Top-down versus bottom-up ecological control in cacao, *Theobroma cacao* L.

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***Theobroma cacao* L. (Malvaceae *sensu lato*) is one of the most important agricultural tree crops in the tropics. However, little is known about whether *T. cacao* is controlled via top-down (herbivore) or bottom-up (resource limitation) processes in plantations and in natural forests. This question was investigated in this study by planting seedlings of *T. cacao* in plots of primary and secondary tropical wet forest in northeastern Costa Rica, with a simultaneous planting of the same variety of seedlings in an adjacent reconstructed plantation that had a thin overstory of high canopy shade trees. Leaf growth and leaf damage (herbivory) were measured in the cacao grown under the contrasting systems over a three-year period, with one to two censuses per year. Seedlings grown in plantations were observed to have significantly higher amounts of leaf damage than seedlings grown in secondary or primary forest. Nonetheless, plantation-grown cacao grew much faster, had more leaves, and had larger leaves than forest-grown individuals. Furthermore, plantation-grown cacao plants were the only ones to produce flowers and fruits, and they did so within three years. This study demonstrates that the growth and survival of *T. cacao* is likely controlled by resource limitation (bottom-up control) rather than herbivory (top-down control), and that individuals in high light plantations reach reproductive status even with high rates of herbivore pressure. These findings can inform the choice of efficient cocoa farming system and management strategies to be adopted by cacao farmers in Costa Rica and other cocoa producing countries.**

Keywords: Agro-forestry, cacao, cocoa, Costa Rica, farming system, growth, herbivory, shade cover, survival

Theobroma cacao L. Malvaceae *sensu lato* (Alverson et al. 1999), cacao or "cocoa", as it is commonly known, is one of the most economically important crops in Central and South America. Well known for the provision of chocolate, cocoa, and vegetable butter, *T. cacao* has been cultivated for millennia and furnishes a $107 billion industry, accounting for the livelihoods of 40-50 million farmers in Central and South America and Africa (United States Department of Agriculture: Foreign Trade Service, Wood and Lass 1985). Cacao is grown primarily as a small-scale crop, with plantations or groves usually less than four hectares in size, and with a shade canopy of either thinned-out primary or secondary forest or planted shade trees (Bhat 1988, Rice and Greenberg 2000).

Theobroma cacao is native to lowland wet tropical forests in central and South America. Recent genetic evidence places the genus' origin of domestication in South America (de Schawe et al. 2013). Cacao most likely dispersed from Amazonia as a domesticated plant that was grown not for chocolate but for the sweet-tasting pulp that encases the seeds within the pod (Smith et al. 1992). Cacao presumably reached Central America, Mexico and parts of the Caribbean archipelago centuries prior to the Spanish arrival (Hunter 1990), although the exact means for this dispersal remain controversial (Smith et al. 1992; Schultes 1984; Young 1994). In its natural environment outside of domestication, cacao is a shade-tolerant tree, typically growing along streams, within a partial shade/sun cover, as a tall, slender sub canopy tree bearing pods generally smaller in size than in domesticated cacao (Allen 1981). Wild-grown trees typically produce few flowers and seedling recruitment is slow and sporadic (A.M. Young, unpubl. data).

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Despite the recognized importance of 'cacao' as a crop, little is known about the ecological interactions that enable its survival in various ecosystems. Cacao may be maintained by two different types of trophic interactions: 1) top-down control by a higher trophic level (in this case herbivores), or 2) bottom-up control via resource limitation. Evidence for both types of interactions in plant systems exists (reviewed by Hunter & Price 1992; Turkington 2009). In the top-down control model, population growth at each trophic level is controlled by the one above it with the exception of top predators, which are resource limited (Menge and Sutherland 1976; Bishop 2002; Spiller and Agrawal 2003; Borer et al. 2006; Knight et al. 2006). Conversely, in the bottom-up control model, population growth is controlled by a limited supply of resources, which prevents populations from increasing in relative abundance (White 1978, reviewed by Dyer and Coley 2002; Elser et al. 2007; Hillebrand et al. 2007).

