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Seasonal dynamics of nitrogen cycling for a Prosopis woodland in the Sonoran Desert

Dinamica estacional del ciclo de nitrógeno de un bosque de Prosopis en el desierto Sonorense

P. W. RUNDEL, E. T. NILSEN, M. R. SHARIFI,
Dept. of Ecology and Evolutionary Biology, University of California, Irvine, California 92717, USA

R. A. VIRGINIA, W. M. JARRELL,
Dept. of Soil and Environmental Sciences, University of California, Riverside, California 92521, USA

D. H. KOHL and G. B. SHEARER
Dept. of Biology, Washington University, St. Louis, Missouri 63130, USA

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Abstract Prosopis woodlands in the Sonoran Desert have levels of above-ground biomass and productivity much higher than those predicted for desert plant communities with such low levels of precipitation. A stand of *P. glandulosa* near the Salton Sea, California, has 13,000 kg ha^{-1} above-ground biomass and a productivity of 3700 kg ha^{-1} yr^{-1}. Such a high level of productivity is possible because Prosopis is decoupled from the normal limiting factors of water and nitrogen availability. Soil nitrogen contents for the upper 60 cm of soil beneath Prosopis canopies have 1020 g m^{-2} total nitrogen, 25 per cent of which is in the form of nitrate. Such accumulations of nitrogen may be the result of active symbiotic nitrogen fixation. Early estimates suggest that about 25–30 kg N ha^{-1} yr^{-1} is fixed in these stands. Since Prosopis covers only 34% of the ground surface and its water resources are not limiting, much higher levels of nitrogen fixation and productivity may be possible in managed stands at greater densities.

Resumen Los bosques de Prosopis en el desierto Sonorense tienen niveles de producción de biomasa (parte aérea) y productividad mucho mayores que las predecibles para comunidades de plantas de desierto con muy bajos niveles de precipitación. Los bosques freatofíticos de *P. glandulosa* cerca del Mar de Salton, California, producen 13 000 kg ha^{-1} de biomasa aérea con una productividad 3 700 kg ha^{-1} $año^{-1}$. Tan alto nivel de productividad es posible porque Prosopis no es afectado por los factores que limitan la aprovechabilidad de agua y nitrógeno.

Los primeros 60 cm del perfil del suelo bajo el dosel de Prosopis contienen 1 020 g m^{-2} de nitrógeno total, el 25% existe en la forma de nitrato. Tales acumulaciones de nitrógeno pueden ser el resultado de la fijación simbiótica activa. Los primeros valores estimados sugieren que son fijados entre 25–30 kg N ha^{-1} $año^{-1}$ en estos bosques. Puesto que Prosopis cubre solamente 34% de esta área y sus recursos de agua no son limitantes, puede ser posible la obtención de mayores niveles de fijación de nitrógeno y productividad de los cultivos si se manejan con mayores densidades.

Introduction

Productivity in desert and semi-arid plant communities is generally very low. These low levels of production result from the limiting factors of high water stress and limited nitrogen availability[22]. There are exceptions to this general pattern, however, particularly in desert and semi-arid ecosystems dominated by woody legumes. The genus Prosopis, the mesquites, forms the dominant coverage on millions of square kilometers of arid woodlands in North and South America. There are numerous anecdotal and semiquantitative accounts of high levels of productivity in Prosopis woodlands, but in the past there had been no good quantitative data published.

In recent studies[15] we have measured biomass and productivity rates in a stand of *Prosopis glandulosa* var. *torreyana* in the northwestern Sonoran Desert. Despite a very low mean annual precipitation of only 70 mm yr^{-1} at our study site near the Salton Sea in southern California, we have found a standing above-ground biomass of 13,000 kg ha^{-1} with a net production of 3700 kg ha^{-1} yr^{-1}. We have found even higher values for biomass and productivity in a second stand near Catavina in Baja California Norte, Mexico[10]. These levels of productivity far exceed those of other desert ecosystems, which generally range from 150–1000 kg ha^{-1} yr^{-1}.

Our hypothesis has been that Prosopis is able to reach such remarkable levels of productivity because it is decoupled from the normal limiting factors of water and nitrogen availability. It is well established that deep roots of Prosopis tap permanent water tables at great depths, making water available throughout the year[11]. Water alone, nevertheless, will not ensure high productivity without readily available nitrogen for growth. Such nitrogen is normally not present in desert soils[21]. Symbiotic nitrogen fixation, however, could provide a source for such nitrogen[2]. In this paper we report on our studies of the seasonal and long-term dynamics of nitrogen cycling in *Prosopis glandulosa* stands. We describe pool sizes of nitrogen in individual ecosystem compartments as well as the magnitude of fluxes between pools.

