Nitrogen Resorption and Nitrogen Use Efficiency in Cacao Agroforestry Systems Managed Differently in Central Sulawesi

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Cacao agroforestry is a traditional form of agriculture practiced by the people of Central Sulawesi. These agroforestry systems vary from a simple system following selective cutting of forest trees, to a more sophisticated planting design. The cacao was planted under remaining forest covers (CF1), under planted trees (CF2), and between shade trees *Gliricidia sepium* (CP). The objectives of this study were to quantify nitrogen use efficiency (N NUE) and nitrogen resorption in cacao agroforestry systems. The N NUE at the ecosystem scale (N NUE$_{ES}$) for the cacao agroforestry systems were compared with the natural forest. The results showed that CP produced the highest litterfall and cacao foliar nitrogen. CP and CF1 produced litterfall and the nitrogen resorption that not were significantly different. In contrast, CF2 produced the lowest litterfall, hence required lower nitrogen supply. The nitrogen resorption of CF2 was less than that of CF1 and CP. However, N NUE in cacao plant (N NUE$_C$) of CF2 was higher than that of the CP. The N NUE$_{ES}$ of either CF1 or CF2 were similar to that of the natural forest, but higher than that of the CP. Using shade trees in cacao plantations increased foliar nitrogen concentration, nitrogen resorption, N NUE$_C$ and N NUE$_{ES}$; thus, might be one reason for a higher productivity of cacao in unshaded systems.

Key words: cacao agroforestry system, cacao foliar nitrogen, nitrogen resorption, N NUE

INTRODUCTION

Agricultural and forest lands in the tropics have been subjected to unprecedented development pressures for the past several decades (Collier *et al*. 1994; Janzen 1998). Millions of hectares of primary forest have been degraded by logging (Putz *et al*. 2000) and millions more were converted into intensively used agricultural areas (Lenne & Wood 1999). At the same time, traditional agroforestry, perennial, and long-fallow shifting cultivation systems (i.e. forest farming) have been displaced by monocultures techniques (Thrupp 1998). The role and importance of agricultural lands, particularly traditional forest farming systems, have been neglected in global biodiversity conservation efforts (Thrupp 1998; Fox *et al*. 2000).

In closed-canopy forests, both external micro-climatological factors and plant metabolic processes vary from the top of the canopy to the forest floor. As a consequence, pronounced vertical gradients occurred in the physiology of foliage in the forest canopies (Ishii *et al*. 2000; Lewis *et al*. 2000). The foliage also responds to factors that vary through the canopy, such as foliar nitrogen (N) and N translocation or resorption efficiency (Ishii *et al*. 2000; McDowell *et al*. 2000).

An agroforestry system such as shade-grown cacao (*Theobroma cacao*) is one alternative land use such as in slash-and-burn agriculture and is recommended for sustainable development in the humid tropics (Johns 1999).

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Cacao is shade-tolerant and can grow under a canopy of trees maintained, regenerated, or replanted from the traditional tropical forest (Beer *et al*. 1998). Hence, its inclusion into a forest agro-ecosystem can maintain biodiversity and ecological services provided by the native forests (Rice & Greenberg 2000; Glor *et al*. 2001).

Nitrogen is a major constituent of chlorophyll and is involved in the carboxylating enzymes of the photosynthesis, especially Rubisco (Waring & Schlesinger 1985). The difference in N concentration of foliage tissue generally reflects the differences in enzyme concentration (McGuire *et al*. 1995). Foliar N concentration depends on many variables, including soil N mineralization and nitrification rates, soil C/N ratio, plant species, temperature, and irradiance (Yin 1994; MaGill *et al*. 1996; Ollinger *et al*. 2002). Species traits, N availability, and climate are the three controlling factors that likely determine canopy foliar N concentration (Pan *et al*. 2004).

