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par **Pablo SILES GUTIERREZ**

Hydrological processes (water use and balance) in a coffee (*Coffea arabica* L.) monoculture and a coffee plantation shaded by *Inga densiflora* in Costa Rica

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A mi esposa
Patricia Talavera
La mujer más linda del mundo y la persona que me ha apoyado cuando nadie más lo hizo

A la Pacha Mama, Gaia, la madre tierra: nuestra madre

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Titre de la thèse:

Processus hydrologiques (utilisation de l'eau et bilan) dans deux systèmes caféiers (*Coffea arabica L.*) : (1) une monoculture et (2) une parcelle ombragée par *Inga densiflora* au Costa Rica

présentée par Pablo Siles Gutierrez pour l'obtention du titre de Docteur de l'Université Henri Poincaré (Nancy I)

le 14 décembre à 10h30

Résumé

En zones marginales, les arbres d'ombrage augmentent la production de café arabica en améliorant le microclimat et la fertilité du sol. En zones optimales, ces effets sont plus controversés mais les systèmes agroforestiers (SAF) procurent toujours d'autres services tels que la lutte antiérosive ou la diversification des productions. Le présent travail compare en zone optimale du Costa Rica une monoculture (MC) et un SAF avec *Inga densiflora* Benth en termes de microclimat, productivité et bilan hydrique.

Par rapport à MC, les arbres d'ombrage ont réduit la radiation globale de 40-50%, les températures maximales foliaires du caféier de 6°C en journée et le VPD foliaire, mais augmenté de nuit les minimales foliaires de 0,5°C. Selon l'année, les arbres ont augmenté l'interception de la pluie (12% à 85%) et la transpiration du système (29% à 33%) mais réduit le ruissellement de 50% et le drainage (1% à 14%). Le SAF a augmenté l'interception (13% de la pluie) par rapport à MC (7%) lorsque le LAI total augmentait de plus d'une unité. Les arbres ont réduit l'égouttement, augmenté l'écoulement le long des troncs et ont contribué pour 40-50% à la transpiration du SAF avec des caféiers transpirant moins qu'en MC. L'assèchement profond du sol sous SAF indique une certaine complémentarité avec les arbres utilisant vraisemblablement des ressources en eau non accessibles au caféier.

Malgré l'absence de compétition en eau dans ces conditions de site, la production de café a été réduite de 29% en SAF par rapport à MC du fait d'une radiation et floraison réduites. Par contre, la production de biomasse a été multipliée par 3, contribuant au stockage du carbone et à la production d'énergie.

Mots Clés :

Bois de feu, conductance stomatique, cycle de l'eau, écoulement de tronc, égouttement, évaporation, flux de sève, interception de la lumière, ombrage, rendement en café, système multistrate, température foliaire, transpiration, tropiques humides, utilisation de l'eau.

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Hydrological processes (water use and balance) in a coffee (*Coffea arabica* L.) monoculture and a coffee plantation shaded by *Inga densiflora* in Costa Rica

presented by Pablo Siles Gutierrez to opt for the degree of Doctor in Science at the University Henri Poincaré (Nancy I)

December 14 at 10h30

Summary

Under suboptimal site condition for arabica coffee cultivation the shade trees increase the coffee production due to an enhancement of the microclimate and the soil fertility. Under optimal site conditions, the use of shade are more controversial, nevertheless the agroforetry systems (AFS) provide others services as the reduction of erosion and the diversification of production. The present study compare in optimal site conditions in Costa Rica a coffee monoculture (MC) and AFS with *Inga densiflora* Benth in terms of microclimate, productivity and water balance.

In reference to MC, the shade trees reduced the global radiation between 40% to 50%, the maximal coffee leaf temperature to 6°C, the leaf to air VPD during the day and increased the leaf temperature in 0,5°C during night. According to the year of measurement, the trees increased the rainfall interception (12% to 85%) and the total system transpiration (29% to 33%), at the same time trees reduced the runoff (50%) and the drainage (1% to 14%). The trees reduced the throughfall, increased the stemflow and contributed 40% to 50% to the total transpiration of the AFS reducing the coffee transpiration in the AFS. In other hand, higher reductions in the AFS compared to MC in soil water in depper soil layers indicate a complementarity interaction in the use of water between coffee and trees.

Despite the absence of water competition under these site conditions, the coffee yield was reduced by 29% in the AFS in comparison to the MC, due to a reduction in the radiation and flowering intensity. In other hand, the total aerial biomass was 3 times in the AFS compared to MC, contributing to carbon sequestration and renewable energy.

Key words:

Fuelwood, stomatal conductance, water cycle, stemflow, evaporation, sap flow, light interception, shade, coffee yield, multi-strata system, leaf temperature, transpiration, tropic humid, water use.

Titulo de tesis:

Procesos hidrológicos (utilización de agua y balance) en un sistema de monocultura de café (*Coffea arabica L.*) y una plantación de café sombreada por *Inga densiflora* en Costa Rica

presentado por Pablo Siles Gutierrez para la obtención del titulo de Doctor de la Universidad Henri Poincaré (Nancy I)

el 14 de diciembre a las 10h30

Resumen

En zonas marginales, los árboles de sombra aumentan la producción de café arabica mejorando el microclima y la fertilidad de suelo. En zonas óptimas, los efectos de la sombra son más controversiales, aun así los sistemas agroforestales (SAF) proveen siempre otros servicios tales como la lucha antierosiva o la diversificación de producción. El presente trabajo compara en una zona óptima de Costa Rica un sistema de monocultura (MC) y un SAF con *Inga densiflora* Benth en términos de microclima, productividad y balance hídrico.

Con respecto al MC, los árboles de sombra redujeron la radiación global de 40-50%, las temperaturas foliares máximas de café en 6°C durante el día y el VPD foliar, pero aumento los mínimos foliares durante la noche en 0,5°C. Según el año, los árboles han aumentado la intercepción de la lluvia (12% a 85%) y la transpiración del sistema (29% a 33%) pero redujo la escorrentía en 50% y el drenaje (1% a 14%). El SAF aumento la intercepción de la lluvia (13% de la lluvia) con respecto al MC (7%) cuando el LAI total aumento en mas una unidad. Los árboles redujeron el goteo, aumentaron el escurrimiento del tronco y contribuyeron entre 40-50% a la transpiración de SAF reduciendo la transpiración de café en comparación de MC. Una mayor reducción de humedad en los horizontes profundos del suelo en SAF indica una cierta complementariedad con los árboles utilizando realmente recursos hídricos no accesibles al café.

A pesar de la ausencia de competencia por agua en estas condiciones de sitio, la producción de café fue reducida en 29% en el SAF con respecto al MC debido a una reducción en la radiación y floración. Por otro lado, la producción de biomasa en SAF fue 3 veces la de MC, contribuyendo a la fijación de carbono y a la producción de energía.

Palabras claves:

Leña, conductancia estomática, ciclo del agua, escurrimiento de tronco, evaporación, flujo de savia, intercepción de la luz, sombra, rendimiento de café, sistema multi-estrato, temperatura foliar, transpiración, trópico húmedo, utilización de agua.

Table of content

1 GENERAL INTRODUCTION 1

1.1 COFFEE 1
1.1.1 The coffee plant, related species and origin 1
1.1.2 Distribution and economical importance, markets 2
1.1.3 Importance of the coffee as a crop in Mesoamerica 4
1.2 ECO-PHYSIOLOGY OF COFFEE 5
1.2.1 Edaphic and climatic boundaries for acceptable yield of C. arabica 5
1.2.2 Photosynthesis and stomatal conductance 6
1.3 THE IMPORTANCE OF COFFEE AGROFORESTRY SYSTEMS IN MESOAMERICA 7
1.3.1 Current agroforestry practices 7
1.3.2 Use of Inga as shade tree in coffee AFS 8
1.3.3 Description of the genus Inga 9
1.3.4 Major effects of the use of shade in coffee plantations 9
1.3.5 New arguments in favor of agroforestry 13
1.3.6 Biological interactions in AFS, with a special focus on water competition 14
1.3.7 What remains to be documented on coffee water relations? 17
1.4 MY RESEARCH HYPOTHESES 17
1.5 MY RESEARCH QUESTIONS 18

2 MATERIAL AND METHODS 19

2.1 SITE DESCRIPTION AND EXPERIMENT 19
2.2 METEOROLOGY AND MICROCLIMATE 19
2.2.1 Radiation transmission and interception 20
2.2.2 Leaf temperature 20
2.2.3 Soil water content 20
2.3 INGA DENSIFLORA GROWTH 22
2.4 COFFEE GROWTH 22
2.4.1 LAI dynamics 22
2.4.2 Yield monitoring 22
2.4.3 Coffee biomass monitoring 22
2.5 WATER BALANCE 22
2.5.1 Rain Interception 23
2.5.2 Transpiration 23
2.5.3 Runoff 24

3 RESULTS AND DISCUSSION 26

3.1 INFLUENCE OF TREES ON MICROCLIMATE 26
3.2 INFLUENCE OF SHADE TREES ON COFFEE GROWTH AND YIELD 29
3.2.1 Yield 29
3.2.2 Coffee LAI and biomass 30
3.3 TREES GROWTH AND TOTAL SHOOT BIOMASS 33
3.4 INFLUENCE OF TREES ON WATER BALANCE COMPONENTS 35
3.4.1 Rainfall interception loss 35
3.4.2 Transpiration 39
3.4.3 Runoff 48
3.4.3 Soil volumetric water 49
3.5 WATER BALANCE AT PLOT SCALE 51
3.6 COMPETITION FOR WATER 53

4 CONCLUSIONS AND PERSPECTIVES 54

4.1 INFLUENCE OF TREES ON THE MICROCLIMATE EXPERIENCED BY COFFEE PLANTS 54
4.2 INFLUENCE OF TREES ON COFFEE YIELD AND BIOMASS 54
4.3 INFLUENCE OF TREES ON WATER BALANCE 55
4.3.1 Canopy Rainfall Interception 55
4.3.2 Transpiration 55
4.3.3 Runoff 56
4.4 WATER USE AND TREE-CROPS INTERACTIONS 56
4.5 PERSPECTIVES 57

5 REFERENCES 58

List of Figures

Figure 1 . Dynamics of the world coffee production (ab) and price paid to producers (c) during the period 1976 to 2005 (Source: ICO, modified by the author)..... 2

Figure 2 . Dynamics of areas planted with coffee (a) and production of green beans (b) in Mesoamerica during the period 1990-2005 (FAO-STAT, modified by the author)..... 4

Figure 3. Employments generated by the coffee sector in countries of Central America in 2001 (Source: Castro et al., 2004, modified by the author)..... 5

Figure 4. Annual time-course of incident and transmitted radiation and percentage of shade of *Inga densiflora* in an agroforestry system at San Pedro de Barva, Costa Rica. 26

Figure 5. Mean diurnal time courses of global, intercepted and transmitted radiations for (a) April 2005 (dry season) and (b) October 2005 (rainy season) below the *Inga* canopy in AFS plot (Values are means of 2 weeks of measurements)..... 27

Figure 6. Mean diurnal time courses of transmitted radiation at 1 m and 3 m away from the trunk of *Inga densiflora* in an agroforestry system in San Pedro de Barva, Costa Rica, for (a) April 2005 (dry season) and (b) October 2005 (rain season)..... 28

Figure 7. Mean diurnal leaf temperature (ab) and mean diurnal differences in leaf temperature (cd) at different coffee canopy strata between monoculture and an agroforestry system shaded with *Inga densiflora* in San Pedro de Barva, Costa Rica, for April 2005 (dry season, left panels) and July 2005 (rainy season, right panels). 29

Figure 8. Coffee berry dry matter per plant (a) and coffee green bean yield (b) in monoculture (MC) and in an agroforestry system (AFS) shaded with *Inga densiflora* in San Pedro de Barva, Costa Rica during 6 consecutive production cycles. 30

Figure 9. Leaf area index (a) and number of leaves per plant (b) for coffee plants in monoculture (MC) and in an agroforestry system (AFS) in San Pedro de Barva, Costa Rica. 31

Figure 10. Biomass (MT ha^{-1}) of the different coffee components in an agroforestry (AFS) and monoculture plot (MC) in San Pedro de Barva, Costa Rica..... 31

Figure 11. Diurnal time courses of incident PPFD and net CO_2 assimilation of coffee leaves during the dry season (a: February; b: March 2005) and wet season (c: August; d: September) in MC and AFS at San Pedro de Barva, Costa Rica. (Values are averages of 4 leaves in 4 plants measured over a period of 1 hour ± CI). 32

Figure 12. Average net CO_2 assimilation rate, stomatal conductance (gs), PPFD and leaf to air VPD at 8 dates during 2005 for the dry and wet seasons in MC and AFS at San Pedro de Barva, Costa Rica (from February to April, dry season; August and September, wet season)..... 33

Figure 13. Dynamics of basal area and total shoot biomass of *Inga densiflora*, (a) shoot biomass in monoculture (MC) and in agroforestry system (AFS) in San Pedro de Barva, Costa Rica, for (b) 2004 and (c) 2005. 34

Figure 14. Average throughfall (with standard error) versus gross rainfall in 2004 (a) and 2005(b) in two coffee agricultural systems (AFS and MC) in the Central Valley of Costa Rica (for 2004, MC: r^2= 0.99, TF=-0.59+0.89*GR; AFS: r^2=0.97, TF=-0.85+0.77*GR; for 2005, MC: r^2= 0.97, TF=-0.53+0.87*GR; AFS: r^2= 0.97, TF=-0.45+0.80*GR). 35

Figure 15. Stemflow (mean ±SE) versus gross rainfall for (a) coffee in MC and AFS, and (b) for *Inga densiflora* in agroforestry system in San Pedro de Barva (Central Valley of Costa Rica) in 2005..... 36

Figure 16. Mean hourly coffee sap flow rate (SF), reference evapotranspiration (ETo; measured in open field) and photosynthetic photon flux density (PPFD) based on ten consecutive days and four coffee plants in AFS or in MC for a dry month (February) and wet month (September) in San Pedro de Barva, Costa Rica (values ± se are means over four plants during monitoring ten days). 39

Figure 17. Diurnal time course of stomatal conductance of coffee leaves during the dry (a: February; b: March 2005) and wet season (c: August; d: September) in MC and AFS at San Pedro de Barva, Costa Rica. (Values are averages of 4 leaves in 4 plants)..... 40

Figure 18. The diurnal time course of PPFD, leaf temperature and leaf to air VPD of coffee leaves during the dry season (a: February; b: March 2005) and the wet season (c: August; d: September 2005) in MC and AFS at San Pedro de Barva, Costa Rica. (Values are averages of 4 leaves in 4 plants measured over a period of 1 hour). 41

Figure 19. Relationships between daily coffee transpiration (a&b) and coffee transpiration over ETo (c&d) versus daily ETo (FAO, 1998) in MC (left panels) and in AFS (right panels) at San Pedro de Barva, Costa Rica. (Daily transpiration values are extrapolations to ha from four coffee plants)..... 42

Figure 20. Response of coffee stomatal conductance to leaf-to-air VPD (a) and PPFD (b) in a MC and an AFS at San Pedro de Barva, Costa Rica. (Values represent average of 4 leaves per plant)..... 43

Figure 21. Relationships between R (ratio of coffee transpiration over ETo) and soil volumetric water content (VW) in MC (a) and in AFS (b) at San Pedro de Barva, Costa Rica. (Values represent daily averages for one to two weeks of measurements. MC: r^2=0.70, R=3.13*VW-0.52; AFS: r^2=0.73, R=1.36*VW-0.09). 43

Figure 22. Relationships between R (ratio of coffee transpiration over ETo) and LAI in MC (a) and in AFS (b) at San Pedro de Barva, Costa Rica. (Values represent daily averages for one to two weeks of measurements. MC: r^2=0.98, R=0.17*LAI; AFS: r^2=0.98, R=0.11*LAI). 44

Figure 23. Relationships between hourly reference evapo-transpiration (ETo) and the ratio of coffee transpiration over ETo on a ground area basis (a) and on a leaf area basis (b) in MC at three coffee

LAI values at San Pedro de Barva, Costa Rica. (LAI Value of 4.5 m^2 m^{-2} coincides with the peak of the wet season and hence highest soil volumetric water content, while other LAI values coincide with 2 dry seasons; values represent means of one week long measurements)..... 45
Figure 24. Relationships between the ratio SF/ETo on a leaf area basis in MC versus ETo (a) and versus VPD (b) in wet and dry soil conditions during the dry season of 2004 at San Pedro de Barva, Costa Rica. (Values are means of measurements over one week for dry soil conditions and over eleven days for wet soil conditions). 46
Figure 25. Relationships between coffee stomatal conductance (gs) and leaf to air VPD, PPFD and leaf temperature in wet and dry soil conditions during the dry season of 2004 at San Pedro de Barva, Costa Rica. (Values represent average of 12 leaves per plant). 46
Figure 26. Relationships between reference evapo-transpiration (ETo) and (a) daily transpiration (Ec) and (b) T/ETo (ratio of *I. densiflora* transpiration over ETo) in an agroforestry system at San Pedro de Barva, Costa Rica..... 47
Figure 27. Relationships between gross rainfall and runoff during the wet season of 2004 (a) and 2005 (b) in MC and in AFS at San Pedro de Barva, Costa Rica. (Values are means of 3 repetitions per system). (for 2004, MC: r^2=0.75 RO=0.17+0.0021*GR^2; AFS: r^2=0.75 RO=0.12+0.0015*GR^2, for 2005, MC: r^2=0.75 RO=0.08+0.0016*GR^2; AFS: r^2=0.75 RO=0.001+0.00091*GR^2)..... 48
Figure 28. Cumulative runoff during 2004 (a) and 2005 (b) in MC and AFS at San Pedro de Barva, Costa Rica. (Values are means of 3 repetitions per system). 49
Figure 29. Time courses of volumetric soil water content at depths of (a) 0-60 cm, (b) 60-120 cm, (c) 120-150cm and 150-200cm (d) in coffee monoculture (MC) and coffee agroforestry system (AFS) in San Pedro de Barva, Costa Rica, measured from July 2003 to October 2005. 50
Figure 30. Mean soil moisture content at three dates at different soil depths in the MC and AFS at San Pedro de Barva, Costa Rica. (a, b: dry season 2004; c: beginning rainy season 2004)..... 51

List of Tables

Table 1. Statistical summary of regressions for daily stemflow versus gross rainfall in two different coffee agricultural systems (MC and AFS) in the Central Valley of Costa Rica. (Note: The equation for coffee stemflow is $S_{CP}= a(P_g^b)$ for daily rainfall < 10 mm and $S_{CL}= a + bP_{g,}$, for rainfall > 10 mm; S_C is the daily coffee stemflow amount (mm) and P_g is gross rainfall (mm). The equation for *Inga* stemflow is $S_I= a(P_g^b)$; S_I is the daily *Inga* tree stemflow (mm)). 37
Table 2. Total rainfall, throughfall, stemflow and canopy interception during the monitoring periods (June to September 2004 and July to November 2005) in two different coffee agricultural systems (AFS and MC) in the Central Valley of Costa Rica. 38
Table 3. Annual rainfall, reference evapo-transpiration (ETo) and estimated water use by coffee plants in MC and coffee plants and shade trees in AFS under optimal coffee cultivation conditions of San Pedro de Barva, Costa Rica for 2004 and 2005. 47
Table 4. Annual water balance in MC and AFS under optimal coffee cultivation conditions of San Pedro de Barva, Costa Rica for 2004 and 2005. 52
Table 5. Water balance during the dry and rainy seasons for 2004 and 2005 at a depth of 200 cm in MC and AFS in San Pedro de Barva, Costa Rica. 52

List of photographs

Photography 1. The *Coffea arabica* plant with details of buds, leaves, flowers and fruits..... 1
Photography 2. Lanscape view of a Arabica coffee grown under the shade of *Inga* trees (P. Vaast). 3
Photography 3. Close up view of coffee plants grown under the shade of *Inga* trees (P. Vaast). 3
Photography 4. View of the experimental coffee plot grown without shade (monoculture) on the research station of CICAFE, San Pedro de Barva, Heredia, Costa Rica (JM. Harmand)..... 21
Photography 5. View of the experimental coffee plot grown under the shade of *Inga densiflora* trees on the research station of CICAFE, San Pedro de Barva, Heredia, Costa Rica (JM. Harmand). 21
Photography 6. Detailed views of measurements of *Inga* stemflow (a) and coffee stemflow (b) on the research station of CICAFE, San Pedro de Barva, Heredia, Costa Rica. 25
Photography 7. Detailed views of the measurements of tree sap flow with “Granier” sensors (a) and coffee sap flow with Dynamax gauges (b) on the research station of CICAFE, San Pedro de Barva, Heredia, Costa Rica. 25
Photography 8. Detailed views of the measurements of water runoff (a) and soil water content with TDR (b) on the research station of CICAFE, San Pedro de Barva, Heredia, Costa Rica. 25

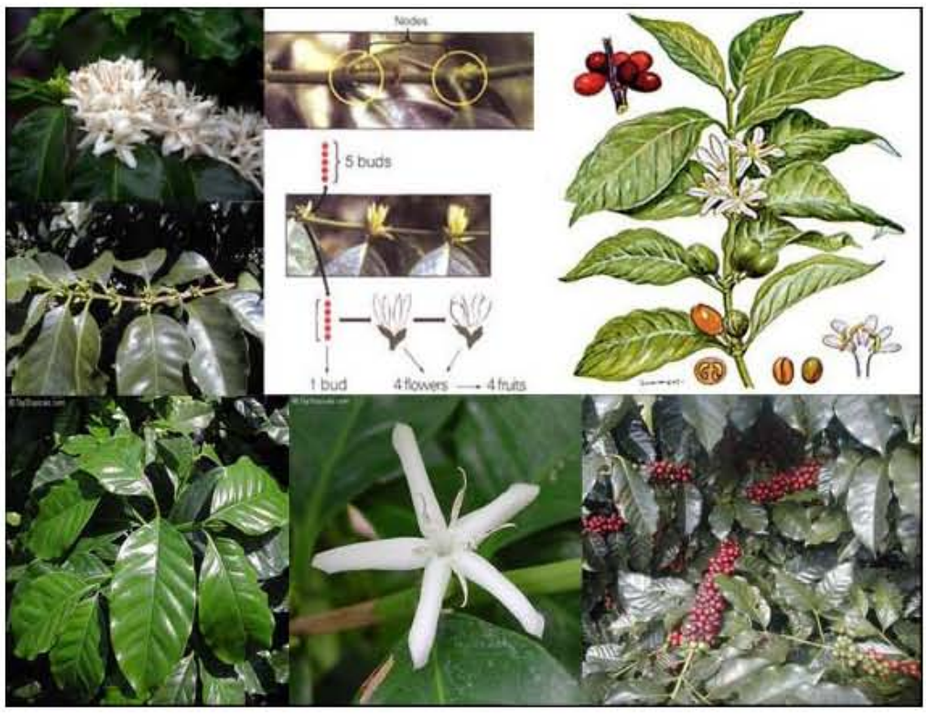
1 GENERAL INTRODUCTION

1.1 Coffee

1.1.1 The coffee plant, related species and origin

The genus *Coffea* (L.) of the Rubiaceae family is composed of around 100 species and is closely related to *Psilanthus* (20 species), both genera are composed of small, hermaphrodite trees or shrubs originated in the Paleotropics (Charrier and Eskes 2004; Taylor 2001; Wintgens 2004). Three species, *C. arabica*, *C. canephora* and *C. liberica*, are cultivated and represent almost the whole world coffee production (Charrier and Eskes 2004; Taylor 2001; Wintgens 2004). Plants from the genus *Coffea* present simple opposed leaves, sometimes with domatia, free interpetiolar stipules, acuminate generally persistent. Inflorescences conglomerate in the axils. The flowers are sessile or pedicellate, the hypantium variously shaped, with corolla hipocrateriform, white or pink, with 5-8 lobes; stamens 4-8 sessile, the stigmas 2, ovary 2-locular, ovule 1 per locule. Fruits or cherries are composed of two coffee beans, each with a longitudinal slit (Charrier and Eskes 2004; Dwyer 1980; Taylor 2001).

Coffea arabica (L.), the most important species in the coffee trade, originated from Ethiopia, but is widely cultivated in the world (reported from 30 m up to 1700 m of altitude in Nicaragua, for example, as cited by Taylor (2001). The species is a small shrub that can be 2 to 12 m tall in natural vegetation. With opposite leaves, 8-15 cm length and 2.5-10 cm wide, acuminated at the apex, attenuated or widely cuneate at the base, 7-10 secondary veins, petiole 6-15 mm length, stipule 3-12 mm length, inflorescences with bracteoles to 2 mm length, sub-sessile flowers, lobes 5, 9-20 mm length, and fruits 10-16 mm length and 8-13 mm wide (Photograph 1) (Taylor, 2001; Dwyer, 1980).



Photography 1. The *Coffea arabica* plant with details of buds, leaves, flowers and fruits.

In non-equatorial regions (>5° latitude north and south) such as Mesoamerica (Southern states of Mexico and Central America) as well as Ethiopia, Hawaii, Southern Brazil and Zimbabwe, coffee plants present a single, 10 month long cycle of growth and fructification. On the contrary, in equatorial regions (such as Kenya and Colombia) that are crossed twice a year by the inter-tropical convergence zone resulting in two dry seasons and two wet seasons, two periods of growth and fructification per year occur in coffee plants (Cannell 1985; Wormer and Gituanja 1970).

1.1.2 Distribution and economical importance, markets

In the world trade, coffee represents the second leading commodity (after petroleum) and provides a livelihood to an estimated 25 million families around the world (in Latin America, Africa and Asia). The world coffee market spans some 71 countries of which 51 are significant producers and 20 are key consumers (Castro et al. 2004; De Franco 2006). The world coffee production increased by 90% from 1976 to 2005, with the most important increments in Asia and South America, especially Brazil (Figure 1a). Africa and Mesoamerica experienced decreases in the percentage of world coffee production in comparison to Asia and South America (Figure 1b). In Asia, the most relevant increase in production happened in Vietnam.

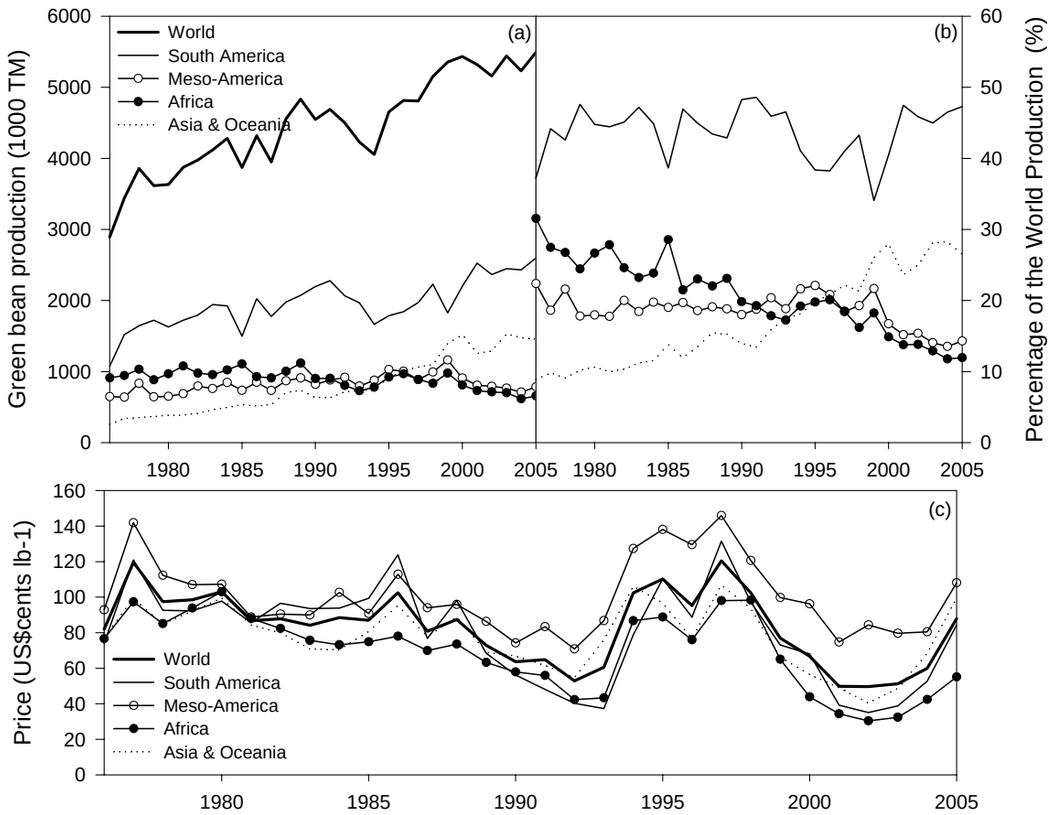
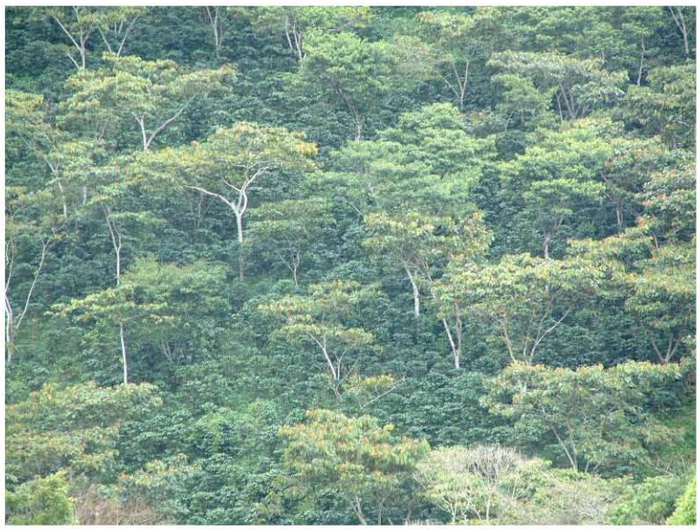


Figure 1 . Dynamics of the world coffee production (ab) and price paid to producers (c) during the period 1976 to 2005 (Source: ICO, modified by the author).

The Mesoamerican region was once the second largest production region in the world after South America (Brazil & Colombia). However due to low prices in the international market and high production costs, it has fallen to the third place after the 2000 cycle, close to African producers (Figure 1 bc).



Photography 2. Lanscape view of a Arabica coffee grown under the shade of *Inga* trees (P. Vaast).



Photography 3. Close up view of coffee plants grown under the shade of *Inga* trees (P. Vaast).

1.1.3 Importance of the coffee as a crop in Mesoamerica

In Mesoamerica, coffee production represents an important component of the growth domestic production and was for decades the most important product of exportation; for example, coffee represents 20% of total value of exportations in 2005 in Nicaragua in which the agriculture represents the 18% of the gross national product (De Franco 2006). In Costa Rica with a more industrialized economy, the economic importance of coffee is lower when compared to other countries of Central America, as agriculture represents only 8.5% of the gross national product (GDP), but with coffee and banana still representing the most important crops. The economic importance of coffee in the Meso-American region has been reduced due to the development of other crops such as pineapple, *Ananas comosus* (L.) Merr. in Costa Rica and the low international coffee prices during the period 1998-2005. Still, there has been a steady increase in areas planted with coffee in the region for the last 2 decades, although the total production is stabilized after a decrease in 2000-2002 (Figure 2).

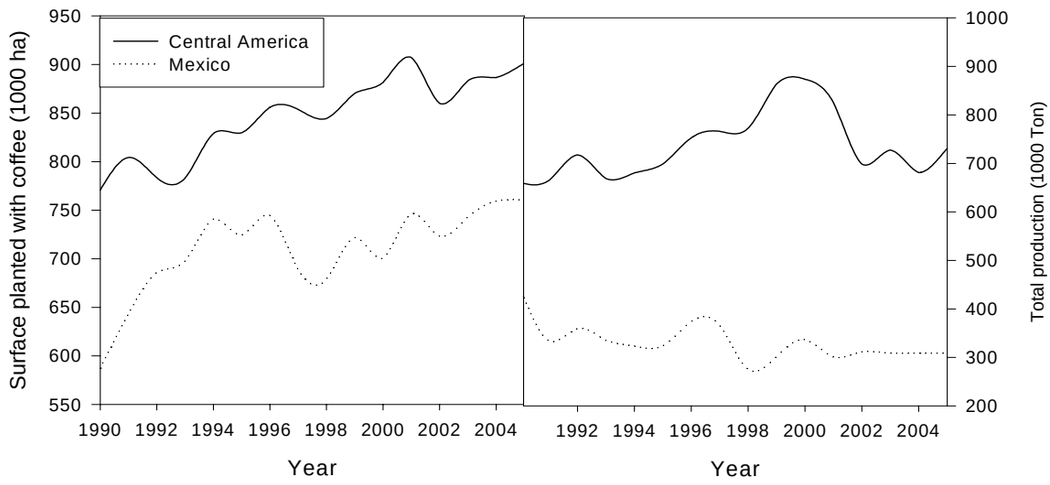


Figure 2 . Dynamics of areas planted with coffee (a) and production of green beans (b) in Mesoamerica during the period 1990-2005 (FAO-STAT, modified by the author).

According to various sources, coffee generates employment for almost 2 million people in Central-America (Figure 3). Coffee generates 700 000 jobs in Guatemala while it generates 300000 jobs in Costa Rica and in Nicaragua; around 30 000-50 000 are direct employments (farmers) and 270 000-250 000 indirect employments in the coffee industry (Castro et al. 2004; De Franco 2006).

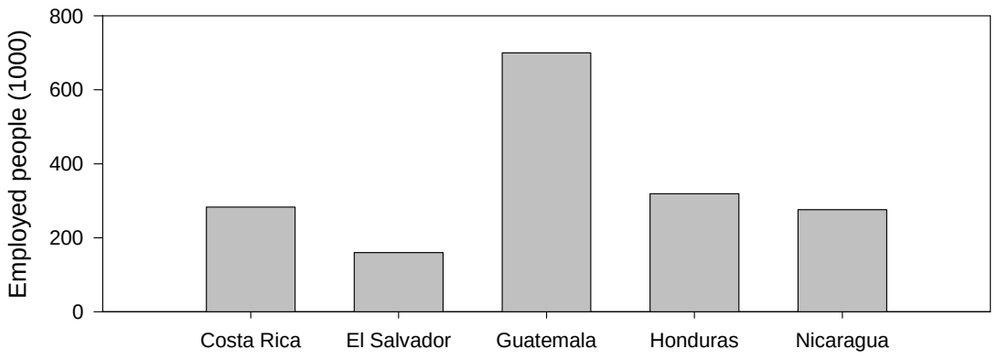


Figure 3. Employments generated by the coffee sector in countries of Central America in 2001 (Source: Castro et al., 2004, modified by the author).

Due to low international prices, coffee farmers must follow various strategies to maintain an acceptable profitability of their coffee systems; the most important ones are: improvement of coffee quality, production diversification (such as additional timber production) and payment for environmental services via local schemes or commercialization to eco-certified markets (Beer et al. 1997; Castro et al. 2004).

1.2 Eco-physiology of coffee

1.2.1 Edaphic and climatic boundaries for acceptable yield of *C. arabica*

1.2.1.1 Temperature and altitude

Temperature is the climatic factor with the highest impact on the physiology of arabica coffee plants; the optimal mean annual temperature range for this species is 18-21^{o}C (Descroix and Snoeck 2004; ICAFE 1998) In the tropics, altitude is strongly related to temperature and indirectly to rainfall, thus the optimal altitude range for coffee production is between 1200 to 1700 m around Equator. However, the production zones in Costa Rica are located in the range of 500 to 1700 m while they range from 30 to 1600 m in other countries of Central America, which represent areas out the optimal range of altitude for coffee production (ICAFE 1998; Taylor 2001). Temperature above the optimal value (>23 ^{o}C) induces an accelerated vegetative development at the expense of reproductive development and a hastened ripening of fruits, leading to loss of quality. Continuous exposure of coffee to high temperatures (>30 ^{o}C) results in depressed growth and abnormalities such as leaf yellowing and growth of tumors at the stem base. Furthermore, the combined effect of high temperature and a prolonged dry season during blossoming may cause a high abortion rate of flowers (DaMatta, 2004).

1.2.1.2 Rainfall

The rainfall pattern must include a few months of low or no rain for coffee flowering induction (Alvim 1973; Alvim 1977; Barros et al. 1978; Wrigley 1988). The optimal range for annual rainfall is between 1400 to 2000 mm. However, coffee grows under a wide range of rainfall from 1000 to over 4000 mm per year. High annual rainfall (2500 -4000 mm) does not cause a significant decrease in the production if drainage is adequate (Descroix and Snoeck 2004; ICAFE

1998). On other hand, high rainfall throughout the year is often responsible for scattered harvests and low yields, reduction in the quality of coffee beans and increases in the harvesting costs (Barros et al. 1978).

1.2.1.3 Vapour pressure deficit

Atmospheric vapour pressure deficit (VPD) has direct effects on coffee physiology as high VPD induces stomatal closure above values of 1.5 to 2.0 kPa (Rena et al. 1994). It has also some negative effects at VPD values lower than 0.3 kPa on the quality of coffee beans and as this increases the risk of fungal diseases. For these reasons, it is considered that an annual mean VPD ranging from 0.3 to 1.0 kPA is optimal (Descroix and Snoeck 2004; ICAFE 1998).

1.2.1.4 Soil types and fertility

Coffee thrives well in alluvial or colluvial soils with favorable texture as well as in volcanic formations. In the Central American, Colombian and Mexican highlands for example, the optimal and most common soils for coffee are recent volcanic soils with depths ranging from100 to 200 cm, slope between 0 to 30%, soil organic matter of 2 to 5 % and cation saturation of 20 to 35% (Descroix and Snoeck 2004; ICAFE 1998).

1.2.2 Photosynthesis and stomatal conductance

1.2.2.1 A shade-adapted species

Coffea arabica L., the most important coffee species, is believed to have evolved as an under-storey tree in the mid-elevation tropical forest from Ethiopia. As an under-storey plant, coffee grows under constant shade, where it is not exposed to high temperatures and VPD, and experiments a short period of drought (Maestri and Barros 1977). Therefore, coffee leaves present features of shade leaves such as low light compensation point for photosynthesis, low rate of photosynthesis at high light intensities, susceptibility to photo-inhibition and low chlorophyll a to chlorophyll b ratio (Rena et al. 1994). However, coffee leaves display a wide plasticity in its adaptation to irradiance as showed by the wide range of radiation conditions in which the coffee is cultivated. Thus, the coffee plant is considered as a shade-adapted species, rather than as a typical shade plant (DaMatta 2004).

1.2.2.2 Photosynthesis

Coffee displays a C3 photosynthetic metabolism. The CO_2 compensation point of photosynthesis is in the range 30-70 ppm at temperatures of 20-25^{o}C (Rena et al. 1994). The rate of photosynthesis under ambient CO_2 and saturating irradiance (photosynthetic photon flux density (PFFD) of 600 to 900μmol m^{-2} s^{-1}) is moderately high (7-12 μmol CO_2 $m^{-2}s^{-1}$) at 20 ºC (DaMatta 2004; Franck 2005; Rena et al. 1994). However, photosynthesis can decrease to values as low as 0.6 to 1.2 μmol CO_2 $m^{-2}s^{-1}$ at high temperatures and high irradiance probably due to stomatal closure and photo-inhibition (Cannell 1972; Cannell 1985; DaMatta and Maestri 1997; Ramalho et al. 1999; Ramalho et al. 2000; Ramalho et al. 1997). Nitrogen (N) seems to be a key factor to improve tolerance to photo-inhibitory effects due to high and prolonged irradiance exposure. Thus, for both arabica and robusta coffees, photo-inhibition might not result in a decrease in

photosynthesis under a high N fertilization regime (DaMatta 2004; DaMatta and Maestri 1997; Franck 2005; Ramalho et al. 2000).

1.2.2.2.1 Effect of leaf temperature on photosynthesis

The negative effect of temperature on coffee photosynthesis has been reported early in the past century with net CO_2 assimilation decreasing at temperature above 24 ^oC (Nunez et al. 1968; Nutman 1937). This temperature effect was confirmed by several authors (Kumar and Tieszen 1980a; Kumar and Tieszen 1980b) in studies where plants experienced a decrease in net CO_2 assimilation due to a reduction in stomatal conductance for temperatures in the range of 25 to 35^oC. For this reason, it is assumed that CO_2 assimilation may be reduced in leaves completely exposed to high irradiance due to the high temperatures reached in tropical regions, which are in the order of 10 to 15 ^oC above the air temperature (Cannell 1985).

1.2.2.2.2 Effect of water stress on photosynthesis

Photosynthetic rate can be affected by water stress via two main ways: a) due to stomatal closure and b) non-stomatal factors related to low activity of enzymes and carbohydrate accumulation (Kumar and Tieszen 1980b). At low water potential, coffee photosynthesis is reduced due to low values of stomatal conductance and hence a reduction of the supply of CO_2 (DaMatta and Ramalho 2006; Kumar 1979; Kumar and Tieszen 1980a; Kumar and Tieszen 1980b; Nunez 1979). The non-stomatal limitation of photosynthesis represents a reduction in photosynthesis independently to the supply of CO_2 and stomatal conductance. This non-stomatal limitation of photosynthesis has been extensively reported for many species such as *Quercus rubra*, *Acer rubrum*, *Populus didentata*, and *Sinapis alba* (Briggs et al. 1986; Cornic et al. 1983), for which the reduction in net CO_2 assimilation due to water stress was not the result of stomatal closure as CO_2 was not limiting. At a water potential of -3.0 MPa, the non-stomatal limitation of photosynthesis explained 90% of the reduction of coffee photosynthesis (Kanechi et al. 1996). This non-stomatal limitation was not related to the total protein, RUBISCO (ribulose-1-5-bifosfato carboxilasa-oxidaxe), chlorophyll content or activity of the electron chain, but with the activation state of RUBISCO, independent of a restricted supply of CO_2 to the leaf as a result of stomatal closure. Additionally, Coffea arabica seems to be more susceptible to non-stomatal limitation of photosynthesis than *C. canephora* (DaMatta et al. 1997).

1.3 The importance of coffee agroforestry systems in Mesoamerica

1.3.1 Current agroforestry practices

The natural adaptation of coffee to shade has been a strong argument in favor of the development and maintenance of agroforestry practices in coffee production. However, little information is available on how these practices have evolved in Mesoamerica (Beer et al. 1997; DaMatta 2004; Leon 1998a; Leon 1998b; Muschler 2004). Originally, coffee was introduced during 1720-1724 to America via the French colonies (Guadalupe, Guyana, Haiti and Martinique). When the commercial coffee production was initially developed in Haiti and Jamaica, no special reference

was reported regarding agroforestry practices. In Costa Rica, coffee began to be commercially cultivated in 1833 and in Colombia during the second half of the nineteenth century. Still, there is no mention, during this initial period, of the use of shade trees by the coffee industry in Latin-American countries. The adoption of shade was reported to begin in 1865 in Costa Rica and in 1872 in Colombia, mainly with the use of *Erythrina* species in lowlands and *Inga* species in highlands (Leon 1998b).

Nowadays, most shade trees used in association with coffee belong to the Fabaceae family due to their capacity to fix nitrogen. Even though farmers may not be aware of this property, they observe their beneficial results in terms of soil fertility. Genera such as *Albizia*, *Inga*, *Leucaena* of the Mimosoideae and *Erythrina* and *Gliricidia* of the Papilioniodeae are common in coffee systems, especially in Mesoamerica (Lambot and Bouharmont 2004; Leon 1998b; Muschler 2004; Muschler 1999).

In Costa Rica, the most common species in coffee agroforestry systems (AFS) is *Erythrina poeppigiana* (Muschler 1997; Muschler and Bonnemann 1997; Muschler 1999; Muschler 2001). Nonetheless, studies on the botanical composition of coffee systems showed more diverse shade vegetation that anticipated. For example, 62 tree species were reported in coffee AFS of the region of Turrialba, Costa Rica; 63 species in the region of Miraflor, Nicaragua; 124 species in the region of Tapalapa, Chiapas, Mexico; and 46 species in the region of Jitotol de Zaragoza, Chiapas (Escalante and Somarriba 2001; Linkimer et al. 2002; Llanderal and Somarriba 1999; Peeters et al. 2003; Yépez et al. 2002; Zuniga et al. 2004). Additionally, there is a recent tendency to incorporate timber trees in coffee AFS to improve profitability, especially during periods of low coffee prices. Timber trees associated with coffee are numerous such as *Cordia alliodora*, *Eucalyptus deglupta*, *Eucalyptus grandis*, *Terminalia ivorensis*, *Terminalia amazonia*, *Cedrela odorata*, *Alnus acuminata*. Among them, *C. alliodora* has been shown to develop at such rate in AFS that it compensates the reduction in coffee yield (Beer 1992; Beer et al. 1997; Hernandez et al. 1997).

1.3.2 Use of *Inga* as shade tree in coffee AFS

With the exception of Costa Rica where *Erythrina poepigiana* is the most abundant species in coffee AFS, the genus *Inga* has been used predominantly as a shade tree in coffee and cacao (*Theobroma cacao*) in Mesoamerica (Leon 1966; Leon 1998a; Pennington 1998). It is worth mentioning that *Inga* is used as a shade tree in agroforestry only in America, possibly because it is endemic of this continent. The history of the use of *Inga* (in the Neo-tropics) extends back to 2000 years when it was cultivated for its edible fruits (*Inga feuillei* called Pacae in Peru) by the tribes Chimu and Mochica in Peru (Leon 1966; Leon 1998a; Pennington 1998). However, the use of *Inga* fruits possibly began independently in different regions in the Neo-tropics and with different species. In Mesoamerica, the domestication of the genus began with *I. juinicuil*, *I. densiflora* and *I. sapionoides* as source of fruits (Leon 1998a; Leon 1998b).

Despite the large diversity of the genus, only few species have been used in AFS with coffee or cacao. For example, Peeters et al. (2003)cited that coffee AFS in Mexico are predominated by only four native *Inga* species: *Inga latibracteata* Harms, *I. oerstediana* Benth. *I. punctata* Willd, and *I. pavoniana* Donn (Peeters et al. 2003). In Costa Rica (and other Central American countries

such as Nicaragua and Guatemala), few species of *Inga* (*I. punctata, I. densiflora, I. oerstediana, I. edulis, I. spectabilis, I. juinicuil* among others) are mentioned as shade tree species in coffee and cacao plantations (Zamora and Pennington 2001). However, possibly up to a total of 20 *Inga* species are in use in coffee AFS, which shows the importance of this neo-tropical genus as a shade tree in coffee AFS in this region (Lambot and Bouharmont 2004; Leon 1998b; Muschler 2004; Muschler 1999; Yépez et al. 2002). Interestingly, this genus can provide many ecological services in coffee and cocoa AFS such as soil protection and restoration, improved soil retention of water, nitrogen fixation and carbon sequestration, additionally to the production of high quality fuel-wood generated by pruning (Fernandez 1998; Hands 1998; Murphy and Yau 1998; Pennington 1998).

1.3.3 Description of the genus *Inga*

The genus *Inga* is very diverse, composed of around 300 species widely distributed from Mexico to Uruguay and found throughout the lowlands and mountainous regions of the humid tropical America (Leon 1966; Pennington 1998; Sousa-Pena 1993; Sousa-Pena 2001; Zamora and Pennington 2001). The speciation of the genus was concentrated in the past 10 million years, with many species arising as recently as 2 million years ago, which coincides with the most recent major uplifts of the Andes. Consequently, the largest center of diversity for *Inga* is in the Andean foothills of the Western Amazon (Bermingham and Dick 2001; Richardson et al. 2001). Thus, in Brazil for instance, 140 species have been reported, and only 80 species for the Mesoamerican region (Pennington 1998; Zamora and Pennington 2001). In Costa Rica, 53 Inga species are reported and 32 in Nicaragua (Sousa-Pena 2001), 33 species in Mexico (Peeters et al. 2003), representing the tree genus with the highest species diversity, and with 12 species reported as endemic (Zamora and Pennington 2001). Furthermore, the genus tends to be species-rich in different moist forest when local floras (florulas) are compared. For example, Gentry (1990) cited *Piper*, *Ficus*, *Inga Ocotea*, *Psychotria*, *Philodendron*, *Anturium* and *Miconia*, as the most speciose genera in moist forest of Costa Rica, Panama, Brazil and Ecuador (Gentry 1990).

1.3.4 Major effects of the use of shade in coffee plantations

Shade trees in coffee plantations present advantages and disadvantages for farmers, therefore the decision regarding their incorporation in coffee plantations depends on the farmers' goal, the specific environmental conditions of the site and the availability of inputs (Beer et al. 1997; Fernandez and Muschler 1999; Muschler 2004; Muschler and Bonnemann 1997; Muschler 1999). The effects of associated trees in coffee production systems can be grouped into two categories: (a) the effects of shade trees on the micro-environment; and (b) their effects on the crop itself and its management.

1.3.4.1 Effects of shade trees in coffee agroforestry systems

There are many arguments to use shade trees in coffee AFS with respect to their ecosystem services; the main ones are: biodiversity conservation, carbon sequestration and greenhouse gases reduction, soil fertility improvement and water resource preservation (due to erosion control and nutrient leaching reduction).

1.3.4.1.1 Biodiversity

Generally, shaded coffee plantations support many tree species that provide a multistrata canopy. Consequently, they are important refuges for biological richness for groups such as trees and epiphytes, mammals, birds, reptiles, amphibians, and arthropods (Moguel and Toledo 1999). Biotic diversity is vastly larger in AFS than in monoculture (MC). This is becoming more and more important as protected areas in the Mesoamerican region are decreasing in size and hence coffee AFS can play an increasingly important role as corridors between these conserved forest areas (Perfecto et al. 1996).

