# INSTITUTO POTOSINO DE INVESTIGACIÓN CIENTÍFICA Y TECNOLÓGICA, A.C.

## POSGRADO DE CIENCIAS APLICADAS

# Understanding the role of *Pinus cembroides* and *Quercus potosina* in water and nutrient dynamics in a semi-arid forest ecosystem of central-northwest Mexico applying the functional matrix approach

Tesis que presenta

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que se desarrolló bajo la dirección de

**Dra. Elisabeth Huber- Sannwald**
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*Nuestra recompensa se encuentra*
*en el esfuerzo y no en el resultado.*
*Un esfuerzo total es una victoria completa.*

***Mahatma Gandhi***

A mis padres

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# Resumen

Cada especie presente en los ecosistemas posee características específicas a través de las cuales interactúa con el ambiente, influyendo simultáneamente en varios procesos funcionales del ecosistema. La teoría de la matriz funcional permite entender el efecto de estas características de las especies en varios procesos de los ecosistemas así como entender cual es la aportación de cada especie individual cuando se encuentran coexistiendo con otras especies. Este trabajo evalúo el papel de *Pinus cembroides* y *Quercus potosina* en la dinámica hidrológica y nutrimental de un ecosistema forestal semiárido del centro-noroeste de México aplicando la teoría de la matriz funcional. Este estudio fue llevado a cabo en el periodo que comprende entre junio del 2006 a noviembre del 2008. El estudio se realizó en tres tipos de rodal seleccionados en un bosque semiárido y que incluyeron: rodales monoespecíficos de *Q. potosina*, rodales monoespecíficos de *P. cembroides* y rodales mixtos de pino-encino. Derivado de este estudio, se encontró que la matriz funcional que resulta de las características inherentes en morfología, fisiología y composición química de ambas especies generó diferentes efectos en la redistribución del agua de lluvia (escurrimiento foliar, escurrimiento fustal y escurrimiento superficial), así como en el reciclamiento de nutrientes que ocurre a través de la producción de hojarasca y descomposición del mantillo. Este efecto, sin embargo, es modificado cuando las especies dominantes se encuentran en rodales monoespecíficos y/o mixtos. Así, la apertura del dosel, el diámetro del tronco, la capacidad de retención de agua por el mantillo y su volumen, fueron rasgos inherentes que controlaron los flujos de las diferentes fracciones del agua de lluvia dentro de cada rodal. Paralelamente, la cantidad de agua en cada evento de lluvia también jugo un papel importante en el desencadenamiento de algunos de los procesos hidrológicos. En otros aspectos, los tipos de rodal fueron diferentes en la producción de hojarasca y en la cantidad de nutrientes que recircularon a través de la hojarasca. Sobre la productividad y el ciclo de nutrientes, el presente estudio resalta los siguientes aspectos; la importancia de los eventos extremos en el ciclo de nutrientes a través de la producción de hojas verdes en la hojarasca, con lo que respecta a especies de lenta descomposición como *P. cembroides*, este proceso no siguió los mecanismos esperados cuando se incuba en mezcla con *Q. potosina*. Al mismo tiempo, la perdida de masa de la especies de rápida descomposición (*Q. potosina*) fue favorecida en la mezcla durante la primera etapa de descomposición. Finalmente, otro resultado importante de este trabajo tiene que ver con la capa de mantillo en la superficie del piso forestal, la cual ejerce un importante control sobre la transferencia e intercambio de agua y nutrientes entre la atmosfera, el dosel y el suelo dentro de los ecosistemas forestales. Así, la presencia de parches de vegetación con una sola especies o en mezcla contribuye a la gran variabilidad espacio temporal de los procesos hidrológicos y del ciclo de nutrientes en los ecosistemas forestales del centro-noroeste de México.

**Palabras clave**: *Quercus potosina*, *Pinus cembroides*, procesos funcionales, ciclo de nutrientes, descomposición de mantillo mixto, producción del mantillo, escurrimiento fustal, escurrimiento superficial.

# Abstract

The species present in ecosystems have specific traits through which they interact with the environment, influencing simultaneously in several ecosystem processes. The functional matrix approach contributes to understanding the multiple effects of these species characteristics on several ecosystem processes simultaneously as well as to understanding the contribution of each single species when it occurs alone and when it co-occurs with other species. This work evaluated the role of *Pinus cembroides* Zucc. and *Quercus potosina* Trel. in water and nutrient dynamics in a semi-arid forest ecosystem of central-northwest Mexico applying the functional matrix approach. This study was carried out in the period from June 2006 to November 2008 considering three different stand types which included: monospecific stands of *Q. potosina*; monospecific stands of *P. cembroides* and mixed oak-pine stands. Derived from this study, the functional matrix that results from inherent traits in morphology, physiology and chemical composition of each species generated different effects in rainfall redistribution (throughfall, stemflow, and runoff), as well as in the nutrient recycling that occurs through litterfall production and litter decomposition. This effect, however, is modified when the dominant species occur in monospecific or mixed stands. Thus, the openness of the canopy, stem diameter, litter water content and litter volume were inherent traits that controlled the flux of different fractions of rainfall within each stand. At the same time, the size of rainfall event also played an important role in triggering some hydrological processes. In other aspects, the stand types were different in litterfall production and in nutrient cycling. The present study highlights the following aspects: the importance of extreme events in the nutrient cycling through green leaves in the litterfall, with respect to the species of slow decomposition like *P. cembroides.,* These processes did not follow the expected mechanisms when they were incubated with *Q. potosina* leaf litter. In addition, the mass loss rate of litter of the faster decomposing species (*Q. potosina*) was stimulated in the mixture during the first stage of decomposition. Finally, another important result of this work was related to the layer of the forest floor surface, which had an important control over transfer and exchange of nutrients and water between atmosphere, the canopy and the soil, within forest ecosystems. Thus, the presence of tree patches consisting of single species or mixtures contributes to a remarkable spatial-temporal variability of hydrological processes and nutrient cycling in semiarid forest ecosystems of central-northwest Mexico.