Nutrient resorption is a process in which nutrients are withdrawn from leaves prior to abscission and redeployed in developing tissues. Nutrients resorption prior to abscission is one of key processe by which plants conserve them. Resorption may occur throughout leaf's life, particularly as they become progressively shaded (Ackerly & Bazzaz 1995; Hikosaka 1996). This process reduces the likelihood of nutrient loss in litter dropped on the forest floor (Bormann *et al*. 1977). Subsequently, the withdrawn nutrients are redeployed in new tissue, such as leaves and reproductive structures, or stored for later use (Wright & Westoby 2003). On average, plants withdraw about 5-80% of leaf nitrogen via resorption. The

proportion of nutrients withdrawn from leaves (the resorption efficiency) varies widely between species and environmental condition. For example, less than 5 up to 80% of leaf N, and 0 up to 95% of leaf P may be resorbed (Aerts 1996; Lambers *et al*. 1998; Aerts & Chapin 2000). In infertile habitats, nitrogen in senescent leaf is reduced to lower levels than in fertile habitats (Wright & Westoby 2003).

Nutrient or fertilizer use efficiency concepts generally describe how well does plants or a production system use nutrients. The efficiency of plant nutrient use is simply the inverse of nutrient concentration in senescent leaf. Consequently, plants from nutrient-poor habitats are typically more efficient in their N use than plants from nutrient-rich habitats (Vitousek 1982; Tateno & Kawaguchi 2002). Nutrient use efficiency (NUE) as an index may help explain species distributions across landscapes that vary in soil fertility and other resources (Vitousek 1982; Schlesinger *et al*. 1989).

The objective of this study was to quantify N NUE and nitrogen resorption in cacao leaf from three types of cacao agroforestry systems over one year. In this study, we collected fully-developed and senescent cacao leaf, soil samples, and litterfall.

MATERIALS AND METHODS

Study Sites. The studies were conducted in three different types of cacao agroforestry systems at the northeastern margin of Lore Lindu National Park (LLNP), located in Central Sulawesi, Indonesia ca. 75 km southeast of Palu. The whole sites were located between 120°1' - 120°3'30"E and 1°29'30" - 1°32'S at an elevation of 800 m to 1100 m in Toro village, Kulawi district, Central Sulawesi, Indonesia. The average of relative humidity at Toro village is 87.2%, the mean of monthly temperature was 22.9 °C, the average annual global radiation was 17.48 MJ m^{-2}, and the total annual precipitation in 2005 recorded in the study sites was 2055.6 mm.

Three different cacao agroforestry systems were selected in the buffer zone of LLNP. They were (i) the system under a remaining forest cover (CF1), (ii) the system under local shade trees (CF2), (iii) the system without forest cover, but with planted shade srees, *Glyricidia sepium* (CP). The natural forest (NF) was used as the undisturbed ecosystem compared to N NUE$_{ES}$ cacao agroforestry systems. Environmental characteristics of study sites were presented in Table 1. The CF1 was dominated by *T. cacao, Coffea robusta, Arthocarpus vrieseanus, Turpinia sphaerocarpa,* and *Horsfieldia*

Table 1. Environmental characteristics of the natural forest (NF) and three cacao agroforestry systems (CF1, CF2, and CP) in Toro village, Central Sulawesi, Indonesia

Environmental characteristics	NF	CF1	CF2	CP
Tree density (sum of trees/0.5 ha)*	592	304	244	604
Basal area* (m²)	58.4	31.5	6.6	13.2
Exposition	95° E	110° E	100° E	100° E
Air humidity (%)**	95.7	92	91.4	86.3
Temperature (°C)**	20.4	21.5	21.8	22.9
Canopy cover (%)**	89.7	72.1	69.4	49.8
Altitude (m asl)	1006	832	802	799
Slope (%)	80	70	35	20

*Ramadhanil (2006), **Bos *et al.* (2007)

costulata. The species that dominated CF2 were *T. cacao, Erythrina subumbrans, Syzigium aromaticum, Arenga pinnata,* and *Bischofia javanica,* while CP was dominated by *E. subumbrans, T. cacao, G. sepium, Mellochia umbellate, Piper aduncum* (Ramadhanil 2006). Topography of study sites was relatively flat with different slope (Table 1). Planting distance in the CF1 and CF2 was unregulated, but not the CP. Planting distance in CP was 3 x 3 m. Plot size was 30 x 50 m in every study site. In the study area, cacao trees were mainly hybrids ("Trinitario" type) between the "Criollo" and "Forastero" varieties. The age of cacao trees were 5-15 years old.