Materials and methods

Field studies were carried out at Harper's Well near the southern margin of the Salton Sea in the Sonoran Desert of California. Here *Prosopis glandulosa* dominates an extensive woodland community. Total Prosopis cover is 33.9% within the stand, with all other perennials providing a total of 4% additional coverage. The stand elevation is −30 m, with a permanent ground water supply at a depth of 5 m in the soil. Biomass and productivity measurements necessary to calculate total nitrogen levels in above-ground biomass were determined using a dimensional analysis technique modified from that of Whittaker and Marks[23]. Individual tissue components were analyzed at roughly four-week intervals for their nitrogen contents by micro-Kjeldahl techniques. Soils to 60 cm depth at 30 cm intervals were analyzed for total nitrogen as well as organic nitrogen, nitrate-nitrogen and ammonium-nitrogen.

Results and discussion

Nitrogen pools

Soil nitrogen pools under the canopies of *Prosopis glandulosa* are remarkably high. The mean total nitrogen content of the upper 60 cm of soil under these canopies in our study site was 1020 g N m^{-2} in 1980 (Table 1). By comparison,

Table 1. Nitrogen (g N m^{-2}) in the upper 60 cm of soil under (canopy) and not under (non-canopy) individual Prosopis in Sonoran desert Prosopis stands

N-fraction	Canopy	Non-canopy	Total
Organic-N	762	103	294
NO_3^--N	253	55	112
NH_4^+-N	5	2	3
Total	1020	160	409

open areas between canopies of individual Prosopis contained only 160 g N m^{-2}, while adjacent areas outside of the stand had only 45 g N m^{-2}. Very little nitrogen was present at greater depths in the soil. Even more surprising than the high levels of total soil nitrogen under Prosopis canopies was the proportion of nitrate in this total. Nitrate comprised 25% of the total soil nitrogen pool, with concentrations as high as 1000 mg NO_3–N kg dry soil^{-1}. This concentration of nitrate far surpasses that of even most agricultural soils. Ammonium-nitrogen concentrations were quite low in comparison to NO_3–N concentrations, but also high in relation to NH_4–N concentrations in agricultural soil.

The total above-ground nitrogen content of *Prosopis glandulosa* at Harper's Well was 54.6 g N m^{-2} of canopy area. We lack good data for below-ground tissues. During July 1980 (the period of maximum leaf biomass) nearly 60% of above-ground biomass nitrogen was contained in woody branches and trunks (Fig. 1). Leaves, reproductive tissues, and new stems comprised the remainder with 19.9, 11.9 and 2.1% of the total, respectively. On a weight basis, individual tissues varied greatly in %N. In mid-March 1980, at the peak of the spring

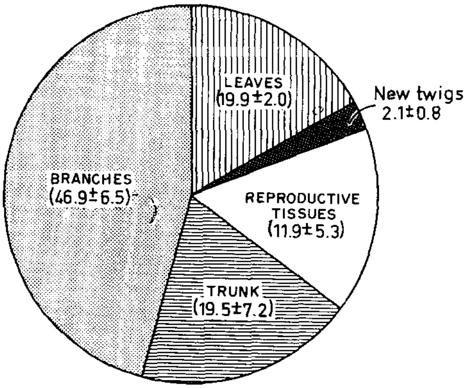

Fig. 1. Above-ground nitrogen distribution in *Prosopis glandulosa*, in July 1980. Values in parentheses represent per cent distribution ± standard errors.