**Key words:** *Quercus potosina*, *Pinus cembroides*, functional processes, nutrient cycling, mixed litter decomposition, litterfall production, rainfall, throughfall, stemflow, runoff.

## General Introduction

Forest ecohydrology studies the functional interrelationship between hydrology and ecosystem processes at the catchment scale (Rodríguez-Iturbe, 2000; Zalewski, 2000). With the ecohydrological approach fundamental understanding of the interaction of ecological and hydrological processes and thus of a 'dual regulation' mechanism can be gained. This is highly pertinent in the light of the role of forest ecosystems in nutrient cycling and water retention in a local and globally changing environment (Zalewski, 2000; Wilcox *et al*., 2003). Hydrological, ecological and geochemical processes are tightly coupled, particularly in water-limited environments (Chesson *et al.,* 2004) such as pinyon forests and dry tropical forests and woodlands, where biological activity and nutrient availability are highly synchronized with water availability (Murphy and Lugo, 1986; Breshears and Barnes, 1999). These forest ecosystems occur in frost-free areas where mean annual temperature is higher than 17°C, mean annual rainfall is between 250-2000mm and the annual ratio of potential evapotranspiration and precipitation (ET:P) exceeds unity (Murphy and Lugo, 1986). Overall, dry forests exhibit lower productivity, lower stature and less canopy stratification than do other forests. Also, the leaf area index (total plant leaf area per ground area) of dry forests is significantly greater than that of wet forests (Murphy and Lugo, 1986).

The structure of a forest is determined by tree species-specific characteristics such as size, shape and spatial distribution, which together with a unique combination of leaf evolutionary traits (lifespan, phenology and chemical composition) determine the input, redistribution and throughput of material and energy through the forest canopy before they reach the forest floor (Spies, 1998; Waring and Running, 1998). Therefore, it is important to understand seasonal changes of species traits, how they interact with changing environmental conditions and the interaction among tree species. Several theories have been proposed to relate species effects to functional aspects of ecosystems. The functional matrix approach (Eviner and Chapin, 2003) is an integrative approach that relates specific species traits to multiple functions such that each species could potentially influence simultaneously several functions of an ecosystem. Consequently, species are functionally unique and cannot be simply replaced by other species without altering ecosystem function. For instance, a multi-species forest canopy determines the quantity and composition of seasonal and annual litterfall produced, which in turn controls the rate of organic matter being recycled and mineral nutrients being made available for plant growth (Prescott, 2002). At the same time, forest tree canopy influences the interception of rain water and redistribution through throughfall and stemflow (Wilcox *et al.,* 2003). On the forest floor, species influence rain water interception and storage through specific litter attributes such as water-holding capacity (Waring and Running, 1998; Sayer, 2006) thereby influencing water infiltration, hydraulic conductivity and runoff (Wilcox *et al.,* 2003), and ultimately the microclimate for litter decomposition (Breshears *et al.,* 1998).

The effect of species interaction on ecosystem function may be either interactive or additive depending on the ecosystem process and species identity. For instance, a *Pinus pseudostrobus* - *Quercus* spp. mixed tree canopy intercepted up to 23% more rainfall than the respective monospecific stands; similarly, mixed tree canopies deposited significantly more mineral nutrients through throughfall than pure pine or oak canopies. These differences were a consequence of greater leaf biomass of mixed than pure stands (Cantú-Silva and González-Rodríguez, 2001). Also, species composition influenced nutrient cycling and productivity in different ways; e.g., Binkley *et al.* (1992) found that greater nutrient use efficiency of *Eucalyptus* and greater nutrient cycling under *Albizia* enhance light capture and higher nutrient use efficiency in mixed stands.

*Pinus cembroides* Zucc. (Mexican pinyon) and *Quercus potosina* Trel. (San Luis Potosi oak) are the dominant tree species of the semiarid pine-oak forest in North and Central Mexico (Rzedowski, 1978). *Pinus cembroides* and *Q. potosina* occur in islands of pure or mixed stands, and *Q. potosina* grows generally on more fertile sites than *P. cembroides* (Rzedowski, 1978). *Quercus potosina* has deciduous leaves, which are shed in a single major shedding event, while *P.*

*cembroides* has 3-4 yr old needles, whose oldest cohorts are usually shed in episodic shedding events (Robert, 1977; Zavala and García, 1991). *Quercus potosina* shows slower growth than *P. cembroides*. Selective wood extraction and uncontrolled use of those tree species (pinyon harvesting, firewood, grazing, etc.) (Romero-Manzanares and García, 2000) have altered species distribution patterns and thus the spatial and temporal dynamics of structural and architectural tree/forest canopy elements that may potentially affect hydrological and nutrient cycling processes.

