

Early stage of single and mixed leaf-litter decomposition in semiarid forest pine-oak: the role of rainfall and microsite

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Abstract It is well known that inherent characteristics of forest species constitute the main control of litter decomposition. In mixed forest, chemical interactions occurring through precipitation turn mechanisms of litter decomposition very uncertain and difficult to predict. Early-stage leaf litter decomposition of *Quercus potosina* and *Pinus cembroides* and their controls were examined based on Ostrofsky's decomposition mechanisms. From June 2007 to May 2008, litterbags with pure and mixed leaf-litter of *Q. potosina* and *P. cembroides* were incubated in situ in monospecific and mixed tree stands, respectively. Sampling was carried out 3, 6, 9, and 12 months after incubation. After 12 months, two phases of decomposition of pure and mixed litter were identified; an early phase with a greater rate of mass loss of the labile litter fraction (k_L ; soluble compounds) and a later phase with a lower rate of mass loss of the recalcitrant litter fraction (k_R ; lignin). The labile

fraction lost was observed at three and 6 months of incubation, which coincided with the months of highest rainfall likely triggering a rapid release of soluble carbon compounds from leaf litter. Results also indicate that leaf-litter from *Q. potosina* had higher concentration of soluble compounds and lower lignin concentration than leaf litter from *P. cembroides*. Observed facilitative and inhibitory mechanisms for mass loss in *Q. potosina* and *P. cembroides* were controlled by interaction between physico-chemical litter characteristics and rainfall.

Keywords *Quercus potosina* · *Pinus cembroides* · Semiarid forest · Litter mixtures · Early stage decomposition · C:N · Lignin:N · Mass loss

Introduction

Decay of litterfall through physical (e.g. leaching) and biological (e.g. microbial activity) processes are an important source of organic and inorganic nutrients for tree growth (Melillo et al. 1982; Berg and McClaugherty 2008). Most of our understanding of decomposition mechanisms derives from mass loss studies using single species leaf litterbags (Coûteaux et al. 1995; Aerts 1997; Gartner and Cardon 2004). In naturally mixed forest ecosystems, the forest floor receives litter from a mixture of co-occurring tree species. Species may differ however, in the timing,

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quantity and quality of leaf-litter production and consequently in decomposition rates (Gallardo and Merino 1993; Berg and Laskowski 2006; Ball et al. 2008; Pérez-Harguindeguy et al. 2008; Vivanco and Austin 2008). Mixed leaf-litter properties act on decomposition through: (i) species-specific litter nutrient concentration, toughness, toxicity (Melillo et al. 1982; Pérez-Harguindeguy et al. 2000), (ii) litter water holding capacity (Mingzhong et al. 2009), (iii) species-specific effects enhancing or inhibiting belowground mineralization processes (Vivanco and Austin 2008), (iv) interaction dynamics of soil fauna and litter species diversity (Hättenschwiler and Gasser 2005), and/or (v) facilitative or inhibitory effects on decomposition of individual species litter types in mixed litter conditions (Ostrofsky 2007).

Although, it is acknowledged that litter chemistry is the prevailing endogenous control of litter decomposition in a wide variety of ecosystems (Meentemeyer 1978; Coûteaux et al. 1995; Austin and Vitousek 2000), macroclimate is the dominant external control (Berg et al. 1993; Coûteaux et al. 1995; Murphy et al. 1998). Previous work has identified three phases of decomposition: an early phase of leaching and decomposition of labile soluble compounds, unshielded cellulose and hemicellulose (Virzo De Santo et al. 1993), an intermediate phase of decomposition of lignified carbohydrates, and a final phase of decomposition of recalcitrant (i.e. lignin) litter fractions (Coûteaux et al. 1998; Berg and Laskowski 2006). Leaching is principally caused by early rainfall events, which may be particularly strong in semiarid climates leading to massive resource leaching (Gallardo and Merino 1993; Virzo De Santo et al. 1993; Coûteaux et al. 1995; Martin et al. 1997; Murphy et al. 1998; Santa-Regina and Tarazona 2001a, b). Thus, during early decomposition litter may release pulses of soluble chemicals including plant mineral nutrients, to which semiarid plants are well adapted for efficient uptake and growth (Schlesinger et al. 2006).

In mixed litter, the rate of early stage decomposition may be controlled by four principal mechanisms (Ostrofsky 2007): (1) acceleration of mass loss of slowly processed recalcitrant leaves in the presence of rapidly decomposing leaves high in concentrations of labile compounds and nutrients that favor rapid colonization of decomposer communities; (2) reduction of decaying rate of rapidly decomposing leaves

when co-occurring with slowly decomposing leaves due to high concentrations of water-soluble defense or inhibitory compounds (e.g. tannins and other phenolics); (3) structural stability of leaf litter beds might either provide a more persistent habitat for decomposing organisms, thereby accelerating decomposition rates of slowly decomposing leaves, or protecting rapidly processed material from abrasion and leaching, thereby slowing down decomposition rates, (4) since none of these effects are mutually exclusive, both facilitative and inhibitory mechanisms could occur simultaneously, so that observed mass rate changes in mixed-litter decomposition may represent the net effect of multiple processes (Ostrofsky 2007).

Pinus cembroides Zucc., (Mexican pinyon) and *Quercus potosina* Trel. (San Luis Potosi oak) are two important tree species (Rzedowski 1978) of the semiarid forests of Sierra San Miguelito in Central-Northern Mexico. Both species can be found forming single and mixed stands. Historical references suggest that the current tree-species distribution is a result of selective harvest of *Quercus* wood. Therefore, the importance of understanding the contribution of each forest species to decomposition may allow assessing impacts of land use change on nutrient cycling. Among the inherent species traits that may influence decomposition and biogeochemical cycles, *Q. potosina* exhibits deciduous leaves, which are shed at the peak of the dry season in a major shedding event (Pérez-Suárez et al. 2009). *Pinus cembroides* in contrast, is a coniferous species that presents 3–4 year old leaves, whose oldest cohorts are usually shed during the dry season (Zavala and García 1991; Pérez-Suárez et al. 2009). *Quercus potosina* litter shows lower C:N and lignin:N ratios than *P. cembroides* (Pérez-Suárez et al. 2009). Further, litter beds of *Q. potosina* exhibit higher water holding capacity than those of *P. cembroides* (Pérez-Suárez et al. 2009), likely speeding up decomposition. In semiarid regions, 47% of total annual precipitation corresponds to rainfall events of 5 mm, while 2–23% to events larger than 30 mm (Loik et al. 2004), playing an important role in nutrient washing and leaching from litter (Pérez-Suárez et al. 2009). Hence, given the higher litter quality of *Q. potosina* this forest species might decompose more rapidly than *P. cembroides* independently of stand type (monospecific or mixed). Equally, considering the higher water holding capacity of broadleaf litter of *Q. potosina*, these litter

beds may create a more favorable microclimate for decomposition than *P. cembroides* litter beds. Overall, very little information exists for the above mentioned litter interactions in semiarid forest ecosystems.

