

# Carbon-nitrogen interactions in fertility island soil from a tropical semi-arid ecosystem

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## Summary

1. Biological nitrogen (N) fixation by symbiotic and free-living organisms is considered the main pathway for N soil enrichment in desert and semi-desert ecosystems. This fact is more noticeable in tropical ecosystems where legume species have a high relative abundance. However, this biological fixation pathway does not guarantee the maintenance of soil N pools, and N conservation pathways are important in understanding controls over soil N cycling.

2. In dryland ecosystems, desert plants can form a 'fertility island' (FI) as soils beneath plants show higher concentrations of N and organic matter.

3. Here we assess how carbon (C) and N may interact to conserve soil N within the FI soil of two legume species (*Prosopis laevigata* and *Parkinsonia praecox*), one a known N-fixer and the other believed not to fix N, as well as within adjacent bare ground soil. In a semi-arid tropical ecosystem in central Mexico, we examined spatial patterns in C and N pools and transformation rates, and we investigated seasonal variations in these relationships.

4. Results show that FI soil C and N could be linked to total N storage through net C and N immobilization in microbial biomass and heterotrophic microbial activity. Soil under *P. laevigata* canopy had greater total N as well as N accumulated in microbial biomass than soil under *P. praecox* and bare ground soil. Nevertheless, inorganic N and potential net N mineralization rates were similar under soils of both species, although we expected higher inorganic N and N-mineralization values in N-fixer species to explain the greater total N. Higher total N concentrations under *P. laevigata* probably result from greater inputs of organic C and a higher potential net C mineralization rate in comparison to *P. praecox* and bare ground soil.

5. Even though N input and output values were not measured, the results highlight the importance of assessing the role of organic C, heterotrophic microbial activity, and N storage in microbial biomass in order to understand controls over N retention in soil N cycling. Thus, soil C-N interactions could be a control factor of N soil conservation in this tropical semi-arid ecosystem.

**Key-words:** available N, C and N immobilization in microbial biomass, C and N mineralization, fertility islands, nitrification, *Parkinsonia praecox*, *Prosopis laevigata*, Tehuacán-Cuicatlán Region

## Introduction

Nitrogen (N) limits primary productivity in many terrestrial ecosystems, among them arid and semi-arid systems (West & Skujinš 1978; Peterjohn & Schlesinger 1990). The main N input pathways available to soil are N biological fixation, organic N mineralization to inorganic forms, and atmo-

spheric deposition (Paul & Clark 1996). The relative contribution of the different N input pathways can vary in different ecosystems (Vitousek *et al.* 2002). In arid and semi-arid ones, atmospheric deposition is typically not the main source of N soil input (West & Skujinš 1978). On the other hand, N biological fixation by cyanobacteria in soil crusts and by bacterial symbionts associated with legumes is considered to be an important soil N input pathway, although the quantities of N fixed through these pathways are relatively small (West & Skujinš 1978; Rhychert and Skujinš 1974). However, N fixation input, whether by

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free-living or symbiotic bacteria, does not guarantee that incorporated N is preserved in soil. For example, there is evidence showing that cyanobacteria are inefficient in retaining N, and it is estimated that losses caused by denitrification constitute up to 99% of fixed N (West & Skujinš 1978; Peterjohn & Schlesinger 1990; Vitousek *et al.* 2002 and content references).

Biological N fixation by bacterial symbionts is considered an even more important N input pathway to the soil of dry and semiarid tropical ecosystems than to soils of temperate or boreal ecosystems that have a lower abundance of legume plants (Vitousek & Sanford 1986; Sprent *et al.* 1996; Castellanos *et al.* 2001; Altamirano-Hernández *et al.* 2004; González-Ruiz *et al.* 2008). Nevertheless, regardless of legume dominance, the availability of water and nutrients other than N (mainly P) can limit N fixation rates in terrestrial ecosystems, and may also regulate soil N conservation.

Nitrogen limitation in arid ecosystems may be exacerbated by high soil N losses due to erosion, leaching, and ammonia volatilization and/or denitrification. If these outputs exceed N inputs from biological N fixation, soil N pools would be expected to decline. Thus, pathways that inhibit soil N from loss will allow the building and maintenance of soil N pools; while our understanding of N conservation in dryland ecosystems remains incomplete, there is a growing body of evidence that suggests that carbon (C) and N interactions may promote soil conservation in a variety of ecosystems (Castellanos *et al.* 2001; Vitousek *et al.* 2002; Teixeira *et al.* 2006; González-Ruiz *et al.* 2008).

The mineralization of organic C caused by heterotrophic microbial activity may form part of a mechanism favouring N retention in soil due to a reduction in the intensity of processes that convert N to forms that are highly susceptible to loss in soil (i.e. nitrification; Montaña, García-Oliva & Jaramillo 2007). At the same time, it can promote the immobilization of N in microbial biomass, leaving N free from other loss pathways such as erosion, leaching, ammonia volatilization, and denitrification. Several studies have shown direct relationships between microbial activity, C storage in soil, and N retention in microbial biomass (Vitousek & Matson 1984 in temperate forest ecosystems; Montaña, García-Oliva & Jaramillo 2007 in dry tropical forest; for other ecosystems, see Vitousek *et al.* 2002).

Soil N distribution in arid and semi-arid zones is related to the occurrence of Fertility Islands (FIs). FIs are defined as desert trees or shrubs, usually legumes, with high N and organic matter concentrations under their canopies, contrasting with areas outside canopies (García-Moya & Mckell 1970; Tiedemann & Klemmedson 1973; Charley & West 1975; Virginia & Jarrel 1983; Cross & Schlesinger 1999). Synonyms are 'N accumulation patches' (Nishita & Haug 1973; Charley & West 1975), 'fertile islands' (Garner & Steinberger 1989), and 'resource islands' (Schlesinger *et al.* 1990, 1996; Camargo-Ricalde & Shivcharn 2003). It is not clear how FI mechanisms can maintain N in FI soil (Barth & Klemmedson 1982). Understanding these retention mechanisms is vital because FIs affect the productivity of other organisms, such

as plants growing under their canopy (Schlesinger 1997; Schlesinger & Pilmanis 1998; Aguiar & Sala 1999; Puigdefábregas & Pugnaire 1999) and can affect plant species richness, abundance, and the quality of interactions in their area of influence (Escudero *et al.* 2004; Perroni-Ventura, Montaña & García-Oliva 2006). Usually, FIs have been given properties of biological N fixation by bacterial symbionts, but not all species that promote FIs have the ability to fix N (Allen & Allen 1981; Sprent 1987; Bryan, Berlyn & Gordon 1996).