Considering the differences in canopy structure, leaf lifespan (deciduous *vs.* evergreen), leaf and litter chemical composition and the external control of biogeochemical and hydrological cycles by seasonal rainfall patterns, the general objective of this study was to understand the role of monospecific and mixed forest stands of *P. cembroides* and *Q. potosina* in spatiotemporal water and nutrient dynamics of these water-limited ecosystems adopting the functional matrix approach. The principal questions of this study were the following: (1) Do the functional matrices of leaf traits of *P. cembroides* and *Q. potosina* confer differential species effects on various hydrological processes (Chapter 1), nutrient return through litterfall (Chapter 2), and litter decomposition (Chapter 3)? (2) Do leaf functional matrices of *P. cembroides* and *Q. potosina* influence nutrient and hydrological cycling differently when these species occur in monospecific or mixed stands (Chapter 1-3)?, and (3) to which degree, do *P. cembroides* and *Q. potosina* contribute to the spatiotemporal dynamics in hydrological processes and nutrient cycling in these semiarid forest ecosystems?

These questions were addressed in the three chapters of this thesis. Chapter I details the effects of *P. cembroides* and *Q. potosina* in monospecific and mixed stands on the interception and redistribution of rainfall (throughfall, stemflow and runoff) over a 21-months period. Chapters II and III address the effects of the two tree species and their seasonal variation on nutrient cycling. Chapter II specifically, determined the quantity and quality of senesced and green litterfall reaching the forest floor considering both the phenological trajectory of leaf development and extreme weather events. Chapter III examined the effect of composition and quality of leaf litter and microenvironment on the dynamics of mass loss and nutrient loss. In the final conclusions, the principal results and perspectives of this investigation are presented and future research directions proposed.

## References

Binkley, D., Dunkin, K.A., DeBell, D., and Ryan, M.G. (1992). Production and nutrient cycling in mixed plantations of *Eucalyptus* and *Albizia* in Hawaii. *For. Sci.* **38**, 393-408.

Breshears, D.D. and Barnes, F.J. (1999). Interrelationship between plant functional types and soil moisture heterogeneity for semiarid landscapes within the grassland/forest continuum: a unified conceptual model. *Landscape Ecology* **14**, 465-478.

Breshears D., D., Nyhan, J.W., Heil, C.E. and Wilcox, B.P. (1998). Effects of woody plants on microclimate in a semiarid woodland: soil temperature and evaporation in canopy and intercanopy Patches. *Int. J. Plant Sci.* **159**, 1010–1017.

Cantú-Silva, I. and González-Rodríguez, H. (2001). Interception loss, throughfall and stemflow chemistry in pine and oak forests in northeastern Mexico. *Tree Physiol*. **21**, 1009-1013.

Chesson P., Gebauer, R.L.E, Schwinning, S., Huntly, N., Wiegand, K., Ernest, M.S.K., Sher, A., and Novoplansky, A. (2004). Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia* **141**, 236-253.

Eviner, V.T. and Chapin III, F.S. (2003). Functional matrix: a conceptual framework for predicting multiple plant effects on ecosystem processes. *Ann. Rev. Ecol. Evol. Syst.* **34**, 455-85.

Murphy, P.G. and Lugo, A.E. (1986). Ecology of tropical dry forest. *Ann. Rev. Ecol. Syst.* **17**, 67-88.

Prescott, C.E. (2002). The influence of the forest canopy on nutrient cycling. *Tree Physiol.* **22**, 1193-1200.

Romero-Manzanares, A. and García M.E. (2002). Estabilidad y elasticidad de la composición florística de los piñonares de San Luis Potosí, México. *Agrociencia* **36**, 243-254.

Robert, M.F. (1977). Notas sobre el estudio ecológico y fitogeográfico de los bosques de *Pinus cembroides*, Zucc., en México. *Ciencia Forestal* **10**, 49-58.

Rodríguez-Iturbe, I. (2000). Ecohydrology: a hydrologic perspective of climate–soil–vegetation dynamics. *Wat. Resour. Res.* **36**, 3–9.

Rzedowski, J. (1978). Vegetación de México. Limusa. México.

Sayer, E.J. (2005). Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. *Biol. Rev.* **80**, 1-31.

Spies, T.A. (1998). Forest structure: a key to the ecosystem. *Northwest Science* **72**, 34-39.

Waring, R.H. and Running, S.W. (1998). Forest Ecosystems: Analysis at Multiple Scales. Academic Press, New York.

Wilcox, B.P., Breshears, D.D., and Allen, C.D. (2003). Ecohydrology of resources-conserving semiarid woodland: effects of scale and disturbance. *Ecol. Monog.* **73,** 223-239.

Zalewski, M. (2000). Ecohydrology—the scientific background to use ecosystem properties as management tools toward sustainability of water resources. *Ecol. Engine*. **16**, 1–8.

Zavala, C.F. and García, M.E. (1991). Fenología y crecimiento del brote anual de *P. cembroides* Zucc., de San Luis Potosí, México. *BIOTAM* **3**, 5-14.

# CHAPTER 1

## Species-specific effects on rainfall redistribution in a semiarid forest of central-northwest Mexico

### Summary

Canopy structure, leaf shape and phenology constitute inherent traits of forest tree species that exert important controls on functional processes of forest ecosystems. Thus, changes in species composition and abundance may alter stand and canopy characteristics of forests, and thus the redistribution of rainfall and hydrological processes, in general. Three different tree assemblages were selected in a semiarid forest of pine-oak in central-northwest Mexico including monospecific stands of *Quercus potosina* and *Pinus cembrodies* and mixed stands of oak and pine. From June 2006 to June 2008, we measured total precipitation and three water fractions passing the stand canopies including throughfall, stemflow and superficial runoff. Some forest stand features were also characterized. Overall, throughfall, stemflow and runoff were controlled by monthly precipitation rather than by the stand or species characteristics (canopy transmittance and stem diameter). Thus, throughfall occurred only with rainfall events larger than 1.4 mm for all stand types. Stemflow did not differ between species and occurred at rainfall events larger than 4.6 mm. Differences in the water fluxes between stand types occurred only at the peak of rainfall and this was consistent in all three years of monitoring. Stand type influenced both throughfall and runoff through canopy openness, while individual species influence stemflow through stem diameter. The results showed that the hydrological processes of rainfall redistribution are affected differentially by tree species, and stand composition and rainfall size in semiarid forest from Northern Mexico.