The objective of this study was to examine potential interspecific influences (as proposed by Ostrofsky 2007) of tree species litter on the dynamics of decomposition of newly shed *Q. potosina* and *P. cembroides* leaves. In particular, the aim was to identify whether facilitative or inhibitory mechanisms control early stage decomposition rate of oak and pine litter when occurring in mixture (Ostrofsky's hypotheses 1 and 2) compared to single litter conditions using standard decomposition bags. Additionally, the study examined the net effect of litter bed types in single and mixed-species stands by incubating standard substrate (cellulose) in different litter microenvironments (Ostrofsky's hypothesis 3). Hence, using a fast-decomposing (*Q. potosina*) and a slow-decomposing semiarid forest species (*P. cembroides*), we tested the following hypotheses: (1) in a mixture of broadleaf and needle litter in litterbags, the recalcitrant *P. cembroides* needles will decay more rapidly in the presence of *Q. potosina* litter than under pure *P. cembroides* conditions (H_1 , mechanism 1—see above). (2) High phenolic concentration of *P. cembroides* litter in a litterbag mixture will slow down the decay rate of *Q. potosina* litter compared to decay rates of *Q. potosina* in pure litter bags (H_2 , mechanism 2—see above). (3) Regarding potential integrated effects of different litter bed types (H_3 , mechanism 3—see above) on decomposition of a standard material, mixed pine-oak litter will create microenvironments in a non-additive fashion compared to single species litter beds such that the decay rate of cotton strips in the two pure stands will be significantly different from the decay rate of cotton strips in mixed stands (Pataki et al. 1998; Yan et al. 2004; Mingzhong et al. 2009).

Materials and methods

Study site

The study was conducted in a pine-oak forest ecosystem in the Sierra San Miguelito, at the southernmost extension of the physiographic province Mesa Central in central Mexico (Cardona 2007). The experiment was set up in a sub-watershed close to

the community “La Amapola” (101°08′–101°04′ W; 22°00′–22°04′ N) (INEGI 2002) at an altitude of 2,400 m a.s.l. The region is characterized by temperate semiarid climate (García 1988) typically with 8 months of dry season (from October to May) and 4 months of wet season (from June to September).

Average annual precipitation in this region reaches 530 mm, while average monthly temperatures range between 12°C in winter (December–February) and 21°C in summer (June–August). Parent material is an igneous rhyolite rock with poorly developed Leptosol soils (FAO's classification system, WRB 2006). The landscape is characterized by abrupt and irregular topography with a high proportion of rock outcrops, and slopes steeper than 30°. The litter layer is 10–15 cm deep, composed of fresh litter on the top, partially decomposed litter below and relatively homogeneous humus at the bottom.

The vegetation is characterized by a young and homogeneous (age and size) forest dominated by *Pinus cembroides* Zucc., and *Quercus potosina* Trel., and includes *Pinus johannis* Rob Pass., other *Quercus* spp., *Yucca* spp., *Dasylyrion* spp. (Rzedowski 1978) and understory species belonging to the genera *Opuntia*, *Agave*, *Mammillaria* and *Euphorbia* (Rzedowski 1978). The average age for the two key species is around 81 ± 8 years (Cetina-Alcalá et al. 1985). More details of tree, litter and litter bed characteristics are presented in Table 1.

Litterbag preparation

Along the sub-watershed, recently shed leaves were collected between March and April 2007 using four 1 m² elastic nets spread below *Q. potosina* and *P. cembroides* tree canopies in each experimental plot. In the laboratory, litter was spread on trays and located on top of the lab tables for 4 days to allow for air drying at room temperature (26°C). Based on an analysis of 10 subsamples of each litter type, air-dried litter exhibited 5% moisture content. Collected litter was cleaned from any foreign material and thoroughly mixed to ensure purity and homogeneity of samples. Litterbags (20 cm × 20 cm) were assembled using a polyethylene mesh (1.0 mm × 1.5 mm). The mesh size was intended to minimize litter loss; however, it may have impeded the incorporation of mesofauna decomposers. To prepare pure *Q. potosina* and *P. cembroides* litterbags, ten grams of air-dried

Table 1 Characteristics of forest stands and soil in semiarid forest from Central-Northern Mexico

	<i>Q. potosina</i>	<i>P. cembroides</i>	Mixed
Tree height (m)	2.5 ± 0.06	4.2 ± 0.2	
Stem diameter (cm)	11.8 ± 0.40	16.30 ± 0.47	
Shoot density (individuals/ha)	2325 ± 193	950 ± 185	2000 ± 492
Leaf litter dry mass (kg ha ⁻¹ y ⁻¹)	2820 ± 307	1360 ± 128	2427 ± 248
Canopy transmittance	0.43 ± 0.03	0.19 ± 0.02	0.29 ± 0.02
Average age	81 ± 8	81 ± 8	
Soil texture	Sandy loam	Sandy loam	Sandy loam
Soil pH	4.37	5.21	4.54
Soil P (mg/kg)	6.93	5.96	6.03
Soil C (%)	5.14	5.47	3.75
Soil N (%)	0.30	0.33	0.22

leaf-litter were evenly spread inside the litterbags. Mixed leaf-litterbags included equivalent amounts (5 g: 5 g) of air dried leaves of both species. Litterbags were sealed, labeled and anchored in the soil with non-corrosive nails. Additionally, empty litterbags were installed as blanks to monitor and correct for unintended litter incorporation into litterbags. Five samples (30 g each) of *Q. potosina* and *P. cembroides* leaf-litter were analyzed to determine initial litter quality (Table 2).