Based on the assumption that C-N interactions regulate soil N availability and conservation, this paper explores C-N interactions in soil under the canopy of two FI legume species (*Prosopis laevigata* and *Parkinsonia praecox*) and bare ground areas adjacent to FI species during wet and dry seasons in a tropical semi-arid ecosystem in central Mexico. It is assumed that C mineralization carried out by heterotrophic soil microbiota promotes maintenance of a portion of soil N in high-energy reduced forms less susceptible to leaching and denitrification (i.e. ammonium and N in microbial biomass). Thus, it is expected that (a) the predominant N mineral form is ammonium, not nitrate; (b) the relationship between C mineralization and different N pools (i.e. total N, ammonium, and N in microbial biomass) is positive; and (c) a positive outcome of the relationship between net N immobilization in microbial biomass and net N mineralization occurs during the wet season (i.e. when conditions for leaching or volatilization are expected to increase).

## Materials and methods

### STUDY AREA

The study was done in the Zapotitlán Valley (18°20'N, 97°28'W), a local basin in the Tehuacán Valley in the state of Puebla, Mexico. The bottom of the valley (1400 m a.s.l.) has a mean temperature of 21 °C with rare freezing events and receives an average rainfall of 380 mm y<sup>-1</sup> with a wet summer seasonal precipitation pattern. Soil is Xerosol marine sediment limestone rock derived; it consists of 41% sand, 37% silt, and 22% clay in the first 20 cm (C. Montaña, unpublished data). According to Leopold (1950), this area corresponds to 'arid tropical scrub' dominated by shrubs and small trees (under 3 m tall), interspersed with columnar cacti of over 10 m (Dávila *et al.* 1993; Montaña & Valiente-Banuet 1998). In contrast to semi-arid zones in North American desert with FIs, at present Zapotitlán Valley vegetation is not grassland derived but, in all likelihood, comes from tropical dry forest (Rzedowski 1978). Root production of up to a depth of 15 cm has been estimated at 14 kg ha<sup>-1</sup> y<sup>-1</sup> (Pavón, Briones & Flores-Rivas 2005).

### FI SPECIES STUDIED

*Prosopis laevigata* (Humb. & Bonpl. Ex Willd.) and *Parkinsonia (Cercidium) praecox* (Ruíz & Pavón) Hawkins coexist in similar densities as small trees in Zapotitlán Valley.

*Prosopis laevigata* has N fixation reports (see Eskew & Ting 1978; Felker & Clark 1980; Allen & Allen 1981) and is evergreen (Pavón & Briones 2001). *Prosopis praecox* is a non N-fixing species (see Allen & Allen 1981; Sprent 1987; Bryan, Berlyn & Gordon 1996), and is deciduous in the dry season (Pavón & Briones 2001). Both species have a

wide distribution across the American continent (Evenari, Noy-Meir & Goodall 1985). Perroni-Ventura, Montaña & García-Oliva (2006) found that soil nutrient concentrations (e.g. N and P) varied under the canopy of both species and that this variability was correlated with plant species richness and abundance. Barth & Klemmedson (1982) noted a link between shrub size and N accumulation in soil under its canopy for one *Prosopis* (*P. juliflora*) and one *Cercidium* (*C. floridum*) species, the former corresponding to a greater accumulation of N in its soil than the same size *Cercidium* shrub.

#### SOIL SAMPLING

Sampling points covered most of the valley area (ca. 45 km<sup>2</sup>) between 1400 and 1600 m a.s.l. Mineral soil at a depth of 0–10 cm was collected from 20 randomly selected sampling points. Three different microsites or microhabitats were sampled at each sampling point (under *FI-P. laevigata* canopy; under *FI-P. praecox*, and in bare areas). To control effects due to tree size, we selected individuals of similar size for each sampling point species pair. *P. laevigata* canopy cover varied from 3.3 to 40.9 m<sup>2</sup> and plant height varied from 2.1 to 3.6 m, while *P. praecox* canopy cover varied from 5.8 to 39.0 m<sup>2</sup> and plant height from 2.4 to 3.6 m. To control effects due to soil heterogeneity and topographical position, bare areas and bases of the two trees at each sampling point were located no more than 20 m apart. Soil sampling was done at the end of the wet season (October) in 2001 and again at the end of the dry season (April) in 2002. In each case, three sub-samples (pooled afterward to compose a single composite sample) were collected beneath the canopy of ten individuals from each FI species and ten from bare areas. Under trees, each of the three sub-samples was collected in an area 5–35 cm from the trunk. In bare areas, three subsamples were collected from around a central point on a 5 m<sup>2</sup> plot that was far from any shrub or tree. All soil samples were stored in black bags and kept at ca. 4 °C for ca. one month before analysis.

#### LABORATORY ANALYSIS

In order to ascertain the degree of soil alkalinity, active soil pH was measured in a solution with one part soil and five parts water. Pool sizes of total C and N, available C and N (TOC and inorganic N, respectively), and microbial C and N were estimated in both FIs and bare areas. Organic C concentration was determined with an automatic CO<sub>2</sub> analyzer UIC model CM5012. Total N soil concentration was measured after acid digestion with Kjeldahl's modified method (Technicon Industrial System 1977) using a Braun-Luebbe auto analyzer 3 (Norderstedt, Germany). Available forms of N (ammonium and nitrate) were analyzed with the Binkley & Hart method (1989) using a Braun-Luebbe auto analyzer 3 (Norderstedt, Germany). Soil microbial form estimation was carried out through the measurement of C concentration ( $C_{mic}$ ) and microbial biomass N ( $N_{mic}$ ) with the Brookes *et al.* (1985) fumigation-extraction chloroform method, using efficiency values postulated by Joergensen (1996).  $C_{mic}$  was determined in a UIC model CM5012 CO<sub>2</sub> automatic analyzer and  $N_{mic}$  in a Braun-Luebbe auto analyzer 3 (Norderstedt, Germany). Due to the high carbonate concentration at our study sites, we subtracted inorganic C values measured in a CO<sub>2</sub> automatic analyzer UIC model CM5012 from  $C_{mic}$  extracts. The organic soluble C value obtained from non-fumigated extractions was considered labile C.

To estimate C transformation and the potential rate at which N becomes available in soil, the potential net C mineralization rate (PNCMR) was determined as well as net N mineralization (NNM).