**Key words:** throughfall, stemflow, runoff, *Pinus cembroides*, *Quercus potosina*

## 1.1 Introduction

Tree species composition and canopy structure contribute to the dynamics of hydrological processes in forest ecosystems. Each tree species has a unique combination of leaf morphological, branch, stem, bark and rooting characteristics related to life form, lifespan, leaf area index (LAI, projected leaf area per unit ground area), stem diameter, and tree height, etc. (Spies, 1998), which all influence the interception, retention and redistribution of precipitation and consequently its spatiotemporal distribution on forest floor (Deguchi *et al.,* 2005). Thus, species traits greatly control internal water cycling both at the tree canopy, soil surface and rooting zone. At the canopy level, rainfall interception by leaves and branches, and throughfall, i.e. the water passing through canopy gaps, are determined by canopy saturation and species phenological changes in canopy structure (Carlyle-Moses *et al.*, 2004; Deguchi *et al.*, 2005; Pypker *et al.*, 2005). Stemflow, another transfer mechanism of rain water from the canopy to the soil, depends on the diameter and storage capacity of stems (Návar *et al.,* 1999; Levia and Frost, 2003), bark surface roughness, and leaf and twig position in the canopy (Návar, 1993). Thus, canopy interception, throughfall and stemflow all contribute to the rain water fractions that ultimately reach the forest floor (Návar *et al.,* 1999; Toba and Ohta, 2005; Krämer and Hölscher, 2009). In the Tamaulipan thorn scrub community in northeastern Mexico, net rainfall (water that reaches the ground) consisted of 78% throughfall, 3% stemflow and 19% interception of gross precipitation (Návar *et al.,* 1999). A study by Cantú-Silva and González-Rodríguez (2001) showed that canopy interception was higher in mixed (23%) than in monospecific stands of *Pinus pseudostrobus* Lindl. (19.2%) and *Quercus* spp. (13.2%) and that stemflow was lower in mixed (0.03%) than in monospecific stands (0.60 % and 50% for pine and oak, respectively).

In addition to species characteristics, tree stand composition by one or more species may also influence hydrological processes (Cantú-Silva and González-Rodríguez, 2001; Carlyle-Moses, 2004). For instance, mixtures of coniferous and deciduous species may increase rain interception compared to monospecific stands (Cantú-Silva and González-Rodríguez, 2001). Litter on forest floor absorbs and stores water thereby modifying infiltration and runoff. Thus, tree species abundance, litter quantity and quality, and litter water holding capacity (the maximal amount of water litter is able to retain) differentially influences important hydrological processes (evaporation, runoff and infiltration) in forest ecosystems (Zhuowen *et al.,* 2006; Mingzhong *et al.,* 2009). According to Zhuowen *et al.* (2006) litter water holding capacity is higher in coniferous forests, intermediate in mixed coniferous-broadleaved forests and lowest in broadleaved forests, and this depends also on the degree to which litter is decomposed.

With respect to rainfall characteristics, timing, frequency and intensity of rainfall are critical determinants of the size of different water fluxes (Toba and Ohta, 2005; Krämer and Hölscher, 2009). In temperate forests of northeastern Mexico, stemflow occurred only after rainfall events greater than 4 mm (Cantú-Silva and González-Rodríguez, 2001). In semiarid regions, 47% of total annual precipitation corresponds to rainfall events ≤ 5 mm and 2-23% to events larger than > 30 mm (Loik *et al*., 2004*).* Thus, global change factors affecting climate or species composition could potentially determine the quantity and redistribution of rainwater, and thereby alter water availability for plant growth, plant-plant interactions and ecosystem function (Mbano *et al.,* 2009). Little is known as to how species and tree stand characteristics and rainfall patterns influence key hydrological processes in semiarid forest ecosystems in central-north Mexico.

Semiarid forests of central-north Mexico have been affected by diverse land use change types including timber and fuelwood extraction, pinyon harvesting, forest grazing and conversion to pastures (Lanner, 1981). These multiple impacts have induced shifts in the distribution and abundance of *Pinus cembroides* Zucc. (Mexican pinyon) and *Quercus potosina* Trel. (San Luis Potosi oak) the two dominant tree species that occur in patches of both pure and mixed stands (Pérez-Suárez *et al.,* 2009). Both species exhibit different leaf morphological traits: *Q. potosina* is a broadleaved deciduous species with concave leaves, while *P. cembroides* is an evergreen species with needle leaves with 3-4 year lifetime. Both species develop open canopies at low heights. Previous studies showed that conifers typically exhibit a higher rainfall interception than broadleaved species when growing in the same environment (Moreno *et al.,* 1993; Cantú-Silva and González-Rodríguez, 2001).

The aim of this study was to examine how tree species and forest stand characteristics of semi-arid pine-oak forests influence the fractionation and redistribution of precipitation water. Questions of this study included the following: (1) Do tree species differentially influence the size of throughfall, stemflow and runoff, when grown in monospecific and mixed stands? (2) How does the size of rainfall events influence these water fluxes?