Table 2 Initial litter chemistry (means ± 1 SE; n = 5) of *Q. potosina* and *P. cembroides*

Component	<i>Q. potosina</i>	<i>P. cembroides</i>
Moisture content (%)	4.60 (±0.07)*	4.86 (±0.05)
Ash (%)	6.38 (±0.36)***	1.97 (±0.09)
Solubles (%)	51.89 (±0.27)***	40.02 (±0.34)
Celullose (%)	22.84 (±0.47)*	24.75 (±0.40)
C (%)	54.76 (±1.82)	55.88 (±1.78)
N (%)	0.93 (±0.02)	0.94 (±0.04)
P (%)	0.04 (±0.00)*	0.05 (±0.00)
K (%)	0.30 (±0.03)*	0.21 (±0.01)
Ca (%)	0.81 (±0.01)***	0.46 (±0.03)
Mg (%)	0.10 (±0.00)	0.10 (±0.01)
Na (%)	0.01 (±0.00)	0.00 (±0.00)
Mn (ppm)	1139.20 (±80.67)***	183.00 (±5.26)
Lignin (%)	27.69 (±0.89)***	34.65 (±0.61)
C:N ratio	58.99 (±3.25)	60.47 (±4.25)
Lignin:N ratio	29.71 (±0.91)***	37.45 (±2.26)
N:P ratio	20.07 (±0.84)**	14.94 (±1.21)

* $P = 0.05$; ** $P = 0.01$; *** $P = 0.001$, NS not significant ($P > 0.05$)

Experimental set-up

Plots of monospecific and mixed *Q. potosina* and *P. cembroides* stands were randomly distributed along a 2000 m long watershed used as the study area. Four replicates of each forest stand were chosen yielding a total of 12 plots. Plots were selected considering similar topographic features, landscape position, exposition (N facing) and altitude to minimize potential confounding effects. Plots where decomposition bags were deployed consisted of an area of 3 m × 3 m maintaining a minimum distance of 30 cm between litterbags and 1 m to 1.5 m from tree trunks. Litterbags and blanks were randomly intermingled in the plots. A total of 112 bags were placed per forest stand (28 per plot; 16 litterbags and 12 blanks); altogether, 336 litterbags were placed in the study area for this experiment. The study was initiated on May 30, 2007, just before the rain season started. On four sampling dates (August and November, 2007; February and May, 2008) seven (4 litterbags making up one subsample and 3 blanks) litterbags were collected per plot.

The first 6 months of incubation coincided with the wetting cycle and the second 3 months with the drying cycle. To examine the control of rain on the rate of litter decomposition and litter nutrient dynamics, four standard rain gauges were placed along the 12 plots. Accumulated rain was recorded following each individual rainfall event. Additionally, on each plot two soil psychrometers (PST-55, WESCOR) were inserted 10 cm deep into the litter layer, where soil water potential was recorded biweekly from June

2007 to July 2008. From each plot, two litter samples from a 20 cm × 20 cm area were collected to evaluate gravimetric water content from each litter type (pure *P. cembroides*, pure *Q. potosina*, and mixed), from the top 10 cm of the litter layer.

Determination of litter mass loss

At each sampling date (after 3, 6, 9 and 12 months of incubation), a total of 48 leaf litterbags and 36 blanks were collected and kept in separate plastic bags that were stored in ice chests for transportation. At the laboratory of the Division of Environmental Sciences, IPICYT, San Luis Potosi, Mexico, the content of each leaf litterbag was dried in an oven at 70°C for 72 h until reaching constant mass. Prior to drying, the content of mixed-leaf litter samples was separated into pine needle and oak leaf litter fractions. After collection, separation and drying, four leaf litter types were obtained including pure *Q. potosina* and *P. cembroides* leaf-litter, and separated *Q. potosina* and *P. cembroides* leaf-litter from mixed samples. For the blank bags, the content was dried and the weight used to correct for potential incorporation of external litter material during the incubation period. To account for any mineral soil attached to leaf litter samples, approximately 0.5 g of each subsample were combusted in a muffle furnace at 550°C during 4 h to determine the remaining ash-free dry matter content (% AFDM), which was then used to correct for leaf litter dry mass according to:

$$FLi = (SaAFDM)/(LiAFDM)$$

where *FLi* corresponds to the sample mass inside the bag (which is organic matter), *SaAFDM* corresponds to *AFDM* as percentage of the total sample, and *LiAFDM* represents the *AFDM* as percentage of the initial litter sample (Harmon et al. 1999). Mass loss was expressed as the proportion of *AFDM* remaining.

Chemical analysis of leaf-litter quality

Leaf-litter samples were analyzed for total carbon (C) and nitrogen (N) of pulverized material with an Elemental Analyzer (Costech ECS 4010). Sample aliquots were ground with a WileyTM mill and passed through a No. 20 stainless steel mesh (1 mm mesh size). Afterwards the material was processed with an ANKOM²⁰⁰ Fiber Analyzer to obtain: Neutral

Detergent Fiber (NDF), Acid Detergent Fiber (ADF), and Acid Detergent Lignin (ADL). Soluble compounds, cellulose and lignin content were calculated by standard methods of selective hydrolysis using differences of filterbag weights under sequential extractions of NDF, ADF and ADL. Accordingly, the NDF procedure removes soluble cell components from leaf-litter such as simple sugars and amino acids, so that %NDF corresponds to the remaining non-soluble fraction. The soluble cell material (referred here as soluble compounds) corresponded to lost material. Acid Detergent Fiber removes cellulose from the sample leaving a residue of lignin and “lignin-like” compounds such as cutine, acid detergent insoluble nitrogen, and acid insoluble ash. Thus, ADL is the lignin content after digestion with sulfuric acid and cellulose content is calculated as the difference between %ADF and %ADL. Additionally, leaf litter subsamples were analyzed for dry mass (105°C for 48 h), moisture content, and ash mass (500°C for 5 h). Finally, lignin:N ratios were calculated from the original data.

Soluble carbon was determined from 24 h leaf litter extracts on pure water, using the total organic carbon analyzer (TOC-VcsN, SHIMADZU model TNM-1).

Standard cotton strip decomposition tests

To examine integrated microenvironmental effects of different litter bed types on decomposition rates (Hypothesis 3), a cellulose degradation test was implemented using a standard unbleached 100% cotton fabric (96% pure cellulose; Belnap et al. 2005). Sets of cotton strips (6 cm-wide and 15 cm-long) were wrapped up in aluminum foil, autoclaved for 30 min at 121°C to reduce risk of litter layer contamination. On each plot, five labeled cotton strips were inserted 1.0 cm deep into the litter layer (without bending) at an angle of 3°. To insert the cotton strips, the lower 4 cm of the strip was folded over a blade of a straight flat shovel and carefully inserted into the litter layer, leaving approximately 5 mm protruding out of the surface. A total of 20 cotton strips were buried per litter bed type (mixed and pure oak and pine). Incubations lasted for 30 days during both the dry (February) and the wet season (June). At the end of incubation periods, cotton strips were carefully extracted, placed between

sheets of blotting paper, wrapped in foil packs and stored under cool conditions. In the laboratory, soil and roots were carefully removed from cotton strips. When moist, strips were first dried at room temperature (24–26°C). Afterwards, strips were wrapped in aluminum foil and autoclaved (121°C, 30 min). For each cotton strip, tensile strength was determined at the College of Textile Engineering at the Instituto Politecnico Nacional, Mexico City. Our assumption was that tensile strength measures indirectly cloth decomposition by cellulolytic activity in the litter layer and it is expressed in units of force (Newton) (Belnap et al. 2005).