Many studies have recorded higher faunal diversity in AFS than in MC, sometimes with records in coffee AFS similar or higher than in forest areas. For example, more foraging ants, beetles, and non-formicid hymenopterans were recorded in coffee AFS when compared to MC (Perfecto and Snelling 1995). In a premontane moist forest at elevations of 1200 to 1800 in Panama, two species of Neotropical army ants (*Eciton burchelli* and *Labidus praedator*) were present only in forest and shade coffee, but not in MC (Roberts et al. 2000). In Nicaragua, a study of primates behavior showed that coffee AFS can be used as corridors between forest fragments for howler monkeys (*Alouatta palliata*) and possibly other forest mammals (Williams-Guillén et al. 2006). For birds, shaded coffee may play an important role in maintaining local biodiversity, and acts as buffer areas around forest patches, even if shaded coffee may be beneficial mostly for generalist species (including several migratory species), but of lower values for forest specialists (Tejeda-Cruz and Sutherland 2004). Coffee AFS with the presence of large shade trees (such as some *Inga* species) have a positive influence even on the diversity of epiphytic species, despite the less diverse and more homogeneous communities in coffee plantations than in forests (Hietz 2005).

1.3.4.1.2 Soil erosion and lixiviation control

Nowadays, soil erosion is an important concern in agriculture. In Mesoamerica, coffee is planted very often on medium to high slopes, as described for Miraflor in Nicaragua where the average slope was 29% and a range from 2% to 70% (Zuniga et al. 2004). An experiment conducted in the Andes (slope = 31%) demonstrated that erosion of the most biologically active fraction of the soil profile (<4mm) was larger in MC systems than in AFS coffee plantations with values of 1.57 and 0.73 t ha^{-1} y^{-1}, respectively during the period of crop establishment (Ataroff and Monasterio 1997). Soil erosion is the result of high runoff, thus, on minimal slope (1%) the recorded runoff of 3% of annual rainfall in MC was comparable to 2% in AFS (Avila et al. 2004; Harmand et al. 2007). Nevertheless, these authors suggested that the higher litter layer in AFS of 8.5 t DM ha^{-1} compared to 2.5 t DM ha^{-1} in MC was a better protection of the soil surface against rain splash (Harmand et al. 2006). Similar results have been reported in other AFS such as alley cropping, in which the runoff was reduced substantially with the inclusion of trees (Lal 1989a; Lal 1989b). Furthermore, the inclusion of shade trees in coffee plantations may reduce nutrient leaching and water contamination with nitrate and other harmful substances. Harmand et al (2007) showed that in highly fertilized coffee plantations, the inclusion of *E. deglupta* as a shade tree: 1) increased N uptake during the dry season and N accumulation in litter and permanent biomass; 2) slightly reduced water drainage; and 3) reduced NO_3^- leaching especially when coffee berry production was low. Nevertheless, in years of high production of coffee in full sunlight, the negative effect

of shade on coffee production could offset the advantage of N accumulation in trees as a mean of reducing N leaching. Hence, the inclusion of shade trees in coffee plantations intensively managed requires reducing N fertilization input in order to match plant needs and reduce NO_3^- leaching (Harmand et al. 2006).

1.3.4.1.3 Carbon sequestration and reduction of greenhouse gases

Tropical AFS can play an important role in the sequestration of carbon (C), hence acting as a sink and reducing CO_2 concentration in the atmosphere. The potential C sequestration in AFS is estimated between 12 and 228 Mg ha^{-1} with a mean value of 95 Mg ha^{-1} (Albrecht and Kandji 2003). After 7 years, the aerial biomass accumulation of a coffee AFS accounted to 28.4 Mg ha^{-1} compared to 11.4 Mgha^{-1} in a MC, which showed the potential of tree inclusion to C sequestration in the coffee sector (De Miguel et al. 2004). In other coffee AFS, a C sequestration of 11 Mg ha^{-1} yr^{-1} over 10 years was reported in which 6 Mg ha^{-1} yr^{-1} corresponded to the shade tree aerial component (Albrecht and Kandji 2003). Reporting data from experiments and published literature, Harmand et al. 2006a showed that for approximately a ten year period, the conversion of coffee MC to AFS resulted in an additional mean annual increment in aerial phytomass (biomass + litter) varying from 1 t C ha^{-1} y^{-1} in the case of regulated shade by *E. poeppigiana*, to 1.7 – 3.1 C ha^{-1} y^{-1} in the case of shade timber trees. However, AFS may also generate greenhouse gases such as N_2O. For example, an AFS with *Inga densiflora* increased slightly the emission of N_2O in comparison to coffee MC, while N fertilizer was responsible for 70% of the emission (Hergoualc'h et al. 2007).

1.3.4.2 The effects of shade trees on coffee and its management

Additionally to their ecological impacts at the ecosystem level, shade trees influence directly the coffee plant and its management; trees influence the microclimate and hence, coffee productivity and quality as well as soil fertility through nutrient cycling, N-fixation and soil organic matter enhancement (Beer 1987; Beer et al. 1997; Vaast and Snoeck 1999; Willey 1975).

1.3.4.2.1 Influence of trees on soil fertility

Trees in AFS can improve the fertility of coffee soils (or many other associated crops) through the three following ways: a) an increase in nutrient supply (N-fixation) and a reduction of nutrient output (reduction of runoff and lixiviation); b) a more efficient nutrient cycling by means of a stable decomposition and a conversion of nutrients in more labile forms (for example P); and c) an improvement of the soil environment for a more favorable root growth through an improvement of the soil physical properties (Buresh and Tian 1997; Khanna 1997; Vaast and Snoeck 1999; Willson 1985).

In coffee AFS with legume trees, N-fixation and nutrients recycling are important ways of improving soil fertility and sustaining crop production (Harmand et al. 2006). For example, N input from shade tree litterfall alone could represent approximated 95 kg N ha^{-1} y^{-1} (Aranguren et al. 1982). In a coffee AFS with *Erythrina poeppigiana*, the biomass obtained from the pollarding added 330, 269, and 173 kg N ha^{-1} y^{-1} depending on whether the pruning frequency was one, two or three times a year, respectively (Russo and Budowski 1986). However, the nutrients added via

pollarding in AFS, represent only a more efficient nutrient cycling and not an extra input of nutrients to the system; thus, only 14% to 50% of the total N in the pollarding originated from N-fixation (Palm 1995). On the other hand, some legume trees used as shade trees contain high content of polyphenols in their biomass, that release N slowly and over a longer period. This effect can increase the fraction of N-organic and the content of soil organic matter (SOM) in the long term (Palm and Sanchez 1990; Palm and Sanchez 1991). Finally, the biomass not only adds nutrients to the soil, but also increases the availability of nutrients to plants. Phosphorus is thought to be one of the most limiting nutrients in tropical soils, but its availability can be improved by the symbiosis with mycorrhizae or by the transformation of non-available inorganic forms to more available organic forms. This later process can be the result of the supply of energy to microorganism, stimulating the roots growth of associated plants or by the reduction of soil P absorption (Buresh and Tian 1997).

1.3.4.2.2 Influence of shade trees on microclimate

On top of their potentially advantageous impacts on soil fertility, shade trees modify the microclimate (light, relative humidity, temperature) for crop growing underneath and may compete with them for resources such as light, water and nutrients (Beer 1987; Beer et al. 1997; Willey 1975).

In a coffee AFS, it has been showed that trees reduced the maximal temperature by an average of 5.4ºC, and increased the minimal temperature by up to 1.5ºC (Barradas and Fanjul 1986). On the other hand, soil evaporation was reduced by 40% in comparison to plantation without trees, due to decrease in VPD and radiation. Vaast et al. (2005) observed a reduction in coffee transpiration under shade trees in the southern region of Costa Rica. On basis of the physiological responses of coffee to environmental factors, it is commonly accepted that the shade of trees is important mostly in regions of sub-optimal environmental conditions to coffee growth (Fernandez and Muschler 1999). Very often, these regions present environmental limitations such as temperatures higher than 30^{o}C, high VPD, low water availability.

1.3.4.2.3 Influence of trees on yield and coffee quality

It has been suggested that the negative influence of shade trees on coffee yield is the product of lower whole-tree carbon assimilation, greater stimulus to vegetative rather than flower buds, and fewer nodes formed per branch and flower buds at existing nodes (Cannell 1974; Cannell 1975). From past and current research on coffee photosynthesis, seems unlikely that the shade of trees strongly reduces coffee photosynthesis due to coffee adaptation to shade. Indeed, it has been demonstrated that the most important negative impact of trees on coffee yield, is through lower flower induction and hence the lower number of productive nodes on a branch (Franck 2005). As a consequence of shade, coffee plants generally have lower fruit loads (Franck 2005), but shade also influences other variables of agronomic importance, as follows:

- larger individual leaf size, longer leaf longevity, reduction in leaf specific mass and hence a lower carbon investment for a similar LAI with coffee shade grown compared to sun grown plants (Franck 2005).

- An enhanced vegetative growth and carbon reserves in branches and roots of shade grown plants with lower fruit loads (Cannell 1971; Cannell 1974).
- A reduction of the branch mortality, phenomenon known as dieback (Clowes 1973).
- These last two effects allowing a better flower induction and a better yield during the next production cycle, hence reducing bi-annual production (Vaast et al. 2005a; Vaast et al. 2005b).

However, in compensation to yield reduction, shade improves quality in coffee. Shaded plants produce coffee beans of larger size and higher quality, and hence improve farmers' income (Vaast et al. 2005a; Vaast et al. 2005b; Vaast et al. 2002). In Guatemala, shade and altitude improved quality with shade grown coffee plants producing a higher portion of beans with larger size and increased chlorogenic acid and sucrose concentration (Guyot et al. 1996). In Costa Rica, shade improved quality in a sub-optimal zone for coffee cultivation, with mean bean weight and size increasing with increasing shade from full sun to 80% of shade (Muschler 2004; Muschler 1999; Muschler 2001).

1.3.5 New arguments in favor of agroforestry

1.3.5.1 Quality and niche markets

The certification of coffee for sustainable and environmentally friendly production practices potentially adds value to the coffee product and can increase profitability for farmers that follow the recommended practices of certification schemes. This niche market is divided into five main certifications: Organic, Fair Trade, Rainforest, Starbucks and Bird Friendly certified; although, new ones are underway such as Nespresso AAA and 4C. The market for these certifications seems to increase between 10 to 20% per year, especially in Europe (50%), United States (39%), Japan (9%) and Canada and Taiwan (2%). From this point of view, agroforestry practices can increase the profitability of coffee farming since all these certification programs require or recommend the use of shading trees, in addition to other ecological and social requirements; therefore, there is a direct link between environmental conservation and the market for coffee. For example, Bird Friendly Coffee is marketed by conservation groups and birders' associations (Castro et al. 2004).

1.3.5.2 Environmental services

Environmental services such as carbon sequestration, microclimate regulation, water regulation, water supply, soil preservation, erosion control and sedimentation, nutrient cycling, pollination of crops, waste treatment, are critical for the Earth's life, and therefore their total economic values could represent twice the GNP of the world if properly valued (Costanza et al. 1997). The concept of payment for environmental services has risen as a tool to incentive and to promote sustainable land uses. For the society at large, the most important environmental services to be included in incentive schemes to land owners include:

1. Carbon sequestration
2. Water resource protection
3. Biodiversity conservation

4. Enhancement of landscape scenic beauty

In Central America, payments for environmental services have been developed at national scale only in Costa Rica since 1996 (article 46 of the Law 7575), but it is in early stages of development in other neighboring countries. Thus, the development of policies for payment for environmental services could represent an additional income for farmers that maintain agro-forestry practices, since these payments are focused on the financial retribution of land owners for the services brought by their environmentally friendly practices to the benefit of the local communities, states or globally. However, until recent years in Costa Rica, the concept of environmental service was focused in forest and forest plantations, excluding AFS, although more recently AFS have been included in policies of environmental services as water resource protection and carbon sequestration.

1.3.6 Biological interactions in AFS, with a special focus on water competition

In most cases, water is considered to be the most limiting resource in crops or forest tree physiological processes. Stomata mediate a significant fraction of the annual flux of water between the soil and the atmosphere. Guard cells regulate the flux of CO_2 and H_2O at leaf level with apoplastic abscisic acid (ABA) stimulating stomatal closure. Stomata respond to stimuli of hormone signalling, light, water status, CO_2, temperature and other environmental variables (Schroeder et al. 2001), resulting in complex physiological and environmental mechanisms operating across several spatial and temporal scales. Short-term water stress generally results in stomatal closure and a reduction in canopy hydraulic conductance that influence transpiration rates (Jones 1998).

In coffee, stomata are located in the abaxial surface of leaves at densities of 230 to 285 mm^{-2} (Kumar 1979). Stomatal closure is promoted by ABA; high levels of ABA reduce K^+ concentration in the guard cells and induce both tugor loss and closure. Coffee stomatal conductance was described as highly sensitive to irradiance (Nutman 1937). Thus at low irradiance, there was an increment in stomatal aperture with an increment in irradiance, while an opposite effect was found at high irradiance. Similar results have been reported with low conductance under high solar radiations (Alvim and Havis 1953; Wormer 1965). Using a mixture of water and iso-propanol, Wormer (1965) also found that stomatal aperture was negatively related to temperature, VPD and solar radiation, with a major effect of temperature values above 24^o C. More recently, studies showed that the stomatal conductance in coffee depends on water availability, evaporative demand of the environment and leaf temperature. Moreover, a strong dependence of the stomatal conductance has been established with air VPD (Fanjul et al. 1985; Hernandez et al. 1989; Rena et al. 1994). These authors found that stomatal conductance was strongly reduced at values of air VPD higher that 1.5 kPa. Furthermore, the negative effect of the radiation on stomatal conductance appeared to be the result of intertwined effects of photosynthetic photon flux density (PPFD) and VPD. Thus, the maximal stomatal conductance occurred in the morning hours and decreased with increasing VPD and PFFD. When stomatal

conductance was normalized by PFFD, a clear curvilinear relationship was observed between stomatal conductance and VPD, with a low effect of PFFD (Gutierrez et al. 1994).

Additionally to the stomatal conductance effect on the transpiration, Gutierrez and Meinzer (1994) estimated the crop evapotranspiration coefficient (Kc=ETc/ETo) using the Bowen ratio-energy balance technique in coffee fields at different stages of canopy development. They obtained that the average Kc was among 0.58 to 0.79 in fields planted with 1 to 4-year-old coffee plants. Also, they showed that Kc varied seasonally due that measurement made between July and August and again between September and November 1991 presented significant variation. Crop transpiration alone, determined with the stem heat balance technique, comprised from 40% to 95% of Kc as the leaf area index increased from 1.4 to 6.7, showing a strong influence of the LAI in the crops transpiration. Additionally to this estimate on coffee crop coefficients (Kc), the FAO manual on crop evapotranspiration (Allen et al. 1998) presented values for coffee in the range of 0.90 to 1.10, when they used the FAO version of the Penman-Monteith equation to estimate ETo.

However, few studies on coffee transpiration have been carried out in AFS (Kanten and Vaast 2006). Despite the potentially beneficial effects of AFS, there is a common concern regarding tree competition with crops for limited resources, such as water (Beer 1987). It is known that a larger use of resources occurs in a mixed system compared to a monoculture. Thus, the agroforestry benefits are to be expected only when there is complementarity for resource capture between trees and associated crops (Cannell et al. 1996).

For this reason, the understanding of the interactions between trees and crops in AFS is critical for their management and implementation in various regions. In temperate regions, humid tropics and semiarid tropics, competition for water has been identified as the major determinant of productivity in alley cropping systems (Govindarajan et al. 1996; Hauser et al. 2005; Rao et al. 1997). It has been claimed that root management which includes species selection, spacing, nutrient distribution, and shoot pruning, among others, is essential for reducing the competition for nutrients and water between crops and associated trees. Plants tend to avoid excessive root competition by spatial segregation; as a consequence, associated plant species develop vertically stratified root systems, leading to complementarities in the use of soil resources (Schroth 1998). However, it has been reported that trees in AFS are not always efficient in accessing or recovering water and nutrients from the sub-soil and hence represent a source of competition with the main crop (Hauser et al. 2005). In alley cropping systems with maize (*Zea mays* L.) associated to black walnut (*Juglans nigra* L.) or red oak (*Quercus rubra* L.), reduction in yield (50%) is associated to water competition even if shade also reduced the photosynthetically active radiation (Gillespie et al. 2000). Furthermore, competition for soil water was reported to be substantial during 2 years in an alley cropping system with maize (*Zea mays* L.) and silver maple (*Acer saccharinum* L.). This was concluded after observing that for maize associated with trees without a root barrier (that prevents tree roots from colonizing soil areas exclusively dedicated to maize roots), soil water content, predawn and midday water potential, and midday net photosynthesis of maize plants adjacent to the tree rows were reduced compared to plants in the center of the alley cropping or in monoculture (Miller and Pallardy 2001). Additionally to maize or sorghum, there is evidence of water competition in alley croppings with other crops. In an AFS

with pecan (*Carya illinoensis*) and cotton (*Gossypium hirsutum*) in a sandy loam soil (Rhodic Paleudult) in Jay, Florida, there was evidence of water competition. Thus, plots with root barriers that restricted invasion of tree roots into crop root zone, presented higher soil water content and resulted in better cotton growth (height, leaf area, and fine root biomass) than the treatments without roots barriers (Wanvestraut et al. 2004).

Nonetheless, there are differences in the water use among species and competition also depends upon resource availability for the main crop and characteristics of associated trees. An example is provided with Grevillea (*Grevillea robusta* A. Cunn.; Proteaceae) for which deep rooting pattern is reported to result in low levels of water competition with the associated crops (Howard et al. 1996). In an alley cropping with cowpea (*Vigna unguiculata* L.; Leguminosae), trees presented 85% of the total root water uptake from below the crop rooting zone (below 60 cm of soil), suggesting a high degree of below-ground complementarity (Howard et al. 1996). In addition, a redistribution of soil water from deeper horizons to drier surface horizons by root system has been documented and termed "hydraulic lift", as mentioned for *Grevillea robusta* and *Eucalyptus camaldulensis*. However, the reverse phenomenon occurs after surface horizons are rewetted and water transported by roots from superficial to deeper soil horizons showing that there is a "hydraulic redistribution" of water due to tree roots (Burgess et al. 1998). This phenomenon is cited in other studies in which different tree species associated (*Acacia crassicarpa*, *Acacia julifera*, *Acacia leptocarpa*, *Leucaena pallida* and *Senna siamea*) with continuous maize (*Zea mays* L.) cultivation. Thus, trees transpired more water than natural fallow vegetation or monoculture plots during the dry season, but this pattern was reversed after rainfall when plots with planted trees contained greater quantity of stored water (Nyadzi et al. 2003).

Despite tree water competition in AFS, significant differences are expected to exist between tree species due to their water use per unit leaf area. Thus, indigenous tree species are thought to be better adapted and to compete less in a dry environment than exotic species. However, some studies have shown an opposite relation, for example, in a parkland in Senegal, the indigenous tree species *Acacia seyal* used more water per unit leaf area than all other species. On the contrary, the exotic species *Azadirachta indica* consistently used less water per unit leaf area than most other species, irrespective of season (Deans and Munro 2004).

The competition for water also depends on resource availability, soil depth and annual rainfall pattern as much as the tree species. For example, crop yields were reduced in a shallow Alfisol by the presence of *Leucaena leucocephala* due to water competition, but the severity of the competition was higher in years of low rainfall and for long-duration crops such as castor bean (*Ricinus comunis*) and pigeonpea (*Cajanus cajan*) (Rao et al. 1991).

It has been suggested that productivity of natural vegetation under savannah trees generally increases as rainfall decreases, while the opposite occurs in agroforestry. Thus, in the savannah, the beneficial effects of microclimatic improvement (e.g. lower temperatures, reduced radiation and evaporation losses) are greater in more xeric environments, because mature savannah trees have a high proportion of woody above-ground structure compared to foliage, so that the reduction in soil evaporation is larger than tree transpiration. On the contrary, the beneficial effects of trees in AFS in terms of microclimate improvement are negated by a reduction in soil moisture due to increasing interception losses and tree transpiration (Ong and Leakey 1999).

However, most of the literature focused on water competition was developed for alley cropping systems whereas there is a lack of information on how trees interact with perennial crops in AFS, especially for water partitioning. In coffee, the use of shade trees depends on social and biophysical factors (Fournier 1988; Muschler 2004; Muschler and Bonnemann 1997). It is suggested that shade trees can be associated with coffee in suboptimal regions, however it is thought that inadequate shade (species, tree densities) could reduce coffee production due to water competition, especially during the dry period. In addition, water must be freely available during the period of fruit expansion (Beer et al. 1997; Carr 2001; Muschler 1997). In coffee AFS, little information is available on the water use by coffee and associated trees, and possible water competition. Water use in 3 coffee AFS was higher in comparison to MC, but a higher water use itself does not indicate water competition (Kanten and Vaast 2006). There are many published studies on the positive influence of trees on microclimate (Barradas and Fanjul 1986; Beer 1987; Muschler 1997; Muschler 2004; Muschler and Bonnemann 1997), but few studies on water use (Kanten and Vaast 2006) and none on the water components of the water budget to draw conclusions on the possible negative effects of trees on water balance.

1.3.7 What remains to be documented on coffee water relations?

The current knowledge on water use by coffee is incomplete. Although stomatal conductance responses to microclimate are well documented, there are very few studies about water use at the whole plant level under field conditions and at plot level. Furthermore, there is little information on water use in long term experiments and on the influence of climate and soil factors on transpiration of coffee plants under various production systems. Particularly, there is little information on coffee water use in agroforestry systems along climatic and soil gradients, which can help to assess the role of associated trees with respect to water use and competition.

1.4 My research hypotheses

From the physiological (agronomic) point of view, the optimal site conditions for coffee cultivation are in the altitude range from 1200 to 1800 m. This has been explained by the fact that at temperatures above 24 ^{o}C, the net photosynthesis decreases and is reduced markedly above 34 ^{o}C (Cannell 1985; DaMatta 2004a; Nunez et al. 1968). Thus, the use of shade trees has been recommended in Central America for areas with relatively high mean annual temperatures (sites at low altitude) and less fertile soils, especially in Costa Rica (Barros et al. 1978; Muschler 2004; Muschler and Bonnemann 1997). On the contrary, under the most appropriate conditions for coffee culture (high altitude with relatively low annual mean temperature, high water availability and nutrient supply), shade of associated trees reduces coffee yield significantly whenever compared to full sun, intensive coffee monoculture (Beer et al. 1997; Muschler 1997; Muschler 2004; Muschler 1999; Vaast et al. 2007; Vaast et al. 2005c; Vaast et al. 2005d). However, the use of shade trees depends on factors such as: production objectives, environmental factors, and level and quality of inputs available to improve the environment of the coffee production system (Fournier 1988; Muschler 2004; Muschler and Bonnemann 1997). Thus, monoculture coffee plantations are recommended if agrochemical inputs, mechanization, irrigation and modern, high-

yielding varieties are available (Beer et al. 1997; Muschler 1997). On the other hand, if conservation of natural resources are important goals, then agroforestry systems are recommended, especially if producers are interested in producing certified coffee (Organic Coffee, Fair Trade Coffee, Rainforest certification and Bird Friendly coffee), or if AFS are included in schemes for payments of environmental services. The use of shade is a common practice in most of the countries in Mesoamerica, especially north of Costa Rica, with the genus *Inga* as an important component of the shade stratum in agroforestry systems. However, the competition for resources, especially water, is a common concern of farmers with the use of shade trees in coffee systems. Trees influence plot water budget in AFS via all the water components. Effectively, trees are thought to increase rain interception and total transpiration of the system, but to reduce runoff and increase infiltration. The increment in total transpiration has lead to the thinking that shade trees compete for water with coffee plants grown underneath, especially during the dry season. However, few studies have taken into account all the components of the water budget and how trees affected these components. The importance of the use of *Inga* in agroforestry systems under optimum climate conditions for coffee culture has driven us to assess the effects of *Inga densiflora* on the bean yield and biomass of coffee, as well as its effect on the water balance at plot level (rain interception, transpiration and runoff) during two consecutive years of production in regions with optimal climate conditions for coffee.

1.5 My research questions

With the development of this thesis, I have tried to answer the following questions:

- How does *Inga densiflora* as shade tree species modify the microclimate of a coffee canopy in an agroforestry system?
- How does *Inga densiflora* as shade tree influence bean yield and biomass of coffee plants?
- How does *Inga densiflora* as shade tree influence the components of the water balance (rainfall interception, runoff and transpiration) at plot level?
- In which way is the transpiration of coffee plants affected by the presence of shade trees: reduction or increase of stomatal conductance; reduction in water availability for the system; modification and buffering effect of the micro-climate? How important is the stemflow of coffee and of trees? Can it be ignored in water budget as it is routinely the case?

2 MATERIAL AND METHODS

2.1 Site description and experiment

The study was conducted during 2004-2005 on the experimental farm of the research station of the Coffee Institute of Costa Rica (ICAFE), located in San Pedro de Barva in the Central Valley of Costa Rica (10°02'16'' N, 84°08'17'' O; 1200 m above sea level). According to the life zones of Holdridge, the region is classified as a premontane rain forest, with a mean annual temperature of 21°C and an annual precipitation of 2300 mm with a pronounced dry season from January to April (Mata and Ramirez 1999). However, the annual rainfall was particularly high with 3245 and 2684 mm during 2004 and 2005, respectively and unevenly distributed throughout the year with 94% and 93% during the wet season from May to November for 2004 and 2005, respectively. The annual Penman-Monteith reference evaporation (ETo), estimated by the equation of FAO from meteorological data (Allen et al. 1998), amounted to 1310 and 1177 mm yr^{-1} for 2004 and 2005, respectively.

The soil is derived from the weathering of volcanic ashes, belongs to Andisols and is classified as Dystric. As typically for Andisols, it is characterized by a loamy-clayey texture, well-structured, deep and permeable, with a low bulk density and high organic matter content (Mata and Ramirez 1999). The soil cation exchange capacity (CEC) is high due to the presence of allophones, with a low pH, relative high values of organic carbon (3.6% -3.7%) and moderate values of exchangeable Ca, Mg and K.

The experimental area presented two adjacent coffee plots: an agroforestry system (AFS) and a second one, a monoculture (MC) without shade trees. Coffee (*Coffea arabica* L.var. Caturra) was planted in 1997 with a spacing of 2 m between rows and 1 m within a row, which resulted in densities of 5000 and 4773 coffee plants ha^{-1} for MC and AFS, respectively, and with an average of 3 coffee stems per planting hole. In AFS, *Inga densiflora* (Benth) was planted within the coffee rows at a spacing of 6 x 6 m (277 trees ha^{-1}). Two shade management practices were applied in AFS: during the period from 1997 to 2002, trees were highly pruned at least twice a year, while from 2003 to 2005 the pruning intensity was lighter in order to provide a more substantial shade for the coffee plants (30-50%). The plots were equally intensively managed with a fertilization composed of 250 N; 15 P_2O_5; 110 K_2O; 70 MgO; 5 B_2O_3; 50 S and 60 CaO kg ha^{-1} yr^{-1}, following the recommendations of ICAFE (ICAFE 1998).

2.2 Meteorology and microclimate

An automatic weather station was installed in an open area next to the experimental plots and meteorological variables were monitored. A Vaisala temperature and relative humidity probe (Model HMP 35C, Campbell Scientific, Logan, UT) was used to determine VPD. The photosynthetic photon flux density (PPFD) was measured with quantum sensors (SOLEMS PAR-CBE 80, Palaiseau, France) and wind speed with an anemometer (Model 05103-5 Wind-monitor). Rainfall was measured with a tipping bucket gauge (Model ARG 100). Rainfall, temperature, humidity and quantum sensors were connected to a data logger (CR10X Campbell Scientific Instruments), measured every 30s and average values over 15 minutes were recorded to

the datalogger memory; the measurements were made throughout the 2 year period, except for days when the devices failed due to technical problems or for periods that coincided with main holidays.

2.2.1 Radiation transmission and interception

To determine the shade level for coffee plants in AFS, PAR-CBE 80 sensors were fixed on the top of the orthotropic stem on 4 four coffee plants under shade trees. Coffee plants positioned at 1 m and 3 m from shade trees were selected. Additionally, hemispherical photos were taken to study the spatial variability of transmittance at seven dates throughout the two years of monitoring. The hemispherical photos were taken above the coffee canopy at 100 grid points in a 400 m^2 plot divided in 2m x 2m squares. The hemispherical photographs were analyzed with the Gap Light Analyzer (GLA) software.

2.2.2 Leaf temperature

The influence of shade trees on coffee leaf temperature was measured with copper-constantan micro-thermocouples attached to the underside of seven leaves per system during the period of April to August 2005. The monitored leaves were selected on branches located in three strata (upper, medium and lower) of the coffee plant canopy. Mean values over 15 minutes were then recorded to a datalogger (CR10X Campbell Scientific Instruments).

2.2.3 Soil water content

The method used was the TDR (Time Domain Reflectometry) technique that has been extensively employed to measure soil water content in the field with different probe designs. The TDR method measures the apparent velocity of electromagnetic waves traveling in a wave guide defined by the probes inserted into the soil. The time between the arrival of reflections marking the soil surface and the end of the probes can be estimated from the TDR wave form on the cable tester screen. The TDR method measures the average water content of the soil embedding the probes. The probes may be installed vertically to yield the average water content at one point, or horizontally, yielding the average water content at one depth. In this study, the TDR-probes were installed in both systems, with six and nine TDR probes installed in MC and AFS, respectively. Soil water content was monitored in the layers 0-30, 30-60, 60-90, 90-120 and 120-150 cm. Measurements were undertaken every ten days in each probe and for each 30 cm layer with a portable apparatus (MP-917, ESI, Environmental Sensors Inc.). In many circumstances, it appeared that soils with different characteristics behaved similarly and did not need to be calibrated individually. Nonetheless, soil was sampled monthly in this study during one year, with an auger at the 0-30, 30-60, 60-90, 90-120 and 120-150 cm depths at approximately 1 m away from each TDR probe and at 50 cm away from the coffee plant. At the same time, time reflectrometry was measured on each probe in order to calibrate TDR measurements in each layer of each probe with respect to the soil water content measured after a 48h of soil oven-drying at 105°C.



Photography 4. View of the experimental coffee plot grown without shade (monoculture) on the research station of CICAFE, San Pedro de Barva, Heredia, Costa Rica (JM. Harmand).



Photography 5. View of the experimental coffee plot grown under the shade of *Inga densiflora* trees on the research station of CICAFE, San Pedro de Barva, Heredia, Costa Rica (JM. Harmand).

2.3 Inga densiflora growth

The growth of *Inga* trees was recorded through measurements of of stem diameter at breast height (DBH at 1.3 m) on all individuals (41) in October 2002, January 2004, July 2004, January 2005 and August 2005. During 2004, allometric relationships based on non-linear regressions were developed to provide reliable estimates of the total above-ground biomass and that of leaves, trunk and branches.

2.4 Coffee growth

2.4.1 LAI dynamics

Coffee leaf area index (LAI) was estimated at seven dates during the study: August 2003, February 2004, September 2004, February 2005, April 2005, June 2005 and October 2005. The total plant leaf area was measured on eight individual plants per system (MC and AFS). In each of the 16 plants, the length and width of all individual leaves were measured, then the individual leaf area was estimated by the following equation: Area= 0.69*Length*Width, (R^2 = 0.96), obtained by the regression analysis of the measured area, length and width of 100 leaves. The total plant leaf area was estimated from the cumulated value of the all leaves. LAI of the plantation was estimated as the coffee plant density multiplied by the total leaf area per plant.

2.4.2 Yield monitoring

Annual coffee yield was measured from 1999 to 2005. In both systems, 10 sub-plots of 15 coffee plants were monitored annually. The annual coffee yield was obtained by the summing of 4 to 5 biweekly harvest events per year, during the harvest season that extended from November to the end of January. Data from individual plot were extrapolated to yield per ha with the density of plants per ha; yield in green coffee bean was obtained from sub-samples after wet processing and drying of berries.

2.4.3 Coffee biomass monitoring

Coffee biomass was measured on eight coffee plants in July 2004, January 2005 and July 2005. Fresh weight of stems, branches and leaves was measured for each stem and sub-samples of these components were taken and oven dried at 60°C during 72h.

2.5 Water Balance

The classical water balance equation representing the mass conservation law was used, considering water flux densities entering and leaving a soil volume element of 200 cm depth, integrated over time.

The following equation was used:

$$P - I - T - R - D + \Delta S = 0$$

Where P = rainfall; I = rainfall interception; T = crops transpiration; ΔS = variations of soil water content in the 0-200 layer; R = runoff; and D = deep drainage below the 200 cm depth, all expressed in mm.

2.5.1 Rain Interception

2.5.1.1 Throughfall

Throughfall was monitored in both systems from June to September in 2004 and from May to November during 2005. In each plot, 72 home-made rain-gauges (25 cm high and 82 cm^2 sampling area) were placed on the ground. The localization of all the gauges took into account the heterogeneity of coffee and tree canopies. In AFS, the 72 rain gauges were distributed in three repetitions of four sets (with 6 rain gauges) and located at 1.0, 2.2, 3.0 and 3.6 m distances from the *I. densiflora* stems. In MC, sets of rain gauges were placed at 4 m to 8 m apart in a rectangular design (see methodological details below in the section “rainfall interception loss”).

2.5.1.2 Stemflow

2.5.1.2.1 Coffee

Coffee stemflow was measured on 12 plants in each system. The stemflow device consisted in a collecting cup sealed around the stem, where collected water was diverted by plastic flexible tubing into a bucket placed on the floor. The stemflow volume of water collected from each tree was measured after each rainfall event during the rainy season of July to October 2005. To estimate daily stemflow of coffee in each plot (mm d^{-1}), the mean stemflow volume per stem was multiplied by the respective coffee density of each of the two systems.

2.5.1.2.2 Inga densiflora

Inga densiflora stemflow was measured on 6 trees using collars constructed with 25 mm thick polyethylene plastic tubes that were slit opened and then sealed on the stem in an upward spiral. The water collected by the collar was diverted by flexible tubing into a bucket placed on the ground. The stemflow volume of water collected from each tree was measured after each rainfall event during the rainy season of June to October 2005. To estimate daily stemflow of trees (mm d^{-1}), stemflow volumes were multiplied by the tree density (277 stems ha^{-1}).

2.5.1.3 Rainfall interception loss

Rainfall interception loss in both systems (MC and AFS) was calculated, for each rainfall event, as the difference between the registered gross rainfall in the open and the amount of measured throughfall plus stemflow.

2.5.2 Transpiration

2.5.2.1 Coffee

A stem heat balance method was used to estimate transpiration rate on coffee plants. In each system, four commercial stem sap flow gauges (Dynamax Inc., Houston, Texas) were installed ranging from 25 to 30 mm in diameter. The stem sap flow gauges (model SGB 35) were operated under the control of a datalogger CR10X (Campbell Scientific Inc., Logan, Utah). The data were monitored every minute, and mean values were stored every 15 min in a SM192 storage module.

For each monitored coffee stem, the leaf area (LA in m^2) was determined. Coffee sap flow (FS) was originally measured in g s^{-1} $stem^{-1}$, and then expressed in g h^{-1} m^{-2} of foliar area (FA). To estimate the daily coffee transpiration per hectare, the mean daily coffee transpiration per unit basal area was multiplied by the total coffee basal area per hectare estimated from stem measurements on a group of 156 coffees per system (312 m^2).

2.5.2.1.1 Gas Exchange

Gas exchange was recorded during 8 dates between February and September 2005 on fully developed leaves (third to sixth pair of leaves from the branch tip) using a CO_2/H_2O infrared gas analyzer (LCPro, ADC BioScientific Ltd., Hoddesdon, UK) connected to a broadleaf chamber. Measurements were taken on attached leaves in the upper third of coffee canopy and in the peripherical position on the branches of 4 trees per system. Four leaves per tree were monitored for a total of 32 measurements (2 systems [MC and AFS] x 4 trees x 4 leaves). Gas exchange was measured in each system sequentially and in the same order for all monitoring rotations. This sequence was repeated several times during the monitoring day in order to capture an abbreviated diurnal response to daily environmental changes. Measurements included morning, afternoon, and late afternoon measurements.

2.5.2.2 *Inga densiflora*

Sap flow was monitored with 2-cm long radial sap flow probes (Granier 1985; Granier 1987). Each sensor is composed of two probes; one heated continuously by a constant electrical source and the other one not heated. The dissipation of heat from the upstream heated needle increases with increasing sap flow rate. During conditions of zero sap flow, such as nighttime, the temperature difference between the lower and the upper probes represents the steady state temperature difference caused by the dissipation of heat into non-transporting sapwood. The sap flux density is computed through an empirical relationship validated by Roupsard et al (2006) as follow:

$$dF = 12.42\left[\frac{\Delta T_{max} - \Delta T}{\Delta T}\right]^{1.231}$$

where dF (l dm^{-2} s^{-1}) is the average sap flow density, ΔT the temperature difference between the two probes and ΔT_{max} is the baseline (maximum) temperature difference for the data set of the day. Sap flow was measured on four trees (11 stems) that were selected to represent the stem diameter distribution of the stand. Diameter at breast height of these trees ranged from 9.4 to 14.2 cm. Stand transpiration was computed as the product of the total basal area and the mean sap flow density of measured trees.

2.5.3 Runoff

Runoff was measured in both MC and AFS systems during the 2004 and 2005 rainy seasons by means of galvanized square frames of 1 m^2 and 15 cm height. Three frames were installed per system with each frame buried into the soil to a 7-cm-depth. Following every rainfall, water from surface runoff was collected at the bottom of the frame through a tube connected to a 30-L plastic can.



Photography 6. Detailed views of measurements of *Inga* stemflow (a) and coffee stemflow (b) on the research station of CICAFE, San Pedro de Barva, Heredia, Costa Rica.



Photography 7. Detailed views of the measurements of tree sap flow with “Granier” sensors (a) and coffee sap flow with Dynamax gauges (b) on the research station of CICAFE, San Pedro de Barva, Heredia, Costa Rica.



Photography 8. Detailed views of the measurements of water runoff (a) and soil water content with TDR (b) on the research station of CICAFE, San Pedro de Barva, Heredia, Costa Rica.

3 RESULTS AND DISCUSSION

3.1 Influence of trees on microclimate

Shade trees modified the microclimate primarily through a reduction in light transmittance. In AFS, the amount of transmitted radiation through the shade tree canopy depended upon time (solar angle), season of the year and distance from tree stem. During the dry season, the daily transmittance was higher than during the rainy season, with values of 45% compared to only 30% (Figure 4).

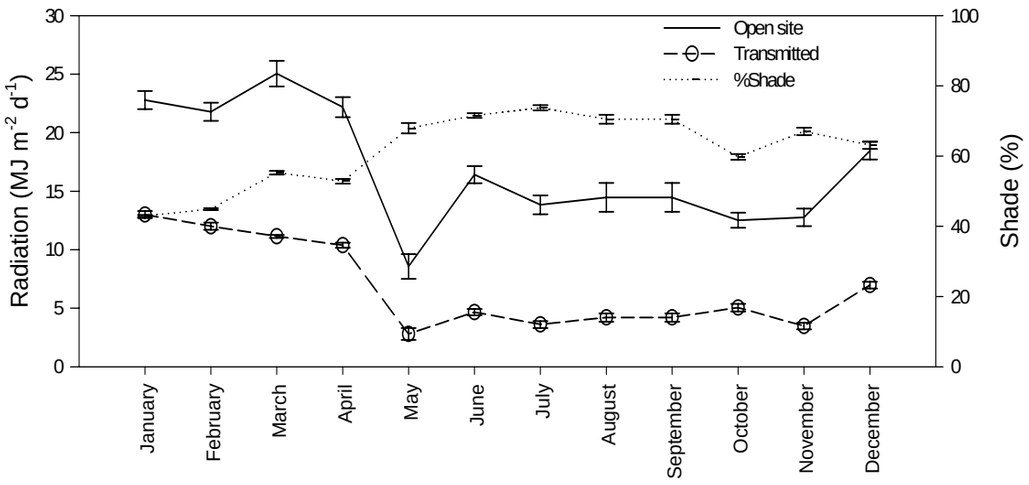


Figure 4. Annual time-course of incident and transmitted radiation and percentage of shade of *Inga densiflora* in an agroforestry system at San Pedro de Barva, Costa Rica.

However, the percentage of transmitted radiation also varied greatly throughout the day during both seasons. During the dry season, transmittance averaged 29% in the morning (7:00-9:00), 43-55% around midday (10:00-15:00) and 33% in late afternoon (15:00-18:00). During the rainy season, the daily pattern differed significantly with the highest values (28% to 35%) registered in the morning (7:00 to 11:00) and low values (15% to 20%) thereafter (Figure 5 ab). The lower values and different pattern of radiation transmittance during the wet season in comparison to the dry season are explained by differences in canopy development and phenology of the shade trees.

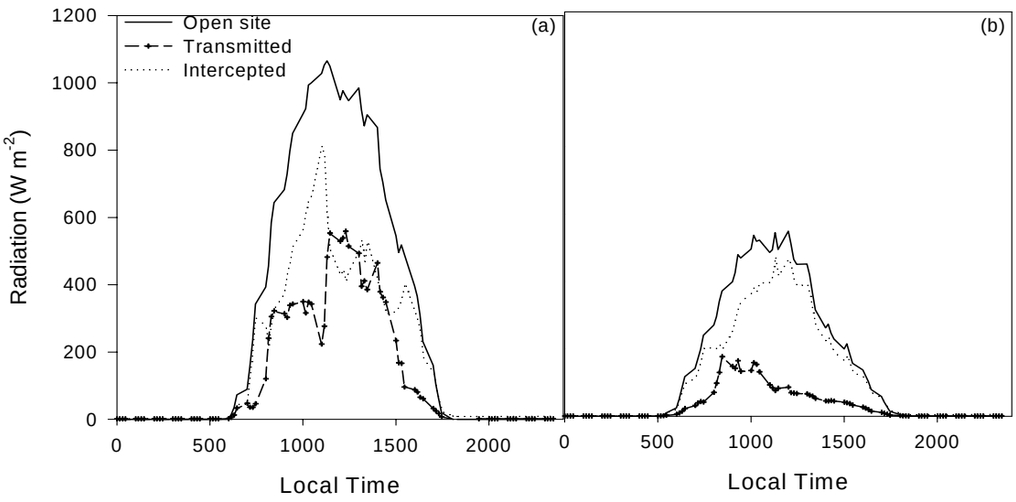


Figure 5. Mean diurnal time courses of global, intercepted and transmitted radiations for (a) April 2005 (dry season) and (b) October 2005 (rainy season) below the *Inga* canopy in AFS plot (Values are means of 2 weeks of measurements).

Despite the low light transmittance in AFS, shade levels seemed to be in the acceptable range for coffee (40 to 70%) according to many studies (Beer 1987; Beer et al. 1997; Muschler 2004; Vaast et al. 2005c; Vaast et al. 2005d). These low radiation levels for coffee canopy are generally acceptable for low altitude conditions due to the shade tolerant features of coffee (Cannell 1975; Cannell 1985; DaMatta 2004; DaMatta and Maestri 1997; Franck 2005; Kumar 1979; Kumar and Tieszen 1976; Kumar and Tieszen 1980a). Due to all these features, coffee photosynthetic rate seems to be at the maximum at intermediate shade levels (PPDF around 1000 µmol m^{-2} s^{-1}) in many coffee growing conditions (Beer et al. 1997; Franck 2005; Franck et al. 2006; Nutman 1937; Vaast et al. 2002). However, tree canopy caused substantial local variation in shade level depending on the proximity of coffee plants to shade trees. The percentages of radiation transmitted at distances of 1 and 3 meters from shade trees were significantly different (Figure 6), as reported by many others authors for various agroforestry systems (Feldhake 2001; Ong et al. 2000). Trees produced a low transmittance of around 25% of radiation close to their stems, while the transmittance was much higher further away, but coupled with a higher variability along the day.

This variability in transmittance may have profound effects on the growth and inter-specific competition of under-story plants, especially weeds (Staver et al. 2001). This also generates micro-environments affecting coffee functions such as transpiration (Kanten and Vaast 2006) and photosynthesis (Franck 2005; Vaast et al. 2005a; Vaast et al. 2002).

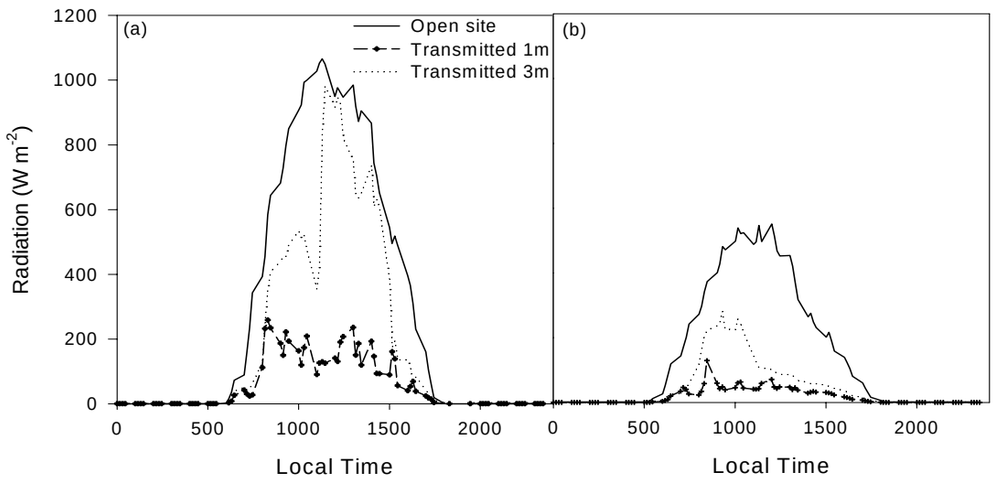


Figure 6. Mean diurnal time courses of transmitted radiation at 1 m and 3 m away from the trunk of *Inga densiflora* in an agroforestry system in San Pedro de Barva, Costa Rica, for (a) April 2005 (dry season) and (b) October 2005 (rain season).

In addition, shade of *I. densiflora* showed a substantial moderating influence on the thermal leaf environment. During the 2 dry seasons, coffee leaves without shade experimented temperatures higher than air temperature whereas leaf temperature of shaded coffee was always lower than air temperature (Figure 7ab). However, during the wet season the average leaf temperature of coffee without shade was similar to the air temperature, but maintaining higher values with respect to coffee under shade. Shade induced leaf temperature differences of 1^{o}C up to 7^{o}C with respect to coffee leaves in full sun, depending on time of the day, season and leaf position within the coffee canopy (Figure 7cd).

The modifying effects of shade trees on the leaf temperature, air humidity and wind speed in the under-storey has been documented in various coffee AFS of Costa Rica (Siles and Vaast 2003; Vaast et al. 2005c; Vaast et al. 2005d) and Mexico (Barradas and Fanjul 1986). This reduction in leaf temperature is of particular importance since the temperature for an optimal photosynthesis of arabica coffee is in the range between 18 to 24 ºC (Kumar y Tieszen, 1976; Cannel, 1985; Vaast et al, 2005; Franck et al, 2006) and with a detrimental effect of temperature above 25 ºC related to stomatal closure (Nunes *et al*. 1968, Kumar y Tieszen, 1980; Fanjul et al, 1985; Guttierez et al, 1994, Dauzat et al, 2001, van kanten and Vaast, 2006). Furthermore, other authors, working on different agroforestry systems, cited a positive effect of the temperature reduction on crop establishment, reduced soil temperature and evaporation, and enhanced activity of soil organisms (Ong et al, 2000; Rao et al, 1998; Martius et al; 2004).

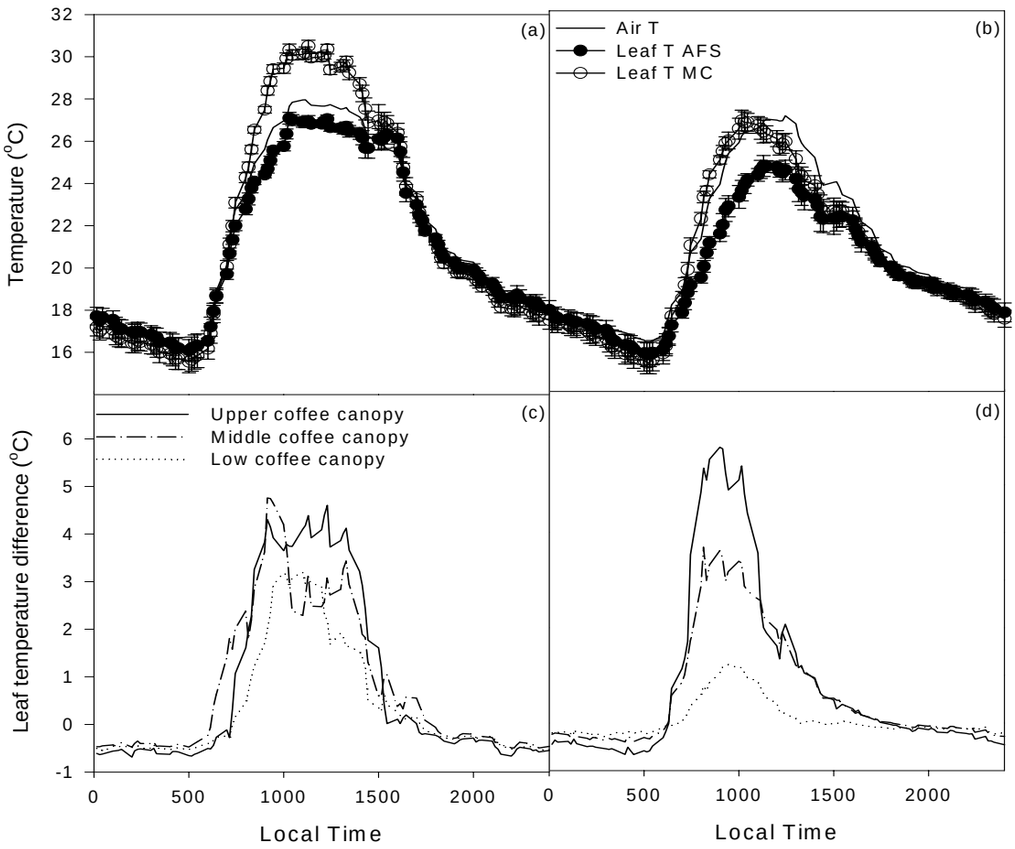


Figure 7. Mean diurnal leaf temperature (ab) and mean diurnal differences in leaf temperature (cd) at different coffee canopy strata between monoculture and an agroforestry system shaded with *Inga densiflora* in San Pedro de Barva, Costa Rica, for April 2005 (dry season, left panels) and July 2005 (rainy season, right panels).