## 1.2 Materials and Methods

### **1.2.1** Study site

The study was carried out in a sub-watershed nearby to the community “La Amapola” (101°08’-101°04’ W, 22°00’- 22°04’ N) (INEGI, 2002) in the Sierra San Miguelito, an uplifted plateau area in the southernmost part of the physiographic province of Mesa Central in central Mexico (Cardona, 2007). Elevations range between 2,100 and 2,800 meters above sea level. The landscape is characterized by abrupt and irregular topography dominated by slopes steeper than 30°. Parental material consists of igneous Rhyolitic rocks with poorly developed soils classified as Leptosols according to FAO’s classification system (Cardona, 2007). The forest floor is characterized by surface accumulation of moor humus, including fresh litter, partially decomposed litter, and relatively homogeneous humus. Overall, the depth of this organic layer is highly variable (0-20 cm) at small spatial scales (< 20 cm), because of abundant rock outcrops and deep pockets of litter accumulation between them.

The region is characterized by a temperate semiarid climate (García, 1988) with 8 months (from October to May) of dry season and 4 months of wet season (from June to September). Average annual precipitation in this region reaches 530 mm and average monthly temperatures range between -3 °C in winter (December-February) and almost 21°C in summer (June-August) (García, 1988; INEGI, 2002). The vegetation is characterized by semiarid pine-oak forests with *Pinus cembroides* Zucc. and *Quercus potosina* Trel. as the most abundant tree species, with intermingled *Pinus johannis* Rob Pass., other *Quercus* spp., *Yucca* spp. and *Dasylirion* spp. (Rzedowski, 1978). The understory includes species of the genera *Opuntia*, *Agave*, *Mammillaria* and *Euphorbia* (Robert, 1977; Rzedowski, 1978).

### **1.2.2** Monitoring design

Along a 2 km sub-watershed (Photo 1.1 A and B), four 10m x 10m plots of three forest stand types were selected including monospecific *P. cembroides* and *Q. potosina,* and mixed stands with both species. Stand characteristics such as tree density and stem diameter (cm) were measured in each plot at the beginning of the study.

After each rainfall event the following measurements were taken in each stand type. Stemflow (in liters per rainfall event; Photo1.2A and B) and surface runoff (in liter per $m^2$; Photo 1.2 C and D) were measured from June 2006 to October 2008; while throughfall (in liters per rainfall event; Photo 1.3) was measured from June 2007 to October 2008. Stand throughfall was collected in a gutter (2 m long x 0.1 m wide x 0.1m high) attached to the run-off construction 30 cm above the forest ground ,and then channeled to a 20 L-container positioned beneath the tree canopy. For stemflow, a plastic half-tube was attached to the tree trunks in a spiral-like manner and connected to a 4 L plastic container at the bottom of the tree. In plots of monospecific stands, stemflow was collected from one tree, while in plots of mixed stands stemflow was collected from one tree of each species. For surface runoff measurements, a stainless steel structure (3.0 m long x 1.0 m wide x 0.5 m high) built of metal sheets (3 mm thick) was inserted into the soil (10 cm deep), and sealed with concrete. Runoff structures were oriented parallel to the slope. An opening down-slope of the runoff structure was connected to a 200L container. For gross rainfall measurements, four standard rain gauges were installed in open treeless areas along the 12 plots. Following each rainfall event, the throughfall and stemflow containers were emptied and the volume measured. For the runoff plots, a yard-stick was inserted into the run-off collector and the humid height measured with a ruler. Volume runoff was then estimated considering the diameter of the container and the change in height between readings. After one week without rain events, the water table height was measured to account for evaporation losses.

To estimate canopy openness as an indirect indicator for rain interception, light transmittance was calculated as the photosynthetically active radiation (PAR; proportion of direct sunlight and skylight passing through the canopy; Pierce and Runing, 1988) passing through the leaf and branch canopy.

