

Dynamics of leaf litter humidity, depth and quantity: two restoration strategies failed to mimic ground microhabitat conditions of a low montane and premontane forest in Costa Rica

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Abstract: Little is known about how restoration strategies affect aspects like leaf litter's quantity, depth and humidity. I analyzed leaf litter's quantity, depth and humidity yearly patterns in a primary tropical lower montane wet forest and two restored areas: a 15 year old secondary forest (unassisted restoration) and a 40 year old *Cupressus lusitanica* plantation (natural understory). The three habitats are located in the Río Macho Forest Reserve, Costa Rica. Twenty litter samples were taken every three months (April 2009-April 2010) in each habitat; humidity was measured in 439g samples (average), depth and quantity were measured in five points inside 50x50cm plots. None of the restoration strategies reproduced the primary forest leaf litter humidity, depth and quantity yearly patterns. Primary forest leaf litter humidity was higher and more stable ($\bar{X}=73.2$), followed by secondary forest ($\bar{X}=63.3$) and cypress plantation ($\bar{X}=52.9$) (Kruskal-Wallis=77.93, n=232, p=0.00). In the primary (Kruskal-Wallis=31.63, n=78, p<0.001) and secondary (Kruskal-Wallis=11.79, n=75, p=0.008) forest litter accumulation was higher during April due to strong winds. In the primary forest (Kruskal-wallis=21.83, n=78, p<0.001) and the cypress plantation (Kruskal-wallis=39.99, n=80, p<0.001) leaf litter depth was shallow in October because heavy rains compacted it. Depth patterns were different from quantity patterns and described the leaf litter's structure in different ecosystems though the year. Rev. Biol. Trop. 60 (3): 1041-1053. Epub 2012 September 01.

Key words: restoration strategies evaluation, leaf litter humidity, leaf litter quantity, leaf litter depth, leaf litter structural complexity.

Tropical forests have undergone extensive deforestation throughout the world (Geist & Lambin 2002, Quesada *et al.* 2009, FAO 2010), increasing the need to develop scientific restoration efforts. The selected restoration strategy will impact soil quality, biodiversity, aquifer recharge and forest environmental services. However, the effects of restoration strategies on different ecosystem components are not well known and the importance of deterministic and stochastic factors needs more discussion (Chadzon 2008).

In Costa Rica all restoration strategies leave understory to natural ecological succession (or "unassisted restoration"), but the canopy establishment follows three major types:

natural ecological succession ("do nothing restoration"), native plant species plantation, and introduced plant species plantation (like *Cupressus lusitanica*) (Cusack & Montagnini 2004, Jiménez 2005, Murillo 2005, Bonilla *et al.* 2008, Sampaio *et al.* 2008, Quesada *et al.* 2009, Barrientos & Monge 2010, Cole *et al.* 2010, Castellanos-Barliza & León 2011). More complex restoration options like direct transfer of intact habitat islands or seed addition (Watts *et al.* 2008) are not common in Costa Rica.

Restoration strategy selection in Costa Rica is a consequence of political and economic national strategies (Jiménez 2005, Murillo 2005). Nevertheless, the application of a restoration strategy should take into account

technical assessments (De Camino 2005), or management plans that include all the complex elements of an ecological restoration program (Windhager 1999, Fernández 2006, Clewell & Aronson 2008).

Selection of a restoration strategy impacts micro and macro-scale elements, such as soil temperature, litter quality, soil respiration rates, nitrogen availability, microbial biomass, faunal community composition, among others, that would influence the functioning of the restored forest or ecosystem (Ayres *et al.* 2009a). Therefore, technical analysis of restoration strategies require multi-disciplinary and ecosystem level studies. However, to achieve such knowledge it is important to understand the dynamics of several phenomena: understory composition; forest temperature and moisture; litter production, structure, humidity, and decomposition rates; soil erosion, plant dispersion, etc. In Costa Rica the study of these phenomena was started by L.A. Fournier in the 20th century (Fournier & Camacho de Castro 1973, Fournier & Herrera de Fournier 1978).