3.2 Influence of shade trees on coffee growth and yield

3.2.1 Yield

In AFS, the cumulative yield during six consecutive years was 10% lower than that recorded in MC. However, tree shade management in AFS was heavier in the period from 1997 to 2002 compared to the period from 2003 to 2005. Clearly, this influenced coffee yield and no statistical difference was found from 1999 to 2003 between AFS and MC when shade trees were pruned twice a year and shade was light. On the contrary, coffee yield in AFS was significantly reduced by 29% compared to MC during the period from 2003 to 2005 due to a denser tree shade (Figure 8). The highest yield reduction (38%) was registered during the last year of the study when the actual light transmittance varied between 40 to 50%.

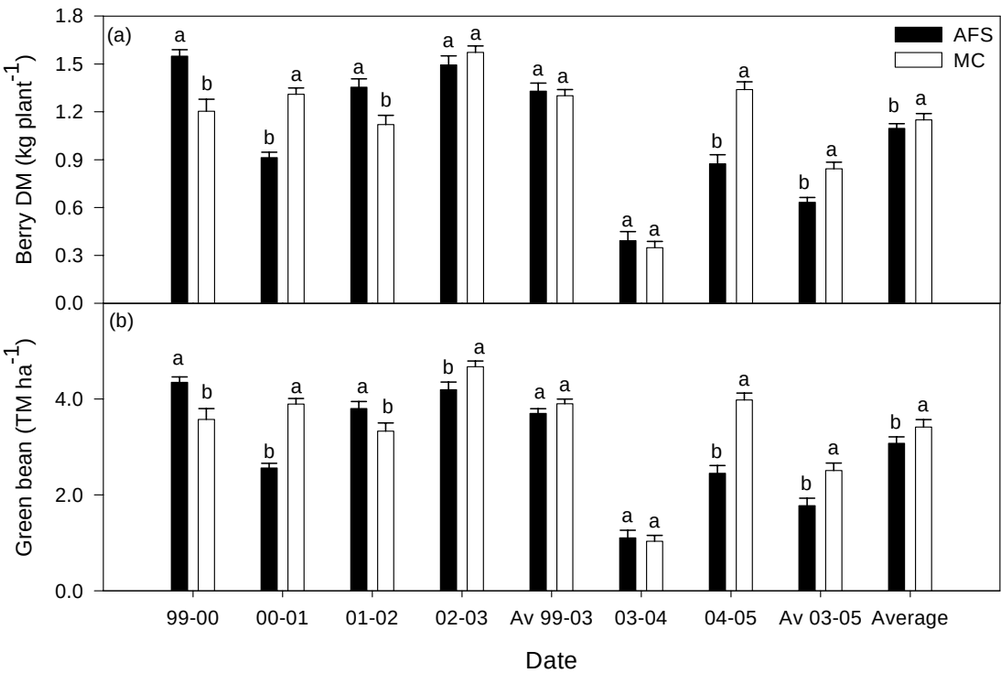


Figure 8. Coffee berry dry matter per plant (a) and coffee green bean yield (b) in monoculture (MC) and in an agroforestry system (AFS) shaded with *Inga densiflora* in San Pedro de Barva, Costa Rica during 6 consecutive production cycles.

Coffee yield reduction by shade is well documented in AFS with yield components such as fruiting nodes and fruits per node strongly affected by low light levels even when other ecological factors were favorable (Soto-Pinto et al. 2000; Vaast et al. 2005a). However, a yield reduction in the range of 10 to 20% can be financially compensated if a premium price is paid for improved quality (i.e. larger bean size and higher cup quality) as demonstrated in sub-optimal and optimal conditions of Central America (Guyot et al. 1996; Vaast et al. 2005a; Vaast et al. 2005b).

3.2.2 Coffee LAI and biomass

Values of coffee LAI in AFS and MC were not statistically different during the first 5 monitoring dates, but were lower in AFS during June and October 2005. Although coffee under shade displayed larger individual leaf sizes, coffee plants presented similar LAI values in AFS and MC due to a larger number of leaves per coffee plant in MC than in AFS (Figure 9ab). Thus, shading by *I. densiflora* had a significant effect on coffee leaf traits such as enhancing specific leaf area (SLA) and mean individual leaf area in AFS compared to MC (data non-shown, see detailed in article 1). Other authors have reported in coffee a highly significant effect of uniform artificial shade on leaf traits such as SLA, individual leaf area, and leaf nitrogen content (Franck 2005; Vaast et al. 2005a; Vaast et al. 2005b).

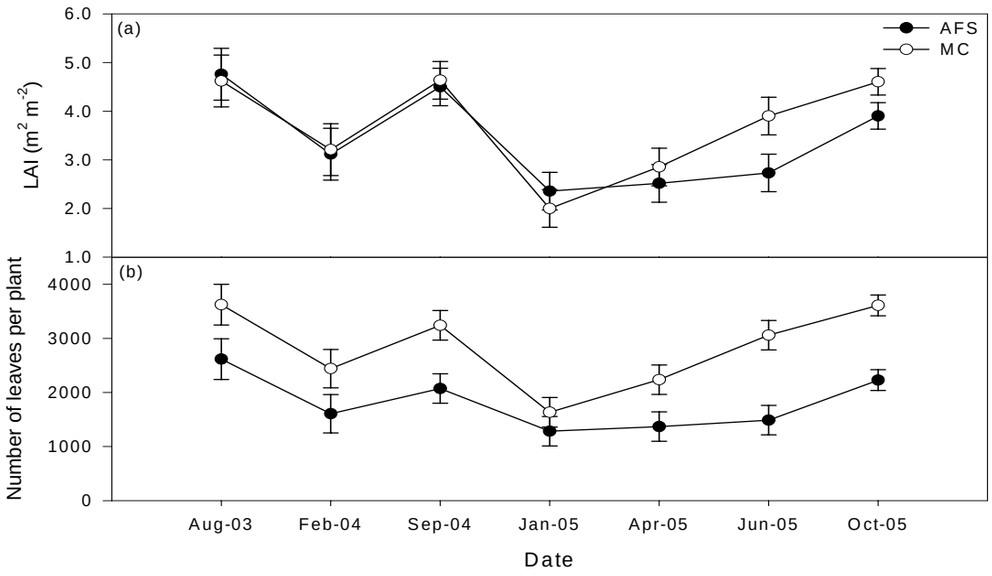


Figure 9. Leaf area index (a) and number of leaves per plant (b) for coffee plants in monoculture (MC) and in an agroforestry system (AFS) in San Pedro de Barva, Costa Rica.

Coffee plant dry matter was not significantly affected by shade as shown by the absence of difference for shoot biomass between AFS and MC, except for lower values of leaf dry matter and LAI during the wet season 2005 in AFS compared to MC (Figures 9 & 10). This is consistent with the commonly accepted belief that shade has little effect on the total carbon gain and hence coffee biomass (Cannell 1974; Cannell 1985; Franck 2005).

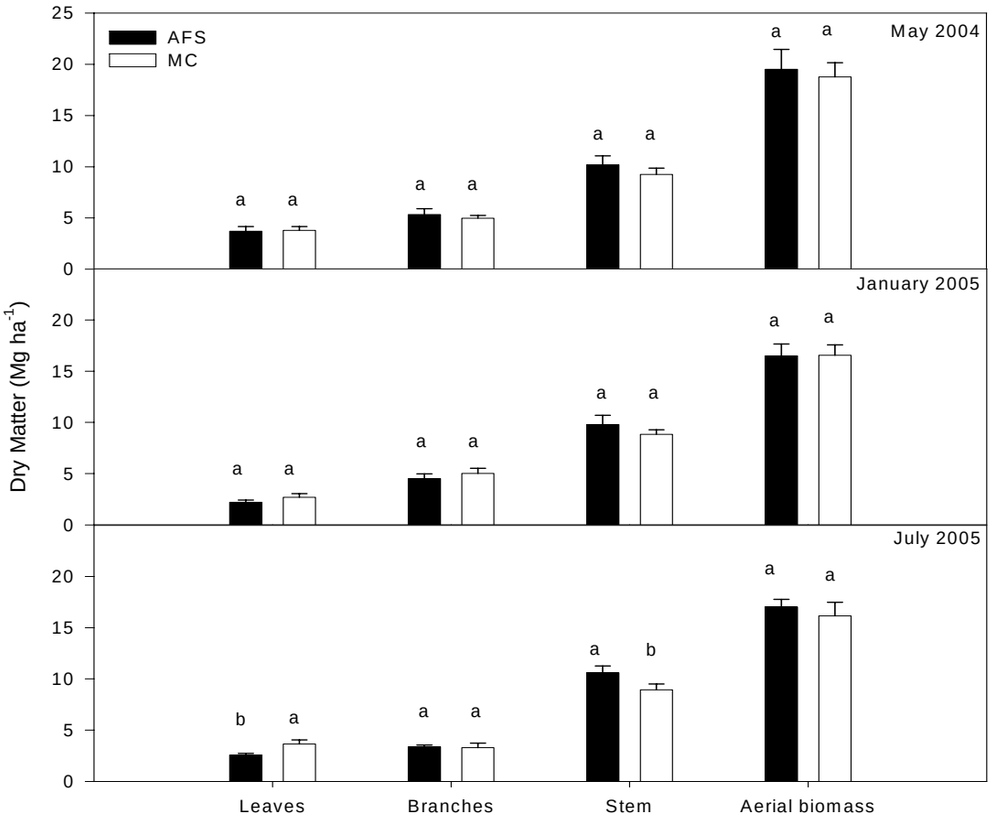


Figure 10. Biomass (MT ha^{-1}) of the different coffee components in an agroforestry (AFS) and monoculture plot (MC) in San Pedro de Barva, Costa Rica.

Data of photosynthesis during four dates (2 during the dry season and 2 during the wet season) suggested that, despite the lower values of irradiance (PPFD) at leaf level in coffee under shade, the CO_2 net assimilation was in average not different from values measured in MC (Figure 11).

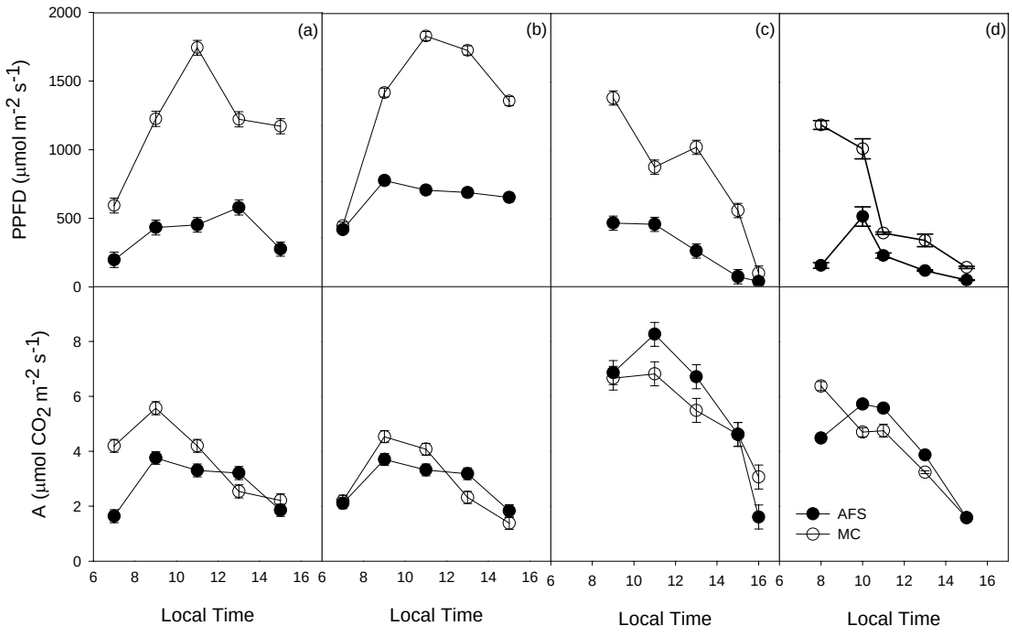


Figure 11. Diurnal time courses of incident PPFD and net CO_2 assimilation of coffee leaves during the dry season (a: February; b: March 2005) and wet season (c: August; d: September) in MC and AFS at San Pedro de Barva, Costa Rica. (Values are averages of 4 leaves in 4 plants measured over a period of 1 hour ± CI).

The daily average values of net CO_2 assimilation from 8 dates during 2005 also showed no significant differences ($P<0.05$) between coffee in AFS and in MC, except in February 2005 (Figure 12). Even with higher values of PPFD in MC, the similar values in net CO_2 assimilation in both systems could be explained by the higher values of gs in AFS compared to MC. These higher gs values in AFS were the result of lower values of leaf to air VPD in AFS than in MC. This fact showed the shade effect on microclimate (PPFD, leaf to air VPD and leaf temperature) and hence its impact on physiological processes in the coffee plant. Without any significant effect observed on net CO_2 assimilation, these results suggest that shade trees reduced primarily yield through a reduction in the number of productive nodes and flowering intensity of coffee. These results are in agreement with another study where shade of 75%, 50% and 25% reduced coffee fruits to 66%, 33 and 13% compared to plants without shade, due to a reduction on the number of flower in coffee plants, but none on canopy photosynthesis and overall biomass production (Franck 2005).

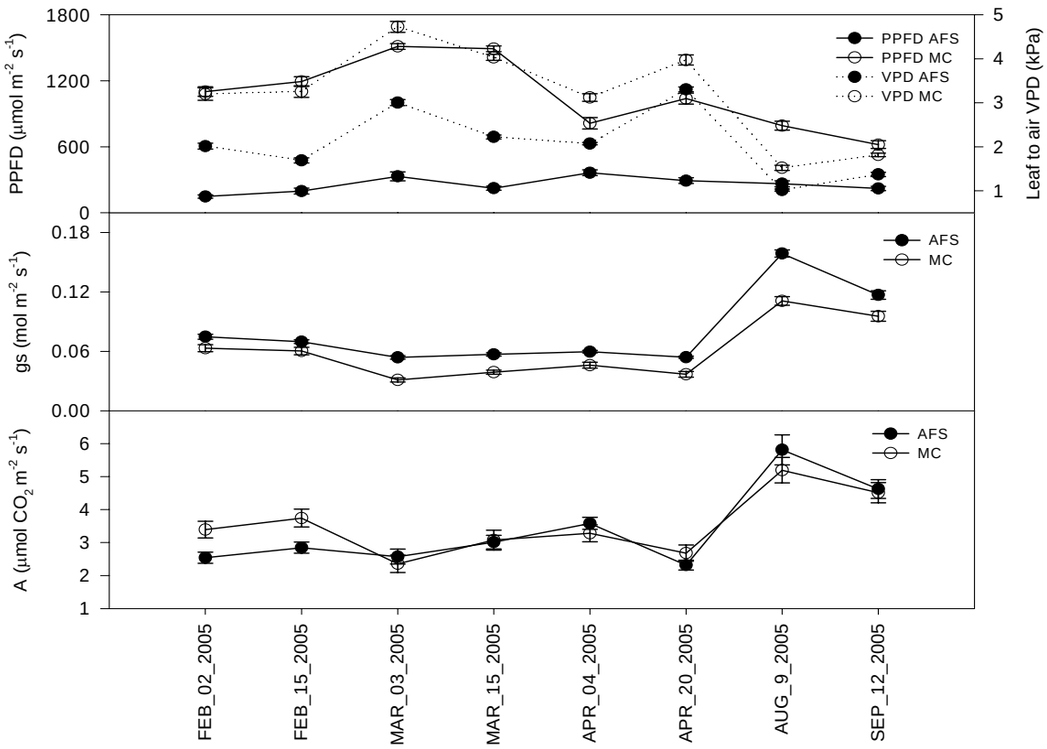


Figure 12. Average net CO_2 assimilation rate, stomatal conductance (gs), PPFD and leaf to air VPD at 8 dates during 2005 for the dry and wet seasons in MC and AFS at San Pedro de Barva, Costa Rica (from February to April, dry season; August and September, wet season).

The small and not significant differences in coffee biomass showed an absence of competition for resources between the shade tree species and coffee in AFS under the optimal conditions and intensive fertilization regime of the present study. Indeed, no sign of competition for water was observed, especially during the four months of the dry season as the monitoring of soil moisture did not show evidence of any effect of shade trees on soil water availability in the soil layers from 0 to120cm (data shown below) where the most if not all the coffee root system was concentrated (data shown in article 1). Even though AFS plot transpired more, the reduction in soil water was evident only during the dry season of 2004 and in the deeper soil layer (120-150). Generally, competition for nutrients is also cited as a major concern in coffee AFS (Beer et al. 1997), but was unlikely in the present study due to the large annual fertilizer applications (250 kg N; 15 kg P; 110 kg K) in excess of export by coffee berry production in a fairly fertile soil (Harmand et al. 2007).

3.3 Trees growth and total shoot biomass

As a result of the heavy pruning (twice a year) of *Inga* trees during the first 5 years, the annual mean increments in basal area and shoot biomass of *Inga* trees were low with values of 0.83 m^{-2} ha^{-1} yr^{-1} and about 2.55 Mg ha^{-1} yr^{-1}, respectively (Figure 13 a). From the fifth year (2003) onwards, shade was regulated less heavily (only once a year) and the annual mean increment in basal area and aerial biomass of *Inga* trees increased substantially with values of 1.9 m^{-2} ha^{-1} yr^{-1} and 5.8 Mg ha^{-1} yr^{-1}, respectively (Figure 13a).

For the whole monitoring period of 8 years, the annual mean increments in basal area and shoot biomass of *Inga* trees were relatively low wit values of 1.2 m^{-2} ha^{-1} yr^{-1} and 3.8 Mg ha^{-1} yr^{-1}, respectively (Figure 13a) compared with data of another study in Jatun Sacha, Ecuador (Pennington 1998). Despite the fact that tree density in AFS was lower than in a pure stand, the individual annual tree growth was smaller in the present site than in Ecuador, which showed the strong reducing effect of tree pruning in AFS on the growth of *Inga* trees. However, growth during five to six years reached a value of 7.8 Mg ha^{-1} yr^{-1}, which is comparable to the growth in other localities. *Inga* displayed a larger growth biomass production as compared to other Fabaceae species such as *Erytrhina* and *Gliricidia*. Moreover, the wood of various *Inga* species is preferred as source of fuelwood for cooking due to its fast growth rate and the fact that it burns well without much smoke (Hands 1998; Murphy and Yau 1998; Pennington 1998).

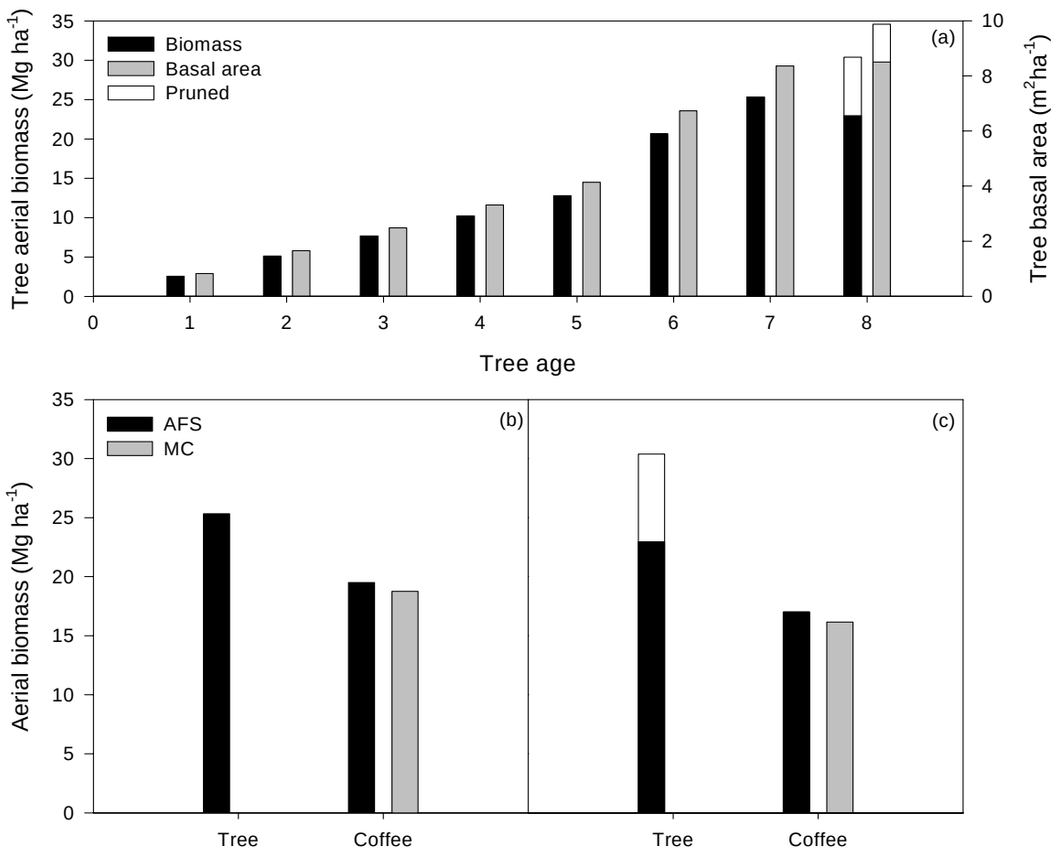


Figure 13. Dynamics of basal area and total shoot biomass of *Inga densiflora*, (a) shoot biomass in monoculture (MC) and in agroforestry system (AFS) in San Pedro de Barva, Costa Rica, for (b) 2004 and (c) 2005.

Despite the low tree growth rate in the present site, the combined shoot biomass of coffee and shade trees was 3 times higher in AFS than in MC (Figure 13b). This demonstrates the advantage of a mixed system in terms of biomass production. This biomass accumulation represents an important carbon sequestration by the agroforestry system and an appreciable source of renewable fuel of economic importance to farmers (Martínez Acosta 2005; Murphy and Yau 1998).

3.4 Influence of trees on water balance components

3.4.1 Rainfall interception loss

3.4.1.1 Throughfall

Regressions of throughfall versus gross rainfall were computed from 86 and 140 single rain events for 2004 and 2005, respectively, with rainfall ranging from 0.25 to 60 mm (Figures 14 a & b). Statistical analyses demonstrated that regression slope was significantly ($P < 0.05$) higher in MC than in AFS during the two consecutive years, whereas intercepts were similar for both systems.

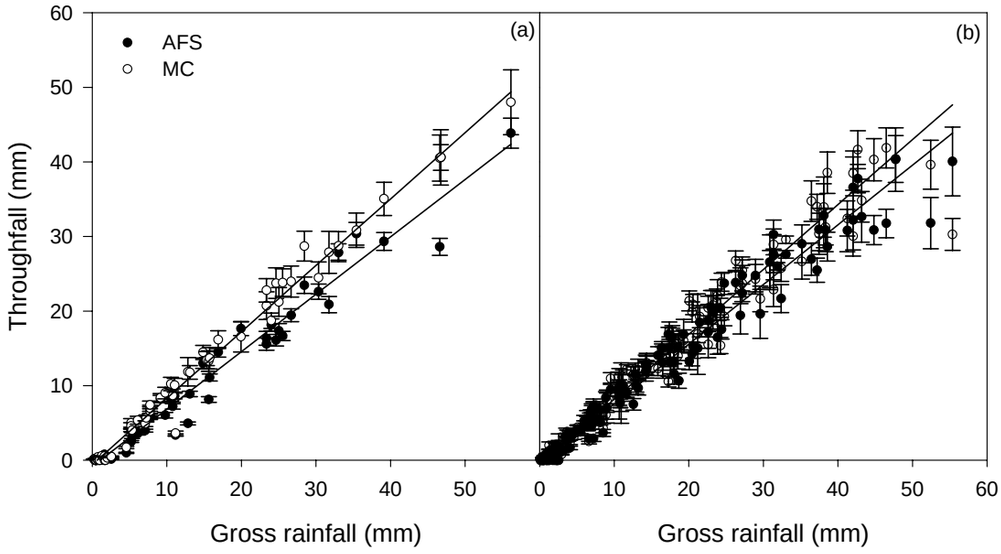


Figure 14. Average throughfall (with standard error) versus gross rainfall in 2004 (a) and 2005(b) in two coffee agricultural systems (AFS and MC) in the Central Valley of Costa Rica (for 2004, MC: r^2= 0.99, TF=-0.59+0.89*GR; AFS: r^2=0.97, TF=-0.85+0.77*GR; for 2005, MC: r^2= 0.97, TF=-0.53+0.87*GR; AFS: r^2= 0.97, TF=-0.45+0.80*GR).

Additionally, there was also a statistically significant difference in the regression slopes in AFS between 2004 and 2005, which could be attributed to the difference in LAI in both components (shade tree and coffee). No difference was observed in MC which is consistent with the non-significant difference in LAI observed for MC between the wet seasons 2004 and 2005. Other studies (Huber and Iroumé 2001; Marin et al. 2000) showed that canopy cover or LAI influenced the canopy water-storage capacity, and therefore throughfall. As mentioned previously, there was no difference in coffee LAI during the 2004 wet season between AFS and MC with an estimated LAI of 4.64 and 4.71 m^2m^{-2}, respectively. However, coffee LAI was different between the two systems in the wet season 2005 with an estimated LAI of 3.80 and 4.60 m^2 m^{-2} for AFS and MC, respectively. Additionally, LAI of shade trees estimated by hemispherical photographs was 1.32 and 1.22 m^2 m^{-2} for 2004 and 2005, respectively, showing a small but significant difference, even if LAI estimation from photographs were not very precise and fully reliable. Consequently, total

LAI (coffee + tree) was higher during 2004 in AFS (5.96 m^2 m^{-2}) than in MC (4.71 m^2 m^{-2}) whereas values were rather similar (5.02 and 4.60 m^2 m^{-2}, respectively) during 2005.

The cumulative throughfall (in % of gross rainfall as presented in Table 2) ranged between 72.8% and 85.1% for both systems, however the ranges reported in the literature for various forest types and climatic zones are very large from 55 to 90%, probably due to the differences in canopy structure and climatic conditions, which makes it difficult to compare with the present results (Huber and Iroumé 2001; Marin et al. 2000). On the other hand, the present data are consistent with the throughfall measured by Harmand et al. (2007) under coffee monoculture (83%) and shaded coffee with *Eucalyptus deglupta* (82%) at a low altitude area in Southern Costa Rica (Harmand et al. 2007). These two systems presented relatively low LAI of 2.74 and 3.5 m^2 m^{-2}, respectively. On the other hand, the present throughfall values are quite different from those reported from several coffee plantations in Colombia with similar climatic conditions (41-54%) where data on LAI were not reported (Jaramillo 2003; Jaramillo and Chaves 1998; Jaramillo and Chaves 1999).

3.4.1.2 Stem flow

In both systems, the relationship between coffee stemflow and gross rainfall could be described as a power function when rainfall was below 10mm and a linear function when rainfall was above 10mm (Figure 15 a, Table 1). There was a significant difference (P= 0.06) in stemflow between systems with higher values recorded in AFS than in MC.

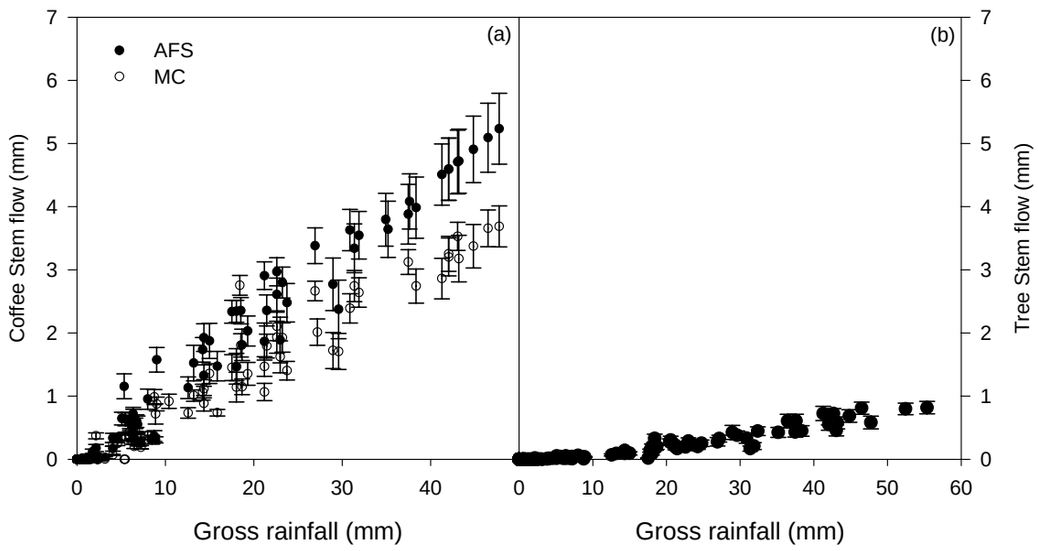


Figure 15. Stemflow (mean ±SE) versus gross rainfall for (a) coffee in MC and AFS, and (b) for *Inga densiflora* in agroforestry system in San Pedro de Barva (Central Valley of Costa Rica) in 2005.

Table 1. Statistical summary of regressions for daily stemflow versus gross rainfall in two different coffee agricultural systems (MC and AFS) in the Central Valley of Costa Rica. (Note: The equation for coffee stemflow is $S_{CP}= a(P_g^b)$ for daily rainfall < 10 mm and $S_{CL}= a + bP_{g,}$, for rainfall > 10 mm; S_C is the daily coffee stemflow amount (mm) and P_g is gross rainfall (mm). The equation for *Inga* stemflow is $S_I= a(P_g^b)$; S_I is the daily *Inga* tree stemflow (mm)).

Coffee system	A	B	se	R^2	*n*	*A*
MC						
Coffee (S_{CP})	0.004	2.313	0.495	0.917	82	0.0001
Coffee (S_{CL})	0.176	0.068	0.005			0.0001
AFS						
Coffee (S_{CP})	0.025	1.641	0.303	0.955	82	0.0001
Coffee (S_{CL})	0.054	0.106	0.006			0.0001
Inga	0.002	1.578	0.077	0.929	102	0.0001

Coffee stemflow represented up to 10% of rainfall and should not be ignored when computing plot water budget. The present study appears to be the first to monitor stemflow in coffee plantations as no reference was found in the literature. This is probably due to the fact stemflow was ignored in hydrological studies because low values (<2%) found in previous studies on perennial systems (Levia and Frost 2003). Thus, when stemflow is not taken into account, it is computed as rainfall interception and results in errors in drainage estimation.

The relationship between *Inga* tree stemflow and gross rainfall could be described by a power function (Figure 15b, Table 1). In general, tree stemflow represented a low portion of the combined stemflow in AFS. Most of the gross rainfall events with less than 4 mm did not result in any tree stemflow and values less than 1 mm were registered even for the highest rainfall events (60 mm). Coffee canopy operated as a funnel collector with the funneling ratio, defined as F=V / (BG) where V is the stemflow volume, B is the stem basal area, G is the incident gross rainfall in mm, was 68 and 48 in AFS and MC. In comparison, the funneling ratio for *I. densiflora* was estimated to be only 20. Again a comparison with the values found in the literature is difficult due to the large range in the funneling ratios (7 to 112), mostly due to differences in canopy architecture of the species studied (Levia and Frost 2003). In the present study, the differences in the funneling ratio between coffee and *I. densiflora* can also be explained by differences in architecture. Generally, larger stemflow rates are observed in small plants with multiple stems such as coffee in comparison with taller trees with a single stem, probably due to the fact that horizontal or downward tree branches inclined outward may not intercept and funnel rainfall towards the tree center to be drained as stemflow. Instead, rainfall is drained as throughfall once the canopy becomes water saturated (Carlyle-Moses 2004; Levia and Frost 2003; Marin et al. 2000).

The differences in the funneling ratio and resulting stemflow between coffee plants in AFS and MC can be explained by the architectural differences in plants grown under shade compared to plants grown in full sun. Shaded coffee plants were generally 40 cm taller with longer branches than the ones in MC; this could be appreciated by the significant higher stem and branches biomass in AFS. In some studies (Levia and Frost 2003), a positive relationship has been

observed between the stem length and the generation of stemflow, presumably taller plants having the potential to produce greater stemflow because of a greater projected stem surface area.

3.4.1.3 Rainfall canopy interception

Using stemflow equations developed during 2005, daily stemflow and interception losses were estimated for 2004. As a consequence of a higher LAI in AFS in 2004 compared to 2005, there were differences in throughfall and estimated interception losses between years. Thus, these data support the general hypothesis that vegetation with higher LAI intercept higher rainfall, since LAI played a major role in the interception loss via a direct increase storage capacity of the canopy, surface of evaporation and consequent evaporation flux. Cumulated throughfall, stemflow and interception represented 76.8%, 11.8% and 11.4% for AFS and 83.2%, 7.2% and 9.6% for MC during 2005 (Table 2). During 2004, they were estimated at 72.8%, 11.7% and 15.5% for AFS and 85.1%, 6.0% and 8.9% for MC. Thus, the derived values of cumulative canopy interception loss for both systems in 2004 and 2005 were similar to values found in the literature for other vegetation types ranging from 7% to 30% (Marin et al. 2000; Price and Carlyle-Moses 2003).

Table 2. Total rainfall, throughfall, stemflow and canopy interception during the monitoring periods (June to September 2004 and July to November 2005) in two different coffee agricultural systems (AFS and MC) in the Central Valley of Costa Rica.

System	Total rainfall	Throughfall		Stemflow		Interception	
	(mm)	(mm)	(%)	(mm)	(%)	(mm)	(%)
June-Sept. 2004							
AFS	1426	1038	72.8	167*	11.7	221	15.5
MC	1426	1214	85.1	84*	6.0	126	8.9
July-Nov 2005							
AFS	1725	1324	76.8	204	11.8	196	11.4
MC	1725	1434	83.2	124	7.2	167	9.6

* During 2004, only throughfall was monitored and values of stemflow were estimated using equations developed during 2005 in Table 1.

AFS presented a large difference in canopy interception loss between 2004 and 2005, due probably to differences in LAI. During 2005, AFS presented a difference of only 0.4 m^2 m^{-2} in total LAI in comparison to MC. On the other hand, in 2004 with a higher difference in LAI, MC presented a 15% higher throughfall in comparison to AFS; this high difference in throughfall was the mirror image of the higher total interception loss in AFS, even with a higher stemflow. In addition, AFS not only presented differences in LAI, but also in plantation structure (2 canopy layers) which influenced the way water reached the soil surface. In AFS, throughfall was lower than in MC for all rainfall categories, compensated partly by a larger stemflow. Therefore, under similar LAI (for instance during 2005), trees influenced the water fluxes, but with a small impact on total interception. When LAI was higher, not only the water fluxes were influenced but also the total interception.

3.4.2 Transpiration

On a leaf area basis, coffee transpiration was higher during the dry season than in the wet season in both systems. The higher coffee transpiration can be attributed to the larger evaporative demand in the dry season. Furthermore, coffee transpiration was larger in MC than in AFS, irrespective of the season (Figure 16). Under hot and sub-optimal conditions of Southern Costa Rica, higher coffee transpiration has already been reported in MC than in AFS (Kanten and Vaast 2006). In the present optimal site, higher coffee transpiration on a ground area basis in MC than in AFS was due to the combination of higher leaf transpiration in MC compared to AFS with similar LAI in both systems (data shown above).

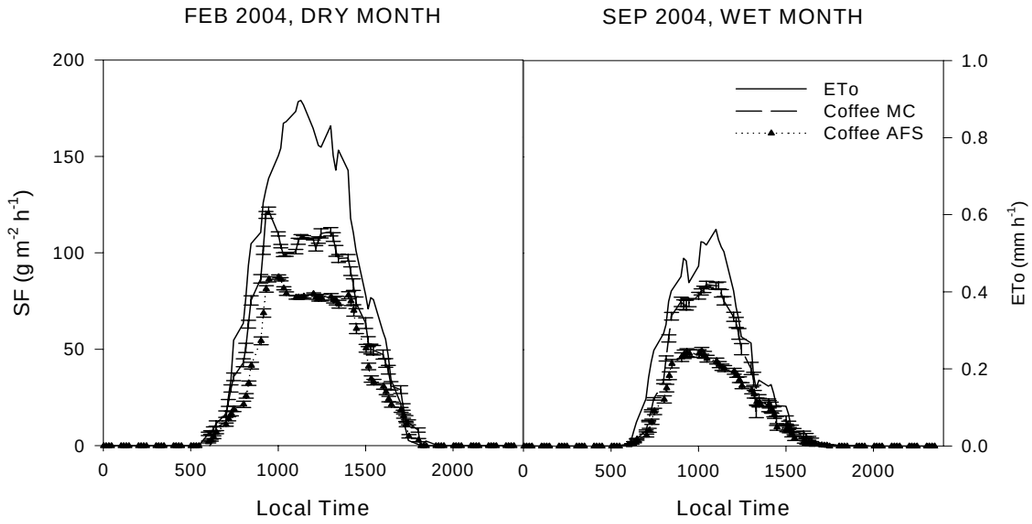


Figure 16. Mean hourly coffee sap flow rate (SF), reference evapotranspiration (ETo; measured in open field) and photosynthetic photon flux density (PPFD) based on ten consecutive days and four coffee plants in AFS or in MC for a dry month (February) and wet month (September) in San Pedro de Barva, Costa Rica (values ± se are means over four plants during monitoring ten days).

Even though coffee without shade presented a higher transpiration rate compared to coffee under shade on a leaf area (and hence on ground area basis), the stomatal conductance of coffee under AFS presented higher values when compared to MC in the wet season, and to a lower extent during the dry season (Figure 17).

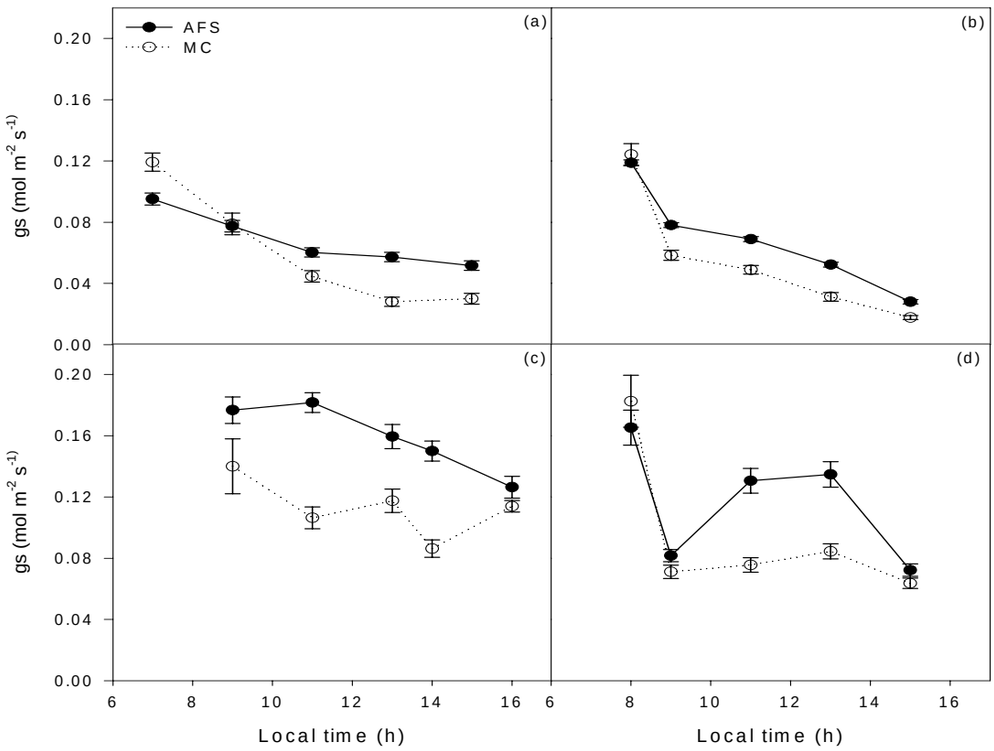


Figure 17. Diurnal time course of stomatal conductance of coffee leaves during the dry (a: February; b: March 2005) and wet season (c: August; d: September) in MC and AFS at San Pedro de Barva, Costa Rica. (Values are averages of 4 leaves in 4 plants).

The higher transpiration rate of coffee without shade compared to coffee under shade can be explained by a larger evaporative demand of coffee in MC than in AFS. In AFS, coffee plants received less radiation due to the fact that *Inga* trees intercepted 50% to 60% of the global radiation (as estimated by hemispherical photographs) in the dry season and wet season, respectively. Furthermore, leaf temperature at midday was 3 to 6 ^{o}C higher in MC than in AFS. Additionally, values of VPD, PPFD, and temperature at the leaf level recorded during the gas exchange measurements (using a CO_2/H_2O infrared gas analyzer; LCPro, ADC BioScientific Ltd., Hoddesdon, UK) were higher in MC that in AFS (Figure 18).

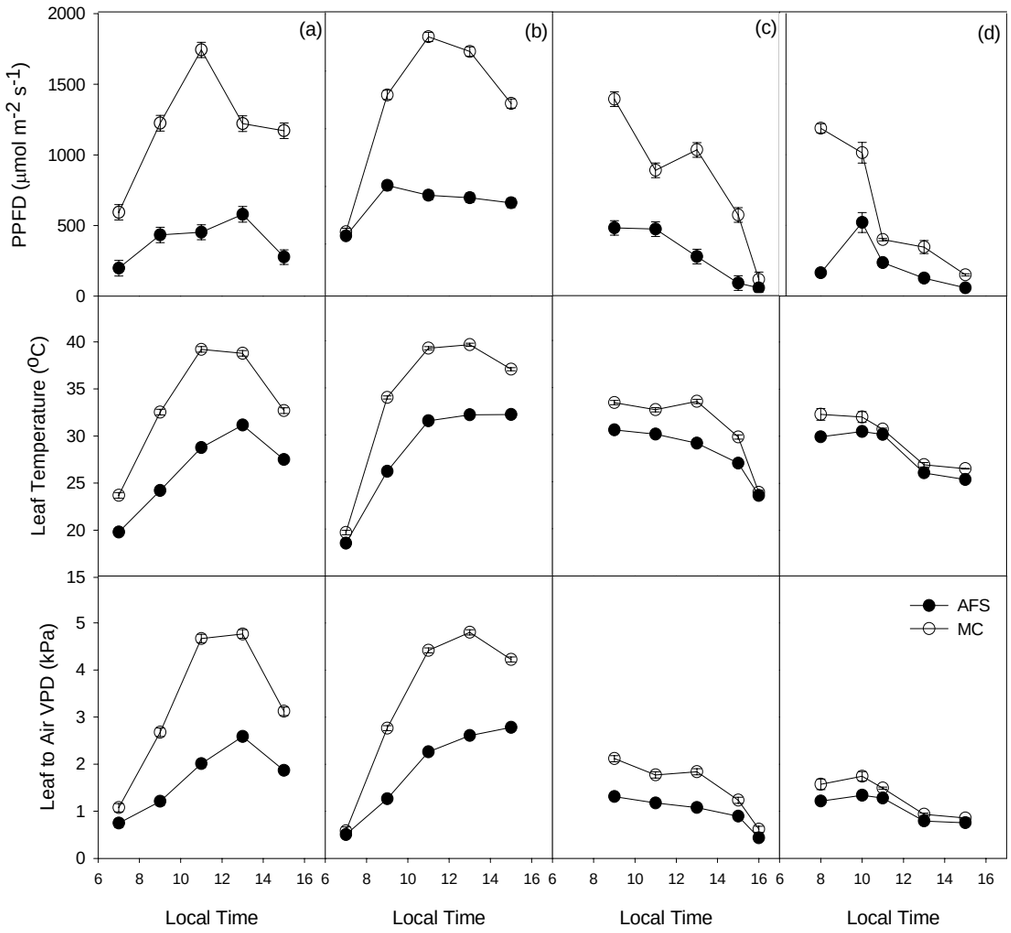


Figure 18. The diurnal time course of PPFD, leaf temperature and leaf to air VPD of coffee leaves during the dry season (a: February; b: March 2005) and the wet season (c: August; d: September 2005) in MC and AFS at San Pedro de Barva, Costa Rica. (Values are averages of 4 leaves in 4 plants measured over a period of 1 hour).

Daily values showed that coffee transpiration was controlled by ETo, but tended to reach a plateau at values around 4 mm d^{-1} (Figure 19). Moreover, the ratio T/ETo decreased significantly above an ETo threshold of about 2 mm d^{-1}. This response may be attributed to a decrease in stomatal conductance with an increase in VPD as documented in many tropical forest species (Oren et al. 1996; Phillips et al. 1999).

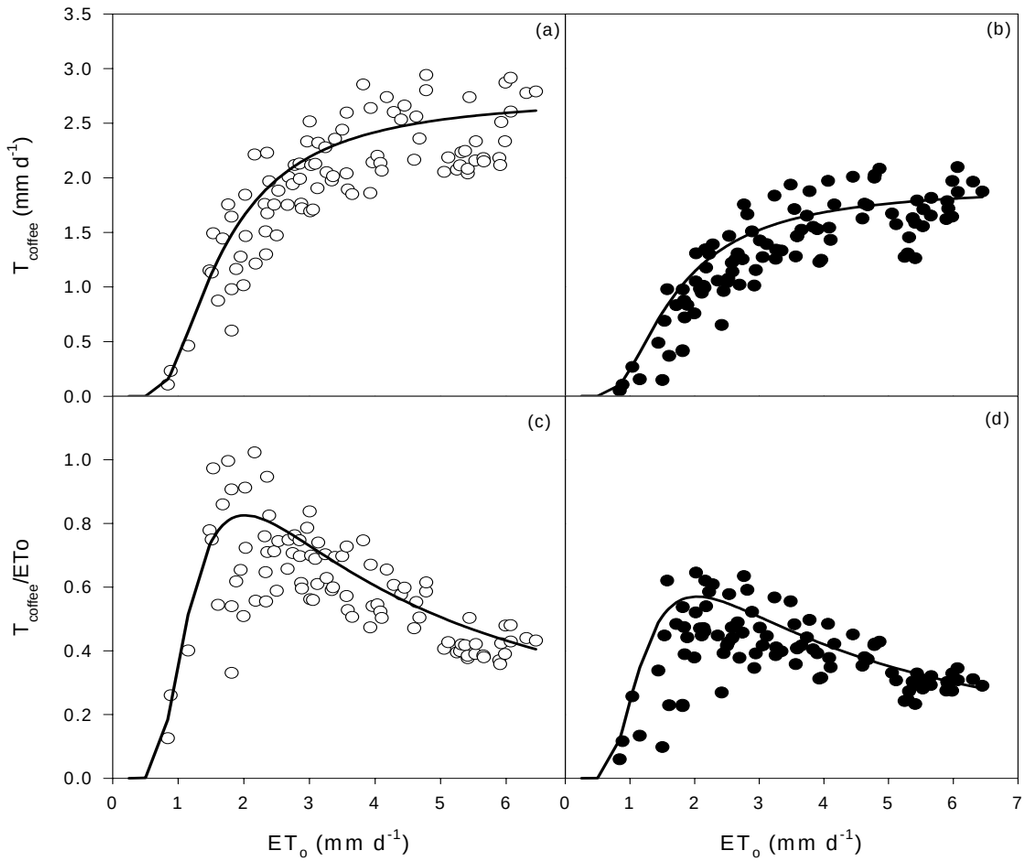


Figure 19. Relationships between daily coffee transpiration (a&b) and coffee transpiration over ETo (c&d) versus daily ETo (FAO, 1998) in MC (left panels) and in AFS (right panels) at San Pedro de Barva, Costa Rica. (Daily transpiration values are extrapolations to ha from four coffee plants).

Stomatal conductance showed a tight relationship with leaf VPD, but a less clear one with PPFD, irrespective of the season and whether plants grew in AFS or MC (Figure 20). Previous studies have demonstrated that high values of air VPD and air temperature (Fanjul et al. 1985; Gutierrez et al. 1994; Hernandez et al. 1989; Kumar 1979; Kumar and Tieszen 1980b; Wormer 1965) and more recently also leaf to air VPD and leaf temperature (Gutierrez et al., 1994) induce stomatal closure in coffee plants like in many other species and hence affect transpiration. A study in Hawaii showed that stomatal conductance in coffee was high in the morning and declined along the day with increasing VPD and solar radiation (Gutierrez et al. 1994). In the present study, stomatal conductance presented a clear reduction for air VPD values above the range of 1.5 to 2.0 kPa, even during the wet season and high soil moisture (at field capacity).