Also, net nitrification (NN) was used as an estimate of potential ammonium transformation into soil nitrate (Paul & Clark 1996) and as a potential estimate of nitrifying microbial activity (Binkley & Hart 1989). PNCMR was estimated on the basis of the Coleman *et al.* (1978) method, by measuring CO<sub>2</sub>-C collected in soil-incubated NaOH traps in a growth chamber at 25 °C for 13 days, humidified with deionized water to maintain the soil field's capacity. NNM was estimated as net ammonification plus net nitrification according to Binkley & Hart (1989). NN was calculated based on nitrate concentration at the end of an incubation period, subtracting nitrate concentration before incubation (Binkley & Hart 1989). Net N and C immobilization in microbial biomass ( $NN_{micI}$  and  $NC_{micI}$ ) was used as a measure of soil N protection from losses by leaching and/or denitrification (Paul & Clark 1996) as well as from microbial turnover (see Luo *et al.* 2006).  $NN_{micI}$  and  $NC_{micI}$  were calculated on the basis of the difference between final and initial incubation concentrations, according to Binkley & Hart (1989).

#### STATISTICAL ANALYSIS

Seasonal variations in pH, total and available C, and N pools from the field samples were statistically examined with a split-plot ANOVA (Montgomery 1991) with microsite ( $n = 20$ , under *P. laevigata* and *P. praecox* canopies and bare areas) as main plot and season as subplot ( $n = 2$ , wet and dry season). This approach was also used to analyze  $C_{mic}$ ,  $N_{mic}$ , labile C and  $NN_{micI}$  ( $n = 10$ ),  $NC_{micI}$  ( $n = 9$ ), and C and N transformation rates (PNCMR, NNM, and NN;  $n = 20$ ) with data from the incubation study. Box-Cox transformations were performed to normalize data when necessary. We compared interaction means using Tukey's honestly significant difference (HSD) with Bonferroni's sequential correction (Rice 1989). The relationships between nutrient pools and transformation rates (independent variables) and certain potential fluxes (net nitrification and net C mineralization rate; dependent variables) in each season were analyzed by stepwise multiple-regression analyses. The model used to analyze net nitrification included PNCMR, ammonium, nitrate, TOC, total N,  $C_{mic}$ ,  $N_{mic}$ , and labile C as independent variables. The model used to analyze the potential net C mineralization rate included NNM, NN, ammonium, nitrate, TOC, total N,  $C_{mic}$ ,  $N_{mic}$ , and labile C as independent variables. Only independent variables with a statistically significant ( $P \leq 0.05$ ) slope were accepted in each model. Net C and N immobilization frequency distributions for all soil samples in each season were done to observe seasonal variations of soil N protected by microbial biomass. All statistical analyses were performed using S-PLUS 2.1 software (Mathsoft 1999).

## Results

#### SOIL PH

Water and CaCl<sub>2</sub> pH were slightly more alkaline in bare areas ( $8.6 \pm 0.04$  in water) than in soils under *P. laevigata* and *P. praecox* ( $8.5 \pm 0.03$  in water), but only water pH differed according to season ( $8.6 \pm 0.03$  in the wet season vs. the dry season  $8.5 \pm 0.03$  in the season; Tables 1–3).

#### CONCENTRATION OF TOTAL AND MICROBIAL C AND N POOLS

Total C and N,  $C_{mic}$ , and  $N_{mic}$  pools were different among microsites but did not differ between seasons (Table 1). The

Response	Factors					
	Microsite		Season		Microsite × Season	
	F	P	F	P	F	P
pH						
pH (H <sub>2</sub> O)	8.4	0.001	10.8	0.002	1.1	0.3
pH (CaCl <sub>2</sub> )	21.0	<0.0001	1.9	0.2	1.1	0.4
Total forms						
TOC	22.3	<0.0001	1.8	0.1	1.7	0.2
Total N	63.6	<0.001	0.7	0.4	0.4	0.4
C : N ratio	7.66	0.002	0.234	0.6	2.57	0.09
Microbial pools						
C <sub>mic</sub>	15.12	0.0001	1.98	0.2	0.47	0.6
N <sub>mic</sub>	15.1	0.0001	1.18	0.3	2.26	0.1
Available pools						
Labile C	11.1	0.0007	42.6	<0.0001	0.01	0.9
NH <sub>4</sub> <sup>+</sup> -N	51.4	<0.0001	133.8	<0.0001	0.48	0.6
NO <sub>3</sub> <sup>-</sup> -N	3.91	0.03	3.48	0.07	6.2	0.005
Potential fluxes						
PNCMR	107.5	<0.0001	16.9	0.0002	1.8	0.2
NNM	4.8	0.01	0.2	0.7	0.2	0.9
NN	61.5	<0.0001	77.4	<0.0001	0.6	0.6

FI, fertility island; TOC, total organic carbon; C<sub>mic</sub>, microbial C; N<sub>mic</sub>, microbial N; NH<sub>4</sub><sup>+</sup>, N Ammonium; NO<sub>3</sub><sup>-</sup>, N Nitrate; PNCMR, potential carbon mineralization rate; NNM, net nitrogen mineralization; NN, net nitrification.

concentrations of Total C and Total N were highest in soil under *P. laevigata* (29.7 ± 2.3 and 2.9 ± 0.1 mg g<sup>-1</sup> dry-soil respectively), intermediate under *P. praecox* (22.1 ± 1.6 and 1.9 ± 0.1 mg g<sup>-1</sup> dry-soil) and lowest in bare areas (15.3 ± 1.3 and 1.2 ± 0.1 mg g<sup>-1</sup> dry-soil, Table 2). The highest concentrations of C<sub>mic</sub> were under tree canopies (1127.4 ± 132.1 and 880.7 ± 104.6 µg g<sup>-1</sup> dry-soil under *P. laevigata* and *P. praecox* respectively). The concentration of N<sub>mic</sub> was higher (81.4 ± 9.0 µg g<sup>-1</sup> dry-soil under *P. laevigata*) than under the soil of *P. praecox* (53.7 ± 8.0 µg g<sup>-1</sup> dry-soil) and both concentrations were higher than that found in

bare areas (29.3 ± 4.0 µg g<sup>-1</sup> dry-soil Table 2). The C : N ratio was higher in bare areas (15.2 ± 1.7) than under *P. laevigata* (10.3 ± 0.6) and had an intermediate value under *P. praecox* (11.7 ± 0.8, Table 2), which indicates greater concentrations of recalcitrant elements in open areas than under *P. laevigata* canopies.

