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Contribution of nitrogen from litter and soil mineralization to shade and sun coffee (*Coffea arabica* L.) agroecosystems

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Abstract: Coffee (*Coffea arabica* L.) production is important for its economic, ecological and social values in tropical areas. Whether coffee is grown under shade (SHD) or full sunlight (SUN), may have a direct impact on soil nitrogen (N) cycling, which can affect yield and agroecosystem sustainability. We studied N cycling in coffee farms in three municipalities in Puerto Rico and evaluated three ecosystem types in each: SUN coffee, SHD coffee and secondary forest (FOR). Aboveground litter dry matter and litter N inputs were quantified. Litter dry matter inputs (t ha^{-1} year^{-1}) were higher in SHD (2.15) and FOR (1.83), and were significantly greater than SUN (1.40). Litter N inputs (kg N ha^{-1} year^{-1}) were significantly lower in SUN (31) than in SHD (52) and FOR (43). Cycling of N was evaluated in detail in the municipality of Las Marias in SHD and SUN coffee. Litter N inputs (kg N ha^{-1} year^{-1}) to soil were significantly different between FOR (41) and SHD (56). The standing stock of N in aboveground biomass SHD was ~3 times that in SUN, and total N input was twice that in SUN. However, soil N standing stocks were similar in SHD and SUN, indicating faster litter N turnover in SUN than in SHD ecosystems. By contrast, net soil N mineralization rates (kg N ha^{-1} year^{-1}) were ~2 times higher in SHD (96) than in SUN (49), indicating that soil N turnover is greater in SHD than SUN. Our results suggest that litter N is mineralized at a slower rate in SHD than in SUN, whereas soil N is mineralized at a slower rate in SUN than in SHD. Higher inputs of N to soil, and soil N turnover in SHD may result in improved coffee production and associated forest biomass N uptake. Higher soil N mineralization rates in SHD coffee suggest improved ecosystem sustainability than in SUN coffee, presumably due to higher microbial activity, greater microbial diversity and substrate availability.

Resumen: La producción de café (*Coffea arabica* L.) es importante por sus valores económicos, ecológicos y sociales en las zonas tropicales. Si el café se cultiva bajo sombra (SHD) o a pleno sol (SUN) puede tener un impacto directo sobre el ciclo del nitrógeno del suelo (N), lo que puede afectar el rendimiento y la sostenibilidad del agroecosistema. Estudiamos el ciclo del N en fincas cafetaleras en tres municipios de Puerto Rico y evaluamos tres tipos de ecosistemas en cada una: café SUN, café SHD y bosque secundario (FOR). Cuantificamos la materia seca aérea del mantillo y los aportes de N del mantillo. Los aportes de materia seca del mantillo (t ha^{-1} año^{-1}) fueron más altos en SHD (2.15) y FOR (1.83), y fueron significativamente mayores que en SUN (1.40). Los aportes de N del mantillo (kg N ha^{-1} año^{-1}) al suelo fueron significativamente menores en SUN (31) que en SHD (52) y FOR (43). Se evaluó en detalle el

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ciclo de N en el municipio de Las Marías en café SHD y SUN. Los aportes de N del mantillo (kg N ha^{-1} $año^{-1}$) al suelo difirieron significativamente entre FOR (41) y SHD (56). El almacemamiento de N en la biomasa aérea en SHD fue ~ 3 veces mayor que en SUN, y el aporte total de N fue el doble que en SUN. Sin embargo, el almacenamiento de N en el suelo fueron similares en SHD y SUN, lo que indica que el recambio de N del mantillo es más rápido en los ecosistemas SUN que en los SHD. En contraste, las tasas netas de mineralización de N en el suelo (kg N ha^{-1} $año^{-1}$) fueron ~ 2 veces mayores en SHD (96) que en SUN (49), lo que indica que el recambio de N del suelo es mayor en SHD que en SUN. Nuestros resultados sugieren que el N del mantillo se mineraliza a un ritmo más lento en SHD que en SUN, mientras que el N del suelo se mineraliza a un ritmo más lento en SUN que en SHD. Los aportes mayores de N hacia el suelo y el mayor recambio de N en el suelo en SHD pueden resultar en una producción mejorada de café y en la captación asociada de N forestal.Las tasas más altas de mineralización de N del suelo en SHD sugieren que allí la sostenibilidad es más alta que en SUN, probablemente debido a la mayor actividad microbiana, una mayor diversidad microbiana y una mayor disponibilidad de sustrato en el café SHD.