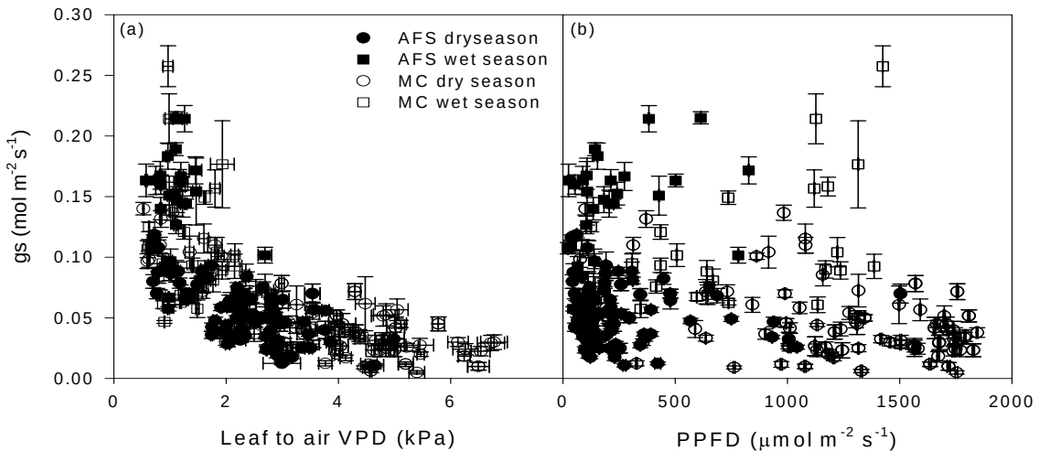


Figure 20. Response of coffee stomatal conductance to leaf-to-air VPD (a) and PPFD (b) in a MC and an AFS at San Pedro de Barva, Costa Rica. (Values represent average of 4 leaves per plant).

The interactive effect of soil moisture and VPD on stomatal conductance has been little studied in coffee. However, it seems that a high evaporative demand (i.e., as with a large VPD) reduces leaf stomatal conductance even when soil moisture is not limiting (Fanjul et al. 1985; Hernandez et al. 1989; Kanechi et al. 1995). Nonetheless, the season of low soil water content (the dry season) generally presents the highest values of VPD and ETo (Kanten and Vaast 2006), which makes it difficult to separate the effects of these factors on stomatal conductance and hence transpiration in field studies.

In the present study, soil moisture seemed to play a strong influence on the ratio of coffee transpiration over ETo (R: T/ETo) in MC and AFS. The ratio T/ETo increased linearly with increasing soil moisture (Figure 21).

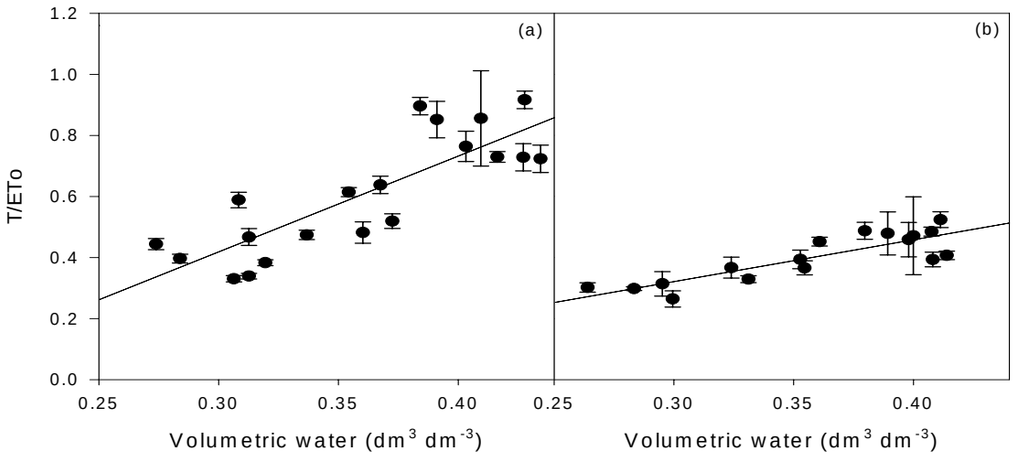


Figure 21. Relationships between R (ratio of coffee transpiration over ETo) and soil volumetric water content (VW) in MC (a) and in AFS (b) at San Pedro de Barva, Costa Rica. (Values represent daily averages for one to two weeks of measurements. MC: r^2=0.70, R=3.13*VW-0.52; AFS: r^2=0.73, R=1.36*VW-0.09).

The ratio T/ETo and LAI showed also a linear relationship in both systems; thus high R values during the wet season can be attributed to higher LAI values in the wet season compared to the dry season (Figure 22). The relationship between coffee transpiration and LAI has been already

highlighted for coffee (Gutierrez and Meinzer 1994) as they showed that coffee transpiration increased from 40% up to 95% of ETo when coffee LAI increased from 1.4 to 6.7 m^2 m^{-2}. On other hand, this is a quite common response for many types of canopies; for example, a strong relationship between canopy conductance (and hence transpiration) and LAI has been showed in 20 different tree stands in temperate and tropical regions (Granier et al. 2000).

Thus, the independent effect of soil moisture on coffee transpiration in this site conditions cannot be separated from the effect of the microclimatic variables (as VPD and ETo) and LAI, since during the dry season coffee presented the low values of LAI and higher values of ETo and VPD. Leaf area index of others species decrease after water stress, due to shedding of older leaves and low development of young ones; this illustrates that the loss of leaves is a frequent response to water stress due to soil or microclimate variables. In some temperate deciduous forests, the dominant factor controlling seasonal canopy conductance and stand transpiration is the degree of defoliation; nonetheless, soil moisture strongly affects water use by forests as it exacerbates canopy defoliation (Oren and Pataki 2001). However, the soil water deficit reduces the stomatal conductance, due that the abscicic acid produced in the roots contributes to the stomatal on many species (Tardieu and Simonneau 1998). But for coffee, stomatal conductance declines sharply with increasing evaporative demand irrespective of the soil water status, which show that the most limiting factor on transpiration is the microclimatic conditions (DaMatta 2004b).

It seems however that in this specific site due to the depth of the soil and the deep rooting of coffee (200 cm data presented in chapter 1), the soil moisture is not a limiting factor on transpiration and the microclimatic variables such as VPD, temperature, radiation and ETo influence more directly the coffee transpiration via a reduction in stomatal conductance. On other hand, during the dry season the LAI reduce sharply due to leaf shedding reducing the ratio T/ETo of the coffee crop.

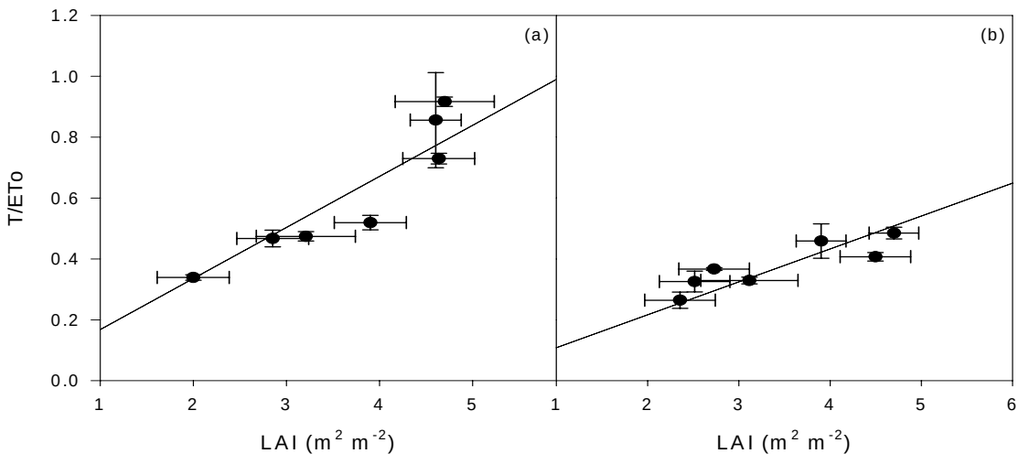


Figure 22. Relationships between R (ratio of coffee transpiration over ETo) and LAI in MC (a) and in AFS (b) at San Pedro de Barva, Costa Rica. (Values represent daily averages for one to two weeks of measurements. MC: r^2=0.98, R=0.17*LAI; AFS: r^2=0.98, R=0.11*LAI).

The present results on coffee the ratio T/ETo estimated every 15 minutes at 3 different LAI values showed that for larger LAI values, the values of the ratio T/ETo (on a ground area basis)

were larger when plotted against ETo. Larger LAI were mostly observed during the wet season with soil volumetric water near the field capacity whereas low LAI predominated in the dry season. However, when the ratio sap flow (SF)/ETo estimated on a leaf area basis was plotted against ETo, the response of the ratio SF/ETo was similar for all LAI ranges and hence soil water moisture (Figure 23). For the 3 LAI values, the response of the ratio SF/ETo to ETo showed that the ratio SF/ETo reached a maximum value at low ETo, and then decreased at values higher than 0.4 mm h^{-1}, independently of the soil water status.

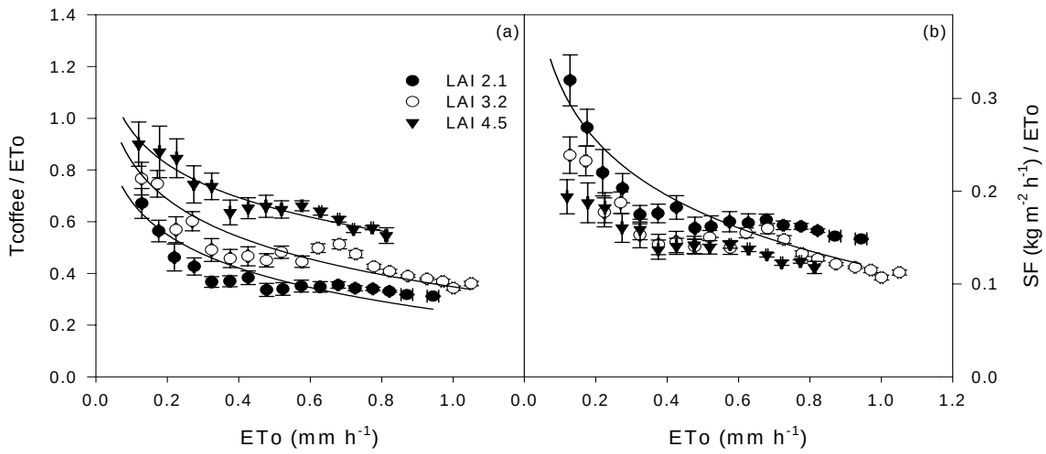


Figure 23. Relationships between hourly reference evapo-transpiration (ETo) and the ratio of coffee transpiration over ETo on a ground area basis (a) and on a leaf area basis (b) in MC at three coffee LAI values at San Pedro de Barva, Costa Rica. (LAI Value of 4.5 m^2 m^{-2} coincides with the peak of the wet season and hence highest soil volumetric water content, while other LAI values coincide with 2 dry seasons; values represent means of one week long measurements).

To further investigate this aspect, continuous monitoring of sap flow was undertaken on two coffee plants in MC for a period of one week when the soil was dry (0.31 dm^3 dm^{-3}) and with a low LAI of 3.2 m^2 m^{-2} and for eleven days after irrigation to increase soil water to field capacity (0.42 dm^3 dm^{-3}) in order to isolate the effects of soil water availability from that of LAI and microclimate (ETo, VPD). For low ETo values, high values of the ratio SF/ETo were observed for both set of soil conditions (wet and dry) without any significant differences (Figure 24). At ETo values above 0.40 mm h^{-1}, the ratio SF/ETo presented a higher reduction during the period with low soil water than during the period of high soil water. When the ratio SF/ETo was plotted against VPD, a similar pattern was observed for both soil conditions; i.e. a strong reduction in the ratio SF/ETo with increasing VPD.

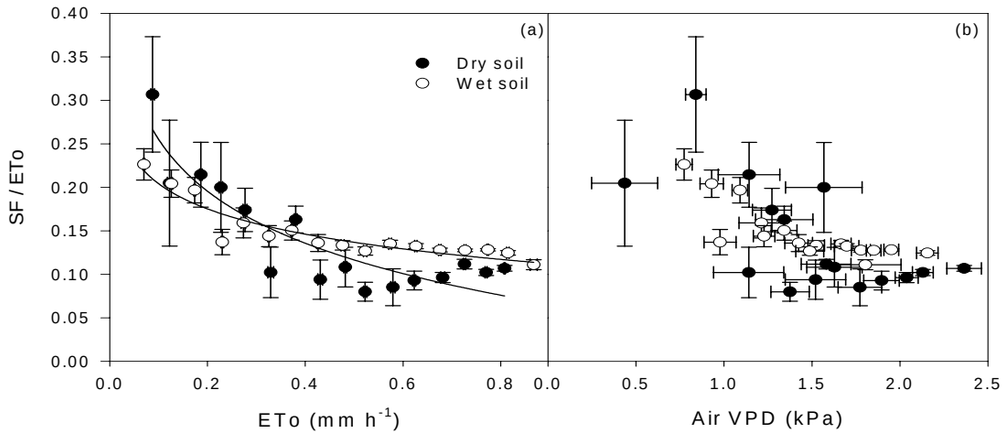


Figure 24. Relationships between the ratio SF/ETo on a leaf area basis in MC versus ETo (a) and versus VPD (b) in wet and dry soil conditions during the dry season of 2004 at San Pedro de Barva, Costa Rica. (Values are means of measurements over one week for dry soil conditions and over eleven days for wet soil conditions).

When mean coffee stomatal conductance (gs) was plotted as a function leaf to air VPD, PPFD and leaf temperature, it was clear that gs was declining with an increasing VPD, contrary to other variables where a higher variability was observed (Figure 25). Even though, there was an apparent reduction in stomatal conductance with an increase in PPFD or leaf temperature, these relationships could be due solely to the fact that there was an increment in VPD with the increments in PPFD and leaf temperature. As previously mentioned, many authors (Carr 2001; Fanjul et al. 1985; Gutierrez et al. 1994; Kanten and Vaast 2006) observed that there is a strong limitation in stomatal conductance in coffee plants at air VPD values higher than 1.5 kPa, even under well watered soil conditions.

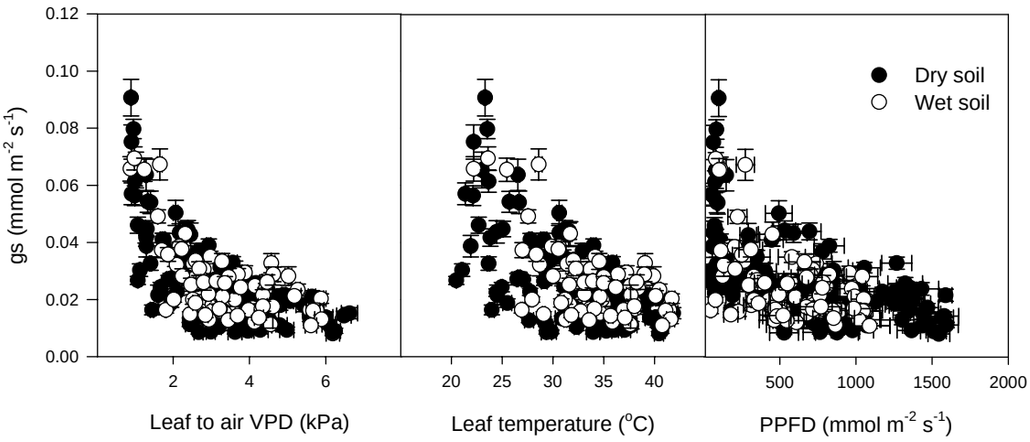


Figure 25. Relationships between coffee stomatal conductance (gs) and leaf to air VPD, PPFD and leaf temperature in wet and dry soil conditions during the dry season of 2004 at San Pedro de Barva, Costa Rica. (Values represent average of 12 leaves per plant).

For *Inga densiflora*, there was a decrease in sap flow rate with increasing sapwood depth; this has been shown for other species in temperate and tropical zones (Nadezhdina et al. 2002; Roupsard et al. 1999). In the present study, this was taken into account with sap flow measurements at different depths to get a better estimation of tree transpiration. The present results provide

insights on the processes controlling transpiration of *Inga densiflora*, with the highest T/ETo values observed during the wet season at low ETo values, but high soil moisture (Figure 26). Tree transpiration reached a maximal transpiration for daily values of ETo in the range of 3 to 4 mm d^{-1}; this is generally attributed to a stomatal closure. Indeed, several studies have shown that stomatal conductance in trees is sensitive to environmental variables such as VPD and PPFD (Jarvis 1976; Motzer et al. 2005). However, little information is available in the literature on transpiration of *Inga* species.

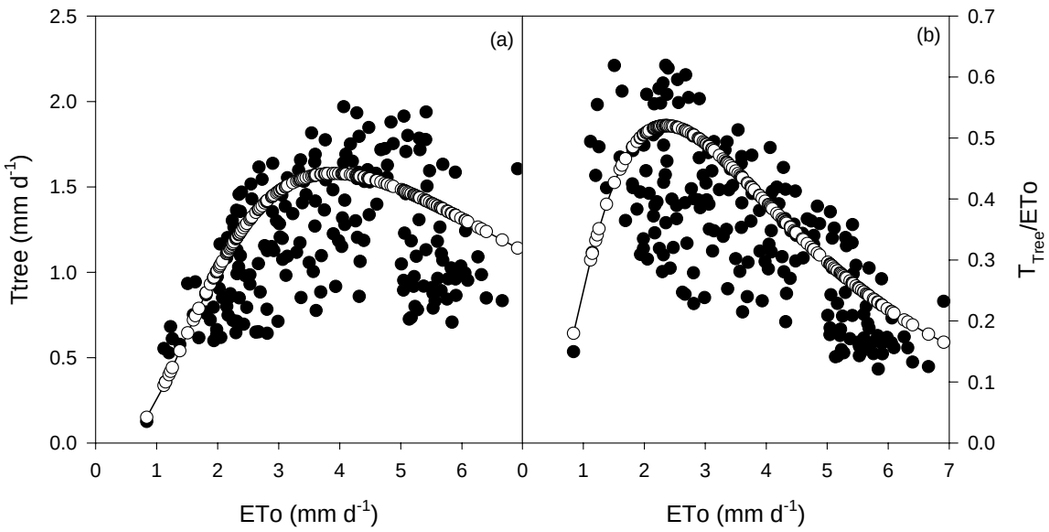


Figure 26. Relationships between reference evapo-transpiration (ETo) and (a) daily transpiration (Ec) and (b) T/ETo (ratio of *I. densiflora* transpiration over ETo) in an agroforestry system at San Pedro de Barva, Costa Rica.

The transpiration of *Inga densiflora* accounted for 40% - 50% of the total water use of AFS. Even though these values seem high with respect to the low density of trees (277 ha^{-1}) and a basal area of 6.7 to 8.5 m^2 ha^{-1}, they appeared consistent with the amount of solar radiation intercepted (46% to 60%). Over the monitoring period of 2 years, the combined transpiration of *Inga densiflora* and coffee in AFS was higher than that of coffee alone in MC (Table 3).

Table 3. Annual rainfall, reference evapo-transpiration (ETo) and estimated water use by coffee plants in MC and coffee plants and shade trees in AFS under optimal coffee cultivation conditions of San Pedro de Barva, Costa Rica for 2004 and 2005.

			Water use (mm yr^{-1})			
Year	Rainfall (mm yr^{-1})	ETo (mm yr^{-1})	Coffee in AFS	Tree	Total AFS	Coffee in MC
2004	3245	1310	544	464	1008	785
2005	2633	1178	437	468	905	678

3.4.3 Runoff

Runoff was dependent upon the rates of gross rainfall in both systems (MC and AFS) for the two years of measurements (Figure 27). In both systems, runoff was noticeable with rainfall above 5 mm and became important for rainfall above 20 mm. Runoff was larger in MC than in AFS at higher rainfall.

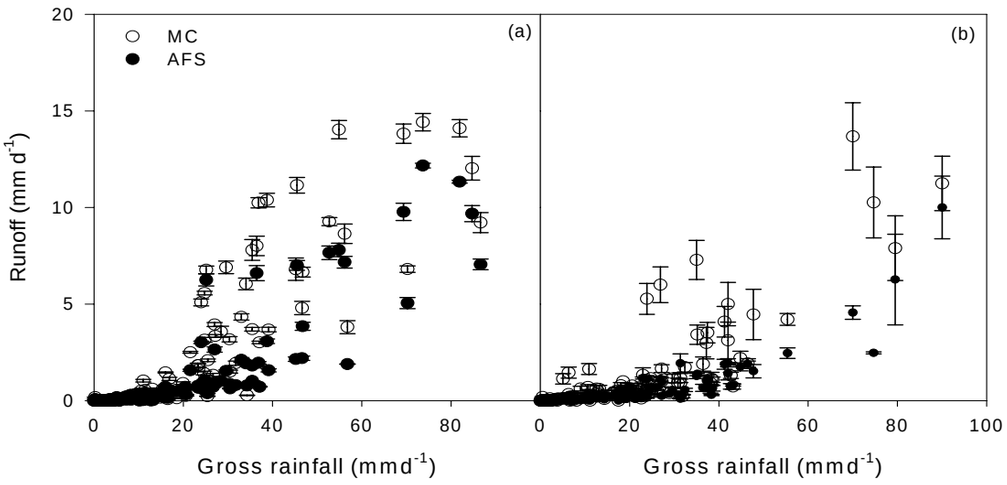


Figure 27. Relationships between gross rainfall and runoff during the wet season of 2004 (a) and 2005 (b) in MC and in AFS at San Pedro de Barva, Costa Rica. (Values are means of 3 repetitions per system). (for 2004, MC: r^2=0.75 RO=0.17+0.0021*GR^2; AFS: r^2=0.75 RO=0.12+0.0015*GR^2, for 2005, MC: r^2=0.75 RO=0.08+0.0016*GR^2; AFS: r^2=0.75 RO=0.001+0.00091*GR^2)

Runoff was higher in MC compared to AFS for both years and during all the monitoring periods (Figure 28). Furthermore, it was at its highest rates during the 2004 wet season due to higher rainfall intensities in September and October as Costa Rica was affected by the hurricane Ivan. Thus, during 2004 the rainfall accounted for 3245 mm and exceeded by 1000 mm the mean annual rainfall registered the previous years. Cumulative runoff were statistically different between both systems (P=0.07), and represented 9.7% and 5.6 % of the total annual rainfall in MC and AFS, respectively, during 2004 and 7.6 and 3.3% during 2005 in MC and AFS.

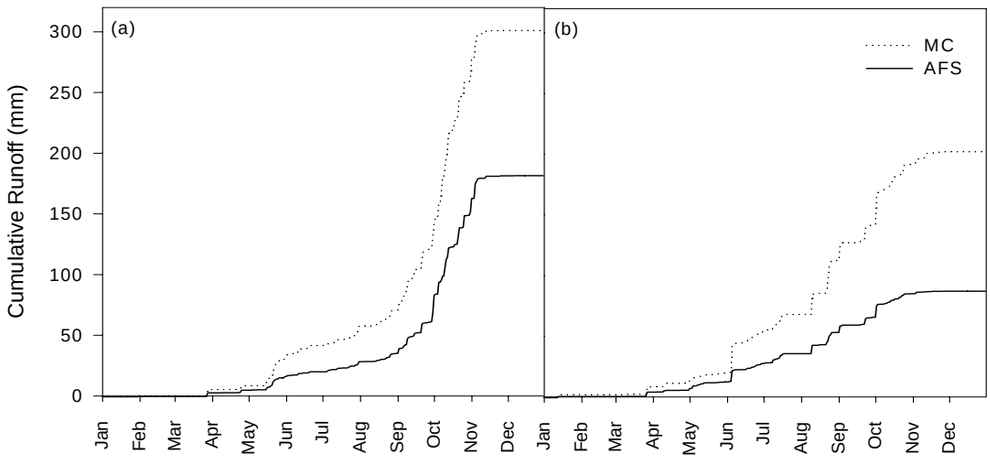


Figure 28. Cumulative runoff during 2004 (a) and 2005 (b) in MC and AFS at San Pedro de Barva, Costa Rica. (Values are means of 3 repetitions per system).

Higher values of runoff in MC compared to AFS are explained by a lower litter ground cover in MC (3.1 Mg DM ha^{-1}) than in AFS (5.0 Mg DM ha^{-1}) (Harmand et al 2007) and higher sealing soil surface in MC increasing rain splash and horizontal water flow as well as a higher bulk soil density limiting water infiltration, as showed in other AFS (Lal 1989a; Lal 1989b). Lower rainfall intercepted by the vegetation in MC, hence higher water on the soil surface could also have contributed to higher runoff in MC than in AFS.

3.4.3 Soil volumetric water

There were no significant differences in soil water content between systems during the monitoring period of over two years in the soil layers from 0 to 120 cm. However, AFS presented significantly ($p<0.05$) lower water content at deeper layers (120-200cm), especially during the dry season 2004 as a result of its higher water use (Figure 29). As showed above, AFS transpired more (30%) than MC, due to the presence of *Inga* trees. Nonetheless, this also suggested that shade trees used water from deeper horizons compared to MC, showing there was complementarity in the use of the resource water.

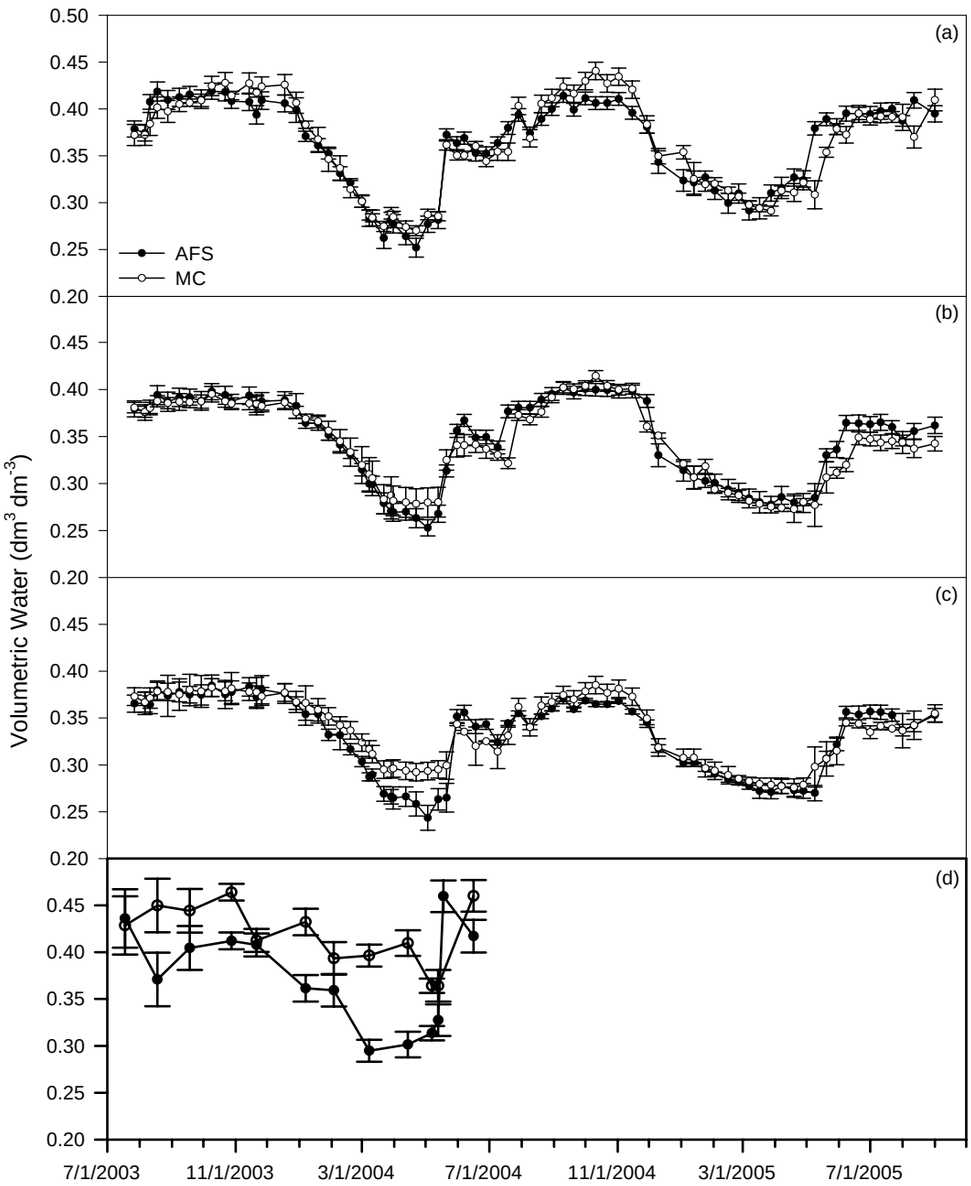


Figure 29. Time courses of volumetric soil water content at depths of (a) 0-60 cm, (b) 60-120 cm, (c) 120-150cm and 150-200cm (d) in coffee monoculture (MC) and coffee agroforestry system (AFS) in San Pedro de Barva, Costa Rica, measured from July 2003 to October 2005.

This water use originating from deeper horizons in AFS can be seen clearly in the relatively higher reduction of volumetric soil water content at depths exceeding 120 cm during the dry season in AFS than in MC (Figure 30a, b). On the contrary, there were no observed differences in water content in the surface horizons betwen MC and AFS. At the beginning of the rainy season, soil moisture remained low in the 120-200 cm layer, but was very high especially below 250 cm. This showed that soil water remained available in great amount below 200 cm depth during all the dry season.

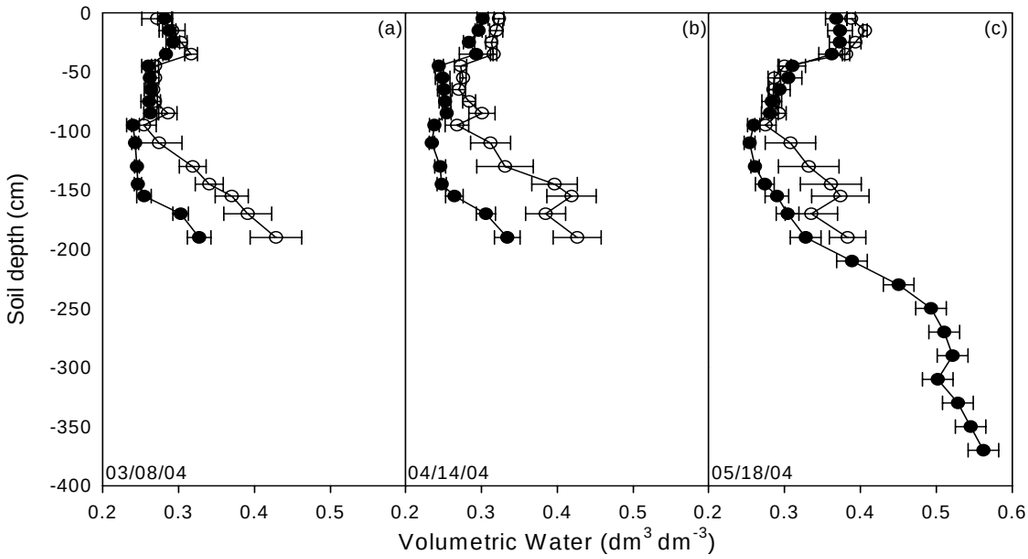


Figure 30. Mean soil moisture content at three dates at different soil depths in the MC and AFS at San Pedro de Barva, Costa Rica. (a, b: dry season 2004; c: beginning rainy season 2004).

Trenches dug to a depth of 200 cm exposed fine roots at this depth suggesting that roots could reach deeper layers and eventually get access to deep available water. Additionally, as already demonstrated for this type of soil in Nicaragua (Maraux and Lafolie 1998), capillary rise was likely to contribute to plant water uptake (until 2 mm day^{-1}) during the dry season.

3.5 Water balance at plot scale

The annual total transpiration was 28% and 33% higher in AFS than in MC for 2004 and 2005, respectively. The annual canopy interception loss in AFS was also higher during both years, but with a more important difference during 2004 than 2005. Runoff was higher for both years in MC compared to AFS (Table 4). As already reported for coffee and other agroforestry systems, trees affect all the components of the water balance (Beer et al. 1997; Kanten and Vaast 2006; Ong et al. 2000; Rao et al. 1997).

Table 4. Annual water balance in MC and AFS under optimal coffee cultivation conditions of San Pedro de Barva, Costa Rica for 2004 and 2005.

Year		Rainfall	PET	Transpiration			Runoff		Interception	
				MC	AFS		MC	AFS	MC	AFS
				Coffee	Coffee	Tree				
2004	(mm)	3245	1310	785	544	464	302	182	233.3	426.6
	(%)	100	40.4	24.2	16.8	14.3	9.3	5.6	7.2	13.1
2005	(mm)	2685	1178	678	437	468	203	88	241	273
	(%)	100.0	43.9	25.3	16.3	17.4	7.6	3.3	9.0	10.2

In summary, trees in AFS reduced water runoff, but increased rainfall interception and total vegetation transpiration. As a consequence, the annual total sum of interception plus runoff and transpiration in AFS was 50% and 47% of the rainfall for 2004 and 2005, respectively, while it accounted for 41% and 42 % in MC during 2004 and 2005.

Table 5. Water balance during the dry and rainy seasons for 2004 and 2005 at a depth of 200 cm in MC and AFS in San Pedro de Barva, Costa Rica.

Year	System	Period	Rainfall (mm)	Runoff (mm)	Interception (mm)	Transpiration (mm)	∆ S (mm)	Balance (mm)
2004	MC	Dry season	99	5	14	243	-110	-53
2004	AFS	Dry season	99	3	22	303	-161	-67
2004	MC	Rainy season	3132	297	216	478	83	2060
2004	AFS	Rainy season	3132	179	400	618	168	1768
2005	MC	Dry season	192	11	21	290	-69	-62
2005	AFS	Dry season	192	6	26	407	-54	-193
2005	MC	Rainy season	2495	191	222	402	88	1592
2005	AFS	Rainy season	2495	82	248	519	73	1573

Water balance established during the dry season between 07/01/04 and 14/04/04 showed higher actual evapotranspiration (AET) and a greater reduction in soil water content in AFS than in MC (Table 5). Furthermore, a water balance deficit (higher in AFS than in MC) could have been compensated by plant water uptake in deeper layers than the 200 cm depth or by capillary rise as already suggested. Compared to MC, this higher water requirement of AFS in the dry season was compensated by water uptake in the deeper soil layers associated with a reduction of evaporative demand and coffee transpiration under shade.

Water balance established during the rainy season between the 14/04/04 and the 10/12/04 showed a higher drainage in MC (2060mm) than AFS (1768mm). This was due to the combined effect of lower AET (Interception and Transpiration) during the rainy season and a lower amount of rainfall required at the beginning of the rainy season in order for the soil water content to reach field capacity in MC.

During the rainy season of 2005 (28/04/05 to 15/12/04), the two systems presented similar LAI associated with rather similar interception of rainfall. Therefore, differences in soil water between

systems were only due to higher transpiration in AFS. The excess of water reaching the soil in MC was associated with a higher runoff than in AFS, which resulted in rather similar water drainages in both systems.

3.6 Competition for water

In many agroforestry systems, competition for water appears to be an important interaction between associated trees and crops, resulting in yield reduction of the main crop (Govindarajan et al. 1996; McIntyre et al. 1997; Rao et al. 1997). However competition for water is more likely in the semi-arid tropics (annual rainfall of 600 to 700 mm and a long dry season) or shallow soils (with a rooting depth < 60 cm). In the present study, the annual rainfall largely exceeded the Penman-Monteith reference evapo-transpiration (ETo) and the actual vegetation transpiration in both systems (Table 3). Even though the dry season lasts 5 months (mid-December to mid-April), rainfall were frequent and represented 29% (183mm) and 35% (196mm) of ETo during the dry seasons of 2004 and 2005, respectively. Thus, rainfall represented 32% and 47% of AFS transpiration during the dry seasons of 2004 and 2005, respectively, while it accounted for 40 % and 66% of the transpiration in MC for the same periods. The rooting depth for both systems was at least until 200 cm, which represented rather high available water soil storage (323 mm in MC and 310 mm in AFS).

Furthermore, coffee fruit development took place during the wet season when the soil was maintained at field capacity by high and frequent rainfalls. In his review on coffee water requirements, Carr (2001) emphasized that water supply is not likely to be a limiting factor in regions where rainfall coincides with fruit development. On the contrary, if fruit development experiences a short dry season as in equatorial regions with bi-modal rainfall patterns fruit size and quality could be negatively affected by water limitation. In the present conditions, the reduction in coffee yield in AFS is not likely due to water competition, because the period of rapid fruit expansion coincided with the rainy season which represented 90% of the annual rainfall with no soil water limitation.

4 CONCLUSIONS AND PERSPECTIVES

From the data gathered over a period of more than 2 years, it appears that the effects of *Inga densiflora* on: a) the microclimate of coffee plants; b) coffee yield and biomass; and c) water balance at plot scale, can be summarized as follows.

4.1 Influence of trees on the microclimate experienced by coffee plants

The major effects of shade trees on the microclimate experienced by coffee plants can be summarized as a reduction in the transmitted light and air and leaf coffee temperature extremes. The transmittance of light in AFS ranged between 40 to 55 % of the global radiation (as estimated by hemispherical photographs) and 45% to 30% of PPFD. The leaf temperature in AFS was reduced by 1 to 6^{o}C compared to leaf temperature in MC. These variables affected the physiological behavior of coffee and hence bean yield. Temperature extremes seemed to be a more important factor than light, under these field conditions, since it can affect photosynthesis via a reduction of stomatal conductance or non-stomatal factors. It can be hypothesized that the effect of trees on coffee leaf temperature is likely to be more important in lowlands where coffee is cultivated under suboptimal conditions with temperatures values higher than 26^{o}C (below 800m of altitude).

4.2 Influence of trees on coffee yield and biomass

The present results showed that coffee production was quite similar in both systems with a mean decrease of 10% in yield for AFS compared to MC over 6 production cycles. Indeed, yield was not statistically different between AFS and MC during the period from 1999 to 2003 when tree pruning was heavy. On the contrary, shade tree significantly reduced coffee yield by 29% in AFS compared to MC during the period from 2003 to 2005 when tree pruning was lighter; the strongest reduction of 38% was observed during 2004. Clearly, it can be concluded that in these optimal conditions with no water or nutrient limitations, the shade tree development of later years combined with a lighter pruning regime led to a noticeable decrease in coffee yield due a lower light transmittance (40-55%). On the other hand, total shoot biomass production was significantly larger in AFS and amounted to 3 times that produced in MC, which can be a source of household energy and revenue diversification, especially in period of low coffee prices. Thus, there seems to be no reason to consider *Inga*-shaded plantations less productive than MC in optimal conditions, especially considering the fact that coffee AFS results in coffee of high quality and provides environmental benefits such as C sequestration, conservation of soil fertility and water quality.

4.3 Influence of trees on water balance

4.3.1 Canopy Rainfall Interception

Associated trees influenced rainfall loss through canopy interception via an increase in the total LAI, and hence enhanced canopy storage capacity and surface of evaporation. During 2004 when the total LAI (tree + coffee) was higher in AFS than in MC, the canopy interception loss was also higher. During 2005 when the total LAI was similar in both systems, only small differences were detected between these systems. Even though trees had a small impact on total interception, they affected the partitioning of gross rainfall, reducing throughfall and increasing stemflow. Differences in coffee stemflow between AFS and MC were due to a modification of the architecture of coffee plants, with larger stems and branches in coffee under shade. Shade trees (*I. densiflora*) had a small influence on the total interception loss in AFS.

4.3.2 Transpiration

The present results on transpiration allow us to have a better idea of this important process in coffee in MC and AFS. However, the present observations are restricted to optimal conditions for coffee cultivation; i.e. an altitude of 1200 m, a fertile and deep volcanic soil with a high fertilization regime, and an intermediate dry season that allows coffee plants to have one main flowering period and a rather concentrated harvesting season.

Still, the following conclusions can be drawn:

- The water use of coffee plants in MC was higher than in AFS on leaf area and ground area bases. This was due to higher evaporative demand in MC compared to AFS. On the other hand, coffee plants in AFS presented higher stomatal conductance than in MC as previously documented. Nonetheless, the present study has the advantage of combining measurements of stomatal conductance and sap flow measurements for both coffee and associated plants. Therefore, this study shows that even though shade trees provide better microclimatic conditions (decreased leaf to air VPD and reduced leaf temperature) for coffee plants which allowed to maintain higher rates of stomatal conductance, these coffee plants still transpired less than plants in full sun due to the buffered microclimate and lower evaporative demand compared to MC.
- High VPD and ETo reduced stomatal conductance and therefore coffee transpiration rate could not keep up with respect to the evaporative demand in both systems. Coffee stomatal conductance decreased above leaf VPD values of 2.0 kPa. PPFD did not appear to have a straightforward influence on stomatal conductance reduction. Still, ETo values above 0.4 mm h^{-1} seemed to reduce the hourly coffee T/ETo ratio independently of the soil water content.
- Soil water content did not seem to be a limiting factor of coffee and tree transpiration after 2 years of monitoring. During the wet season, the ratio T/ETo of coffee was higher than in the dry season. However, 3 factors had a strong influence on coffee transpiration: ETo, soil water and LAI. The wet season with the highest values of T/ETo generally presented lowest values of ETo, and highest values of soil water and LAI, which makes it difficult to separate the effect of each factor on transpiration. Nevertheless, it was clear

that VPD and ETo reduced coffee stomatal conductance, independently of the soil water content and LAI. Thus, the reduction in transpiration due to low values of soil water is analyzed as being mostly the result of a reduction in LAI, and hence in these site conditions soil water influence on stomatal conductance seems to be secondary whenever high values of VPD and ETo are present.

- The estimated annual transpiration of AFS was 29% and 33% higher than coffee MC in 2004 and 2005, respectively. Nevertheless, the AFS water use was no more than 32 % and 33% of the total rainfall in 2004 and 2005, respectively.

4.3.3 Runoff

The present data support the idea of lower runoff and hence soil erosion in AFS in comparison to MC, as found in other AFS studies. These data allow us to propose the following explanations for lower runoff in AFS than in MC:

- Trees reduce runoff by increasing rainfall interception. Still, rates of rainfall interception presented little differences in both systems in 2005. Nonetheless, trees affected the way by which water reached the soil surface, through an increase in stemflow and a reduction in throughfall. This is of major importance as it reduces the direct impact of rain drops to the soil surface.
- Trees reduce runoff by increasing soil litter. The soil litter has a protective effect on the soil, reducing the direct impact of rain drops and increasing infiltration via an enhanced soil surface roughness.
- Consequently, it is quite certain that the reduced runoff in AFS is the result of the combined effects of reduction in throughfall and of enhanced soil litter.

4.4 Water use and tree-crops interactions

This study suggests that shade trees in coffee AFS affect all components of the water balance. As observed in other studies, the transpiration and rainfall interception were higher in AFS compared to MC; this resulted during 2004 (longer dry season compared to 2005) in lower soil water content in AFS, especially in deeper layers. Tree and coffee plants showed complementarity for water use as trees certainly took up water from deep layers that were not accessible by the shallower coffee root system. Furthermore, a facilitative interaction for water use occurred as shade trees improved the coffee transpiration efficiency as demonstrated by the higher values of stomatal conductance and similar values of net photosynthesis of coffee leaves in AFS compared to MC. On the other hand, during the rainy season there was ample water availability due to a large annual rainfall (> 3000 mm). For this reason, under the site conditions of the central valley in Costa Rica characterized by high rainfall (>2500 mm) and deep, fertile soils, competition for water between coffee and associate trees was not observed and competition for nutrients was unlikely due to the high fertilization regime. Thus as mentioned above, the lower coffee yield in AFS in comparison to MC, can be attributed to reduction in light available for coffee that affects coffee flowering and not competition between coffee and associated shade trees for water or nutrients.

4.5 Perspectives

- The present data present the possibilities to model water balance at plot scale in both systems (MC and AFS) and compare the output of the model with the measurements made during this study.

- Research should be continued for exploring the influence of shade trees on the productivity and water balance in coffee plantations, taking into account different soil types, tree species and various ecological conditions to better understand water partitioning between trees and coffee plants.

- To develop a decision making tool in term of species selection and management according local ecological conditions, farmers' strategies and market opportunities.

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SECOND PART

Article 1

Microclimate and productivity in a coffee agroforestry system with *Inga densiflora* in optimal conditions in Costa Rica

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Keywords: Coffee yield, fuelwood; light interception, leaf temperature; Shade trees

Microclimate and productivity in a coffee agroforestry system with *Inga densiflora* in optimal conditions in Costa Rica

Abstract

The influence of shade trees on coffee productivity depends on many interacting factors such as soil and climatic conditions, coffee and tree species, fertilization regime, shade management, and pest and disease management. The advantages of associating shade trees in coffee agroforestry systems (AFS) are commonly thought to be mostly restricted to poor soil and sub-optimal ecological conditions. Thus, the objective of this study was to investigate under optimal coffee cultivation conditions the impact of *Inga densiflora*, a very common shade tree in Central America, on the microclimate, yield and vegetative development of shaded coffee in comparison to coffee monoculture (MC).

Maximum temperature of shaded coffee leaves was reduced by up to 5^{o}C relative to coffee leaf temperature in MC. The minimum leaf temperature at night was 0.5^{o}C higher in AFS than air temperature demonstrating the buffering effects of shade trees. Water use in AFS was higher than in MC as judged by the monitoring of water availability in the soil depths colonized by roots, but competition for water or nutrients between coffee and associated trees was negligible due to the high rainfall and ample fertilization regimes. Coffee production was quite similar in both systems during the establishment of shade trees, however a yield decrease of 29% was observed in AFS compared to MC with a decrease in radiation transmittance of 40% to 50% during the latter years and in the absence of an adequate pruning. Aerial biomass production was significantly higher in AFS and amounted to 3 times the biomass produced in MC, which can be a source of household energy and farmers' revenue diversification. Thus, there seems to be no reason to consider *Inga*-shaded plantations less productive than MC in optimal conditions, especially considering the fact that coffee AFS result in high quality coffee and provide environmental benefits such as C sequestration, conservation of soil fertility and water quality.

Introduction

The coffee plant present features of a shade plant, with a low light compensation point and photo-inhibition at high solar radiations (Rena et al., 1994, Kumar y Tieszen, 1980, Franck, 2005). However, coffee is cultivated under different climate conditions and agricultural practices. Coffee growing under agroforestry systems may be advantageous with respect to coffee growing in monoculture for the following aspects: 1) by modifying the microenvironment, shade trees reduce coffee stress and flowering intensity, and hence overbearing and dieback of coffee plants; and 2) trees also enhance soil fertility by nitrogen fixation, soil organic matter accumulation and improved nutrient cycling (Beer, 1987; Willson, 1985; Barradas y Fanjul, 1986, Vaast et al., 2002). On the other hand, shade trees may compete with coffee for resources such as light, water and soil nutrients (Beer, 1987; Willey, 1975). For these reasons, trees can reduce coffee yield in optimal growing conditions, especially when tree density is high (Muschler, 1999; Tavares et al, 1999; Viera et al, 1999).

The influence of shade trees on coffee depends on the soil and climatic conditions, but also on the coffee species used and the agricultural practices such as fertilization regime, and pest and disease control. It is claimed and mainly demonstrated that advantages of associated shade trees in coffee production are mostly important in poor soils and under sub-optimal ecological conditions (Muschler, 1998 & 1999). Thus, the objective of this study was to investigate in optimal coffee cultivation conditions the impact of *Inga densiflora*, a shade tree predominant in coffee areas of Central America, on the microclimate, yield and growth of coffee as well as the growth of the shade tree itself.

Materials and methods

Site description and experimental design

The study was conducted on the experimental farm of the research station of the Coffee Institute of Costa Rica (ICAFE), located in San Pedro de Barva in the Central Valley of Costa Rica (10°02’16’’ N, 84°08’17’’ O) at an altitude of 1200 m. The climate is relatively cool with a mean annual temperature of 21°C, a mean annual precipitation of 2300 mm and with a pronounced dry season from January to April.

The experimental design included two adjacent coffee plots: a shaded one or agroforestry system (AFS) with an area of 1500 m^2 and a second one without shade trees or monoculture (MC) with an area of 1200m^2. In both plots, coffee was planted in 1997, following a coffee monoculture, with a spacing of 2 m between rows and 1 m within a row, which resulted in densities of 5000 and 4773 coffee plants ha^{-1} for MC and AFS, respectively, and with an average of 3 coffee stems per planting hole. In AFS, *Inga densiflora* (Benth) was planted within the coffee rows at a spacing of 6 x 6 m (277 trees ha^{-1}). The plots were equally intensively managed with a fertilization regime composed of 250 N; 15 P_2O_5; 110 K_2O; 70 MgO; 5 B_2O_3; 50 S and 60 CaO kg ha^{-1} yr^{-1}, following the recommendations of ICAFE (1998).

The site had between 2% to 8% slope from north to south. The soil is derived from the weathering of volcanic ashes, belongs to the Andosols (IUSS-WRB, 2006), and is classified as a Dystric Haplustands. It is characterized by loamy clay texture; it is typically well-structured, deep and permeable, with low bulk density and high organic matter content (Mata and Ramírez, 1999). The soil nutrient concentrations were adequate due to frequent fertilizations of coffee and the naturally high soil fertility of the volcanic soil. There were small differences in soil properties from one sub-plot to another (Table 1). The CEC were high in both sub-plots due to the high content of allophones. Both soils had low pH, relative high values of organic carbon (3.6% and 3.7%) and moderate values of exchangeable Ca, Mg and K.

