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Litterfall Dynamics Under Different Tropical Forest Restoration Strategies in Costa Rica

Danielle Celentano[1,5], **Rakan A. Zahawi**[2], **Bryan Finegan**[1], **Rebecca Ostertag**[3], **Rebecca J. Cole**[4], and **Karen D. Holl**[4]

[1] Tropical Agricultural Center for Research and Higher Education (CATIE), 7170 Turrialba, Costa Rica

[2] Organization for Tropical Studies (OTS), Las Cruces Biological Station, Apdo 73-8257, San Vito de Coto Brus, Costa Rica

[3] University of Hawaii, Hilo, Hawai 96720, U.S.A.

[4] Environmental Studies Department, University of California, Santa Cruz, California 95064, U.S.A.

ABSTRACT

In degraded tropical pastures, active restoration strategies have the potential to facilitate forest regrowth at rates that are faster than natural recovery, enhancing litterfall, and nutrient inputs to the forest floor. We evaluated litterfall and nutrient dynamics under four treatments: plantation (entire area planted), tree islands (planting in six patches of three sizes), control (same age natural regeneration), and young secondary forest (7–9-yr-old natural regeneration). Treatments were established in plots of 50 × 50 m at six replicate sites in southern Costa Rica and the annual litterfall production was measured 5 yr after treatment establishment. Planted species included two native timber-producing hardwoods (*Terminalia amazonia* and *Vochysia guatemalensis*) interplanted with two N-fixing species (*Inga edulis* and *Erythrina poeppigiana*). Litter production was highest in secondary forests (7.3 Mg/ha/yr) and plantations (6.3), intermediate in islands (3.5), and lowest in controls (1.4). Secondary forests had higher input of all nutrients except N when compared with the plantation plots. *Inga* contributed 70 percent of leaffall in the plantations, demonstrating the influence that one species can have on litter quantity and quality. Although tree islands had lower litterfall rates, they were similar to plantations in inputs of Mg, K, P, Zn, and Mn. Tree islands increased litter production and nutrient inputs more quickly than natural regeneration. In addition to being less resource intensive than conventional plantations, this planting design promotes a more rapid increase in litter diversity and more spatial heterogeneity, which can accelerate the rate of nutrient cycling and facilitate forest recovery.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp.

Key words: ecological restoration; nutrient inputs; plantations; secondary forest; tree islands.

Tropical forests are among the most important biomes on earth. They house high levels of biodiversity (Losos & Leigh 2004), maintain critical ecosystem services (Noble & Dirzo 1997), and exchange large quantities of carbon and water with the atmosphere (Townsend *et al.* 1992, Field *et al.* 1998). These forests are also threatened by widespread deforestation, particularly in Latin America, where land is being converted rapidly to agricultural uses (FAO 2006). In addition to altering ecosystem structure, tropical deforestation provokes changes in local, regional, and global nutrient cycles with high environmental and social costs (Millennium Ecosystem Assessment 2005).

The majority of tropical forests are sustained by soils with moderate to low fertility (Vitousek & Sanford 1986). Biomass holds a considerable proportion of the nutrients that are potentially available to the biota, and plants have developed highly adapted mechanisms for the acquisition and retention of nutrients (Lambers *et al.* 2007, Walker & Reddel 2007). This characteristic makes some tropical areas especially vulnerable to deforestation, where not only nutrient capital is removed but nutrient cycles are also disturbed, increasing nutrient leakage from the system (Walker & Reddel 2007).

In this context, secondary forests play an important role in mitigating human impacts. In addition to providing habitat, conserving biodiversity, and supplying material goods, they restore ecosystem services such as nutrient cycling (Ewel 1976, Zou *et al.* 1995, McDonald & Healey 2000, Ostertag *et al.* 2008). Patterns and dynamics of natural succession differ greatly at the stand scale within and between regions (Van Breugel *et al.* 2007), and, in some areas, the recovery of tropical forests can be strongly limited by a range of biotic and abiotic factors including lack of seed dispersal, seedling competition with introduced pasture grasses, and decreased soil nutrient availability (Uhl 1987; Nepstad *et al.* 1996; Holl 1999, 2002). Indeed, strategies to overcome these barriers to forest recovery are particularly needed in the tropics, given the large areas of degraded lands (Lamb *et al.* 2005) and the need to maintain essential ecosystem functions.

Approaches to forest restoration vary depending on levels of site degradation, residual vegetation, desired outcomes, and budget (Chazdon 2008). Planting 'tree islands' may be more cost-effective and less labor intensive than conventional tree plantations, as fewer trees need to be planted per hectare (Holl *et al.* in press). This design aims to create structural complexity that facilitates recovery by mimicking the natural regeneration process known as nucleation, where patches of successional vegetation create microhabitats favorable to later-successional species establishment and attract seed dispersers (Yarranton & Morrison 1974, Zahawi & Augspurger 2006, Fink *et al.* 2009, Cole *et al.* in press). Active restoration strategies may increase litterfall and nutrient inputs when compared with areas under natural processes.

