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# Leaf litter decomposition of tree species in three successional phases of tropical dry secondary forest in Campeche, Mexico

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## Abstract

Leaf litter decomposition rate and nitrogen, carbon and phosphorous (NCP) concentration of three species: *Croton lundellii* Standl., *Metopium brownei* (Jacq.) Urban and *Manilkara zapota* (L.) van Royen were evaluated in different phases of development (3, 13 and >50 years old) of secondary dry forest in Campeche, Mexico, to test two hypotheses: (1) leaf decomposition rate is higher in older successional stages of secondary dry forest; (2) decomposition rate is more rapid in pioneer species than late successional species, because of differences in substrate quality. The litterbag method was employed to evaluate decomposition. Results indicated that decomposition was related to forest development phase but the strongest influence was due to leaf chemical composition. Decomposition was fastest in *C. lundellii*, intermediate in *M. brownei* and slowest in *M. zapota*. The C/N, C/P ratios and total N and P concentrations were good indicators of decomposition rates across species in all successional stages. In comparing leaf litter collected locally and decomposed in situ, the earlier successional phase showed higher decomposition rates than later stages of succession. Neither N concentration or C/N ratio explained this difference, but it was correlated with higher P concentration.

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**Keywords:** *Croton lundellii*; *Metopium brownei*; *Manilkara zapota*; Litter quality; Decay rate; Succession

## 1. Introduction

The leaf litter deposition and decomposition are recognized as critical pathways of organic matter and nutrient flux in tropical dry forest systems (Melillo et al., 1982; Proctor, 1983; Alvarez et al., 1992). The leaf litter aboveground is the main input of nutrients to the soil (Herbom and Congdon, 1998; Martínez-Yrizar,

1995; Montañez, 1998). The production and decomposition of leaf litter in dry forests are influenced by the seasonality of precipitation and plant composition (Anderson and Swift, 1983; Cuevas, 1995). During the wet season, conditions for growth and activity of soil microorganisms are improved, thus increasing decomposition rate. Studies on soil invertebrates show that during the dry season the soil fauna moves deeper in the soil (Prieto et al., 1999). Due to this difference between dry and wet season, in some tropical dry forests an inhibition of decomposer community results in a transient accumulation of litter on

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the forest floor during the dry season (Swift and Anderson, 1989).

In dry forests on the Yucatan Peninsula, litter production (Whigham et al., 1990, 1991) and decomposition of fine and coarse woody detritus (Harmon et al., 1995) have been studied, but leaf litter decomposition along a successional gradient was not investigated. Montañez (1998) found that leaf litter decomposition of tree species in home gardens depended on season and species, where a slow decomposition occurred during the dry season and fast during the rainy season. Different decomposition rates among tropical species have been documented (Babbar and Ewel, 1989; Alvarez and Becerra, 1996; Montañez, 1998; Sundarapandian and Swamy, 1999), and leaf quality, especially the C/N ratio, has been proposed as a sound predictor of decomposition rate (Heal et al., 1997). Because the floristic composition and forest structure changes during secondary succession (Brown and Lugo, 1990), decomposition will depend on the age of the forest (Coleman and Crossley, 1996). If pioneer species have high decomposition rates due to higher leaf nutrient content, then slower decomposition can be expected in mature forests. On the other hand, old-growth forests may be more efficient in the recycling of nutrients (Brown and Lugo, 1990), and we may expect higher decomposition rates in these forests.

The major problem in dry forest is land use conversion, which entails disruption of ecological processes like productivity, hydrological process, soil erosion and nutrient cycling, and biodiversity loss (Mass, 1995).

The objective of this study was to evaluate the leaf litter decomposition rate of tree species in three different growth phases of tropical dry secondary forest (3, 13 and >50 years old). Two hypotheses were tested: first, that decomposition rate is higher in older successional stages of secondary dry forest, and second, that it is higher in pioneer species relative to late successional species due to differences in substrate quality.

## 2. Study area

The study was carried out on the rim of the Calakmul biosphere reserve in the state of Campeche, southern Mexico. The reserve is situated between

17°45' and 19°15'N, 89°15' and 90°10'W. This zone comprises one of the largest well-preserved tropical dry forest in southern Mexico. Approximately 34% of the total area (723,185 ha) corresponds to the core area, which is surrounded by a human populated buffer zone (Díaz, 2000). About 50,000 inhabitants coming from 26 states of the Mexican Republic have settled in 120 villages since the 1970s. The community of “El Refugio” (northeastern part of the reserve, 107 inhabitants) was chosen because there are a number of permanent plots established by the land cover and land use change project of Clark University, Harvard forest and ECOSUR financed by NASA (Turner et al., 2001).

Topography is relatively flat and characterized by a karstic plateau, reaching a maximum elevation of 380 m above sea level. This plateau shows an altitudinal gradient, decreasing from South to North in the reserve (García and March, 1990). The soils are classified as rendzina, gleysol, litosol and vertisol (FAO, 1970; García and March, 1990). The climate, according to the Köppen system modified by García (1973), is seasonally dry subhumid (Aw) with a summer rainy season (June–October). The annual precipitation is around 945 mm, and the mean annual temperature is ca. 22 °C. The dry season extends between February and May. In August, there is a short dry season (locally named “canicula”). Monthly rainfall and temperature distribution during the study period are presented in Fig. 1.