One of the basic components of a tropical forest is the litter that accumulates on the ground, it constitutes an essential part of nutrient cycling (Wardle 2002, Álvarez-Sánchez & Harmon 2003, Ayres *et al.* 2009a, Castellanos-Barliza & León 2011). The vegetation that is chosen in a restoration program will define temperature and soil humidity, mainly due to canopy density, stratus structure, sunlight that can reach understory and soil, leaf litter production and decomposition rate, and tree falling rate, among others (Mosquera *et al.* 2007). It also defines: soil physical and chemical properties (Ayres *et al.* 2009a); understory plant species composition; litter composition coming from the canopy and understory; leaf litter nutrients, production and decaying rate (Mosquera *et al.* 2007, Scherer-Lorenzen *et al.* 2007, Hättenschwiler *et al.* 2008, Vivanco & Austin 2008); organism diversity (Vasconcelos 1999, Naranjo-García 2003, Doblas 2007, Sánchez *et al.* 2007, Bonilla *et al.* 2008, Castro-Díez *et al.* 2008, Ayres *et al.* 2009c); and forest regeneration and recovery rates and patterns

(Letcher & Chadzon 2009). It has been shown, that the replacement of native by exotic species affects the litter production rate, nitrogen content and nutrient release during decomposition (Bonilla *et al.* 2008, Castro-Díez *et al.* 2008).

Many studies have been performed on leaf litter production (Bonilla *et al.* 2008), decomposition rates (Álvarez-Sánchez & Harmon 2003, Castro-Díez *et al.* 2008, Ayres *et al.* 2009b, c), nutrient release (Ayres *et al.* 2009a, Castellanos-Barliza & León 2011) and on litter organism diversity and its impact on decomposition rates (Fournier & Herrera de Fournier 1978, Barrientos 2000, Palacios-Vargas *et al.* 2007, Ayres *et al.* 2009a). Despite the large number of species that inhabit the leaf litter, few studies have been done on its structural properties, dynamics and relation with organisms.

A high diversity of angiosperms is characteristic of tropical forests and allows the establishment of a structurally complex and diverse leaf litter layer, even if there is an accumulation of leaves belonging to the nearest plant, a phenomenon known as “home field” (Gholz *et al.* 2000, Ayres *et al.* 2009a, Ayres *et al.* 2009b). To my knowledge, no leaf litter structural complexity hypotheses or indexes have been built. Future ecologic work on this matter should consider plant species diversity, litter quantity, vertical space covered (depth), accumulation and decomposition rate, hyphal density (as hypha may be attaching litter layers) and diversity of type texture and shape of material added to the litter.

A more complex litter layer has more species and organisms, probably because it provides more area to hide from predators, feed and lay eggs (Barrientos 2000, Sabo *et al.* 2005, Palacios-Vargas *et al.* 2007, Sabu *et al.* 2008). In addition, the amount of litter defines the amount and rate of the interactions in the different trophic levels (Sabo *et al.* 2005). But contrary to what could be expected, Ayres *et al.* (2009c) found that litter decomposes more rapidly near the plant that produces it. This is probably the result of specialization by decomposers.

Litter also retains soil humidity longer than bare soil (Anderson 1990), allowing water to percolate instead of rapidly evaporating. Litter makes forest humidity more stable by keeping water (Díaz-Fernández *et al.* 2006, Ruiz *et al.* 2009), and prevents rain's direct impact on the soil, reducing erosion (Di Stefano & Fournier 2005).

Rainfall and litter humidity are key factors in a complex interplay of processes. There is a negative relationship between litterfall and rainfall (Mosquera *et al.* 2007), which at least in some tropical forests can be attributed to the presence of deciduous plants (Fournier & Camacho de Castro 1973). However, rainfall is crucial for litter decay (Cornejo *et al.* 1994, Castellanos-Barliza & León 2011) and correlates with microbial biomass (Schimel *et al.* 1999) and abundance of other organisms (Bonilla *et al.* 2008). Litter humidity affects the community living under, in and on the litter, because in many cases species migrate vertically in order to achieve optimal environmental conditions (Barrientos 2000, Naranjo-García 2003, Doblas 2007). Another important finding is that extreme drought and occasional rewetting cause water stress, which significantly reduces biomass and microbial biodiversity and causes changes in the structure of the decomposers community (Schimel *et al.* 1999).

