopies of N fixing and non-N fixing trees (Barth & Klemmedson, 1982). Pumping of nutrients from deeper layers undoubtedly occurred to result in the increased soil P under large *Prosopis* canopies. However, this increased soil P was only 13 kg ha^{-1} vs. 4.4 Mg ha^{-1} increase for N and a 17.7 Mg ha^{-1} increase for soil C.

Even the increased soil P under tree legumes may not be entirely due to redistribution of soluble P. Legumes have been found to be more efficient in obtaining P from insoluble sources than grasses (Drake & Steckel, 1955). This has been attributable to the increased cation exchange capacity of legume root systems that lowers the calcium activity of the soil solution facilitating the release of P from insoluble Ca-P compounds (Drake & Steckel, 1955).

Texas cattlemen routinely contract for the mechanical removal of small diameter (< 7 cm), closely spaced (1–3 m) *Prosopis* that are about 3–4 m tall. As assessed by

the %Ndfa of the leaves and trunk, most of these small trees are actively fixing N (Table 3). However these trees have not yet accumulated soil C and N concentrations above the background levels (Table 2) and at this high stand density the trees shade out the grasses and provide intense competition for water. Thus, they have not increased soil fertility levels to compensate for their detrimental effects on forage production. Therefore, at this stand density, it would seem prudent to conduct the thinning and pruning programme outlined by Patch & Felker (1997) to reduce the forage competition while continuing to build soil organic C and N.

For many years the perspective of Martin (1948) prevailed that *Prosopis* did not fix N in field settings since nodules could not be located. However, the work of Johnson & Mayeux (1990) strongly suggested that *Prosopis* was the major source of fixed N in the arid regions of Texas since nodules were found on five of 10 sites examined, and soils capable of producing nodules on seedlings were found on the other five sites. However, Johnson & Mayeux (1990) had no direct confirmation of N-fixation on their sites. The fact that we obtained greater than 77%Ndfa for the wood on six of the seven sites clearly demonstrates significant N-fixation in the field.

Not only do these stands fix nitrogen, but the quantities of N fixed are very significant in economic terms, unlike blue-green, algal-lichen crusts and non-symbiotic fixers which fix at rates of only 1–2 kg ha⁻¹ yr⁻¹ (Loftis & Kurtz, 1980).

It is possible to estimate the age of the trees and thus the annual accretion rates. Depending on the level of management of sapling stands, Patch & Felker (1997) measured a range of annual growth rates of 0.5 cm to 1.2 cm (basal diameter). At these growth rates, the 60-cm diameter trees would range from 50 to 120 years of age. If the soil increase of 4.4 Mg N ha⁻¹ and 17.7 Mg C ha⁻¹ was observed for a 25% canopy cover, then there would be 1.1 Mg ha⁻¹ additional N and 4.4 Mg ha⁻¹ additional C for the top 20 cm depth. Thus, the net annual accrual of soil N and C would range from 9 to 22 kg N ha⁻¹ and from 35 to 88 kg C ha⁻¹. Since appreciable losses of the soil N have occurred in the form of denitrification, the inputs from N-fixation must have been considerably greater than the long-term accrual.

Abrams *et al.*, (1990) measured the increase in soil C and N among three *Prosopis* species in a 10-year old irrigated trial in California. They found that *P. glandulosa var torreyana* had the greatest accumulation of soil N with values under and away from the canopy of 1051 kg ha⁻¹. From the 10-year age of this plantation (established in 1977 not 1980) the annual increment was calculated to be 100 kg N ha⁻¹ yr⁻¹.

Perhaps the single greatest loss of N from arid ecosystems is from grazing. Only 17% of the N ingested by domestic livestock was estimated to be exported from the ecosystems in the form of animal tissues (Woodmansee, 1978). In contrast, Gist & Sferra (1978) estimated that 45% of the N ingested by sheep was lost to the atmosphere from ammonia volatilization of urine and faeces. For example, if a 450 kg range animal consumed 10 kg dry matter of 1.5% N (9.4% protein) for 365 days, then 55 kg of N would be consumed of which 25 kg would be lost from the ecosystem. At a 2 kg N ha⁻¹ yr⁻¹ input from blue-green algae and rainfall, about 12 ha would be required from lichens and rainfall to balance the N losses from one 450 kg animal.