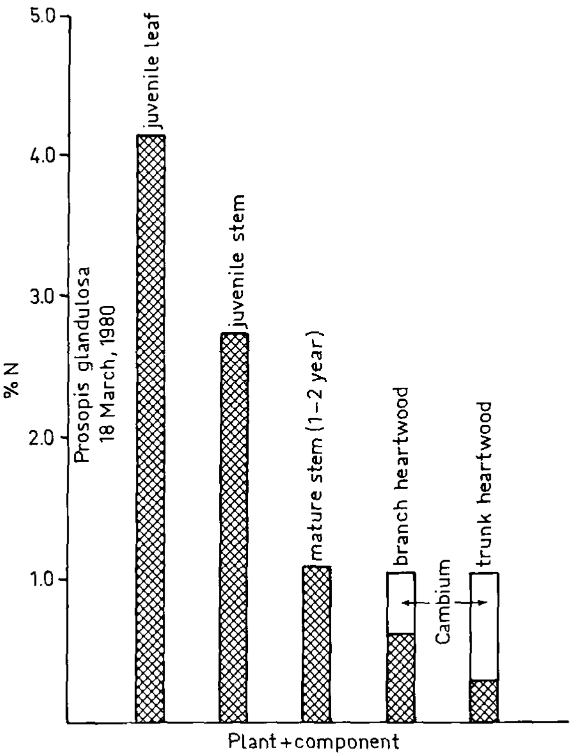

Fig. 2. Per cent N (dry weight basis) in *Prosopis glandulosa* tissues in March 1980.

growth period, juvenile leaves contained over 4% N and new stems 2.7% N (Fig. 2). The previous year's stems had about 1.1% N while older woody tissues had less than 0.7% N. Nitrogen concentrations of new tissues changed rapidly, however, during this early period of growth. New leaves contained more than 5% N when they first formed, but the N-content dropped rapidly as the leaves matured over the next two months (Fig. 3). There was very little decline in leaf nitrogen concentration from late April to January when the majority of leaves were abscissed. A very similar seasonal progression of nitrogen concentrations occurred with new stems, although the levels of nitrogen were lower (Fig. 3). For leaves, our data suggest that the rapid early decline in leaf per cent N was largely a function of dilution as the leaves expanded and became heavier on an area basis. Leaf specific weights (mg cm^{-2}) of Prosopis leaflets increased until early May (Fig. 4), but nitrogen specific weights (mg N cm^{-2}) did not vary greatly after mid-March.

Monthly data on the seasonal dynamics of above-ground biomass components and the nitrogen concentration of these components allowed us to calculate the mean daily rate of nitrogen accumulation for each sample period. These data indicate a very high rate of nitrogen accumulation in leaves early in

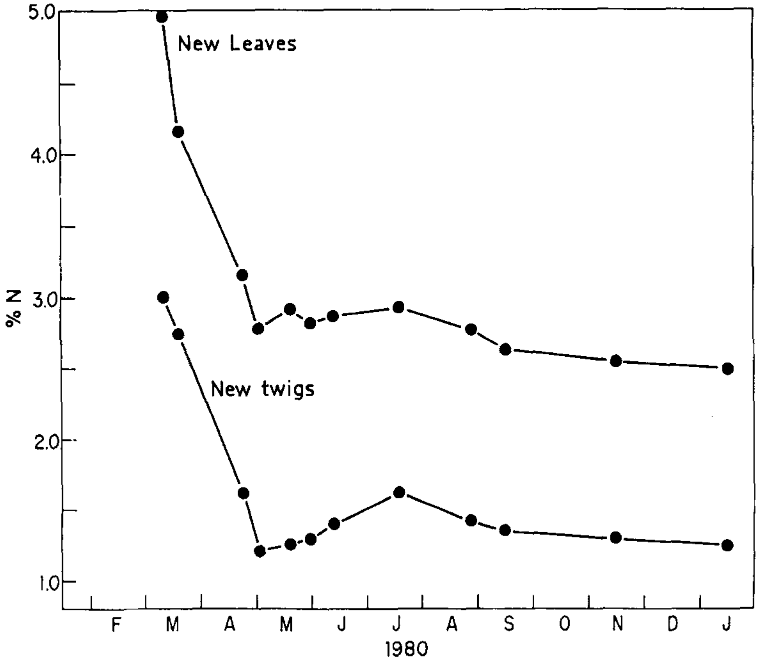

Fig. 3. Change in per cent N in *Prosopis glandulosa* leaves and stems with age.