Experimental Set-Up. The experiment was began in March 2005 and ended in March 2006. Ten litter traps (1 x 1 m, 50 cm above the ground) were installed at 20 subplots on each plot. Litter was collected at monthly intervals for one year (March 2005 to February 2006). The litter was taken to the laboratory and dried to constant dry weight at 80 °C. The total litterfall was obtained by weighing the samples. Nitrogen content in litterfall was determined with Kjeldahl method.

Leaves were collected at three-monthly intervals over one year (March 2005 to March 2006) from the three types of cacao agroforestry systems. At each collecting time, three to five leaves samples (fully-developed leaves and senescent leaves) were collected from five cacao trees from each plot. The senescent leaves were yellowish and easily dropped by shaking the branch. Fully-developed leaves and senescent leaves from each sampling period were thoroughly washed and air dried then kept in oven at 60 °C for 48 hours. Grounded dried leaves were stored in paper bags for chemical analyses. Leaf nitrogen concentration was determined with Kjeldahl method.

Soil samples were also collected at three-monthly intervals over one year using a soil core down to 15-20 cm depth. At each collecting time, twenty five soil samples were collected randomly in each plot. Soil samples for soil nitrogen content determination, were stored in sealed plastic bags at 4 °C until analysis. The total soil N content was determined with Kjeldahl method.

The nitrogen use efficiency of the cacao plants (N NUE$_C$) in the agroforestry system was calculated according to Vitousek (1982) and Tateno and Kawaguchi (2002):

N NUE$_C$ =1 / nitrogen concentration in senescent leaf (%)

The nitrogen use efficiency at the ecosystem scale (N NUE$_{ES}$) in the cacao agroforestry system and in the natural forest as a control was calculated according to Vitousek (1982):

$$\text{N NUE}_{ES} = \frac{\text{Litterfall production (g m}^{-2}\text{ y}^{-1})}{\text{N content in litterfall (g m}^{-2}\text{ y}^{-1})}$$

The proportional nitrogen resorption was calculated according to Sharma and Pande (1986):

$$\text{Resorption (\%)} = \frac{\text{Nd} - \text{Ns}}{\text{Nd}} \text{ x } 100\%$$

where Nd: N in fully-developed leaf, Ns: N in senescent leaf

Statistical Analyses. Data of annual litterfall, foliar nitrogen content, N resorption, soil nitrogen content, N NUE_C and N NUE_{ES} were analyzed using general linear models (GLMs). All post hoc tests were carried out using Tukey's HSD test. Relationship between parameters was analyzed using regression and Pearson correlation analysis. All analyses were caried out using SPSS 13.0 software.

RESULTS

The cacao agroforestry systems investigated in this study were in the local people's plantations at the border LLNP. These plantations were never fertilized. Means of annual litterfall, cacao foliar nitrogen content, nitrogen resorption, soil nitrogen content, and N NUE_C in the cacao agroforestry systems were presented in Table 2. Means of annual litterfall, cacao foliar nitrogen content, nitrogen resorption, and N NUE_C were differed significantly (P = 0.02, P = 0.004, P = 0.03, and P = 0.03, respectively) among the three agroforestry systems, but those of soil nitrogen content were not (P = 0.07). The CF2 had a mean of annual litterfall of 497.7 g m^{-2} y^{-1} which was not significantly different from that of CF1 but significantly lower than that of the CP. Foliar nitrogen content of cacao under the CF2 (1.2%) was not different from that of the CF1 (1.3%) but lower than that of CP (1.5%). The CF2 had the highest value of N NUE_C (97.3%).

The relationships between cacao foliar nitrogen content (in fully-developed leaf) and canopy cover and temperature revealed different patterns (Figure 1). The relationship between foliar nitrogen content and canopy cover showed a negative correlation (Pearson's r = - 0.36), while foliar nitrogen content and temperature showed a positive correlation (Pearson's r = 0.34). Increasing canopy cover would decrease temperature in the forest. Canopy cover was not related to cacao foliar nitrogen content (r^2 = 0.13).

The relationship between cacao foliar nitrogen content (in fully-developed leaf) and soil nitrogen content was poor (r^2 = 0.14, Figure 2). However, significant correlation occured between soil nitrogen content and cacao foliar nitrogen content (in fully-developed leaf) (Pearson's r = 0.38, P = 0.003).

