Trends in leaf traits, litter dynamics and associated nutrient cycling along a secondary successional chronosequence of semi-evergreen tropical forest in South-Eastern Mexico

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Abstract: Trends in structural and chemical leaf traits along a chronosequence of semi-evergreen tropical forest and their correlation with litter production and decomposition and associated carbon (C) and nitrogen (N) fluxes were assessed. Leaves of 15 dominant species in each plot were collected to measure leaf area, specific leaf area (SLA), C and N concentration and C:N ratio. Litterfall was measured and litter decomposition experiments were set up in 16 experimental plots in a chronosequence of secondary and mature forest. All five leaf traits combined discriminated the secondary forests from mature forest. SLA, N and C:N were significantly correlated to litter decomposition rates. Litter decomposition was significantly slower in mature forest compared with secondary forests. The N concentration of litter was lowest during the dry season, when litterfall was highest. N concentration in fresh leaves was higher than in litter, indicating that N is re-absorbed before leaf abscission. Leaf dynamics and associated nutrient cycling differ significantly between secondary forests and mature forest. Ecosystem-level leaf structural and chemical traits are good predictors of the stage of the forest and explain well the differences in decomposition rates between secondary and primary forests.

Key Words: leaf chemical traits, leaf decomposition, leaf structural traits, secondary succession

INTRODUCTION

Litter quality and production are important for the functioning of forested ecosystems (Berglund & Ågren 2012, Melillo *et al.* 1993). Litterfall determines the input of soil organic matter that generates microclimatic conditions that favour habitats for decomposers (da Silva *et al.* 2018, Handa *et al.* 2014) and maintains carbon stocks and nutrient fluxes that sustain soil fertility (Aryal *et al.* 2015, Lu & Liu 2012). Leaves represent up to around half of above-ground net primary productivity in tropical forests, but this proportion varies with climate and seasonality (Aryal *et al.* 2015, Zhang *et al.* 2014), forest type and species composition (Handa *et al.* 2014, Rentería & Jaramillo 2011). In tropical forest with dry season(s), litterfall correlates negatively with precipitation (Aryal *et al.* 2015, Zhang *et al.* 2014). In the dry season, when litterfall is high, leaves tend to have low nutrient concentrations to reduce nutrient loss (Bernier *et al.* 2008, Lorenz & Lal 2010).

Nitrogen and carbon concentrations and C:N ratio are leaf chemical traits that are correlated to litter quality and decomposition rates (Jackson *et al.* 2013, Zanne *et al.* 2015). Leaf structural traits, such as leaf area (LA) and specific leaf area (SLA), reflect the investment of energy to optimize photosynthesis and to protect the leaves against herbivory (Poorter & Bongers 2006, Wright *et al.*

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2004). Leaf traits and nutrient cycles at the ecosystem level depend on species composition that changes during succession (Chazdon 2014).

Succession in general starts with pioneer species that have leaves that tend to be highly palatable, with high N concentration but with short lifespan (Kazakou *et al.* 2009, Pérez-Harguindeguy *et al.* 2000). As succession advances, these species are replaced by shade-tolerant species that are characteristic of mature forests (Aide *et al.* 2000, Saldarriaga *et al.* 1988). These species grow slowly, have leaves with low N concentration, high C:N ratio (Kazakou *et al.* 2006, Pérez-Harguindeguy *et al.* 2000), and low SLA (Bakker *et al.* 2011). These changes in leaf quality during succession influence the decomposition of the litter (Bakker *et al.* 2011, Matsuki & Koike 2006). To provide a realistic description of the decomposition process, several studies have used double exponential equations to separate the volatile and stable parts of the leaf litter (Corbeels 2001, Wieder & Lang 1982, Xu & Yuan 2017). Other studies have analysed leaf traits in successional stages of tropical evergreen forest (Boukili & Chazdon 2016, Hölscher *et al.* 2003, Lohbeck *et al.* 2012). In semi-evergreen forests, information is available about changes in litterfall and nutrient transfer during succession (Aryal *et al.* 2015, Read & Lawrence 2003), and changes in decomposition rates (Xuluc *et al.* 2003), but these are not related to changes in leaf traits. Therefore, the primary goal of this study is to contribute to our understanding of the changes in leaf traits, litterfall production and decomposition rates that occur during secondary succession in a semi-evergreen tropical forest in South-Eastern Mexico. We hypothesize that leaf traits in secondary forest are characterized by high N and SLA associated with high photosynthetic efficiency, opposed to the leaves in mature forest with low N and SLA that are considered as conservative strategies. These changes in leaf traits are correlated to slower leaf decomposition in mature forests, and we expect that the high investments in nutrient-rich leaves in secondary forests are partially maintained in the tree through foliar nutrient resorption before leaf abscission.

METHODS

Study site

The study site is located in the buffer zone of the Calakmul Biosphere Reserve (CBR), Campeche, South-East Mexico. The experimental plots were established in 2012 in two communities: Cristobal Colon and El Carmen (Aryal *et al.* 2014, 2015). The area is of karstic origin with rolling limestone hills and ridges that range from about 100 to 360 m asl (Vester *et al.* 2007). The soils in the uplands are dominated by lithosols and rendzinas; the lowland

plains are characterized by small differences in relief, in which so-called bajos (small depressions) occur, which are dominated by vertisols where water accumulates during the rainy season (Bautista *et al.* 2011, Turner 2001, Vester *et al.* 2007) and often dry out in the dry season.

The climate of the region is tropical sub-humid with rainfall varying between 900 to 1400 mm y^{-1} (with major portions of the rainfall from June to October) and mean annual temperature of around 26°C (García *et al.* 2002). Three seasons can be distinguished: October– January, the season dominated by cold and rainy fronts coming from the north, February–May, dry and relatively cool, and June–September, with tropical rain storms and relatively hot (Figure 1).

Semi-evergreen tropical forest is the dominant eco-system in the region (Rzedowski 1978, Turner 2001), of which large parts have been converted to slash-and-burn agriculture, creating a mosaic of agricultural lands mixed with secondary forests in various stages of development (Aryal *et al.* 2014), and patches of remnant mature forests. The characteristic species of young secondary forest (YSF) are *Lonchocarpus guatemalensis*, *Bursera simaruba*, *Hampea trilobata*, *Lonchocarpus rugosus* and *Thevetia ahouai.* The medium-aged secondary forest (MSF) is dominated by *Lonchocarpus guatemalensis*, *Croton icche*, *Guettarda combsii*, *Coccoloba reflexiflora* and *Eugenia ibarrae.* The most abundant species in advanced secondary forest (ASF) are *Croton arboreus*, *Lonchocarpus guatemalensis*, *Bursera simaruba*, *Guettarda combsii* and *Eugenia winzerlingii*. In mature forests (MF) *Pouteria reticulata*, *Gymnanthes lucida*, *Piper yucatanense*, *Eugenia ibarrae*, *Nectandra salicifolia* and *Manilkara zapota* dominate (adapted from Aryal *et al.* 2014, 2015; full names in Appendix 1).