Litter humidity is affected by rainfall, litter composition and canopy cover, as well as by type, thickness and permeability of the soil (Álvarez-Sánchez & Harmon 2003, Díaz Fernández *et al.* 2006, Sampaio *et al.* 2008). All these factors are modified with deforestation and establishment of a different flora community (Vasconcelos & Laurance 2005, Bonilla *et al.* 2008); therefore, any restoration process should consider these factors. However, litter humidity has been studied almost exclusively in relation to forest fires in temperate regions and lowland tropical dry forests (Odiwe & Muoghalu 2003, Dezzeo & Chacón 2006, Ruiz *et al.* 2009).

The effect of different restoration strategies on humidity, structure, temperature, species composition and nutrient release of forest litter

has not been analysed. This study analysed three variables that are important to understand leaf litter complexity and general patterns that affect biodiversity in the forests (leaf litter humidity, depth and quantity) in a primary forest, a secondary forest and a plantation.

MATERIALS AND METHODS

Research area: The study was carried out in Orosi Valley, Costa Rica, at Reserva Forestal Río Macho. This reserve limits with the Tapantí-Macizo Cerro de la Muerte National Park, which has more than 58 000ha of primary forest. The dry season goes from December through April, whereas the rainy season runs from May through November.

Three habitats were selected: a primary forest (or "old growth forest" according to Clark (1996)) near the "El llano" water dam (9°45'56.07" N - 83°51'47.11" W, 1 640msm), in a tropical lower montane wet forest area with ultisol humult soil; a secondary forest (or "young secondary forest" according to Clark (1996)) left to natural succession for about 15 years (9°45'29.52" N - 83°51'23.27" W, 1 684 msm), in a tropical lower montane wet forest area with ultisol humult soil, and a *Cupressus lusitanica* plantation that has been without management for nearly 40 years and therefore has a poorly developed understory dominated by hardwood leaves species (9°47'52" N - 83°51'51" W, 1 309msm). The *C. lusitanica* plantation belongs to a tropical humid premontane forest area and the soil is inceptison dys-trandep. The three places have similar slopes, all of over 40°.

Sampling: Samples were collected every three months in each habitat: January 2010, April 2009, July and October 2009. Due to logistic problems the cypress plantation was sampled in April 2010 instead of April 2009.

In each sampling date a 200m randomly selected transect was set at least 10m away from any trail to avoid border effect and away of tree gaps to avoid the effect of direct sun evaporation on litter (Camargo & Kapos 1995).

Along each line, 20 sampling plots (50x50cm) were chosen with a digital random number generator. Samples were collected between 9:00am and 2:00pm, to standardize the daily humidity fluctuation (Ruiz *et al.* 2009) and also because this is the time of the day with less rain and where re-humidification by atmospheric water vapour is less important (Pyne *et al.* 1996, Dirks *et al.* 2010).

One leaf litter sample (mean 439g, SD=188, min=89, max=1 470) was collected in each 50x50cm plot. In each plot all litter was collected including small branches less than 5mm in diameter, fragmented litter and humus (representing successive decaying stages), only bare soil, living plants, stones and branches bigger than 5mm in diameter were left. Litter samples were kept in a plant oven (60°C) for several days until constant dry weight was reached to apply the formula: Humidity percentage=(wet weight-dry weight)/wet weight*100.

Litter depth was measured in each plot with a standard millimetric ruler in five independent places of a 50x50cm subplot. Average leaf-litter depth for each plot was calculated. Litter quantity was assessed by the number of hardwood leaves that could be threaded with an ice pick (10cm long, 3.5mm diameter) (five samples were taken for each plot) in a 50x50cm subplot. Cypress needles were not considered in this methodology as they do not form layers. Leaf layers were analysed because they are useful structural elements for litter tropical dwellers (Naranjo-García 2003, Doblás 2007, Palacios-Vargas *et al.* 2007, Eaton *et al.* 2011).

All statistical analyses were performed with Statgraphics Centurion XV. Leaf-litter humidity comparisons were made between habitats and between sampling dates (Kruskal-Wallis ANOVA). Litter abundance and depth were analyzed in relation to each other (Spearman correlation), and to humidity, habitat and sampling date (Kruskal-Wallis ANOVA).

RESULTS

Leaf litter humidity comparison between habitats

Primary forest had the wettest litter ($\bar{X}=73.2$, $n=77$, $SD=11.6$, $min=8$, $max=87$), followed by the secondary forest ($\bar{X}=63.3$, $n=75$, $SD=16.8$, $min=12$, $max=94$) and cypress plantation ($\bar{X}=52.9$, $n=80$, $SD=14.6$, $min=21.3$, $max=77.6$) (Kruskal-Wallis=77.93, $n=232$, $p=0.00$).