Cacao is known to have a large generalist pest community and many native insects have adapted to utilize the existing crop plant resources in South and Central America (Lara Eduarte 1957). Thus, cacao may be subject to top-down control. If cacao establishment is limited from the top-down by herbivores, we would expect seedling performance (as measured by growth, leaf production and reproduction) to be suppressed the most where herbivory is highest. Alternatively, if performance is limited from the bottom-up via resource availability, one would expect cacao seedlings to perform best where resource availability (in this case, light) is highest, regardless of the amount of herbivory.

To test whether cacao is controlled by bottom-up or top-down processes, the difference in seedling establishment and performance over five years was examined during this study in three distinct environments: 1) a traditionally planted cacao plantation with a lightly shaded overstory consisting of *Erythrina spp.* trees; 2) a heavily shaded primary forest; and 3) a moderately shaded secondary forest. The level of herbivory was quantified among the three different habitat types and addressed two specific questions: 1) How do cacao seedlings respond to environmental conditions that differ in levels of resource availability and herbivory? 2) Is cacao performance (and, by extension, population growth) controlled more by top-town processes (herbivory) rather than by bottom-up processes (resource limitation)?

Methods

Study species

The genus *Theobroma* includes 20 species of cauliflorous trees, all of which are native to tropical America (Cuatrecasas 1964; Rondon and Cumana-Campos 2005). Most members of the genus are shade-tolerant understory species. Several of the species are cultivated locally, but none are as widely cultivated as *T. cacao. Theobroma cacao* is largely pollinated by small-bodied midges (Diptera: Ceratopigonidae and Cecidomyiidae; Hernandez 1965; Kaufmann 1973, 1975; Soetardi 1950; Soria 1970; Wellensiek 1932; Young 1985). Flowers are receptive for one day and unpollinated flowers drop after 24-48 hours (Young 1986). The leaves of *T. cacao* L. are browsed by generalist Orthopterans, such as grasshoppers and crickets (Lara Eduarte 1957).

Site establishment

We conducted a five-year study at the Tirimbina Rainforest Center (formerly Finca La Tirimbina) in northeastern Costa Rica, which is located near the Rio Sarapiqui and the town of La Virgen (10°23'N, 84°07'W), Heredia Province. The elevation of Tirimbina is approximately 220 meters above sea level. The entire region consists of gentle to steep rolling hills, with roughly half of the area devoted to agriculture. The study sites are within a long-term forest study at Tirimbina managed by Centro Agronómico Tropical de Investigación y Enseñanza (CATIE).

We established 29 total plots between 15 December 1996 and 16 January 1997. Each plot was 10 x 10 meters in which we planted 16 cocoa seedlings, each 3 meters apart. Eight of these plots were in a 25 year-old secondary forest that was situated on relatively flat terrain and had been cleared in 1972. In the primary forest, we established twenty plots in five separate sites (4 plots per site). The primary forest area consisted of large, mature forest tree species such as *Pentaclethra macroloba* (Willd.) Kuntze and *Ceiba pentandra* (L.) Gaertn interspersed with several scattered light-gaps surrounded by small patches of older second-growth tree species. In the plantation, we established a single block of 300 *T. cacao* L. seedlings within an 80 x 30 m area. Additional cacao seedlings were planted in July 1999 in all plots to account for high initial mortality due to transplant shock. A total of 128 seedlings was added in the primary forest, 80 seedlings in the secondary forest, and 124 seedlings in the plantation. In the pasture plots, grasses and other small brush were removed periodically by machete in accordance with usual management practices for cocoa plantation.

Each plot was marked using 16 small plastic tubes, each with a unique metal tag identifying the seedling number within that plot. The metal tags used to mark and identify each seedling in the forest plots were coded with three numbers: site, plot and seedling number. For the pasture plot, where it was relatively easy to locate seedling positions, we did not use tags, but instead we used a map indicating the location of each seedling. Prior to planting the cacao in the pasture plot, the area was cleared of brush by machete and *Musa* spp. (banana) were planted along with a fast-growing permanent tree shade of *Erythrina spp* to provide shade. The *Musa* were cut once the *Erythrina* were established. The *Erythrina* ("poro") shade trees were established by obtaining live cut stems from a nearby forest (Chilamate) and pushing the stems into the ground during the rainy season early in the study.