Statistical analysis

Differences in mass loss among four leaf-litter types (pure and mixed *Q. potosina* and *P. cembroides* litter) considering four consecutive sampling dates were examined with a repeated measures analysis of variance with leaf-litter type and incubation time as main factors. To describe the dynamics of temporal mass loss (decomposition constant; k), the temporal decay of remaining mass on time was fitted to a double exponential decay model (Wider and Lang 1982; Ostrofsky 2007):

$$M_t = M_L e^{-k_L t} + M_R e^{-k_R t}$$

where M_t is the leaf-litter mass remaining at time t , M_L corresponds to the labile mass fraction at time zero, M_R describes the initial recalcitrant mass fraction, k_L is the decay constant for the labile fraction, k_R is the decay constant for the recalcitrant fraction, and t is time in months.

To test for differences in litter quality as a measure of litter decomposability (N, C, Soluble Compounds, cellulose, lignin, soluble C, and, C:N and lignin:N ratios) a two way ANOVA model was applied with leaf litter type and incubation time (0, 3, 6, 9, and 12 months) as main factors. For post hoc comparisons of mass loss and nutrient concentration Tukey's multiple mean comparison test was applied. Although the time is one of the sources of variability for this design, repeated measures ANOVA was not applied because of determinations of litter quality were carried out on different litter bags (experimental units) each harvesting time; instead the two way ANOVAs was used.

Relationships between accumulated rainfall and mass loss were examined using Pearson's correlation analysis. Tensile strength of cotton strips was analyzed with a two-way ANOVA using a factorial design with season (dry and rain) and microsite (monospecific *Q. potosina*, monospecific *P. cembroides* and mixed stands) as main factors. Water content of litter types (oak, pine and mixed) was compared using a one-way ANOVA. Prior to analysis, data were tested for normality using Shapiro-Wilk's test. Response variables that did not show a normal distribution were log transformed. Post hoc multiple mean comparisons were carried out with a Tukey's test using a significance level of $P \leq 0.05$. All statistical analyses were conducted using the SAS Statistical software (SAS Institute, Inc. 2002–2003).

Results

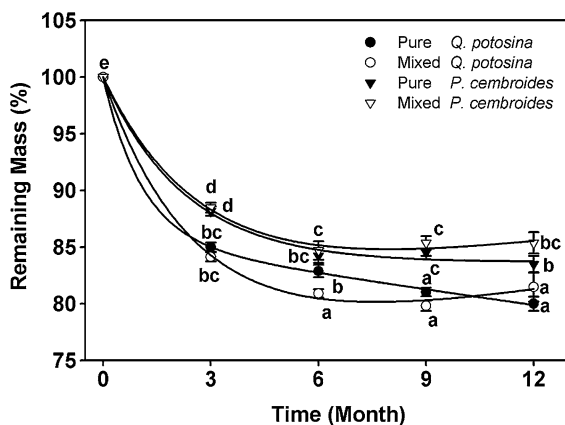
Mass loss

Leaf-litter decomposition (reported as remaining mass) exhibited a decay pattern that fit well to a double exponential decay model ($R^2 > 0.97$; Table 3). Estimated early (first 3 months) decomposition rates, k , of the labile litter fraction were significantly higher than k of the recalcitrant litter fraction in all four leaf-litter types (Table 3). Decomposition rates of pure *Q. potosina* litter were almost twice as high as k observed for both pine litter types. However, there were no differences in k for either labile or recalcitrant fractions when comparing pure and mixed litter incubations. Except for pure *Q. potosina* litter the recalcitrant fraction did not decay during this early incubation period.

Overall, mass loss showed a pronounced seasonal decline in the first 3 months of incubation leveling out during the dry months in all four litter types (Fig. 1; time \times leaf-litter type interaction $P = 0.0212$). Overall, during the whole incubation period *Q. potosina* exhibited greater leaf-litter mass loss than *P. cembroides*. Thus, after three incubation months, mass loss by *Q. potosina* leaf-litter ($15.0 \pm 0.40\%$; $P \leq 0.05$) was 27% higher than mass loss observed in *P. cembroides* leaf-litter ($11.8 \pm 0.41\%$). Mixed *Q. potosina* leaf litter showed 11.7% greater mass loss than pure leaf-litter ($19.1 \pm 0.37\%$ vs. $17.1 \pm 0.55\%$; $P \leq 0.05$) (Fig. 1) after

Table 3 Double exponential decay constants (k) and fits (R^2) for the early labile litter fraction (k_L ; $\pm 1SE$; $P = 0.05$) and the later recalcitrant litter fraction (k_R ; $\pm 1SE$; $P = 0.05$) in twolitter types (*Quercus potosina*, *Pinus cembroides*) and two incubation conditions (pure and mixed litter)

Leaf-litter type	Condition	Labile (k_L)	Recalcitrant (k_R)	R^2
<i>Q. potosina</i>	Pure	11.10 ± 2.94^a	0.0690 ± 0.01^a	0.998
<i>Q. potosina</i>	Mixed	6.90 ± 3.73^{ab}	0.00 ± 0.07^a	0.977
<i>P. cembroides</i>	Pure	5.29 ± 2.44^b	0.00 ± 0.06^a	0.985
<i>P. cembroides</i>	Mixed	6.25 ± 3.76^b	0.00 ± 0.06^a	0.972

Different letters in rows indicate significant differences among litter condition and litter type at $P \leq 0.05$ **Fig. 1** Curve-fit of double decay function to percentage of ash-free dry mass (AFDM) remaining considering pure and mixed *Q. potosina* and *P. cembroides* leaf-litter during 1 year of in situ litter incubation. Vertical bars are one standard error ($P \leq 0.05$). Different letters indicate significant differences ($P \leq 0.05$)

6 months of incubation, whereas, *P. cembroides* litter mass loss did not differ between pure and mixed incubations at any time.