It is instructive to compare the amount of N fixed by a single large tree to other N inputs. Using the equations of El Fadi *et al.* (1989), a 50-cm basal diameter tree would have a fresh weight of 1208 kg. Using the 80% dry matter coefficient and the value of 3% leaves of total standing biomass and 3% N in the leaves (Villagra & Felker, 1997), this 50-cm diameter tree would produce 28.8 kg of leaves and 0.86 kg of N annually. Given the ranges of 5 to 60% Ndfa observed in this study, the N fixed in the leaf litter would range from 0.043 to 0.52 kg annually. Since a 50-cm diameter *Prosopis* can produce as much as 40 kg of 13% protein (2% N) in *Prosopis* pods (Oduol *et al.*, 1986), it is possible that an equivalent amount of fixed N could occur in litter from these pods.

Implications of soil development under semi-arid tree legumes in global carbon sequestration

In addition to the maximum soil C increase over background of 5.7 g kg^{-1} that we observed under the canopies of *Prosopis*, other workers have found values under *vs.* outside the canopies of 1.7 g N kg^{-1} and 19 g C kg^{-1} *vs.* 0.2 g N kg^{-1} and 3.2 g C kg^{-1} in California (Rundel *et al.*, 1982; Virginia & Jarrell, 1983), 0.49 g N kg^{-1} and 5.0 g C kg^{-1} *vs.* 0.24 g N kg^{-1} and 2.7 g C kg^{-1} in Arizona (Tiedemann & Klemmedson, 1973), 0.49 g N kg^{-1} and 3.1 g C kg^{-1} *vs.* 0.42 g N kg^{-1} and 1.9 g C kg^{-1} in India (Shankar *et al.*, 1976), and 1.3 g N kg^{-1} and 15 g C kg^{-1} *vs.* 1.0 g N kg^{-1} and 13.8 g C kg^{-1} in Texas (East & Felker, 1993). Connin *et al.*, (1997) only measured organic C under *Prosopis* in New Mexico and found values under *vs.* away of 2.1 *vs.* 1.3 g C kg^{-1} . Generally these soil values were for the top 30 cm depth.

Assuming a normal bulk density of 1.55 g cm^{-3} soil, a 30-cm soil depth, and 100% canopy cover, the absolute changes would correspond to a range in increase over background of soil C from 5.6 (Texas site) to 73.5 Mg ha^{-1} (California site). At 25% canopy cover, these increases would correspond to changes of about 1.4 to 18.4 Mg ha^{-1} soil C increase. Under the same assumptions, our maximum soil C increase would correspond to 26.5 or 6.6 Mg ha^{-1} at a 25% canopy cover.

The area to which this technology might be applicable is uncertain but extensive. A classic work on the extent of tree legumes *Acacia* and *Prosopis* in the dry tropics by the FAO expert A.L. Griffiths (1961) suggested that these species occurred on 31.2 million km^2 . If this area could be managed to obtain an additional soil C increase of 2 Mg ha^{-1} , the global sequestration would be $6.2 \times 10^9 \text{ Mg}$ of carbon. While the increase in C we suggest is lower on an annual basis than that reported for Canadian boreal forests (2.4 Mg ha^{-1}) (Chen *et al.*, 1999) due to the fact that the surface area of the worlds semi-arid/arid regions is 100 times larger than the Canadian boreal forests, the total impact from semi-arid/arid lands ($6.2 \times 10^9 \text{ Mg}$ of carbon) is much larger than the Canadian boreal forests. Our hypothesis that semi-arid lands could be managed to sequester $6.2 \times 10^9 \text{ Mg}$ of carbon compares favourably to the projected 2000 total world carbon emissions of $6.9 \times 10^9 \text{ Mg}$ of carbon. This value also compares favourably to the need to reduce the projected 2010 emissions of $8.5 \times 10^9 \text{ Mg}$ to 95% of the 1990 carbon emissions ($6.1 \times 10^9 \text{ Mg}$) for a $2.74 \times 10^9 \text{ Mg}$ reduction in global emissions (EIA, 1995, 1996).