Litterfall represents the main transfer of organic matter and mineral elements from aboveground vegetation to the soil surface

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[5] Corresponding author; e-mail: danielle@catie.ac.cr

(Vitousek & Sanford 1986). It increases rapidly in the first years of succession (Ewel 1976); once the canopy is closed, however, there is no obvious trend in litterfall production with increasing stand age (Ewel 1976, Lugo 1992, Zou *et al.* 1995, Ostertag *et al.* 2008), species richness (Scherer-Lorenzen *et al.* 2007), or diversity (Wardle *et al.* 1997). Nevertheless, tree species alter litter chemistry and influence decomposition (Zou *et al.* 1995, Xuluc-Tolosa *et al.* 2003), which in turn affect nutrient availability and successional pathways (Vitousek & Walter 1989).

In this study, we evaluated litter dynamics in a large-scale restoration experiment in southern Costa Rica. The project compares natural regeneration to two active restoration strategies (uniform mixed-tree plantation and tree islands; Holl *et al.* in press) as models for restoration that may be applicable in other tropical regions. Both restoration systems use two native timber-producing hardwoods (*Terminalia amazonia* and *Vochysia guatemalensis*) interplanted with two nitrogen-fixing tree species (*Erythrina poeppigiana* and *Inga edulis*). *Inga edulis* has been shown to increase soil nutrient availability through litterfall, thus creating better conditions for seedling establishment (Nichols *et al.* 2001, Nichols & Carpenter 2006).

Our specific objectives were to evaluate litter production and leaf litter nutrient concentration and inputs to the forest floor in the 5-yr-old active restoration strategies and compare them with same-aged areas undergoing natural succession and young secondary forests (7–9 yr) that had similar structure to the plantations. We hypothesized that: (1) both active restoration strategies would have higher litter and nutrient inputs than the areas with natural regeneration due to differences in tree density and canopy closure; and (2) litter production would be similar in uniform mixed-tree plantation and young secondary forests as a result of comparable canopy cover.

METHODS

STUDY SITES.—This study was conducted from September 2008 through August 2009 at six sites located between Las Cruces Biological Station (8°47′7″ N, 82°57′32″ W) and the town of Agua Buena (8°44′42″ N, 82°56′53″ W) in Coto Brus county in southern Costa Rica (Fig. 1). Over the past 60 yr, most of the region was cleared and converted to agricultural use, primarily coffee production. In the last 15 yr, shifts in the global coffee market led to conversion of coffee plantations to cattle pasture and the fallowing of marginal agricultural lands, resulting in numerous patches of young successional forests (Rickert 2005). Today, around 25 percent of the original forest remains, mostly as small fragments (Daily *et al.* 2001). The forest in this region is classified as a tropical premontane rain forest (Holdridge *et al.* 1975).

Study sites span an elevation range of 1000–1300 m asl and are mostly steeply sloping. Average temperature in the region (21°C) varies little during the year and annual precipitation averages 3500 mm with a distinct dry season from December to March. The sites had been used for agriculture for 18–50 yr before the start of the study and most were burned once or twice soon after clearing, but not thereafter (see Holl *et al.* in press for more detailed site descriptions). Sites were either recently abandoned pastures generally dominated (> 80% cover) by *Pennisetum purpureum* Schumach and/or *Urochloa brizantha* (Hochst. Ex. A. Rich.) R. D. Webster, or coffee farms dominated by a mixture of forage and nonforage grasses, forbs, and *Pteridium arachnoideum* (Kaulf.) Maxon.

Soils (inceptisols) are acidic (pH ~5.6, Al acidity > 1.4 cmol/kg and acid saturation > 20%), and have very low phosphorus (3.0 ± 0.4 mg/kg SE), low to moderate levels of exchangeable cations (Ca: 8.7 ± 1.1 cmol/kg; Mg: 2.8 ± 0.3 cmol/kg; K: 0.4 ± 0.1 cmol/kg) and very high concentrations of Fe (132.8 ± 7.8 mg/kg). Bulk density averaged 0.63 g/cm^3 (± 0.03) and organic matter was high (> 10%; Celentano 2010).

EXPERIMENTAL DESIGN.—At each of the six sites, three treatment plots of 50 × 50 m were established in June–July 2004. Treatments are plantation (Pl; entire area planted with a mix of four species); islands (Is; planting six tree islands of three sizes: 4 × 4, 8 × 8, and 12 × 12 m); and control (Co; no planting/natural regeneration; Fig. 2).