Leaf litter humidity according to season

Dry season: During January the driest place was the plantation ($\bar{X}=31.1\%$) followed by the secondary forest ($\bar{X}=48.9\%$) and the primary forest ($\bar{X}=74.7\%$) (Kruskal-Wallis=35.75, $n=59$, $p<0.001$) (Fig. 1). During the April samplings the litter humidity was similar in the primary forest and the cypress plantation, but the secondary forest was dryer (Kruskal-Wallis=12.99, $n=55$, $p=0.0015$) (Fig. 1).

Wet season: During the July and October samplings the cypress plantation was drier (July $\bar{X}=60.6\%$, October $\bar{X}=59.9$) than the other two habitats (primary forest: July $\bar{X}=75.6\%$, October $\bar{X}=79.4\%$) (secondary forest: July $\bar{X}=72.6\%$, October $\bar{X}=77.6\%$) (July, Kruskal-Wallis=31.68, $n=60$, $p<0.001$) (October, Kruskal-Wallis=35.31, $n=58$, $p<0.001$) (Fig. 1).

Leaf litter humidity yearly pattern according to habitat

Primary forest: Litter was drier during the April sampling (Kruskal-Wallis=33.28, $n=77$, $p<0.001$), but the difference between the driest and the wettest sampling was of only 15.8% (\bar{X} max=79.4%, \bar{X} min=63.6%) (\bar{X} max=mean maximum, \bar{X} min=mean minimum) (Fig. 1).

Secondary forest: Litter humidity pattern shows a longer period of low litter humidity

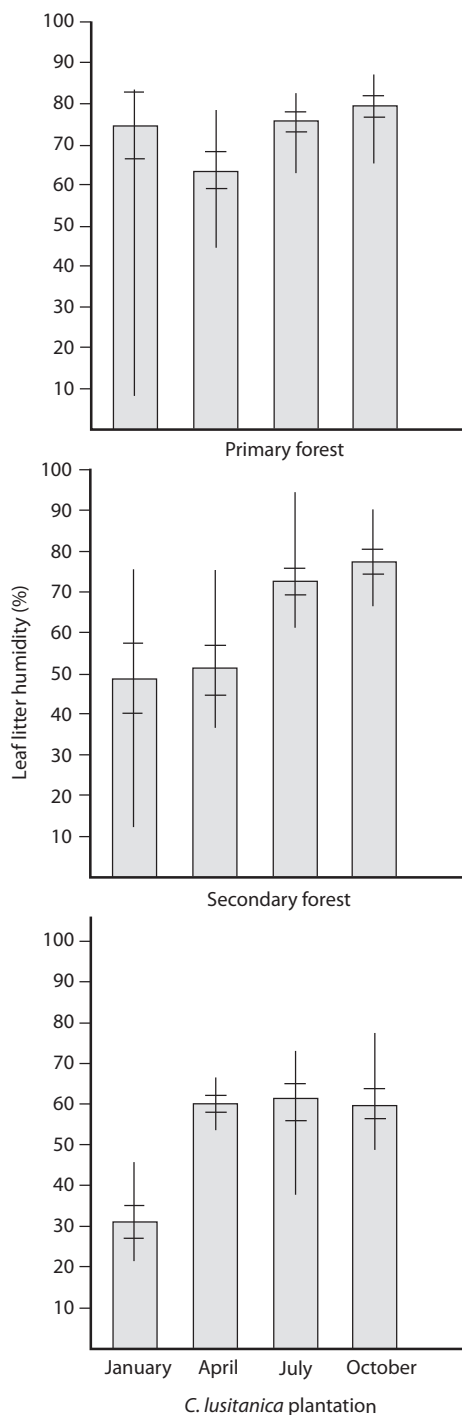


Fig. 1. Leaf litter humidity percentage in the three studied habitats. Vertical lines on bars referred to minimum and maximum. Horizontal lines on bars referred to standard deviation.

than in the primary forest and the *C. lusitanica* plantation. In this habitat the litter was dryer during the January and April samplings (Kruskal-Wallis=49.16, $n=75$, $p<0.001$), and the difference between the driest and the wettest sampling was of 28.7% (\bar{X} max=77.6%, \bar{X} min=48.9%) (Fig. 1).