Experimental design

The experiments were set up in 16 permanent forest monitoring plots, with four plots in each of four stages of succession: young (YSF, around 8 y old), medium-aged (MSF around 15 y), advanced secondary forests (ASF, around 25 y) and mature forests (MF, not cleared for more than 100 y). In a separate study, a forest inventory was carried out in the same plots, that is used here to determine tree species composition (Aryal *et al.* 2014).

Leaf traits

We collected leaves from the 15 most abundant tree species in each plot, with a total of 61 species (out of 149 species present in all plots). These species represented between 63% and 92% of all standing trees
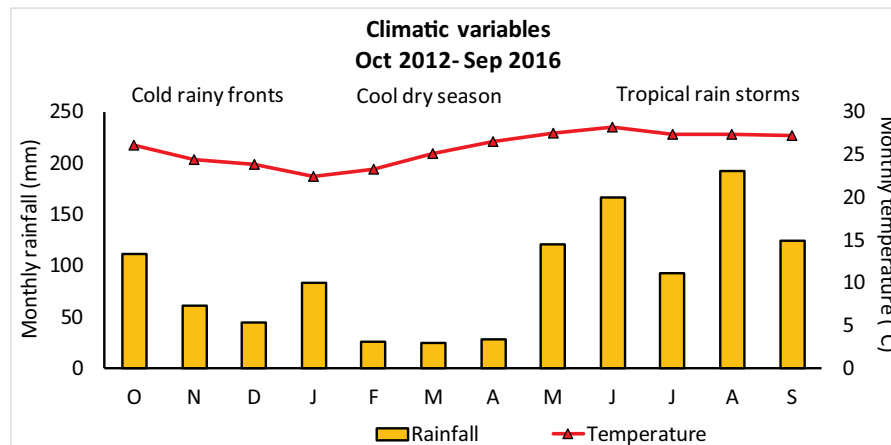
Figure 1. Average monthly temperature and precipitation for the study region between 2012 and 2016, obtained from the meteorological station, Xpuhil, Calakmul, Campeche, Mexico. Data courtesy of the Comisión Nacional de Agua (CONAGUA), Campeche.

> 5 cm diameter at breast height (1.3 m). The collected leaves were photosynthetically active with no signs of herbivory. For small trees, we collected leaves from the crown, and for medium and tall trees we sampled those leaves partially or completely exposed to vertical sunlight (Cornelissen *et al.* 2003). The following leaf structural traits were determined for each collected leaf. (For species with compound leaves, leaflets were used as a sample unit, Poorter *et al.* 2004.)

The LA was measured by scanning fresh leaves with an EPSON Perfection V300 and the area represented by each leaf surface estimated with Adobe Photoshop (0.1 mm). The SLA was calculated, dividing LA by dry weight. One leaf of each tree was ground (excluding the midrib) (Cornelissen *et al.* 2003), sieved through a 0.5-mm mesh and C concentration, N concentration and C:N ratio determined with a Perkin-Elmer CHNO/S 2400 analyser.

The leaf traits measured for each species were extrapolated to the plot level, where the trait value of each species was multiplied by the relative importance of this species in each plot (the relative importance of each species was derived from the inventory data and calculated as the sum of the relative basal area and relative abundance of this species). The weighted trait values were summed within a plot and divided by the percentage of the total relative importance of all species for which a trait value was determined, to obtain the ecosystem-level leaf trait value of the particular plot.

Litterfall

In each plot, litterfall was collected monthly from October 2012 to September 2016 in 12 circular litter traps of 0.5 m^2 (Cuevas & Medina 1986), placed in each monit-

oring plot. All the traps were placed at a height of about 1 m from the ground surface. The litter samples were collected in paper bags and transported to the laboratory for processing. The samples were oven-dried at 70°C for 3 d to obtain stable dry weight and separated into leaves, twigs and bark, fruits and flowers. These components were weighed separately.

Nutrient concentration of litterfall and litter on the forest floor

Carbon and nitrogen concentration and the C:N ratio of litterfall, collected in October 2015, February, June and September 2016, were analysed with a Perkin-Elmer CHNO/S 2400 analyser, to determine intra- and inter-annual variation of litter quality.

To evaluate possible differences in C and N concentration in the litter layer of the successional stages, four random samples from the forest floor were collected in October 2016 within each plot, and each sample was separated in three layers: Oi, the organic horizon characterized by relatively intact plant material, Oe, the organic horizon characterized by partly decomposed organic matter, and Oa, the organic horizon of fully decomposed organic matter (humus). The samples were subsequently dried, weighed and a subsample of each layer was analysed for carbon and nitrogen concentration and C:N ratio with a Perkin-Elmer CHNO/S 2400 analyser.

Decomposition experiments

The litterbag method was used to analyse the decomposition process (Cuevas & Medina 1986). Litterbags were

made from polyethylene of 150×150 mm with 1-mm mesh size on the bottom part of the bag and 2 mm at the upper part to allow access to the litter by macrofauna during the decomposition process (Karberg *et al.* 2008). We established two decomposition experiments in each of the 16 plots. For the first experiment, we used the litterfall collected within the plot (mixed and cut into pieces) and 10 g of which was put into each litterbag, and then placed in the same plot where the leaves were collected. For the second experiment, we used a standard litter from a single, widespread species (*Piscidia piscipula*; 10 g in each litterbag) which was placed in all plots as a control.

Thus, a total of 34 litterbags were placed in each of the 16 plots. Half of these litterbags contained the mixed litterfall from that particular plot (plot litter), and the other half the standard litter of *Piscidia piscipula.* One litterbag of each experiment and each plot was re-collected weekly during the first month, fortnightly during the next 2 mo and monthly for the next 9 mo to complete a year, from October 2015 to September 2016, with a total of 17 collection dates. This collection pattern allowed us to detect and separate the fast decomposition of soluble parts from the slower decomposition of the more stable elements.