Plantation and island treatments were planted with four species: two native timber species *T. amazonia* (J. F. Gmel.) Exell (Combretaceae) and *V. guatemalensis* Donn. Sm. (Vochysiaceae) interplanted with two naturalized fast growing N-fixing tree species *E. poeppigiana* (Walp.) O. F. Cook (Fabaceae), and *I. edulis* Mart. (Fabaceae). Species selection was based on: (1) high survival in prior studies in the region (> 80%), rapid height growth rates (1–2 m/yr) and broad canopy cover development in the first few years; and (2) availability in local nurseries (Nichols *et al.* 2001, Carpenter *et al.* 2004, Holl *et al.* in press). A total of 86 trees were planted in island treatments (344 trees/ha) and 313 trees in each plantation (1252 trees/ha). Seedlings were planted in alternating rows of *Vochysia/Terminalia* and *Inga/Erythrina*, and were separated by 4 m within rows and 2.8 m across rows (see Holl *et al.* in press for additional details of experimental layout).

We also sampled young secondary forests (7–9 yr growth) near three of the six sites. We selected the closest secondary forest that met our criteria of similar land use history and similar structure to plantations (canopy height, closure, and stem density), *i.e.*, canopy height of 5–15 m, overhead cover of 45–90 percent, and stem density (dbh ≥ 2 cm) of 1406–6875 stems/ha. We did not find any nitrogen-fixing trees in these secondary forest plots. Plot design approximated that of restoration treatments. Twenty-one plots in total were sampled in our experiment.

LITTERFALL SAMPLING.—Litter was collected twice monthly from 12 litterfall traps in each 50 × 50 m plot ($N = 252$) from 1 September 2008 to 30 August 2009 (24 sampling periods). Traps were constructed from fine gauge (0.5 × 0.5 mm) mosquito netting suspended in an inverted pyramid from circular wire hoops and mounted on 60 cm tall legs (area = 0.25 m^2). A rock in the bottom of each trap prevented it from being emptied by the wind. In the island treatment, one trap was installed inside each medium and large island, two were placed within a 2 m perimeter of where trees were planted, and the remaining six were located in unplanted areas

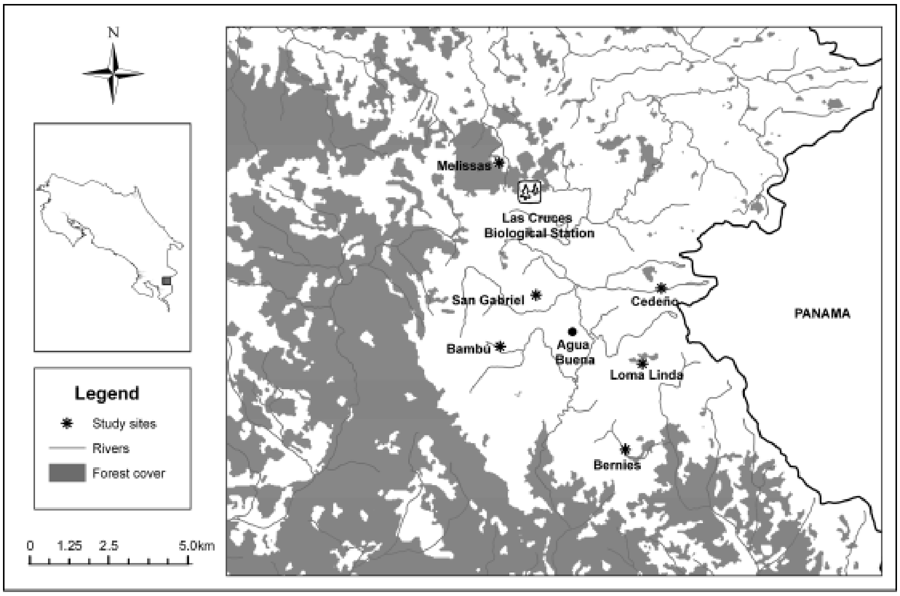

FIGURE 1. Distribution of study sites in Coto Brus County in southern Costa Rica.

($\geq$ 2 m from the base of trees planted in islands; Fig. 2). In other treatments, groups of three litter traps (separated by 4–10 m) were distributed in each of the four quadrants of the plot.

Litter was sorted into leaves, reproductive parts, woody tissue, and miscellaneous. Mass data were reported as a dry weight (48 h at 65°C) for every collection. To determine the individual contribution of each planted tree species to the litterfall, all leaves and flowers were separated by vegetation category (the planted tree species, grasses, other dicotyledons, and unidentified plant material) for the first sampling of every month. We did not separate species in the secondary forest; all species in this treatment was classified as other dicotyledons.