Species involved

Coffea arabica L. "Caturra" is a highly productive dwarf variety, but depends on intensive fertilization to maintain a high productivity. Coffee forms its flower buds mainly on branches that developed during the previous year. In the present experiment, flowering initiated after the first rains at the beginning of April-May and the peak of harvest occurred in December and January.

Inga densiflora Benth. (*I. langlassei, I. microdonta, I. mollifoliola, I. montealegrei, I. monticola, I. sordida, I. titiribiana*) is a fast-growing legume tree species distributed from Mexico to Brazil. It is used as a shade tree for coffee and cocoa from Mesoamerica to Brazil and is well adapted to a wide altitudinal range (100–1400 m), but is more common above 600 m (Leon, 1966; Soussa, 1993; Zamora and Pennington, 2001). This is a low tree (on average 6-18 m and up to 30 m in height) with an irregular canopy and leaves slightly hairy. It produces flat and banana-shaped fruits, up to 30 cm long, sometimes sold in markets of Colombia and Costa Rica. Its wood is of low timber value and is mainly used as fuel wood. Consequently, this tree species is mostly used as a service tree in agroforestry systems as it provides shade for coffee and mulch through pruning during the production cycle. In the present experiment, trees were managed to maintain 2-3 stems, with an annual pruning of the lower branches in the month of October to reduce the excessive shade for coffee during the late period of the rainy season, according to the recommendations of ICAFE (1998).

Meteorology

An automatic weather station was installed in an open area next to the experimental plots and meteorological variables were monitored during the two years (2004-2005) of experimental data collection. Relative humidity (RH in %) and air temperature (T in °C) were measured by sensors (HMP45C, Campbell Scientific Corp., Logan, UT) at a height of 2 m. The photon flux density (PFD) was measured with quantum sensors (SOLEMS PAR-CBE 80, Palaiseau, France) and wind speed with an anemometer (Model 05103-5 Wind-monitor) also installed at a height of 2 m. Rainfall was measured with a tipping bucket gauge (Model ARG 100), with a resolution of 0.2 mm, providing information on intensity and duration of every rainfall. Values were measured every 30s and averages

over 15 minutes were recorded with a datalogger (CR10X Campbell Scientific Instruments). Additionally, two manual standard rain gauges were installed in the field and daily monitored in the morning hours after each rain event of the previous day since rain mainly falls during afternoon hours at the study site. Quarter-hourly reference evapo-transpiration (*ETo* in mm) was estimated by the FAO Penman-Monteith equation (Allen et al. 1998) with inputs (wind speed, T, RH and solar radiation estimated from PFD values) from the meteorological station in the open.

Radiation transmission and interception

Level of shade was measured as the proportion of PFD intercepted by shade tree canopy relative to PFD in the open during 10 days (day 7 to day 16) per month during the 2 years of study. PAR-CBE 80 sensors were fixed on the top of the orthotropic stem of each coffee plant monitored for sap flow to measure PFD availability for coffee under shade trees. Values were measured every 30s and averages over 15 minutes were recorded with a datalogger (CR10X Campbell Scientific Instruments). Coffee plants positioned at 1 m and 3 m from shade trees were selected. Additionally, hemispherical photos were taken to study the spatial variability of transmittance (see below) at seven dates throughout the two years of monitoring.

Leaf temperature

Leaf temperature was measured with a copper-constantan micro-thermocouple attached to the underside of seven leaves per system. These leaves were selected on branches located in three strata (upper, medium and lower) of the coffee plant canopy. For each stratum, selected leaves were located at the periphery or in the middle part of the branch. Values were measured every 30s and averages over 15 minutes were recorded with a datalogger (CR10X Campbell Scientific Instruments). During the measurements, all sensors and cables were placed in the shade to avoid heating effects due to direct sun exposure.

Soil water content

Time domain reflectrometry (TDR) probes were installed in both systems to periodically monitor soil volumetric water content. Six and nine TDR probes were installed in MC and AFS, respectively, at 50 cm away from coffee plants. The soil volumetric water content was monitored in the following layers: 0-30 cm, 30-60 cm, 60-90 cm, 90-120 cm and 120-150 cm. Every 10 days, measurements were undertaken with a portable apparatus (MP-917, ESI, Environmental Sensors Inc.) reading time reflectrometry of each probe and for every layer. During one year, soil was sampled monthly with an auger at the same depths at approximately 1 m away from each TDR probe and at 50 cm away from coffee plants in order to calibrate the time reflectrometry of each probe and every layer with the soil water content measured after 48 h of soil oven-drying at 105°C.

Plantation characteristics

Tree growth and biomass monitoring

In AFS, stem diameter at breast height (DBH at 1.3 m) of all the individual shade trees (41 trees) was measured in October 2002, January 2004, July 2004, January 2005 and August 2005 to estimate the total tree trunk basal area of the plantation. The biomass of ten and seven trees of *I. densiflora* was measured in 2004 and 2005, respectively. Allometric relationships based on non-linear regression analyses were developed to provide reliable estimates of the total above-ground tree biomass and that of leaves, trunks and branches. These relationships enabled to estimate tree growth non-destructively throughout the experimental period.

Additionally, seasonal estimation of tree leaf area index (LAI) was carried out with hemispherical photographs. Based on the general phenological characteristics of the shade trees observed on the ICAFE research station, two series of hemispherical photographs were undertaken; one series during the dry season (February) when trees shed their foliage and a second one during the rainy season (August-September) when the foliage density is high. The hemispherical photographs were taken above the coffee canopy at 100 grid points in a 400 m^2 plot divided in 2m x 2m squares. The hemispherical photographs were analyzed with the Gap Light Analyzer (GLA) software.

Coffee growth and biomass monitoring

In both systems, coffee stem basal diameter was measured as the average of two perpendicular measurements at 10 cm above soil surface in a sub-plot area of 312 m^2 (156 coffee plants) in January 2004, August 2004, January 2005 and August 2005. These measurements were used to estimate the total coffee stem basal area in each coffee system as the total sum of the basal area of individual plants per plot and then multiplied by 32.05 to estimate the total coffee basal area per hectare. The leaf area of eight coffee plants was measured per system to estimate coffee LAI in February 2004, September 2004, February 2005, April 2005, June 2005 and October 2005. The measurement of plant leaf area consisted for each coffee plant in the measurements of the length and the width of all the individual leaves of that plant; the individual leaf area was estimated from an equation deriving the leaf area from the product of leaf length (L) and width (W) (Leaf area= 0.69LxW, R^2 = 0.96). As these measurements were labor intensive and time-consuming, a simplification was developed to estimate LAI which consisted in counting all the leaves of a coffee plant and then multiplying this total leaf number by an average leaf area. Biomass measurements were carried out on eight coffee plants in May 2004, January 2005 and July 2005. For each coffee plant, all the stems were taken into account and their total length and basal diameter (at 10 cm above soil surface) were recorded. Fresh weight of stems, branches and leaves was measured. For each plant, sub-samples of these components were taken and oven dried at 60°C during 72h to estimate their dry biomasses and thereafter to extrapolate the total biomass of each component.

The specific leaf area (SLA) of coffee was measured for both systems on 6 plants and at four strata within the coffee canopy, located on the node positions 8th, 22nd, 37th and 51st from the stem top. Individual leaves were scanned and images processed with an image-scanning program (Whinrhizo, V.3.9, Regent Instruments) to determine precisely their leaf area. Individual leaves were oven dried at 60°C during 72h and weighted thereafter with a high precision balance to derive their individual SLA.

Yield monitoring

Coffee production was measured during 6 consecutive harvests from 1999 to 2005. In both MC and AFS, harvest was monitored on 10 rows (sub-plots) constituted of 15 coffee plants. The annual production was obtained by summing the weights of coffee fresh fruits harvested during the 4-5 biweekly harvest events of the harvest season. Data were extrapolated to yield per ha and the green bean coffee yield was obtained from sub-samples after wet processing of berries.

Roots studies

Measurements of fine root (d < 2mm) biomass, length density, volume and mean diameter of coffee in MC and coffee together with shade tree in AFS were undertaken during the rainy seasons of 2005. Roots were sampled with a cylindrical auger of 80mm internal diameter. In AFS, the root variables were studied with respect to the following factors: (1) distance from the nearest shade tree; (2) position relative to the coffee row and inter-row; and (3) soil depth. To assess the effect of distance to the nearest shade tree on the root system, samples were collected on a diagonal across each plot at 1.5 m and 3.6 m from the trees. At both distances from the tree, soil from the coffee row and inter-row were sampled. Samples on the coffee row were collected at 50 cm from the coffee stem. Samples on the coffee inter-row were collected 1 m from the coffee stem. Finally, to study the vertical distribution of fine roots, at each position and distance, samples were collected down to 100 cm depth in 10 cm increments. Sampling at a greater depth was restricted by the length of the auger, but additional samples were collected in a pit at the distance of 3.6 m from the tree down to 200 cm depth with 10 cm increments.

After sampling, soil cores were stored at 10^{o} C and processed within two week. Roots were separated from soil and organic debris to evaluate root length density; volume and mean root diameter by scanning of collected roots and processing data with a root image-scanning program (Whinrhizo, V.3.9, Regent Instruments). For AFS, roots were not separated accordingly to plant species due to the difficulty in distinguishing roots of *Inga densiflora* from that of *Coffea arabica*.

Analytical methods

Data were analyzed with SAS release 8 (SAS Institute Inc., Cary, NC, USA, 1999). For the microclimate variables (PFD and leaf temperature), mean and confidence intervals were computed. For coffee yield, coffee biomass, root density and SLA, analyses of variance (Anova) and Newman and Keuls (NK) test were computed. Regression analyses were performed to develop allometric relationships for the biomass of *Inga densiflora*.

Results

Climate characteristics

The annual rainfall was particularly high with 3245 mm and 2685 mm during 2004 and 2005, respectively (Table 2). Rainfall was unevenly distributed throughout the year with 3057 mm (94%) and 2495 mm (93%) during the wet season from May to November for 2004 and 2005, respectively. Monthly rainfall ranged from 0 mm to 650 mm for the driest month and the wettest one, respectively. Monthly Penman-Monteith reference evaporation (ETo) varied between 70 to 170 mm and amounted to 1310 and 1178 mm yr^{-1} for 2004 and 2005, respectively. Monthly ETo was higher than monthly rainfall from December to April, but the cumulative rainfall accounted for 188 mm (27% of ETo) and 190 mm (30% of ETo) in 2004 and 2005, respectively (Table 2).

Effects of trees on microclimate

The mean diurnal time course of transmitted radiation through shade tree canopy in AFS depended on the solar angle and season (Figure 1). During the dry season (2004), the mean percentage of transmittance (of the photosynthetic radiation) was 40% whereas it was only 25% during the wet season. The percentage of transmitted radiation also varied greatly throughout the day. In the dry season (2004), it averaged 29% in the morning hours (7:00-9:00) with the lowest values of 14-13% registered at 8:00-9:00, 43-55% around midday to early afternoon hours (10:00-15:00) and 33% in the late afternoon hours (15:00-18:00). During the wet season (2004), the daily pattern was different than in the dry season with the highest values (28% to 35%) registered in the morning hours (7:00 to 11:00) and low values (15% to 20%) thereafter.

Total daily incident radiation values for coffee in AFS were influenced by the time of the year, not only due to natural climatic fluctuations of the radiation along the year, but also due to the loss of foliage during the dry season and canopy pruning, and hence reduction in shade level during the month of September in the middle of the wet season (Figure 2). During both years (2004 & 2005), shade level was lower in the dry season reaching values of 40% to 50% whereas values were in the range of 70-75% in the wet season. During the dry months (January to April), the radiation in the open site was higher due to low cloudiness so that the total daily radiation available for coffee was almost 50% higher in the dry season than in the wet season in both systems.

The discontinuous nature of the tree canopy caused substantial local variation in shade level depending on the proximity of coffee plants to shade trees. The percentages of the radiation transmitted at distances of one and three meters from shade trees were significantly different (Figure 3). In the dry season, transmitted radiation measured at one meter represented only the 23% of the radiation measured in the open, while it represented 60% at three meters. Furthermore, the solar angle affected the pattern of the transmittance; at three meters from the shade tree, the highest values of transmittance were recorded around midday with values of 95%, while values were in the range of 30% to 35% in the morning and the afternoon. At a distance of one meter, the highest values

were registered between 9:00 to 11:00, after which they decreased to 15-19%. During the wet season, the differences in transmittance between the two distances were also important, but with lower values of transmittance at 3 meters reaching their maximum (50-65 %) in the morning hours (9:00 to 11:00) whereas the highest values at one meter ranged from 24% to 35% between 8:00 to 13:00.

The shading pattern of the central plot in AFS was determined using a grid of hemispherical photographs. During the wet season, it was possible to find areas which received up to 60-70% of the total radiation whereas other areas received only 10-20% (Figure 4). According to the analysis of hemispherical photographs during the dry season, 50% of the plot area in AFS received less than 50% of radiation whereas 88% of the plot area received less than 50% of radiation during the wet season.

Seasonal differences between the mean LAI of *I. densiflora* at plot scale were relatively small, but highly significant. The overall decrease in LAI from the wet season 2004 to the dry season 2005 was about 35% (or 0.47 m^2 m^{-2}), which translated into a seasonal change in the light transmittance (estimated by hemispherical photographs) to the canopy of coffee plants (Table 3). These changes were substantial in some part of the plantation with 79% of the grid points experiencing increases in radiation transmittance from 5% to 45%. Furthermore, LAI decreased by 0.15 to 0.75 m^2 m^{-2} for 80% of these grid points (Figure 5). Changes in LAI were further displayed by subtracting the LAI values of the wet season from the LAI values of the dry season (Figure 5). Local changes in LAI at single grid points ranged from –1.95 to 1.35 m^2 m^{-2}. Although mean LAI for the entire grid area differed significantly between seasons, roughly 24% of the total area was not effected by these changes (considering only values $\geq$ 0.45 m^2 m^{-2} as significant changes).

Measurements of leaf temperature in un-shaded coffee canopy and in coffee canopy grown under shade of *I. densiflora* showed a substantial moderating influence of shade on the thermal environment. During the dry and wet seasons, coffee leaves without shade experimented temperatures higher than air temperature whereas leaf temperature of shaded coffee was always lower than air temperature (Figure 6). Still, the differences between non-shaded leaf temperature and air temperature were less important during the wet season. Mean maximum shaded coffee leaf temperature was reduced by up to 5^{o}C relative to coffee leaf temperature in monoculture (Figure 7). The minimum leaf temperature at night was 0.5^{o}C higher in AFS than air temperature demonstrating the buffering effects of shade trees.

Effect of trees on soil water content

The lowest values of soil volumetric water content were registered from February to April corresponding to the last month of the dry season, when it reached values of 0.28 dm^3 dm^{-3}. During the time of the study, the MC and AFS profiles showed similar soil water content at the 0-60 cm depth as well as at the 60-120 depth (Figure 8). Therefore, the effect of shade trees on the soil water content was not apparent in the layer of 0-120cm for the complete period of the study. On the contrary, the soil moisture for the deeper layer of 120-150 cm was significantly lower in AFS than MC. This difference was

more pronounced during the dry season 2004 due to low rainfall in December 2003 and a marked dry season that ended late at the beginning of May 2004, compared to the dry season 2005 which was less pronounced and with rainfalls registered during the months of March and April.

Effect of trees on coffee growth and production

Annual coffee green bean yield for the six production cycles (1999/2000 to 2004/2005) were found to be higher at the experimental site for both systems (MC and AFS) than the average national yield (1.7 MT ha^{-1}), except for 2003/2004 (Figure 9). The cumulative yield over six consecutive years was 10% lower in AFS than in MC. However, tree shade management in AFS was heavier in the period from 1997 to 2002 compared to the period from 2003 to 2005. Clearly, this influenced coffee yield and no statistical difference was found from 1999 to 2003 between AFS and MC when shade trees were pruned twice a year and shade was light, corresponding to the low rate of growth of shade trees in the first years. On the contrary, coffee yield in AFS was significantly reduced by 29% compared to MC during the period from 2003 to 2005 due to a denser tree shade (Figure 9). The highest yield reduction (38%) was registered during the last year of the study when the actual light transmittance varied between 40 to 50%.

Coffee stem basal area was higher in MC than in AFS (Figure 10). This effect resulted from differences in coffee stem diameter together with plant density. Above-ground biomasses of individual coffee plants were not significantly different in AFS and MC during the two year period of monitoring, with the exception of the last measurement for which coffee plants in AFS had lower leaf and higher stem dry matter compared to MC. Estimated total above-ground coffee biomasses were at their highest during the wet season 2004 (Table 4), possibly due to a low yield during the previous year which allowed plants to allocate a higher amount of carbohydrates to vegetative growth. During the wet season 2004 when both aerial and below-ground biomasses were measured, the biomasses of tap root and coarse roots accounted for 20% of the total biomass, but no significant differences were observed between systems.

Although shade provided by *I. densiflora* had no effect on coffee biomass, it strongly influenced leaf characteristics such as SLA. Indeed, SLA of shaded coffee plants was significantly higher than that of sun-grown coffee plants in all leaf positions within the coffee canopy (Figure 11). SLA increased with increasing levels of shade, with the highest LSA values observed in the lowest strata of the plant canopy and with a linear and significant relationship between SLA and branch rank for both systems. A higher R^2 was registered for MC than for AFS and the slope and intercept were shown to be significantly different for the two regression equations ($P<0.05$). Other leaf characteristics were influenced by the shade of *I. densiflora* such as leaf width, length and area (Table 5). At the 3 monitoring dates, mean coffee leaf area was larger in AFS than in MC. Furthermore, a reduction in the mean leaf area was registered in MC during the dry season 2004, whereas the mean leaf area in AFS was more stable with similar values

during dry and wet seasons. Despite this higher mean leaf area of shaded coffee, LAI in both systems was similar from August 2003 to April 2005 (Figure 12). During the wet season 2005, LAI in MC was significantly ($P<0.05$) higher than in AFS and its increase started earlier and was bigger than in AFS. Coffee plants in MC had more leaves per plant than in AFS. During the dry season 2004, shaded coffee plants lost only 33% of their leaves, whereas coffee plants in MC lost 39%. In 2005, plants in AFS lost 39% of their leaves, whereas plants in MC lost up to 50% which represented a more important reduction in LAI in comparison to 2004, and even more so in MC.

Root characteristics

Fine root biomass, length and mean diameter were not affected by the proximity of shade trees in AFS no statistical differences were observed between samples taken at 1 m or 3.5 m from the tree stem (data not shown). This pattern was in accordance with that of aboveground data for which coffee plants closer to shade trees were similar to that of coffee plants farther away from shade trees.

In both systems, coffee roots were concentrated within the coffee rows and showed a marked decline in the inter-rows. Indeed, the average root biomass and root length differed significantly between the inter-row and the row zone (Figures 13, 14 and 15). Root biomass and diameter were significantly lower in MC than in AFS in the first 40 cm of soil in the inter-row (Figures 13 and 15). Nevertheless, no differences were found within the rows in the terms of root characteristics between the two systems. In both systems, the root distribution within the rows was relatively homogenous in the first 60 cm of soil where 75% of the total fine root biomass of the top 100 cm was concentrated. On the other hand, only 50% of the root biomass was present in the first 60 cm in the inter-row in MC in comparison to 70% in AFS, which demonstrated not only a difference in biomass but also in term of distribution.

Tree growth

Inga densiflora trees were severely pruned at approximately 1.3 m above ground after 2 years of growth in order to force trees to branch and to grow on two to three stems. Thereafter, regular pruning of the basal branches ensured that trees continued to grow on these stems and precluded excessive shading of the under-storey coffee plants. Destructive measurements were undertaken to develop allometric equations from tree stems of 7 years (2004) and 8 years (2005); these stems had DBH between 8.5 cm and 18.5 cm and a total biomass between 17.2 kg and 67.0 kg. The relationships between DBH and biomasses (total, stem, branches and leaves) could be described as power functions (Figure 16). The stem represented the main biomass component of the aerial tree biomass in the AFS, followed by secondary branches and leaves (Table 6).

After 5 years, trees were well established with a mean DBH of 8.5 cm, a minimum of 5.1 cm and a maximum of 12.4 cm. At the age of 8 years, the mean DBH was 13.5 cm with a minimum of 9.3 cm and a maximum of 19.1 cm. After 5 years, the stem basal area was 4.2 $m^2\,ha^{-1}$, whereas it was 9.9 $m^2\,ha^{-1}$ at 8 years with a mean annual increment of 1.2 m^2

ha^{-1} yr^{-1} for the period of 8 years, but with the highest annual increment observed during the fifth year with 2.5m^2 ha^{-1} yr^{-1} compared to the mean increment of 0.83m^2 ha^{-1} yr^{-1} for the first five years. For the monitoring period of 8 years, the mean annual biomass increment was 3.8 Mg ha^{-1} yr^{-1} with a total estimated biomass of 12.8 (Mg ha^{-1}) after five years and 30.4 Mg ha^{-1} after 8 years, which showed a low annual increment during the first 5 first years with 2.6 3.8 Mg ha^{-1} yr^{-1} compared to 7.86 and 4.67 for the latter years (Figure 17). However, 17 tree stems were cut at a height of 1 m during the last year to derive the allometric equations and the rest of the trees were pruned to eliminate small branches just above coffee canopy. These practices caused a reduction of 1.4 m^2 ha^{-1} in terms of the basal area and 7.4 MT ha^{-1} in term of tree aerial biomass.

The density of *Inga* trees (278 trees ha^{-1}) did not influence the total aerial biomass of coffee plants at the ages of 7 years (2004) and 8 years (2005). The estimated coffee biomasses at plot scale were not found to be significantly different between systems, even though coffee density was slightly lower in AFS than in MC. Nonetheless, the total biomass per plot was 2.4 and 2.9 times higher in AFS (44.8 and 47.4 Mg ha^{-1}, 2004 and 2005 respectively) than in MC (18.8 and 16.2 Mg ha^{-1}, 2004 and 2005 respectively), due to the contribution of the shade tree biomass (56% and 64% of total biomass for 2004 and 2005) which was quite higher that the total coffee biomass (Figure 18).

Discussion

Effects of shade trees on microclimate

In the present study, the canopy of *I. densiflora* trees had a strong influence on the microclimate experienced by coffee plants growing underneath. Shade modified the microclimate primarily through a reduction in light availability. Furthermore, the transmitted light was probably partially depleted in red wavelengths affecting the specific leaf area and architecture of the under-story plants as documented by Staver et al (2001). Light availability (PFD estimated by sensors on the top of plants) for the coffee canopy in AFS varied between 50% to 25% of the open radiation in the dry season and the wet season, respectively. These reductions are in the acceptable range for coffee (40 to 70%) according to many studies (Beer et al, 1998; Muschler, 1998; Vaast et al, 2005). The low values of radiation during the wet season are explained by the high development of associated shade tree canopies. In the central region of Costa Rica, farmers commonly pruned shade trees to reduce shade level for coffee. For *Inga* species, a partial prune is generally used, which consists in cutting down selected branches and leaving 2 or 3 main branches per tree for maintaining a homogenous shade (Muschler, 1999). These low levels of radiation for the coffee canopy in AFS are common and acceptable because coffee photosynthetic rates are at their maximum at intermediate shade levels (PFD of 600 to 900 µmol m^{-2} s^{-1}) in many coffee growing conditions (Nutman, 1937; Beer et al, 1998; Vaast et al, 2005a; Franck et al, 2006). Indeed, coffee presents the characteristics of a shade adapted plant with a low light compensation point (15-20 µmol m^{-2} s^{-1}), low

values of light saturation (500 and 900 µmol m^{-2} s^{-1} for shade and sun leaves, respectively) and photo-inhibition at high radiation values, especially under water or nitrogen limiting conditions (Kumar and Tieszen, 1976; Kumar and Tieszen, 1980; Cannell, 1985; da Matta and Maestri, 1997; Franck, 2005).

In the present study, radiation distribution below the canopy of *Inga* varied notably with distance to the shade tree and time of day as reported by many authors for various agroforestry systems (Feldhake, 2001; Ong et al, 2000; Vaast et al, 2005). Trees cast a shadow in their close surroundings resulting in a low transmittance of around 25% of radiation but with a quite stable daily pattern, while the transmittance is much higher further away from shade trees but coupled with a higher variability along the day. In this study, large changes in transmittance at small scale clearly indicated that a characterization at the whole canopy scale might not be sufficient to adequately describe the light availability for coffee plants growing underneath and the micro-environment effects on coffee physiological responses such as transpiration (van Kanten and Vaast, 2005) and photosynthesis (Franck et al, 2006). This variability in light transmittance resulted in sizeable changes in the light micro-climate and may have profound effects on the growth and inter-specific competition of under-story plants and perhaps seed germination for some species (Staver et al, 2001).

Shade trees influence other microclimate variables such as temperature, humidity and wind as highlighted for coffee by many studies (Barradas and Fanjul, 1986; Fernández and Muschler, 1999; Muschler, 1999; Dauzat et al, 2001; Vaast et al, 2005). In the present study, temperature differences between coffee leaves in the open and under shade were found to vary between 1^{o}C and 7^{o}C depending on time of the day, season and leaf position within the coffee canopy. These leaf temperature differences were similar to the one reported in the literature for other coffee systems. In Mexico, Barradas and Fanjul (1986) reported that the presence of *Inga* trees (205 trees ha^{-1}) reduced the daily maximum temperature by 4-5^{o}C and increased the minimum temperatures by 1-2^{o}C. Similarly, 40 to 70% of shade provided by *Erythrina poeppigiana* or *Terminalia ivorensis* or *Eucalyptus deglupta* lowered leaf and soil temperatures in low elevation coffee zones to levels that are closer to optimum for coffee (Muschler, 1998; Siles et Vaast, 2003; Angrand et al, 2004). For most coffee researchers, this reduction is of particular importance since the temperature range is between 18ºC to 24ºC for an optimal photosynthesis of Arabica coffee (Kumar y Tieszen, 1976; Cannel, 1985; Vaast et al, 2005; Franck et al, 2006) and with a detrimental effect of temperature above 25 ºC related to stomatal closure (Nunes *et al*. 1968, Kumar y Tieszen, 1980; Fanjul et al, 1985; Guttierez et al, 1994, Dauzat et al, 2001, van kanten and Vaast, 2006). Furthermore, additional positive effects of trees in AFS are also cited such as temperature reduction on enhanced crop establishment, reduced soil temperature and evaporation, and enhanced activity of soil organisms (Ong et al, 2000; Rao et al, 1998; Martius et al; 2004).

Effect of the trees on soil moisture

In many agroforestry studies, water competition between various crops and associated trees appeared to be the most important factor causing a yield reduction of the associated crop (Rao et al, 1998; McIntyre et al, 1997; Govindarajan et al, 1996). However, most of these water studies in AFS have been carried out in the semiarid tropics, with a maximum of 600 to 700 mm during the cropping season. In the present study, the annual rainfall greatly exceeded the Penman-Monteith reference evapo-transpiration (ETo) with a rainfall to ETo ratio of 2.47 and 2.27 in 2004 and 2005, respectively. Soil water recharges were frequent during the relatively long dry season of 5 months (December to April) during which ETo exceeded rainfall. Indeed, rainfalls represented 27% (188mm) and 30% (190mm) of ETo during the dry seasons 2004 and 2005, respectively, and hence this accounted a significant soil water recharge during the dry season. The water use in AFS was higher than in MC. Nonetheless, shade trees did not reduce significantly the soil moisture over the profile down to a depth of 120 cm over 2 years of monitoring, but did significantly at deeper soil depth (120-150 cm). Thus, it can be argued that there was complementarity in the use of the water capture in AFS, due to the fact that the higher water use in AFS was not concentrated in the upper soil layers and trees took up a large part of water and probably nutrients from the sub-soil and hence reduced the source of competition with the main crop. The complementarity in the use of resources have been reported before, and it has been suggested that benefits from agroforestry are to be expected only when there is complementarity of resource capture by trees and crops (Cannell et al., 1996). For example, Grevillea (*Grevillea robusta* A. Cunn.; Proteaceae) has been reported to result in low levels of water competition with the associated crops due to its deep rooting pattern (Howard et al., 1996). Additionally to complementarity, a redistribution of soil water from deeper horizons to drier surface horizons by root systems has been documented and termed "hydraulic lift", as mentioned for *Grevillea robusta* and *Eucalyptus camaldulensis* (Burgess et al., 1998).

Effects of shade trees on coffee biomass and yield

In the present study, shade by *I. densiflora* resulted in a low decrease (10%) of coffee yield over six years in comparison with MC; however during the latter years, the reduction in coffee yield accounted for 38% due to the fact that shade trees presented higher growth rates and hence provided a denser shade. These values are in accordance with reports of many authors demonstrating that coffee yield generally decreased by 10% to 30% under shade conditions, depending on local ecological conditions and altitude in Central America (Beer et al, 1998; Staver et al, 2001; Vaast et al, 2005). In Chiapas, Mexico, Soto-Pinto et al (2000) reported that more than 50% of the coffee plantations gave poor yield (between 50 and 500 kg/ha) because they were maintained under too high shade tree densities ranging from 100 to 998 trees ha^{-1} that considerably reduced light availability for coffee. Similar observations were recently reported in Costa Rica for coffee associated with timber tree species (*Cordia alliodora*, *Terminalia amazonia* and *Eucalyptus deglupta*) in three low-altitude regions of Costa Rica where tree densities

were too high and tree management virtually non-existent (Dzib et al, 2007). Angrand et al (2004), working in AFS with *Eucalyptus deglupta* and *Terminalia ivorensis*, found that a reduction in light availability decreased the number of fruiting nodes, flowers and fruits in coffee AFS with respect to MC in the Southern, low altitude region of Costa Rica. Franck (2005) also observed a strong reduction in flowering intensity and hence fruit load down to 10 % of the one registered in full sun for coffee exposed to an artificial shade of 75% and in the absence of other limiting conditions. These observations confirmed the suggestions made by Cannell (1975, 1985) that the most important components of the coffee yield, i.e. fruiting nodes and fruits per node, are both affected by low light levels even when other ecological factors are favorable. Consequently, poor management of the shade strata such as the absence of shade tree thinning and inadequate canopy pruning is generally responsible for low coffee yield and has led to recommendations of shade elimination, especially at medium to high altitude in Central America. With a proper shade management, a yield reduction in the range of 10% to 20% can be financially compensated by the premium paid for improved quality (i.e. bigger bean size and cup quality) as demonstrated in sub-optimal and optimal conditions of Central America (Guyot et al, 1996; Vaast et al, 2005b & 2006). Furthermore, shade generally buffers the strong alternate bearing pattern of coffee observed in MC under optimal ecological conditions (Beer et al, 1998; Vaast et al, 2006), which results in more stable revenues for coffee farmers over the years. In the present study, shade trees did not reduce coffee alternate bearing pattern probably due to the combination of low tree density and intense pruning management which resulted in a low tree growth rate during the first years and also the high fertilization in highly favorable ecological conditions. Other authors (Beer et al, 1998; Staver, 2001) have suggested or demonstrated (Muschler, 1997, 1999) that shade reduced coffee productivity in optimal conditions (1000 m to 1300 m) and on fertile soils in Central America, where the beneficial effects of shade in regulating the microclimate (temperature and relative humidity) and improving soil fertility were less important. The intensive practices in optimal conditions promoted in the region are generally based on a reduction in shade accompanied by an enhanced reliance on high-yielding cultivars planted at high densities, intensive use of chemical inputs and frequent pruning (Perfecto et al., 1996). The advantage of shade in coffee AFS is more important in sub-optimal conditions such as low altitude and in soils of low fertility (Beer et al, 1998).

No significant differences in coffee dry matter components were observed between AFS and MC with the exception of lower values of coffee leaf dry matter and LAI during the wet season 2005 in AFS. The low differences in coffee biomass showed an absence of competition for resources between the shade species and coffee in AFS under the optimal conditions and intensive fertilization regime of the present study. Although the shade of *I. densiflora* did not affect coffee biomass, it had a significant effect on coffee leaf traits such as enhancing SLA and mean individual leaf area in AFS compared to MC. Vaast et al (2005) and Franck (2005) also found a highly significant effect with uniform shade provided by artificial shade on leaf traits such as SLA, individual leaf area, and leaf

nitrogen content. Despite the higher individual leaf area of coffee in AFS, LAI in AFS and MC were similar during the first 5 monitoring dates and over a period of 18 months, but was lower in AFS during the last rainy season from June to October 2005. Similar LAI values can be explained by a higher quantity of leaves per coffee plant in MC that compensated the lower mean individual leaf area. It is worth mentioning that for both systems the seasonal variation in LAI followed that of the soil moisture as reported by Matoso et al (2004).

Despite the relative low light transmittance of 40% to 50%, estimated by hemispherical photographs, and high aerial shade tree biomass, small but significant differences were observed in terms of biomass and distribution of roots between MC and AFS. In AFS, the higher root biomass observed in the inter-row than on the coffee row might be due to the soil colonization by tree roots, but the attempt to differentiate coffee and tree roots was unsuccessful. On the coffee row, no significant differences in root biomass were observed between MC and AFS. In AFS, this pattern of root biomass may indicate that the colonization of the tree shade was more important in the inter-row zone than in the row. In another study on roots of *Eucalyptus deglupta* associated with coffee, Schaller et al (2003) showed that there was a complementary in root distribution of coffee and shade trees that promoted a more homogeneous distribution in AFS than in MC, hence suggesting an enhanced efficiency in terms of soil exploration and exploitation. This complementary in root distribution between the shaded crops (with more superficial root systems) and associated trees (with deeper root systems) is generally cited as the main reason for the low competition for nutrients and water in AFS (Beer et al, 1998). In the present study, the low competition for soil resources could be explained by the deep and easily colonized volcanic soil, which allowed root colonization down to more than 200 cm (data not shown).

In the present study, no sign of water competition was observed, especially during the five months of dry season. In the upper soil layers (0-120 cm), soil moisture was not affected by the presence of shade trees. On the other hand, a decrease of soil water availability at the deeper depth of 120-150 cm in AFS compared to MC suggested that shade trees tapped water resources deeper than coffee in MC, showing that there was complementarity in the use of soil water between coffee and trees. Furthermore, coffee vegetative and reproductive growth was concentrated in the wet season during which there was no water limitation due to the fact that rainfall exceeded ETo and soil was almost constantly at field capacity. Competition for nutrients is often cited as a major concern in coffee AFS (Beer et al, 1998), but was unlikely in the present study due to the large annual applications of fertilizers (250 kg N; 15 kg P; 110 kg K) in excess of plant uptake (Harmand et al, 2007) in a fairly fertile soil and thus can be excluded as an explanation of the observed coffee yield reduction in AFS compared to MC. Therefore, it appears that in the present study light reduction is the most probable cause for the reduction in coffee yield in AFS, since the shade affected directly the production of productive nodes and flowers buds, and that no other limiting effect was apparent when comparing the systems.

The basal area and biomass of *Inga* trees were 9.9 m^2 ha^{-1} and 30.4 MT ha^{-1} at 8 years, with a mean annual increment of 1.2 m^{-2} ha^{-1} yr^{-1} and 3.8 MT ha^{-1} yr^{-1}, respectively. These values appeared to be low when compared with the annual increments of 9.9 MT ha^{-1} yr^{-1} for *I. densiflora* after 3 years in plantation in Jatun Sacha, Ecuador (Pennington, 1998). Despite the fact that the tree density was 4 times higher in Ecuador, the individual tree increment was still higher in comparison with the one observed on the present site. This can certainly be attributed to the management on multiple stems and regular pruning in the present site as opposed to forest-like management without pruning in Ecuador. Other coffee AFS studies reported similar values for stem basal area and aerial biomass accumulation with respect to the present study (Suarez et al, 2004; de Miguel et al, 2004). With the coffee biomass in AFS being not affected by the shade of *I. densiflora*, the combined aerial biomass of coffee and shade trees was 3 times higher than in MC. This demonstrates the advantage of a mixed system in terms of biomass productivity and accumulation. This aerial biomass accumulation represents an important carbon sequestration by the system. Albrecht and Kandji (2003) considered agroforestry systems as a major potential sink for carbon (C), with trees managed together with crops and/or animals. Despite the fact that AFS represents an important C sink, can be classified as 'forests' (COP Marrakech, 2001) and helps prevent deforestation (COP Nairobi, 2006), farmers managing coffee in AFS do not benefit from financial rewards as AFS are not currently taken into account within the framework of the Clean Development Mechanism of the Kyoto Protocol. Nonetheless, coffee AFS provide a renewable fuel which is of economic importance to farmers. Indeed in Central America where *Inga* species predominate in coffee plantations, the fuel-wood produced is an important resource for rural families as household energy and/or revenues (Beer et al, 1998; Vaast et al, 2007). Murphy and Yau (1998) recorded high calorific values of different *Inga* species and concluded that these calorific values combined with high biomass productivity represent a great potential in terms of energy for the coffee regions.

Conclusion

The major effects of shade tree on the microclimate experienced by coffee plants can be summarized as 1) a reduction in the transmitted light and 2) an improvement of the microclimatic conditions through the reduction of air and leaf coffee temperature extremes. Even if the water use in AFS was higher than in MC, competition for water (as well as nutrients) was certainly negligible due to the high rainfall an ample fertilization, contrary to many AFS studies in which competition for water and nutrients explained the reduction in crop yield. In the present study, light reduction is the most obvious reason for coffee yield reduction since radiation strongly influences the productive nodes and flower buds.

The present results showed that coffee production was quite similar in both systems during the establishment of shade trees, however a yield decrease of 38% was observed in AFS compared to MC with a decrease in radiation transmittance of 40% to 50% during

the latter years and in the absence of an adequate pruning. This low yield reduction over 6 consecutive production cycles can be attributed to frequent tree pruning combined with an intensive fertilization and highly favorable ecological conditions for coffee cultivation. Aerial biomass production was significantly higher in AFS and amounted to 3 times the biomass produced in MC, which can be a source of household energy and revenue diversification. Thus, there seems to be no reason to consider *Inga*-shaded plantations less productive than MC in optimal conditions, especially considering the fact that coffee AFS provide environmental benefits such as C sequestration, conservation of soil fertility and water quality.

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Tables and figures

Table 6 Soil characteristics under *Inga densiflora* (AFS) and in monoculture (MC) at research site in San Pedro de Barva, Costa Rica.

Soil properties		System	
		MC	AFS
pH[a]		4.92+0.24	4.67+0.06
Total C[b]	(%)	3.60+0.14	3.70+0.16
Total N[b]		0.32+0.01	0.36+0.01
CEC[c]		42.47	44.12
Ca[d]	(cmol kg^{-1})	6.25	5.22
Mg[d]		2.08	2.48
K[d]		1.50	2.34
Sand[e]		36.9+0.9	40.6+0.7
Silt[e]	(%)	35.3+1.0	37.1+0.4
Clay[e]		27.9+1.0	22.3+0.7
WFPS[f]	At field capacity	0.65	0.69
	At wilting point	0.39	0.40

[a] pH was measured in a water suspension. [b] Total soil C and N contents by total combustion using a Thermo Finnigan analyzer. [c] The cation exchange capacity (CEC) was analysed as described by Sumner and Miller (1996). [d] The exchangeable Ca, Mg were extracted with KCl and K and P extracted in sodium bicarbonate (Olsen). [e] Texture was determined by the method of Bouyocos. [f] The water field pore space (WFPS) at field capacity and at wilting point (pressure plate) were determined as described by Henríquez and Cabalceta (1999).

Table 7. Monthly rainfall and potential evapo-transpiration (PET) during the monitoring period (2004-2005) at research site in San Pedro de Barva, Costa Rica.

Month	2004		2005	
	Rainfall (mm)	PET (mm)	Rainfall (mm)	PET (mm)
January	44	133	44	157
February	7	136	1	136
March	45	171	79	126
April	87	146	66	111
May	542	77	284	88
June	384	94	428	70
July	272	88	259	90
August	237	98	373	79
September	620	84	381	80
October	645	77	603	65
November	357	91	167	73
December	5	114	0	104
Total	3245	1310	2685	1178

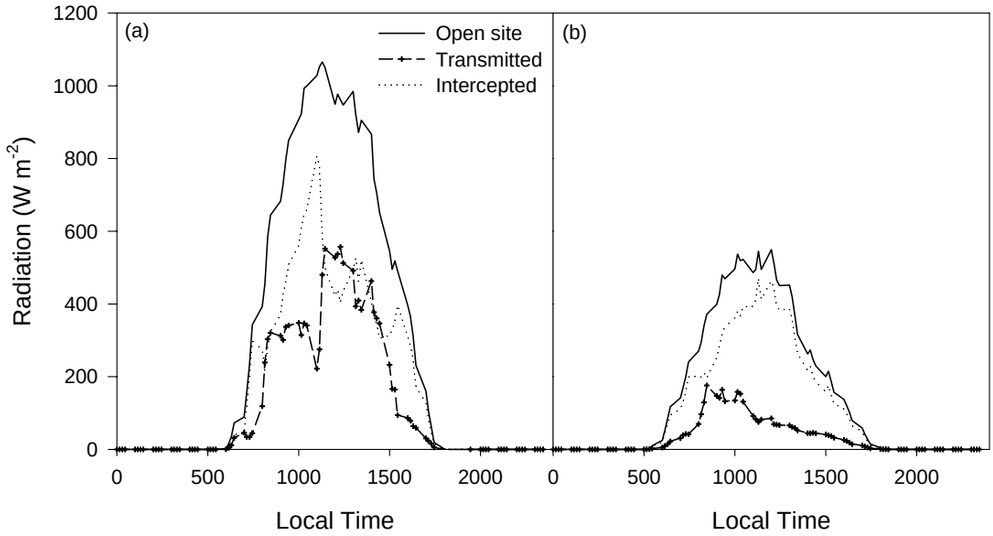


Figure 31. Mean diurnal time courses for global radiation, intercepted and transmitted radiations of *Inga densiflora* in an agroforestry system at San Pedro de Barva, Costa Rica, measured during 15 days in (a) April 2005 (dry season) and (b) October 2005 (rainy season).

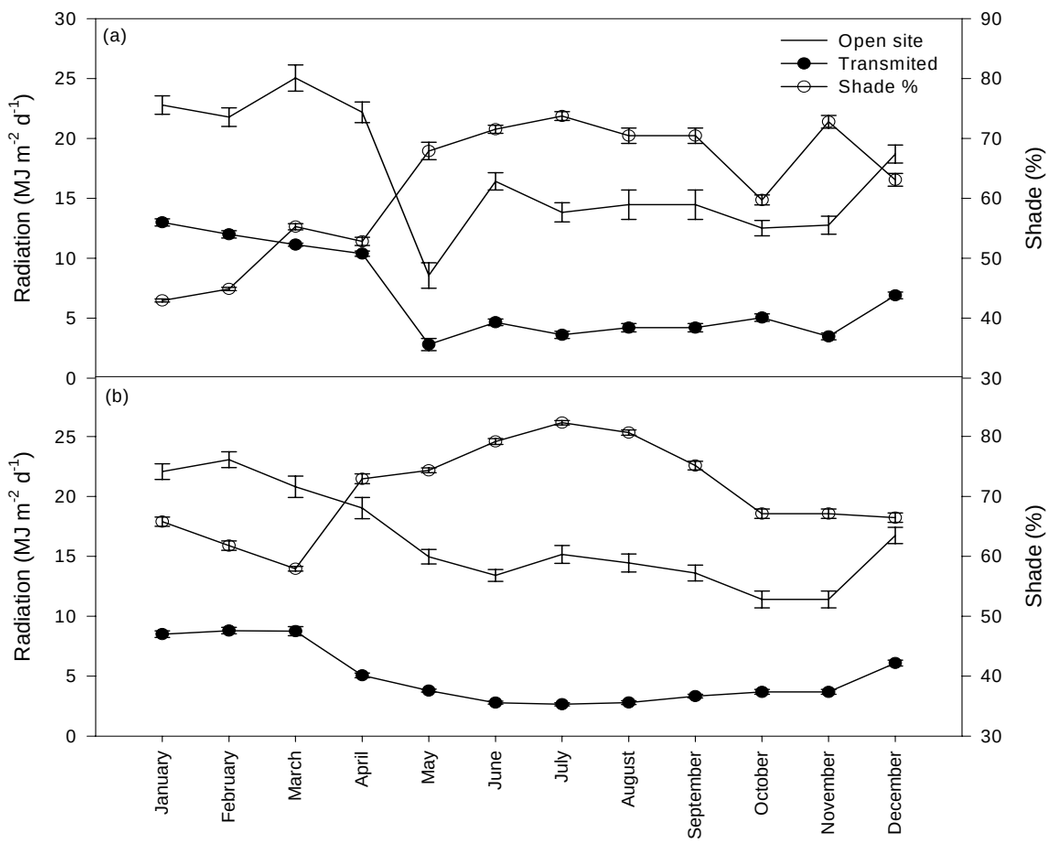


Figure 32. Dynamics of transmitted radiation and shade of *Inga densiflora* in an agroforestry system in San Pedro de Barva, Costa Rica, in (a) 2004 and (b) 2005.

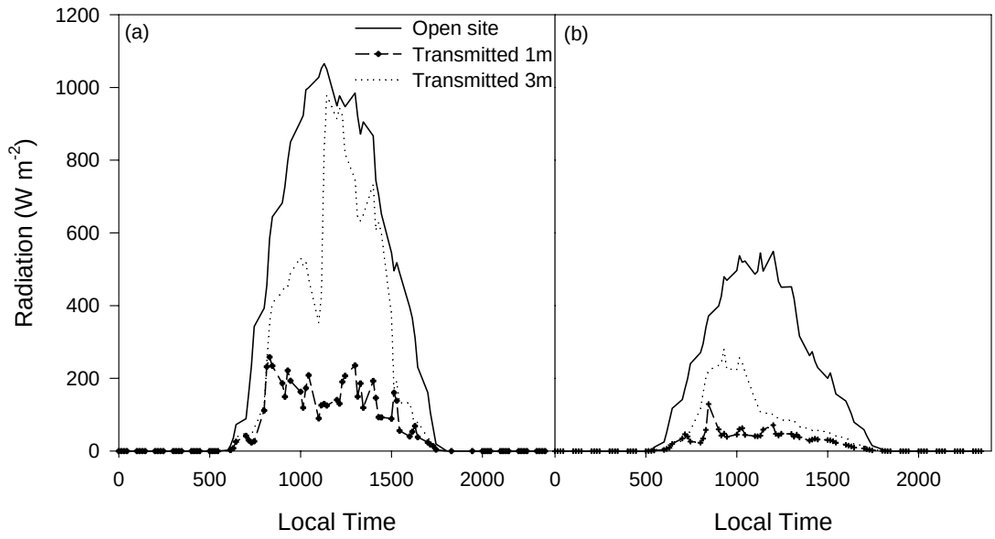


Figure 33. Mean diurnal time courses for transmitted radiation at 1 m and 3 m from the shade of *Inga densiflora* in an agroforestry system in San Pedro de Barva, Costa Rica, measured during 15 days in (a) April 2005 (dry season) and (b) October 2005 (rainy season).

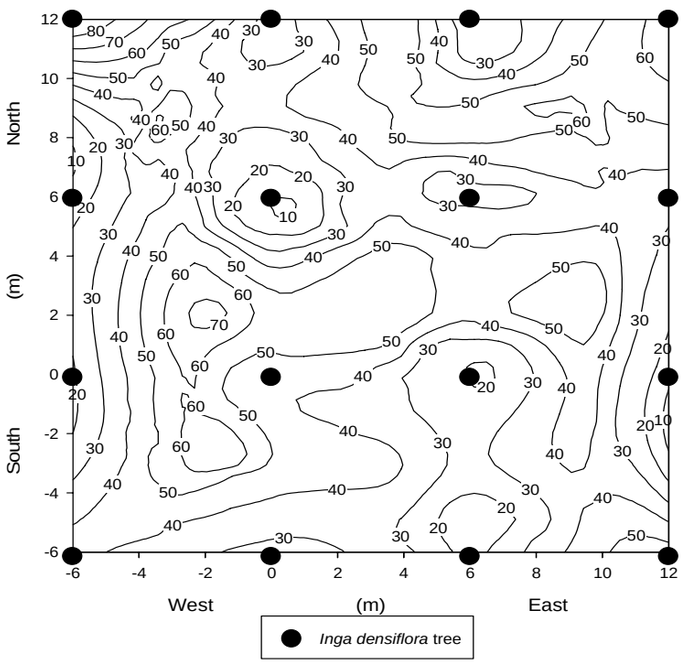


Figure 34. Variation in the percentage of transmitted radiation through the canopy of *Inga densiflora* in an agroforestry system (as determined via hemispherical photographs) in San Pedro de Barva, Costa Rica, for July 2005 (rainy season).

Table 8. Seasonal changes in canopy openness, LAI and radiation transmittance of the canopy of *Inga densiflora* in an agroforestry system in San Pedro de Barva, Costa Rica, estimated from hemispherical photographs.