The litterbags were carefully removed from the soil to avoid loss of litter and put into a paper bag. In the laboratory, the outer parts of the litterbags were carefully cleaned with forceps to eliminate soil particles, emerging fine roots, seedlings and other material that was attached to the bags. The remaining litter was oven-dried at 70°C for 48 h and weighed to 0.001 g. Subsamples of litter collected in each plot at months 0, 4, 8 and 12 were ground in a mill to pass through a sieve to assess C concentration, N concentration and C:N ratio with a Perkin-Elmer CHNO/S 2400 analyser.

Subsamples of all litter components (litterfall, litter from litterbags and forest floor) were combusted in a furnace at 550°C for 4 h, to determine ash content (Ostertag *et al.* 2008) and all weights were corrected according to the per cent of ash to obtain ash-free weights.

Decomposition rates

To estimate the decomposition rates we tested three models, the single exponential model (Eq. 1; Olson 1963); a modification of the single exponential model, where time is added as an independent variable (Eq. 2; Kelly & Beauchamp 1987) and the double exponential model, which separates the decomposition rates of the volatile and stable parts of the leaf mass (Eq. 3; Wieder & Lang 1982):

$$M_t = M_0 e^{(-kt)} + \varepsilon \qquad (1)$$

$$M_t = M_0 e^{(-kt^p)} + \varepsilon \qquad (2)$$

$$M_t = A.M_0 e^{(-k_1 t)} + (1 - A)M_0 e^{(-k_2 t)} + \varepsilon \qquad (3)$$

Where, M_0 is the initial mass, M_t is the remaining mass at a certain time, t is time (mo), ε is the random error; k, k_1 and k_2 are the unknown decay constants estimated from the data, and p the time-dependent relative decomposition rate, A represents the fraction of stable leaf mass and $(1-A)$ the volatile fraction, where k, k_1, k_2, p, A and $(1-A)$ are parameters, estimated from the leaf litter weights in the 17 litterbags collected during the 1-y experiment.

In all cases, equation 2 and 3 gave the best fit. Of these two models, we selected the double exponential model (eq. 3), when k_1 (decomposition rate constant of the stable fraction of the leaf) and A (the proportion of stable leaf mass) were significant, otherwise we applied the modified simple exponential model (eq. 2) with the time-dependent relative decomposition parameter t.

Statistical analysis

To test how the successional stage was related to leaf traits, we applied a discriminant analysis with all selected standardized leaf traits as independent variables with the program XLSTAT. We applied a Pearson correlation coefficient to assess possible correlations among the leaf traits, and between the leaf traits and remaining litter in the litterbags after 1 y of decomposition (RemLeaf).

Differences between successional stages, months and years of collected leaf litterfall, C concentration, N concentration and C:N ratio were tested with a repeated-measures ANOVA and differences between groups (stages, months and years) were determined with the Tukey HSD test ($P < 0.05$).

Statistical differences of litter decomposition rates between the four successional stages were tested with a repeated-measures ANOVA and we applied the Tukey HSD ($P < 0.05$) to test for significant differences between stages, using the monthly remaining weight as dependent variables.

Differences between stages in C concentration, N concentration and C:N ratio of litter from the litterbags were tested with a repeated-measures ANOVA and a Tukey HSD post hoc test ($P < 0.05$).

Differences in C concentration, N concentration and C:N ratio of fresh leaves, litter from litter traps and forest floor were analysed with a factorial ANOVA and a Tukey HSD post hoc test ($P < 0.05$) was applied to identify significant differences between either successional stages or pools with the program Statistica 8.

Table 1. Ecosystem-level leaf traits with SE in four successional stages of semi-evergreen forests around the Calakmul Reserve, Campeche, Mexico; YSF = young secondary forest; MSF = medium-aged secondary forest; ASF = advanced secondary forest and MF = mature forest. LA = leaf area, SLA = specific leaf area, C = carbon concentration, N = nitrogen concentration and C:N = carbon nitrogen ratio. Lowercase letters denote significant differences between successional stages (ANOVA, Tukey HSD, P < 0.05).

	YSF	MSF	ASF	MF
LA (cm^2)	32.9 ± 2.8	33.6 ± 2.2	31.1 ± 0.9	35.4 ± 3.0
SLA (cm^2 g^{-1})	155 ± 4.1^b	171 ± 7.7^b	150 ± 7.8^b	123 ± 3.3^a
C (%)	43.7 ± 0.2	43.4 ± 0.5	43.4 ± 0.4	43.2 ± 0.5
N (%)	1.83 ± 0.1^b	1.93 ± 0.1^b	1.85 ± 0.1^b	1.55 ± 0.1^a
C:N	32.4 ± 1.8^{ab}	29.3 ± 1.5^a	30.8 ± 1.6^{ab}	36.2 ± 1.3^b

Table 2. Pearson correlation coefficients between standardized leaf traits (calculated at plot level) and remnant litter of semi-evergreen forests around the Calakmul Reserve, Campeche, Mexico. LA = leaf area, SLA = specific leaf area, C = carbon concentration, N = nitrogen concentration, C: N = carbon nitrogen ratio and Remleaf = litter remaining in litterbag after 1 y. Significant correlations are indicated as * for P < 0.05 and ** for P < 0.01.

|	LA	SLA	C	N	C:N
SLA	− 0.04				
C	− 0.003	− 0.001			
N	− 0.39	0.80**	0.001		
C:N	0.36	− 0.75**	0.12	− 0.98**	
RemLeaf	0.29	− 0.68**	0.41	− 0.52*	0.55*

RESULTS

Leaf traits

SLA was lowest in mature forest and did not differ among the earlier stages, and likewise, foliar N concentration was also lowest and C:N highest in mature forest (Table 1). This reduction in N concentration reflects the lower leaf nutrient quality in MF. Leaf area and C concentration presented no significant differences among stages (in Appendix 1 we present the stages and average leaf traits of all the species we collected and analysed).

The discriminant analysis separated MF completely, whereas the selected leaf traits did not allow a complete separation of the secondary stages. The first axis of the discriminant analysis explained about 94% of the variation between the stages, mainly due to the differences in SLA and C and N concentrations (Figure 2).

SLA and foliar N concentration were negative correlated with the mass of leaf litter remaining in litter bags after 1 y (RemLeaf; Table 2), whereas C:N ratio was positively correlated with RemLeaf; in other words, lower SLA and N, and higher C:N ratio values slowed down decomposition.

Table 3. Annual leaf litterfall (Mg ha^{-1}) with SE in young (YSF), medium-aged (MSF), advanced (ASF) secondary forests and mature forest (MF) of semi-evergreen forests around the Calakmul Reserve, Campeche, Mexico. Uppercase letters indicate statistical differences between successional stages within a specific year, lowercase letters indicate statistical differences between years within a successional stage (ANOVA, Tukey HSD, P < 0.05).