Leaf litter chemical content and nutrient inputs to forest floor.—Leaf litter was analyzed for percent concentrations of total C, total N, Ca, Mg, K, P, and mg/kg for Cu, Mn, Zn, and Fe at the onset of the study (October 2008) and for three time periods (December–February 2009, March–May 2009, and June–August 2009) using bulked samples. Total C and N were analyzed using the combustion method with an automated analyzer (Thermofinigan, Flash EA 1112 Series). Nutrient concentrations (Ca, Mg, K, P, Cu, Mn, Zn, and Fe) were determined as follows: plant tissue samples were dried (70°C), milled, sieved using a 1 mm mesh (18/ASTM; Díaz & Hunter 1978, Association of Official Agricultural Chemists 1984, Mills & Jones 1996), and analyzed on a Thermo Spectronic (Helios alpha, Waltham, MA, U.S.A.) for P and an Atomic Absorption Spectrophotometer (AAnalysist 100, Perkin Elmer, Waltham, MA, U.S.A.) for other nutrients. Given the low variability in leaf nutrient concentration among sampling periods, we present the mean nutrient concentration for all time periods. Leaf nutrient inputs to the forest floor (referred to hereafter as nutrient inputs) were estimated using total leaf production for the year multiplied by average nutrient concentration.

Canopy variables.—Canopy cover directly above each trap was determined using a spherical densiometer in February, May, and August 2009 and averaged. Individual trees above each litter trap were

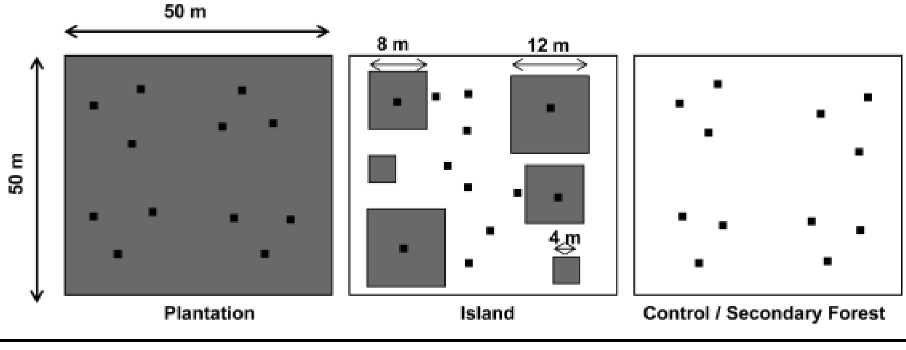

FIGURE 2. Plot and litter traps (black square) layout. In plantation and control, litter traps are located alongside the permanent vegetation sampling plots. Gray, area planted with tree seedlings; White, unplanted areas.

identified and their height measured. To determine the actual diversity of litter, we estimated a canopy species diversity index (d) per plot according to Margalef diversity index (Margalef 1958): $d = [(S - 1)/\ln N]$; where S is the number of species and N is the total number of individuals. We used all species visible in the densiometer mirror above each of the 12 litter traps in each plot to calculate the index at the plot level (Table S1). On average, 17 individuals per plot were used for this estimation.

DATA ANALYSES.—Our experiment was set up as an incomplete block design (the secondary forest treatment was replicated at three of six sites) with site as a blocking factor. Differences in litterfall (total production, each component, and leaf and flower species) among restoration strategies were analyzed using a mixed-model analysis of variance with treatments as fixed factors and site as a random factor, and means were compared according with Fisher's LSD test. The same analysis was used to compare leaf nutrient concentrations and inputs, site conditions, and canopy variables for each treatment. Because of heterogeneous variance for total litterfall and litterfall components, a separate model correcting for heteroscedasticity was run using the function 'varIdent' in R® (version 2.7.2; R Core Development Team 2009). We also analyzed data using a complete block design (four treatments repeated in three sites); these results were consistent with the mixed-model outputs for the incomplete block design so we do not report these other model results.

Correlations between litterfall and canopy variables were examined through path analysis. Correlations between leaf nutrient concentration and canopy species diversity index were also assessed using path analysis. Multiple regression models were used to test the relationship between monthly litter production and leaf nutrient concentrations, the number of species, and the diversity index. In the multiple regression models using total litter production, we used the residual value from the mixed model analyses as the dependent variable to avoid confusion with treatment effects. All statistical analysis and graphics were executed with InfoStat/P® (version 2009; Di Rienzo *et al.* 2009) and R® (version 2.7.2; R Core Development Team 2009). We report means ± SE throughout and consider $P \leq 0.05$ as significant.

RESULTS

LITTERFALL PRODUCTION.—Litter production was highest in secondary forests and plantations, intermediate in island plots, and lowest in controls (Table 1). Litterfall consisted of mostly leaves in all treatments (Pl = 87% ± 1, Is = 88 ± 1, Co = 89 ± 1, SF = 77 ± 1). Leaf and wood fall showed the same pattern as total litter (Table 1), whereas production of miscellaneous material was greatest in secondary forest, intermediate in the planted treatments, and lowest in the control. Production of leaves, wood, and miscellaneous material (Fig. 3) was greater between January and March (drier months) with a peak in February. Biomass of reproductive parts was higher in secondary forests and peaked in April (Table 1; Fig. 3).