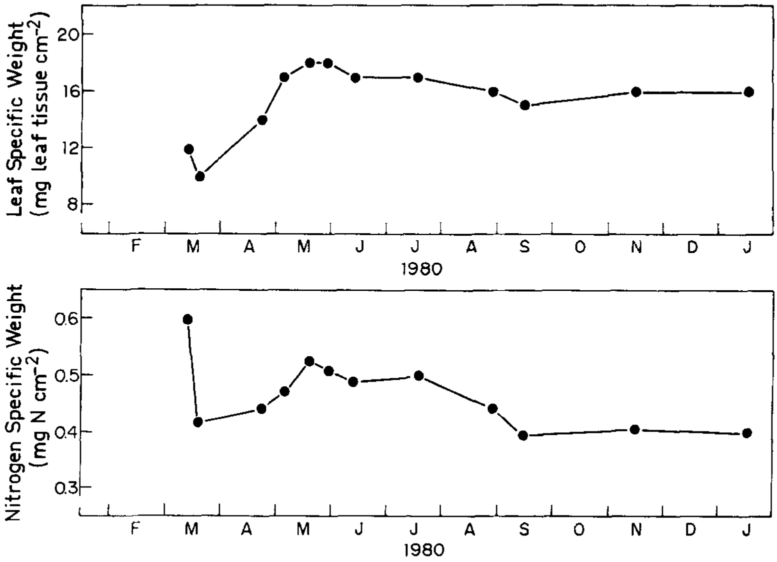

Fig. 4. Changes in leaf specific weight (mg dry leaf tissue cm^{-2} leaf area) and N concentration (mg N cm^{-2} leaf area) in *Prosopis glandulosa* with age.

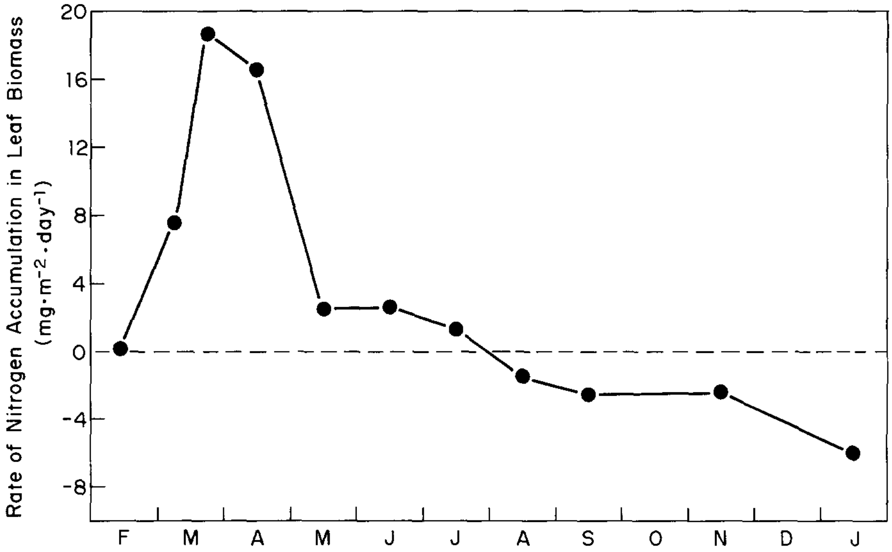

Fig. 5. Rate of nitrogen accumulation in leaf biomass of a *Prosopis glandulosa* community in the Sonoran Desert, California.

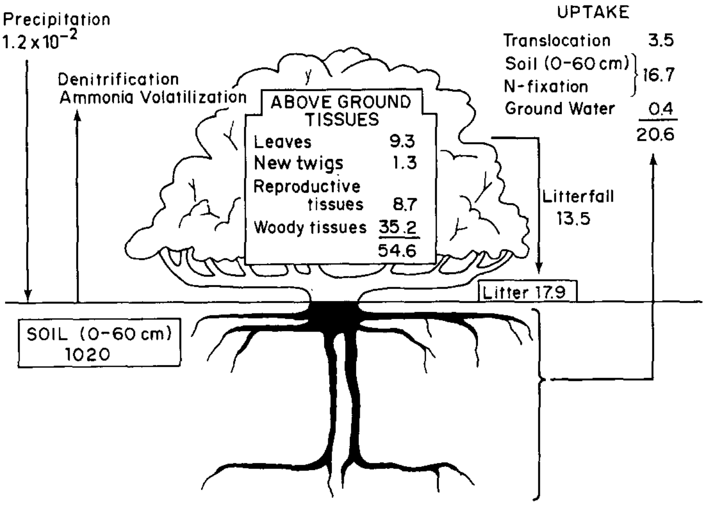

Fig. 6. Nitrogen cycling beneath the *Prosopis glandulosa* canopy. Units for N pools are g N m^{-2}, and for fluxes, g N m^{-2} yr^{-1}. Uptake is based on above-ground biomass only.