Seedling establishment

All of the cacao seedlings were a variety called "Matina", obtained from seeds in Finca Experimental La Lola (Young 1983) with the cooperation of CATIE. These seeds were germinated in small plastic bags at a cocoa nursery at La Florida, a site near Tirimbina. "Matina" cacao is a Forastero (Cheesman 1944; Wood & Lass, 1985) in origin and is among the earliest types of cocoa grown in the region of La Lola in Limon Province near the Caribbean coast. At the time of planting, the cacao seedlings were 12-15 cm tall. Almost double the number of seedlings were planted in the primary forest plots to account for the more spatially variable conditions caused by light gaps and large primary forest trees. In March 1997 the plots were finalized and the study began.

Seedling census

The seedlings were surveyed seven times between March 1997 and July 2003. These censuses were scheduled at varying times during the growing season (September 1997, April 1998, September 1998, March 1999, February 2000, September 2000 and March 2003), which allowed us to more fully capture the variation in leaf damage that occurred over the growing season. For each census seedling height, stem width, the total number of leaves, leaf width and length, and leaf damage were measured. Missing seedlings were noted as a means of measuring survival rates in all plots. Later in the census, flowers and pods were also counted so that we could quantify the establishment of reproductive adults. Leaf damage, presumably by chewing insects, was measured on a six-point scale of damage: 0% loss, 0-5%, 5-25%, 25-50%, 50-75%, 75-95% and 100% loss. We then converted these categories into “minor,” “moderate” and “heavy” leaf damage levels.

In February 2000, we collected the leaf with the greatest damage from each seedling to determine the main contributors to leaf damage. A total of 80 leaves was collected from primary forest seedlings, 41 from secondary forest and 136 from the pasture plot. Collected leaves were snipped off with scissors and were traced on paper to estimate damage and to describe the various patterns of damage (Figure 1).

Data analysis

To address the unbalanced experimental design, we used the mixed effects analysis of variance tool in the R statistical software (version 3.0.2) package “nlme” (Pinheiro et al. 2014). For each response variable (leaf number, leaf damage, leaf surface area, mortality) habitat (Plantation, Primary Forest, Secondary Forest) was used as the fixed effect and site as a random variable to account for the variably nested experimental design.

Results

The secondary forest seedlings had significantly more leaves than the primary forest seedlings ($F_{2,\ 2088}$=393.94, p=2 x e^{-4}, fixed effect=habitat, random effect=site, Fig. 2a). Cacao plants grown in plantations under *Erythrina spp.* had significantly larger leaves ($F_{2,296}$=167.66, p<0.001, fixed effect=habitat, random effect=site) than those grown in either primary or secondary forests. Primary forest cacao plants had significantly more total leaf damage than secondary forest ($F_{2,\ 692}$=8.433, p=0.04, fixed effect=habitat, random effect=site). Primary forest cacao plants had significantly more total leaf damage than secondary forest ($F_{2,\ 692}$=8.433, p=0.04, fixed effect=habitat, random effect=site, Fig. 2b). Cacao in plantations experienced significantly more heavy ($F_{2,\ 692}$=39.64, p=0.007, fixed effect=habitat, random effect=site) and moderate damage due to herbivory ($F_{2,\ 692}$=29.22, p=0.007, fixed effect=habitat, random effect=site) than cacao in primary or secondary forests. Minorly damaged leaves were not significantly different between habitat types ($F_{2,\ 692}$=1.14, p=0.43, fixed effect=habitat, random effect=site). Leaves with damage of 0-5% and 5-25% were classified as minorly damaged, 25-50 and 50-75% were considered moderately damaged, and 75-95% and 95-100% were considered heavily damaged.