Litter production was negatively correlated ($r = -0.87$, $P < 0.0001$) with canopy openness (Pl = 35 ± 3%, Is = 62 ± 4, Co = 85 ± 3, SF = 16 ± 1), and positively correlated ($r = +0.74$, $P < 0.0001$) with canopy height (Pl = 5.8 m ± 0.2, Is = 4.2 ± 0.24, Co = 3.2 ± 0.2, SF = 7.4 ± 0.4). The number of species (Pl = 4.3 ± 0.2, Is = 4.2 ± 0.7, Co = 3.5 ± 0.8, SF = 7.3 ± 0.9) and canopy diversity index (Pl = 1.11 ± 0.06, Is = 1.14 ± 0.23, Co = 0.94 ± 0.28, SF = 2.22 ± 0.30) were significantly greater in secondary forests than in other treatments (Number of species: $F = 5.8$, $P = 0.0112$; diversity index: $F = 5.7$, $P = 0.0110$; Table S1). Neither the number of species ($P = 0.08$) nor the diversity index ($P = 0.15$), however, correlated with litterfall. *Inga edulis* contributed the vast majority of leaf and flower biomass in plantations (70% and 89%, respectively) and islands (47% and 70% respectively; Table 2). Besides *Inga*, only *Erythrina* produced flowers (small quantities) among the species planted. There were large differences in litter production across sites (range 1.1–5.7 Mg/ha) with two sites (Cedeño and Bernie; Fig. 1) having significantly lower litter production than the others ($F = 31.4$, $P < 0.0001$).

LEAF LITTER NUTRIENTS CONTENT AND INPUTS.—Secondary forests had greater concentrations of Ca, Mg, K, Zn, and Mn in leaf litter than did restoration treatments (Table 3). Treatments in which N-fixing species were planted (plantation and island) had greater concentrations of N, higher ratios of C:Ca, C:Mg, and C:K, and lower ratios of C:N than control and secondary forest (Table 3). In turn, leaf C concentration was significantly lower in the control. Other nutrients (P, Cu, and Fe) and the ratio of C:P did not differ among treatments.

Leaf concentration of Ca was positively correlated with both canopy diversity index ($r = +0.51$, $P = 0.0175$) and the number of species ($r = +0.44$, $P = 0.0454$). Together, these two variables explained 43 percent of Ca variation (multiple regression $P = 0.0061$), 28 percent of Mg ($P = 0.0507$), and 37 percent of P ($P = 0.0155$).

TABLE 1. *Annual litterfall production (Mg/ha) by component between September 2008 and August 2009 (± SE) in plantation, island, control, and secondary forest. Values with the same letter are not significantly different (*p ≤ *0.05) across treatments.*

Production (Mg/ha/yr)	Control	Island	Plantation	Secondary forest	F	P
Leaves	1.23 ± 0.29^a	3.06 ± 0.43^b	5.40 ± 0.39^c	5.43 ± 0.39^c	154	< 0.0001
Wood	0.07 ± 0.03^a	0.22 ± 0.05^b	0.48 ± 0.06^c	0.65 ± 0.08^c	45.8	< 0.0001
Reproductive	0.07 ± 0.04^a	0.16 ± 0.07^a	0.31 ± 0.07^b	0.59 ± 0.09^c	33.8	< 0.0001
Miscellaneous	0.07 ± 0.02^a	0.12 ± 0.03^b	0.12 ± 0.02^b	0.51 ± 0.06^c	29.8	< 0.0001
Total	1.41 ± 0.36^a	3.52 ± 0.52^b	6.29 ± 0.48^c	7.29 ± 0.53^c	129	< 0.0001