	YSF	MSF	ASF	MF
Yr 1	3.4 ± 1.1^A	5.6 ± 0.8^{Bb}	5.6 ± 0.9^{Bab}	3.9 ± 0.5^{AB}
Yr 2	5.1 ± 1.2	6.2 ± 0.7^B	5.6 ± 0.4^{Ab}	5.3 ± 0.5
Yr 3	4.7 ± 1.1^A	6.1 ± 0.3^{Bb}	6.2 ± 0.2^{Bb}	5.2 ± 1^{AB}
Yr 4	4.6 ± 0.8	4.8 ± 0.2^a	4.8 ± 0.2^a	4.9 ± 0.8
Average	4.4 ± 1.1^A	5.7 ± 0.5^C	5.6 ± 0.4^{BC}	4.9 ± 0.7^{AB}
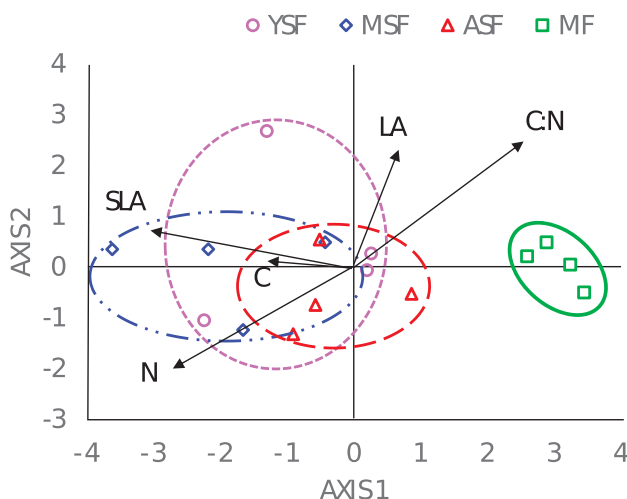
Figure 2. Discriminant analysis to separate successional stages of semi-evergreen forests around the Calakmul Reserve, Campeche, Mexico, with the following leaf traits as explanatory variables: SLA = specific leaf area, LA = leaf area, C = carbon concentration, N = nitrogen concentration and C:N ratio. YSF = young secondary forest; MSF = medium-aged secondary forest; ASF = advanced secondary forest; MF = mature forest.
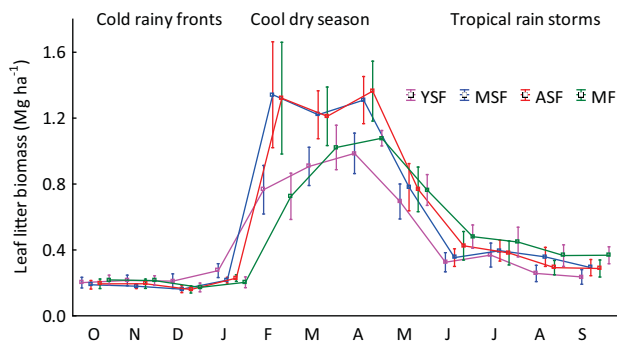
Litterfall

The average annual leaf litterfall presented significant differences among the successional stages (F = 7.19, P < 0.001), with the highest litterfall in MSF (5.7 Mg ha^{-1} y^{-1}), followed by ASF (5.6 Mg ha^{-1} y^{-1}) and lowest in YSF with (4.4 Mg ha^{-1} y^{-1}). Leaf litter production varied between years (Table 3) and within a year (Figure 3). The lower litter production in mature forest was partially compensated by higher flower and fruit production (data not presented). Analysing differences in litter production for each year separately we observed for the first (F = 7.4, P < 0.001) and the third year (F = 3.55; P < 0.05) significant differences among successional stages.

Litterfall in all successional stages was highest from February to May, comprising between 65% and 75% of annual litterfall, which period coincides with the

Table 4. Intra-annual variation of C and N-concentration and C:N ratio in leaf litter with SE collected in semi-evergreen forests around the Calakmul Reserve, Campeche, Mexico. Significant differences between months are indicated with a small letter (ANOVA, Tukey HSD, $P < 0.05$).

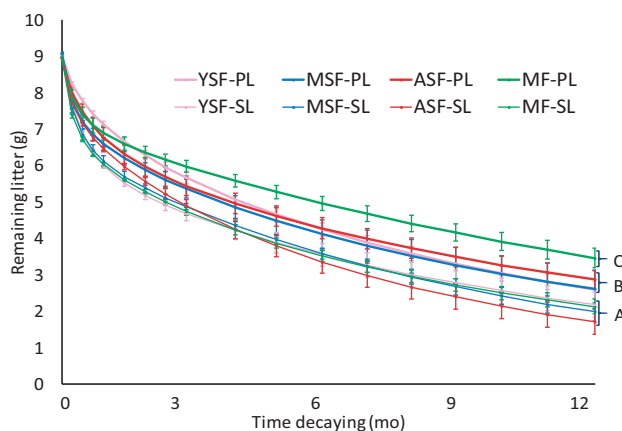|	October 2015 Start cold season	February 2016 Start dry season	June 2016 Start rainy season	September 2016 Rainy season
C %	43.9 ± 0.5^{ab}	43.8 ± 0.3^{ab}	42.8 ± 0.4^{a}	44.9 ± 0.4^{b}
N %	1.54 ± 0.06^{b}	1.53 ± 0.04^{b}	1.11 ± 0.05^{a}	1.98 ± 0.07^{c}
C:N	34.4 ± 1.7^{b}	33.8 ± 1^{b}	46.6 ± 2.4^{c}	27.1 ± 1.1^{a}

Figure 3. Average monthly litterfall in four successional stages of semi-evergreen forests around the Calakmul Reserve, Campeche, Mexico. Uncertainty bars show the 95% confidence interval of the monthly litterfall of the four plots in each successional stage (four plots, 4 y of data). YSF = young secondary forest; MSF = medium-aged secondary forest; ASF = advanced secondary forest; MF = mature forest.


Figure 4. Remaining leaf mass and their standard error during the 1-y leaf litter decomposition experiment in semi-evergreen forests around the Calakmul Reserve, Campeche, Mexico. Letters next to the models reflect the statistical difference between the decomposition trend of plot litter (PL) in MF compared to all secondary stages (MF different from all secondary stages) and the standard litter (SL, different from all plot litter). YSF = young secondary forest; MSF = medium-aged secondary forest; ASF = advanced secondary forest; MF = mature forest.

dry season. This peak was highest in medium and advanced successional stages, but less pronounced in young secondary and mature forest (Figure 3).