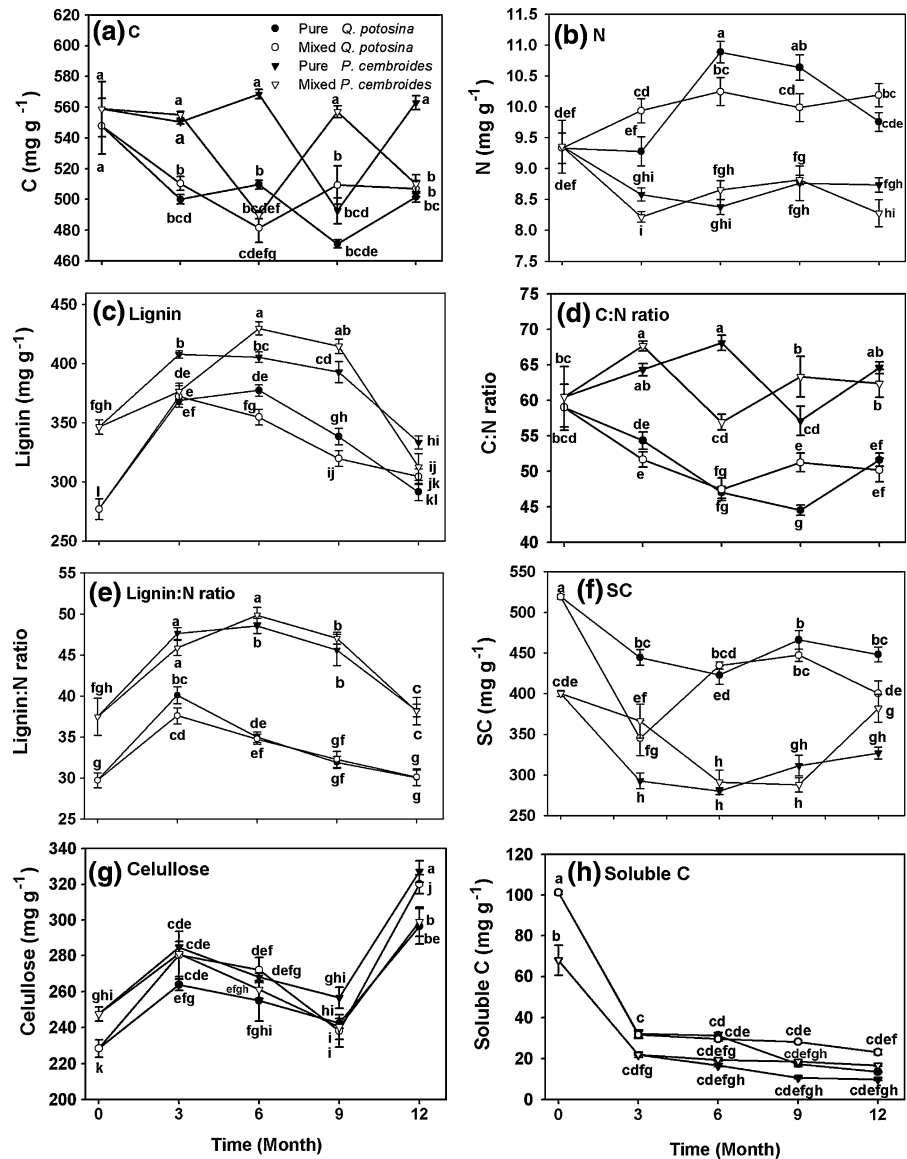
Leaf litter quality

Leaf litter C concentration changed with time, however this depended on litter type (leaf-litter type \times time interaction; $P \leq 0.0001$, Fig. 2a). During the first 3 months of incubation, C concentration of *Q. potosina* litter both in mixed and pure litterbags dropped markedly and remained with similar concentrations thereafter. While C concentration of *P. cembroides* litter did not change during the first 3 months, it decreased significantly after 6 months of incubation in mixed litterbags and after 9 months of incubation in pure litterbags. Nitrogen concentration

of *Q. potosina* litter was on average 2 mg g^{-1} higher than N concentration of *P. cembroides* litter throughout the incubation period (time \times leaf-litter type interaction $P = 0.0001$, Fig. 2b). In *P. cembroides* litter, N concentration declined after 3 months and maintained similar concentrations for the rest of the year, both in mixed and pure litterbags. In both *Q. potosina* litter types, N concentration increased after 6 month of incubation when compared to initial N concentrations; also it was higher for litter in pure than mixed litterbags after 6 and 9 months of incubation, however it was similar for both litter types after 12 months (Fig. 2b). The C:N ratio (time \times leaf-litter type interaction $P = 0.0001$, Fig. 2d) displayed similar temporal dynamics as litter C concentration for both pure and mixed *P. cembroides* and *Q. potosina* leaf litter. Except for the initial C:N ratio, overall *Q. potosina* litter exhibited lower C:N ratios than *P. cembroides* litter.

Also, leaf-litter types and incubation periods caused significant differences in lignin concentration (Fig. 2c), lignin:N ratios (Fig. 2e), and soluble compounds (Fig. 2f) concentrations (leaf-litter type \times time, $P \leq 0.0001$). In general *P. cembroides* leaf-litter (pure and mixed) exhibited higher lignin concentration than *Q. potosina* litter (Fig. 2c). Lignin concentration started with 280 mg g^{-1} and 350 mg g^{-1} for *Q. potosina* and *P. cembroides*, respectively, raised by about 80 mg g^{-1} half a year later and dropped again to initial values after 1 year. However, there were differences with respect to lignin concentrations in litter of pure and mixed litterbags. In case of *P. cembroides*, after 3 months, lignin concentration of litter in mixed bags was lower than that in pure bags, while after 6 and 9 months lignin concentration was higher in mixed than in pure bags. In case of *Q. potosina*, the pattern was reverse, with higher lignin

Fig. 2 Concentration variations (mg g^{-1}) for **a** carbon, **b** nitrogen, **c** lignin, **d** C:N ratio, **e** lignin:N ratio, **f** SC (soluble compounds), **g** cellulose, and **h** Soluble C (soluble Carbon) in remaining mass of decomposing leaf-litter. Bars with different letters indicate statistical differences. The source of variation, Leaf-litter type by year fraction interaction; $P = 0.0001$ for all litter chemical fractions except cellulose (**g**); $P = 0.7130$



concentration of litter in pure bags than in mixed bags. Leaf-litter lignin:N ratios were higher for *P. cembroides* than for *Q. potosina* throughout the incubation period; however, no differences occurred between pure and mixed litter samples (Fig. 2e). Regarding cellulose concentration, except for the initial higher cellulose concentrations observed in *P. cembroides* litter, no differences in cellulose concentrations between litter types occurred (leaf litter type and time, $P = 0.01$, Fig. 2g). In general, cellulose concentration rose at 3 months, dropped at 9 months and rose again at 12 months.