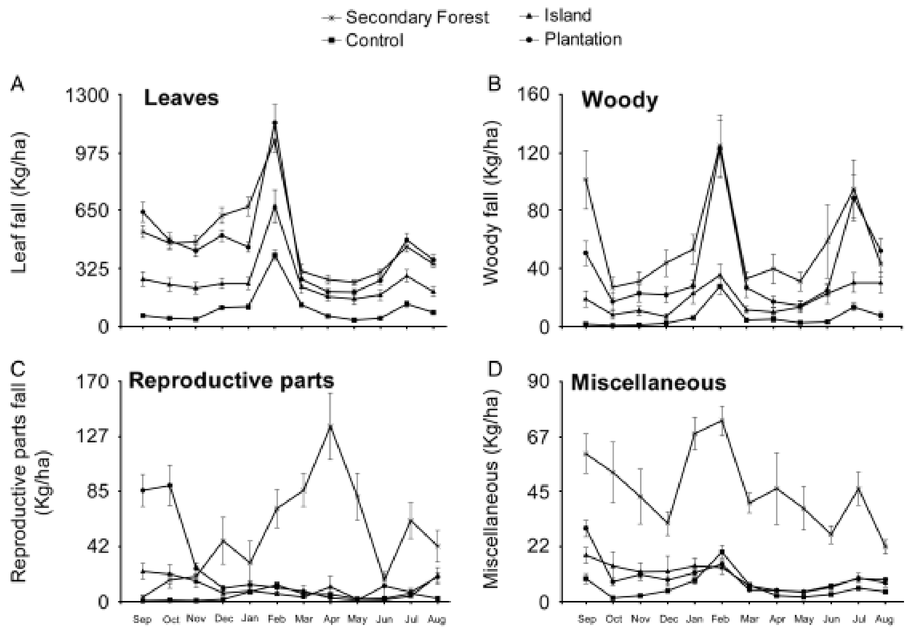

FIGURE 3. Mean monthly production (kg/ha; ± SE) between September 2008 and August 2009 of: (A) leaves; (B) wood; (C) reproductive parts; and (D) miscellaneous in the two active restoration treatments (plantation and island), control and secondary forest in Coto Brus, Costa Rica.

The model was not significant for K ($R^2 = 0.23$, $P = 0.0966$) and micronutrients ($P > 0.2$).

The total litter input of N was highest in plantations, intermediate in islands and secondary forests, and lowest in controls, although the difference between plantations and secondary forests was only marginally significant given high among-site variation in plantations (Table 4). Carbon input was similar in secondary forests and plantations. Secondary forests had greater litter inputs of Ca, Mg, K, P, Zn, and Mn (Pl and SF did not differ for P and Mn). Controls consistently had the lowest input of all nutrients, and islands were slightly higher (plantation and islands did not differ for P, K, Mg, Zn, and Mn).

DISCUSSION

Degraded areas are widespread throughout the tropics. Developing an understanding of ecological processes such as litter dynamics under different tropical forest restoration strategies, as compared with natural regeneration, is important for the evaluation of proactive methods and to recommend restoration practices for

TABLE 2. *Percent (mean ± SE) of total leaf and flower fall grouped by species (October 2008–August 2009) in plantation, island, and control*[a]*. Values with the same letter are not significantly different (*$p < 0.05$*) across species composition.*

	Leaves (%)			Flowers (%)		
Species composition[b]	Control	Island	Plantation	Control	Island	Plantation
Inga edulis	1 ± 0^{a}	47 ± 10^{b}	70 ± 5^{c}	2 ± 1^{a}	70 ± 14^{b}	89 ± 2^{b}
Erythrina poeppigiana	4 ± 3^{a}	11 ± 3^{a}	15 ± 4^{b}	1 ± 1^{a}	1 ± 0^{a}	1 ± 1^{a}
Vochysia guatemalensis	0 ± 0^{a}	5 ± 4^{a}	$5 \pm 2^{a,b}$	0 ± 0^{a}	0 ± 0^{a}	0 ± 0^{a}
Terminalia amazonia	0 ± 0^{a}	2 ± 1^{a}	3 ± 1^{a}	0 ± 0^{a}	0 ± 0^{a}	0 ± 0^{a}
Grasses	$40 \pm 2^{a,b}$	15 ± 11^{a}	2 ± 1^{a}	50 ± 15^{b}	15 ± 12^{a}	5 ± 3^{a}
Other dicots[c]	56 ± 2^{b}	$20 \pm 6^{a,b}$	$6 \pm 1^{a,b}$	47 ± 15^{b}	14 ± 5^{a}	5 ± 1^{a}
F	6.9	5.4	88.8	8.4	11.9	537.7
P	0.0003	0.0012	< 0.0001	< 0.0001	0.0012	< 0.0001

[a] All species in the Secondary Forests were classified as other dicotyledons.

[b] Unidentified leaf and flower material represented less than 2% in all treatments.

[c] For potential species composition, please refer to the list of canopy species in Table S1.