***Cupressus lusitanica* plantation:** Litter was driest during the January sampling (Kruskal-Wallis=44.1617, $n=80$, $p<0.001$) and the difference between the driest and the wettest sampling was 29.5% (\bar{X} max=60.6%, \bar{X} min=31.1%) (Fig. 1). The wettest sampling mean (60.6%) in this habitat was even drier than the driest sampling mean in the primary forest (63.6%).

Leaf litter depth and quantity in the three studied habitats in a year

Thicker litter layer and greater quantity of leaves were associated with greater levels of litter humidity (Litter quantity, Spearman correlation $r=0.3$, $n=232$, $p=0.000$) (r =correlation, n =sample size), (Litter depth, Spearman correlation $r=0.27$, $n=232$, $p=0.000$). The litter depth (Kruskal-Wallis=78.95, $n=233$, $p=0.0$) (Fig. 2A) and quantity (Kruskal-Wallis=92.47, $n=233$, $p=0.0$) (Fig. 2B) were higher in the primary forest followed by the secondary forest and the cypress plantation.

Leaf litter depth and quantity yearly patterns according to habitat

Litter quantity pattern in primary (Kruskal-Wallis=31.63, $n=78$, $p<0.001$) (Fig. 3) and secondary forest (Kruskal-Wallis=11.79, $n=75$, $p=0.008$) (Fig. 3) show that leaf is more abundant in April and decreases until January. A completely different pattern was found in the cypress plantation where October is the sampling with more leaf abundance while April had the fewest (Kruskal-Wallis=7.77, $n=80$, $p=0.0509$, marginally significant).

Litter depth in primary forest (Kruskal-Wallis=21.83, $n=78$, $p<0.001$) (Fig. 4) and *C. lusitanica* plantation (Kruskal-Wallis=39.99,

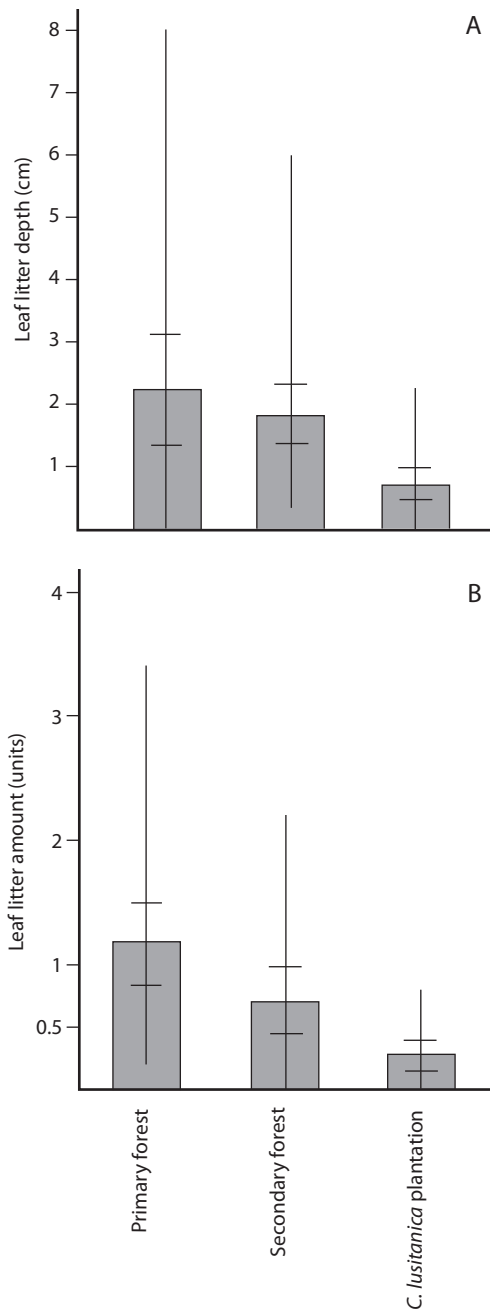


Fig. 2. A. Litter mean depth (in cm) in the three studied habitats. **B.** Litter mean quantity of leaves (in leaf units) in three studied habitats. Vertical lines on bars referred to minimum and maximum. Horizontal lines on bars referred to standard deviation.