None of the cacao plants in the forest plots reached reproductive maturity, whereas the plantation cocoa trees were producing flowers and pods within three years (Table 1). By February 2001, one quarter (74 of 300) of the trees in the plantation had flowers and pods and average number of floral buds and open flowers was significantly higher than in either the primary or secondary forests, which produced no floral buds or open flowers (Table 1). Cacao in primary and secondary forest plots remained in the seedling-to-small sampling stage for the entire study, and those in the primary forest were shorter in height but thicker in stem width than those in secondary forest plots. The mean stem diameter and height of cocoa in the primary forest were 4.36 cm (±1.19, N=90) and 43.54 cm (±2.65, N=90), whereas mean stem diameter of and height of cocoa in the secondary forest were 0.47 (±0.07, N=50) and 49.89 cm (± 3.71, N=50).

Based upon representative samples of tracings done on damaged leaves (Fig. 1), most herbivore damage was done by chewing insects as opposed to damage from falling debris such as twigs. The presence of large orthopterans in the plantation cacao was noted and *Trigona* spp. (stingless bee) was observed stripping the soft, pliable red meristem leaf tissue of cacao in the plantation.

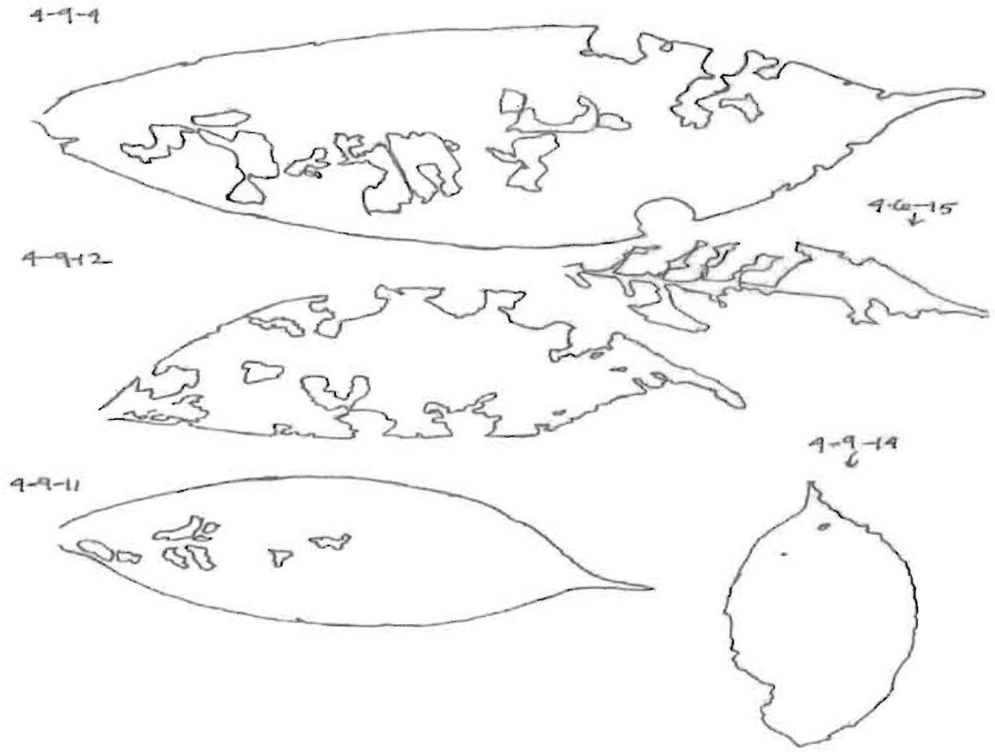

Figure 1: Examples of leaf damage experienced by *Theobroma cacao* L. in three forest types at Tirimbina Rainforest Center, Costa Rica. These examples of leaf tracings represent the type of qualitative data used to diagnose orthopteran herbivory on mature *T. cacao* leaves. Leaf damage was categorized as light, moderate and heavy at each of the censuses during the course of the study and the categories were used to describe herbivory patterns stated in methods in each of the forest types.