Resumo: A produção de café (*Coffea arabica* L.) é importante pelo seu valor económico, ecológico e social em áreas tropicais. O regime de cultivo, sob sombreamento (SHD) ou em plena luz solar (SUN), pode ter um impacto direto sobre o ciclo do azoto no solo (N), o que pode afetar a produtividade e sustentabilidade do agroecossistema. Estudou-se o ciclo do N em fazendas de café em três municípios em Porto Rico e avaliaram-se três tipos de ecossistemas em cada um: café SUN, café SHD e floresta secundária (FOR). A massa aéreaseca de folhada e as entradas de N foram quantificadas. Os inputs de biomassa seca de folhada (t ha^{-1} ano^{-1}) foram maiores no regime SHD (2,15) e FOR (1,83), e significativamente maiores do que para SUN (1,40). As entradas de N (kg N ha^{-1} ano^{-1}) libertado pela folhada foram significativamente menores no SUN (31) do que em SHD (52) e FOR (43). A reciclagem de N foi avaliada em detalhe no município de Las Marias em cafeais SHD e SUN. Os inputs de N da folhada no solo (kg N ha^{-1} ano^{-1}) foram significativamente diferentes entre FOR (41) e SHD (56). O estoque de N na biomassa aérea em SHD era aproximadamente 3 vezes superior do que em SUN, e a entrada total de N foi duas vezes maior do que em SUN. No entanto, o estoque de N no solo foi semelhante em SHD e SUN, indicando uma rotação mais rápida do N na folhada em SHD do que em SUN. Em contraste, as taxas liquidas de mineralização do N no solo (kg N ha^{-1} ano^{-1}) foram aproximadamente 2 vezes maiores em SHD (96) do que em SUN (49), indicando que a taxa de rotação de N no solo é maior em SHD do que em SUN. Os nossos resultados sugerem que o N da folhada é mineralizado a umataxamaior em SHD do que no SUN, enquanto que o N do solo é mineralizado a uma taxa mais baixa em SUN do que em SHD. Entradas mais elevados de N no solo, e uma taxa de rotação de N no solo em SHD, podem resultar na melhoria da produção de café e da captação de N na biomassa florestal associada. Maiores taxas de mineralização do azoto no solo em café SHD sugerem melhoria da sustentabilidade destes ecossistemas do que nos cafeais SUN, provavelmente devido à maior atividade microbiana, maior diversidade microbiana e disponibilidade de substratos no cafezal SHD.

Key words: Agroecosystem sustainability, coffee production, nitrogen cycling, shade coffee, soil nitrogen mineralization.

Introduction

Coffee (*Coffea arabica* L.) is one of the most important trade commodities in the tropics (Quintero & Ataroff 1998). In Puerto Rico, coffee production has social, economic and ecological importance since it is primarily confined to the mountainous interior portion of the island, which has limited agricultural production options, has highly weathered soils prone to erosion, and limited employment opportunities. In 1828, Puerto Rico had about 7,000 ha of coffee grown under partial shade, which increased to 77,000 ha by the beginning of the 20th century (Borkhataria *et al.*

2012; Vega 2008). By the mid-1950s many coffee farms were abandoned, due to low yields, decreased labour availability, increasing production costs, and emphasis on industrial production (Weaver & Birdsey 1986). These abandoned farms reverted to secondary forests and pasture. The coffee industry was revitalized by Vicente-Chandler *et al.* (1968) who identified management practices that produced high economic yields using dwarf - type high-yielding varieties, high planting density, full sunlight, and intensification of fertilizer usage. Currently there are approximately 22,000 ha under coffee production in Puerto Rico, of which ~60 % is grown under full sunlight, with the remaining 40 % grown under some form of partial shade (USDA 2009). During 2008-2009, coffee production in Puerto Rico was estimated at 3,864 t and was ranked fourth among all commodities in terms of gross agricultural production, with a farm-gate value of $20.61 million (DAPR 2011).

Coffee yields under shade in Puerto Rico and elsewhere can be 40 % lower than under full sunlight (Abruña *et al.*1965b; Haggar *et al.* 2011). Higher yields under full sunlight are attributed to the increased photosynthetic expression of the crop, but which must come at the expense of increased nutrient and pesticide management. Coffee intercropped with trees has been promoted for its ability to reduce nutrient losses from runoff and leaching by increasing evapotranspiration and nutrient accumulation in the biomass (Tully *et al.* 2013). It is suggested that sun coffee has lower C and N recycling efficiency which leads to higher N losses (Tully *et al.* 2012). Because of increased input costs and sustainability concerns, coffee growers continue to seek alternative management approaches such as organic production, and are reverting to the use of leguminous and timber trees to provide some level of shading. Indirect benefits result from coffee grown under shade, especially at lower nutrient input levels and at low altitudes. For example, lower biodiversity has been reported under sun coffee (Borkhataria *et al.* 2006, 2012; Greenberg *et al.* 1997; Perfecto *et al.* 1996). Coffee under full sunlight, which has a lower over-storey vegetative canopy cover and decreased surface litter, may be more vulnerable to erosion (Smith & Abruña 1955) and nutrient runoff losses (Semidey *et al.* 2002; Sotomayor-Ramírez *et al.* 2007), adversely affecting soil functioning and ecosystem sustainability (Hergoualc'h *et al.* 2012). Coffee under shade has greater total leaf area, fewer dead branches, longer branches, and bigger and thinner leaves (Jaramillo-Botero *et al.* 2009). Fruit weight, bean size, and beverage quality all have been shown to improve as a result of shading (Muschler 2001; Vaast *et al.* 2006). However, other studies have shown that coffee grain-size distribution was not different between sun and shade coffee (Vicente-Chandler *et al.* 1968), and sensory attributes were negatively influenced by shade (Skovmand-Bosselmann *et al.* 2009).