TABLE 3. *Mean leaf fall nutrient concentration (± SE) for four periods of analysis in plantation, island, control, and secondary forest. Values with the same letter are not significantly different* ($p < 0.05$) *across treatments.*

	Control	Islands	Plantation	Secondary Forest	*F*	*P*
Percent						
C	43.1 ± 1.0^{a}	45.9 ± 1.0^{b}	47.7 ± 0.3^{b}	46.0 ± 0.4^{b}	9.7	0.0016
N	1.53 ± 0.15^{a}	2.10 ± 0.17^{b}	2.38 ± 0.12^{b}	1.60 ± 0.09^{a}	10.3	0.0012
Ca	1.58 ± 0.17^{a}	1.45 ± 0.12^{a}	1.36 ± 0.10^{a}	2.14 ± 0.05^{b}	5.5	0.0130
Mg	0.39 ± 0.03^{b}	0.27 ± 0.03^{a}	0.23 ± 0.02^{a}	0.40 ± 0.05^{b}	11.0	0.0009
K	0.50 ± 0.05^{a}	0.46 ± 0.06^{a}	0.42 ± 0.04^{a}	0.84 ± 0.04^{b}	10.0	0.0014
P	0.12 ± 0.01	0.10 ± 0.01	0.10 ± 0.01	0.14 ± 0.02	–	0.2424
mg/kg						
Cu	12.3 ± 2.2	12.4 ± 1.4	12.1 ± 0.8	9.75 ± 0.08	–	0.5300
Zn	92.4 ± 9.0^{b}	40.5 ± 3.8^{a}	27.8 ± 1.9^{a}	73.3 ± 6.6^{b}	27.7	0.0001
Mn	$322 \pm 44^{b,c}$	$268 \pm 50^{a,b}$	254 ± 48^{a}	351 ± 75^{c}	5.8	0.0109
Fe	157 ± 23	159 ± 17	144 ± 16	129 ± 8	–	0.3005
Ratios						
C:N	29.6 ± 2.8^{b}	22.7 ± 2.0^{a}	20.3 ± 1.0^{a}	29.0 ± 1.5^{b}	7.8	0.0037
C:Ca	$28.7 \pm 2.7^{a,b}$	$32.6 \pm 2.4^{b,c}$	36.0 ± 2.9^{c}	21.6 ± 0.7^{a}	5.4	0.0140
C:Mg	113 ± 8^{a}	187 ± 23^{b}	220 ± 16^{b}	119 ± 13^{a}	12.3	0.0006
C:K	$89.0 \pm 7.1^{a,b}$	$109 \pm 15^{b,c}$	120 ± 10^{c}	55.0 ± 2.7^{a}	5.8	0.0110
C:P	388 ± 39	466 ± 31	500 ± 38	358 ± 52	–	0.0916

landowners and public agencies. Although litter dynamics during secondary succession are well studied (Ewel 1976, Zou *et al.* 1995, McDonald & Healey 2000, Ostertag *et al.* 2008), few investigations have compared secondary forests and plantations (Cuevas *et al.* 1991, Lugo 1992) and to our knowledge no publication has examined litter fall in tree islands.

LITTER PRODUCTION AND QUALITY.—Litter production was much higher in the two active restoration strategies studied (uniform mixed-tree plantation and tree islands) as compared with areas under natural regeneration (controls) after 5 yr. Indeed, most of the control areas were dominated by pasture grasses, which represent an important barrier to forest recovery (Holl 2002). In the active restoration treatments, the fast growing N-fixing species (*I. edulis* and *E. poeppigiana*) provided canopy cover and quickly shaded out grasses and other ruderal vegetation (Holl *et al.* in press). Plantations showed higher litter production than islands due to higher tree density and canopy cover, a result consistent with previous studies that demonstrate a strong correlation of litter production with canopy cover and aboveground biomass increases; thus litterfall represents an important measure of net primary productivity (Clark *et al.* 2001, this study).

Litter production in the plantation treatment was similar to secondary forests that were 3–5 yr older, so from a production standpoint, plantations may be a better restoration strategy than tree islands over the short term. Previous studies, however, suggest that stand age is a key factor affecting litterfall but only in the first decade or so after lands are removed from agriculture; after canopy closure there is no clear correlation between litterfall production and stand age (Ewel 1976, Lugo 1992, Zou *et al.* 1995, Ostertag *et al.* 2008). We hypothesize that treatment differences in terms of litterfall rates will likely disappear over time. Although plant species density and diversity were higher in secondary forest plots, these structural variables were not correlated with litter productivity, as in previous studies (Lugo 1992, Wardle *et al.* 1997, Scherer-Lorenzen *et al.* 2007). The higher biomass of reproductive parts in secondary forest plots is likely due to species composition and the longer time since abandonment for these plots, during which time more trees had reached reproductive maturity.