The vegetation types in the area correspond to tropical semi-evergreen forest (selva mediana subperennifolia), tropical low semi-evergreen forest (selva baja subperennifolia) and secondary forest (Lundell, 1934; Miranda, 1958; Rzedowski, 1981; Flores et al., 1990; Flores and Espejel, 1994). These types are classified as tropical dry forest in the Holdridge system (Murphy and Lugo, 1986). The forest in this study is characterized by the presence of both evergreen and deciduous species. Canopy height is between 15 and 25 m. The characteristic tree species are *Manilkara zapota* (L.) van Royen, *Vitex gaumeri* Greenman, *Lysiloma latisiliquum* (L.) Benth., *Bursera simaruba* (L.) Sarg., *Metopium brownei* (Jacq.) Urban, *Brosimum alicastrum* Swartz, *Piscidia piscipula* (L.) Sarg., *Malmea depressa* (Baill.) R.E. Fries, *Guetarda combsii* Urban, *Thouinia paucidentata* Radlk., *Thevetia gaumeri* Hemsley,

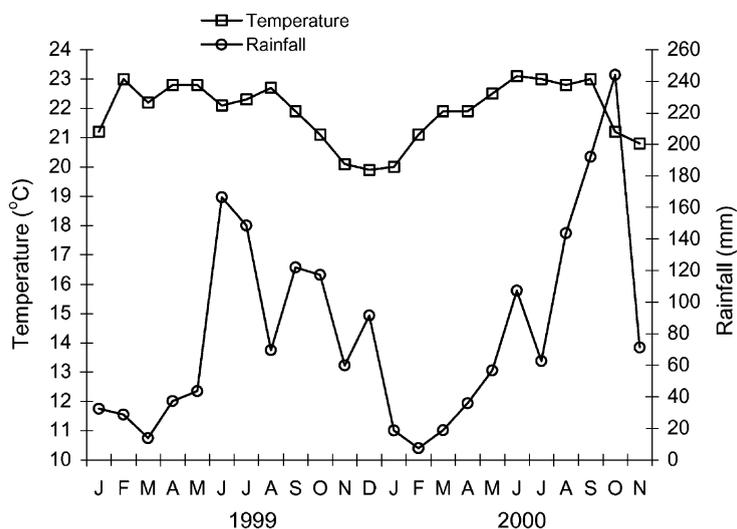


Fig. 1. Ombrothermic diagram recorded during 1999–2000 in the Zoh Laguna weather station, 30 km from El Refugio, Campeche, Mexico.

*Lonchocarpus rugosus* Benth., *Croton lundellii* Standl., and *Cecropia obtusifolia* Berthol.

### 3. Methods

#### 3.1. Forest stand selection

During 1999, a number of circular permanent plots (500 m<sup>2</sup>) were established in secondary forest stands of known age, all of which have been used for slash and burn agriculture. D. Pérez (personal communication) described the floristic composition and forest structure in these permanent plots and D. Lawrence (personal communication) determined the litterfall dynamics and soil physical and chemical characteristics. Three successional stages with different environmental conditions were chosen: (1) secondary forests 3 years old reaching 2–3.5 m in height dominated by young trees, shrubs (>1 cm and <4.5 cm dbh) and climber plants; (2) secondary forests 13 years old with a high density of trees (>4.5 cm and <16 cm dbh) and shrubs 5–8 m tall; (3) mature forest more than 50 years old, dominated by tall trees (>30 cm dbh) reaching 13–16 m in height (D. Pérez, personal communication). Two plots of each successional phase were chosen from the plots formerly established in the litterfall collection experiment.

#### 3.2. Leaf litter decomposition of tree species

A leaf litter decomposition experiment was carried out during a period of 7 months from April to October, 2000. Three plant species were used in the experiment: *C. lundellii* Standl., an early successional deciduous species; *M. brownei* (Jacq.) Urban; a late successional deciduous species, and *M. zapota* (L.) van Royen, an evergreen late successional species. These species were typical components of forest composition and structure in the study area (D. Perez, personal communication). Entire leaves of *C. lundellii* and *M. brownei* were harvested directly from adult trees during February and March, just before abscission. Then they were oven dried at 60 °C for 72 h. Recently fallen leaves of *M. zapota* were collected under the trees, taking care that all leaves were in a similar condition. Leaf litter was used to determine decomposition because this plant organ represents a substantial portion (50–80%) of the total aboveground litter production in terms of biomass (Toky and Ramakrishnan, 1983a; Alvarez et al., 1992; Martínez-Yrizar, 1995; Montañez, 1998; Sundarapandian and Swamy, 1999). Because of their relatively higher nutrient concentration, they represent the major nutrient input as well (Toky and Ramakrishnan, 1983b; Alvarez et al., 1992). Furthermore, leaves decompose faster than twigs and other woody materials (Anderson and

Swift, 1983), thus providing rapid inputs to the soil nutrient cycle.

Leaf decomposition was evaluated through the litterbag technique described by Swift and Anderson (1989) and Alvarez et al. (1992). This technique has proven useful in delineating and analyzing differences in decomposition rate (Coleman and Crossley, 1996). Mesh bags 15 × 20 cm in size with 2 mm mesh were filled with 30 g of dried leaves from one of the species (Montañez, 1998). The leaves of an individual species were mixed to obtain an uniform mixture before filling the mesh bags. The 1–2 mm mesh size was considered sufficiently small to prevent losses of litter due to breakage, but sufficiently large to permit the access of decomposers (Sundarapandian and Swamy, 1999). On April 1, three replicates of six litterbags per species were labeled and placed on the forest floor at random on the border of each plot. A total of 54 leaf litterbags were set out in each plot (108 in each successional phase), with 324 bags for the entire study.