Fertilizer nitrogen (N) recommendations for coffee production in Puerto Rico vary from 170 to 340 kg N ha^{-1} $year^{-1}$ in plantations older than four years (Vicente-Chandler *et al.* 1968). Maximum fertilizer N response rates for coffee (var. Bourbon) grown under full sunlight and high planting densities have been demonstrated at 340 kg N ha^{-1} $year^{-1}$ (Abruña *et al.* 1959; Abruña *et al.* 1965a). As N export in the harvested fruit can be nearly ten times lower than crop response, inefficient use of fertilizer nutrients increases potential losses to the environment via leaching, runoff, denitrification and volatilization (Harmand *et al.* 2007; Rice & Havlin 1994; Tully *et al.* 2012). Thus, there is a need to re-evaluate the current crop and nutrient management strategies for coffee developed for Puerto Rico - originally developed in the 1960s - in order to lower the potential negative impact of fertilizer N use, increase biodiversity, reduce erosion and reduce crop production costs. This requires a quantitative understanding of N inputs and N mineralization rates relative to losses, including crop needs. Because there are many soil, management and cropping scenarios for coffee production systems, there is a need to understand and quantify the fraction of fertilizer N utilized by the coffee plant, the contribution of N from soil organic matter mineralization, plant litter decomposition, and N fixation by associated leguminous trees that provide shade, on a site-specific basis (Fellini & Bergamo 2008; Harmand *et al.* 2007; Quintero & Ataroff 1998). A better description of the soil and ecosystem functions in sun and shade-grown coffee will eventually be used to provide recommendations that will serve to increase coffee production and sustainability.

In this study, we assess non-fertilizer N inputs and soil N transformations for coffee grown under full sunlight or shade by quantifying the contribution of N in the litter and soil net N mineralization under field conditions. We used adjacent secondary forest sites for comparison. We hypothesized that coffee under shade would have greater N inputs from recycled over-storey plant

Table 1. Geographic description and climatologic characteristics of experimental sites.

Site	Ecosystem[1]	Latitude N	Longitude W	Elevation (m asl)	Mean annual precipitation (mm)	Mean annual temperature (°C)
Jayuya	SUN	18°10'05"	66°37'50"	765	1935	23
	SHD	18°09'41"	66°38'46"	785		
	FOR	18°09'44"	66°38'46"	817		
Lares	SUN	18°11'43"	66°50'55"	575	2290	24
	SHD	18°11'59"	66°50'49"	636		
	FOR	18°11'46"	66°50'55"	605		
Las Marías	SUN	18°14'44"	67°00'25"	297	1870	26
	SHD	18°14'39"	67°00'08"	288		
	FOR	18°14'43"	67°00'26"	285		

[1] SUN, SHD, and FOR correspond to coffee under full sunlight, coffee under partial shade, and secondary forest, respectively.

Table 2. Selected soil physical and chemical properties for coffee under sun (SUN) and shade (SHD) and secondary forest (FOR).

Site	Ecosystem	pH	Total organic C ($g\ kg^{-1}$)	Total N ($g\ kg^{-1}$)	sand (%)	silt (%)	clay (%)
Jayuya	SUN	4.13	33.4	3.37	16	20	64
	SHD	4.00	40.1	4.30	21	34	46
	FOR	4.56	68.7	6.80	25	29	46
Lares	SUN	4.27	26.0	2.83	31	23	46
	SHD	4.00	41.8	4.20	11	31	58
	FOR	4.30	50.9	4.27	21	23	56
Las Marías	SUN	4.23	42.2	4.37	20	18	62
	SHD	4.20	31.3	3.20	16	20	64
	FOR	5.73	42.0	4.27	24	26	50

biomass that would result in higher soil N mineralization rates.

Materials and methods

This study was carried out in farms located in three municipalities, namely Jayuya, Lares, and Las Marías (Table 1). The soils were: an Oxisol of the Los Guineos series *(very fine, kaolinitic, isothermic Humic Hapludox)* in Jayuya, an Inceptisol of the Anones series (*fine, parasesquic, isohyperthermi, Humic Drystrudepts*) in Lares, and an Ultisol of the Humatas series (*very fine, parasesquic, isohyperthermic, Typic Haplohumults*) in Las Marías (Beinroth *et al.* 2003). Within each location, experimental plots were established in coffee ecosystems under partial shade (SHD), under full sunlight (SUN), and secondary forest (FOR). Selected soil physical and chemical properties for the sites are shown in Table 2. The treatments were arranged in the field in a randomized complete block design with three replicates, with plot sizes of about 400 m^2.

The most important forest species in terms of relative abundance and basal area in the FOR sites were *Spathodea campanulata*, *Guarea guidonia*, *Schefflera morototoni*, *Syzigium jambos* and *Inga vera* (López-Rodríguez 2008). In the SHD sites the dominant over-storey species were *Inga vera*, *Inga laurina*, *Citrus sinenis* and *Inga fagifolia*. All sites were in the very-humid subtropical life-zone (Holdridge 1996). Forest stand ages were between 30 and 40 years (López-Rodríguez 2008).

The primary coffee varieties were a mixture of Arabica origin (Caturra, Borbón and Limaní) and the age of the plantations varied from 8 to 15 years. On average, the planting density (plants ha^{-1}) was 3,500 and 2,500 in SUN and SHD, respectively. Fertilizer nutrient applications followed by the farmers were lower than those recommended by UPRM-CCA (1998), and estimated to be 48, 30 and 60 kg ha^{-1} of N, P_2O_5 and K_2O, respectively, in SUN, and 35, 14, and 43 kg ha^{-1} of N, P_2O_5 and K_2O, respectively, in SHD (López-Rodríguez 2008).