Table 1: The average number floral buds per individual and average number of open flowers per individual of *Theobroma cacao* L. plants across three habitat types at Tirimbina Rainforest Center, Costa Rica

Habitat	Date	Number of individuals	Average # of floral buds per individual (± Standard error)	Average # of open flowers per individual (± Standard error)
Plantation	March, 1999	15	34.00 (±9.63)	5.27 (±1.87)
	March, 2003	150	61.09(±3.04)	8.70(±0.59)
Primary Forest	March, 1999	286	0(±0)	0(±0)
	March, 2003	176	0(±0)	0(±0)
Secondary Forest	March, 1999	128	0(±0)	0(±0)
	March, 2003	208	0(±0)	0(±0)

Plantation grown *T. cacao* L. produced significantly more floral buds per plant and open flowers per plant at both collection times. *T. cacao* L. grown in both primary and secondary forests produced no floral buds or open flowers during any data collection period.

Discussion

Whether populations are controlled by top-down or bottom-up processes has been a long-standing question in ecology (Hairston et al. 1960). To date, there have been dozens of studies supporting either bottom-up or top-down control (reviewed by Power 1992, Leibold et al. 1997), suggesting that different, and often co-occurring populations may be controlled by entirely different processes. Determining the exact processes that control agricultural crops is of critical importance because it allows for the implementation of informed and efficient management strategies. Plants that are limited by herbivores from the top-down would be unlikely to increase yield in response to additional resources. By contrast, plants that are limited by resource availability (bottom-up) would be unlikely to have increased yield with the addition of pesticides.

Our data indicate that cacao growth and survival are controlled from the bottom-up by resource limitation, and not by top-down processes such as insect herbivory. Resources such as light, water, and nutrients are often limited in tropical forests, and resource limitation appears to control cocoa growth in this study. While multiple resources may have contributed to the pattern of higher growth in the current study, light is often the most limiting resource in the understory (Holste et al. 2011; Schnitzer et al. 2008) and may have been responsible for our findings. Wild *T. cacao* commonly occurs along breaks in the forest canopy along streams, rivers and light gaps created by tree falls (Allen 1981; Schultes 1984), suggesting that cacao is a naturally light-demanding species.

By contrast, high levels of herbivory were less important to performance in the cacao observed in this study. Nearly 75% of the plants in the plantation experienced high levels of herbivory, yet the greater abundance of resources, presumably light, permitted them to grow considerably more and to reach reproductive maturity despite herbivore-induced loss of leaves. By contrast, less than half of the leaves in secondary and primary forests sustained insect damage yet these plants produced fewer leaves and had significantly smaller leaf area despite the escape from pest pressure. Additionally, leaves in the plantation were more likely to experience damage ranked as "heavy" or "moderate", with significantly less damage ranked as "minor", while damage ranked as "minor" was the largest damage contributor for cocoa in both the primary and secondary forests (Figure 2d). Therefore, cacao seedling growth, survival, and reproduction appears to be suppressed where light is limited, but not by top-down control from insect herbivory.

This study demonstrates that cacao is able to thrive in plantation settings despite suffering the highest levels of leaf herbivory, indicating that resource limitation limits growth of this important agricultural plant. Our findings are consistent with other studies supporting bottom-up control of plant species populations. In the temperate zone, understory plants are often limited by nitrogen and light availability, both bottom-up control mechanisms (Catovsky and Bazzaz 2002). Similarly, water availability has been found to limit plant communities in semi-arid and arid regions (Baez et al. 2006). In tropical forests, light is often considered to be the single most limiting factor for plant growth and survival. For example, at La Selva Biological Station in Costa Rica, Holste et al. (2011) found that understory woody seedling growth increased significantly when exposed to higher light, nitrogen, and phosphorus availability indicating a strong role of bottom-up processes in limiting establishment in tropical understory communities. Our data indicate that these bottom-up processes similarly limit the growth and reproductive output of *Theobroma cacao* an agriculturally important tropical tree.