There can also be substantial amounts of woody biomass per ha in semi-arid regions. In a survey of *Prosopis* stands that ranged from 18,000 stems ha^{-1} to 6 stems ha^{-1} , Felker *et al.* (1990) found that the total fresh biomass ranged from about 8 Mg ha^{-1} to 100 Mg ha^{-1} with 100 stems of 30 cm diameter having the greatest total biomass. Assuming a 50% moisture content and a C/dry weight conversion of 40%, the standing C content of these stands would range from 2 to 20 Mg ha^{-1} . Non-irrigated plantations of unselected genetic stock of *Prosopis* were found to have a standing dry biomass of 69 Mg ha^{-1} at the end of 10 years growth for an annual dry biomass growth increase of 6.9 Mg ha^{-1} (Duff *et al.*, 1994).

As Swisher (1997) pointed out, carbon storage in above-ground biomass that may be later harvested and used is not sufficient for long-term carbon storage and therefore does not sustainably reduce the carbon stock in the atmosphere. In contrast, the build up of soil C would be a long-term permanent increase provided that land degradation was prevented. Also, as Swisher (1997) has pointed out, this increase in C storage must be viewed as a one-time increment on the land. Batjes (1998) has also suggested that 'enhanced sequestration of atmospheric carbon dioxide in the soil ultimately ... may well provide a more lasting solution than temporarily sequestering carbon dioxide in the standing biomass though reforestation'

Following the Kyoto summit there has been vigorous emphasis on reducing global carbon dioxide levels (UNFCCC, 1997). Our results indicate that given modest

increases in soil C (by temperate soil standards) over the very extensive arid lands, a significant global reduction in carbon dioxide could occur from implementation of forestry with *Prosopis* and *Acacia*.

The Global Environment Facility (GEF) established after the Rio Summit (Global Environment Facility, 1996), has the mission to be the financial mechanism for global environmental amelioration. Two of the four mandates were alleviation of the problems of global climate change, biodiversity and land degradation as it relates to these areas (Global Environment Facility, 1996). Within land degradation, the GEF has particularly identified the need for cross-sectorial approaches to desertification, deforestation and promotion of sustainable use of arid and semi-arid ecosystems. The GEF recognizes that 'Degrading dryland soils and burning of biomass are globally significant sources of greenhouse gases', and that GEF objectives will include 'Carbon sink protection, enhancement and restoration projects that improve carbon storage in biomass and soils to control degradation, especially desertification and deforestation'.

Clearly given these global mandates and the significant environmental, social and economic benefits to be accrued from sustainable management of tree legumes like *Prosopis* to enhance C and N sequestration in arid soils, globally significant efforts should be made to manage and utilize this potential.

Conclusions

The high percentages of Ndfa in wood and leaves on the seven random sites chosen in Texas clearly indicates that *Prosopis* is actively fixing N. Furthermore the levels of N and C are present in quantities that are very significant in economic and ecological terms. Thus, the hypothesis that *Prosopis* does not create islands of fertility by N-fixation must be rejected. As the trees become larger, the percent of both N and P in the leaves increases, as does the level of soil N and P. There is a tendency for the leaf $\delta^{15}\text{N}$ to increase with tree age suggesting that %Ndfa declines with tree age. The leaf $\delta^{15}\text{N}$ is closely coupled with soil $\delta^{15}\text{N}$, while the trunk $\delta^{15}\text{N}$ is more directly coupled to the N fixation process. The highly significant negative regression between soil nitrate and % Ndfa in the leaf clearly is evidence that as the soil under *Prosopis* develops, the N fixation process declines.

The management of semi-arid ecosystems for cattle, fuelwood and cabinet wood uses should recognize the drain on the ecosystem from volatilization of excreted N and incorporate tree legumes in these systems to balance N input/output ratios.

A growing body of worldwide evidence in semi-arid savannas suggests that basic soil physical properties that are primarily determined by organic C are much more limiting to sustainable productivity than previously recognized. Thus, more attention should be given to inclusion and management of tree legumes in arid ecosystems solely for the benefit of increasing soil C to improve soil physical properties.

When the small increases in C per hectare resulting from tree legume N-fixation are aggregated on the extensive areas to which subtropical tree legumes are adapted, globally significant impacts on C sequestration are possible.

Despite the cumbersome and difficult task of working with large trees in uneven, aged native stands, this work illustrates that standard techniques can be successfully used to estimate N-fixation by these trees in the field. Future research should be directed towards developing management techniques to enhance N-fixation and soil development by tree legumes at the whole stand level.

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