Soil sampling and analysis

Between 12 and 15 soil subsamples were taken from each plot to a depth of 15 cm, homogenized and a subsample taken to the laboratory for processing. Soil moisture was determined gravimetrically after drying at 105 °C. Soils were sieved to pass a 2-mm mesh and air-dried. Soil total organic C and total N concentrations were determined by automated dry combustion ((Carlo-Erba 1500 series II Thermo-Fisher, Waltham, MA). Soil pH was determined using a 1:2 soil/water ratio. Particle size distribution was determined by the Bouyoucos method (Day 1965).

Litter sampling and analysis

Litter was captured in 0.35 m^2 (0.5 m × 0.7 m) wire-mesh baskets (openings of 1.44 cm^{-1} mesh) to reduce water-logging. One basket was randomly placed in each plot, beneath over-storey trees and between coffee plants. The collected litter was removed monthly from November 2006 to October 2007 and dried to a constant weight at 60 °C. The dried litter was ground in a Wiley mill to pass a 40-mesh and stored in a sealed container at room temperature. The C and N concentrations of a composited litter sample from each agroecosystem was determined by automated dry combustion. The monthly deposition of C and N was calculated based on the product of litter dry matter and C and N concentration. The annual inputs of litter dry-matter biomass, C, and N were calculated from the sum of the monthly values.

Soil N mineralization

The three ecosystems in Las Marías - SUN, SHD and FOR - were used for evaluation of soil net N mineralization rates using an *in situ* covered-core method (Hart *et al.* 1994; Raison *et al.* 1987; Schepers & Meisinger 1994). Specifically we followed the approach used by Raison *et al.* (1987) which is based on the sequential measurement of changes in the quantity of soil mineral N (NH_4^+-N plus NO_3^--N) in the cores (N_C; no N uptake by roots) and in unconfined bulk soil (N_S) as a function of time. The soil cores consisted of polyvinyl chloride (PVC) pipes (20 cm length, 7.6 cm diameter) with 0.5 cm- dia side holes to improve gas exchange with the bulk soil. The areas where the tubes were inserted were not fertilized during the experimental period. An initial background measurement ($T_{0,s}$) of soil mineral N was performed by taking three subsamples from each plot to a depth of 15 cm. At each sampling date, two adjacent (30 cm apart) PVC cores with a sharpened bottom edge were carefully inserted into the soil to a depth of 15 cm to avoid soil compaction and preserve soil structural integrity. Each column was fitted with a PVC cap to prevent water infiltration, and to reduce NO_3 leaching and NH_3 volatilization. The cores remained in the soil for 21 days ($T_{1,c}$). At this time (T_2), the first set of columns were removed, a second set of columns ($T_{2,c}$) was inserted into the soil and a sample of bulk soil was obtained ($T_{1,s}$). This procedure was repeated on seven consecutive instances over a 24-week period from November 2006 to May 2007. After the cores were removed, soil samples were stored in polyethylene bags at 5 °C. Soil moisture was determined gravimetrically by drying at 105 °C for 48 h. Soil NH_4^+-N and NO_3^--N were determined by distillation after extraction with 1 M KCl using a 2.7:1 extractant/soil ratio (Keeney & Nelson 1982).

The net N mineralization rate (N_{min}) over a specific time period (T_i) was calculated from the difference between mineral N (NH_4^+-N + NO_3^--N) concentration (mg N kg^{-1} soil) measured from the incubation tube at $T_{i,c}$ and mineral N concentration measured from the ambient soil sample prior to incubation ($T_{i-1,s}$), divided by the number of days elapsed between the two sampling times, using equation [1]:

$$N_{min} = (NT_{i,c} - NT_{i-1,s}) / (T_i - T_{i-1}) \qquad [1]$$

All values were converted from concentration to mass per unit area basis using measured soil bulk density and sampling depth. The annual (52-week) rate of mineralization was estimated by linear extrapolation from the cumulative total measured during the 24-week period.

Statistical analysis

A two-way analysis of variance on litter dry matter, and C and N content in litter was performed with site and agroecosystem as factors using Infostat (2006). Data were square-root transformed as necessary to comply with assumptions of normality and variance homogeneity. Tukey's test

Table 3. Inputs of litter dry matter and litter C and N as influenced by site and ecosystem.

Ecosystem[1]	Litter dry matter ($t\ ha^{-1} yr^{-1}$)			Litter N ($kg\ N\ ha^{-1} yr^{-1}$)			Litter C ($kg\ C\ ha^{-1} yr^{-1}$)		
	Jayuya	Lares	Las Marías	Jayuya	Lares	Las Marías	Jayuya	Lares	Las Marías
SUN	1.39 a[2]	1.15 a	1.65 a	32 a	29 a	32 a	648 a	612 a	536 a
SHD	2.09 b	1.97 b	2.37 b	50 b	50 b	56 b	1095 b	1132 b	1111 b
FOR	1.56 ab	2.08 b	1.86 ab	49 b	39 ab	41 ab	733 ab	960 b	941 b

[1] SUN, SHD, and FOR correspond to coffee under full sunlight, coffee under partial shade, and secondary forest, respectively.
[2] Columns with different letters within an inputs type and site are significantly different ($P \leq 0.05$).

was used to detect differences among means ($P < 0.05$). Soil net N mineralization rate data were analyzed using a split-plot arrangement in randomized complete block design with agroecosystem as the main plot and time as the subplot. Differences in weekly rates of field N mineralization, rates of field N mineralization averaged over time, and cumulative N mineralization were analyzed using ANOVA.