Figure 3 showed that there was a poor relationship between litterfall production and nitrogen resorption in the CF1, CF2, and CP. The correlation between litterfall and nitrogen resorption was not significant either (Pearson's r = 0.22, P = 0.08).

There was also a poor relationship between soil nitrogen content and nitrogen resorption in cacao agroforestry systems (Figure 4). However, significant correlation occured between

soil nitrogen content and nitrogen resorption (Pearson's r = 0.3, P < 0.05).

The efficiency of plant utilizing soil nutrients for producing biomass may indicate its capability to optimize growth at a given soil nutrient content. The relationship between cacao N NUE_C in the cacao agroforestry systems and soil nitrogen content showed that there was a trend of decreasing N NUE_C with the increasing of soil nitrogen content in cacao agroforestry systems (Figure 5), although the relationship was not significant. We found that the natural forest (NF) as the undisturbed ecosystem was not different from CF1 nor CF2 for N NUE_{ES} at the ecosystem scale, but had significantly higher values (P < 0.01) than CP. The N NUE_{ES} in CP (64.53)
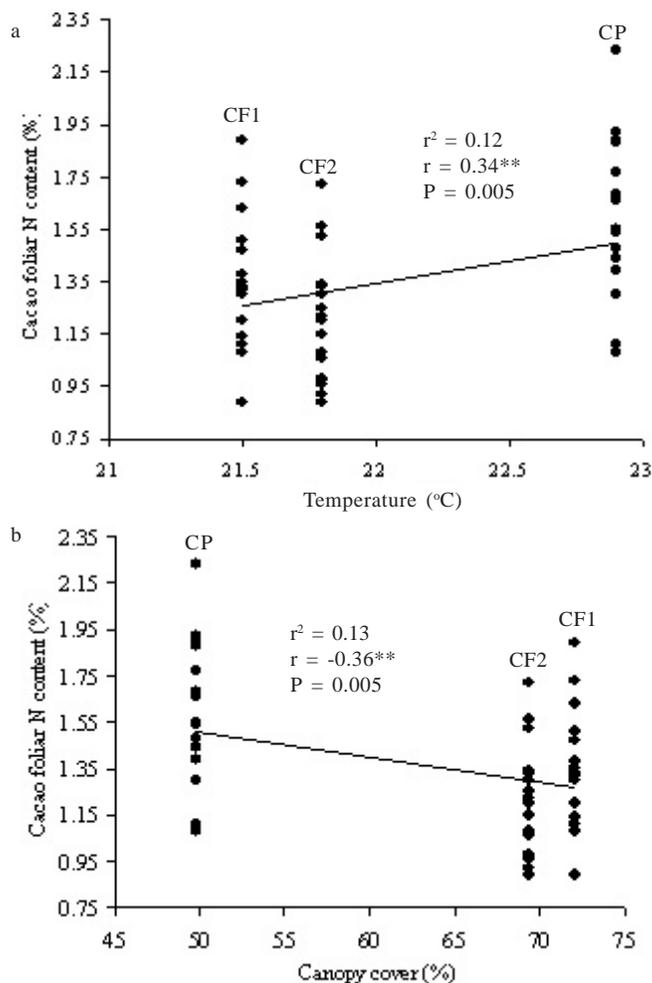

Figure 1. Cacao foliar nitrogen (%) in relation to (a) temperature (ºC) and (b) canopy cover (%) in three cacao agroforestry systems (CF1, CF2, and CP) in Toro village, Central Sulawesi, Indonesia. **Significant differences given at P < 0.01.

Table 2. Mean annual litterfall, N in fully-developed leaf, N resorption, soil N content, and N NUE_C in three cacao agroforestry systems (CF1, CF2, and CP) in Toro village, Central Sulawesi, Indonesia

Cacao agroforestry sysems	Annual litterfall (g m^{-2} y^{-1})	N fully-developed leaf (%)	N senescent leaf (%)	N resorption (%)	Soil N content (mg kg^{-1})	N NUE_C
CF1	693.4 ± 21.9ab	1.3 ± 0.05ab	1.1 ± 0.04ab	17.6 ± 2.5b	511.1 ± 102.1a	91.1 ± 7.4ab
CF2	497.7 ± 27.7a	1.2 ± 0.05a	1.0 ± 0.04a	12.7 ± 2.0a	582.6 ± 112.9a	97.3 ± 5.4a
CP	822.9 ± 37.8b	1.5 ± 0.07b	1.3 ± 0.06b	14.4 ± 1.9ab	583.5 ± 106.8a	80.7 ± 12.0b