The C and N concentrations of the litterfall varied significantly within a year with the highest concentration during the rainy season (September), when litterfall was lowest, and lowest at the onset of the rainy season (June), when litterfall started to drop down. The C:N ratio showed an opposite trend to N, with highest values (46.6) in June, when N was lowest (1.11) and lowest C:N values (27.1) in the rainy season, when N was highest (1.98, Table 4).

Litter decomposition

The rate of litter decomposition of the control species (standard litter) did not differ significantly between the successional stages, indicating that environmental conditions did not influence decomposition rates between the stages. The loss of leaf mass of the litter mixture was significantly lower in mature forest, compared with the three successional stages and were all significantly lower than the decomposition rates of the control species (Figure 4). In most cases model 3 was selected, except when k_1 or A was insignificant (Appendix 2). Both model 2 and 3 showed better fits to the data (Appendix 3). Model 3 separated well the fast decomposition of the volatile parts (Appendix 4).

C and N concentrations in the remaining litter changed during the decomposition experiment, with no statistical differences among successional stages. Particularly the N concentration in the remaining litter fluctuated significantly during the decomposition process, decreasing sharply between months 2 and 4 of the experiment. In the last two measurements, N concentration increased slowly in all stages, possibly due to a variation in the litter mixture in the bags, or fungus contamination that could not be removed. The C concentrations dropped in all stages, as expected, with the highest loss in the first 2 mo and lower loss in subsequent periods (Figure 5a, b).

Net loss of both C and N mass was initially fast in all stages. Loss of C mass was highest during the first 2 mo, whereas the proportion of N mass loss was highest in the subsequent 2 mo (Figure 5c, d). Remnant N mass fluctuated a little between months 4 and 8 in MSF and ASF, similar to the increase in N concentration.
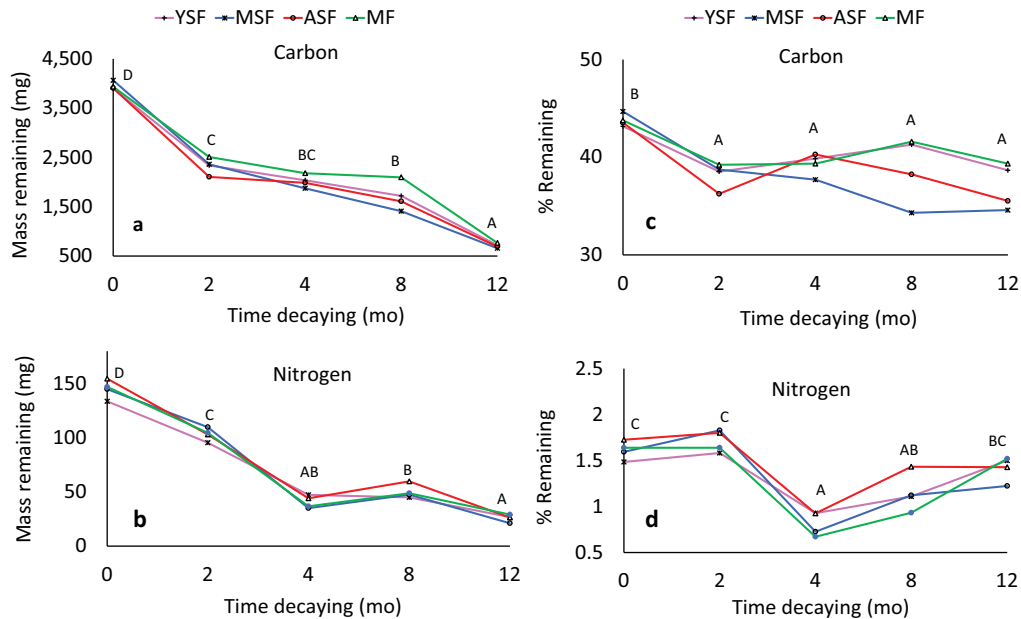
Figure 5. Carbon (C) and Nitrogen (N) mass (in mg) and concentration (in %) during the decomposition of the litter mixture in four successional stages of semi-evergreen forests around the Calakmul Reserve, Campeche, Mexico. Figure 5a = C mass, 5b = N mass, 5c = C concentration, 5d = N concentration. Capital letters in each figure indicate significant differences between dates (Tukey, P < 0.05). YSF = young secondary forest; MSF = medium-aged secondary forest; ASF = advanced secondary forest; MF = mature forest.

C concentration of litter in the traps was significantly higher than the C concentration of the various horizons on the forest floor due to loss of C during decomposition, as expected. C concentration showed a downward trend from litter in traps, little decomposed litter on the forest floor (Oi) and was lowest for highly decomposed material (Oe and Oa, Figure 6a). The N concentration of fresh leaves collected from the trees on average exceeded that of litter collected in the litter traps of the same month. There were significant differences in N concentrations of fresh leaves between different stages, with highest concentrations in MSF and lowest in MF, but we did not find any differences in N concentrations between successional stages for the litter collected from traps and litter on the forest floor (Figure 6b). C:N ratio decreased slowly from fresh leaves to litterfall and litter on the forest floor, although some variation was observed in young secondary forest (Figure 6c).

DISCUSSION

Leaf traits and their relation to the rate of decomposition

SLA and N concentration showed significant differences between secondary and mature forest, with lower values of SLA and N concentrations in mature forest, as has been observed in other studies (Matsuki & Koike 2006). C concentrations in leaf litter from secondary forests were somewhat higher than in mature forest, but with no significant differences. Moura *et al.* (2016) also found higher C concentrations in intermediate secondary forests. The differences observed in SLA and N concentration can be attributed to the leaf economic spectrum (LES), which explains that vascular plants trade-off rapid resource acquisition against resource conservation (Jackson *et al.* 2013, Poorter & Bongers 2006). Secondary species (with resource acquisitive leaves) have high SLA and N concentration in leaves. In contrast, dominant species of MF generally have lower SLA and N concentration (considered as resource conservative) of leaves (Bakker *et al.* 2011, Kazakou *et al.* 2006, Pietsch *et al.* 2014, Quested *et al.* 2007). The leaves of species in mature forests also tend to stay longer on the tree than leaves of species from early secondary stages (leaf lifespan, LL), which is also considered part of the LES (Wright & Westoby 2000), although we were not able to assess this.