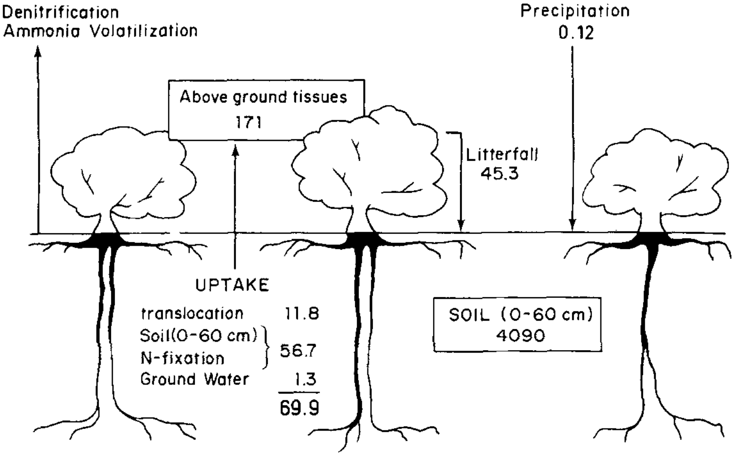

Fig. 7. Nitrogen cycling in a *Prosopis glandulosa* community in the Sonoran Desert, California. Biomass-N pools (kg N ha^{-1}) and fluxes (kg N ha^{-1} yr^{-1}) are for *Prosopis glandulosa*, and uptake is based on above-ground biomass only.

the growing season (during March), and then a rapid decline that continued through April. Very little net accumulation of nitrogen in leaves took place through the early summer, and by mid-summer there was a net loss of nitrogen from the above-ground biomass as leaf abscission began to occur (Fig. 5).

Nitrogen fluxes

Most external inputs and outputs from our system are relatively easy to account for since they are so small. For the inputs, we have considered precipitation input, animal inputs, and nitrogen fixation. With a mean annual precipitation of only 70 mm, we calculate that precipitation inputs of nitrogen are only about 1.2×10^{-2}g N m^{-2} yr^{-1} (assuming a mean rainwater-N concentration of 0.17 mg Nl^{-1}; Schlesinger and Hasey[13]). Animal inputs through fecal accumulation by vertebrates is primarily an internal recycling factor in our Prosopis stand, but some very small net input of nitrogen may come from birds or larger carnivores which feed outside the stand. Nitrogen fixation is a very important input, however. While our preliminary data suggest that free-living fixation by bacteria, bluegreen algae and lichens is very small, we present data below to suggest that symbiotic fixation by nodules of Prosopis must be very great.

Outputs of nitrogen from our ecosystem could occur through leaching, ammonia volatilization, denitrification and erosion. Although we have not directly measured the first two of these fluxes, they are clearly negligible factors because of the very low levels of precipitation, low soil ammonia concentrations, and a soil pH of 7–7.5, which should inhibit ammonia volatilization[6]. Our measurements of denitrification using the acetylene inhibition method[13] suggest that about 0.05 g N m^{-2} of canopy cover is lost following a 50 mm artificial rainfall, but this amount is again insignificant in the overall nitrogen budget[20]. Nitrogen lost by erosion and surface runoff is difficult to quantify. In the majority of years, as in 1980, there is no significant nitrogen loss by erosion. During exceptional years, however, sheet flow flooding across the stand can be considerable; it clearly has occurred in the past. While such events may only occur a few times a century, they are an important consideration in long-term models of nitrogen cycling.

Using our data for 1980 we have calculated a simple flow model for nitrogen cycling beneath the canopy of Prosopis at Harper's Well (Fig. 6). Of the 54.6 g N m^{-2} of above-ground biomass nitrogen beneath the canopy, 20.3 g N m^{-2} was in new leaves and twigs, reproductive tissues and the new increment of woody tissues. The quantity of nitrogen reabsorbed before leaf tissue loss by abscission is a minimum estimate for nitrogen which could be translocated from stored tissues into the new nitrogen pool (11.8 kg N ha^{-1} yr^{-1}). From measurements of seasonal transpiration fluxes through the foliage of the Prosopis canopies[10], we can calculate that only about 0.04 g m^{-2} of nitrogen uptake could occur from groundwater (where NO_3–N is present at 1 mg N l^{-1} or less). The remaining 16.7 g N m^{-2} taken up must come from a combination of uptake from surface roots and from symbiotic nitrogen fixation. This, of course, is a minimum estimate since we do not know the quantity of nitrogen accumulated in roots.