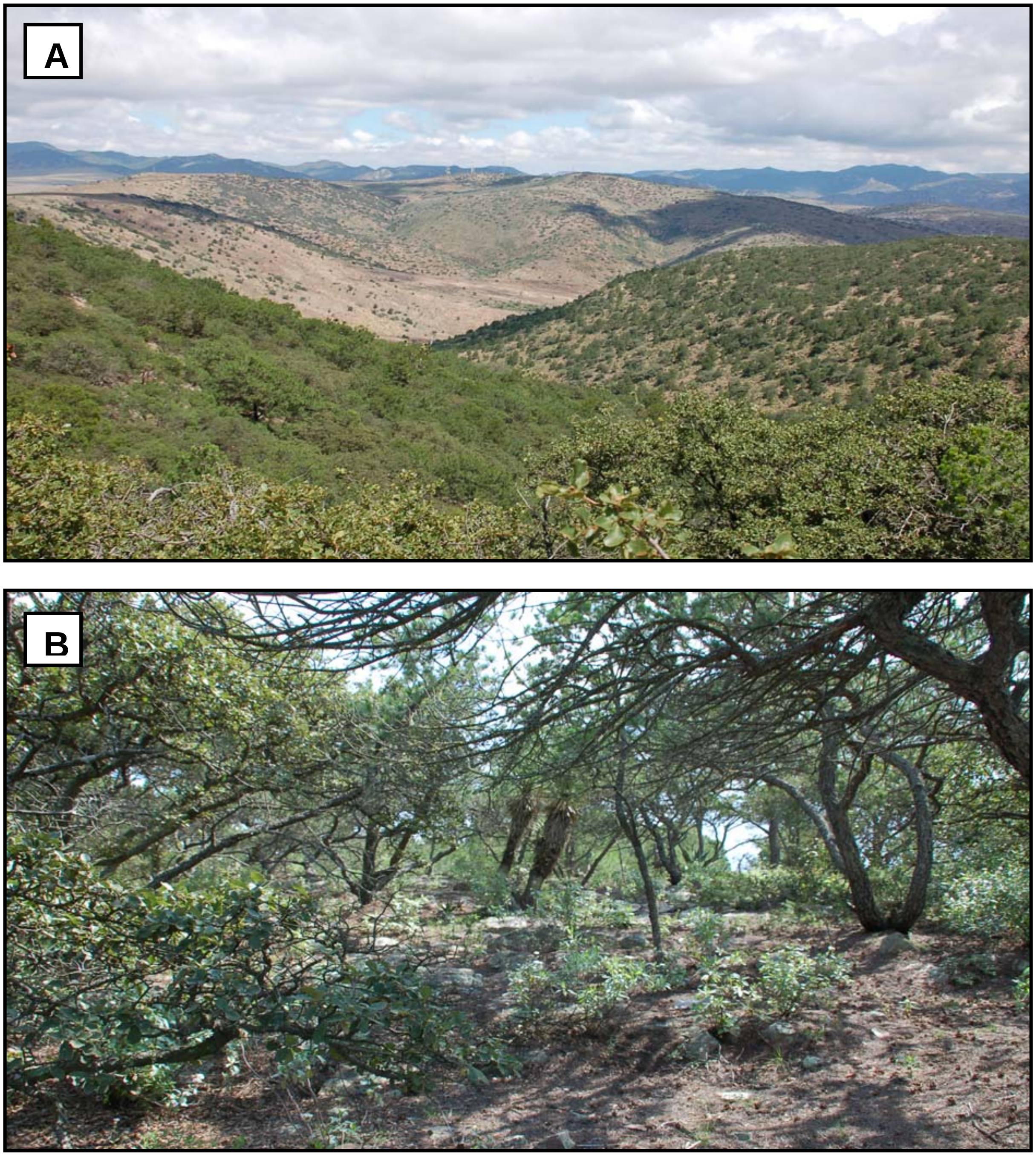


**Photo 1.1** Panoramic view of the sub-watershed and study site (left side of sub-water watershed; N-exposed slope) in the Sierra San Miguelito, San Luis Potosi, Mexico (A) and typical internal structure of pine-oak forests in this area (B).