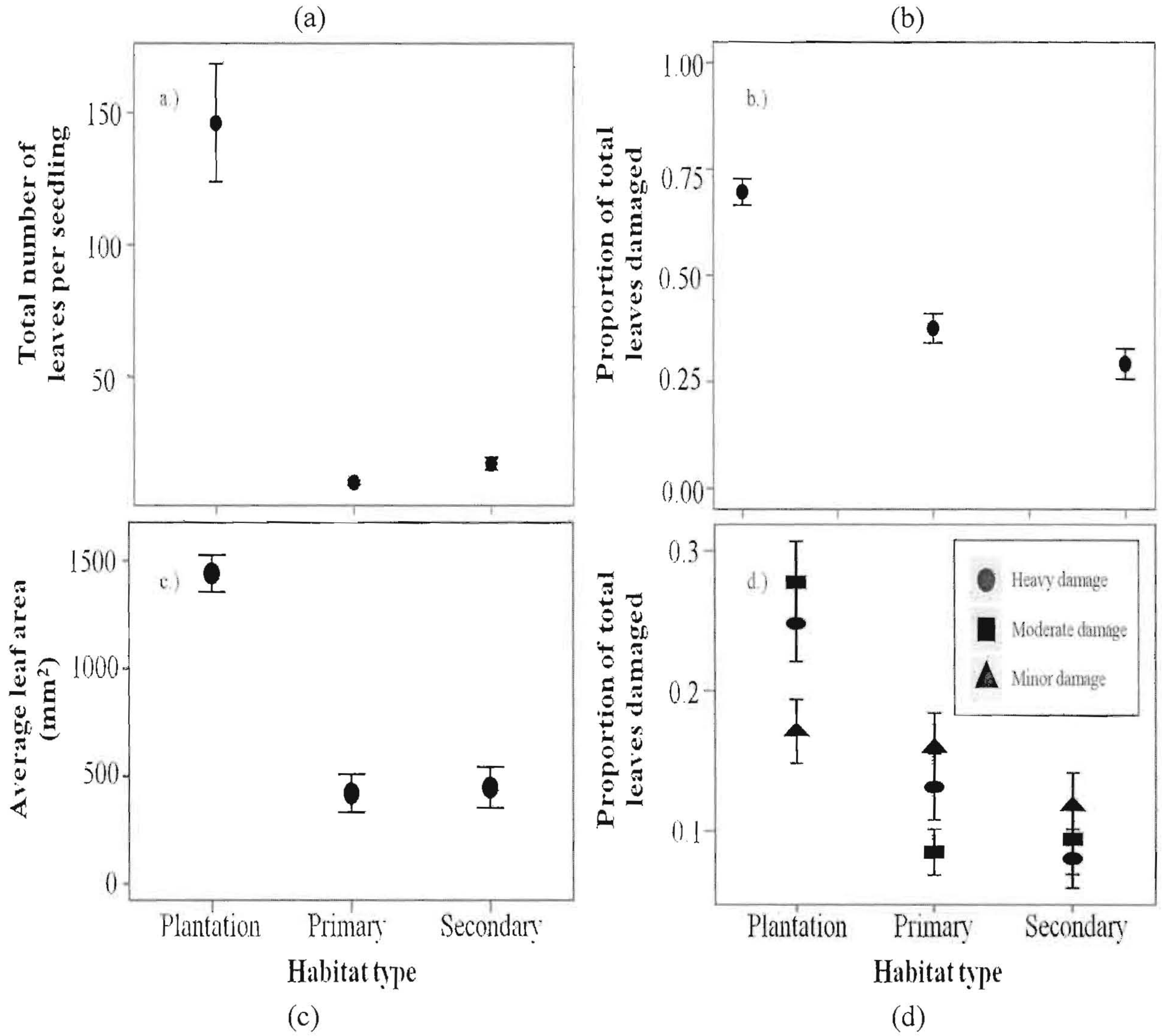

Figure 2: The proportion of *Theobroma cacao* L. leaf number, area, and herbivory in three habitat types at Tirimbina Rainforest Center, Costa Rica. (a) Cacao plants growing in plantations had significantly more leaves than plants in both primary and secondary forest.(b) Cacao plants in plantations had significantly more damage than cacao plants in either primary forest or secondary forest. (c) Cacao plants grown in plantations under *Erythrina spp.* had significantly larger leaves than those grown in either primary or secondary forests. Leaf area of cacao plants in the primary and secondary forests did not differ significantly. (d) Cacao in plantations experienced significantly more heavy and moderate damage due to herbivory than cacao in primary or secondary forests. Minorly damaged leaves were not significantly different between habitat types. Leaves with damage of 0-5% and 5-25% were classified as minorly damaged, 25-50 and 50-75% were considered moderately damaged, and 75-95% and 95-100% were considered heavily damaged.

The importance of resource availability in cacao cultivation has been demonstrated in this study. However, the choice of cacao farming system adopted by farmers, particularly smallholders, who cannot afford high input systems, must be informed by consideration of a combination of ecological (environmental), social and economic trade-offs. In Costa Rica, the value of agro-forestry based cacao farming has been recognised (Ramirez et al. 2001).

This agro-forestry system is in keeping with the advantages of "establishing landscapes with natural habitats and resources that favour pollinator population survival and services" (FAO 2009). For example, coffee farms located in close proximity to forested areas in Costa Rica were found to benefit from greater diversity and number of pollinators visiting the coffee plants (FAO 2009). This translates into increased coffee yields and improved coffee quality. This finding is relevant for cacao since pollination efficiency is a limiting factor in cocoa productivity. Maintaining optimum pollinator population levels in cacao farming systems is crucial. Furthermore, agro-forests provide other ecosystem services such as carbon sequestration. Waldron et al. (2015) have described how this service, provided by biodiverse, agro-forest cacao systems, can be used as an incentive for farmers to practice profitable, eco-friendly agroforestry. This service is achieved through the application of the United Nations REDD (reducing emissions from deforestation and forest degradation) programme of sustainable certification of cacao agroforests (eco-labelling), which rewards farmers with carbon credits. Waldron et al. (2015) also demonstrated how yield may be improved under shade by the retention of an optimum number of shade trees (100 per hectare in the cacao agro-forests studied).