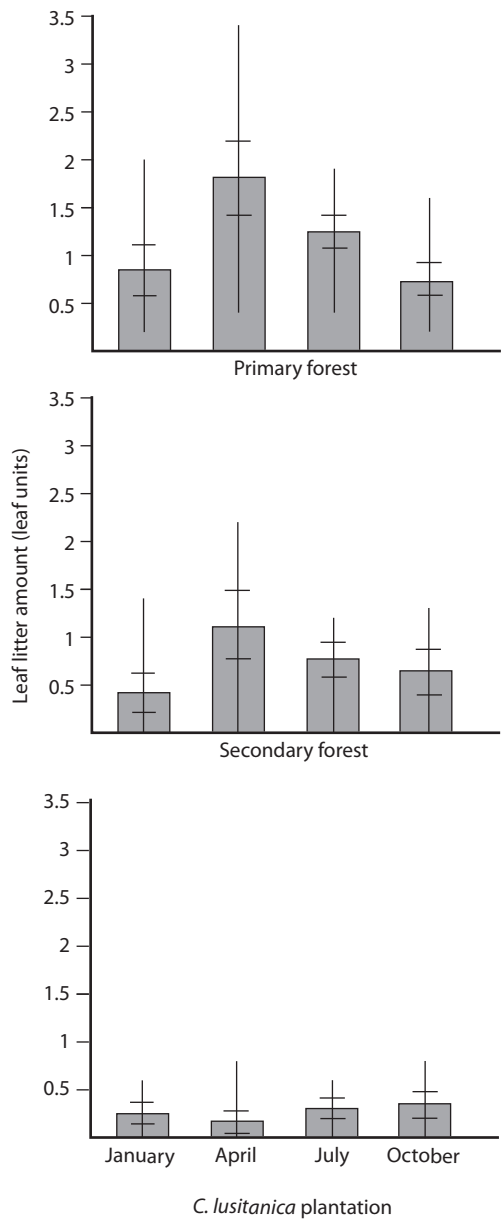


Fig. 3. Leaf litter mean quantity of leaves (in units). Vertical lines on bars referred to minimum and maximum. Horizontal lines on bars referred to standard deviation.

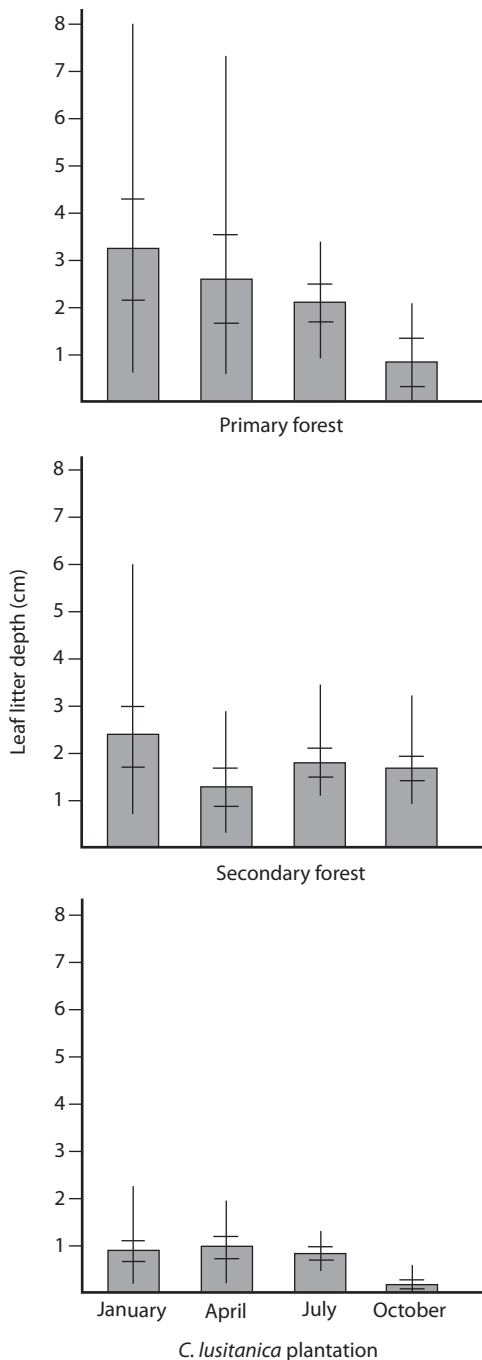


Fig. 4. Leaf litter mean depth (in cm). Vertical lines on bars referred to minimum and maximum. Horizontal lines on bars referred to standard deviation.