### 3.3. *In situ decomposition of local leaf litter*

In order to compare the decomposition of the total litter deposition and decomposition among different successional stages, bags containing local leaf litter were deployed as well. These bags were filled with 30 g of the leaf fraction, obtained from litterfall harvested in four traps (1 × 1 m<sup>2</sup>) during February and March. Additional 18 mesh bags of local leaf litter were placed in each plot (36 per successional stage). A total of 108 bags were employed for the study of in situ decomposition of local leaf litter.

At six time intervals (35, 63, 91, 125, 156 and 190 days after start of experiment) three bags per species and three of the local leaf litter samples were retrieved from the plots for analysis. The analysis consisted of measuring the mass of leaves left in the bag after drying in paper bags in an oven at 60 °C for 72 h. Differences between the mass at the beginning of the experiment and that at the different time periods were calculated to evaluate leaf decomposition (Singh and Gupta, 1977).

### 3.4. *Nutrient concentration*

Chemical analyses were undertaken to determine leaf litter quality for each species and local leaf litter

sample, and to track changes in leaf litter quality during the experiment. Total carbon (C), nitrogen (N), and phosphorous (P) concentration were determined in subsamples from each litterbag before the experiment, and each time a bag was taken out for measurement of remaining mass. After dry weight was measured, the leaves in all three bags per species were mixed and milled to generate homogeneous, composite samples for the analysis. Determination of N and P was done using a modified Kjeldahl method (Harris, 1970) followed by photometric analysis (AOAC, 1994). Total organic matter was estimated using the Walkley and Black method (Anderson and Ingram, 1993). Organic carbon contents were calculated from the organic matter values using a conversion factor of 0.58 g C per gram of organic matter.

### 3.5. *Statistical analysis*

To describe and compare the decomposition rates between ages of secondary forest development and among tree species, a repeated-measures analysis of variance (von Ende, 1993;  $p < 0.10$ ) was used with fixed factors and split-plot nested design. The plots were the subjects; time was the within-subject factor, and treatment (tree species nested in successional stages) the between-subject factor. This analysis took into account the correlation between dates and allowed comparison and fitting of the response patterns (shape of the curve). We obtained the Huynh-Feldt corrected probability (von Ende, 1993) to decide rejection or acceptance of the differences with time and the time by treatment interactions ( $p < 0.10$ ). A similar analysis was employed to compare leaf quality between species nested in environmental condition (successional stages). The same procedure was applied to compare the local leaf litter loss and leaf quality among stages of secondary forest development, followed by a Tukey test (Steel and Torrie, 1988). A linear model was applied to calculate annual decay rate constants ( $k$ ) from dry mass remaining for each tree species and for the local leaf litter sample (Wieder and Lang, 1982).

The dry mass remaining equation was :  $X_t = -k^*t + X_0$

where  $X_t$  is the remaining mass (g) at time  $t$  (days),  $X_0$  the initial leaf mass, and  $k$  is the decomposition rate constant (yr<sup>-1</sup>). The linear model is defined such that

the absolute decomposition rate is constant throughout decomposition, while the relative decomposition rate increases with time (Wieder and Lang, 1982). This model can be applied as well when leaf litter decomposition decreases slowly (Montañez, 1998). The correlation between litter quality and annual decay rate constant was realized based on mean values of C/N ratio, C/P ratio, N and P concentration obtained during the six measurements.

## 4. Results

### 4.1. Leaf litter decomposition

Decomposition rate (Fig. 2) showed no significant overall effect of successional stage ( $p > 0.1$ ) but a strong effect of species ( $F_{2,3} = 132.7$ ;  $p = 0.001$ ). Fig. 3a shows that the decomposition was not constant in time ( $F_{5,15} = 277.5$ ;  $p < 0.001$ ) and varied for each species along time ( $F_{10,15} = 7.40$ ;  $p < 0.001$ ). Furthermore, decomposition was slightly, but significantly higher (0.78 g,  $p < 0.010$ ) in the mature forest than in the 3 year old forest (Fig. 2).

Leaf litter mass loss for all species followed a similar pattern through time (Fig. 3a). Decomposition increased with the onset of the rainy season from June to beginning of August (63–125 days) then stayed low and relatively constant for the latter part of the study (125–190 days). However, *C. lundellii* started losing mass first (Fig. 3a), followed by *M. brownei* and later by *M. zapota*. *C. lundellii* showed the greatest mass loss at 190 days (44.3% or 13.3 g of the original mass), *M. brownei* showed intermediate loss (30% or 9.0 g), and *M. zapota* showed the lowest mass loss (26.3% or 7.9 g).