	2004		2005	
	Dry season	Wet season	Dry season	Wet season
Canopy openness (%)	33.4±0.7	30.25±0.6	43.97±0.7	33.8±0.7
LAI (m^2 m^{-2})	1.14±0.04	1.32±0.03	0.85±0.03	1.22±0.04
Radiation transmittance (%)	43.2±1.2	40.4±1.1	54.72±1.3	41.7±1.4

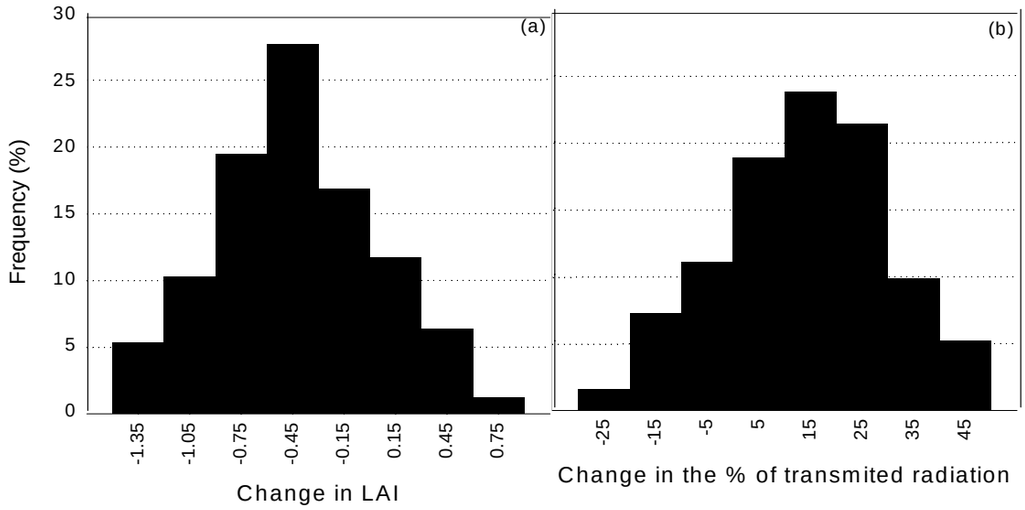


Figure 35. Percentage of change in (a) LAI of shade tree and (b) transmitted radiation estimated via hemispherical photos between the wet season and dry season in an agroforestry system planted with *Inga densiflora* in San Pedro de Barva, Costa Rica.

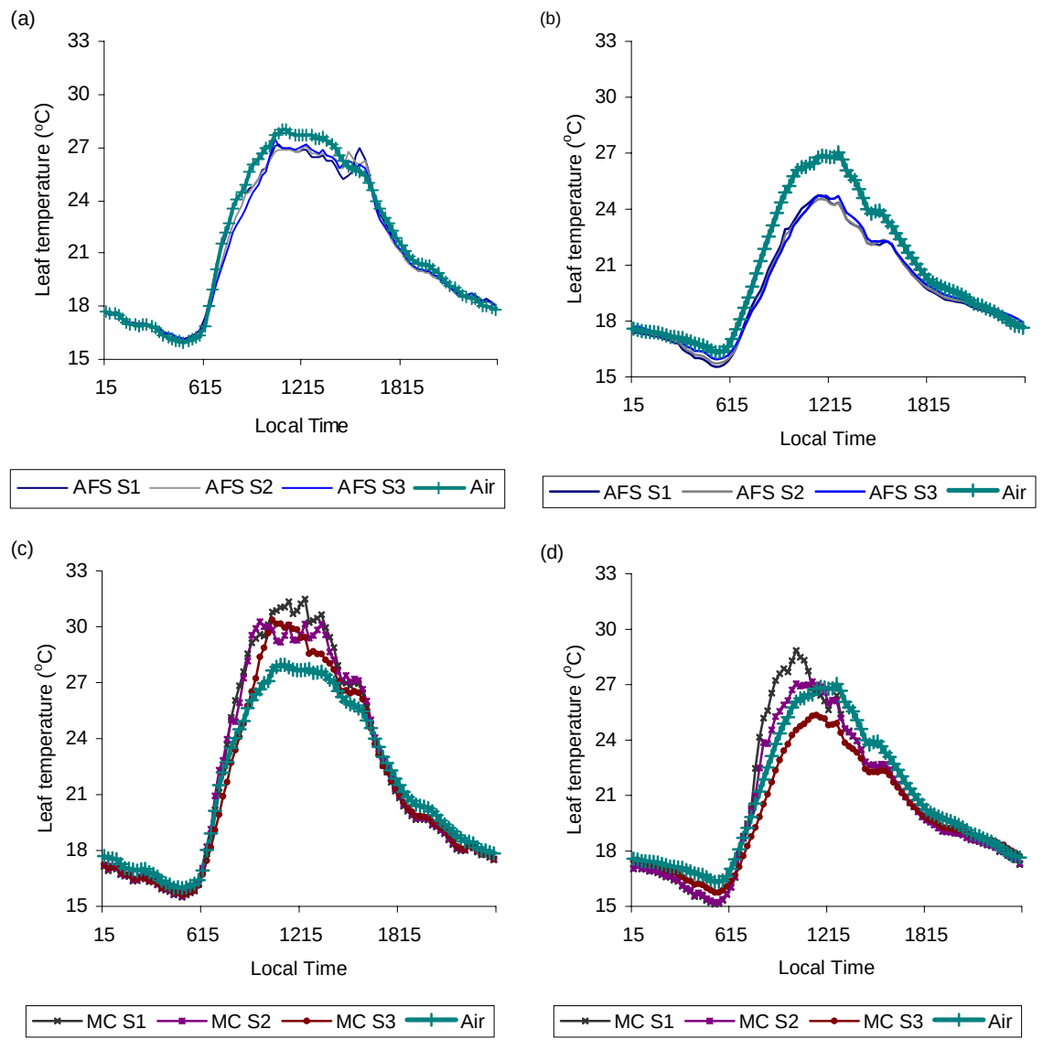


Figure 36. Mean diurnal courses of coffee leaf temperature in different coffee canopy strata in an agroforestry system (a dry season in April 2005, b rainy season in July 2005) shaded by *Inga densiflora* and in monoculture (c dry season in April 2005, d rainy season in July 2005) in San Pedro de Barva, Costa Rica, S1: upper coffee canopy stratum; S2: middle coffee canopy stratum; S3: low coffee canopy stratum. (Values are averages of a month of measurements).

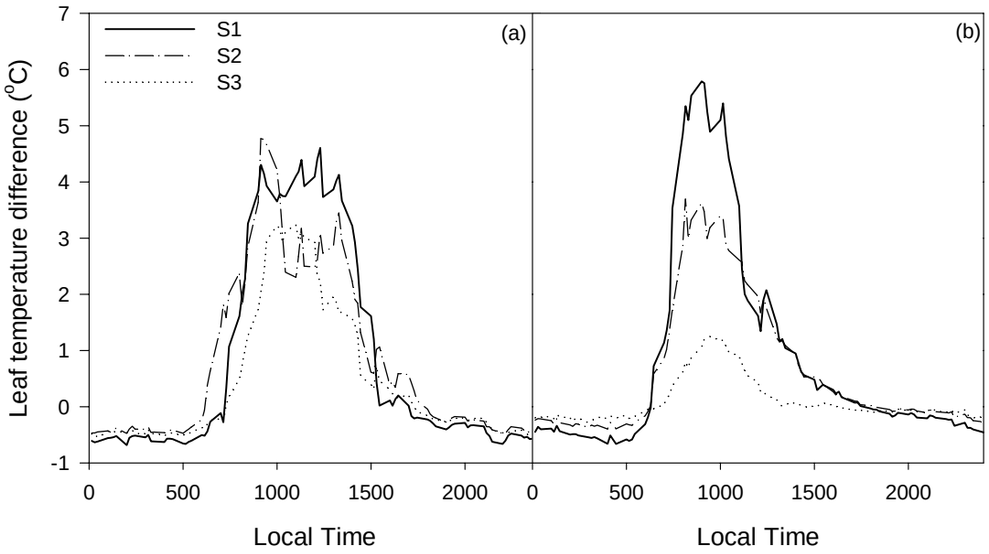


Figure 37. Mean diurnal differences in coffee leaf temperature at different strata between monoculture and agroforestry system shaded with *Inga densiflora* in San Pedro de Barva, Costa Rica, for (a) April 2005 (dry season) and (b) July 2005 (rainy season); S1: upper coffee canopy stratum; S2: middle coffee canopy stratum; S3: low coffee canopy stratum. (Values are averages of a month of measurements).

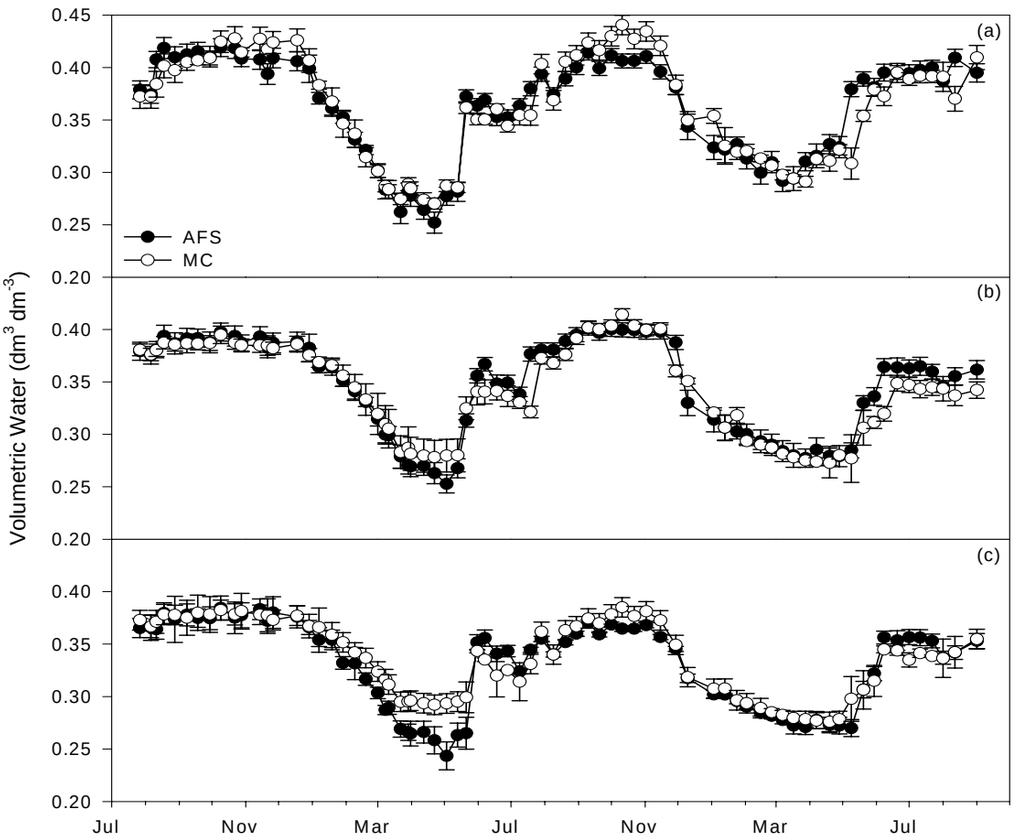


Figure 38. Volumetric soil water content at depths of (a) 0-60 cm and (b) 60-120 cm in coffee monoculture (MC) and coffee agroforestry system (AFS) in San Pedro de Barva, Costa Rica, measured from July 2003 to October 2005.

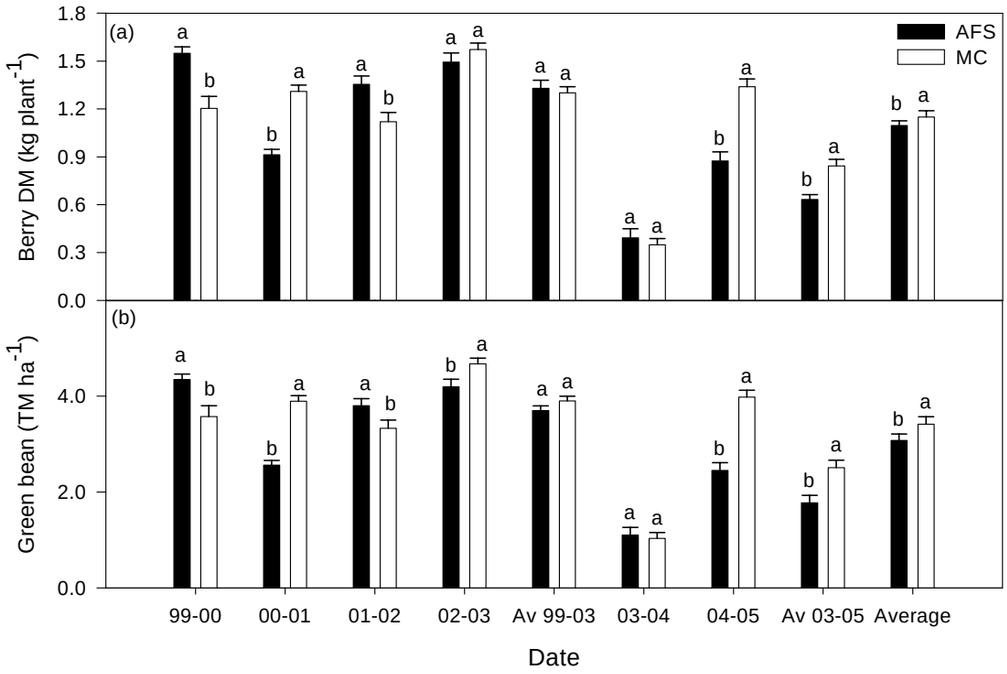


Figure 39. Coffee berry dry matter per plant (a) and coffee green bean yield (b) in monoculture (MC) and in an agroforestry system (AFS) shaded with *Inga densiflora* in San Pedro de Barva, Costa Rica during 6 production cycles.

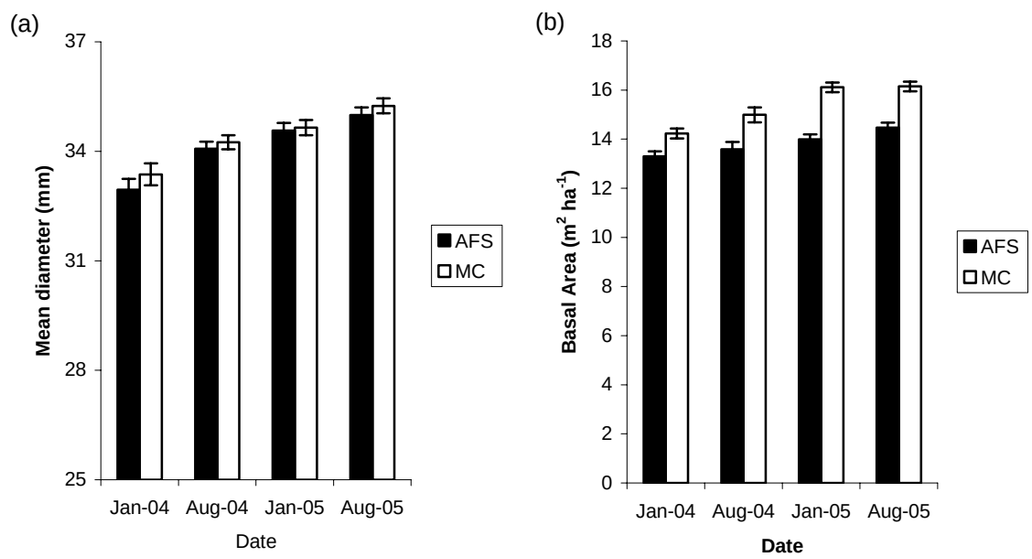


Figure 40. (a) Stem mean diameter and (b) basal area of coffee plants in agroforestry system (AFS) and monoculture (MC) in San Pedro de Barva, Costa Rica.

Table 9. Biomass (DM in Mg ha^{-1}) of the different components of coffee aerial part in agroforestry system (AFS) and monoculture (MC) in San Pedro de Barva, Costa Rica.

	May 2004		January 2005		July 2005	
	Mg ha-^{1}		Mg ha-^{1}		Mg ha-^{1}	
	AFS	MC	AFS	MC	AFS	MC
Leaves	3.7±0.5	3.8±0.4	2.2±0.2	2.7±0.4	2.6±0.2	3.7±0.4
Branches	5.3±0.6	5.0±0.3	4.5±0.5	5.0±0.5	3.4±0.2	3.3±0.5
Stem	10.2±0.9	9.2±0.6	9.8±0.9	8.8±0.4	10.6±0.7	8.9±0.6
Tap Root	3.3±0.1	3.4±0.3	-	-	-	-
Coarse Roots	1.8±0.1	1.8±0.2	-	-	-	-
Total Above	19.2±2.0	18.0±1.4	16.5±1.2	16.6±1.0	16.5±0.8	15.9±1.3
Total Below	5.0±0.3	5.2±0.5	-	-	-	-
Total	24.2±1.9	23.2±1.5	-	-	-	-

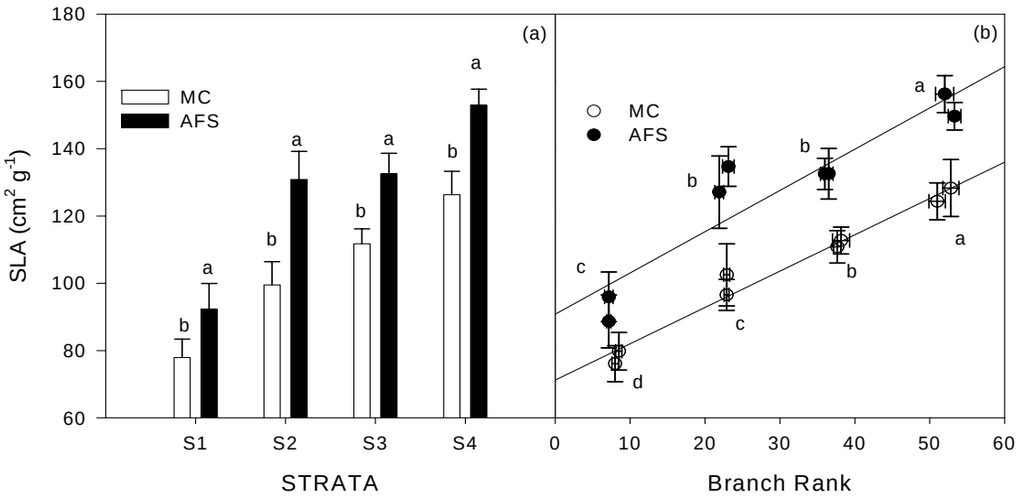


Figure 41. (a) Mean specific leaf area (SLA) of coffee at different plant strata in monoculture (MC) and an agroforestry system (AFS). (b) Relationships between leaf position within the plant canopy and the mean specific leaf area of coffee in monoculture (MC) and in an agroforestry system (AFS) in San Pedro de Barva, Costa Rica. Vertical bars denote SE and different letters denote statistical difference (p=0.05). S1: upper coffee canopy stratum; S2: middle upper coffee canopy stratum; S3: middle low coffee canopy stratum; S4: low coffee canopy stratum. (MC: SLA=71.2+1.08BR, R^2=0.97; AFS: SLA=90.8+1.22BR, R^2=0.87).

Table 10. Effects of the shade tree on coffee leaf traits in monoculture (MC) and in an agroforestry system (AFS) in San Pedro de Barva, Costa Rica. Means are presented ± SE, different letters within a line indicate a significant difference between AFS and MC, Turkey, p=0.05.

	MC			AFS		
	August 2003	February 2004	September 2004	August 2003	February 2004	September 2004
Leaf width (cm)	4.2±0.03b	3.4±0.04b	4.0±0.03b	4.8±0.05a	4.6±0.09a	4.5±0.08a
Leaf length (cm)	9.3±0.07b	7.5±0.08b	8.4±0.07b	10.5±0.08a	10.2±0.19a	10.1±0.12a
Leaf area (cm^2)	30.1±0.4b	21.9±0.4b	28.7±0.5b	38.6±0.7a	36.9±0.5a	34.7±0.7a

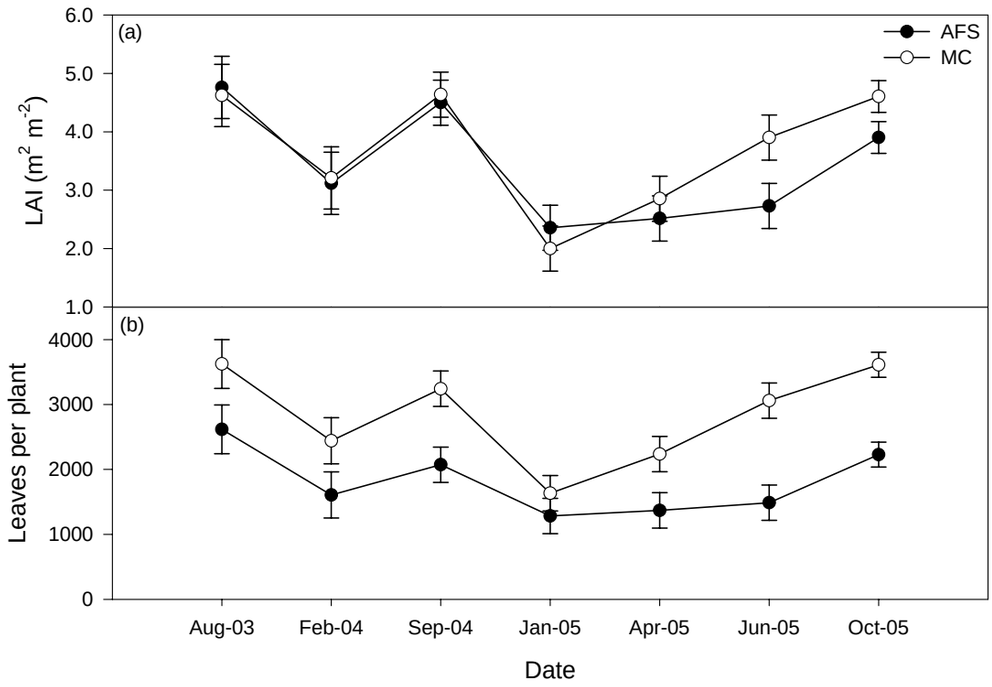


Figure 42. Leaf area index (a) and number of leaves per plant (b) of coffee plants in monoculture (MC) and in an agroforestry system (AFS) in San Pedro de Barva, Costa Rica.

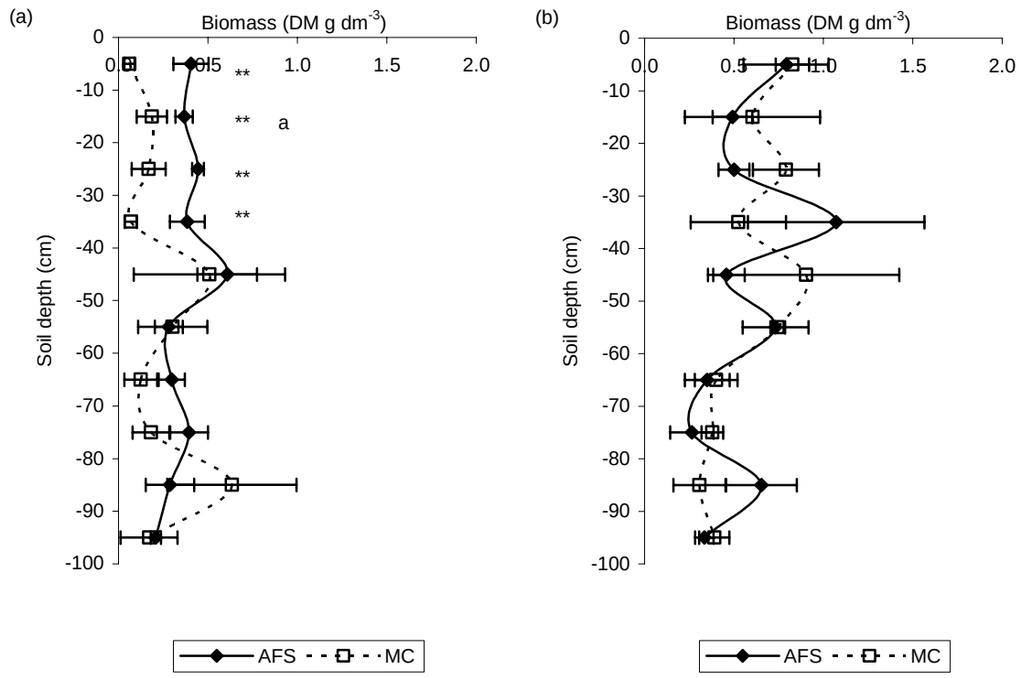


Figure 43. Mean total root biomass (*Inga desnsiflora* + *Coffea arabica*) at different soil depths in monoculture (MC) and in an agroforestry system (AFS) in San Pedro de Barva, Costa Rica, (a) Coffee inter-row and (b) Coffee row. Vertical bars denote SE and ** denote statistically significant differences (α=0.05).

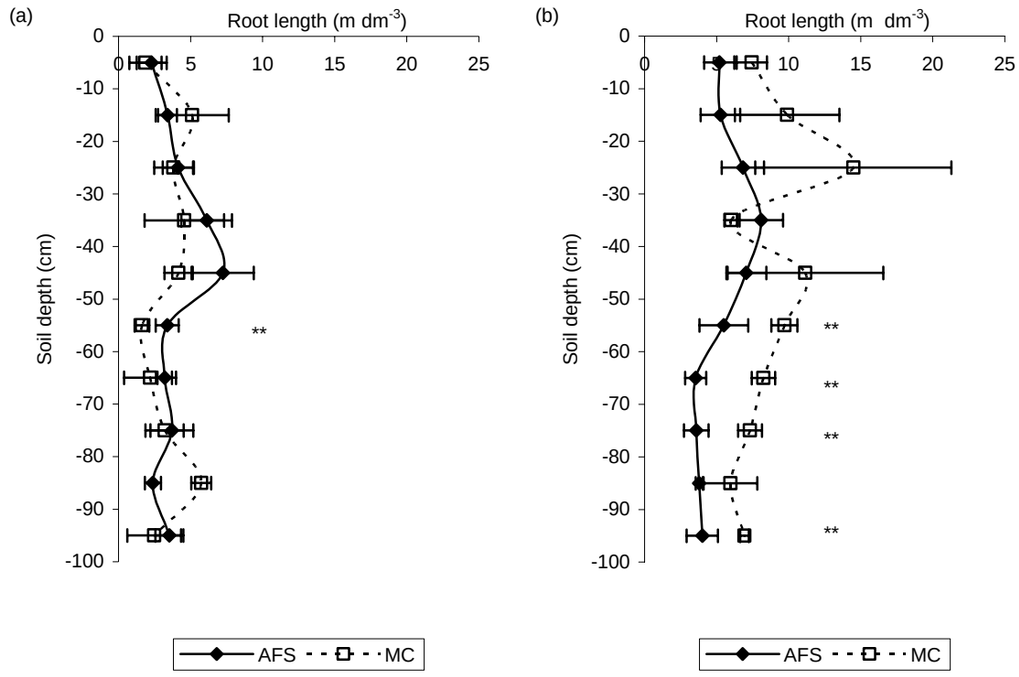


Figure 44. Mean total root length (*Inga densiflora* + *Coffea arabica*) at different soil depths in monoculture (MC) and an agroforestry system (AFS) in San Pedro de Barva, Costa Rica, (a) Coffee inter-row and (b) Coffee row. Vertical bars denote SE and ** denote statistically significant differences (α=0.05).

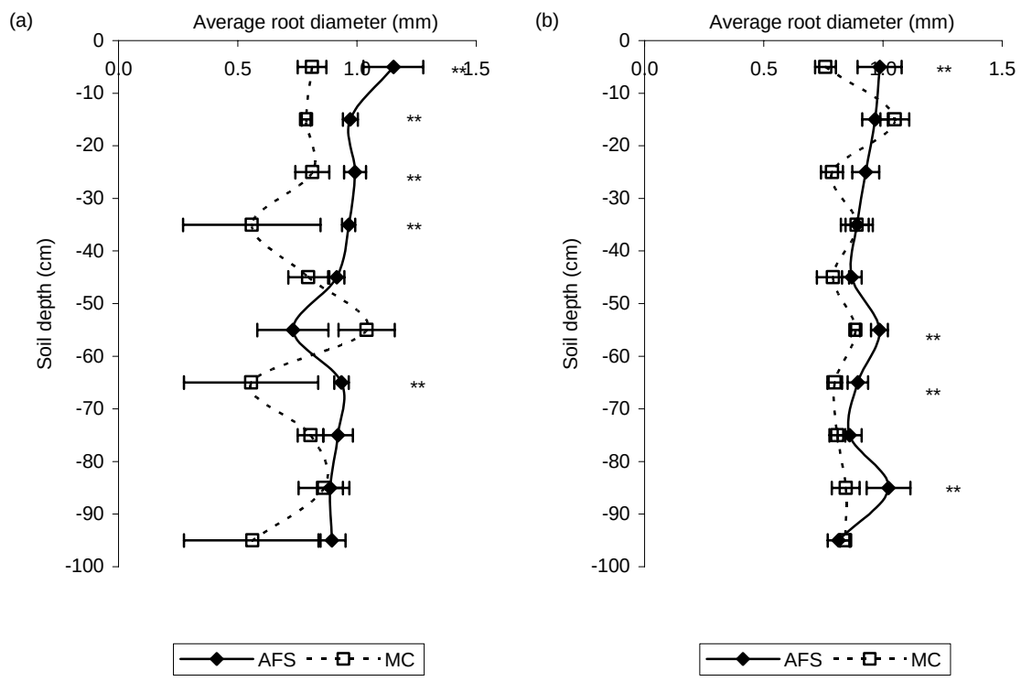


Figure 45. Mean root diameter (*Inga desnsiflora* + *Coffea arabica*) at different soil depths in monoculture and an agroforestry system (AFS) in San Pedro de Barva, Costa Rica, (a) Coffee inter-row and (b) Coffee row. Vertical bars denote SE and ** denote statistically significant differences (α=0.05).

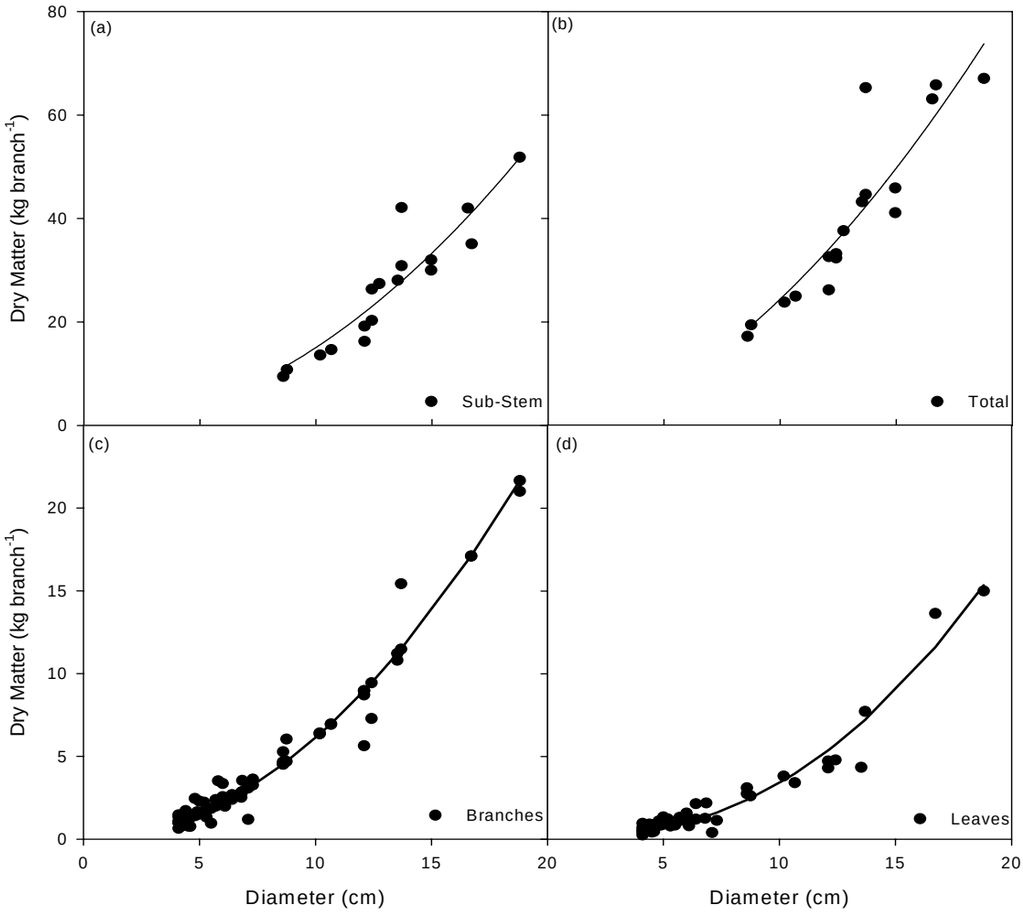


Figure 46. Relationships between (a) sub-stem, (b) total aerial, (c) branches, and (d) leaves dry matter and stem diameter at 130 cm for *Inga densiflora* in an agroforestry system at San Pedro de Barva, Costa Rica.(a: $SSDM=0.128D^{2.04}$, $R^2=0.93$; b: $TADM=0.34D^{1.8}$, $R^2=0.92$; c: $BDM=0.06D^{1.99}$, $R^2=0.93$; d: $LDM=0.014D^{2.36}$, $R^2=0.92$)

Table 11. Biomass (DM in Mg ha^{-1}) of the different components of *I. densiflora* aerial part in agroforestry system (AFS) in San Pedro de Barva, Costa Rica.

	2002	2003	2004	2005
	Mg ha^{-1}			
Stem	7.2	12.2	15.4	18.4
Branches	3.7	5.4	6.3	7.4
Leaves	1.9	3.0	3.7	4.5
Total	12.8	20.6	25.3	30.4

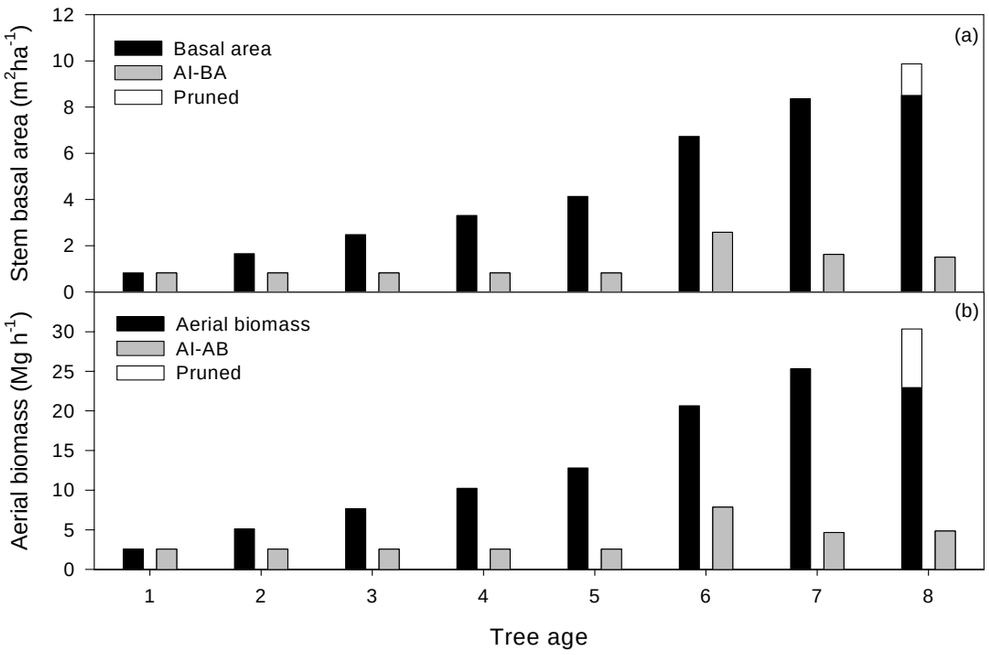


Figure 17. Stem Basal area (a) and total aerial biomass (b) of *Inga densiflora* in an agroforestry system in San Pedro de Barva, Costa Rica. (IA denote Annual increment for each variable).

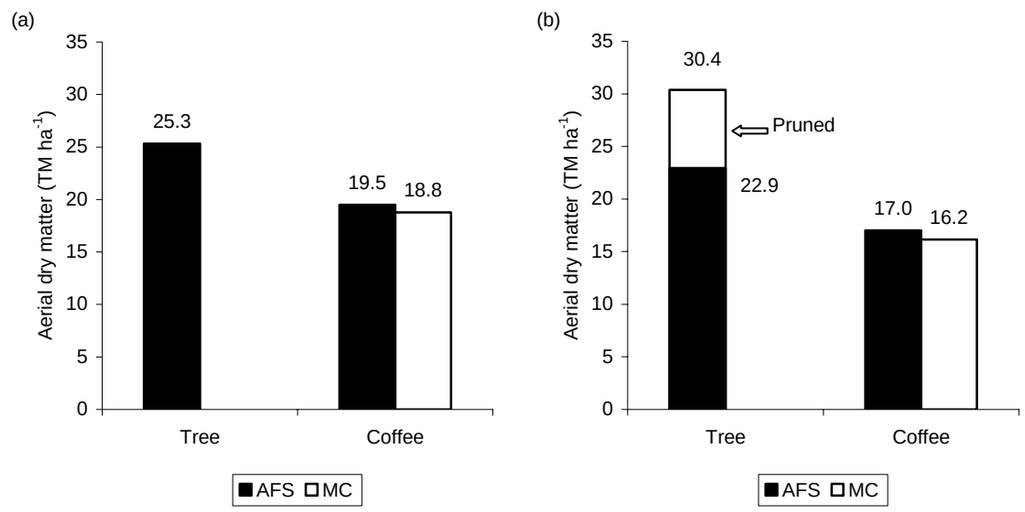


Figure 18. *Inga densiflora* (tree) and coffee aerial biomasses in monoculture (MC) and an agroforestry system (AFS) in San Pedro de Barva, Costa Rica, for (a) 2004 and (b) 2005.

Article 2

Total rainfall interception in coffee (*Coffea arabica*) monoculture and coffee – *Inga densiflo*ra agroforestry system in Costa Rica

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Keywords: troughfall, stemflow, evaporation, wet tropics, multi-strata system, water cycle

Prepared for Journal of Hydrology

Total rainfall interception in coffee (*Coffea arabica*) monoculture and coffee – *Inga densiflo*ra agroforestry system in Costa Rica

Abstract

The inclusion of shade trees in coffee systems can be expected to influence the magnitude of canopy water fluxes such as rainfall interception. Partitioning of gross rainfall through the canopy was studied in two coffee agricultural systems: (1) coffee monoculture (MC) and (2) coffee grown in an agroforestry system (AFS) with *Inga densiflora* as the associated shade tree species, in Costa Rica under annual rainfall of 2300mm. Throughfall, stemflow and gross rainfall were monitored after each rain event over the period of June to November of 2005, which represents 70 % of the cumulative yearly rainfall. Throughfall was also monitored the previous year from June to September 2004. In 2004, the measured throughfall accounted for 72.8% and 85.1% in the AFS and MC, respectively. The estimated stemflow accounted for 11.7% and 6.0% and interception loss for 15.5% and 8.9% in the AFS and MC, respectively. The high differences in throughfall and canopy interception loss between systems can be attributed to high differences in LAI. During the 2005 monitoring period, throughfall accounted for 76.8 and 83.2 % of total rainfall, stemflow for 11.8 and 7.2% and interception loss for 11.4 and 9.7% for the AFS and coffee monoculture, respectively. In the AFS, the coffee plants and the shade trees accounted for 88% and 12% of total stemflow, respectively. The high coffee stemflow, registered in both systems, is the result of the compact coffee architecture composed of multiple-stems. The average funneling ratio for the coffee plants was estimated to be 40 and 60 in the monoculture and the AFS, respectively. The differences in coffee stemflow measured in both systems can be attributed to the shade effect on coffee architecture. This study shows the small influence of shade trees on the total rain interception when the total LAI (tree+coffee) was not higher in the AFS than the MC, whereas shade trees produce differences in water fluxes to the soil by reducing throughfall while increasing total stemflow.

Introduction

More than 32% of the world coffee is grown in Latin America, where it is one of the major sources of foreign exchange (Perfecto 1996). The coffee plant (*Coffea arabica* L.) is a species native of the tropical forests of Ethiopia, where it grows in a complex multi-strata forest (Maestri y Barros, 1977). In Central America, coffee is traditionally grown in agroforestry systems as an under-story plant, consistently with its shade tolerant nature (Franck et al. 2005). In this region, leguminous shade tree species, e.g. *Gliricidia sepium*, *Erythrina spp* or *Inga spp*, predominate in coffee agroforestry systems (AFS) and are managed principally for the benefit of coffee grown underneath (Escalante, 1985; Muschler, 1999; Beer et al.; 1998). This arrangement generally produces a stable production system, providing soil protection by litter from negative effects such as compaction and high runoff and erosion, a moderation effect on microclimate (humidity and temperature) and renewal of soil organic matter (Beer et al. 1998, Muschler, 1999; Fournier, 1988).

The presence of shade trees in coffee plantations influences the hydrologic cycle by affecting rainfall interception, runoff, evapo-transpiration, soil water uptake and infiltration. Three studies have been undertaken in Mexico, Brazil and Costa Rica on coffee and shade tree water consumption in coffee AFS (Jiménez and Goldberg, 1992; van Kanten and Vaast, 2006) or coffee under various irradiance regimes (Fahl et al., 2000) showing that 1) coffee transpiration by unit leaf area decreased with increasing shade level and 2) combined water consumption of coffee and shade tree was higher than that of coffee in monoculture. However, less information is available in the literature on the effects of the shade stratum on the other components of the hydrological cycle, particularly on the rainfall interception loss by coffee and shade tree canopies. The canopy interception loss, which is the water intercepted by the canopy and evaporated to the atmosphere is often an important component of the water balance influencing directly net rainfall input to the soil and water drainage. It represents on average 26% and 13% of rainfall in coniferous forest and foliated deciduous forests, respectively. In tropical rain forest communities, the interception loss represents from 13% to 17% of rainfall (Carlyle-Moses, 2004). In forests of Western Amazonia, the interception loss averages from 12% to 17 % of the rainfall depending of forest canopy cover (Tobon Marin *et al*., 1999) while in Chile it represents from 11% to 39% for broad leaf forests and from 10% to 37% for coniferous forests (Huber and Iroumé, 2001).

Canopy interception loss depends greatly on properties of the respective tree species, such as leaf area and branch angles, vegetation storage capacity (canopy area and stem water storage capacity), evaporation during rainfall, as well as rainfall size and frequency (Hall, 2003). In that sense, trees in agroforestry systems can potentially increase the interception loss due to an increment of overall vegetation storage capacity. Trees can also influence the interception loss, via a modification of the plantation structure (one layer versus two layer system). For example, Huber and Iroumé (2001) found that multi-

strata broad leaf native forests can intercept more rain due to the re-interception of water from higher canopy levels by lower canopies in comparison to plantations of coniferous, generally managed as a single layer system with dominant and co-dominant trees, even if a higher interception loss in coniferous forests is expected, by the high water interfacial tension at the surface of needles and the large LAI.

Most of the studies on interception loss have been carried out in temperate and tropical forests and few publications are found in the literature regarding tropical perennial agricultural systems. Studies of interception in perennial crops (cocoa) show a 13-27% of rain interception, depending on the leaf area index (LAI) and phenological stage (Jaramillo, 2003). Imbach et al. (1989) found an interception loss of 14 and 16 % in cocoa agroforestry systems with *Erythrina poepigiana* and *Cordia alliodora*, respectively. Jaramillo and Chaves (1998 & 1999) found interception losses in coffee agroforestry systems with *Inga sp* that were 2% and 10 % higher than that of a tropical rain forest and a coffee monoculture, respectively.

Generally, throughfall in tropical forests represents 70% to 97% of rainfall in comparison to stemflow with 1%-2%, which is generally ignored in the water balance (Tobon Marin *et al*., 1999; Holscher et al. 2004). Nevertheless, stemflow can vary from 1% to 13% of rainfall in coniferous plantations and from 1% to 8% in broad leaf forests (Huber and Iroumé, 2001). In agricultural systems with banana plantain whose architecture favors a high stemflow, it represents around 9-10% of rainfall (Jimenez and Lhomme, 1994). Higher stemflow values (8-18%) have been reported for smaller-stature forests or forests with a large proportion of small or multiple stem trees (Levia and Frost, 2003). Additionally, it seems that the understory vegetation plays a more important role in the stemflow generation in forest and heterogeneous vegetation. Odiar *et al.* (2004) working in a rainforest of Borneo during a full year cycle, observed that stemflow accounted for 3.5% of gross rainfall, but the understory trees (DBH < 10 cm) played an important role in terms of stemflow, representing 77% of the total stemflow and 90% of the stemflow generated in rainfall events with less than 20 mm.

Thus, the introduction of a shade tree in coffee monoculture could have negative impacts on water balance by increasing the canopy interception losses. The present study was designed to address this question by measuring rainfall and its partitioning after entering the canopy in a coffee monoculture and a coffee agroforestry system. This paper focused on the analysis of two year measurements of rainfall, throughfall, stemflow, the resultant evaporation and the related structure of these systems.

Materials and methods

Site description and experimental design

The study was conducted on the experimental farm of the Research Station of the Coffee Institute of Costa Rica (Icafé), located in San Pedro de Barva in the Central Valley of Costa Rica (10°02'16'' N, 84°08'17'' O; 1200 m above sea level). The mean annual temperature is 21°C and annual precipitation 2300 mm with a pronounced dry season from January to April. The soil, derived from the weathering of volcanic ashes, belongs to Andisols and is classified as a Dystric Haplustands (Mata and Ramírez 1999).

The experimental design included two adjacent coffee plots: a shaded one (1500 m^2) and a second one without trees (1200m^2). In both plots, coffee (*Coffea arabica* L. var. Caturra) was planted in 1997, following a coffee monoculture, with a spacing of 2 m between rows and 1 m within the rows, which resulted in 5000 and 4773 coffee plants ha^{-1} for the monoculture and AFS, respectively. An average of 3 coffee stems was placed in each planting hole, to get three stems per plant. In the AFS, *Inga densiflora* (Benth) was planted within the coffee rows at a spacing of 6 x 6 m (277 trees ha^{-1}). The plots were equally intensively managed with a fertilization of 250 kg N ha^{-1}, 30 kg P ha^{-1} (triple superphosphate), 100 kg K ha^{-1} (KCl), 80 kg Mg ha^{-1} (MgO), 5 B_2O_3; 50 S and 60 CaO kg ha^{-1} yr^{-1}.

Plantation structure characteristics

In the AFS, the diameter at breast height (DBH) of the 38 multi-stem trees was measured in July 2004 and August 2005 to estimate the tree basal area of the plantation. Simultaneously, tree biomass measurements were carried out. According to the architecture of the tree species which consisted of a short simple trunk ramified into two or three sub-vertical branches (substems), an allometric relationship between DBH and biomass of individual vertical branches was determined. A sample of 10 and 7 vertical branches, representing all the diameter classes, was selected among the 38 trees in 2004 and 2005, respectively. These randomly selected branches were cut and substems, secondary branches and leaves were separated and weighed. Additionally, 100 hemispherical photographs above the coffee canopy were taken to estimate canopy openness and LAI of the tree layer in the AFS during July 2004 and August 2005. The hemispherical photographs were analyzed with the Gap Light Analyzer (GLA) software.

In both systems, the stem basal diameter (at 10 cm from the ground) of 156 coffee bushes was measured in a sub-plot area of 312 m^2, during July 2004 and August 2005. Simultaneously, the leaf area of 8 coffee bushes per system was measured to estimate LAI. Biomass measurements were carried out in eight coffee bushes in 2004 and 2005, respectively, where stem, branches and leaves were weighed separately. Canopy storage capacity was estimated by from data of LAI multiplied by the mean water storage capacity of both species, the mean water storage capacity was estimated in seven groups of leaves with an average surface of 1200 cm^2 for each species. The mean water storage

capacity of the leaves was estimated as the difference between the weigh of fresh leaves (recently cut) and the weigh of the leaves wet by the immersion in water for 5 minutes, this difference in water weigh was divided by the surface of the leaves.

Microclimate data

An automatic weather station was installed in an open area next to the experimental plots. Relative humidity (RH in %) and air temperature (Temp in °C) were measured by sensors (HMP45C, Campbell Scientific Corp., Logan, UT) at a height of 2 m. The photosynthetic photon flux density (PPFD) was measured with quantum sensors (SOLEMS PAR-CBE 80, Palaiseau, France) and wind speed with an anemometer (Model 05103-5 Wind-monitor) also installed at a height of 2 m. Rainfall was measured with a tipping bucket gauge (Model ARG 100), with a resolution of 0.2 mm, providing information on intensity and duration of every rainfall. Values were measured every 30s and averages over 15 min were recorded with a datalogger (CR10X Campbell Scientific Instruments). Additionally, two manual standard rain gauges were installed in the field and daily monitored in the morning hours after each rain event of the previous day since rain mainly falls during afternoon hours at the study site.

Throughfall

Throughfall was monitored from June to September in 2004 and from May to November in 2005 with home made rain gauges consisting in plastic bottles (height: 25 cm; sampling area: 82 cm^2) that were placed at ground level. In each plot, 72 rain gauges were distributed in 12 sets (replications), each composed of 6 rain gauges located at various distances from the coffee stem, to take into account the heterogeneity of coffee canopies. As shown on Figure 1, The 6 rain gauges were placed on the coffee row and in the inter-row (at 0 m, 0.5 m and 1.0 m from the coffee row). To take into account the natural variability in throughfall produced by the shade tree canopies, the 72 rain gauges were distributed in three repetitions of four sets (with 6 rain gauges) and located at various distances from the *I. densiflora* stems (1.0, 2.2, 3.0 and 3.6 m) as presented in figure 1. In the monoculture plot, the sets of rain gauges were placed at 4 m to 8 m apart in a rectangular systematic design.