$n=80$, $p<0.001$) (Fig. 4) had their lowest value during the October sampling, while in the secondary forest all the samples had about the same litter depth values, just slightly lower during April (Kruskal-Wallis=10.68, $n=75$, $p=0.014$) (Fig. 4).

DISCUSSION

The findings in this research show that leaf litter humidity in primary forest is higher and more stable around the year than in these restoration habitats. Wind, evaporation, solar radiation and UV-B radiation, soil's capacity to keep humidity, drainage and temperature are some factors that affect litter humidity (Ruiz *et al.* 2009, Dirks *et al.* 2010, Smith *et al.* 2010). In this case, probably the taller and more abundant canopy and understory dicotyledonean foliage cover of the primary forest (personal observation) help keeping the litter's humidity higher and more stable the year around. The structure (quantity and depth) and species composition of the litter may also help keeping high humidity levels (Álvarez-Sánchez & Harmon 2003).

The *C. lusitanica* plantation's litter humidity is lower than in the primary and secondary forest almost the year around. The only exception is in April when the secondary forest is the driest. Nevertheless, the highest litter's humidity in the cypress plantation was 60.6% which is lower than the driest sampling mean in the primary forest (63.6%). This can be attributed to lower values of litter quantity and depth (Ruiz *et al.* 2009), litter decomposition stage (cypress secondary compounds may delay decomposition rates) (Ruiz *et al.* 2009), litter composition (mainly cypress needles), a poorly developed understory (personal observation), a more regular canopy structure and a more homogenous foliage cover (Rodríguez & Cordero, unpublished data).

Secondary forest's and cypress plantation's litter gain and lose more humidity than the primary forest's litter, but during the rainy season, the secondary forest can be almost as humid as the primary forest. The only study known to me that compares angiosperm and

gymnosperm litter humidity was made by Díaz-Fernández *et al.* (2006). This study shows that both kinds are able to keep the same humidity, the only exception are grasses, which are able to keep twice as much. Therefore, the wider humidity range of these habitats may be a result of the lower amount of litter, shallower litter and less developed canopy in the secondary forest, and less developed understory in the cypress plantation (personal observation). This allows the sun to increase litter's temperature and evaporation rate. In the secondary forest, another possible explanation is the abundant grass of the secondary forest, because grass is able to keep more moisture (Díaz-Fernández *et al.* 2006). The grass abundance in the secondary forest may be a result of occasional cattle activity in the area. In future studies the wind speed should also be considered.

It is interesting that litter quantity and litter depth have the same general pattern: primary forest has the highest values, followed by the secondary forest; the cypress plantation has the smallest litter quantity and the shallower litter. Nevertheless, the patterns around the year in the three habitats are different.

In the primary and secondary forest litter quantity had its highest values during the April samplings. This pattern matches the inverse relation between litter productivity and rainfall found by other researchers (Di Stefano & Fournier 2005, Mosquera *et al.* 2007, Sánchez *et al.* 2007). The three studied habitats are within tropical lower montane wet forest and tropical humid premontane forest areas (now altered by human activity), therefore, some deciduous trees occur. Nevertheless, most are evergreen species, and hence these results cannot be attributed only to the leaf fall found in tropical dry forest (Fournier & Camacho de Castro 1973). The litter quantity in Rio Macho primary and secondary forest is probably also a consequence of the strong winds that blow from the beginning of December-March or April. This may have caused a litter accumulation in the April sample. After that, litter decomposes slowly until December when another cycle begins. In addition, it could be

that the low humidity of the dry season reduces the decomposition rate. Nevertheless, this last item should be considered carefully as field studies show contradictions about the relation between litter decaying rate, temperature, rainfall, ultraviolet-B radiation and evapotranspiration (Cornejo *et al.* 1994, Monedero & González 1995, Aerts 1997, Powers *et al.* 2009, Smith *et al.* 2010, Eaton *et al.* 2011, Salinas *et al.* 2011); experimental studies on this topic are needed. This pattern could not be detected in the cypress plantation, maybe as a result of the absence of hardwood trees.