Nitrogen inputs for coffee agroecosystems in Las Marías

We used the data collected in this study for the Las Marías sites, in conjunction with published data, to calculate N inputs for the SHD and SUN coffee agroecosystems. The inputs of N considered in our analysis included: biological N fixation (symbiotic and non-symbiotic), N in wet deposition, fertilizer N, litter-fall N, and soil net N mineralization. The contribution of symbiotic biological N fixation in shaded coffee, based on values for *Inga jinicuil*, has been reported up to 40 kg N ha^{-1} yr^{-1} (Roskoski 1982). Son (2001) estimated an N input of 2 to 3 kg N ha^{-1} $year^{-1}$ from non-symbiotic biological N fixation; however, Avilés-Vázquez (2009) estimated biological N fixation rates from the sum of leaf litter, epiphylls, lichens, and soil at our study sites of 0.173 and 0.329 kg ha^{-1} $year^{-1}$ in SUN and SHD, respectively. We thus used the values given by Avilés-Vázquez (2009) in our calculations. Wet N deposition, based on data from a station in El Verde (northeastern Puerto Rico) from 2000 to 2008, was estimated at 2.8 kg N ha^{-1} $year^{-1}$, for both systems (NADP 2010). The fertilizer N contribution at the site has historically been 48 and 35 kg N ha^{-1} yr^{-1} for SUN and SHD coffee, respectively, which is considerably less than recommended rates by UPRM-AES of 200 to 250 kg N ha^{-1} $year^{-1}$ (UPRM-CCA 1999).

Results and discussion

Litter inputs

Cumulative annual inputs of litter dry-matter and litter C and N were significantly influenced by the interaction between site and ecosystem ($P < 0.05$). Litter dry-matter, C and N inputs were significantly lower in SUN than in SHD for all sites, but SHD was similar to FOR (Table 3). In Jayuya, the highest monthly litter dry-matter input occurred between August and September under SHD, whereas no temporal variation was observed in FOR and SUN. In Lares, the highest litter dry-matter input occurred in August and September in SHD and FOR, and between October and November in SUN. In Las Marías, the highest litter dry-matter input was from November to December in SHD and FOR, and from February to March in SUN. Our observations are in contrast with expected trends in litter-fall, which typically peaks from February to March in Puerto Rico, coincident with the time of lowest rainfall and prior to first annual blossom of coffee trees. This temporal pattern of litter-fall may influence soil mineral N availability, which in turn will influence soil microbial biomass pools and N turnover.

Recently deposited litter quality differed among ecosystems and locations. For example, In Jayuya, the C:N ratio (mean ± standard error) of litter was 15 ± 0.58 in FOR and 21 ± 1.6 in SUN and SHD, whereas in Lares and Las Marías the C:N ratio in FOR (24 ± 2.2) was similar to that in SUN (23 ± 2.4) which was higher than in SHD (17 ± 0.6). The mean N contribution from litter was 31 ± 3.91 kg N ha^{-1} in SUN for all sites, and a mean of 52 ± 6.11 and 43 ± 1.61 kg N ha^{-1} was found for SHD and FOR, respectively. Higher litter C and N inputs to soil were observed in SHD and FOR.

We expected to find lower litter C:N ratios in

FOR and SHD due to the predominance of leguminous trees *Inga* spp. and *Andira inermis*, yet this was observed only in Jayuya. Although our analysis does not allow us to identify the relative N contribution from each species, our litter N concentration values are within the range reported for shade and sun-grown coffee (Dossa *et al.* 2008) and for the same forested species in Puerto Rico, which ranged from 20.1 to 23.7 g kg^{-1} for *Inga* spp., 9.5 to 19.5 g kg^{-1} for *Andira inermis*, and 6.1 to 11.2 g kg^{-1} for *Coffea arabica* (Sanchez *et al.* 1997).

Annual litter dry matter and N inputs in SUN, SHD and FOR in our study were generally lower than those reported in other studies. For example in Venezuela, coffee under sun had litter dry matter input of 3.3 t ha^{-1} year^{-1}, compared to 17.4 t ha^{-1} year^{-1} for coffee under shade (Arellano *et al.* 2004). Similarly De las Salas (1987) reported annual litter inputs ranging from 4.2 to 12.5 t ha^{-1} year^{-1}, with annual N inputs of 57 to 228 kg N ha^{-1} for a range of tropical forests. In Costa Rica, Heuveldop *et al.* (1985) reported an annual litter input of 7.6 t ha^{-1} year^{-1} in coffee under partial shade provided by *Erythrina poeppigiana.* Cardona & Sadeghian (2005) reported annual litter inputs 1.9 to 2.2 t ha^{-1} year^{-1}. In Venezuela, Mogollón *et al.* (1997) quantified N inputs in litter in coffee under shade with legume trees and in association with *Citrus* spp., with values of 141 and 85 kg ha^{-1} year^{-1}, respectively. The differences between our litter inputs and N contribution values and published results are likely due to differences in vegetation abundance and diversity. For example, the planting density (plants ha^{-1}) for coffee in our study was 3,500 in SUN and 2,500 in SHD, generally lower than those in other studies (Babbar & Zak 1995; e.g. Hergoualc'h *et al.* 2008).