Different letter(s) in the same column after the means value indicated significant differences among means (P < 0.05, Tukey HSD test). Data were means ± SE
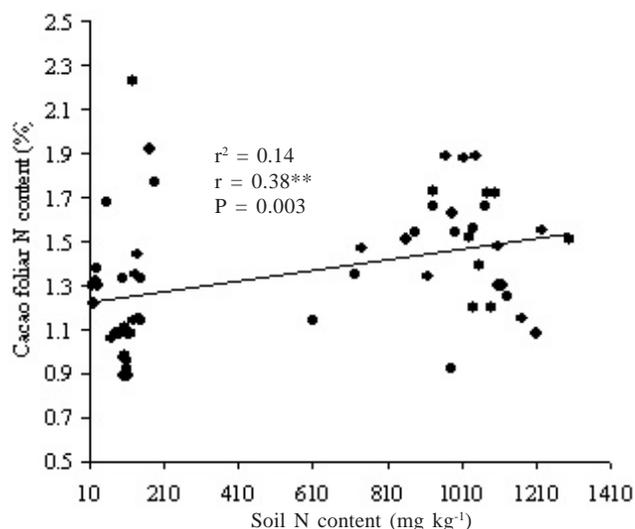
Figure 2. Cacao foliar N content (%) in relation to soil N content (mg kg^{-1}) in three cacao agroforestry systems in Toro village, Central Sulawesi, Indonesia. **Significant differences given at P < 0.01.
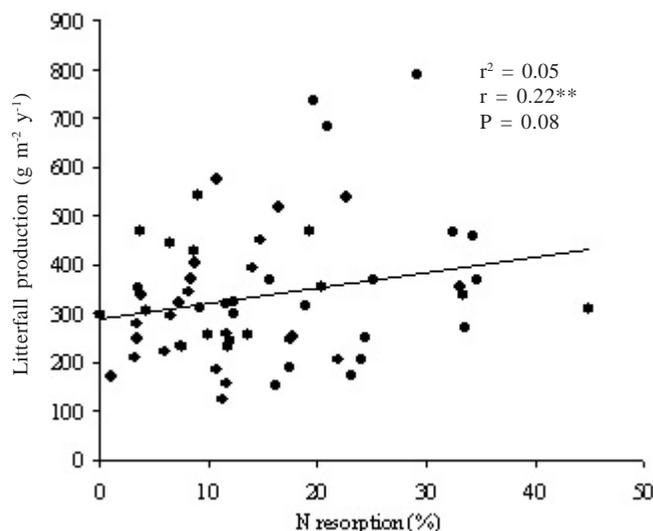

Figure 3. Litterfall production (g m^{-2} y^{-1}) in relation to N resorption (%) in three cacao agroforestry systems in Toro village, Central Sulawesi, Indonesia. **Significant differences given at P < 0.05.
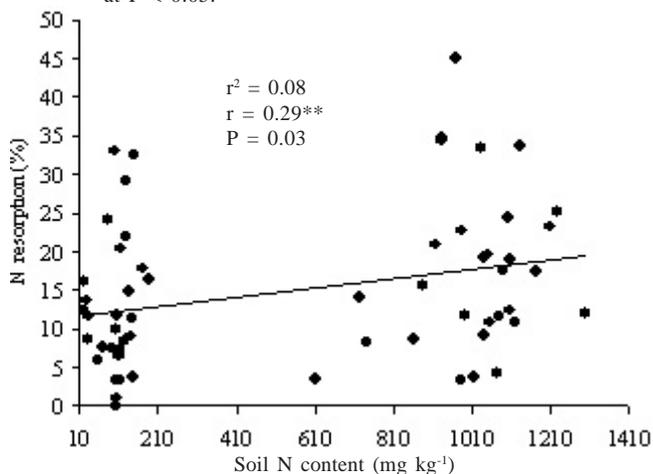

Figure 4. N resorption (%) in relation to soil N content (mg kg^{-1}) in three cacao agroforestry systems in Toro village, Central Sulawesi, Indonesia. **Significant differences given at P < 0.05.