The positive correlation between SLA and N concentration implies that species with higher photosynthetic capacity have higher N concentration and possibly a shorter LL (Hikosaka & Osone 2009, Poorter & Bongers 2006, Matsuki & Koike 2006, Wright *et al.* 2004). Species with a high photosynthetic capacity tend to grow fast, produce leaves with high nutrient concentrations (in our case N), and have few defences against herbivory and microbial activity (Finerty *et al.* 2016, Jackson *et al.* 2013, Poorter *et al.* 2004). Such leaf characteristics were observed in the younger stages of succession in our study, where
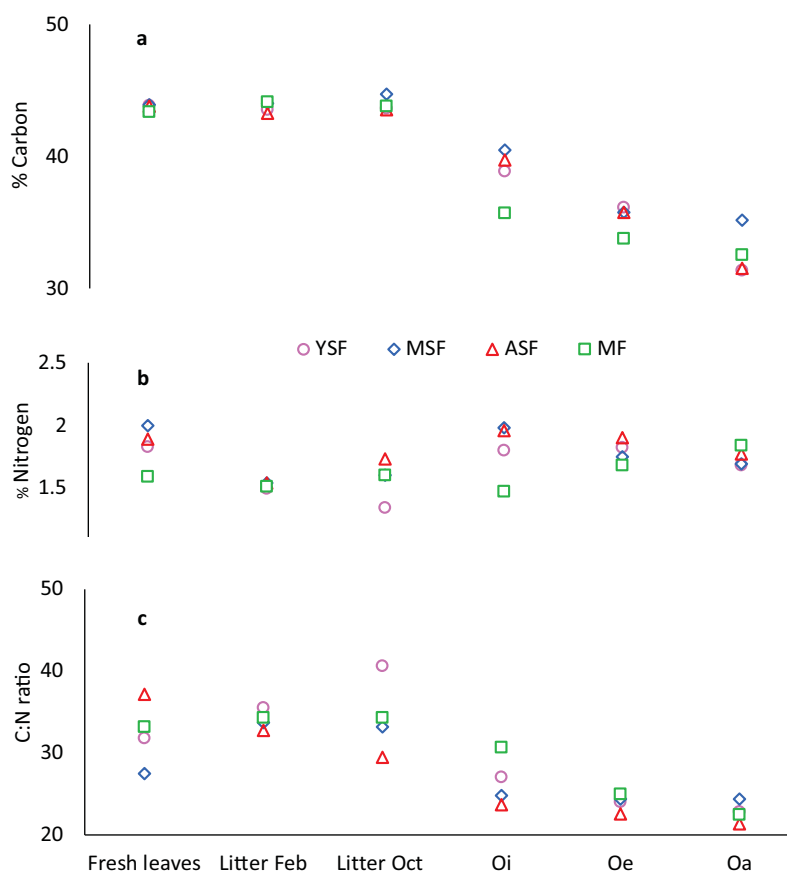
Figure 6. Carbon (a) and Nitrogen (b) concentration and C:N ratio (c) in fresh leaves, litter collected in February (Litter Feb) and October (Litter Oct) and litter from the forest floor in semi-evergreen forests around the Calakmul Reserve, Campeche, Mexico. Oi = fresh litter; Oe = litter in decomposition; Oa = highly decomposed organic material. YSF = young secondary forest; MSF = medium-aged secondary forest; ASF = advanced secondary forest; MF = mature forest.

SLA and N were the leaf traits that separated secondary forests from mature forests. The leaf traits were not able to separate the early, intermediate and advanced secondary stages, possibly due to the fact that the changes in species composition takes more years (Aryal *et al.* 2014) before it will be noted in the ecosystem-level leaf traits.

Since there were no differences among successional stages in decomposition rates of the standard litter, this suggests that litter quality, rather than microclimatic effects, was the main factor driving differences in decomposition rate of the litter between secondary forests and mature forest (Li *et al.* 2017, Szefer *et al.* 2017). The leaf traits SLA and foliar N concentration correlated positively and C:N ratio negatively with decomposition rates, consistent with other studies (Bakker *et al.* 2011, Freschet *et al.* 2012, Pérez-Harguindeguy *et al.* 2000, Taylor *et al.* 1989). The relation between the decomposition rate and N concentration can be attributed to the fact that N concentration directly impacts microbial activity, and thus the decomposition process (Berg & McClaugherty 2008, Cleveland & Liptzin 2007, Seneviratne 2000).

In this study we collected the leaves that were partially shaded and partially exposed to vertical sunlight (Cornelissen *et al.* 2003, Dawkins & Field 1978), as these conditions reflect the dominant condition of the forest environment and are well suited for the purpose of our study (Poorter & Bongers 2006). This may reduce the capacity to compare our results with other studies that have quantified changes in SLA and foliar nutrient concentrations of species across chronosequences of secondary succession (Lohbeck *et al.* 2015), as these authors collected leaves from completely sun-exposed shoots in the upper canopy (Pérez-Harguindeguy *et al.* 2013).

Variation in litterfall and associated nutrient transfer from trees to forest floor

Leaf litterfall varied between years, between months and between successional stages. The average annual leaf litterfall increased from young to intermediate stages of recovery, and decreased slightly in mature forest. These

differences are not significant in separate annual cycles, stressing the importance of collecting litterfall data over longer periods, as pointed out by various authors (Drake *et al.* 2011, Hughes *et al.* 1999, Ostertag *et al.* 2008). The decrease in litterfall in mature forest is partly due to changes in stand structure and species composition (Moura *et al.* 2016, Ohtsuka *et al.* 2010) producing leaves with longer livespans (Matsuki & Koike 2006), and partly due to a transfer of metabolic investments from leaves to reproductive parts (Ryan *et al.* 1997). Seasonal fluctuations in litterfall were correlated with seasonal fluctuations in precipitation, as has also been observed in other studies (Kotowska *et al.* 2016, Sayer & Tanner 2010). This fluctuation is less pronounced in mature forests, possibly due to having leaves with longer LL.

Nutrient concentrations in leaf litter varied among seasons, with highest C concentrations and N concentrations in the rainy season and lowest at the end of the dry season. Read & Lawrence (2003) also pointed out that nutrient concentrations in litter are highest during the wet season. N concentrations of fresh leaves in secondary forests were higher than those in litter from traps, indicating that part of the N in fresh leaves was mobilized to other plant tissues before leaf abscission (Chavez *et al.* 2015), a process known as foliar nutrient resorption (FNR), confirming our hypothesis that these high investments in nutrient-rich leaves in secondary forests are partially preserved before abscission. Neither C nor N concentrations in litter from traps showed differences among the successional stages. C concentration decreased gradually from litter in the traps to the humus horizon on the forest floor, as observed in other studies (Berg & McClaugherty 2008, Ono *et al.* 2013).