#### CONCENTRATION OF ACTIVE OR AVAILABLE FORMS

Labile C showed greater concentrations in soil under FI species canopies (118.9 ± 14.9 and 109.4 ± 11.7 µg g<sup>-1</sup> dry-soil

Variable	n	Microsite					
		Bare area		<i>P. praecox</i>		<i>P. laevigata</i>	
		Mean	±SE	Mean	±SE	Mean	±SE
pH (H <sub>2</sub> O)	40	8.6 <sup>b</sup>	0.04	8.5 <sup>a</sup>	0.03	8.4 <sup>a</sup>	0.03
pH (CaCl <sub>2</sub> )	40	8.2 <sup>b</sup>	0.03	8.0 <sup>a</sup>	0.03	8.0 <sup>a</sup>	0.03
TOC (mg g <sup>-1</sup> dry soil)	40	15.3 <sup>a</sup>	1.3	22.1 <sup>b</sup>	1.6	29.7 <sup>c</sup>	2.3
Total N (mg g <sup>-1</sup> dry soil)	40	1.2 <sup>a</sup>	0.1	1.9 <sup>b</sup>	0.1	2.9 <sup>c</sup>	0.1
C : N ratio	40	15.2 <sup>b</sup>	1.7	11.7 <sup>ab</sup>	0.8	10.3 <sup>a</sup>	0.6
C <sub>mic</sub> (µg g <sup>-1</sup> dry soil)	20	328.2 <sup>a</sup>	79.5	880.7 <sup>b</sup>	104.6	1127.4 <sup>b</sup>	132.1
N <sub>mic</sub> (µg g <sup>-1</sup> dry soil)	20	29.3 <sup>a</sup>	4.0	53.7 <sup>b</sup>	8.0	81.4 <sup>c</sup>	9.0
Labile C (µg g <sup>-1</sup> dry soil)	20	61.6 <sup>a</sup>	10.0	109.4 <sup>b</sup>	11.7	118.9 <sup>b</sup>	14.9
NH <sub>4</sub> <sup>+</sup> -N (µg g <sup>-1</sup> dry soil)	40	4.0 <sup>a</sup>	0.7	11.6 <sup>b</sup>	2.0	11.5 <sup>b</sup>	1.4
PNCMR (µg g <sup>-1</sup> dry soil)	40	12.6 <sup>a</sup>	1.4	37.1 <sup>b</sup>	2.0	45.2 <sup>c</sup>	2.9
NNM (µg g <sup>-1</sup> dry soil)	40	1.5 <sup>a</sup>	0.6	3.5 <sup>b</sup>	1.7	5.2 <sup>b</sup>	1.3
NN (µg g <sup>-1</sup> dry soil)	40	5.0 <sup>a</sup>	0.6	12.1 <sup>b</sup>	0.9	13.0 <sup>b</sup>	1.2

Different letters in each row mean significant differences according to Tukey's honestly significant difference (HSD), with Bonferroni's sequential correction ( $P \leq 0.05$ ). For abbreviations, see Table 1

**Table 1.** F-values for split-plot ANOVA with microsite as main plot (under FI-*P. laevigata* and FI-*P. praecox* canopies, and bare areas) and season as sub-plot (wet and dry season) in total, microbial, and available C and N pools, and potential C and N transformations in a tropical semi-arid ecosystem in central Mexico

**Table 2.** Mean values ± SE in pH, total, microbial, and available C and N pools, and potential C and N transformations per microsite (under FI-*P. laevigata* and FI-*P. praecox* canopies and in bare areas) in a tropical semi-arid ecosystem in central Mexico

**Table 3.** Mean values  $\pm$  SE in pH, available C and N pools, and potential C and N transformations in accordance with season (wet and dry) in a tropical semi-arid ecosystem in central Mexico. For abbreviations, see Table 1

Variable	n	Season			
		Wet season		Dry season	
		Mean	$\pm$ SE	Mean	$\pm$ SE
pH (H <sub>2</sub> O)	60	8.6	0.03	8.5	0.03
Labile C ( $\mu\text{g g}^{-1}$ dry soil)	30	126.2	8.2	67.1	10.7
NH <sub>4</sub> <sup>+</sup> -N ( $\mu\text{g g}^{-1}$ dry soil)	60	4.0	0.3	14.1	1.5
PNCMR ( $\mu\text{g g}^{-1}$ dry soil)	60	35.9	2.6	27.4	2.3
NN ( $\mu\text{g g}^{-1}$ dry soil)	60	6.7	0.5	13.4	0.9

under *P. laevigata* and *P. praecox* respectively) than in bare areas ( $61.6 \pm 10.0 \mu\text{g g}^{-1}$  dry-soil). Similar results were obtained for ammonium ( $11.5 \pm 1.4$  and  $11.6 \pm 1.0 \mu\text{g g}^{-1}$  dry-soil under *P. laevigata* and *P. praecox* respectively vs.  $4.0 \pm 0.7 \mu\text{g g}^{-1}$  dry-soil in bare areas, Table 2). But there were contrasting seasonal differences (Tables 1 and 3). While labile C decreased in the dry season ( $126.2 \pm 8.2 \mu\text{g g}^{-1}$  dry-soil in the wet season against  $67.1 \pm 10.7 \mu\text{g g}^{-1}$  dry-soil in the dry season), ammonium increased from  $4.0 \pm 0.3 \mu\text{g g}^{-1}$  dry-soil in the wet season up to  $14.1 \pm 1.5 \mu\text{g g}^{-1}$  dry-soil in the dry season, Table 3). Nitrate was the only nutrient which showed an interaction between season and microsite (Table 1). This interaction resulted from the fact that nitrate concentration was greater under tree canopies in the dry season ( $2.9 \pm 0.6$  and  $2.3 \pm 0.5 \mu\text{g g}^{-1}$  dry-soil under *P. laevigata* and *P. praecox* against  $0.9 \pm 0.3 \mu\text{g g}^{-1}$  dry-soil in bare areas), while no between microsite-differences were found during the wet season ( $1.6 \pm 0.5$ ,  $1.5 \pm 0.6$  and  $1.9 \pm 0.6 \mu\text{g g}^{-1}$  dry-soil under *P. laevigata*, *P. praecox* and open areas, Table 4). Soil in those three microsites showed a greater ammonium concentration (ca. 2.5-fold in the wet season and ca. 7-fold in the dry season) than nitrate concentration ( $4.0 \pm 0.3$  against  $1.7 \pm 0.5 \mu\text{g g}^{-1}$  dry-soil for ammonium;  $14.1 \pm 1.5$  against  $2.0 \pm 0.5 \mu\text{g g}^{-1}$  dry-soil for