The C/N ratio followed a similar pattern in all species, declining with time as expected during the process of decomposition (Fig. 3b). By the end of the experiment, *C. lundellii*, which began with a lower C/N ratio, still displayed the lowest C/N ratio (mean over all treatments: 36.22). *M. brownei* and *M. zapota*, having high ratios originally, finished with lower C/N ratios (60.40 and 71.51, respectively). Although these two species started with a similar C/N ratio, it was much more variable in *M. zapota* than in *M. brownei* throughout the course of the experiment (Fig. 3b). These differences in leaf quality between

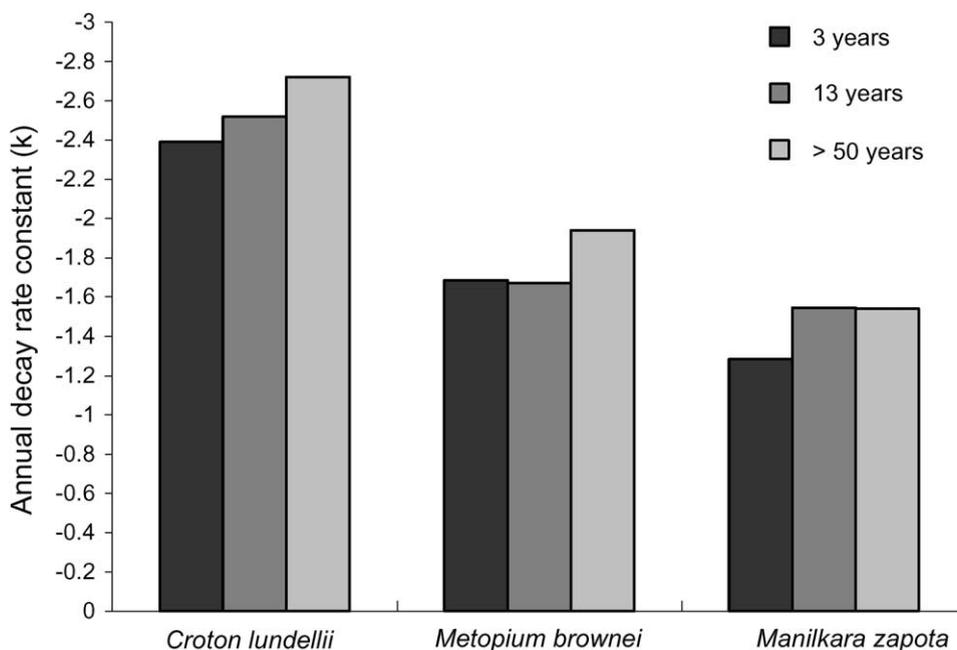


Fig. 2. Decomposition rates constant ( $k$ ) for tree species on three different successional stages of secondary dry forest ( $R^2 > 0.91$ ).

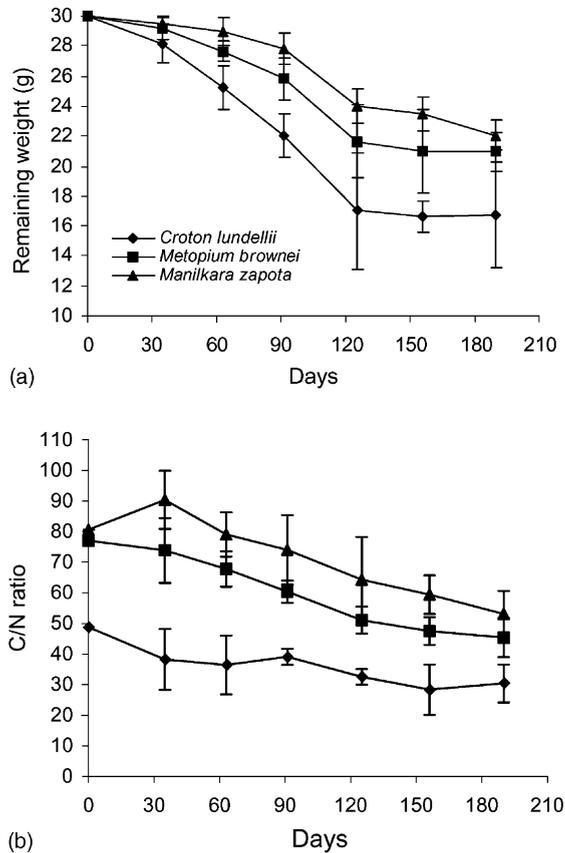


Fig. 3. (a) Leaf dry mass loss (mean  $\pm$  SD); (b) C/N ratio for tree species in tropical secondary dry forest (days 0–35 represent dry season; days 63–190 represent rainy season).

species were significant ( $F_{2,3} = 165.4$ ;  $p = 0.000$ ). The species–time interaction was also significant ( $F_{2,3} = 165.4$ ;  $p < 0.001$ ), indicating that C/N ratios changed at different rates across species.

An analysis of nutrients concentration (Fig. 4) showed a significant effect of species in: total N concentration ( $F_{2,3} = 43.97$ ;  $p = 0.006$ ), total C concentration ( $F_{2,3} = 86.55$ ;  $p = 0.002$ ) and total P concentration ( $F_{2,3} = 35.82$ ;  $p < 0.001$ ). However, there was no effect of successional stage on nutrient concentration ( $p > 0.1$ ). Carbon and N concentrations were significantly different between *C. lundellii* and both *M. zapota* and *M. brownei*, but not between last two species. All species differed in P concentration (Tukey's for all comparisons,  $p < 0.05$ ). Total N concentration significantly increased in the leaf tissue of all three species with time ( $F_{6,12} = 10.68$ ;  $p < 0.001$ ).

The highest values were recorded for *C. lundellii* throughout all time intervals. At the end of the experiment, its N concentration (1.35%) was 50% greater than that of *M. brownei* (0.89%) and 90% greater than that of *M. zapota* (0.77%). Conversely, carbon concentration showed no significant trend with time. Over all, *M. zapota* showed higher total C concentrations (52.7%), followed by *M. brownei* (51.4%) and *C. lundellii* (45.7%). On the other hand, P concentration exhibited a notable increase during the first three sampling periods for *C. lundellii* and *M. brownei*, followed by a decline towards the end of the study. *M. zapota* showed a slight increase in the first months and a subsequent stabilization in P concentration. Phosphorus concentration was highest for *C. lundellii* (0.0381%, averaged over all time intervals), followed by *M. brownei* (0.0359%) and *M. zapota* (0.0345%).