In addition, Franzen and Mulder (2007) concluded that cacao grown under primary forest is the most 'environmentally sound production system'. Siebert (2002) reported that there were fewer weeds when cacao was grown under primary, secondary, or agroforestry shade compared to under full sun or in a plantation system, and this negates the need for herbicides (Clay 2004, cited by Franzen and Mulder 2007). Conversely, weed control is achieved by planting cacao at high density, but this is an intensive (high input) system.

Other benefits of agro-forestry based systems of cocoa production are reduction in soil erosion, buffering of the cacao trees against adverse climatic conditions and pests, and increased efficiency of nutrient utilisation by the trees (Rice and Greenberg 2000; Hartemink 2005). It is noteworthy that in less shaded systems, productivity is superior to that of agro-forest based systems, as demonstrated in terms of reproductive output by this study. However, cultivation of cacao under full or high light conditions is not sustainable. Productivity wanes over time and favourable yields are achieved through application of relatively high inputs such as fertilizers (Ahenkorah et al. 1974). The productivity of trees exposed to full sunlight is limited to 8 to 10 years as opposed to approximately 20 years for cacao grown under adequate shade thus these findings must be integrated over the amount of years this cacao will remain productive (Franzen and Mulder 2007).

The lower incidence of herbivore damage in the agro-forest systems, as was observed in this study, is an advantage of those systems that must be considered in more detail. Increased pest attack (herbivory) in unshaded cacao production systems is well documented and was observed in this study (reviewed by Tscharntke et al. 2011). This heightened pest pressure may warrant the application of expensive and environmentally unfriendly pesticides. The rich insect pest predator diversity in cacao agro-forests for bio-control, compared to that in the less shaded plantation system, may explain this phenomenon and deserves further investigation. However, this advantage in pest pressure may not prove a successful management tool as cacao in the plantation performed better in terms of leaf, fruit, flower, and woody organ production in spite of this higher pest pressure.

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