Concentration of soluble compounds was on average higher in *Q. potosina* litter compared to *P. cembroides* litter. The soluble compounds exhibited a significant decline from initial values, with faster rates in *Q. potosina* litter (3 months) than in *P. cembroides* litter (6 months) (litter type by time interaction $P = 0.0001$, Fig. 2f). After 3 months, the concentration of soluble compounds in *Q. potosina* litter dropped significantly more in mixed than in pure litter bags, while the opposite was observed for soluble compounds concentration in *P. cembroides* litter. After six and 9 months of incubation, soluble

compounds litter concentration was similar in pure and mixed bags for both tree species. After 12 months of incubation, soluble compounds concentration was higher in *Q. potosina* litter of pure bags compared to mixed bags (Fig. 2f). The concentration of soluble carbon dropped in both litter species after 3 incubation months with *Q. potosina* having significantly higher initial soluble C concentrations (litter type main effect; $P = 0.0001$, Fig. 2h). Soluble C concentrations did not differ in litter of pure and mixed litterbags.

Remaining mass of recalcitrant compounds (lignin) exhibited initially a slight increase in both pure and mixed *Q. potosina* (Fig. 3a, $P < 0.001$) to drop after 6 months. Pure *P. cembroides* was constantly declining with an abrupt fall in the 1 year examination, while mixed litter remained similar to original content reaching almost a 30% decline for the 12 months incubation. Mass remaining in soluble compounds followed maximum decline in 3 months incubation (Fig. 3b) leveling out thereafter. Mixed

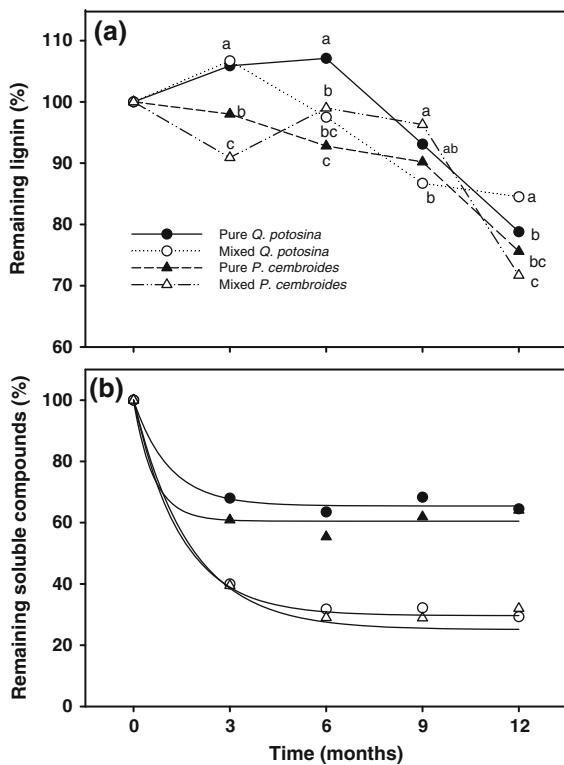


Fig. 3 Temporal dynamics of remaining ligning (a) and remaining soluble compounds (b) in leaf litter of two forest species (*Quercus potosina* and *Pinus cembroides*) under two incubation conditions (pure and mixed)

litter types loose 30–40% more soluble compounds than pure litter types.

Standard cotton strip decomposition test

After a 30-day incubation period in three litter bed types, tensile strength of cotton strips changed in response to bed type (microsite main effect; $P = 0.0082$; Fig. 4) and season (season main effect; $P < 0.0001$; Fig. 4). Overall, tensile strength of cotton strips incubated in mixed litter microsites was significantly lower than of cotton strips incubated in pure *P. cembroides* litter beds. No differences in tensile strength were detected between pure *Q. potosina* and *P. cembroides* litter beds. Tensile strength was ca. around 20% lower in cotton strips incubated during the wet season than during the dry season (Fig. 4).

Regarding environmental conditions prevailing during the study period, total rainfall was 337 mm, with the largest proportion (71%) recorded for the months from June to August. Sixty-five mm were recorded from September to November, while the remaining 32 mm corresponded to spring rain (March to May). Accumulated rainfall explained 97% of mass loss recorded in *P. cembroides* leaf-litter for both pure and mixed incubation conditions ($P < 0.05$; Fig. 5c and d, respectively). In comparison, rainfall explained 88% of mass loss in pure *Q. potosina* litter and only 58% for mixed leaf-litter (Fig. 5a, b).

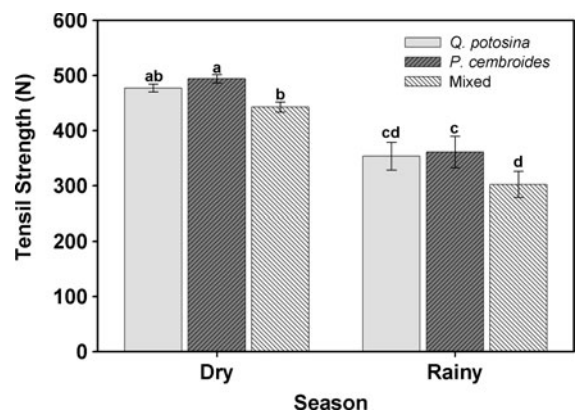
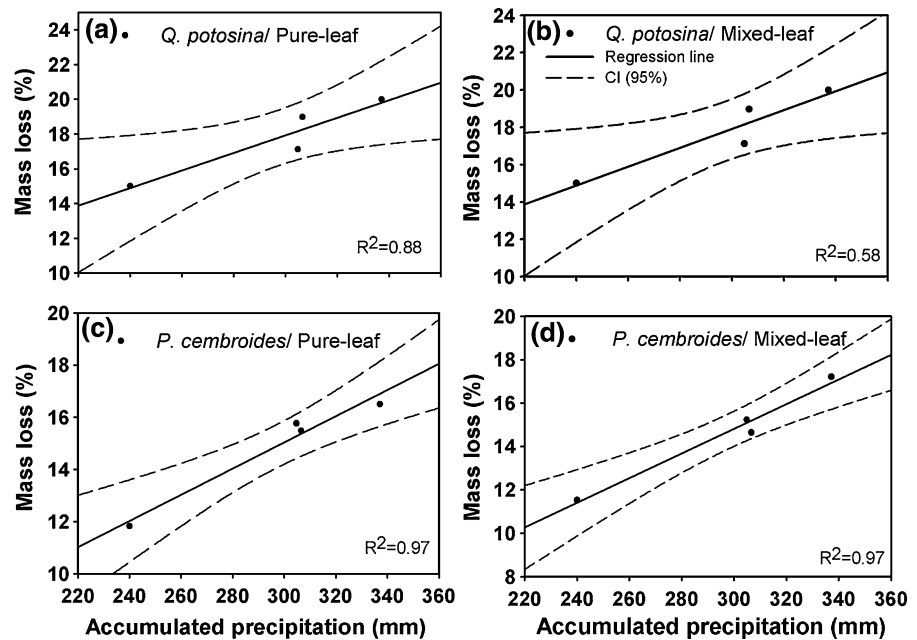