*C. lundellii* had a higher decay rate constant ( $-2.54$ ) than *M. brownei* ( $-1.77$ ) and *M. zapota* ( $-1.46$ ) averaged over all three environmental conditions (all  $R^2$  values  $> 0.91$ ). Statistical analysis showed that decay rates did not differ significantly ( $p > 0.1$ ) between stages of secondary forest development, although there was a trend toward increasing decomposition rate with forest age (Fig. 2). Differences were recorded between  $k$ 's of species ( $F_{2,3} = 52.36$ ;  $p < 0.005$ ), and Tukey's test indicated that all species have markedly different decay rates ( $p < 0.05$ ). Annual decay rate was inversely related to C/N and C/P ratios ( $R^2 = -0.829$ ,  $-0.874$ , Fig. 5a and b) and positively correlated with total N and P concentrations ( $R^2 = 0.7486$ ,  $0.783$ , Fig. 5c and d).

#### 4.2. In situ decomposition of local leaf litter

Both successional stage ( $F_{2,3} = 11.38$ ;  $p = 0.002$ ) and time ( $F_{2,3} = 75.26$ ;  $p < 0.001$ ) had significant effects on decomposition. The mass loss behavior of local leaf litter decomposing in situ was similar in all three phases of secondary forest (Fig. 6a). Cumulative mass loss increased through time, and began to level off after 190 days. Mass loss was higher in the early successional phase during all time intervals. Ultimately, leaf litter from 3 year old forests lost 43% (12.9 g), 33% (9.9 g) and 28% (8.4 g) in 13 and  $> 50$  year old forests, respectively.

The C/N ratio diminished significantly ( $F_{6,12} = 8.79$ ;  $p < 0.001$ ) with time for all successional phases, but

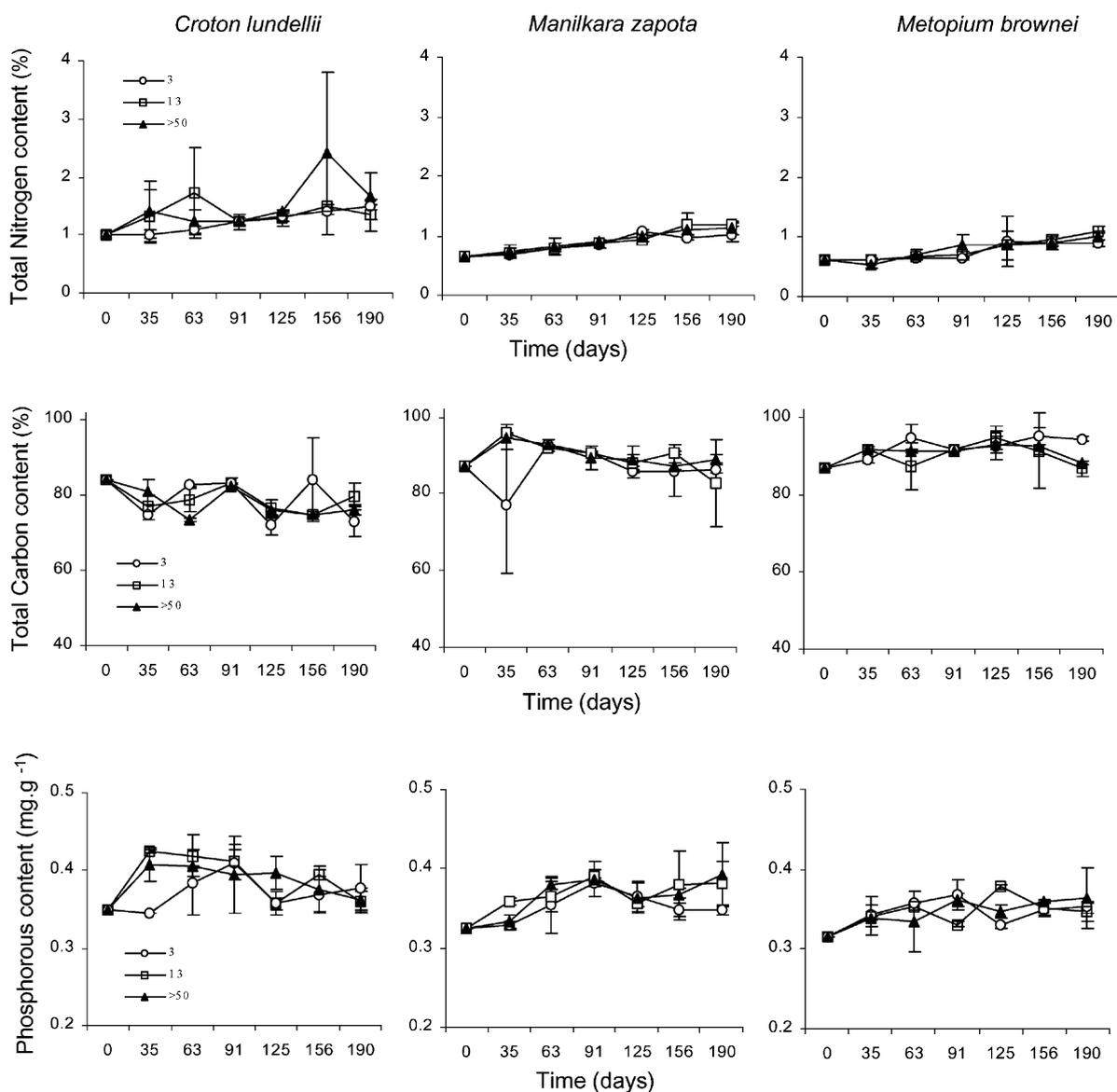


Fig. 4. Leaf litter nutrient concentration for three species during decomposition within three successional stages (3, 13, >50 years) of development of semi-evergreen forest.