The primary forest and cypress plantation showed a litter's depth pattern that has the lowest values in October, while April and January have the highest values. As the studied areas have steep slopes, it would be reasonable to think that some litter is flown downhill by heavy rains, but it is not the case because the amount of leaves in the litter was similar to January. September and October are the wettest months of the year in this area (Herrera 1986, UNESCO 2007). This may produce a compaction effect, leaving less space between leaves. This effect may also help keeping high litter moisture during that time of the year, but it also means that less interleaf space is left for micro and macro organisms. Besides this, another aspect that may strongly affect biota and decaying rates is the oxygen concentration. If litter is more compact and wet it may be also more anaerobic. On the contrary, during January, although there are less leaves in the litter they are more loose and occupy more vertical space. In the secondary forest the lowest litter depth values were obtained in April; further studies are needed to understand this pattern.

Litter depth patterns found in this study are different to litter quantity patterns, because describe different aspects of the litter's structure and they should not be considered equivalents.

It is reasonable to expect that less litter humidity correlated with less litter quantity and depth, but as shown in this research the relation between them is much more complex. Therefore litter humidity, depth and quantity must be analyzed in relation with understory

and canopy foliage cover and composition, and with soil features. In fact litter humidity presents a continuum with soil and understory, therefore many litter dwellers migrate between these strata to achieve better humidity conditions (Naranjo-García 2003, Doblas 2007, Ayres *et al.* 2009a). Complementary research is being conducted on terrestrial molluscs in these plots, showing that their abundance and size distribution is strongly correlated with these factors (Barrientos, unpublished data). It would also be interesting to analyse regeneration patterns in relation to litter humidity and structure.

The selection of a given restoration strategy affects ecosystem features like the litter humidity and structure, that, in return, will determine the biodiversity that can get established in it. Here it is shown that natural succession and reforestation with cypress present litter humidity, depth and quantity patterns that do not resemble conditions in a primary forest floor. Future studies should also analyze if plantations with native species where the understory is left to natural succession, produce patterns of litter humidity, quantity and depth more similar to primary forest. Other aspect not considered in this study is the effect of fragment sizes on these variables (Didham 1998).

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RESUMEN

Poco se sabe acerca de cómo las estrategias de restauración afectan aspectos como la cantidad, profundidad y humedad de la hojarasca. Se analizaron estas variables en un bosque tropical húmedo montano bajo, considerado bosque primario y dos áreas restauradas: un bosque secundario de 15 años (restauración natural) y una plantación de *Cupressus lusitanica* de 40 años con sotobosque restaurado naturalmente. Los sitios estudiados se ubican en la reserva forestal Río Macho, Costa Rica. Los muestreos se realizaron cada tres meses (abril 2009-abril 2010). En cada ocasión se escogieron al azar 20 cuadrículas de 50x50cm de las que se recogió 439g en promedio de hojarasca para medir la humedad por diferencia entre peso seco y húmedo. En cada cuadrícula se midió la profundidad y cantidad de hojarasca haciendo un promedio de cinco puntos. La cantidad se midió con el número de hojas ensartadas en un picahielos. La profundidad se midió con una regla metálica. Ninguna de las técnicas de restauración reproduce los patrones anuales del bosque primario en cuanto a la humedad, profundidad y cantidad de hojarasca. La humedad de la hojarasca del bosque primario es mas alta y estable ($\bar{X}=73.2$), seguida por el bosque secundario ($\bar{X}=63.3$) y el cipresal ($\bar{X}=52.9$) (Kruskal-Wallis=77.93, $n=232$, $p=0.00$). La cantidad de hojarasca acumulada en el bosque primario (Kruskal-Wallis=31.63, $n=78$, $p<0.001$) y el secundario (Kruskal-Wallis=11.79, $n=75$ $p=0.008$) es mayor en abril debido a los fuertes vientos. La profundidad de la hojarasca del bosque primario (Kruskal-wallis=21.83, $n=78$, $p<0.001$) y en el cipresal (Kruskal-wallis=39.99, $n=80$, $p<0.001$) es menor durante octubre debido a que los fuertes aguaceros la compactan. Los patrones de cantidad y profundidad de la hojarasca presentan diferencias, que describen la estructura de la hojarasca en diferentes ecosistemas a lo largo del año.

Palabras clave: evaluación de estrategias de restauración, humedad de hojarasca, cantidad de hojarasca, profundidad de hojarasca, complejidad estructural de hojarasca.

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