Fig. 4 Cotton strip tensile strength (Newtons) incubated under pure and mixed litter bed conditions of *P. cembroides* and *Q. potosina*. Significant sources of variation included Microsite ($P = 0.0082$) and season ($P = 0.0001$), while the interaction microsite by season was not ($P = 0.9029$). Bars with different letters indicate significant differences at $P \leq 0.05$

Fig. 5 Relationships between litter mass loss and accumulated precipitation (four sampling periods) during 1-year leaf litter incubations of pure and mixed *Quercus potosina* litter (a and b) and pure mixed *Pinus cembroides* litter (c and d). Regression lines are depicted with a continuous line and their confidence intervals ($P < 0.05$) with a hatched line



In months with rainfalls amounting to 40 mm, soil water potential ranged on average between -0.01 MPa and -1.05 MPa, while in the dry season (from January to March 2008), soil water potential dropped to -4.3 MPa (Fig. 6a). Concurrently, litter bed temperatures during fall and winter fluctuated around 10 – 12°C , in comparison to 16 – 18°C observed in spring and summer (Fig. 6a). Also, litter water content measured once during the wet season was significantly higher for oak litter than for pine litter ($P = 0.0001$), whereas mixed litter had intermediate water content (Fig. 6b).

Discussion

In this study, early-phase mass loss in both *Q. potosina* and *P. cembroides* occurred principally by leaching of labile soluble compounds including carbon. Mass loss was most pronounced during the initial incubation period (3 and 6 months), which coincided with the period of largest annual rainfall input (240 mm). Mass loss of pure *Q. potosina* leaf-litter occurred more rapidly than mass loss of pure *P. cembroides*, confirming that broadleaf species decompose at a faster rate than coniferous species (Prescott et al. 2000; Alvarez et al. 2008).

While there is ample knowledge on soil microbial, faunal and abiotic controls of litter decomposition rates of individual plant species, less is known of inherent, physicochemical effects of species-specific litter on mixed litter decomposition rates both from a quantitative and qualitative perspective. From a quantitative perspective, in this study, it was proposed that recalcitrant, slowly decomposing *P. cembroides* litter would decay more rapidly in the presence of the faster decomposing *Q. potosina* litter with higher concentrations of labile fractions (hypothesis 1, Ostrofsky 2007) using litter decomposition bags. Contrary to predictions, in this 1-year study, the presence of *Q. potosina* leaf litter did not enhance decomposition rates (k) of *P. cembroides* leaf litter, when compared to decomposition rates of pure *P. cembroides* leaf litter suggesting that its leaf litter has a high structural stability attributable to strongly lignified leaf tissue likely having an overriding control on litter mass loss (Table 2; Fig. 3a). Other studies have made similar observations, in that no distinctive species-specific litter effects were found in decomposition rates of mixed versus pure broadleaf and coniferous litter species (Prescott et al. 2000), or single or multi-species *Nothofagus* litter in Patagonian forests (Vivanco and Austin 2008). In contrast to this study however, Ganjgunte et al.

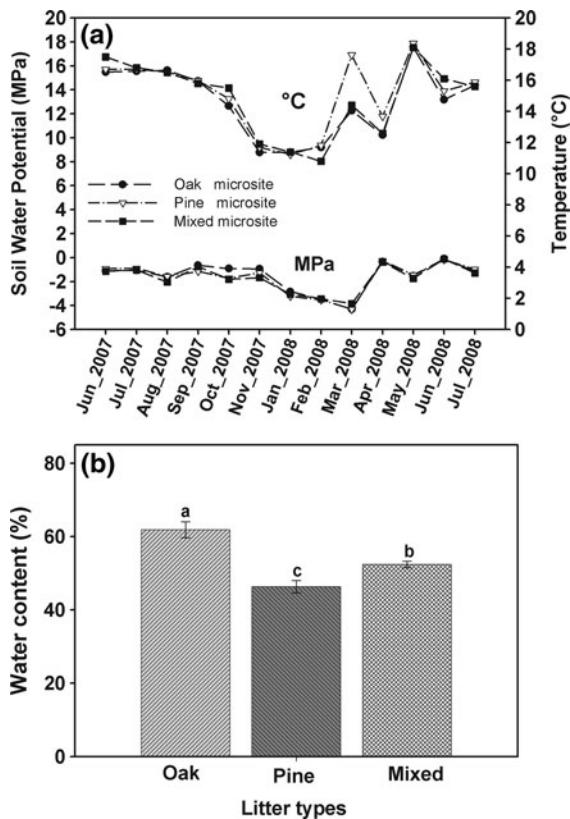


Fig. 6 **a** Monthly values for soil water potential (MPa; left “y” axis; Data taken from For Ecol Mange 258, 2009) and litter temperature (°C at 10 cm deep; right “y” axis) during incubations of leaf litterbags at the study site in Sierra San Miguelito, San Luis Potosi. **b** Gravimetric water content of a surface litter layer (top 10 cm) for pure and mixed conditions of oak and pine stands. Bars with different letters indicate significant differences at $P = 0.0001$

(2005) reported that decomposition of *Pinus radiata* litter was delayed when incubated in the presence of understory species.

Mass loss in *Q. potosina* leaf-litter in contrast, showed a trend opposite to expectations. Accordingly (second hypothesis; Ostrofsky 2007), mass loss of fast-decomposing species (oak) should be reduced in the presence of a slow-decomposing species (pine). In this study however, rate of mass loss of mixed *Q. potosina* litter was greater than that of pure *Q. potosina* leaf litter (Fig. 1). This response occurred after the principal rainfall season 6 months after litter incubation (Fig. 1). The high decay rates coincided with large precipitation events (summing to 239 mm) causing dissolution and leaching of soluble compounds (Table 3 and Fig. 3b). This finding supports previous

studies (Gallardo and Merino 1993; Virzo De Santo et al. 1993), where soluble compounds leaching was the main mechanism for early mass loss during decomposition. In case of *P. cembroides*, accumulated rainfall explained 97% of leaf litter mass loss incubated under pure and mixed conditions, while in case of *Q. potosina* it explained only 88% and 58% of mass loss for pure and mixed leaf litter, respectively (Fig. 5). This result came as a surprise, since it was expected that leaves with higher soluble compounds concentration such as *Q. potosina* would exhibit closer relationship to accumulated rainfall and therefore susceptibility to dissolution, leaching and mass loss. Thus, the precipitation induced leaching processes seemed to have been highly non-linear. Still, where rainfall is markedly seasonal, moisture becomes an important regulator of decomposition and N mineralization as mentioned by Cornejo et al. (1994).