did not differ significantly among phases ( $p > 0.1$ , Fig. 6b). C and N concentration did not differ significantly ( $p > 0.1$ ) among stages. Successional stage was a significant factor only in explaining changes in P concentration ( $F_{2,3} = 18.19$ ;  $p = 0.021$ ). P concentration was moderately higher in early successional forest (0.0382%) than in >50 year old secondary forest (0.0372% or 13 year old secondary forest (0.0366%).

Nutrient dynamics varied depending on the nutrient considered. N concentration increased through time, and C concentration remained steady, whereas P concentration increased initially and then declined.

Estimated annual decay rates were slightly higher ( $k = -2.40$ ) for early than for later successional phases of secondary vegetation ( $-1.95$  and  $-1.94$  for 13 and >50 year old stands, respectively). Decomposition rates

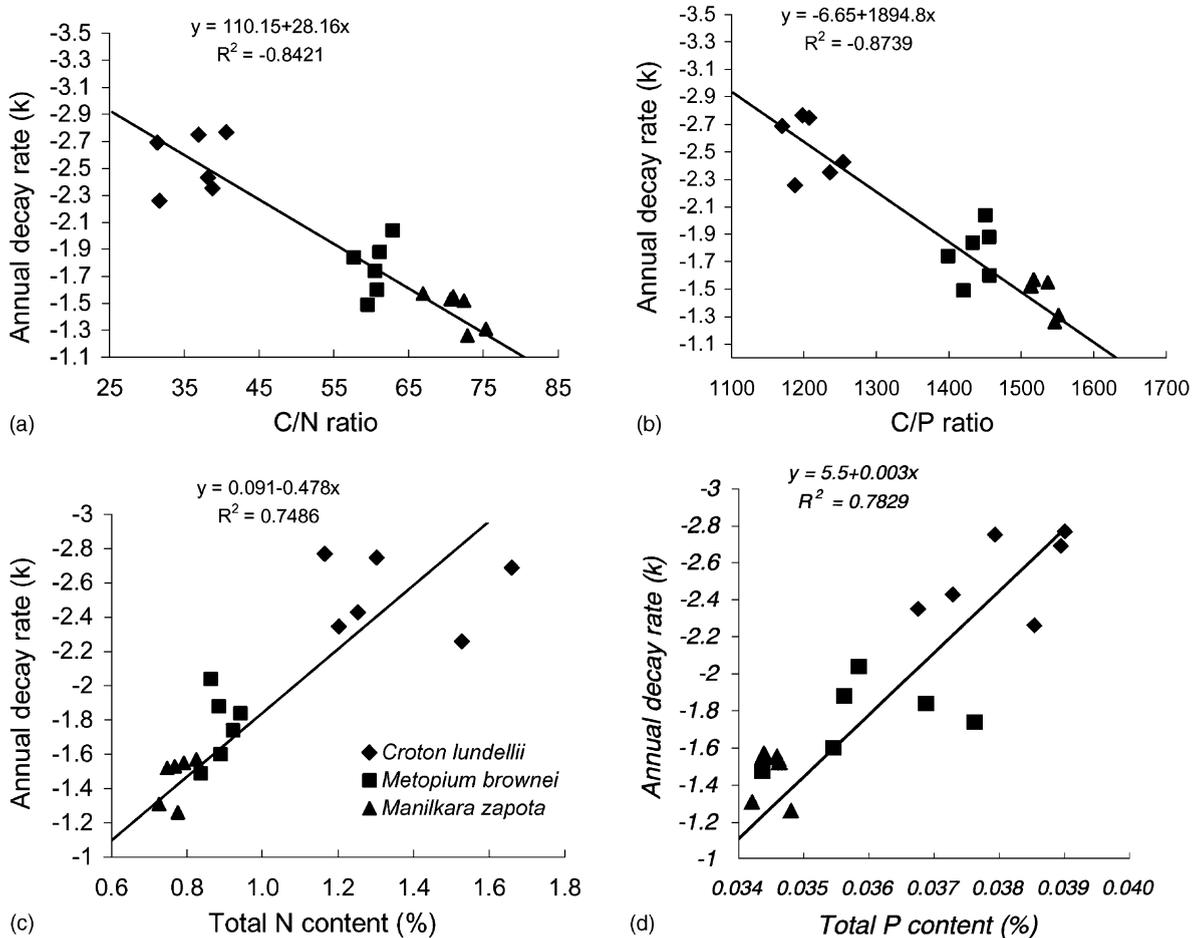


Fig. 5. The relationship between: C/N, C/P ratios (a), (b), total N, P contents (c), (d) and annual decomposition rate ( $k$ ) constant of three types of leaf litter.

did not vary significantly ( $p > 0.1$ ) between phases of secondary forest development.