**Table 4.** Nitrate mean values  $\pm$  SE in accordance with microsite-season interaction in a tropical semi-arid ecosystem in central Mexico. For abbreviations, see Table 1

Variable	n	Bare area	<i>Parkinsonia praecox</i>	<i>Prosopis laevigata</i>
NO <sub>3</sub> <sup>-</sup> -N ( $\mu\text{g g}^{-1}$ dry soil) - wet season	20	$1.9 \pm 0.6^a$	$1.5 \pm 0.6^a$	$1.6 \pm 0.5^a$
NO <sub>3</sub> <sup>-</sup> -N ( $\mu\text{g g}^{-1}$ dry soil) - dry season	20	$0.9 \pm 0.3^a$	$2.3 \pm 0.5^b$	$2.9 \pm 0.6^b$

nitrate, Tables 3 and 4). All available forms were greater under canopies than in open areas (Tables 2 and 4).

#### POTENTIAL FLUXES (PNCMR, NNM, NN)

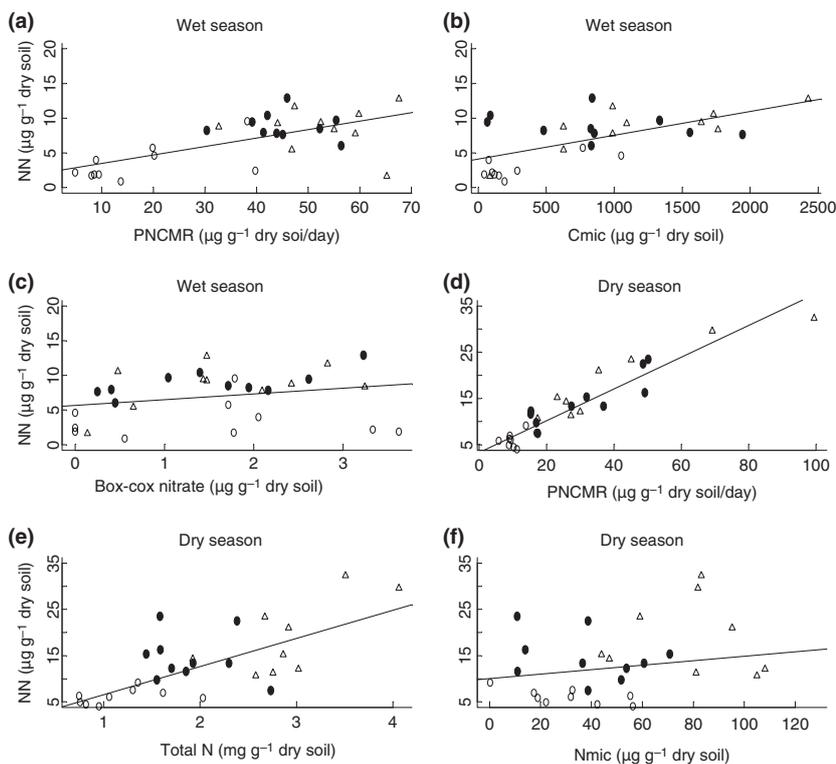
PNCMR differed among microsites ( $45.2 \pm 2.9$ ,  $37.1 \pm 2.0$  and  $12.6 \pm 1.4 \mu\text{g g}^{-1}$  dry-soil under *P. laevigata*, *P. praecox* and open areas respectively, Tables 1 and 2) and was greater in the wet season ( $35.9 \pm 2.6 \mu\text{g g}^{-1}$  dry-soil) than in the dry season ( $27.4 \pm 2.3 \mu\text{g g}^{-1}$  dry-soil, Tables 1 and 3). NNM was higher under tree canopies ( $5.2 \pm 1.3$  and  $3.5 \pm 1.7 \mu\text{g g}^{-1}$  dry-soil under *P. laevigata* and *P. praecox* respectively) than in open areas ( $1.5 \pm 0.6 \mu\text{g g}^{-1}$  dry-soil, Tables 1 and 2), and, contrary to differences in the other potential fluxes, did not show seasonal variability (Table 1). NN was also greater under FI canopies ( $13.0 \pm 1.2$  and  $12.1 \pm 0.9 \mu\text{g g}^{-1}$  dry-soil under *P. laevigata* and *P. praecox* respectively) than in open areas ( $5.0 \pm 0.6 \mu\text{g g}^{-1}$  dry-soil, Tables 1 and 2) but greater during the dry season ( $13.4 \pm 0.9 \mu\text{g g}^{-1}$  dry-soil) than during the wet season ( $6.7 \pm 0.5 \mu\text{g g}^{-1}$  dry-soil, Tables 1 and 3).

#### SOIL C-N INTERACTIONS

PNCMR, C<sub>min</sub>, and nitrate were positively related to NN in the wet season (Table 5, Fig. 1a–c). In the dry season PNCMR, total N, and N<sub>mic</sub> were the variables positively

**Table 5.** Stepwise multiple regression analyses of nutrient pools and transformation rates (dependent variables) with certain potential fluxes (net nitrification and potential net C mineralization rate; independent variables) in a tropical semi-arid ecosystem in central Mexico. Only independent variables with a statistically significant slope at  $P \leq 0.05$  were included in each model. For abbreviations, see Table 1