Table 3. Nitrogen use efficiency (N NUE$_{ES}$) in the natural forest (NF) and three cacao agroforestry systems (CF1, CF2, and CP) in Toro village, Central Sulawesi, Indonesia

Study sites	Annual litterfall (g m^{-2} y^{-1})	N content in litterfall (%)	N NUE$_{ES}$
NF	1367.4 $\pm$ 32.5c	1.15 $\pm$ 0.2ab	94.9 $\pm$ 12.7b
CF1	693.4 $\pm$ 21.9ab	0.92 $\pm$ 0.05a	108.0 $\pm$ 6.7b
CF2	497.7 $\pm$ 27.7a	0.89 $\pm$ 0.08a	109.6 $\pm$ 9.4b
CP	822.9 $\pm$ 37.4b	1.62 $\pm$ 0.15b	63.8 $\pm$ 7.6a

Different letter(s) in the same column after the means value indicated significant differences among means (P < 0.05, Tukey HSD test). Data were means $\pm$ SE
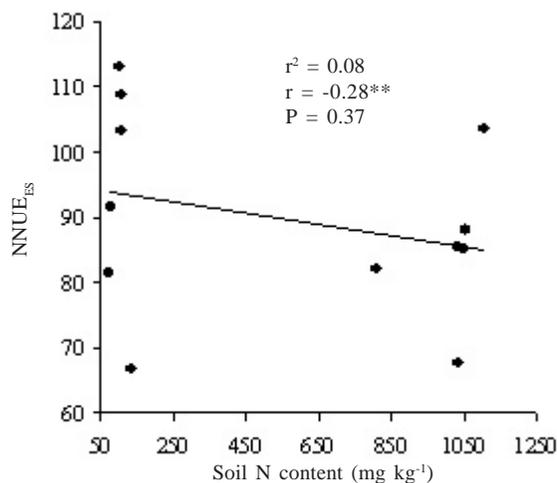

Figure 5. Nitrogen use efficiency at the ecosystem scale (N NUE$_{ES}$) in relation to soil nitrogen content (g kg^{-1}) in the natural forest and three cacao agroforestry systems in Toro village, Central Sulawesi, Indonesia. **Significant differences given at P < 0.05.

was lower than in the other ecosystems (CF1 = 108.19, CF2 = 112.12, and NF = 94.85) (Table 3).

DISCUSSION

The canopy cover in CP cacao agroforestry system (49.8%) was lower compare to the CF2 (69.4%) and the CF1 (72.1%). A lower canopy cover is equivalent to a higher light intensity and also a higher temperature. Wood and Lass (1985) reported that the higher light intensity is a very important factor for cacao productivity. If nitrogen is not limited, the higher light intensity increases linearly the carbon gain of the cacao plants leading to a high biomass production. This was indicated by the higher (P = 0.02) litterfall under the CP (822.9 g m^{-2} y^{-1}) than that under the CF2 (497.7 g m^{-2} y^{-1}), and similar to that under the CF1 (693.4 g m^{-2} y^{-1}). This high biomass production coincided with an elevated supply rate of nitrogen as reflected by the fact that the foliar nitrogen content of cacao under the CP (1.5%) was higher (P = 0.004) than that under the CF2 (1.2%) and similar to that under the CF1 (1.3%). The relationship between foliar N, temperature, and canopy cover indicated that cacao foliar nitrogen content decreased with the increasing of canopy cover, but it increased with the decreasing of temperature. The relationship between canopy cover and foliar nitrogen content was significant (Pearson's r = -0.36) and showed that a greater canopy cover reduces the foliar nitrogen content of the cacao tree (Figure 1). This

finding was similar to that reported by Tateno and Kawaguchi (2002) and Leal and Thomas (2003) mentioning that high light intensity required of high supply of nitrogen reflected in the foliar nitrogen content of mature leaves as a manifestation of plant nitrogen demand.