N mineralization rates

Mean *in situ* soil net N mineralization rates (mg N kg^{-1} week^{-1}) were determined in Las Marias, and were 2.8 ± 1.48, 5.6 ± 2.78 and 5.8 ± 2.23 for SUN, SHD and FOR, respectively (Fig. 1). The cumulative amount of net N mineralized (mg N kg^{-1}) over the 24-week measurement period was 22.5, 44.5 and 46.7 for SUN, SHD and FOR, respectively (Fig. 2). Extrapolated to an annual basis, soil net N mineralization rates were 89.3, 153.3, and 159.4 kg N ha^{-1} year^{-1} for SUN, SHD and FOR, respectively. Net N mineralization in SUN was 56 and 58 % of that in SHD and FOR, respectively. Soil N mineralization will depend on the size of soil C and N pools, yet we did not find

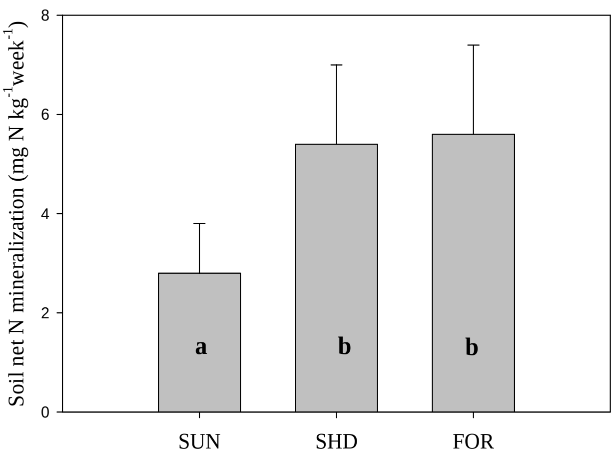

Fig. 1. Mean weekly soil net N mineralization rate for coffee under full sunlight (SUN), coffee under partial shade (SHD) and secondary forest (FOR) ecosystems in Las Marias, Puerto Rico. Bars with different letters indicate significant differences at P ≤ 0.05, using Tukey's test. Vertical bars are standard error of the mean.

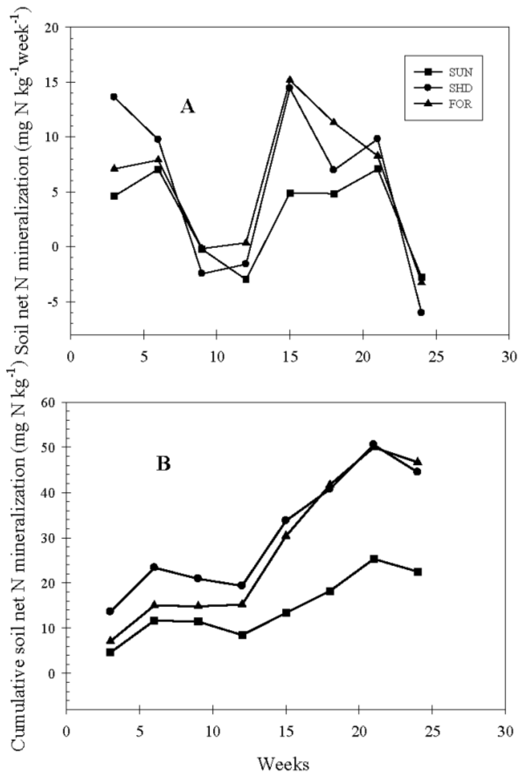

Fig. 2. (A) Instantaneous field rates of net N mineralization and (B) cumulative mineralized N in coffee under full sunlight (SUN), coffee under partial shade (SHD) and secondary forest (FOR) ecosystems in Las Marias, Puerto Rico.

differences in these values beween SHD and SUN, at the depths studied. Other studies have also found soil N mineralization to be higher in SHD than in SUN coffee (Babbar & Zak 1994; Hergoualc'h 2008; Nonato de Souza *et al.* 2012). Our values are similar to those reported by Babbar & Zak (1994) for coffee production under shade (148 kg N ha^{-1} $year^{-1}$) and lower than those under sun (111 kg N ha^{-1} $year^{-1}$).

For all sites and ecosystems in Las Marias, net soil ammonification (NH_4^+-N accumulation) was observed at all sampling dates, except on Week 9, 12, and 24, when negative NH_4^+-N production rates (net loss) was observed (data not shown). Negative NH_4^+-N production rates may be a reflection of losses by volatilization, microbial immobilization and/or nitrification rates that were higher than gross NH_4^+ production. Negative ammonification rates coincided with decreased nitrification rates, suggesting that microbial immobilization and, to a lesser extent volatilization, contributed to lower soil NH_4 availability. The predominant N species in solution was NO_3-N, with levels nearly double those of NH_4^+-N (data not shown).

The temporal patterns of N mineralization were similar across ecosystems, although there were consistent differences in magnitude (Fig. 2). N mineralization rates increased consistently from Week 12 to 21, decreasing from Week 21 to 24. Maximum N mineralization rates were observed on Week 15 for SHD and FOR, with values of 14.4 and 15.2 mg N kg^{-1} wk^{-1}, respectively. The maximum net N mineralization rate for SUN was < 8 mg N kg^{-1} $week^{-1}$. Minimum rates (net N immobilization) were observed at 24 weeks for SHD and FOR and at 12 weeks for SUN, with values of -6.0, -3.3 and -3.0 mg N kg^{-1} $week^{-1}$.