Dependent variable	Regression models- Wet season <sup>a</sup>	R <sup>2</sup>	P
Net nitrification (All microsites)	$-0.173 + 0.088(\text{PNCMR}) + 2.169(\text{C}_{\text{mic}}) + 1.263[(\text{NO}_3^- \text{-N} + 1)^{-1} - 1 / -0.25]$	0.7	<0.0001
Potential net C mineralization rate (Bare area)	$21.327 + 8.18(\text{N}_{\text{Total}}) + 0.0105(\text{NNM}) + 0.116(\text{NH}_4^+ \text{-N})$	0.9	<0.0001
( <i>P. praecox</i> )	$40.786 + 2.90(\text{N}_{\text{Total}}) + 0.0105(\text{NNM}) + 0.116(\text{NH}_4^+ \text{-N})$		
( <i>P. laevigata</i> )	$22.380 + 9.01(\text{N}_{\text{Total}}) + 0.0105(\text{NNM}) + 0.116(\text{NH}_4^+ \text{-N})$		
	Regression models- Dry season <sup>a</sup>		
Net nitrification (All microsites)	$2.38 + 0.304(\text{PNCMR}) + 2.063(\text{N}_{\text{Total}}) - 0.041(\text{N}_{\text{mic}})$	0.9	<0.0001
Potential net C mineralization rate (Bare area)	$1.113 + 1.194(\text{NNM}) + 13.034(\text{C}_{\text{mic}}) + 1.918(\text{NH}_4^+ \text{-N}) - 4.557(\text{N}_{\text{Total}})$	0.9	<0.0001
( <i>P. praecox</i> )	$-8.141 + 2.067(\text{NNM}) + 13.034(\text{C}_{\text{mic}}) + 1.918(\text{NH}_4^+ \text{-N}) - 4.557(\text{N}_{\text{Total}})$		
( <i>P. laevigata</i> )	$-7.229 + 1.645(\text{NNM}) + 13.034(\text{C}_{\text{mic}}) + 1.918(\text{NH}_4^+ \text{-N}) - 4.557(\text{N}_{\text{Total}})$		



**Fig. 1.** Relationships between NN and several independent variables in soils from a tropical semi-arid ecosystem in central Mexico. Regressions were done by pooling data from different microsites: under *FI-P. laevigata* (triangles) and *FI-P. praecox* (closed circles) canopies and in bare areas (open circles). (a–c) Relationships in a wet season model. (d–f) Relationships in a dry season model, see Table 5. For abbreviations, see Table 1. In all cases slopes are statistically significant at  $P \leq 0.05$ .

related to NN (Table 5, Fig. 1d–f). Relationships among variables in each model did not differ among microsites (ANCOVAs not presented).

Total N, NNM, and ammonium were positively related to PNCMR in the wet season (Fig. 2a–c). In the dry season NNM,  $C_{mic}$  ammonium, and total N were the variables positively related to PNCMR (Fig. 2d–g). The response of PNCMR to total N in the wet season and to NNM in the dry season differed according to microsite (ANCOVAs not presented). However, PNCMR responses to total N and NNM were positive for all microsites (Fig. 2). Values for these parameters are shown in Table 5.

#### NET $N_{MIC}$ AND $C_{MIC}$ IMMOBILIZATION

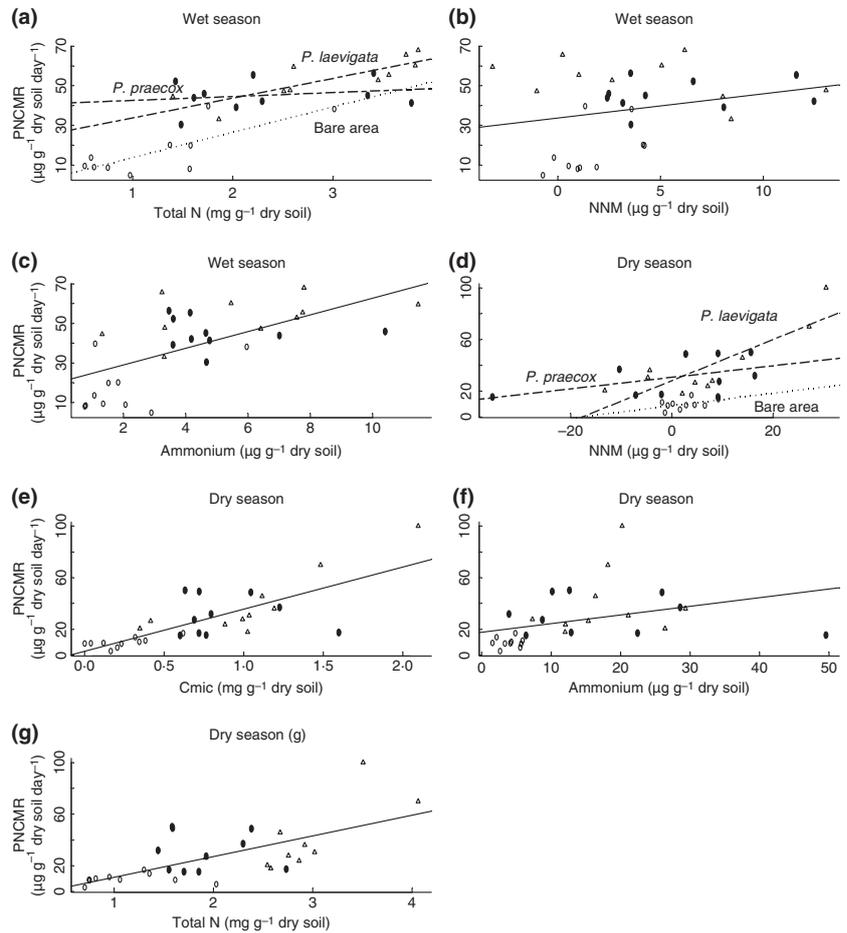
The frequency distributions of  $NN_{mic}$  I and  $NC_{mic}$  I values indicate that in the wet season there are more sample sites with immobilized N and C in microbial biomass than samples with non-immobilized N and C (Fig. 3a–b). In contrast, the reverse is true during the dry season (Fig. 3c–d).