The plant internal nitrogen demand may be satisfied by nitrogen taken up from the soil and/or by nitrogen resorbed from senescent leaf. When soil nitrogen content is high, plants generally prefer to absorb nitrogen from the soil (Baddeley *et al*. 1994; Bowman 1994; Rapp *et al*. 1999; Tateno & Kawaguchi 2002; Wright & Westoby 2003; Singh *et al*. 2005). Cacao trees cultivated in the CP satisfied its internal nitrogen demand by both nitrogen soil uptake and nitrogen resorption. *G. sepium*, the nitrogen-fixing shade tree planted in the CP contributes a good amount of litter, and through decomposition, the soil nitrogen content for plants including cacao trees may improve. Therefore, the cacao trees in the CP benefited from a slight improvement of soil nitrogen content. However, even though the mean of soil nitrogen content under CP was somewhat higher than that in the CF1 or CF2, the differences were not significant. On the other hand, there was a significant relationship (Pearson's r = 0.38, P < 0.01) between cacao foliar nitrogen content and soil nitrogen content showing an increasing foliar nitrogen content with an increasing soil nitrogen content (Figure 2). This type of relationship was similar to that reported by Singh *et al*. (2005).

Nitrogen resorption of the cacao trees grew under CP was 14.4% which less than that of CF1. The cacao agroforestry under the CF1 was located in the foothill region about 80% inclination. In this steep slope, surface runoff was considerable with the consequence that nutrients were washed out into the river below thereby reducing soil nutrient content in the cacao plantation. This situation apparently forced the cacao plants under the CF1 to rely more on a higher resorption of nitrogen (17.6%).

The CF2 has the lowest tree densities and basal area as compared to other study areas. As a result, the litterfall in the cultivation of cacao trees under the CF2 regime resulted in less litterfall, i.e. 497.7 g m² y⁻¹. The cacao trees especially under the CF2 showed a considerably higher weed infestation than those under the CF1 or CP (Ramadhanil 2006). It seems that the cacao trees under the CF2 system suffered from strong competition with weeds. We assume that the weeds accumulated considerable amounts of nitrogen and other nutrients, thus preventing cacao trees from accumulating a higher amount of biomass or litterfall. With a low amount of litterfall, these cacao trees apparently required a smaller supply rate of nitrogen. A relatively small resorption rate (12.7%) seemed to be sufficient to satisfy the internal nitrogen demand. The nitrogen resorption of cacao trees under the CF2 did not differ significantly from that under the CP. This may be taken as an indication that, with respect to root nitrogen uptake, the conditions in both systems were similar, i.e. sufficient regarding soil nitrogen content. However, the internal nitrogen demand differed as a consequence of different litterfall rates.

The relationship between nitrogen resorption and soil nitrogen content in this study indicated a peculiar relationship, where nitrogen resorption increased with increasing soil nitrogen content. The CF1 was located under the canopy of the remaining forest, so the density of shrubs and grasses was small, while the plot of the CP was located in a well maintained cacao plantation using *G. sepium* as shading trees. All plots were infested by weeds during the measurements at various degrees with the heaviest infestation occurring under the CF2. Although the soil nitrogen content was quite high, it appears that competition with weeds reduced the nitrogen available to the cacao trees which may have promoted a higher foliar nitrogen resorption rate.

The nitrogen use efficiency of the cacao trees grew under the CP was lower than that under the CF2. This finding supports the argument of Tateno and Kawaguchi (2002) that plants with high foliar nitrogen content tend to have a lower N NUE$_{ES}$. Comparing the means of N NUE$_{ES}$ at the ecosystem scale among the agroforestry systems and with the natural forest, the results showed that the CF1 and CF2 was not differed from the natural forest, while the N NUE$_{ES}$ of CP was significantly lower than in the other systems. This finding agrees with Smith *et al*. (1998) and Tateno and Kawaguchi (2002) that the N NUE$_{ES}$ of legume trees as nitrogen-fixing species is lower than the N NUE$_{ES}$ in the natural forest. The values of N NUE$_{ES}$ in this work are lower than those reported by Ankilla *et al*. (2002) in Costa Rican lowland forest, but higher than those reported by Smith *et al*. (1998) in Curuá-Una, Brazil.

We conclude that reducing the cover by shade trees in cacao plantations increases foliar nitrogen concentration, nitrogen resorption, and nitrogen use efficiency in the cacao tree, thus, may be one reason for a higher productivity of cacao in unshaded systems. However, more light also promotes weed infestation and thus competition for nitrogen.

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