On a system-wide basis the net nitrogen uptake by above-ground Prosopis biomass is 69.8 kg N ha^{-1} yr^{-1} (Fig. 7). Of this total, 56.7 g m^{-2} comes from the combination of surface root uptake and symbiotic nitrogen fixation.

Nitrogen fixation

What evidence is there that symbiotic nitrogen fixation is taking place in these stands? First, nodules have been found on a young Prosopis individual growing in a moist wash in early spring. However, no nodules have been found in surface soils under larger trees. Second, measurements of the natural ^{15}N abundance of soil and Prosopis tissues indicate an input of symbiotically-fixed nitrogen[8, 19]. Since the $^{15}N/^{14}N$ ratio of soil nitrogen usually exceeds that of the atmosphere, plants that fix N_2 have $^{15}N/^{14}N$ ratios below those of soil nitrogen and associated non-nitrogen-fixing plants[1, 7, 16]. With appropriate sampling techniques, the magnitude of this difference should be proportional to the amount of nitrogen fixed[4]. While our studies of ^{15}N abundance are still in a preliminary stage, our data indicate that nitrogen fixation is actively occurring in *Prosopis glandulosa*. These data suggest that possibly as much as about 50% of total nitrogen uptake may come from fixation.

Our second line of evidence that fixation is important comes from an analysis of the long-term dynamics of nitrogen cycles in our Prosopis stand. Our study site at Harper's Well is located on the old bottom deposits from Lake Cahuila, which covered the present Salton Sea basin up until very recent times. Archeological data suggest that the lake dried *ca.* 400–500 yrs BP. Thus we have a maximum stand age for our calculations. If we take the present canopy soil nitrogen (1020 g N m^{-2}) and subtract the background soil nitrogen (45 g N m^{-2}) from adjacent non-Prosopis sites, we calculate a differential nitrogen accumulation under Prosopis canopies of 975 g N m^{-2}. Assuming a 500 year stand age, the mean annual nitrogen accumulation has been *ca.* 1.95 g N m^{-2} of canopy for this period. On a stand basis this is slightly over 6 kg N ha^{-1} yr^{-1}. Since fixation is the only significant system input of nitrogen, these values represent a minimum figure for mean annual levels of fixation. Expected erosional losses at irregular intervals over the 500 year period would likely increase this maximum level considerably. Since above-ground Prosopis biomass is only 50–75 yrs old (by ring counts), the nitrogen found beneath the Prosopis individuals has probably accumulated over a much briefer time period than the maximum of 500 yrs.

The actual mean level of nitrogen fixation in our stand is undoubtedly higher than our minimum estimates. Erosional losses of nitrogen in irregular surface runoff in the stand certainly occur at irregular intervals. If such losses were of sufficient magnitude to cycle soil nitrogen on a 100 year rather than a 500 year cycle, then stand nitrogen fixation could be about 30 kg N ha^{-1} yr^{-1}. Another estimate of nitrogen fixation can be based on our preliminary figures from ^{15}N abundance measurements that approximately 50% of the total uptake comes from fixation. This suggests that at least 23–36 kg N ha^{-1} yr^{-1} is fixed on a stand basis; including the below-ground nitrogen accumulation in root production may increase this estimate to >40 kg N ha^{-1} yr^{-1}.

These estimated rates of nitrogen fixation in our Prosopis stand are quite similar to those reported for other natural communities in regions with much higher levels of precipitation[12, 18]. Since the high levels of nitrate in the upper 60 cm of soil probably inhibit nodule formation[5], it is not surprising that we have not found nodules in the surface root zone. We hypothesize that nodulation is currently restricted in our stand to the capillary fringe above the ground water table.

Conclusions

The high levels of production and nitrogen fixation we have measured in Prosopis suggest that managed woodlands may provide economically significant sources of wood fuels and forage for sheep or goats. The low total coverage of Prosopis in natural stands is almost certainly related to problems of seedling establishment[9, 17] and not resource availability. So long as water resources do not become limiting, our study suggests that stand levels of nitrogen fixation as high as 150 kg N ha^{-1} yr^{-1} might be possible with plantation growth of selected genotypes of *Prosopis glandulosa*[3]. Such a level would be close to that reached in agricultural production of alfalfa or soybeans. Plantation productivity of Prosopis could be as high as 15,000 kg ha^{-1} yr^{-1}, equally split between new woody tissues and high-quality forage[10].

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