Changes in C and N concentrations and mass during decomposition

Rapid loss of litter C mass within the first 2 mo was probably caused by microbial use of easily assimilated carbohydrates (glucose, cellulose and hemicellulose; Berg & McClaugherty 2008), i.e. positive priming (Li *et al.* 2017). During these first 2 mo, N concentrations remained at the same level in all successional stages, but N started to mineralize rapidly after 2 mo, when almost all of the volatile C had disappeared (derived from the results of the two-component decomposition model used in our analysis, Appendix 4). The remaining more-complex C components, like lignin, tannins and polyphenols, were less attractive for the microbial community (Berg & McClaugherty 2008), which explained the much slower rate of C loss in the subsequent period.

In terms of mass loss, initially the proportion of C loss (around 40%) was much higher than the proportion of loss of leaf mass (around 30%), whereas N mass initially decreased in a similar proportion as leaf mass. In the subsequent period, when the labile C mass had disappeared, the proportion of N loss increased significantly (around 50% and more in 2 mo). After 4 mo, the proportion of C mass loss was similar to the loss of leaf mass, whereas N mass fluctuated a little, possibly due to an increase in fungus contamination of the samples (Berg & McClaugherty 2008, Xuluc *et al.* 2003).

The combination of ecosystem-level leaf structural and chemical traits is a good predictor of the successional stage the forest is in, and explains well the differences in decomposition rates. All the results indicate that leaf dynamics and associated nutrient cycling differ significantly between secondary forests and mature forest. This is very important, taking into consideration that it may take more than 120 y for these forests to recover (Aryal *et al.* 2014). This means that the related ecosystem functions also take a long time to re-establish. This has a major impact on conservation and restoration strategies and on estimates of carbon and nitrogen dynamics at the ecosystem level.

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Appendix 1. Leaf traits of 61 species of secondary and mature semi-evergreen tropical forests of Calakmul, Campeche, Mexico. LA = leaf area (in cm^2); SLA = specific leaf area (in cm^2 g^{-1}); C = carbon concentration (in % of leaf mass); N = nitrogen concentration (in % of leaf mass); C:N = ratio between C and N. YS = young secondary forest; MS = medium-aged secondary forest; AS = advanced secondary forest; M = mature forest.

Family	Species	Stage	LA	SLA	C	N	C:N
Anacardiaceae	*Metopium brownei* (Jacq.) Urb.	YS MS AS	36.1	152	46.7	1.69	34.4
Anacardiaceae	*Spondias mombin* L.	MS AS M	11.3	384	39.9	2.04	26.8
Annonaceae	*Mosannona depressa* (Baill.) Chatrou	YS MS M	39.1	104	41.2	1.63	31.8
Apocynaceae	*Cascabela gaumeri* (Hemsl.) Lippold	YS MS AS	25.5	234	44.2	1.96	28.1
Apocynaceae	*Thevetia ahouai* (L.) A.DC	YS	87.7	146	40.6	1.86	32.5
Araliaceae	*Dendropanax arboreus* (L.) Decne. & Planch	YS MS M	47.4	226	45.8	1.51	37.4
Bignoniaceae	*Handroanthus chrysanthus* (Jacq.) S.O.Grose	M	45.8	304	44.7	2.44	21.4
Burseraceae	*Bursera simaruba* (L.) Sarg.	YS MS AS	30.1	185	42.8	1.53	42.6
Burseraceae	*Protium copal* (Schltdl. & Cham.) Engl.	M	46.4	136	45.2	1.66	31.7
Celastraceae	*Hemiangium excelsum* (Kunth) A.C.Sm.	YS MS AS M	60.9	81	39.4	0.81	65.3
Ebenaceae	*Diospyros salicifolia* Humb. & Bonpl. ex Willd.	YS AS	16.3	113	46.2	0.86	69.2
Euphorbiaceae	*Croton arboreus* Millsp.	MS AS	52.3	161	40.4	1.87	25.5
Euphorbiaceae	*Croton icche* Lundell	YS MS AS M	23.1	137	39.6	1.83	25.4
Euphorbiaceae	*Gymnanthes lucida* Sw.	AS M	32.7	116	38.7	1.72	26.5
Lamiaceae	*Vitex gaumeri* Greenm.	YS AS	51.0	143	44.1	2.13	26.3
Lauraceae	*Nectandra salicifolia* (Kunth) Nees	YS MS AS M	33.4	117	49.1	1.90	31.1
Leguminosae	*Bauhinia divaricata* L.	MS	34.1	174	40.6	2.16	21.9
Leguminosae	*Caesalpinia mollis* (Kunth) Spreng	MS M	37.4	134	46.4	2.44	22.2
Leguminosae	*Calliandra belizensis* (Standl.) Standl	M	0.3	86	39.2	2.09	21.9
Leguminosae	*Haematoxylum campechianum* L.	MS	0.7	146	40.5	1.64	28.7
Leguminosae	*Lonchocarpus castilloi* Standl.	YS MS AS	6.4	226	45.4	3.01	17.7
Leguminosae	*Lonchocarpus guatemalensis* Benth.	YS MS AS M	15.6	208	42.7	2.21	23.6
Leguminosae	*Lonchocarpus rugosus* Benth.	YS MS AS	14.0	197	44.4	2.18	24.6
Leguminosae	*Lonchocarpus yucatanensis* Pittier	MS M	14.9	155	41.9	2.88	17.6
Leguminosae	*Lysiloma latisiliquum* (L.) Benth.	YS MS	0.3	76	46.4	1.82	29.8
Leguminosae	*Mimosa bahamensis* Benth.	YS MS	0.4	106	42.8	2.58	21.7
Leguminosae	*Piscidia piscipula* (L.) Sarg.	YS MS AS	31.7	149	41.3	1.79	30.9
Leguminosae	*Platymiscium yucatanum* Standl.	YS	10.1	155	45.5	2.94	18.0
Leguminosae	*Swartzia cubensis* (Britton & Wilson) Standl.	YS	35.3	188	49.2	2.92	20.2
Malpighiaceae	*Byrsonima bucidifolia* Standl.	M	13.7	171	43.6	1.33	38.2
Malpiguiaceae	*Malpighia glabra* L.	YS MS AS	13.8	121	41.9	1.96	25.0
Malvaceae	*Hampea trilobata* Standl.	YS MS AS	81.8	189	43.3	1.78	31.2
Malvaceae	*Pseudobombax ellipticum* (Kunth) Dugand	AS	36.2	259	42.3	0.91	54.1
Meliaceae	*Cedrela odorata* L.	YS	18.5	223	43.1	2.85	17.7
Moraceae	*Brosimum alicastrum* Sw.	M	46.1	159	39.8	1.90	24.9
Moraceae	*Trophis racemosa* (L.) Urb.	YS AS	21.7	145	38.6	1.91	24.2
Myrtaceae	*Eugenia ibarrae* Lundell	YS MS AS M	31.6	88	43.5	1.24	48.0
Myrtaceae	*Eugenia winzerlingii* Standl.	YS MS AS M	10.9	115	45.3	1.34	45.3
Myrtaceae	*Myrciaria floribunda* (H.West ex Willd.) O.Berg	MS M	10.1	123	46.4	1.19	46.8
Myrtaceae	*Pimenta dioica* (L.) Merr.	M	142	95	43.3	1.16	44.4
Piperaceae	*Piper yucatanense* C.DC.	M	30.4	155	38.1	2.39	19.6
Polygonaceae	*Coccoloba acapulcensis* Standl.	M	49.6	198	43.5	2.08	24.4