The similarity in temporal patterns of N mineralization among all three ecosystems in Las Marías suggests that the dynamics of N mineralization were driven by external forcing factors common to the area, such as climatic patterns. Because all three ecosystems within a site were within a 2-km^2 area, similar temperature and precipitation regimes were expected. N mineralization rates decreased between Week 9 and Week 12, coincident with the tropical winter period from early January to late February. This is generally the coldest and driest part of the year in this area, with precipitation values that are approximately half of the historic yearly average and maximum and minimum air temperatures that are 2.5 and 4.5 °C lower than the yearly average, respectively (NOAA 2012).

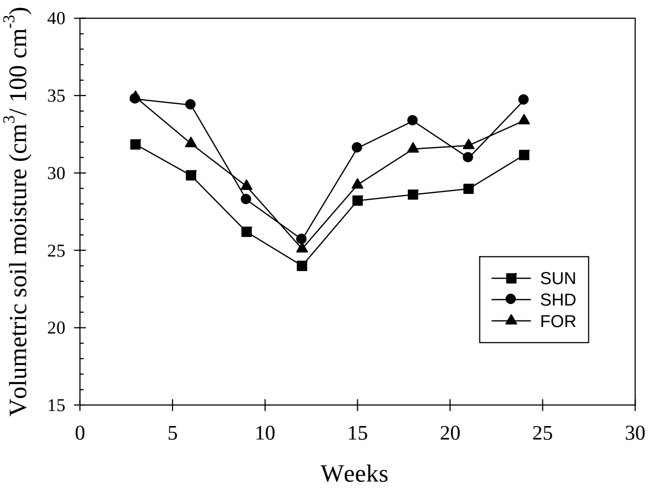

Fig. 3. Gravimetric soil moisture during field incubations for N mineralization in coffee under full sunlight (SUN), coffee under partial shade (SHD) and secondary forest (FOR) ecosystems in Las Marias, Puerto Rico.

Temporal patterns of net N mineralization rates for all three ecosystems generally were also in synchrony with measured soil moisture at each sampling time period (Fig. 3). Soil moisture tended to be higher in SHD and FOR relative to SUN on all sampling dates, although the differences were not significant ($P \geq 0.05$) (Fig. 3). Soil moisture is an important control on N mineralization (Andren *et al.* 1988; Rice & Havlin 1994). Soil microbial activity is reduced as soil moisture decreases relative to field capacity, and increases as soil is initially wetted at the onset of rainfall. Across all ecosystems, soil moisture was weakly correlated to the weekly rate of net N mineralization (r = 0.29), rate of ammonification (r = 0.31) and rate of nitrification (r = 0.19) ($P < 0.05$). The weak correlation may be explained by the fact that, once there is sufficient moisture, other factors control N mineralization: a strong correlation is expected only when soil moisture is limiting. The lowest soil moisture values were observed during Week 9 and 12, and coincided with the lowest (and occasionally negative) values for rates of ammonification, nitrification, and net N mineralization. We could not determine whether the differences in the magnitude of net N mineralization among locations were due to changes in soil factors (e.g. soil texture and mineralogy), or environmental factors such as precipitation, elevation, incident radiation or temperature.

Nitrogen inputs for coffee agroecosystems in Las Marías

Our analysis of N inputs indicates that total N inputs were 58 kg N ha^{-1} higher in SHD than in SUN coffee (Table 4). Nutrient N requirements (supplied by soil N or fertilizer N) of coffee plants increase with yield. Maximum yields (parchment) of different coffee varieties under SUN and SHD coffee (30 % shade) in Puerto Rico have been measured at 1,900 and 1,322 kg ha^{-1}, respectively (Vicente-Chandler *et al.* 1968). Coffee yields in Las Marías were 337 and 135 kg ha^{-1} $year^{-1}$ in SUN and SHD, respectively, equivalent to between 10 and 18 % of maximum. Fertilizer N application rates were about 16 % of maximum recommended rates (based on crop response to fertilizer-N applied). Assuming N extraction levels of 29.6 kg N 1,000 kg^{-1} parchment coffee and a harvest index of 25 to 30 % (Bertsch 2003), total crop N removal was calculated at 46 and 19 kg N ha^{-1} in SUN and SHD coffee, respectively. Total N inputs were greater than coffee N removal by the crop in SUN and SHD, yet excess N inputs were probably not sufficient to maximize yields due to N losses, such as denitrification, volatilization, and runoff, as well as limiting factors other than N (Babbar & Zak 1995; Leal *et al.* 2009; Noponen *et al.* 2012).

Table 4. Summary of N inputs in coffee agroecosystems under sun (SUN) and shade (SHD) in Las Marias, Puerto Rico.

Input (kg N ha^{-1} yr^{-1})	SUN	SHD
Litter N	32	56
Soil N mineralization	49	96
Fertilizer N	48	35
Biological N fixation	0.17	0.33
N Deposition	2.8	2.8
Total N inputs	132	190

Improperly managed shade trees reduce yields of intensively managed coffee by competing for light, moisture, and nutrients. The relative shade in Las Marías was 90 % in SHD coffee (Avilés-Vázquez 2009), although the recommended value is between 30 and 40 % (Soto-Pinto *et al.* 2000). Higher N inputs in SHD did not result in increased coffee yields possibly due to the reduced solar radiation incidence. Thus, the low coffee yields observed could be the result of the combined effects of poor nutrient-N and shade management.