Based on the response dynamics of the measured variables, the rate of mass loss in *Q. potosina* seemed to have been a step-wise process: in the first 3 months, the decay rate of soluble compounds was significantly greater for mixed litter than for pure litter (Figs. 2f, 3b) and this is when soluble compounds and soluble-C concentration declined substantially. For soluble compounds the decline was twice as high in mixed compared to pure litter and the substances released in mixed litter seemed to have been mostly non-C compounds and/or were respired. The reduced control of rain on mass loss in *Q. potosina* could have resulted from a rapid efficient leaching of soluble compounds including soluble C from initial rainstorms (see for instance k_L for pure *Q. potosina*, Table 3 and Figs. 2f, h). Alternatively, the presence of different litter types with contrasting litter chemistry (see Table 2) may trigger a sequence of qualitative changes during decomposition events. For example, early stage leaching and microbial decomposition of labile compounds from one litter type may spatially and temporally overlap with the early stage of lignin decomposition of a more recalcitrant litter type. The interaction of these decomposition processes may reduce the inhibiting effects of lignified structures in cell walls on enzymes to access and release also the labile C fractions inside plant cells (Austin and Ballaré 2010; Pauly and Keegstra 2008) of the more recalcitrant litter type. Co-occurring litter types together support potentially complementary soil microbial functional groups (Hättenschwiler and

Gasser 2005) and thus enhance decomposition of both labile and more recalcitrant fractions of the litter type with higher decomposability, in this case *Q. potosina*.

Ostrofsky's second hypothesis states that in litter mixtures, releases of certain chemical compounds may inhibit litter decomposition. This was manifested with the small soluble compounds fluxes released in mixed *P. cembroides* litter (around 80 mg g⁻¹ more soluble compounds after 3 months incubation) that coincided with large soluble compounds fluxes from mixed *Q. potosina* litter (Fig. 2f). Hence, these results confirm that decomposition of mixed leaf litter may concurrently impose facilitative and inhibitory effects for a single chemical compound as suggested by Hypothesis 3. Our results show additionally that facilitative and inhibitory effects may not only be associated with single chemical compounds but rather, the sequential presence/accumulation of different chemical compounds in litter mixtures may trigger facilitative and inhibitory effects at different temporal scales (after 3 months, e.g. soluble compounds, or after 12 months, e.g. cellulose) and most likely (however not studied in our case) be associated with the development of different microbial populations.

Our data support this potential mechanism; after 3 months litter mixture triggered greater soluble-C release (expressed in soluble compounds concentrations) from mixed rather than from pure *Q. potosina* litter, while soluble compounds release in *P. cembroides* was reduced compared to pure *P. cembroides* litter. However, after 3 months lignin concentration in *P. cembroides* litter from mixed bags was lower than that of pure bags, while no differences in lignin concentrations were observed between mixed and pure *Q. potosina* litter. After 6 months, while soluble compounds concentration was similar for both *Q. potosina* litter types, lignin concentration dropped more in mixed than in pure *Q. potosina* litter. In contrast, *P. cembroides* released more soluble compounds in mixed than in pure litter, while lignin concentration in mixed litter increased and was higher compared to pure litter. This apparently complementary decay dynamics most likely involved population growth of both bacterial and fungal species, which in turn stimulated decomposition of soluble compounds and the breakdown of lignified litter. Previous studies for instance, have reported that water soluble-C is used as an energy source for

microbial metabolism in litter decomposition (Møller et al. 1999; Kalbitz et al. 2000; Neff and Asner 2001).

Another mechanism related to facilitation may be related to the vertical and lateral water fluxes in mixed litter beds. For instance, the study by Pérez-Suárez (2009) examining hydrological fractions in the water cycle of semiarid forest ecosystems reported that lateral water fluxes (runoff) were greater in mixed litter beds consisting of *Q. potosina* and *P. cembroides* than in pure litter beds of *Q. potosina*. Thus, litter bed conditions favoring lateral water flux may enhance soluble compounds leaching and hence litter mass loss as seen in the mixed *Q. potosina* litter. These results highlight the importance of interactions among hydrology, soluble carbon leaching and microbial soluble-C relationships as important factors in regulating mass loss of labile litter fractions (Neff and Asner 2001; Anaya et al. 2007) at different temporal and spatial scales.

The occurrence and potential effect of the micro-environmental heterogeneity generated by different litter types were examined in this study with a response-to-environment approach using a tension resistance test of standard cotton material (Fig. 4). In fact, mixed litter and pure oak litter created different microenvironments with respect to their decomposability of a certain standard substrate (cellulose) (Hypothesis 3). The microenvironments of the different litter types seem to have a stable net effect on decomposition. While litter water content differs for the different litter types, it does not seem to be directly related to this effect. At different times during the study year, mixed litter beds differed from pure beds in litter temperatures and soil water potential. Under mixed conditions, these microenvironmental factors tended to be higher than for pure *P. cembroides* litter beds likely favoring conditions for microbial activity and thus for litter decomposition (Pataki et al. 1998; Schimel et al. 1999; Yan et al. 2004; Berg and McClaugherty 2008). Higher microbial activity was assumed the driving factor leading to the significant reduction in observed tensile strength of cotton strips incubated in the mixed litter in both dry and wet season. Thus, our study provides evidence that leaf litter combinations inhibit and/or accelerate processes in early stage litter decomposition due to their inherent chemical traits and structural characteristics may alter the physical and biotic environmental conditions both in space and time.

Conclusions

Results from this study support that inherent species-specific features of litter play a fundamental role either facilitating or inhibiting litter mass loss and associated chemical compounds which may directly contribute to a—thus far little studied—spatiotemporal dynamics in the N, lignin and overall C-cycle associated with early-phase decomposition. The study demonstrates that the interaction dynamics between litter types are more complex than currently considered in decomposition models such as the one tested in this study (Ostrofsky 2007). We did not witness an acceleration of mass loss for the slowly decomposing *P. cembroides* litter in the presence of the faster decomposing *Q. potosina* litter. Also, we did not observe a clear inhibition in mass loss of the faster decomposing *Q. potosina* litter under mixed conditions. Probably most mass loss at this early decomposition phase was controlled by leaching, however, besides leaching additional subtle mechanisms associated with the interaction of chemical compounds and/or microbial community specialists may have contributed to biotic decomposition suggesting complex interactions that cannot easily be accounted for and introduced into decomposition models. Based on the results of this study, selective tree species extraction as a common form of land use/cover change does not only alter large scale changes in C and N pools but may also lead to changes in small-scale resource dynamics that may feedback on tree species interaction and forest ecosystem function.

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