Stemflow of Inga densiflora

Stemflow on the shading trees (*I. densiflora*) was measured on 6 trees using collars constructed with 25 mm thick polyethylene plastic tubes that were slit, opened and then sealed to the stem in an upward spiral. Water collected by the collar was diverted by flexible tubing into a bucket placed on the floor. The stemflow volume of each tree was measured after each rain event. To estimate daily stemflow of trees in the plot (mm d^{-1}), mean stemflow volumes per tree was multiplied by the density of trees (277 stems ha^{-1}).

Stemflow of coffee plants

Coffee stemflow was measured on 12 plants in each coffee system. Each coffee plant had an average of 3 stems. The coffee stemflow device consisted in a collecting cup sealed around the stem.Water collected in each cup was diverted by a plastic flexible tubing to a bucket placed on the floor. To estimate daily coffee stemflow (mm d^{-1}), the mean stemflow volume per stem was multiplied by the respective coffee density of the two systems. For daily rainfall of above 40 mm the stemflow volume generally reached the capacity of the collectors. Therefore, above this threshold, the stemflow was estimated using relation developed for daily rainfall < 40 mm.

Canopy interception loss

The canopy interception loss was calculated in both systems for each rainfall events, as the difference between the registered gross rainfall in the open and the amount of measured throughfall plus stemflow.

Data analysis

Statistical analyses were performed using various Statistical Analysis System (SAS/STAT, 2004) procedures (UNIVARIATE, GLM and REG). One way analyses of variance (ANOVA) were performed for LAI, canopy openness and biomass components of the shade tree to compare differences between the systems in the 2 consecutive years of measurements. Analyses of variance were carried out to evaluate the effect of coffee systems on the throughfall and stemflow values. Linear regressions between throughfall and gross precipitation were developed and the difference of slopes and intercepts of regressions for each system was tested. Regression equations between stemflow and gross rainfall were performed and the significance of the coefficients was tested by the t-statistic.

Results

Tree and coffee structure and growth

In July of 2004 and August of 2005 at the age of seven and eight years, trees (*I. densiflora*) had dbh of 12.3 cm (min=7.5, max=17.2) and 13.5 cm (min=9.3, max=18.2) respectively, with total basal area of 8.36 and 8.51 m^2 ha^{-1}. LAI of trees estimated by hemispherical photographs was 1.32 and 1.22 for 2004 and 2005, respectively (Table 1). These data corresponded to a lower leaf tree biomass and higher canopy openness in 2005 than in 2004. Even if the tree basal area and stem biomass were higher in 2005, trees presented lower LAI than in 2004. The lower LAI of *I. densiflora* trees in 2005 can be associated with a lower leaf biomass per tree in 2005, due to the pruning of low branches for shade control in October 2004. In addition, a lower tree density occurred in 2005, due to the fact that one vertical branch from 10 individual trees was cut in July 2004 to develop allometric equations for tree biomass evaluation.

During the wet season of 2004, there was no difference in LAI of coffee plants between agroforestry system (AFS) and monoculture (MC), with an estimated LAI of 4.64 and 4.71, respectively. However, coffee LAI showed a significant difference between both systems in the wet season 2005 with an estimated LAI of 3.80 and 4.60 for AFS and MC, respectively. Shade increased coffee leaf width, length and area but the larger number of leaves per coffee bush (or plant) in the MC system (data not shown) resulted in similar LAI in both systems in 2004 and higher LAI in MC in 2005. Additionally, LAI of trees estimated by hemispherical photographs was 1.32 and 1.22 m^2 m^{-2} for 2004 and 2005, respectively, showing a small but significant difference, even if LAI estimation from photographs are not very precise and fully reliable. In 2004, total LAI (coffee + tree) was higher in AFS (5.96) than in MC (4.71) whereas rather similar values of 5.02 and 4.60 respectively were found in 2005. The total coffee basal area at 10 cm depth was higher in monoculture during the two consecutive years, due to bigger stem diameter and a higher coffee plants density in the MC (Table 1). Additionally, the height of coffee plants under shade was significantly higher (2.41 m) compared to plants in the MC (1.95 m). Taller stems and longer branches (visual observation) of coffee plants under shade was confirmed by the larger stem and branches biomass of coffee in the AFS than in MC (Table1) although the difference was significant ($P < 0.05$) only for stems in 2005.

Rainfall characteristics

The annual rainfall was particularly high with 3245 and 2684 mm during 2004 and 2005, respectively; when compared to the average historical average of the site (2300mm). Rainfall in the area was unevenly distributed throughout the year with 3057 mm (94%) and 2495 mm (93%) during the wet season from May to November, in 2004 and 2005, respectively. The monthly rainfall during the dry season (December to April) ranged from 0 mm to 87 mm and averaged 50 mm, while during the rainy season it ranged from 167 to 645, with the highest rainfall rates in September and October (Figure 2a). Monthly Penman-Monteith reference evapo-transpiration (ETo) varied between 70 to 170 mm and

amounted to 1310 and 1178 mm yr^{-1} for 2004 and 2005, respectively. Monthly ETo was higher than monthly rainfall only from December to April (Figure 2a).

During the wet season of 2004, the total rainfall was 3050 mm, 41% of the single rain events were less than 5 mm and these events contributed to 133mm while 5% of these events were above 60mm and contributed to 933mm, representing the 28% of the total annual rainfall (Figure 2b). During the wet season of 2004, the rainfall followed a similar pattern, 37% of the rains events were less than 5 mm (105mm) and 5% (450mm)were above of 60mm, representing 17% of the total annual rainfall. However, during 2005 the total annual rainfall was lower compared to 2004, mostly due to lower cumulative rainfall during the months of May and September compared to the same months during 2004. During the wet season of 2005, a total of 151 events were recorded ranging from 0.5 mm to 105 mm and lasting between 15 min and 8 h, but with most of the events (70%) with more than 5 mm lasting between 2h to 4h. For rainfall events less than 10mm, rainfall intensity ranged between 1 to 24 mm h^{-1} with average values between 1 to 4 mm h^{-1}. On the other hand, the rainfall intensity varied on average from 11 to 14 mm h^{-1} (min=4 mm h^{-1} and max=24 mm h^{-1}) for rainfall classes of more than 10 mm (Table 2).

Throughfall

There was a significant difference in the throughfall between the AFS and the MC, additionally the spatial distribution of throughfall was significantly different in the AFS compared to MC. Thus, the throughfall measured at 50 cm from the coffee line in the AFS was significantly lower than that measured at the same position in monoculture during the two years of study (Table 3). Additionally, the variability in throughfall was quite large in both systems, but with the largest variability observed in AFS. Spatial variability of throughfall, expressed as the percent standard error (SE/mean), was larger for gross rainfall below 10 mm, ranging from 1.5 to 38% (with an average of 17% and 15 % for AFS and monoculture, respectively), while it remained almost constant at 7 % for larger rainfalls (data not shown).

A strong significant and positive linear relation was found between throughfall and gross rainfall in both systems for 2004 and 2005 (Figure 3 a, b). Regressions of throughfall versus gross rainfall were computed from 86 and 140 single events for 2004 and 2005, respectively, ranging from 0.25 to 60 mm. Statistical analyses demonstrated that regression slopes were significantly higher ($P < 0.05$) in MC than in AFS during the two consecutive years, whereas intercepts were similar for both systems. In 2004, the cumulative values of throughfall (expressed in mm and percentage of gross rainfall) for 86 rainfall events (1426 mm) from June to September were 992 mm (72.8%) and 1205 mm (85.1%) for AFS and MC, respectively. On the other hand, the difference of throughfall between systems was smaller in 2005. Values of throughfall for 151 rainfall

events (2500 mm) were 2055mm (83.2 ± 3%) and 1960 mm (76.8 ± 4%) for MC and AFS, respectively. AFS significantly (P= 0.05) reduced total throughfall during both years (2004 and 2005), with a more important effect in 2004 when compared to the MC.

Coffee stemflow

The variability of coffee stemflow depended on the gross rainfall and was higher in AFS than in MC. For daily rainfall of less than 10 mm, the SE (%) was 3.7% and 2.2% for the AFS and MC, respectively, while it was 0.5% and 0.3% for rainfall events higher than 10 mm. In general, coffee stemflow was very low for rainfall below 5 mm (0 mm for rainfall less than 2.5 mm) (table 5). On the other hand, it represented 10.2% and 7.2 % of gross rainfall higher than 10mm (and lower than 40 mm?) for AFS and monoculture, respectively. For rainfall events lower than 5mm stemflow was of low significance in water balance (Table 5). In both systems, the relationship between measured stemflow and gross rainfall could be described as a power function (rainfall < 10mm) and a linear (rainfall >10mm) function (Fig 4 a, b;Table 4). There was a significant difference in stemflow between systems; with higher values registered in AFS. The means of cumulative value of stemflow for 91 monitored rainfall events (1700 mm) were significantly ($p< 0.06$) different with values of 10.6% and 7.5% of the gross rainfall for AFS and monoculture, respectively.

Inga Stemflow

In general, the contribution of tree (*I. densiflora*) stemflow to the net rainfall in AFS was very low with a value of less than 1.2 mm for the highest rainfall events due to the low tree density in AFS in comparison with coffee density. Most of the gross rainfall events with less than 4 mm did not resulted in any tree stemflow. For gross rainfall with less than 14 mm, tree stemflow was very low representing less than 0.5 % of rainfall. The relationship between measured tree stemflow and gross rainfall could be described by a power function (Figure 4c, Table 4). The total stemflow for 110 monitored rainfall events (2000 mm) was 25 mm which represented 1.2 % of the gross rainfall.

Canopy interception loss

The canopy interception loss for small rainfalls (< 1 mm) was very close to the gross rainfall, while for rainfalls around 5 mm it represented up to 50% of the rainfall. Depending on rainfall volume, the percentage of interception loss relative to gross rainfall varied from 75% to 7.2 % and 72 to 7% for AFS and MC, respectively. The relationship between canopy interception loss (expressed in % of gross rainfall) in both systems and gross rainfall was represented by a hyperbolic equation (Figure 5). The percentage of canopy interception loss decreased with increasing rainfall from 5 to 45 mm while the percentage of stemflow remained almost constant (Table 5). Consequently throughfall increased from 24.3% and 27.6% for rainfall events below 1 mm to 80.4% and 85.4% for rainfall events above 40 mm for AFS and MC, respectively (Table 5). The total interception loss for 91 monitored rainfall events in which stemflow and throughfall

were measured (1725 mm) represented 11.4% and 9.7 % (196 mm and 167 mm) of the gross rainfall for AFS and MC, respectively. Although canopy interception loss was large in terms of % for rainfall events with less than 5 mm, in cumulative term it only represented 13% and 15 % of the total interception for AFS and MC, respectively. In other hand, for rainfall events higher than 40 mm the cumulative values of canopy interception loss represented 34% and 30% of the total interception for AFS and MC, respectively.

Cumulated throughfall, stemflow and interception were found to represent 76.8%, 11.8% and 11.4% for AFS and 83.1%, 7.2% and 9.7% for monoculture in 2005 (Table 6). Using stemflow equations developed in 2005, daily stemflow and interception loss were computed for a period in 2004 when the throughfall was monitored. For the 2004 cumulative throughfall, stemflow and interception were 72.8%, 11.7% 15.5% in the AFS and 85.1%, 6.0% and 8.9% in the MC system.

Discussion

Throughfall

Also, the variability of throughfall in both systems decreased asymptotically with an increase in gross rainfall, as already shown by Loustau et al (1992) in a plantation of Maritime pine stand and Price and Carlyle-Moses (2003) for temperate deciduous forest in Canada. For small rainfall events (< 5mm), the higher variability in AFS may be explained by spatial variation in tree canopy and also by the differences in the coffee structure as influenced by the presence of the shading trees. Longer stems and branches of coffee in the AFS than in MC, resulted in significantly lower throughfall at 50cm from the coffee line in AFS than in MC during the two years of study (Table 3). Additionally to the spatial differences between systems, there were lower values of throughfall in the AFS compared to the MC in both years; however, these significant differences in throughfall were higher in the year 2004. The differences in the throughfall between both systems can be explained by the higher total LAI (shading tree and coffee) in the AFS compared to the MC. Total LAI (coffee + tree) was higher during 2004 in AFS (5.96) than in MC (4.71) whereas values were rather similar (5.02 and 4.60 m^2 m^{-2}, respectively) during 2005. Others studies (Tobon Marin *et al*., 1999; Huber and Iroumé, 2001) have showed that canopy cover or LAI influences the canopy storage capacity, and therefore the throughfall. This explanation is also supported by the fact that there were differences in the percentage of throughfall between 2004 and 2005 under AFS, according to higher LAI in both components (shading tree and coffee) in 2004 than 2005, while in the MC no difference was observed in the percentage of throughfall, consistently with the small difference in LAI between the two years

The values of cumulative throughfall which varied between 72.8% and 85.1% of the gross rainfall for both systems, are within the ranges reported in the literature for various forest types and climatic zones (from 55 to 90%, according to canopy structure and

climatic conditions) (Marin *et al*., 1999; Huber and Iroumé, 2001). On the other hand, our data are consistent with the throughfall measured by Harmand et al. (2007) under coffee monoculture (83%) and shaded coffee with *Eucalyptus deglupta* (82%) at the low altitude zone of Costa Rica. The former two systems presented relatively low LAI of 2.74 and 3.5, respectively. However, the present values are quite different from those reported by Jaramillo (2003) in several coffee plantations of Colombia with similar climatic conditions (41-54%), where data on LAI were not reported.

Stemflow

Coffee stemflow represented up to 10% of rainfall and should not be ignored when computing plot water budget. The present study appears to be the first to monitor stemflow in coffee plantations as no reference was found in the literature, This is probably due to the fact it is ignored in hydrological studies because low stemflow values (<2%) were found in other perennial plantations (Levia and Frost, 2003).

In the present study, cumulative stemflow seems high with respect to stemflow values (0.8%-2.0%) registered in studies undertaken in rain forest conditions (Tobon Marin *et al*., 1999, Holscher et al. 2004). Nevertheless, it falls within the range (1 to 27%) mentioned by Levia and Frost (2003) in their review of stemflow studies. For cacao plantations, Levia and Frost (2003) reported cumulative stemflow of only 2% which is probably due to cacao tree structure and low tree density (generally in the range of 1000-1500 cacao plants ha^{-1} compared to over 4500 coffee plants ha^{-1}). However, the stemflow play an important role in the water balance in agricultural systems with plants that favors stemflow as in the case of banana system in which stemflow account 9-10% (Jimenez and Lhomme, 1994).

Coffee plants concentrate the inputs of water and operate as a collection funnel, therefore presenting funneling ratio (FR) values of 68 and 48 in the AFS and the MC system, compared to values of 20 for *I. densiflora* (the FR =V / (BG), where V is the stem flow volume, B is the stem basal area, G is the depth equivalent of incident gross precipitation). These values of FR are within the range of values reported by Levia and Frost (2003) in their literature review (7 to 112).

Additionally, there was an interspecific variation in the coffee FR induced by the changes of architecture due to the shading effect of Inga densiflora in AFS. The differences in the funneling ratio and resulting stemflow between AFS and MC can be explained by the differences in the architecture of the plants under shade and in MC. Shaded coffee plants were generally 40 cm taller with longer branches than the ones in MC; this can be appreciated by the significant higher stem + branches biomass in AFS (table 1). In some studies (Levia and Frost, 2003), a positive relation was observed between the stem length

and the generation of stemflow, presumably taller plants have the potential to produce greater stemflow because a greater projected stem surface area.

The differences in FR and stemflow between coffee and *I. densiflora,* can be explained by the differences in the canopy structure of both species. Larger stemflow rates are observed in small plants with multiple stems in comparison with taller trees with a single stem, due probably to the fact that horizontal or downward inclined branches of trees may not intercept rainfall to the center of the tree to be drained as stemflow, instead it can be drained as throughfall once the canopy is water satured (Tobon Marin *et al*., 1999). Due to the multi-stem architecture and compact canopy of coffee plants, a rather high stemflow is observed comparable to the ones observed in Matorral communities in Mexico where the high stemflow values were explained by a vegetation composed of small multi-stem trees (Levia and Frost, 2003; Carlyle-Moses, 2004).

Canopy interception loss

Even if throughfall and gross rainfall were highly correlated, the relationship between gross rainfall and canopy interception was less prominent, with lower coefficient of determination (0.66 and 0.67 for the ASF and MC). In others words the throughfall percentages can be predicted with high accuracy based on rainfall amounts, whereas the prediction of interception must include others parameters as rainfall characteristics. In other hand, since canopy interception loss can not be measured directly, the error associated with this flux is the residual error associated with throughfall and stemflow and this may explain the fact that canopy interception loss presented higher variability than throughfall and stemflow estimates. Daily values of canopy interception loss ranged from 0.25mm to 6.5mm and from 0.25mm to 5.0 mm in the AFS and the MC, respectively. These values of canopy interception loss seemed high since they are of the same magnitude or higher than the Penman-Monteith potential evaporation (ETo). Values of daily ETo during the wet season were in average 2.7mm, and ranged from 1.1 mm to 6.0mm, higher values ETo are found in the dry season mostly due to higher solar radiation. However, values of event canopy interception seem high, these values are similar that were found in other studies of interception in which values of interception reached 7mm, for example in the rain tropics of the Central Amazonia (Price and Carlyle-Moses, 2003; Tobon Marin, 1999; Carlylle-Moses, 2004).

The relative high difference in rainfall interception between systems was associated with a larger LAI in the AFS (6) than in the MC (4.7), in 2004 the MC presented a 15% higher throughfall in comparison to AFS; higher total interception loss, even with a higher stemflow in AFS. During 2005, a difference of only 0.4 m^2 m^{-2} in total LAI (coffee+tree) between systems was associated with lower difference in total. Though climatic conditions were similar for both systems, differences in canopy interception loss between

the AFS and the MC may be explained by differences in LAI during both years. Thus, these data support the general hypothesis that vegetation with higher LAI intercepts higher rainfall, since LAI played a major role in the interception loss via a direct increase storage capacity of the canopy, surface of evaporation and consequent evaporation flux.

In addition, the trees affected the partitioning of gross rainfall into throughfall and stemflow. Thus under similar LAI (for instance during 2005), the trees presented a small impact on total interception, but influenced the water fluxes. In the AFS the throughfall was lower than in the monoculture systems in all the categories of rainfall, but compensated partially by a larger stemflow. Modifying coffee architecture, shade trees increased the funneling ratio of coffee plants resulting in lower throughfall and higher coffee stemflow rates under shade. Globally, compared to MC, the AFS reduced total annual throughfall and increased annual stemflow, resulting in rather similar total interception rate for both systems when LAI was similar. However, when the inclusion of the tree resulted in larger LAI of the system, not only the partitioning of gross rainfall was modified but also the total rainfall interception was increased in the AFS in comparison to the MC.

Conclusion

Associated trees influenced rainfall loss through canopy interception via an increase in the total LAI, and hence enhanced canopy storage capacity and surface of evaporation. This study shows a small influence of trees (*I. densiflora*) on the total interception loss in coffee agroforestry systems in which the total LAI (tree + coffee) is not significantly higher than the monoculture. The higher increment in the interception loss in the AFS compared to MC ocurred when LAI (tree+coffee) was also higher in the AFS compared to MC. Even when trees were pruned and small differences in LAI and canopy interception loss were found between systems, shade trees affected the partitioning of gross rainfall, modifying its spatial pattern, reducing throughfall, and increasing stemflow. Differences on coffee stemflow between AFS and MC were due to a modification of the architecture of coffee plants.

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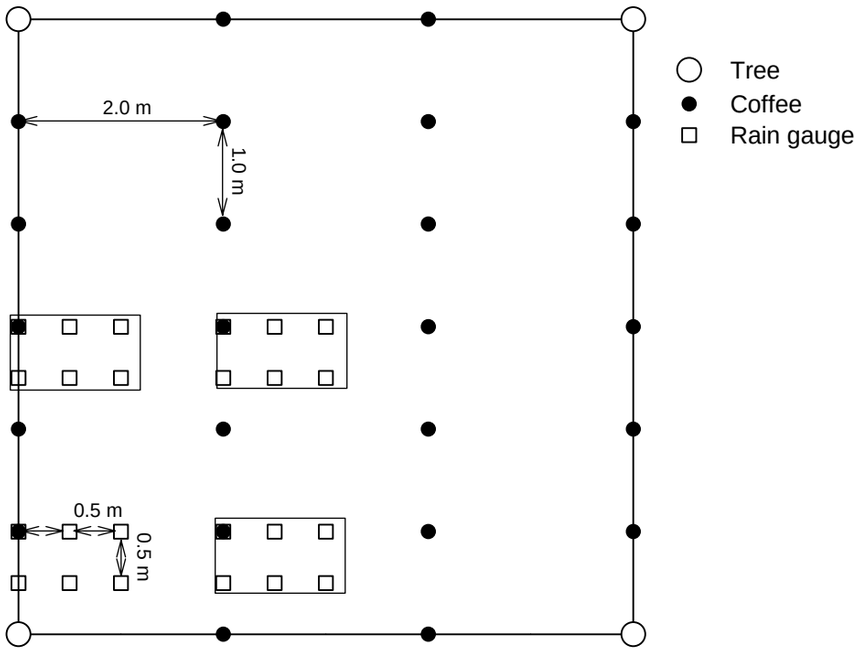


Figure 47. **.** Schematic representation of one repetition layout of the throughfall collectors in the AFS with respect to the coffee plants and *Inga densiflora* stems.

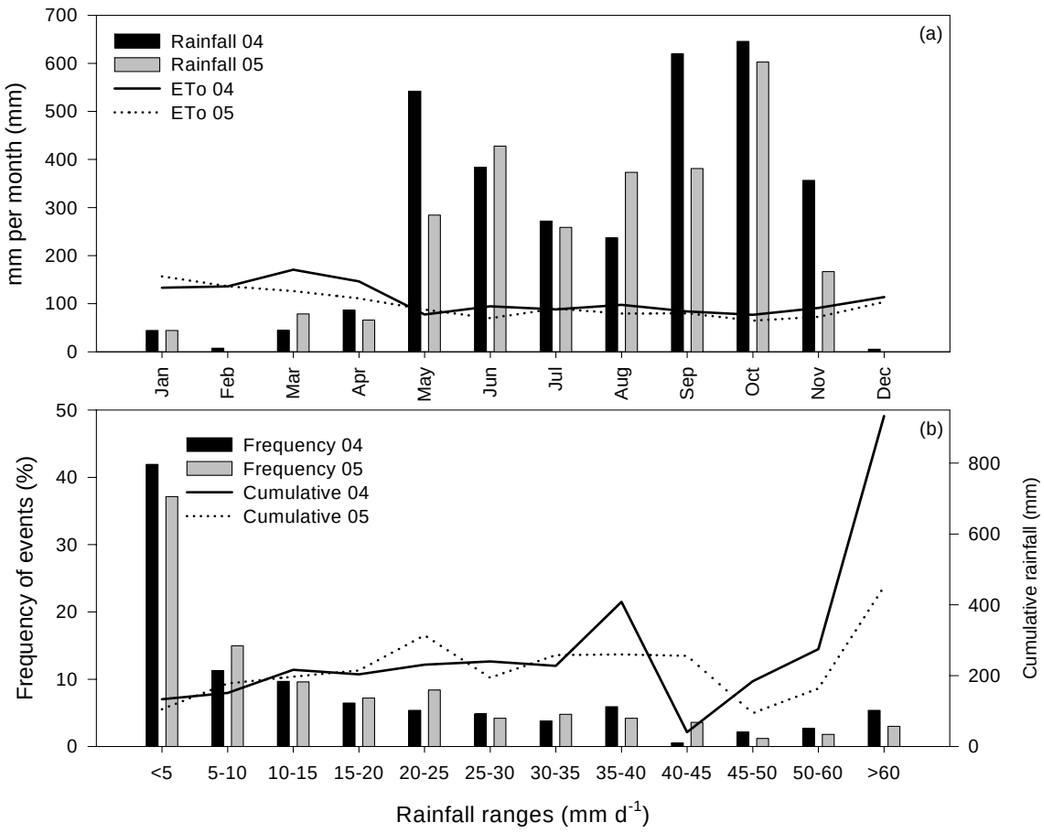


Figure 48. Rainfall characteristics at the research site in the Central Valley of Costa Rica for the years 2004 and 2005. (a) Monthly rainfall and ETo; and (b) frequency and cumulative values of rainfall events for classes of gross rainfall.

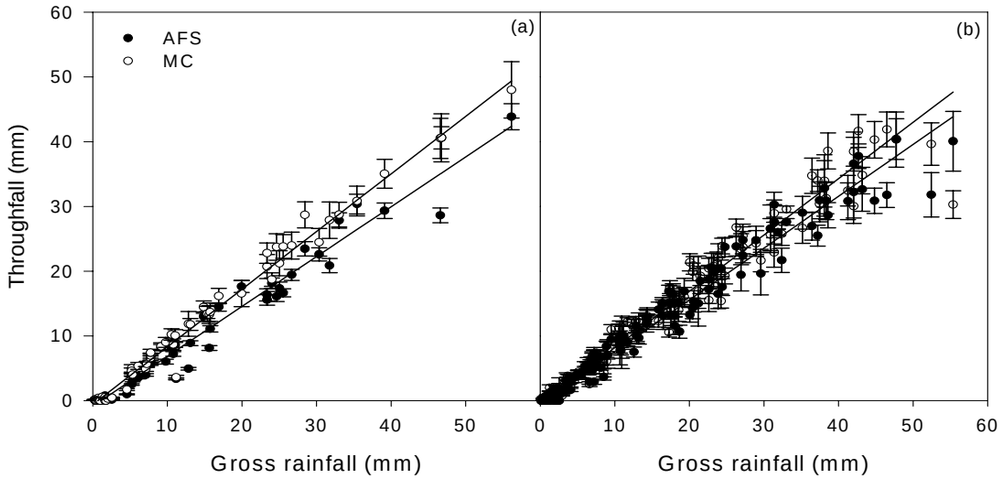


Figure 49. Average throughfall (TF with standard error) versus gross rainfall (GR) in 2004 (a) and 2005(b) in two coffee agricultural systems (AFS and MC) in the Central Valley of Costa Rica (for 2004, MC: r^2= 0.99, TF=-0.59+0.90*GR; AFS: r^2=0.97, TF=-0.85+0.78*GR; for 2005, MC: r^2= 0.97, TF=-0.53+0.87*GR; AFS: r^2= 0.97, TF=-0.45+0.80*GR).

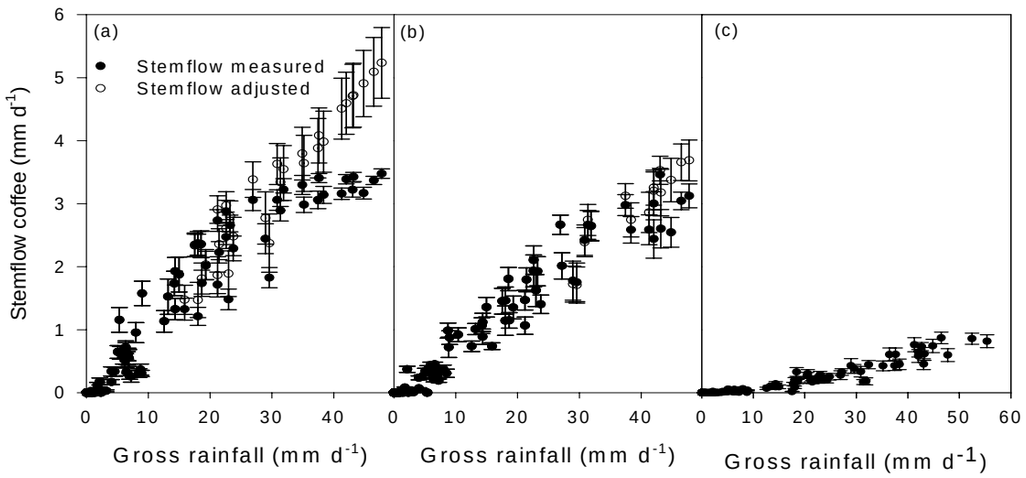


Figure 50. Stemflow (mean ±SE) versus gross rainfall for (a) coffee in AFS, (b) coffee in MC and (c) Inga densiflora in AFS in San Pedro de Barva (Central Valley of Costa Rica) in 2005.

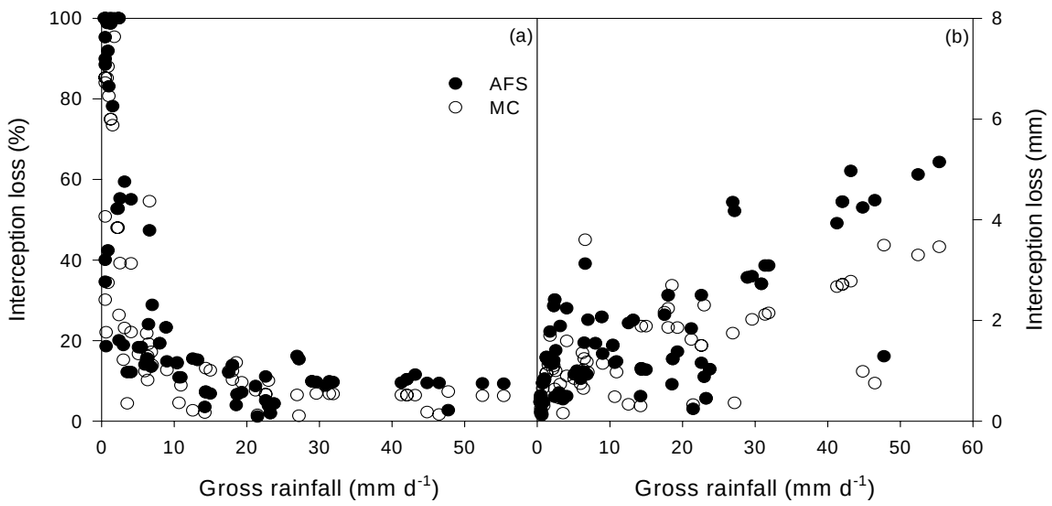


Figure 51. Rainfall loss through canopy interception as a function of gross rainfall in an agroforestry system (AFS) and coffee monoculture in the Central Valley of Costa Rica during 2005.

Table 12. Structure parameters of two coffee systems (monoculture and shaded coffee with *Inga densifllora*) at San Pedro de Barva in the Central Valley of Costa Rica in 2005.

Parameter	Shaded coffee				Monoculture	
	I. densiflora		Coffee		Coffee	
	2004	2005	2004	2005	2004	2005
Canopy openness (%)	30.2± 0.6	32.8± 0.7				
LAI (m^2 m^{-2})	1.32±0.03	1.22±0.03	4.64±0.38a	3.80+0.22b	4.71±0.39a	4.60±0.27a
Canopy storage capacity (mm)	0.18±0.01	0.1±0.01	0.42±0.03	0.34±0.02	0.42±0.04	0.414±0.02
Mean diameter (cm)	12.4	13.5	3.99±0.13b	4.09±0.14b	4.65±0.14a	4.73± 0.15a
Basal area (m^2)	8.36	8.51	13.6	14.1	14.9	16.1
Mean height (m)	8.18±0.37	9.42±0.35	2.41±3a	2.45±5a	1.95±6b	2.01±6b
Biomass						
-Stem (kg $plant^{-1}$)	20.9±3.4b	24.4±3.8a	2.13±0.18a	2.21±0.22a	1.85±0.12a	1.79±0.17b
-Branches (kg $plant^{-1}$)	8.9± 1.3 a	8.9± 1.4b	1.11±0.12a	0.70±0.06a	0.99±0.05a	0.66±0.14a
-Leaves (kg $plant^{-1}$)	5.2±1.0a	4.3± 0.5b	0.77±0.97a	0.54±0.06b	0.76±0.08a	0.73±0.12a

- The statistical test performed on tree biomass compared the year
- The statistical test performed on coffee biomass compared coffee plantations
- Canopy storage capacity was estimated from data of LAI and mean capacity of storage of leaves of *I. densiflora* (0.14 kg m^{-2}) and coffee (0.09 kg m^{-2}).
- Basal area and mean diameter are at breast height (130 cm) for tree and at 10 cm height for coffee

Table 13. Rainfall characteristics (rainfall duration, rainfall intensity and daily gross rainfall) for 7 rainfall classes at San Pedro de Barva in the Central Valley of Costa Rica in 2005.

Rainfall ranges (mm)	N*	Rainfall duration (min)	Rainfall intensity (mm h^{-1})	Gross rainfall (mm d^{-1})
< 1	20	**25.9±4.6**	**1.3±0.2**	**0.6±0.1**
1-5	31	**59.1±10.8**	**4.0±1.1**	**2.4±0.2**
5-10	23	**145±19.1**	**3.8±0.6**	**7.0±0.2**
10-20	21	**130.7±26.5**	**11.1±1.9**	**15.4±0.6**
20-30	20	**147.3±29.9**	**13.4±2.1**	**24.1±0.6**
30-40	10	**217.5±42.9**	**11.7±2.3**	**34.8±0.9**
> 40	13	**336±78.9**	**12.2±3.0**	**59.3±6.4**

* number of monitored rainfall events

Table 14. Effects of the agricultural system, position of rain gauges and distance from *I. densiflora* shade tree on throughfall (expressed in percentage of gross rainfall) in the Central Valley of Costa Rica in 2004 and 2005. Within each line, values followed by the same letter are not significantly different (P < 0.05)

Factor	row	interrow 0.5 m from row	interrow 1. m from row	Average
2004 AFS	54.1±6.8b	60.5±6.8b	93.8±6.8a	**69.5±2.5**
2004 MC	64.3±9.6b	92.3±9.6a	97.5±9.6a	**84.7±5.3**
2005 AFS	72.9±4.5b	71.6±4.5b	93.2±4.5a	**79.3±2.1**
2005 MC	71.0±4.5b	87.7±4.5a	93.0±4.5a	**83.9±2.1**

Table 15. Statistical summary of regressions of daily stemflow versus gross rainfall in two different coffee agricultural systems in the Central Valley of Costa Rica. (Note: The equation for coffee stemflow is $S_{CP}= a(P_g^b)$ for daily rainfall < 10 mm and $S_{CL}= a + bP_{g,}$, for rainfall > 10 mm; S_C is the daily coffee stemflow amount (mm) and P_g is gross rainfall (mm). The equation for Inga stemflow is $S_I= a(P_g^b)$; S_I is the daily *Inga* tree stemflow (mm)).

Coffee system	a	b	b se	R^2	*n*	*P*
Monoculture						
Coffee (S_{CP})	0.004	2.313	0.495	0.917	82	0.0001
Coffee (S_{CL})	0.176	0.068	0.005			0.0001
AFS						
Coffee (S_{CP})	0.025	1.641	0.303	0.955	82	0.0001
Coffee (S_{CL})	0.054	0.106	0.006			0.0001
Inga	0.002	1.578	0.077	0.929	102	0.0001

*Note that the limit of the upper limit of the regression for coffee stem-flow is 45 mm while the upper limit of the Inga stem-flow is 60 mm.

Table 16. Throughfall, stemflow and canopy interception loss percentages of daily gross rainfall for seven rainfall classes in two different coffee agricultural systems (coffee agroforestry system: AFS and coffee monoculture) in the Central Valley of Costa Rica in 2005.

Rainfall ranges	N	% Throughfall		% Stemflow			% Interception	
		AFS	MC	AFS		MC	AFS	MC
				Inga densiflora	Coffee	Coffee		
< 1	12	24.3±8.7	27.6±8.4	0	0	0	74.8±8.9	71.9±8.4
1-5	20	46.6±7.9	51.3±7.7	0.4±0.4	1.5±0.6	1±0.4	51.5±8.2	47.8±7.7
5-10	16	72.0±4.0	73.1±3.0	1.0±0.4	8.6±1.0	5.6±0.5	18.3±4.7	21.3±3.0
10-20	15	75.4±2.6	81.9±2.9	1.0±0.3	10.5±0.6	7.4±0.4	13.2±2.8	10.7±3.1
20-30	12	77.9±3.8	81.4±3.7	1.1±0.2	9.8±1.0	7.4±0.4	11.2±3.8	11.2±3.9
30-40	8	80.5±1.1	*84.9±2.0*	0.5±0.1	10.2±1.5	7.2±1.0	*8.7±2.1*	*8.0±1.7*
> 40	13	*80.4±3.5**	*85.3±3.3**	1.9±0.2	10.6±0.1	7.7±0.1	*7.2±3.5**	*7.0±3.3**

*Extrapolated values obtained from the relation from table 2.

Table 17. Total rainfall, throughfall, stemflow and canopy interception during the monitoring periods in two different coffee agricultural systems (AFS and MC) in the Central Valley of Costa Rica. (Monitoring period during 2004: June to September; and during 2005: July to November)

System	Total rainfall (mm)	Throughfall		Stemflow		Interception	
		(mm)	(%)	(mm)	(%)	(mm)	(%)
2004							
AFS	1426	1038	72.8	167*	11.7	221	15.5
MC	1426	1214	85.1	84*	6.0	126	8.9
2005							
AFS	1725	1324	76.8	204	11.8	196	11.4
MC	1725	1434	83.2	124	7.2	167	9.6

* Note that in 2004 only throughfall was monitored, values of stemflow were estimated using equations developed in 2005.

Article 3

Transpiration of coffee (*Coffea arabica*) and *Inga densiflora* in an agroforestry system in Costa Rica

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Keywords: growth, sap flow, stomatal conductance, transpiration, water use, wet tropics, multi-strata system, water cycle

Transpiration of coffee (*Coffea arabica*) and *Inga densiflora* in an agroforestry system in Costa Rica

Abstract

During 2 years, this study investigated the water use in a coffee monoculture (MC) and an agroforesty system (AFS) with *Inga densiflora* and particularly the influence of the microclimate and soil water availability on the transpiration of coffee plants and shade trees in optimal coffee growing conditions of the central valley of Costa Rica. The results showed that water use of coffee plants was higher in MC than in AFS on leaf area and ground area bases. This was due to a higher evaporative demand in MC compared to AFS where shade trees reduced by about 50% the global radiation and decreased coffee leaf temperature by up to 6°C. Under these conditions, soil water content did not seem to be a limiting factor for coffee transpiration; VPD and ETo reduced the ratio T/ETo, independently of the soil water content. The estimated annual transpiration of AFS was 29% and 33% higher than MC in 2004 and 2005, respectively. Tree water use represented around 40% to 50% of the total annual AFS water use. Nevertheless in the rainy site conditions (> 2600mm yr^{-1}), the AFS water use represented only a 1/3 of the total annual rainfall.

Introduction

In most instances, water is considered to be the most limiting resource in crop or forest tree physiological processes. Stomata mediate a significant fraction of the annual flux of water between the soil and the atmosphere. Stomata respond to stimuli of hormone signaling, light, water status, CO_2, temperature and other environmental variables, resulting in complex physiological and environmental mechanisms operating across several spatial and temporal scales (Schroeder et al. 2001). Short-term water stress generally results in stomatal closure and a reduction in canopy hydraulic conductance that influence transpiration rates (Jones 1998). As coffee plants is believed to have evolved as an under-storey tree in the mid-elevation tropical forest from Ethiopia, stomatal conductance is highly sensitive to irradiance (Nutman 1937). More recently, studies showed that the stomatal conductance in coffee depends on water availability, evaporative demand of the environment and leaf temperature. Moreover, a strong dependence of the stomatal conductance has been established with VPD (Fanjul et al. 1985; Hernandez et al. 1989; Rena et al. 1994). These authors found that stomatal conductance was strongly reduced at values of VPD higher that 1.5 kPa. Furthermore, the negative effect of the radiation on stomatal conductance appeared to be the result of intertwined effects of PFFD and VPD.

Nonetheless, few studies have evaluated coffee transpiration at canopy level in monoculture (Gutierrez and Meinzer 1994). These studies estimated the crop evapotranspiration coefficient (Kc=ETc/ETo) using the Bowen ratio-energy balance technique in coffee fields at different stages of canopy development and showed that the average Kc was between 0.58 to 0.79 for fields planted with 1 to 4-year-old coffee plants. Crop transpiration alone, determined with the stem heat balance technique, comprised from 40% to 95% of Kc as the leaf area index increased from 1.4 to 6.7, showing a strong influence of the LAI on coffee transpiration. Additionally to these coffee Kc estimates, the FAO manual on crop evapotranspiration (Allen et al. 1998) presented values for coffee in the range of 0.90 to 1.10, when the FAO version of the Penman-Monteith equation is used to estimate ETo.

Fewer studies on coffee transpiration have been carried out in agroforestry condtions (Kanten and Vaast 2006). Despite the potentially beneficial effects of agroforesty systems (AFS), there is a common concern regarding competition trees and the associated crops for limited resources, such as water (Beer 1987). It is known that a larger use of resources occurs in a mixed system compared to a monoculture (MC). Thus, the agroforestry benefits are to be expected only when there is complementarity for resource capture between trees and associated crops (Cannell et al. 1996). For this reason, the understanding of the interactions between trees and crops in AFS is critical for their management and implementation in various regions. In temperate regions, humid tropics and semiarid tropics, competition for water has been identified as the major determinant of productivity in alley cropping systems (Govindarajan et al. 1996; Hauser et al. 2005; Rao et al. 1997).

It has been suggested that the productivity of natural vegetation under savannah trees generally increases as rainfall decreases, while the opposite occurs in agroforestry. Thus, in the savannah, the beneficial effects of microclimatic improvement (e.g. lower temperatures, reduced radiation and evaporation losses) are greater in more xeric environments, because mature savannah trees have a high proportion of woody above-ground structure compared to foliage, so that the reduction in soil evaporation is larger than tree transpiration. On the contrary, the beneficial effects of trees in humid AFS in terms of microclimate improvement are negated by a reduction in soil moisture due to increasing interception losses and tree transpiration (Ong and Leakey 1999). However, most of the literature focused on water partitioning was developed for alley cropping systems whereas there is a lack of information on how trees interact with perennial crops in AFS. In coffee cultivation, the use of shade trees depends on social and biophysical factors (Fournier 1988; Muschler 2004; Muschler and Bonnemann 1997). It is suggested that shade trees can be associated with coffee in suboptimal regions while it is thought that inadequate shade (tree species, density and management) can reduce coffee production due to water competition, especially during the dry period. In addition, water must be freely available during the period of fruit expansion (Beer et al. 1997; Carr 2001; Muschler 1997). In coffee AFS, little information is available on the water use by coffee and associated trees, and possible water competition. Water use in 3 coffee AFS was higher in comparison to MC, but a higher water use itself does not indicate water competition (Kanten and Vaast 2006). There are many published studies on the positive influence of trees on microclimate (Barradas and Fanjul 1986; Beer 1987; Muschler 1997; Muschler 2004; Muschler and Bonnemann 1997), but few studies on water use of trees and coffee in a suboptimal site for coffee cultivation (Kanten and Vaast 2006). For this reason, the aim of this paper is to present the water use in AFS during 2 years and the influence of climate and soil factors on transpiration of coffee plants in MC and in AFS, which can help to assess the role of associated trees with respect to water use and competition in optimal coffee growing conditions.

Materials and methods

Site description and experimental design

The study was conducted on the experimental farm of the research station of the Coffee Institute of Costa Rica (ICAFE), located in San Pedro de Barva in the Central Valley of Costa Rica (10°02’16’’ N, 84°08’17’’ O; 1200 m). The climate is relatively cool with a mean annual temperature of 20°C, a mean annual precipitation of 2300 mm and with a pronounced dry season from January to April. The soil is derived from the weathering of volcanic ashes, belongs to Andisols and is classified as a Dystric Haplustands (Mata and Ramirez 1999). The soil nutrient concentrations were adequate due to the frequent fertilization of coffee and the natural high soil fertility of the volcanic soil.

Experimental design and management

The experimental design included two adjacent coffee plots: a shaded one or agroforestry system (AFS) with an area of 1500 m^2 and a second one without shade trees or monoculture (MC) with an area of 1200m^2. In both plots, coffee (*Coffea arabica* L.) was planted in 1997, following a coffee monoculture, with a spacing of 2 m between rows and 1 m within a row, which resulted in densities of 5000 and 4773 coffee plants ha^{-1} for MC and AFS, respectively, and with an average of 3 coffee stems per planting hole. In AFS, *Inga densiflora* (Benth) was planted within the coffee rows at a spacing of 6 x 6 m (277 trees ha^{-1}). The plots were equally intensively managed with a fertilization regime composed of 250 N; 15 P_2O_5; 110 K_2O; 70 MgO; 5 B_2O_3; 50 S and 60 CaO kg ha^{-1} yr^{-1}, following the recommendations of ICAFE (1998).

Species involved

Coffea arabica L. "Caturra" is a highly productive dwarf variety, but depends on intensive fertilization to maintain a high productivity. In the present experiment, the production cycle initiated with flowering after the first rains at the beginning of April-May and ended with the last harvest in December-January.

Inga densiflora Benth. (*I. langlassei, I. microdonta, I. mollifoliola, I. montealegrei, I. monticola, I. sordida, I. titiribiana*) is a fast-growing legume tree species distributed from Mexico to Brazil, well adapted to a wide altitudinal range (100–1400 m), but is more common above 600 m. The wood is of low timber value and is mainly used as fuel wood. This species (as well as a dozen species from this *Inga* genus) is very often used in Central America as a service tree in agroforestry systems providing shade to coffee and mulch through periodic pruning throughout the production cycle (Zamora and Pennington 2001).

Meteorology

An automatic weather station was installed in an open area next to the experimental plots and meteorological variables were monitored during the two years (2004-2005) of experimental data collection. Relative humidity (RH in %) and air temperature (Temp in °C) were measured by sensors (HMP45C, Campbell Scientific Corp., Logan, UT) at a height of 2 m. The photon flux density (PFD) was measured with quantum sensors (SOLEMS PAR-CBE 80, Palaiseau, France) and wind speed with an anemometer (Model 05103-5 Wind-monitor) also installed at a height of 2 m. Rainfall was measured with a tipping bucket gauge (Model ARG 100). Meteorological data were recorded every 15 minutes to a datalogger (CR10X Campbell Scientific Instruments). Quarter-hourly reference evapo-transpiration (*ETo* in mm) was estimated by the FAO Penman-Monteith equation (Allen et al. 1998) with inputs (wind speed, *T*, *RH* and solar radiation estimated from *PPFD* values) from the meteorological station in the open.

Soil water content

Time domain reflectrometry (TDR) probes were installed in both systems. Six and nine TDR probes were installed in MC and AFS, respectively. The soil water content was monitored in the following layers: 0-30 cm, 30-60 cm, 60-90 cm, 90-120 cm and 120-150

cm. Every 10 days, measurements were undertaken with a portable apparatus (MP-917, ESI, Environmental Sensors Inc.) reading time reflectrometry of each probe and for every layer.

Plantation characteristics

Tree growth monitoring

In AFS, stem diameter at breast height (DBH) at 1.3 m of all the individual shade trees (41 trees) was measured in October 2002, January 2004, July 2004, January 2005 and August 2005 to estimate the total tree trunk basal area of the plantation.

Coffee growth monitoring

In both systems, coffee stem basal diameter was measured as the average of two perpendicular measurements at 10 cm above soil surface in a sub-plot area of 312 m^2 (156 coffee plants) in January 2004, August 2004, January 2005 and August 2005. These measurements were used to estimate the total coffee stem basal area in each coffee system. The leaf area of eight coffee plants was measured per system to estimate coffee LAI in September 2003, February 2004, September 2004, February 2005, April 2005, June 2005 and October 2005.

Tree sap flow measurements

Sap flow was measured within a 18m×18m plot, located in the center of the AFS plot, in which solely the four central trees were monitored to avoid possible edge effects, using the temperature difference method of Granier (Granier 1985; Granier 1987). Two cylindrical probes, about 2.2 mm in diameter and 20 mm in length, were implanted in the sapwood of the tree trunks, separated vertically by 15 cm. The probes were installed on the south side of the tree, to minimize direct heating from sunshine, and then shielded with an aluminum protector covered by a plastic sheet to protect sensors from rainfall. The downstream probe was continuously heated with a constant power source, while the unheated upstream probe served as a temperature reference. The dissipation of heat from the downstream heated probe increases with increasing sap flow rate. During conditions of zero sap flow, such as nighttime, the temperature difference between the lower and the upper probes represents the steady state temperature difference caused by the dissipation of heat into non-transporting sapwood. A copper–constantan thermocouple measures the temperature difference between the heated upper needle and unheated lower reference needle. Whole-tree sap flux density is computed through an empirical relationship validated by Roupsard et al (2006):

$$dF = 12.42\left[\frac{\Delta T_{\max} - \Delta T}{\Delta T}\right]^{1.231}$$

where dF (l dm^{-2} s^{-1}) is the average sap flow density, ΔT the temperature difference between the two probes and ΔT_{max} is the baseline (maximum) temperature difference for the data set of the day.

Coffee sap flow measurements

Eight coffee plants, 7 year old, were selected (four per system) with stem diameter at sensor height (35 cm above soil surface) ranging from 25 to 30 mm. Stem-flow sensors (Dynamax Inc., Houston, Texas) were connected to a Campbell Scientific CR10X datalogger (Campbell Scientific Inc., Logan, Utah) reading sap flow rates every minute, averaging and registering values every 15 min to a SM192 storage module.