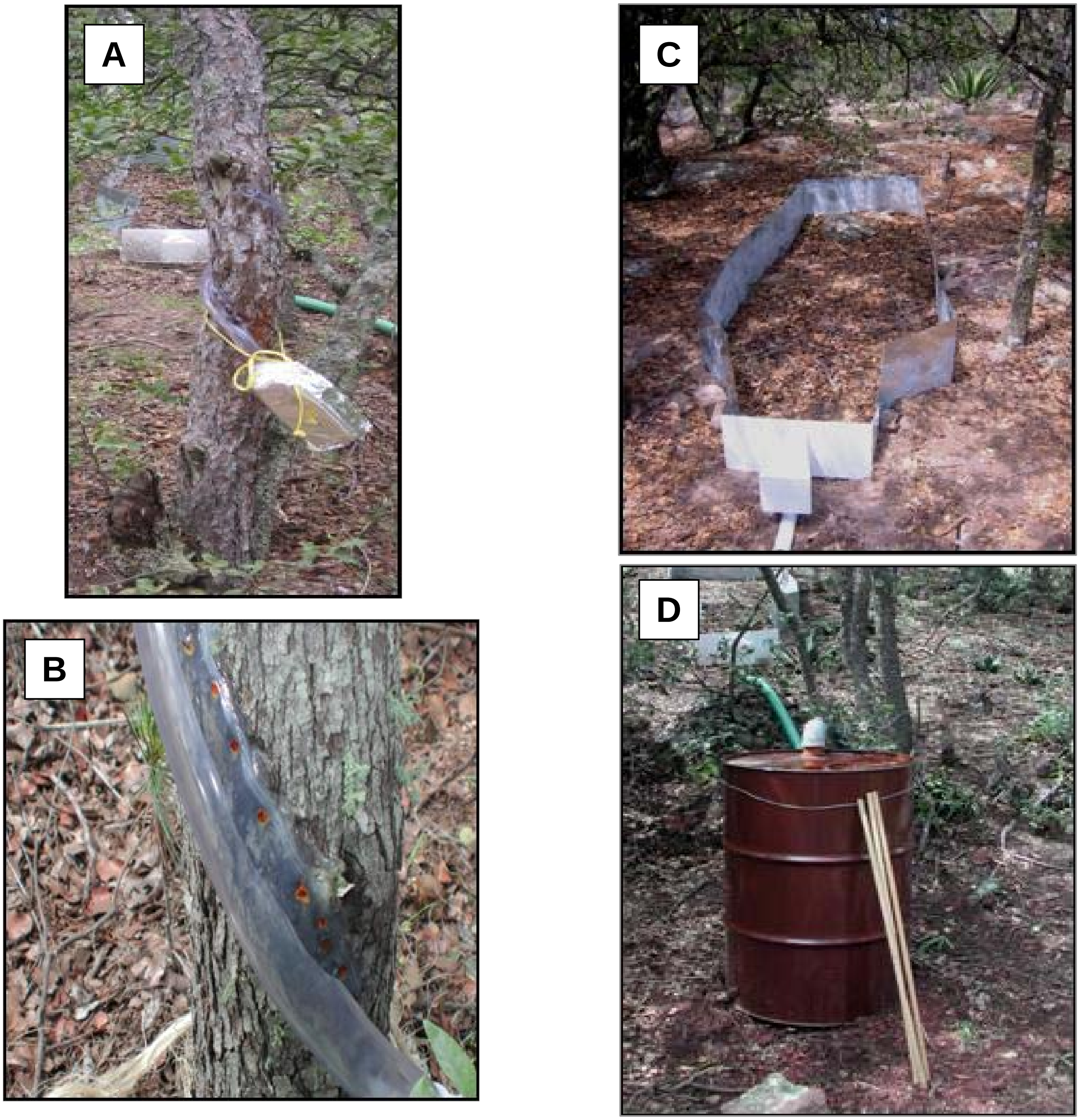


**Photo1.2** Experimental set-up for monitoring stemflow (A and B) and runoff (C and D)

Photosyntetically active radiation was measured with an integrating radiometer (Ceptometer, model SF-80, Decagon Devices, Inc., Pullman, Washington) on July 2009, when foliage of both species was fully developed and litterfall was very low (Chapter 2). Most of the rainfall events occurred while leaf foliage was fully developed. Radiation measurements were taken in linear "sweeps" consisting of 10 measurements at each transversal point of throughfall collectors and runoff plots (below the canopy; Ic).

**Photo1.3** Experimental set-up for monitoring throughfall

For determination of litter water content, two random samples of fresh litter were collected from a 20 cm x 20 cm x 1.0 cm in each plot in July 2007 after a rain event. The samples were put in separate sealed plastic bags and were kept in ice chests during transportation to the laboratory. In the laboratory of the Division of

Environmental Sciences, IPICYT, San Luis Potosi, Mexico, litter samples were immediately weighed and then dried at 70°C for 72 hr in a drying-oven until reaching constant mass. The gravimetric water content was determined for each sample.

### **1.2.3** Statistical analyses

For the analysis of throughfall, stemflow and runoff a repeated measures ANOVA was applied using the mixed procedure in the SAS System (Littell *et al.*, 1998). Canopy type (monospecific *P. cembroides,* and *Q. potosina* stands and mixed pine-oak stands) (between subjects) was the main factor and sampling date the repeated factor (within subjects). Comparisons of stem diameter, light transmittance, litter water content and litter quantity among canopies types were analyzed with one-way ANOVA followed by Tukey's all pairwise multiple comparisons test ($P \le 0.05$). Light transmittance was used as a covariable for the ANOVAs of throughfall and runoff. Stem diameter was used as a covariable for the ANOVA of stemflow. A type I regression analysis was applied to examine the relationship between rainfall events and the dasometric tree characteristics for stemflow, throughfall and run-off. Prior to analysis data were tested for normality using Shapiro-Wilk's test. All variables were normally distributed. For all variables (throughfall, stemflow and runoff monthly) least square means and one standard error are reported. All statistical analyses were performed using SAS System v. 9.1.3 for Windows (SAS System, Cary, NC 2002-2003).

## 1.3 Results

### **1.3.1** Stands characteristics

Regarding dasometric tree species characteristics, stem diameter did not exhibited significant differences (*P* = 0.1626; Annex 1-1) among canopy types (Table 1.1). Tree density was lower in monospecific stands of *P. cembroides* than in monospecific *Q. potosina* stands, while in mixed stands tree density was similar as in monospecific *Q. potosina* stands ($P \leq 0.05$). In addition, monospecific *Q. potosina* stands had 67% and 44% more light transmittance (*P* = 0.0001; Annex 1-2) than monospecific *P. cembroides* and mixed stands, respectively, implying larger canopy gaps. At the forest floor, litter quantity was significantly higher (*P* = 0.0024; Annex 1-3) in monospecific *Q. potosina* stands than in *P. cembroides* stands, while it was intermediate in mixed stands.

**Table 1.1** Characteristics of *P. cembroides*, *Q. potosina* in monospecific and mixed stands in Sierra San Miguelito, San Luis Potosi, Mexico.

| | **Monospecific** | | **Mixed** | |
|---|---|---|---|---|
| | ***Q. potosina*** | ***P. cembroides*** | ***Q. potosina*** | ***P. cembroides*** |
| Tree diameter at breast height (cm) | 11.8 (±0.40)$^{a}$ | 16.30 (±0.47)$^{a}$ | 11.3(±0.11)$^{a}$ | 14.1(±0.20)$^{a}$ |
| Density (trees/ha) | 2,325 (±193)$^{a}$ | 950 (±185)$^{b}$ | 2,000 (±492)$^{a}$ | |
| Canopy transmittance | 0.43 (±0.03)$^{a}$ | 0.19 (±0.02)$^{c}$ | 0.29 (±0.02)$^{b}$ | |
| Litter water content (%) | 61.85 (±2.18)$^{a}$ | 46.30 (±1.69)$^{c}$ | 52.38 (±0.88)$^{b}$ | |
| Litter quantity (g/m$^{2}$) | 124.34 (±10.60)$^{a}$ | 79.24 (±5.46)$^{b}$ | 87.30 (±8.35)$^{c}$ | |

Different letters in columns indicate significant differences among species and stand types at $P \leq 0.05$.

### **1.3.2** Monthly throughfall, stemflow and runoff

Annual rainfall during the study was 227, 404 and 425 mm for the years 2006, 2007 and 2008, respectively. However, for 2006 precipitation was only measured starting mid August.