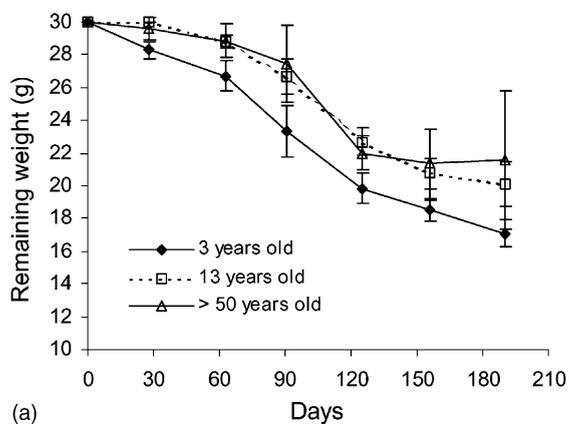
## 5. Discussion

### 5.1. Leaf litter decomposition of individual species

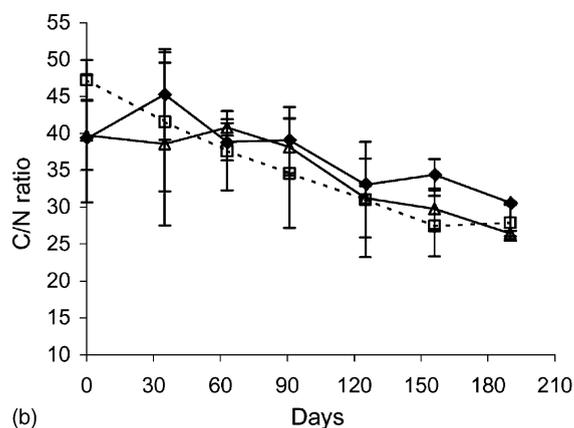
In this study, the results indicate that successional stage does not have a strong effect on decomposition, but the decay rate of individual species associated with those stages varied considerably. The tree species were chosen as representatives of different successional groups: early successional *C. lundellii*, mid successional *M. brownei* and late successional

*M. zapota*. Along this sequence, decomposition rate decreased. This pattern can be explained by indices of leaf litter quality, such as initial N concentration and C/N ratio, which have been widely employed and are relatively easy to determine.

A variety of litter quality indices based on the initial chemical composition have been used as decomposition predictors, such as N concentration or the C/N ratio (Taylor et al., 1989; Zhang and Zak, 1995; Montañez, 1998), the lignin concentration (Meentemeyer, 1978), the lignin-to-N ratio (Melillo et al., 1982), lignin + cellulose, the holocellulose to lignocellulose quotient (McClaugherty and Berg, 1987) and P or C/P ratios (Vitousek et al., 1994). Most of these relations have been established in temperate forest,



(a)



(b)

Fig. 6. (a) Local leaf litter weight loss (mean ± SD); (b) C/N ratio of three phases of secondary forest development.

and the types of litter considered do not encompass a large range of biochemical and physical attributes. Therefore, it is not always possible to generalize these indices to other kinds of vegetation. However, the initial C/N as a general index can provide a broad indication of the decomposition potential (Heal et al., 1997).

We found that *C. lundellii* had both the lowest C/N ratio and highest decay rate, in contrast to *M. zapota* with the highest C/N ratio and the lowest decomposition rate. *M. brownei* showed intermediate behavior. Montañez (1998) found that differences between decay rates of tree species in home gardens could likewise be attributed to C/N ratio. Other studies have made similar findings in a variety of species (Tian et al., 1992; Wieder and Lang, 1982). Zhang and Zak (1995) showed that low C/N and high N measures were correlated with higher microbial activity, and consequently, a higher decomposition rate. Comparing the decomposition rates of the local leaf litter samples and the three species shows that *C. lundellii* has a relatively high rate (Fig. 7).

In addition to the low C/N ratio, higher total N and P concentrations were displayed by *C. lundellii* in contrast with *M. zapota*. During decomposition C is used as an energy source by decomposers while N is assimilated into cell proteins essential for microbial function, thus a higher N concentration in the leaf promotes decomposition (Singh and Gupta, 1977). The effects of a high initial N concentration are most

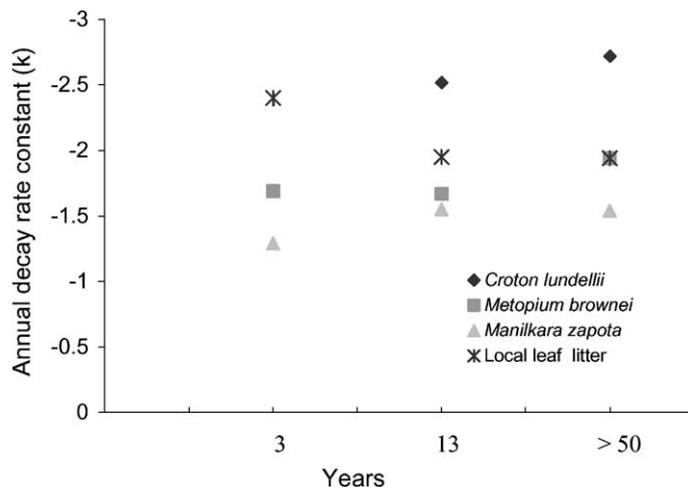


Fig. 7. A comparison approach of decomposition rate of three types of leaf litter and local leaf litter in each successional phase of secondary forest.

marked in earlier stages of decomposition, and then in later stages there is little net change in N concentration as the organic N becomes more resistant to decomposition (Singh and Gupta, 1977). We found that N concentration increased slightly during the experiment. Increases in the N concentration of leaf litter have been found in other studies as well (Melillo et al., 1982; Babbar and Ewel, 1989). There are several possible reasons for the accumulation of N, none of which were tested in this investigation. One or more of follow mechanisms may add nitrogen: fixation, absorption of atmospheric ammonia, throughfall, dust, insect frass, fungal translocation and/or immobilization (Melillo et al., 1982).