Appendix 1. Continued

Family	Species	Stage	LA	SLA	C	N	C:N
Polygonaceae	*Coccoloba cozumelensis* Hemsl.	YS MS AS M	18.1	137	45.1	1.60	34.1
Polygonaceae	*Coccoloba reflexiflora* Standl.	YS MS AS M	54.1	107	44.6	1.27	44.0
Polygonaceae	*Gymnopodium floribundum* Rolfe	AS	11.9	171	43.8	1.59	32.7
Polygonaceae	*Neomillspaughia emarginata* (H. Gross) S.F. Blake	MS AS	60.4	172	44.7	2.38	22.0
Putranjivaceae	*Drypetes lateriflora* (Sw.) Krug & Urb.	M	18.1	99	42.7	0.78	63.8
Rhamnaceae	*Krugiodendron ferreum* (Vahl) Urb.	M	13.4	119	45.0	2.79	18.8
Rubiaceae	*Guettarda combsii* Urb.	YS MS AS	123	101	47.4	1.61	36.9
Rubiaceae	*Randia aculeata* L.	MS AS M	11.0	122	43.2	1.52	34.0
Rubiaceae	*Randia longiloba* Hemsl.	M	24.1	140	39.5	2.27	20.3
Salicaceae	*Zuelania guidonia* (Sw.) Britton & Millsp.	YS MS AS	65.1	236	45.4	2.02	27.1
Sapindaceae	*Allophylus cominia* (L.) Sw.	YS MS AS	28.3	105	40.8	1.55	32.4
Sapindaceae	*Cupania belizensis* Standl.	YS	57.0	148	47.5	2.19	25.3
Sapindaceae	*Melicoccus oliviformis* Kunth	M	11.4	113	46.8	1.42	38.4
Sapindaceae	*Thouinia paucidentata* Radlk.	YS MS AS	8.2	229	42.8	1.80	29.7
Sapotaceae	*Chrysophyllum mexicanum* Brandegee	YS MS AS	16.9	116	42.9	1.47	36.1
Sapotaceae	*Manilkara zapota* (L.) P.Royen	AS M	49.4	101	45.7	1.03	56.9
Sapotaceae	*Pouteria campechiana* (Kunth) Baehni	M	68.4	153	46.4	1.85	30.1
Sapotaceae	*Pouteria reticulata* (Engl.) Eyma	M	38.0	114	43.8	1.48	34.9
Theophrastaceae	*Bonellia flammea* (Millsp. ex Mez) B.Ståhl & Källersjö	M	7.0	117	44.8	1.43	36.5

Appendix 2. Parameter values of the three decomposition models. Non-significant results of model 3 are not presented. Decomposition rate constants are based on loss of litter mass. Model 3 was selected when the results were significant for k_1 and A, else we used model 2, which always showed significant results of both parameters.

$$M_t = M_0 e^{(-kt)} + \varepsilon \qquad (1)$$

$$M_t = M_0 e^{(-kt^p)} + \varepsilon \qquad (2)$$

$$M_t = A.M_0 e^{(-k_1 t)} + (1 - A)M_0 e^{(-k_2 t)} + \varepsilon \qquad (3)$$

		Model 1	Model 2		Model 3		
Age class	Plot No	k	k	p	A	k_1	k_2
YSF	CC02	0.12	0.22	0.65	7.66	0.09	3.09
YSF	CC05	0.14	0.28	0.57			
YSF	EC12	0.12	0.21	0.67			
YSF	EC18	0.16	0.24	0.73	6.96	0.11	1
MSF	CC03	0.22	0.38	0.62	6.95	0.15	3.62
MSF	CC07	0.16	0.35	0.51	7.04	0.1	7.44
MSF	CC08	0.12	0.28	0.5	6.68	0.06	1.7
MSF	EC17	0.1	0.27	0.46			
ASF	CC06	0.13	0.34	0.43	6.14	0.05	2
ASF	CC09	0.17	0.3	0.62			
ASF	EC15	0.15	0.33	0.53			
ASF	EC16	0.1	0.18	0.7	7.62	0.07	1.12
MF	CC01	0.13	0.32	0.47	6.64	0.07	2.6
MF	CC04	0.11	0.26	0.5	7.33	0.07	7.5
MF	EC14	0.1	0.25	0.49	7.19	0.06	5.21
MF	EC29	0.08	0.19	0.52	6.95	0.04	1.02

Appendix 3. Example of the results of the three models applied to the decomposition data of the treatment in plot CC02 corresponding to young secondary forest. The figure demonstates the better fit of models 2 and 3, compared with the widely used model 1, which underestimated the initial and overestimated the final decomposition in all cases.
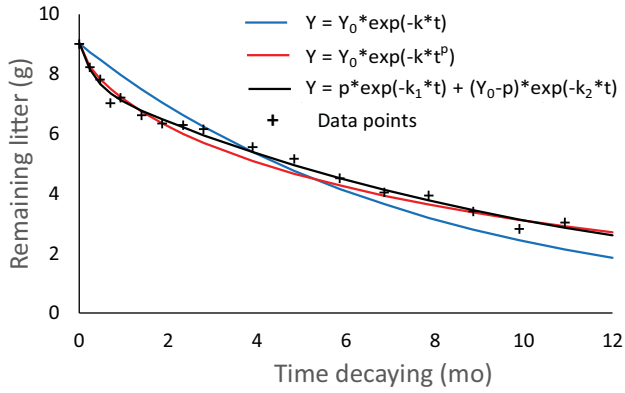
Appendix 4. Decomposition of volatile (blue line) and stable (red line) fraction of leaf litter, plot CC02, applying equation no 3. Note the rapid loss of the volatile fraction (less than 2 mo).