For each monitored coffee stem, leaf area (LA in m^2) was determined by measuring the length (L) and width (W) of individual leaves. Coffee sap flow (FS) was originally measured in g s^{-1} $stem^{-1}$, and then expressed in g h^{-1} m^{-2} of foliar area (FA). Each month, sensors were installed at the same position on the coffee stems for a monitoring period of a week minimum. To estimate the daily coffee transpiration per hectare, the mean daily coffee transpiration per unit basal area was multiplied by the total coffee basal area per hectare estimated from stem measurements on a group of 156 coffees per system (312 m^2). The ratio transpiration/ETo for coffee and *Inga densiflora* was calculated for all the dates in which transpiration was measured.

Analytical methods

Data were analyzed with SAS release 9 (SAS Institute Inc., Cary, NC, USA, 1999). Regression analyses were performed to develop relationships between microclimatic variables and transpiration in coffee and *Inga densiflora*.

Results

Plantation characteristics

Shade affected coffee plant characteristics. Total stem coffee basal area was higher in MC than in AFS. This effect resulted from differences in individual coffee stem diameter together with coffee density as this density was lower in AFS (4773 coffee plants per ha) than in MC (5000 coffee plants per ha). Despite a higher mean leaf area of individual shaded coffee, LAI was similar in both systems from August 2003 to April 2005 due again to the lower coffee density in AFS than in MC. During the wet season 2005, LAI in MC was significantly ($p=0.05$) higher than in AFS and increase in LAI in MC started earlier than in AFS.

Shade trees were well established after 5 years, with a mean DBH of 8.5 cm, a minimum of 5.1 cm and a maximum of 12.4 cm. At the age of 8 years, the mean DBH was 13.5 cm with a minimum of 9.3 cm and a maximum of 19.1 cm. After 5 years, the total stem basal area was 4.2 m^2 ha^{-1} while it was of 8.36 m^2 ha^{-1}at 7 years and 8.51 m^2 ha^{-1} at 8 years.

Climate characteristics

The annual rainfall was particularly high with 3245 and 2684 mm during 2004 and 2005, respectively. In this coffee region, rainfall was unevenly distributed throughout the year with 2900 mm (93%) and 2450 mm (92%) during the wet season from May to November for 2004 and 2005, respectively. Monthly rainfall during the monitoring period ranged from 0 mm to 650 mm for the driest month and the wettest one, respectively. Monthly Penman-Monteith reference evapo-transpiration (ETo) varied between 70 to 170 mm and amounted to 1310 and 1178 mm yr^{-1} for 2004 and 2005, respectively. Monthly ETo was higher than monthly rainfall from December to April, however the cumulative rainfall

during the dry season amounted to 190 mm (29% of ETo) and 196 mm (34% of ETo) in 2004 and 2005, respectively.

The mean daily ETo during the dry season varied between 3.30 and 5.66 mm d^{-1} and 3.20 to 5.14 in 2004 and 2005, respectively. During the 2004 wet season, ETo varied between 1.24 to 3.22 mm d^{-1} with particularly low values in May. During the 2005 wet season, ETo varied from 2.20 to 2.90 mm d^{-1}. On average, cumulative ETo during the wet season (8 months) represented only 60% of ETo during the dry season (4 months). Likewise, global radiation, mean VPD, minimum relative humidity and maximum temperature, differed greatly between the dry and the wet season. Maximum air temperature was notably higher and minimum RH lower during the dry months. Daily variation in air temperature, RH and VPD were also higher during the dry period than during the wet one (Figures 1). Air VPD did not exceed values above 1.0 kPa in the wet season. In contrast, during the dry season, air VPD reached a maximum value of 2.2 kPa (Figures 1) due to high air temperatures and low RH around midday.

Daily pattern of Inga densiflora sap flow at different depths in the sap wood

The sapwood of *Inga densiflora* presented a diffuse-porous structure (vessels disseminated in the entire wood surface) with heartwood absent even in adult trees. For this reason, cylindrical probes were inserted at 0-20 mm, 20-40 mm and 40-60 mm in six trees of 12 cm of DBH to describe the radial profile of sap flow (SF). Generally, the sap flow rate decreased with increasing depth into the sapwood, except for one of the 6 trees monitored presenting a sap flow rate at the intermediate depth of 20-40 mm similar to that of outer depth of 0-20mm. At the deeper depth of 40-60 mm, the sap flow rate tended to be low, but followed the pattern of the shallow depth. In all cases, sap flow measured at intermediate and deeper depths was linearly related to the flow measured at shallow depth with an intercept not statistically different from zero (Figure 2). The good linear relationship showed that the sap flow ratio was relatively constant throughout the day, which allowed us to estimate whole tree sap flow from the measurements at the shallow depth (0-20mm) via correction factors.

During the one week long measurement period, the mean daily cumulative SF at different depths in the six trees showed significant statistical differences. The mean SF ratio for the 20-40mm depth was 0.60 while the Fs ratio was 0.23 for the 40-60mm depth. For an average tree (12.4 cm DBH), the innermost ring area represented a small percentage (3%) of the whole-tree sap flow due to the combination of a smaller area of sapwood and a lower sap flow rate. The outer ring area (0-20 mm) accounted for 71% of the total tree sap flow while the intermediate ring area accounted for 26 %.

Daily pattern of Inga densiflora transpiration in dry and wet periods

The relationship between shade tree canopy transpiration (T) and reference evapo-transpiration (ETo) showed a hyperbolic increase in T with increasing ETo (Figure 3a). A saturation point seemed to be reached at 3.5 mm d^{-1} so that further increases in ETo did

not lead to corresponding increases in T. On the contrary, it appeared that for values of ETo higher than 4 mm d^{-1} T slightly decreased indicating stomatal closure. The relationship between the ratio T/ETo and ETo for I. densiflora showed a maximum value (0.5) for values of ETo in the range of 1.5 mm d^{-1} to 2.5 mm d^{-1} with a strong reduction in T/ETo for ETo values higher than 3 mm d^{-1} (Figure 3b).

Inga densiflora tree daily water consumption

Due to marked seasonal differences in ETo and soil moisture, maximum tree values of T/ETo occurred in the wet season for both years (2004 and 2005). For both years, values of T/ETo reached its minimum in April, which represented the last month of the dry season and when tree foliage density was at its lowest. With the beginning of the wet season, the values of T/ETo tended to increase to reach its maximum value in July 2004, while it reached its maximum values in June and July in 2005. These high values of T/ETo remained constant until the end of the wet season in late December when trees began to shed the leaves.

Coffee transpiration rate in dry and wet periods

Coffee transpiration rates, calculated on a leaf area basis, were higher during the dry season than the wet season for both systems (Figures 4). Furthermore, coffee transpiration rate, calculated on a leaf area basis, was higher in MC than in AFS, irrespective of the season.

During the dry season and for both systems, coffee SF rate started with sunrise (6:30 am, local time), reached a peak at 10:00 am and remained constant until about 3:00 pm, to diminish afterwards with decreasing solar radiation and ETo (Figure 4 a,b). In the wet season, coffee transpiration rate reached a peak around midday when ETo was maximal, without any apparent limitation. In both systems, coffee daily transpiration pattern appeared to follow daily ETo pattern; although coffee SF rate in MC followed daily ETo and PPFD patterns more closely than in AFS. The lower values of coffee SF rate in AFS can be explained by the lower values of PPFD, and hence a lower evaporative demand.

Coffee transpiration versus micrometeorological measurements

On a daily basis, the relationship between coffee T and ETo showed an hyperbolic increase in T with increasing ETo (Figure 5ab). In MC, a maximum T value of 2.7 mm d^{-1} was reached when ETo reached 4 mm d^{-1} while the maximum coffee T value in AFS was 1.7 mm d^{-1}. Above an ETo value of 3 mm d^{-1}, coffee T tended to stabilize and reached a plateau-type indicating stomatal closure. For ETo values higher than 3 mm d^{-1}, T were low when compared with the evaporative demand, which sometimes exceeded 6 mm d^{-1} on sunny days. Thus, in the dry season, coffee transpiration did not exceed more than 2/3 of ETo in MC and approximately 1/3 in AFS.

Over the whole ETo range, the ratio T/ETo for coffee was significantly higher in MC than in AFS (Figure 5cd). The ratio T/ETo for coffee was strongly dependent upon ETo and reaching its maximum value in the ETo range of 1.8 to 2.2 mm d^{-1} in both systems. The maximum T/ETo values were in the range of 0.7 to 1.0 in MC whereas they were

between 0.4 to 0.6 in AFS. After reaching their maximum values, the ratio T/ETo in MC and AFS showed a fast decline with further increase in ETo.

Coffee transpiration versus volumetric soil water

In the present study, the volumetric water moisture was used to show the effect of soil water availability on coffee transpiration. For both systems, the ratio T/ETo progressively decreased when the volumetric soil water decreased from 0.43 down to 0.27; this decrease was more pronounced when volumetric water dropped below 0.4 (Figure 6). There was a strong relationship between the ratio T/ETo and LAI for the 7 monitoring dates where LAI was estimated with accuracy during the monitoring period of 2004-2005. In MC, T/ETo linearly increased from 0.35 to 0.85-0.91 for LAI values from 2.1 to 4.7 while in AFS T/ETo linearly increased from 0.26 to 0.48-0.45 for LAI values from 2.2 to 4.6. Although T/ETo appeared to be strongly related to the soil volumetric water, this could be attributed to the strong relationship between LAI and soil volumetric water. This reflected the fact that soil volumetric water influenced the transpiration by means the reduction of the LAI and its effect on the stomatal conductance is less important than the effect in the reduction of transpiration by leaf drop.

Total estimated water consumption per system

In MC, daily coffee water consumption was high during the 2004 dry season from January to April (varying between 2.1 to 2.6 mm d^{-1}), while in the 2004 wet season (from May to December) these values were lower and ranging from 1.6 to 1.9 mm d^{-1}. During 2005, daily coffee water consumption ranged from 1.2 to 1.3 mm d^{-1} during the wet months. The daily T/ETo values estimated for coffee in MC varied from 0.33 to 0.92, with the lowest values in the dry season (Table 1). During the 2005 dry season, coffee presented its lowest T/ETo values due to the fact that values of LAI were at their lowest.

The daily coffee water consumption in AFS appeared to be lower than in MC for all the monitoring periods. During the 2004 dry season, coffee water consumption in the AFS ranged from 1.4 to 1.8 mm d^{-1} while it was between 1.2 to 1.3 mm d^{-1} during the wet season. During the 2005 dry season, it varied between 1.0 to 1.1 mm d^{-1} while they ranged from 0.7 to 1.0 mm d^{-1} for the wet period. The values of T/ETo for coffee under the shade of *Inga densiflora* varied from 0.26 to 0.65 with typical values of 0.26 to 0.30 during the dry season and 0.45 to 0.50 during the wet season. One exception to this pattern was observed in May 2004 with very low T/ETo values possibly due to low values of ETo, global radiation and large rainfall events during the monitoring period for this month.

During all monitoring periods, the combined transpiration of coffee plants plus shade trees was higher than that of coffee plants grown alone in MC as reflected by T/ETo values (Table 1). Even though coffee water use in AFS was lower than in MC, the total water use was higher in AFS due to that of shade trees. Tree water use represented between 40% to 44% of the total water use in the dry period and 49% to 50% in the wet period. Water use was 10% to 60% higher in AFS than MC.

Discussion

Sap flow ratio and sapwood depth

For *Inga densiflora* 7-8 year old, no difference in coloration between heartwood and sapwood was observed. For other species of *Inga* genus in the Amazon, the presence of diffuse porous structure has been reported and for other tropical trees the presence of diffuse porous represented 80% of the totality of species (Segala and Angyalossy-Alfonso 2000). However, it is unclear if the presence of a dark zone in the xylem delimits the part of the wood that is physiologically active in transporting sap (Ford et al. 2004; Nadezhhdina et al. 2002).

For *Inga densiflora*, there was a decrease in sap flow rate with increasing sapwood depth. This has been shown for other species in temperate and tropical zones. Delzon et al (2004) showed that *Pinus pinaster* Ait. presented a good relationship between sap flow rates and the sapwood depth (Delzon et al. 2004). Nadezhdina et al (2004) also showed a decrease in the sap flow ratio with increasing sapwood depth in dominant trees such as *Pinus sylvestris* L. and *Populus canescens* L. as well as in understory species such as *Prunus serotina* Ehrh. and *Rhododendron ponticum* L. In tropical regions, Roupsard (1996) working with a legume tree, *Faidherbia albida* A. Chev. (*Acacia albida*) (Fabaceae Mimosoideae), found a decrease in the sap flow rate with increasing sapwood depth (Roupsard et al. 1999).

Large errors up to 27% were found when it was assumed that sap flow was uniform over the whole sapwood in trees of 12 cm DHB. Furthermore, it can be observed that linear relationships between outer and inner sap flow rates varied quite noticeably from one tree to another. Hence, it is recommended for every tree that the radial sap flow pattern with depth needs to be determined and correction factors for different depths estimated. Still, this method of inserting the sensors at various depths into the wood after removing the outer sapwood is far from perfect as it artificially induces higher sap flow at deeper depths and hence does not give an accurate account of the decrease in sap flow rate with increasing depth (O. Roupsard, pers. comm.)

Tree sap flow versus ETo

The present results provide insights on the processes controlling transpiration of *Inga densiflora*, with the highest T/ETo values observed in the wet season when low ETo values but high soil moisture were registered. The present differences in tree transpiration at different daily values of ETo are similar to those found in other studies on other species that compared transpiration with respect to environmental variables. For example, in *Citrus sinensis* L. Osbeck, a good correlation was found between canopy transpiration and solar radiation (a major component of ETo) for which a saturation point was observed at about 400Wm^{-2} (Oguntunde et al. 2007). This plateau-type response of trees to ETo, and hence to radiation and VPD are generally attributed to a stomatal closure. Several studies have shown that stomatal conductance in trees is sensitive to environmental variables such as VPD and PAR (Jarvis 1976). Motzer et al (2005) found that daily sap flow correlated linearly with solar radiation for species of the montane

forest (*Trichilia guianensis* Klotzsch; *Psycotria brachiata* Ruiz & Pav. *Ruagea pusbescens tiana* H. Karst), and that additionally VPD seemed to be the main factor influencing the reduction in transpiration during the day (Motzer et al. 2005). Nonetheless, little information is available in the literature on transpiration of *Inga* species to be compared to the present results, which demonstrates the need for further field research for this important Neotropical genus.

Coffee transpiration rate in dry and wet periods

The higher coffee transpiration rates on a leaf area basis in the dry season compared with that in the wet season can be attributed to the high evaporative demand in the dry season. Moreover, coffee without shade presented a higher transpiration rate compared to coffee under shade. This can be explained by the higher evaporative demand of coffee in MC compared to AFS. Light interception data and leaf temperature have showed that plants under the shade of *Inga densilfora*, receive only 50% of the global radiation and the leaf temperature is until 6^{o}C lower than in MC. van Kanten and Vaast (2006) have also reported higher transpiration rates on a leaf area basis in coffee in MC than in AFS. Still, these authors found that even though full sun coffee transpired more, on a leaf area basis, than under shade, daily coffee water consumption per hectare was generally higher under shade than in MC due higher LAI of shade coffee. On the contrary, the present results showed that in MC coffee transpired more on a leaf area basis and on a ground area basis than coffee in AFS due to similar LAI. The present results can be explained by the optimal environmental conditions for coffee growth of the study with mean air temperatures in the range of 20 to 24^{o}C and maximal daily values not exceeding 31^{o}C (ICAFE, 1998) in contrast to the site of van Kanten and Vaast (2006) where environmental conditions were sub-optimal for coffee growth as reflected by lower LAI values of coffee in MC than in AFS.

Coffee transpiration versus micrometeorological measurements and volumetric soil water

Daily values showed that coffee transpiration in both systems were strongly related to ETo, but tended to reach a maximum at ETo values around 4 mm d^{-1}. This response has been attributed to a decrease in stomatal conductance with an increase in VPD as documented in tropical forest species (Oren et al. 1996; Phillips et al. 1999). At all ETo ranges, coffee Kc tended to be higher in MC than in AFS as a result of the higher evaporative demand in MC than in AFS. These coffee T/ETo values in MC were in the range of values of 0.40 to 0.82 reported by Gutierrez and Meinzer (1994b) for plantations with LAI from 1.4 to 6.7 and with high values of ETo (4.6 to 6.6 mm day^{-1}).

The values of coffee T/ETo decreased for ETo values higher than 2 mm d^{-1}. Previous studies have demonstrated that high values of VPD and temperature induced stomatal closure in coffee plants and hence reduced transpiration (Fanjul et al. 1985; Gutierrez et al. 1994; Hernandez et al. 1989; Kumar and Tieszen 1980; Wormer 1965). For example, Wormer (1965) found stomatal closure in coffee plants at high values of temperature, furthermore a linear reduction in the stomatal opening was found with the increase in

VPD and total solar radiation. More recently, Gutierrez et al (1994b) in Hawaii showed that stomatal conductance in coffee was high in the morning and declining along the day with increasing VPD and solar radiation.

In the present study, soil moisture also had a strong influence in coffee T/ETo in MC and AFS. T/Eto increased linearly with increasing soil moisture, until reaching a threshold where soil moisture was no longer limiting for coffee transpiration (0.4 of volumetric water content). Despite the high values of T/ETo with high soil water content in both systems, the ETo in the wet season is low and the LAI presented the highest values, which show the difficulty to separate the influences of these variables. Since a linear relationship between T/ETo and LAI was also observed, the high T/ETo values during the wet season can be attributed to higher LAI values in the wet season than in the dry season. The relationship between crop transpiration and LAI has been already highlighted for coffee by Gutierrez and Mienzer (1994a & b) as they showed that coffee transpiration increased from 40% up to 95% of ETo when coffee LAI increased from 1.4 to 6.7. The strong relationship between canopy conductance (and hence transpiration) and LAI in 20 different tree stands has also been showed by Granier et al (2000). In stands with LAI smaller than 6, the canopy conductance increased linearly with LAI, whereas it did not increase further for LAI larger than 6.0 (Granier et al. 2000). Therefore, the effect of soil moisture on coffee transpiration can be explained via a reduction in leaf area, while the microclimatic variables such as VPD, temperature, radiation and ETo influence coffee transpiration via a reduction in the stomatal conductance. In temperate deciduous forests, the dominant factor controlling seasonal canopy conductance and stand transpiration is the degree of defoliation; thus, soil moisture can strongly affect water use by forests only while canopy leaf area is high (Oren and Pataki 2001).

Generally, the season of high soil water content (wet season) presents the lowest values of VPD and ETo (Kanten and Vaast 2006), which makes difficult to separate the effects of these factors on coffee stomatal conductance. For example, Siles and Vaast (2002) showed higher values of coffee stomatal conductance in the wet season compared to the dry season. However, the wet season presented lower values of leaf temperature, VPD and solar radiation compared to the dry season, which certainly helped to explain the higher values of coffee stomatal conductance during the wet season (Siles and Vaast 2003).

During the dry season, the low coffee T/ETo values suggest limitation of transpiration via a decrease in stomatal conductance due adverse environmental conditions (high VPD and ETo) or limited soil water availability. Low soil water availability decreases leaf water potential and reduces stomatal conductance (Meinzer 1993). However, for coffee, a high evaporative demand (expressed as VPD or ETo) reduces leaf stomatal conductance, even when soil moisture is not limiting (Fanjul et al. 1985; Kanechi et al. 1995). Nevertheless, insufficient information is available to clarify the role of soil humidity and atmospheric humidity on coffee stomatal conductance (Carr 2001). For example, Kanechi et al (1995) showed how stomatal conductance declined with VPD increasing from 1.0 to 3.0 kPa in well watered plants as well than in plants in dry soil. This result has also been recorded in

other species such as rice (*Oryza sativa* L.) which showed that when maintaining a high humidity in the air around the leaves, the effect of soil moisture deficiency was reduced considerably (Singh and Sasahara 1981).

The present results on coffee T/ETo values estimated every 15 minutes at four different LAI values showed that for larger LAI values the ratio T/ETo (on a ground area basis) was larger when plotted against ETo. As mentioned previously, larger LAI were mostly observed during the wet season with soil volumetric water near the field capacity whereas low LAI predominated in the dry season. However, when FS/Eto estimated on a leaf area basis was plotted against ETo, the response of FS/ETo was similar for all LAI ranges and hence the soil water moisture (Figure 7). For the four LAI values, the coffee FS/ETo reached a maximum value at low ETo, and then decreased at values higher than 0.4 mm h^{-1}, independently of the soil water status. Data for coffee plants in AFS showed a similar pattern (data not shown).

In addition to the previous results, continuous monitoring of sap flow was undertaken on two coffee plants in MC for a period of one week when the soil was dry (0.31 dm^3 dm^{-3} and 3.2 of LAI) and for eleven days after irrigation to wet soil and hence to separate the effects of different LAI, soil water and microclimate variables (ETo, VPD). For the period with high soil water availability, coffee plants showed that FS/ETo presented lower sensitivity to ETo and VPD compared with the period with low soil water. For low ETo values, high SF/ETo values were observed for both set of soil conditions (wet and dry) without differences (Figure 8). At ETo values above 0.40 mm h^{-1}, FS/ETo for the period with low soil water presented a higher reduction than for the period of high soil water. When SF/ETo was plotted against VPD, a similar pattern was observed for both soil conditions; i.e. a strong reduction in SF/ETo with increasing VPD. As previously mentioned by other authors (Carr 2001; Fanjul et al. 1985; Kanten and Vaast 2006), it seems that there is a strong limitation in the stomatal conductance in coffee plants with values of VPD higher than 1.5 kPa, even under well watered soil conditions. Nonetheless, well watered plants seem slightly less sensible to VPD (and ETo) at VPD values higher than 1.5 kPa.

Total water use per system

Over the monitoring of more than 2 years, the combined transpiration of *I. densiflora* and coffee in AFS was higher than that of coffee alone in MC. Water use in AFS was 10% to 60%, higher than MC depending on the month; while the total annual transpiration was 29% and 33% higher in AFS than in MC for 2004 and 2005, respectively. These high values of water use at plot level can be explained by the higher combined LAI (tree+coffee) in SAF in comparison to MC. Van Kanten and Vaast (2006) in a sub-optimal coffee zone also found a higher water use in AFS with coffee associated either with *E. deglupta* or *T. ivorensis* or *E. poeppigiana* in comparison to MC. However, van Kanten and Vaast (2006) found that the coffee water use in AFS was higher that in MC, due to reduced coffee LAI in MC despite the higher use of water on a leaf area basis in MC than in AFS. In the present study, transpiration of *Inga densiflora* accounted to 40% - 50% of the total water use; these values seem high with respect to the low density of

trees (277 ha^{-1}) and their total basal area (6.7 to 8.5 m^2 ha^{-1}); however, they appear consistent with the amount of solar radiation intercepted ranging from 46% to 60% (Table 2).

Competition for water

In many agroforestry studies, water competition appeared to be the most important factor with respect to yield reduction of the associated crop (Govindarajan et al. 1996; McIntyre et al. 1997; Rao et al. 1997). Water competition in AFS is most likely in the semiarid tropics with a maximum rainfall of 600 to 700 mm during the cropping season. In the present study, the annual rainfall greatly exceeds the Penman-Monteith reference evapo-transpiration (ETo) and the actual vegetation transpiration in both systems (Table 2). Even though the dry season lasted 5 months (December to April), soil water recharges were frequent and represented 29% (190mm) and 35% (196mm) of ETo during the dry seasons of 2004 and 2005, respectively. Thus, rainfall represented 32% and 47% of AFS transpiration during the dry seasons of 2004 and 2005, respectively, while it accounted for 40 % and 66% of the transpiration in MC for the same periods. Additionally, a reduction in coffee yield due to competition for water in the AFS is not likely because the period of rapid fruit expansion coincided with the rainy season which represented 90% of the annual rainfall with no soil water limitation. In his review on coffee water requirements, Carr (2001) emphasized that water supply is not likely to be a limiting factor in regions where rainfall coincides with fruit development. On the contrary, if fruit development experiences a short dry season as in equatorial regions with bi-modal rainfall patterns fruit size and quality could be negatively affected by water limitation.

Conclusions

The present study on transpiration leads to a better understanding of this important process in coffee under MC and AFS conditions even though observations were restricted to optimal conditions for coffee cultivation; i.e. an altitude of 1200 m, a fertile and deep volcanic soil with a high fertilization regime, and an intermediate dry season.

Still, the following conclusions can be drawn:

- The water use of coffee plants in MC was higher than in AFS on leaf area and ground area bases. This was due to higher evaporative demand in MC compared to AFS. On the other hand, coffee plants in AFS presented higher stomatal conductance than in MC as previously documented.
- High VPD and ETo reduced stomatal conductance and therefore coffee transpiration rate could not keep up with respect to the evaporative demand in both systems. Still, ETo values above 0.4 mm h^{-1} seemed to reduce the hourly coffee T/ETo values independently of the soil water content.
- Soil water content does not seem to be a limiting factor of coffee and tree transpiration after 2 years of monitoring. During the wet season, values of coffee T/ETo were higher than in the dry season. However, 3 factors had a strong influence on coffee transpiration: ETo, soil water and LAI. The wet season with

the highest values of T/ETo generally presented low values of ETo, and high values of soil water and LAI, which makes it difficult to separate the effect of each factor on transpiration. Nevertheless, it was clear that VPD and ETo reduced coffee stomatal conductance, independently of the soil water content and LAI. Thus, the reduction in transpiration due to low values of soil water is analyzed as being mostly the result of a reduction in LAI, and hence in these site conditions soil water influence on stomatal conductance seems to be secondary whenever high values of VPD and ETo are present.

- The estimated annual transpiration of AFS was 29% and 33% higher than coffee MC in 2004 and 2005, respectively. Nevertheless, the AFS water use was no more than 32 % and 33% of the total rainfall in 2004 and 2005, respectively.

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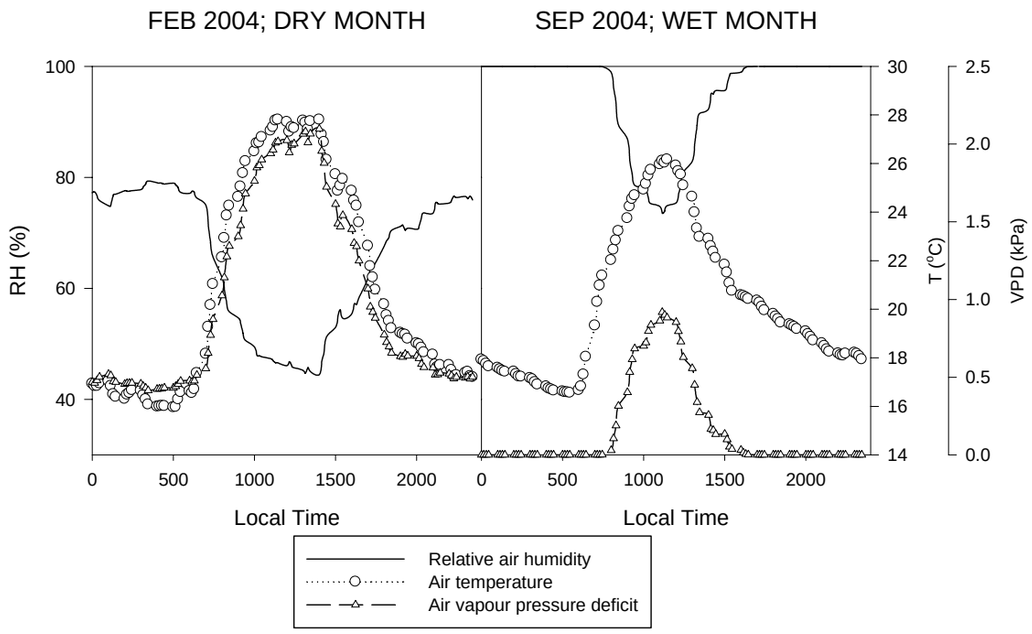


Figure 1. Daily patterns of relative air humidity (RH), air temperature (T) and air vapor pressure deficit (VPD) based on ten consecutive days for a dry month (February) and a wet month (September) at San Pedro de Barva, Costa Rica (values are means over 15 min monitoring periods).

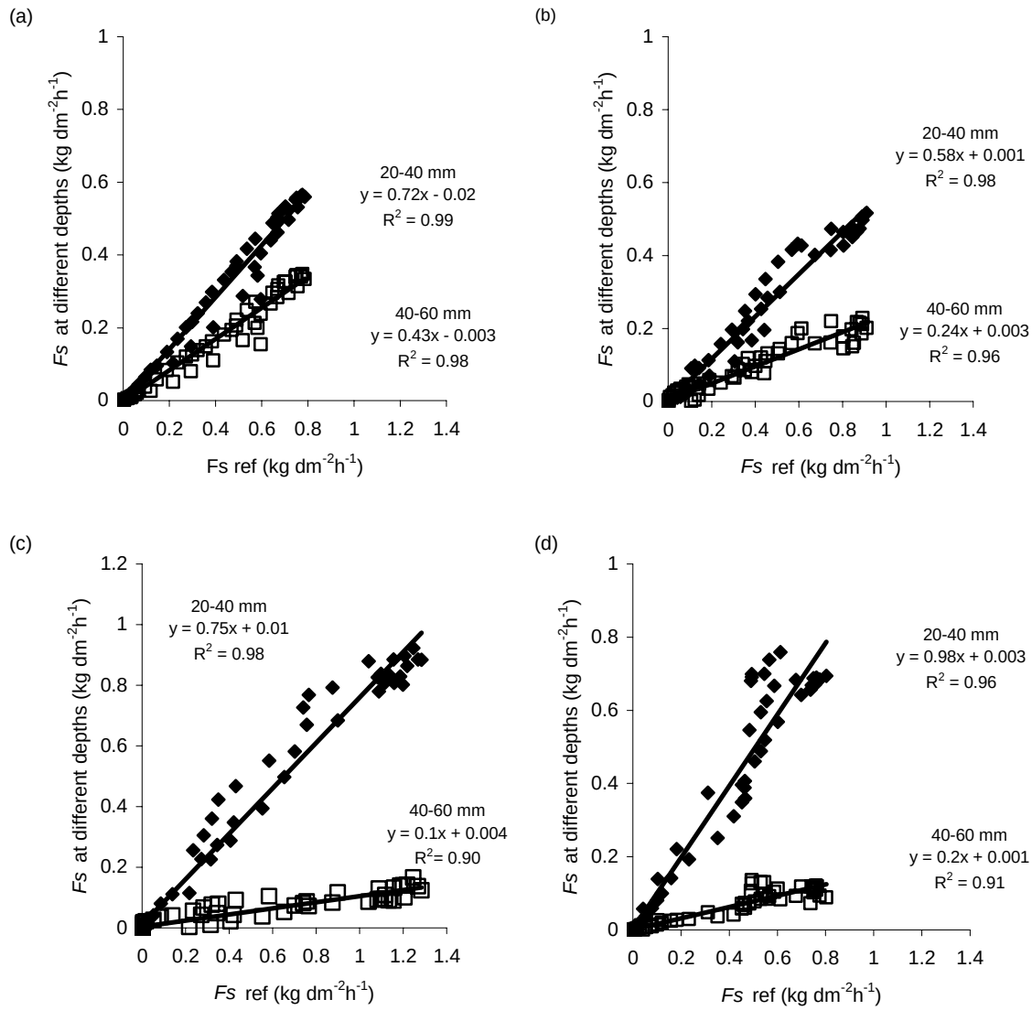


Figure 2. Relationships between values of sap flow at depths of 20-40mm and 40-60mm and the outer depth of 0-20mm during monitoring periods of 15 minutes over 15 days.

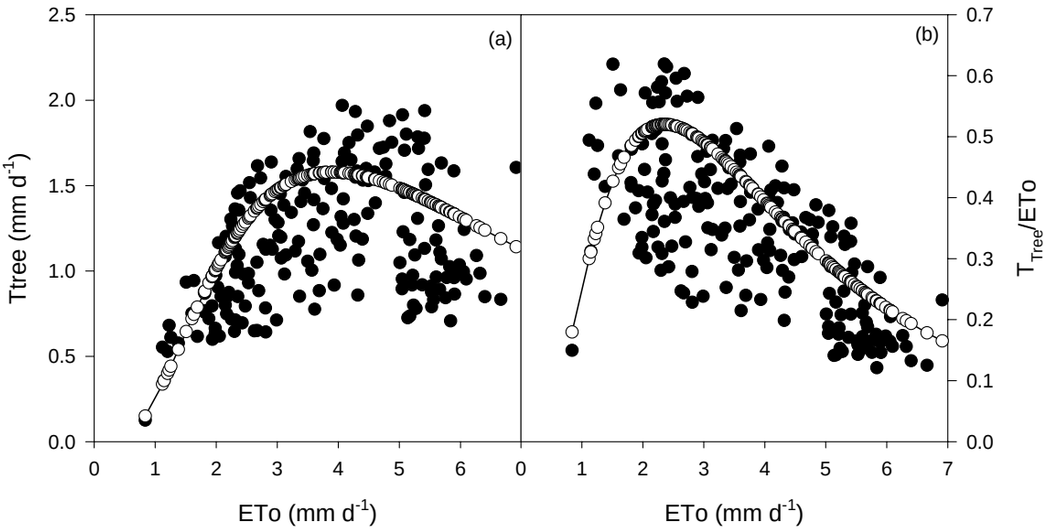


Figure 3. Relationships between reference evapo-transpiration (ETo) and (a) daily transpiration (T) and (b) the ratio T/ETo of *I. densiflora* in an agroforestry system at San Pedro de Barva, Costa Rica.

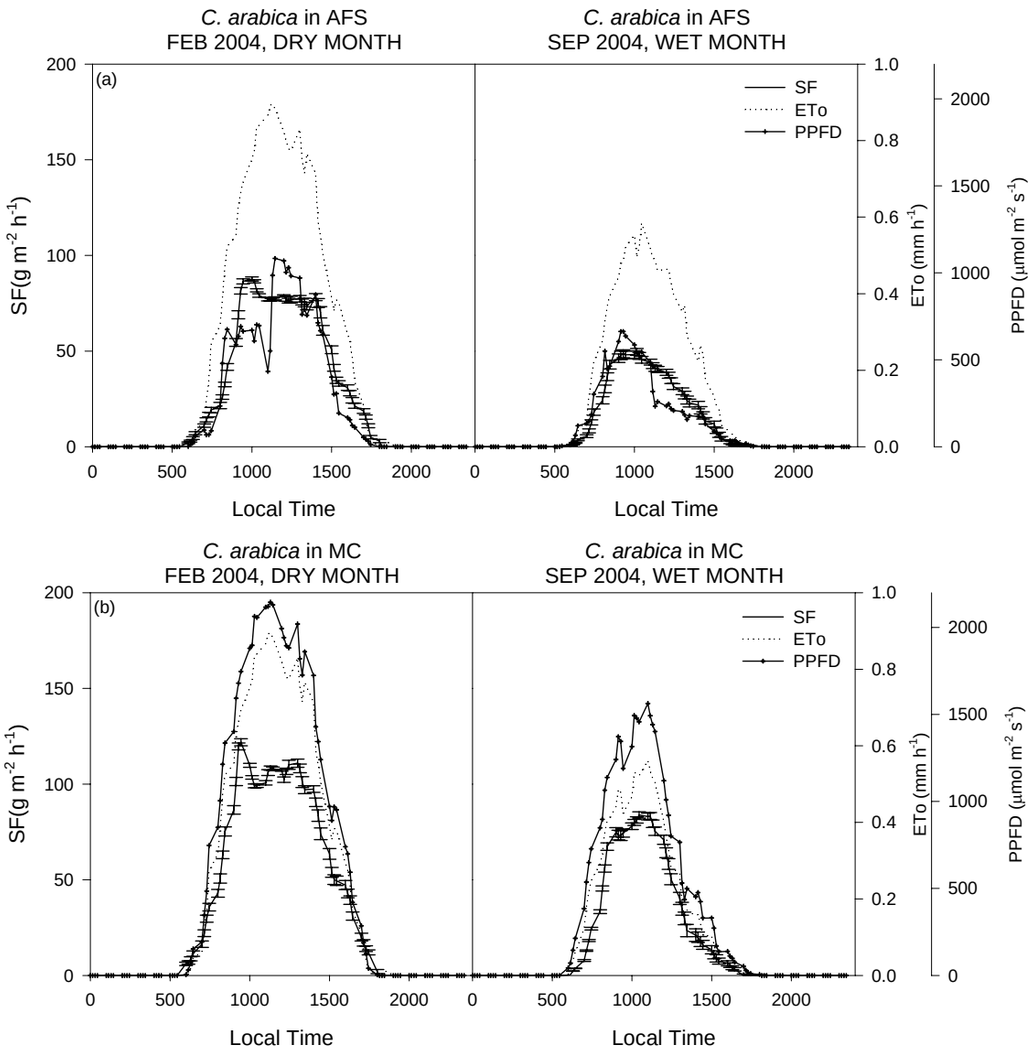


Figure 4. Mean hourly coffee sap flow rate (SF), reference evapotranspiration (ETo; measured in open field) and photosynthetic photon flux density (PPFD) based on ten consecutive days and four coffee plants in AFS (a) or in MC (b) for a dry month (February) and wet month (September) in San Pedro de Barva, Costa Rica (values ± sd are means over periods of 15 min).

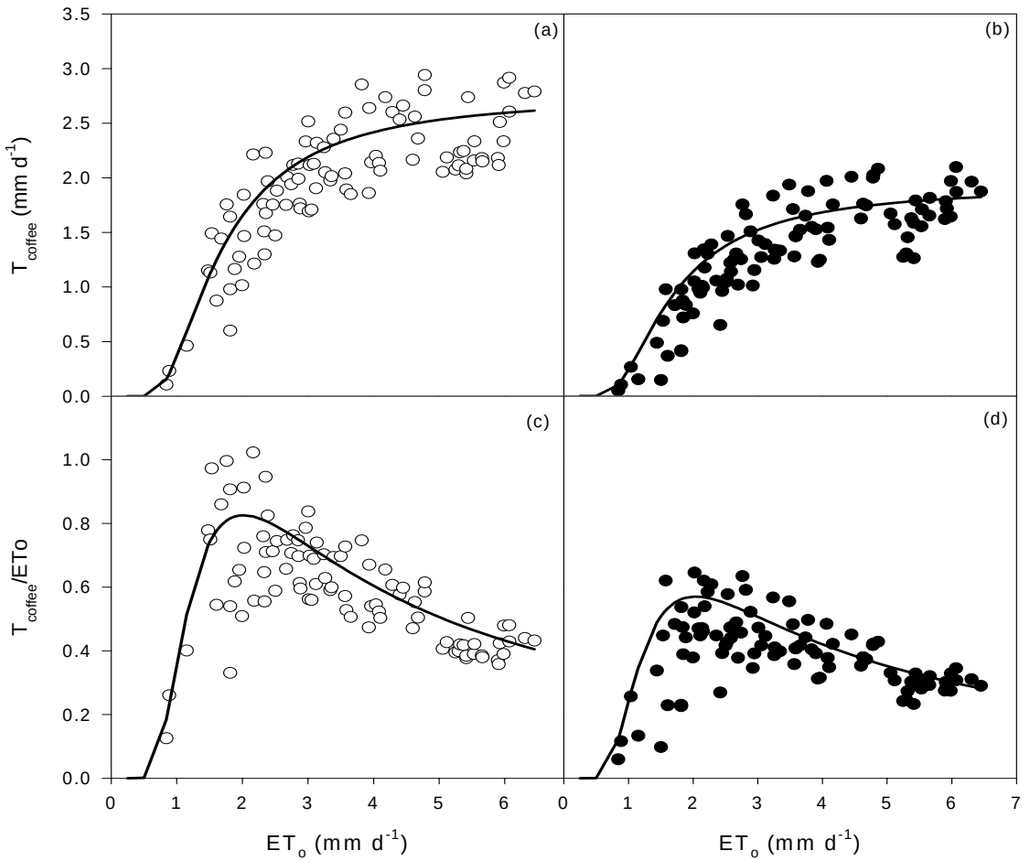


Figure 5. Relationships between daily coffee transpiration (a, b) and T/ETo (c, d) versus daily ETo (FAO, 1998) in MC (left panels) and in AFS (right panels) at San Pedro de Barva, Costa Rica. (Transpiration daily values are extrapolation from four coffee trees to ground unit area)

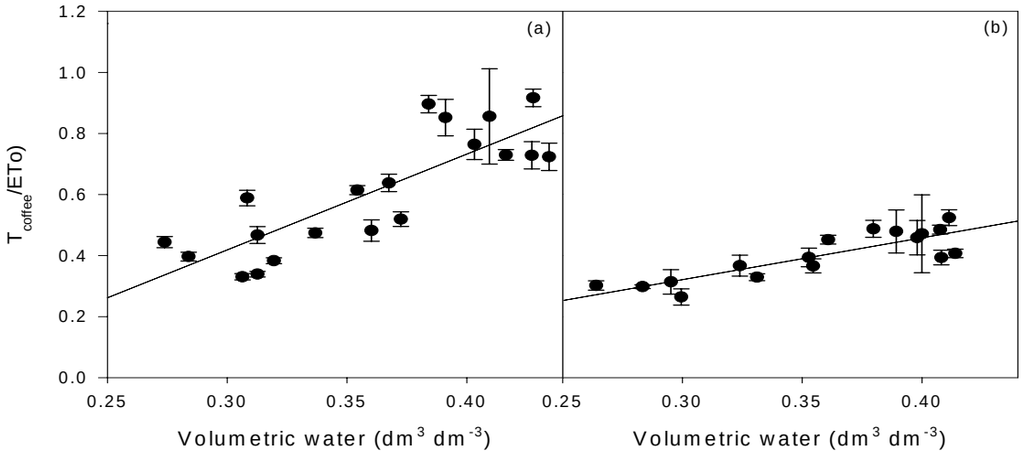


Figure 6. Relationships between T/ETo and soil volumetric water content in MC (a) and in AFS (b) at San Pedro de Barva, Costa Rica. (Values represent daily averages of one or two weeks of measurements. MC: r^2=0.70, T/ETo=3.13*VW-0.52; AFS: r^2=0.73, T/ETo =1.36*VW-0.09).

Table 1 Calculated reference evapotranspiration (ETo) and the ratio T/ETo for coffee and shade trees under optimal coffee cultivation conditions for the period 2003-2005.

Month	Mean ETo (mm day^{-1})	T/ETo	T/ETo		
		Coffee (MC)	Coffee (AFS)	*Inga*	Total AFS
August 2003	2.66	0.90	0.48	0.49	0.97
September	2.51	-	-	-	-
October	1.22	0.92	0.65	0.46	1.10
November	2.44	-	-	-	-
December	3.34	-	-	-	-
January 2004	3.56	0.64	0.45	0.31	0.76
February	5.66	0.47	0.33	0.28	0.61
March	5.42	0.40	0.30	0.28	0.58
April	4.99	0.44	0.30	0.20	0.50
May	1.26	0.37	0.15	0.33	0.48
June	3.22	0.48	0.39	0.43	0.83
July	2.79	0.61	0.49	0.47	0.96
August	2.46	0.76	0.48	0.41	0.89
September	3.04	0.73	0.41	0.38	0.79
October	2.63	0.73	0.52	0.38	0.91
November	3.21	0.72	-	0.31	-
December	3.73	-	0.41	0.40	0.81
January 2005	5.14	0.38	-	0.33	-
February	4.45	0.34	0.26	0.31	0.57
March	3.88	0.33	0.29	0.26	0.55
April	3.19	0.47	0.37	0.25	0.62
May	2.78	0.59	0.37	0.33	0.69
June	2.43	0.52	0.33	0.41	0.74
July	2.90	-	-	0.44	-
August	2.64	0.85	0.43	0.49	0.92
September	2.59	0.86	0.46	0.44	0.90
October	2.32	0.83	0.47	0.42	0.89

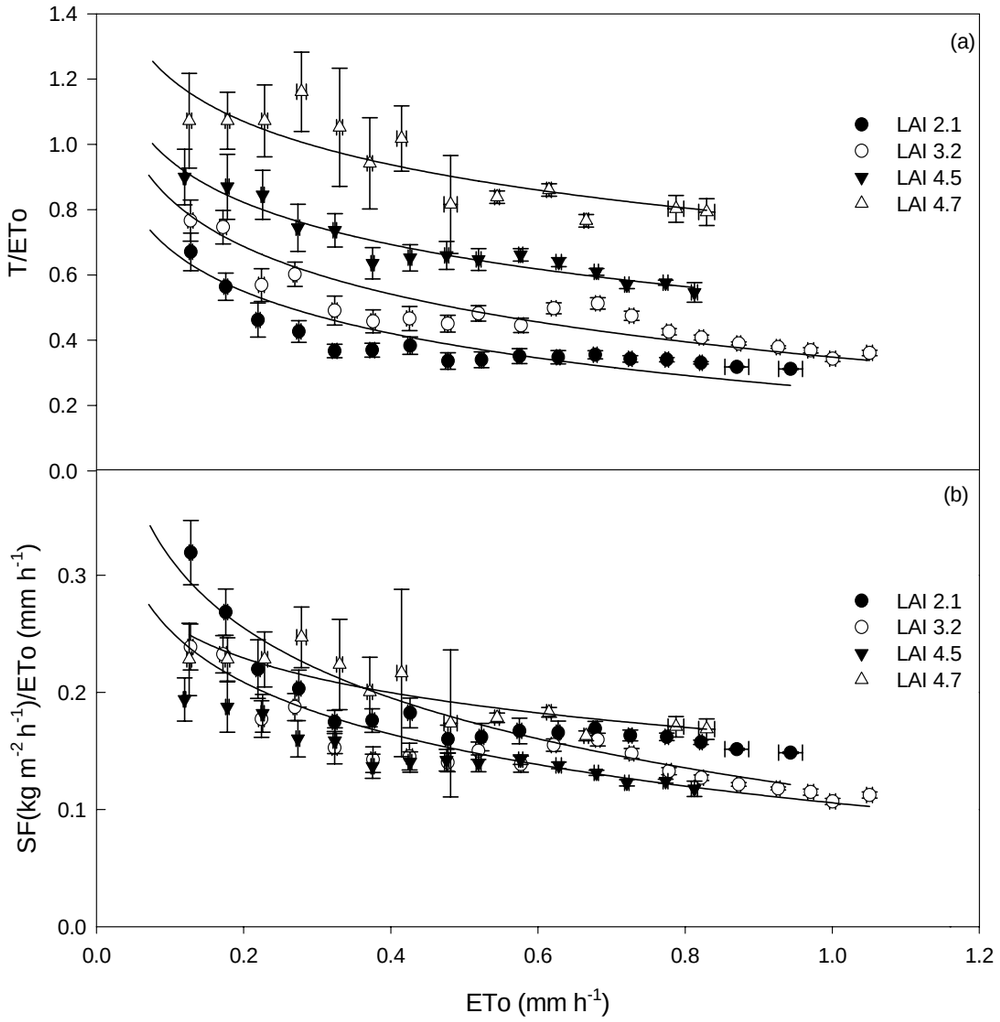


Figure 7. Relationships between hourly reference evapo-transpiration (ETo) and coffee crop coefficient Kc on a ground area basis (a) and coffee transpiration rate on a leaf area basis in MC at four different values of coffee LAI at San Pedro de Barva, Costa Rica. High values of LAI coincide with high values of soil volumetric water content (Values represent means of one week long measurements).

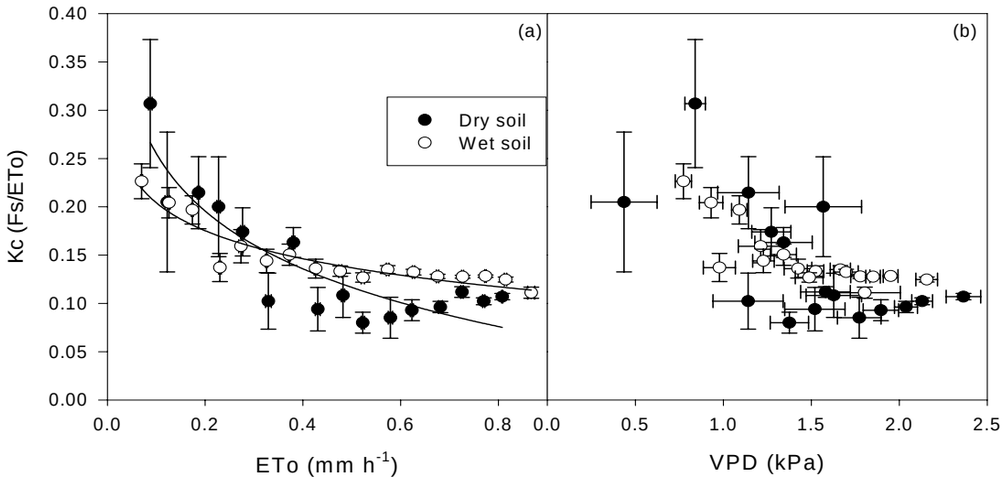


Figure 8. Relationships between coffee crop coefficient (Kc) on a leaf area basis in MC versus ETo (a) and versus VPD (b) in wet and dry soil conditions during the dry season of 2004 at San Pedro de Barva, Costa Rica. (Values are means of measurements over one week for dry soil conditions and over eleven days for wet soil conditions).

Table 2. Annual rainfall, reference evapo-transpiration and estimated water use by coffee plants in MC and coffee plants and shade trees in AFS under optimal coffee cultivation conditions of San Pedro de Barva, Costa Rica for 2004 and 2005.

			Water use (mm yr^{-1})			
Year	Rainfall (mm yr^{-1})	ETo (mm yr^{-1})	Coffee in AFS	Tree	Total AFS	Coffee in MC
2004	3245	1310	544	464	1008	785
2005	2633	1178	437	468	905	678