Nitrogen is one of the most common factors limiting litter decomposition as it determines the growth and turnover of microbial biomass mineralizing the organic carbon (Heal et al., 1997). Net release or net immobilization can be predicted from the organic material's C/N ratio or N concentration. If the ratio of C/N is below 20 or the N concentration is above 2.5%, N will be released and the material decomposes rapidly. If C/N is much greater than 20, N is likely to be immobilized until decomposition and respiration lower the C/N ratio (Heal et al., 1997). All tree species in the study had C/N ratios above 20, with a tendency to diminish through time and to become more similar (Fig. 3b).

Annual decay rate constants ( $k$ ) described (see also Olson, 1963) the fast, intermediate and slow decomposition of *C. lundellii*, *M. brownei* and *M. zapota* respectively. Simple linear regression analysis with annual decay rate constant ( $k$ ) as a dependent variable and C/N, C/P ratios and N, P concentrations as independent variables showed, that these indices of litter nutrient quality accounted for 84.21, 87.39, 74.86 and 78.29% of variance, respectively. Our results confirm that these parameters are good predictors of decomposition rate for different forest development phases in the tropical semi-evergreen forest.

In tropical forests,  $k$  values are often greater than  $-1.0$ , indicating that leaf litter turnover occurs in a year or less than a year (Alvarez et al., 1992). The  $k$  values obtained for the three species in this work were greater than  $-1.0$ , meaning that decomposition could occur within a year or less. Montañez (1998) also found high values for home garden tree species ranging between  $-3.51$  and  $-4.77$ . Turnover rates for the leaf fraction of litter are also greater than  $-1.0$  in

other dry forests. In Chamela, Martínez-Yrizar (1995) determined the  $k$  value of the leaf fraction to be  $-1.39$ , a value in the range of *M. zapota* (also based on fallen leaves). It is important to note that our study was conducted using tissue collected live for two species, rather than naturally senesced leaves. Fallen leaves are likely to decompose more slowly because of changes in N and P content prior to abscission.

The effect of successional phase on decomposition was not statistically significant in terms mass loss, but there was significant difference in decomposition between both young secondary forest and older forests in separate tests (Tukey,  $p < 0.010$ ). Perhaps this lack of significance is due to low number of experimental units (two plots per successional phase) and sampling units (litterbags per species). However, it could simply be the variability among species in the relative influence of the successional environment. Annual decay rates increased with forest age within each species, although the exact pattern varied across species. These data suggest that successional stage may in fact play a role in determining the decomposition rates of species. If decomposition depends on both the chemical composition of the litter and the environment, this study then suggests the optimal environment for decomposition has been reestablished after 13 years but not yet after 3 years of forest development.

## 5.2. *In situ* decomposition of local leaf litter

The local leaf litter decomposition was slightly faster in early successional phases of secondary vegetation than it was in older secondary forests, indicated by higher estimated decay rates. However, this faster decomposition was not correlated with a lower C/N ratio. It was correlated with higher average P concentration throughout the study and with higher initial N concentration. Perhaps slow decomposition of local leaf litter in later phases of secondary vegetation is due to N immobilization. Nitrogen content increased with time in all phases, but did so more dramatically in the 13 year old stands (by 60%) and 50 year old stands (by 37%) than in the 3 year old stands (by 23%). Given these trends, the N/P ratio of litter is likely to be lower in early successional forests. This would suggest a less P-limited environment for the microbial community.

Brown and Lugo (1990) have suggested that secondary forests are generally less efficient than mature

stands in their return of nutrients to the forest floor, regardless of age, soil type and disturbance history. Vitousek (1984) pointed out that secondary forest accumulates small amounts of nutrients in the litter compartment, but returns large amounts in litterfall. Thus, nutrient turnover in the litter of young forests is actually high and may result in positive feedbacks on production and growth. Data from this study agree with Vitousek (1984), showing higher nutrient concentrations and more rapid decomposition in early successional species (Figs. 2 and 6). As we found, Toky and Ramakrishnan (1983b) found that the percentage of nutrients in the leaves is higher during the first years of secondary forest fallows (1–5 years old) than in older fallows (10–20 years old). They also found that, relative nutrient stocks in the soil decreased with the fallow age and nutrient stock in vegetation increased, meaning that nutrients are relatively getting scarce in the soil with fallow age. Thus, decomposition may decrease with successional development because of the dynamics of forest growth as well as the shift in species.

Based on our finding that an early successional species (like *C. lundellii*) had faster decay rates, faster decomposition in early successional forest would be expected. This concurs with the results of our in situ leaf litter experiment. When comparing mass loss of individual species along a successional gradient, the results appear somewhat contradictory, as there was a tendency toward more rapid decomposition in older, rather than younger, forests. Taken together, our studies suggest that litter quality explains more variability in decomposition rates than does environment. In fact, the effects of litter quality and environment appear to work in opposite directions along a successional gradient. Enhanced nutrient content favors more rapid decomposition in young forests, and enhanced microbial environments favor more rapid decomposition in older forests.

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