## Discussion

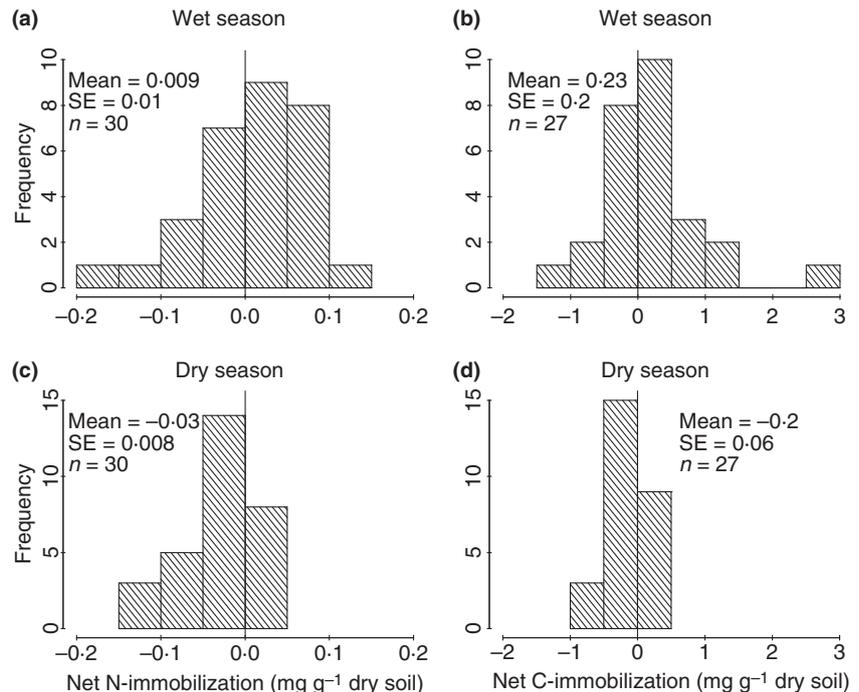
Nutrient spatial distribution in arid and semi-arid soils is associated with plant cover (Noy-Meir 1985; Schlesinger *et al.* 1990; Kieft *et al.* 1998; Mazzarino *et al.* 1998; Austin *et al.* 2004; Schade & Hobbie 2005). The major process that could control N pools and N cycling in these soils are symbiotic N fixation, dry deposition, and N mineralization (West & Skujinš 1978; Chapin, Matson & Mooney 2002). This fact is more noticeable in tropical ecosystems where legume species have a high relative abundance (Vitousek & Sanford 1986;

Sprent *et al.* 1996; Castellanos *et al.* 2001; Altamirano-Hernández *et al.* 2004; González-Ruiz *et al.* 2008). However, it is possible that C mineralization and N immobilization in microbial biomass could contribute to retaining part of the N in the soil, as has been observed in other ecosystems (Vitousek & Matson 1984; Fisher & Binkley 2000; Vitousek *et al.* 2002).

Soil under *P. laevigata* canopy showed greater total N and N in microbial biomass than soil under *P. praecox* and in bare ground soil. Nevertheless, inorganic N and potential net N mineralization rates were similar in FI of both species (Tables 2 and 4). Differing N concentrations in litter and variations in how stored C is processed by microbial biomass under the canopy of each species may help explain these results (see below). The way N is transformed in soil seems to be quite similar for both species (i.e. potential net N mineralization rate and net nitrification) despite the fact that *P. laevigata* has been reported as a N fixer in other arid regions (Eskew & Ting 1978; Felker & Clark 1980; Allen & Allen 1981; Rundel *et al.* 1982), and *P. praecox* as a non-fixer in all cases studied (Allen & Allen 1981; Sprent 1987). N mineralization is known to vary up to 50% between fixer and non-fixer species (Binkley & Giardina 1998). Furthermore, fixer species have a higher ammonium concentration than non-fixers (Paul & Clark 1996; Fisher & Binkley 2000; Vitousek *et al.* 2002). In both FI species, there was a positive relationship between N soil transformation processes and C transformation, C and N in microbial biomass (Fig. 1a,b,d,f) as well as between the C transformation process and total N, net N mineralization, ammonium and C in microbial biomass (Fig. 2). However, the slope of the relationship between the potential C mineralization rate and N transformation processes was higher under *P. laevigata* than *P. praecox* canopy (Fig. 2a,d).



**Fig. 2.** Relationships between PNCMR and several independent variables in a tropical semi-arid ecosystem in central Mexico. Regressions were done for each one of three different microsites or for data pooled from the three microsites: under FI-*P. laevigata* (triangles) and FI-*P. praecox* (closed circles) canopies and in bare areas (open circles) according to the results of ANCOVAs. (a–c) Relationships in a wet season model. (d–g) Relationships in a dry season model, see Table 5. For abbreviations, see Table 1. In all cases slopes are statistically significant at  $P \leq 0.05$ .



**Fig. 3.** (a–b) Frequency distribution plots of estimated values in net microbial N and C immobilization in the wet season (a–b) and dry season (c–d). Histograms were constructed with data obtained from incubation study of samples from three microsites (under FI-*P. laevigata* and FI-*P. praecox* canopies and in bare areas) ( $N = 30$ , i.e. 10 samples per microsite and  $N = 27$ , i.e. 9 samples per microsite). Positive values mean N or C immobilization in microbial biomass, and negative values mean N and C release from microbial biomass.

Soil C mineralization is done by heterotrophic decomposers which get organic C from relatively recent litter inputs and by heterotrophic non-symbiotic N fixers that get their C sup-

ply from the soil environment (i.e. root exudation and root turnover, Paul & Clark 1996; Chapin, Matson & Mooney 2002). The higher organic C and potential net C mineraliza-

**Table 6.** Estimates of C and N in litter and roots of *Prosopis laevigata* and *Parkinsonia praecox* ( $n = 20$  for each species) based on the regression functions proposed by Barth & Klemmedson (1982) for con-specific species

Component	<i>Prosopis laevigata</i>		<i>Parkinsonia praecox</i>	
	C (kg m <sup>-2</sup> )	N (g m <sup>-2</sup> )	C (kg m <sup>-2</sup> )	N (g m <sup>-2</sup> )
Litter	0.381 ± 0.04	30.0 ± 6.1	0.228 ± 0.02	7.5 ± 0.6
Root	0.308 ± 0.04	10.5 ± 1.3	0.157 ± 0.03	3.5 ± 0.6