Secondary forests had higher quality litter (greater nutrient concentration and lower C-to-nutrient ratios) and higher inputs of all nutrients except N when compared with the plantation plots. Different species composition is most likely driving the differences we found between plantations and secondary forests in terms of nutrient quality as in other studies (Zou *et al.* 1995, Scherer-

TABLE 4. *Annual leaf fall nutrient inputs to the forest floor per hectare (± SE) in plantation, island, control, and secondary forest. Values with the same letter are not significantly different* ($P < 0.05$) *across treatments.*

	Control	Islands	Plantation	Secondary forest	*F*	*P*
kg/ha/yr						
C	499 ± 127^{a}	1324 ± 301^{b}	2410 ± 510^{c}	2486 ± 235^{c}	11.6	0.0007
N	18.7 ± 6.0^{a}	62.1 ± 15.6^{b}	123 ± 28^{c}	$87.9 \pm 0.9^{b,c}$	10.2	0.0013
Ca	18.5 ± 5.6^{a}	41.2 ± 8.8^{b}	66.5 ± 13.7^{c}	118 ± 7^{d}	22.8	< 0.0001
Mg	4.54 ± 1.22^{a}	$7.48 \pm 1.87^{a,b}$	10.7 ± 2.3^{b}	22.0 ± 3.7^{c}	10.9	0.0010
K	6.90 ± 2.41^{a}	$14.0 \pm 3.3^{a,b}$	23.1 ± 5.3^{b}	48.3 ± 3.5^{c}	18.4	0.0001
P	1.44 ± 0.40^{a}	$3.01 \pm 0.72^{a,b}$	$5.23 \pm 1.24^{b,c}$	7.53 ± 1.92^{c}	6.3	0.0082
g/ha/yr						
Cu	15.7 ± 6.8^{a}	38.3 ± 10.4^{a}	64.8 ± 16.2^{b}	$53.4 \pm 5.8^{a,b}$	6.3	0.0083
Zn	107 ± 25^{a}	112 ± 19^{a}	130 ± 24^{a}	393 ± 4^{b}	40.7	< 0.0001
Mn	388 ± 138^{a}	$736 \pm 210^{a,b}$	$1317 \pm 453^{b,c}$	1862 ± 338^{c}	7.2	0.0050
Fe	185 ± 49^{a}	443 ± 85^{b}	719 ± 164^{c}	$703 \pm 83^{b,c}$	9.0	0.0021

Lorenzen *et al.* 2007). This suggests that biochemically, plantation and secondary forest will not function in the same way—even if they produce similar amounts of litter. Indeed, litter decomposed faster in secondary forests than other treatments (Celentano 2010). Similarly, Lugo (1992) found that secondary forest litter had higher nutrient concentrations and faster nutrient turnover than plantations, although litter quality in plantations improved over time due to native species enrichment, and some > 17-yr-old plantations had the same litter turnover rate as same age secondary forests (Lugo 1992).

The overwhelming dominance of *I. edulis* (70% of leaf litterfall), an N-fixing species, strongly influenced litter characteristics in our plantation plots. *Inga* litter has a large recalcitrant fraction (Leblanc *et al.* 2006) that can retard decomposition processes (Palm & Sanchez 1990) and soil nutrient availability. In fact, litter accumulation on the forest floor in our plantation plots was much higher compared with secondary forest and islands, and was higher than the annual litter production, because of its low decomposition rate (Celentano 2010).

Dominance by a single species may not be desirable for restoration. The dominant litter can potentially affect nutrient cycling through its effects on soil conditions, litter accumulation rates, and decomposition processes, all of which can influence the recruitment of native species (Carson & Peterson 1990, Molofsky & Augspurger 1992, Mesquita *et al.* 2001). Our results highlight the importance of species choice during restoration efforts, suggesting that litter nutrient characteristics should be taken into account. Although *Inga* also dominated litter fall biomass in the island treatment (47%), distribution among species was more equitable as other dicotyledonous species and grasses comprised a larger proportion. The tree island restoration method increased litter production and nutrient inputs more quickly than natural regeneration and is less resource and labor intensive.

IMPLICATIONS FOR TROPICAL FOREST RESTORATION.—The high variability in litter production and nutrient inputs in our sites underscores the importance of site quality in determining whether restoration succeeds, and the danger of extrapolating the outcomes of restoration strategies that have been tested at only one or two sites. Tree planting is the most widespread strategy to restore tropical forests (Lamb & Gilmour 2003); there is an increasing focus on planting a diversity of native species (Rodrigues *et al.* 2009) but many restoration efforts rely on a small number of commercially available species. Our results show that planting a small number of fast growing trees to facilitate tropical forest recovery promotes the development of a rapid canopy cover that shades out grasses and provides large amounts of litterfall, similar to more diverse secondary forests. High-density large-scale plantings of a few species, however, can result in lower litter quality (measured by nutrient concentration and C-to-nutrient ratios), depending on the species selected. Accordingly, restoration strategies with more heterogeneous planting designs, such as tree islands, are less resource intensive and promote a faster increase in litter diversity and more spatial heterogeneity, which can accelerate the rate of nutrient cycling and facilitate forest recovery. Another strategy to promote higher species diversity and better litter quality would be to plant a larger number of species at the outset or once the canopy has established and site conditions are appropriate for later-successional species, but this approach implies higher costs.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *List of canopy dicot species in the different restoration plots in Coto Brus, Costa Rica.*

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