Estimates of N uptake in coffee (total plant uptake) under SUN are similar to those returned in litter (Table 3). In the case of SHD coffee, the contribution of litter N (56 kg N ha^{-1} $year^{-1}$) is much higher than the estimated vegetative N uptake by coffee plants (14 kg N ha^{-1} $year^{-1}$), with the difference (42 kg N ha^{-1} $year^{-1}$) likely accounted for by N uptake of over-storey shade trees. Values of litter N inputs of 41 kg N ha^{-1} $year^{-1}$ for the FOR ecosystem support this interpretation. Hence, litter N inputs appear to be balanced with vegetative N uptake by coffee in SUN and by coffee and over-storey trees in SHD.

Soil net N mineralization from soil organic matter was the most important source of N input in our coffee agroecosystems, accounting for about 37 % of all N inputs in SUN and 50 % in SHD. Soil N mineralization exceeded crop N uptake in SHD. From an agronomic perspective, the management goal is to maximize the amount of N that the crop takes up from soil N mineralization and litter N decomposition in order to reduce the need to apply fertilizer N. The measured rates of N mineralization are close to organic N inputs (litter plus biologically-fixed N) in SUN and less so in SHD. Litter N inputs were 32 and 56 kg N ha^{-1} $year^{-1}$ for SUN and SHD. This accounts for a higher proportion of N that is eventually mineralized in the soil in SUN. The N mineralized in the soil likely originates from the labile organic matter portion, which is produced by litter decomposition. In the absence of over-storey shade trees, soil in the SUN will have lower root biomass that can serve as precursor for mineralizable N, and lower soil water content, which may limit soil microbial activity.

Litter and soil N turnover in Las Marías

Shade tree plus coffee biomass standing stock N was over ~3 times higher and litter N input was ~2 times higher in SHD than in SUN (Table 5). The differences in over-storey standing stock N were, however, not reflected in soil N stocks, which were only slightly higher in SHD. These results suggest that litter N is turned over faster, and mineralized at a faster rate, in SUN than in SHD, whereas soil N is being turned over faster in SHD than in SUN. The soil organic matter in SUN may have a lower proportion of labile pool (Buyanovsky 1994; Curtin & Wen 1999). Higher inputs of N to soil and soil N turnover in SHD may be offset by improved N uptake of coffee and associated forest biomass uptake. Higher soil N mineralization rates in SHD coffee suggest greater ecosystem sustaina-

Table 5. Stocks of plant biomass, soil and litter, inputs of N from litter and mineralization, and turnover of litter and soil N in coffee agroecosystems under sun (SUN) and shade (SHD) in Las Marias, Puerto Rico.

Parameters	Unit	SUN	SHD
Trees standing stock	ton DM ha^{-1}		13.56
Coffee standing stock	t DM ha^{-1}	7.6	6.61
Secondary forest trees standing stock	t DM ha^{-1}		6.78
Trees+coffee standing stock N	kg N ha^{-1}	95	300.53
Soil N (0-15 cm)	kg N ha^{-1}	7854	8697
Litter N input	kg N ha^{-1} yr^{-1}	32	56
Litter N turnover[1]	yr^{-1}	0.337	0.186
Soil N mineralization	kg N ha^{-1} yr^{-1}	49	96
Soil N turnover[2]	yr^{-1}	0.006	0.011

[1] Litter N turnover was calculated based on the ratio of plant biomass standing stock to litter N input.

[2] Soil N turnover was calculated based on the ratio of soil N stock to soil net N mineralization rate.

bility than in SUN coffee, presumably due to higher microbial activity, and greater microbial diversity and substrate availability in SHD.

Differences in the activities of earthworms between SUN and SHD may also help explain differences between these ecosystems. Earthworms have been shown to accelerate nitrogen mineralization in a broad range of ecosystems (Edwards & Bohlen 1996). Amador *et al.* (2013) reported that earthworms in SHD ecosystems consumed a broader range of food sources, and thus N sources, than those in SUN, based on differences in ^{15}N enrichment between earthworms, soil, and litter - two of their putative food sources. The capacity of earthworms in SHD ecosystems to consume - and presumably mineralize - N from a greater number of trophic levels, may be responsible, at least in part, for greater soil N turnover in SHD than in SUN ecosystems.

Conclusions

Our results indicate that litter and mineralizable soil N contribute a significant amount of N in coffee agroecosystems with low external N inputs, part of which should be available for coffee vegetative growth and fructification. The differences in soil net N mineralization between ecosystems are probably due to differences in aboveground litter inputs, which were expected to be reflected in higher soil organic matter. Although, soil C and N were not different between SHD and SUN, greater N allocation to litter is expected to increase microbial biomass and diversity, which result in improved N cycling. Sotomayor-Ramírez *et al.* (unpublished) found that microbial biomass N was significantly greater in FOR than in SHD, and both were greater than SUN in all locations.

Coffee grown under shade is generally considered to provide enhanced ecological services relative to coffee grown under sunlight because it supports greater plant and animal diversity (Perfecto *et al.* 1996), experiences lower soil erosion (Smith & Abruña 1955), and requires lower inputs of synthetic fertilizers than coffee grown under full sunlight. Although we did not determine the magnitude of N losses from the ecosystems studied, our results suggest that growing SHD coffee may be more sustainable with respect to N management due to lower litter turnover and improved soil N mineralization. Managers need to consider the importance of soil N dynamics in conjunction with crop yields to make decisions regarding which production system to implement.

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