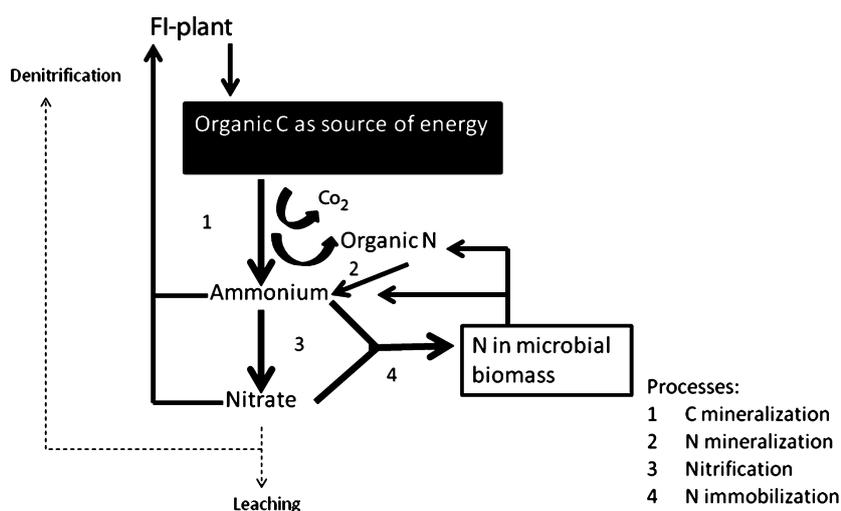
tion rate in soil under *P. laevigata* can be explained as the result of a higher litter input and root C and N production. In the Sonoran Desert, Barth & Klemmedson (1982) showed that the content of different forms of C and total N in *P. juliflora* litter and roots duplicate those of *Cercidium floridum*. These authors present regression equations that predict C and N content for total soil and root biomass, as a function of height, average canopy diameter, and cover area. By applying these equations to data for *P. laevigata* and *P. praecox* we observe higher C and N contents in both *P. laevigata* soil and roots than in *P. praecox* (Table 6). Similarly, Pavón, Briones & Flores-Rivas (2005) found that *P. laevigata* had a litterfall production (including reproductive structures and small and larger leaves) ca. 30% higher than that produced by *P. praecox* in Zapotitlán Salinas. In this context, differences in organic C supply to heterotrophic microbiota activity during the FI species lifetime may—in the long term—result in important differences in soil N stocks. FI species of the same genus and life form of those evaluated in this study are long-lived (ca. 1000–1400 years; McAuliffe 1988). Positive feedbacks between soil C and N accumulation during long periods may result in substantial differences in heterotrophic microbial activity as well as in N immobilization in microbial biomass under different FI species (Fig. 4).

These results show seasonal variation patterns. Soil N availability in the dry season was almost four times higher than in the wet season in Zapotitán Salinas. This pattern is similar in other non tropical arid zones (West & Skujinš 1978;

Austin *et al.* 2004) and tropical dry ecosystems (Jaramillo & Sanford 1995). However, C availability and potential net mineralization were greater in the wet season (Table 3). This suggests a possible limitation of N during the wet season. The C and N availability/limitation pattern can also be observed in immobilization data for C and N in microbial biomass. During the rainy season, a positive balance in C and N immobilization in microbial biomass is observed, while during the dry season the lack of water makes immobilization almost non-existent. The N immobilized in microbial biomass is protected from loss due to leaching and/or denitrification (Paul & Clark 1996; Fisher & Binkley 2000). Although C enters the soil during the dry season, it is unavailable due to the lack of water. In the dry season, the N retention mechanism in microbial biomass (and its acquisition by plants) does not function, causing inorganic N to increase during this time. A larger amount of inorganic N increases the likelihood of nitrate loss due to leaching, denitrification, and/or ammonium volatilization with the first influx of water. It is possible, then, that wet-dry cycles like the ones characteristic of our study site affect microbial functioning in terms of soil N loss and conservation events (see Austin *et al.* 2004; Schmidt *et al.* 2007).

Even though N input and output values were not measured, the results suggest that it is important to include the role of C transformation via heterotrophic microbial activity and N storage in microbial biomass to understand controls over soil N cycling in FI. Thus, N accumulation and conservation in FI soil of this tropical semi-arid ecosystem may be more strongly associated with processes involving C transformations than N symbiotic fixation processes.

Similar relationships between soil C and N transformations have been shown in other tropical ecosystems, such as tropical dry forest (Montaño, García-Oliva & Jaramillo 2007) and tropical wet forest (Vitousek & Hobbie 2000) as well as in other extra-tropical ecosystems (temperate forest, Vitousek & Matson 1984; Fisher & Binkley 2000). According to Montaño, García-Oliva & Jaramillo (2007), N soil transformation is controlled by soil dissolved organic C and heterotrophic microbial activity in a tropical dry forest. With an increase in dissolved organic C, heterotrophic respiration, net microbial



**Fig. 4.** Hypothetical model to explain N retention in FI soil. The model proposes C input and transformation as an energy source in the system. Heterotrophic microbial activity influences the N transformation positively because of C mineralization. The N retained in microbial biomass functions as a N conservation mechanism in soil by limiting its loss from the system due to leaching and/or denitrification. The intensity of C mineralization and N storage in microbial biomass in soil under FI-*Prosopis laevigata* is greater than in soil under FI-*Parkinsonia praecox*; this is reflected in a greater total N stock under FI-*Prosopis laevigata*.

N immobilization, and total N also increase, while N losses due to leaching and denitrification decrease. Vitousek & Hobbie (2000) show the importance of non-symbiotic heterotrophic N fixation activity in the *Metrosideros polymorpha* litter decomposition process in a tropical wet forest. Vitousek & Matson (1984) demonstrated that microbial uptake of nitrogen during the decomposition of residual organic material was the most important process retaining nitrogen in a loblolly pine plantation in North Carolina. May be the most important difference between the influence of FI in deserts and trees in temperate forest is that there is a much larger flow at a higher rate in temperate forests since trees have a larger biomass (see Binkley & Giardina 1998). The range of total annual litterfall in deciduous oak species of temperate areas is from 2300 to 7100 kg ha<sup>-1</sup>y<sup>-1</sup> (Kimmins *et al.* 1985) and average N input via litterfall is 39.5 kg ha<sup>-1</sup>y<sup>-1</sup> for some temperate deciduous forest (Vogt, Grier & Vogt 1986) as compared to 250 ± 5.8 kg ha<sup>-1</sup>y<sup>-1</sup> of litterfall (6.5 ± 1.2 kg ha<sup>-1</sup>y<sup>-1</sup> corresponding to N content) reported by Pavón, Briones & Flores-Rivas (2005) for the tropical semiarid ecosystem where the present study was done.

#### POSSIBLE IMPLICATIONS IN DIFFERENTIAL N ACCUMULATIONS IN FI SOIL

Differential N accumulations in FI soil could have ecological or even evolutionary implications. Desert trees and shrubs affect other life forms that inhabit these ecosystems in ways that are crucial for their existence (Noy-Meir 1985). FI soil N conservation and soil organic C productivity may be reflected in a C-N protection-uptake mechanism at species level, as well as in terms of resource use efficiency and specific productivity ranges. From an evolutionary standpoint, specific FI genotypes with varying capacities to promote soil N conservation by C-N interaction mechanisms (e.g. through different kinds of root exudates production) could promote several biotic interactions (e.g. associated plant-soil microbiota, plant-plant interactions) that may increase reproductive success, with possible repercussions on populations, community, and ecosystem levels (see Bremen & Finzi 1998). However, new approaches are needed in order to test these ideas in a functioning ecosystem context.

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