The repeated measures ANOVA showed that stemflow differed significantly (*P* = 0.0006; Fig. 1.1b, Annex 1-5) among monospecific *Q. potosina,* monospecific *P. cembroides* and mixed stands. However, significant variation in throughfall and runoff was observed considering time and stand type (stand type x time main effect; *P* = 0.0028 and *P* = 0.0001, respectively; Annex 1-4). *Pinus cembroides* stands showed the lowest throughfall in the summer months with average precipitation between 10 and 20 mm (Fig. 1.1), whereas *Q. potosina* and mixed stands had similar throughfall. In contrast, *Q. potosina* exhibited the lowest runoff particularly at the peak of average monthly precipitation in the three observation years (Fig. 1.2). Throughfall (*P* = 0.4572; Fig. 1.1a) and runoff (*P* = 0.5304; Fig. 1.2) main effects were not statistically different among stand types.

Canopy transmittance did not influence throughfall and runoff (ANCOVA; *P* = 0.7217, *P* = 0.6180, respectively). Tree diameter significantly influenced stemflow (diameter; *P* = 0.00023; Annex 1-6). The above test of slope homogeneity showed that even though transmittance did not reduce throughfall fluxes variability in any stand type (*P* > 0.05)

Stem diameter was positively correlated with stemflow (*P* = 0.0001) in *Q. potosina* trees both in monospecific and mixed stands. In case of *P. cembroides,* the relationship was not significant. Light transmittance did not show a significant relationship with runoff in any stand type (Annex 1-7).

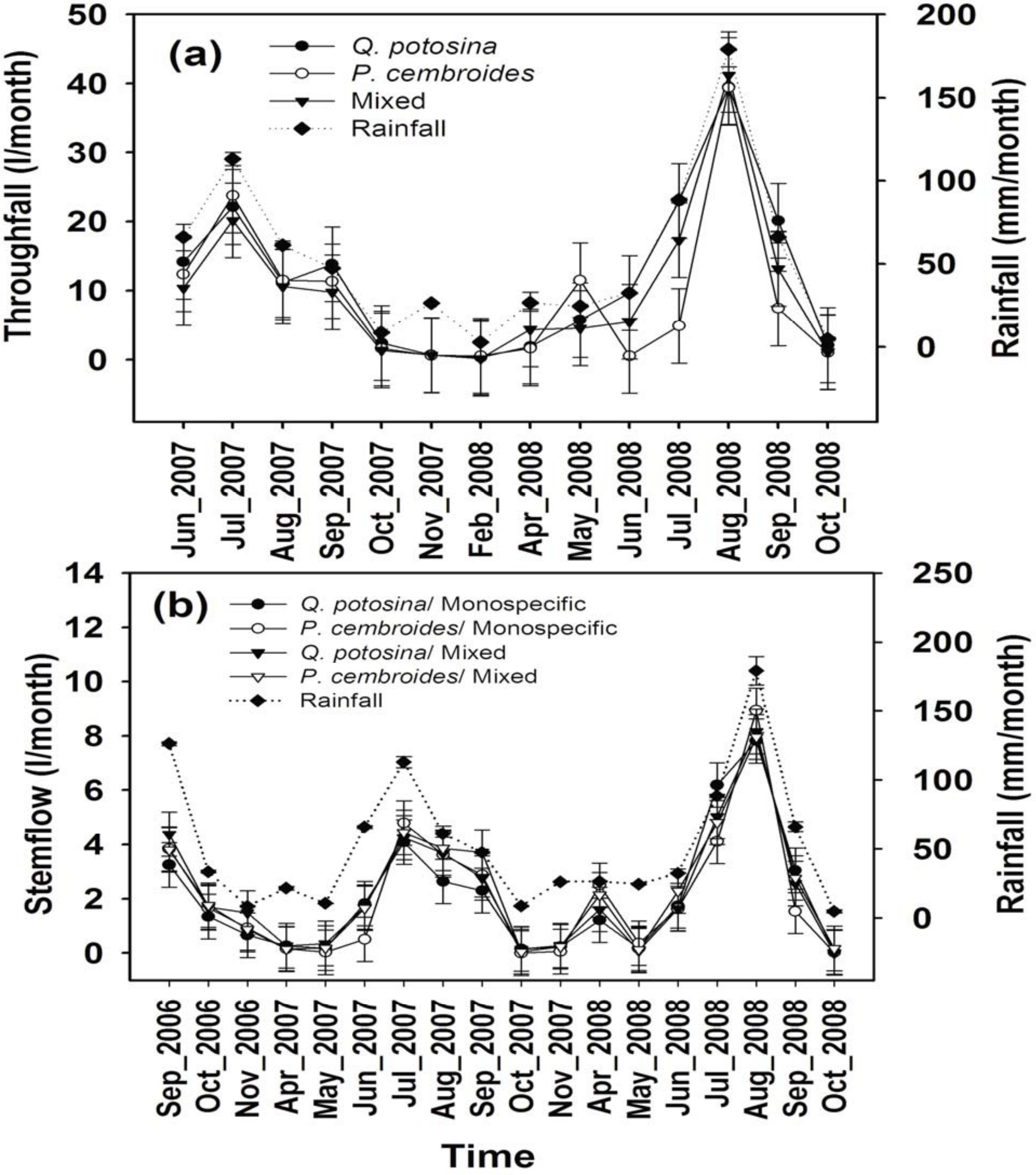


**Figure 1.1** Monthly variation of average throughfall (l/month; left axis; (a)) from June 2007 to October 2008; and monthly average stemflow (l/month; right axis; (b)) from September 2006 to October 2008. The "Y" axes on the right (both graphs) refer to monthly average precipitation (mm/month). Data represent monthly means for each stand type.

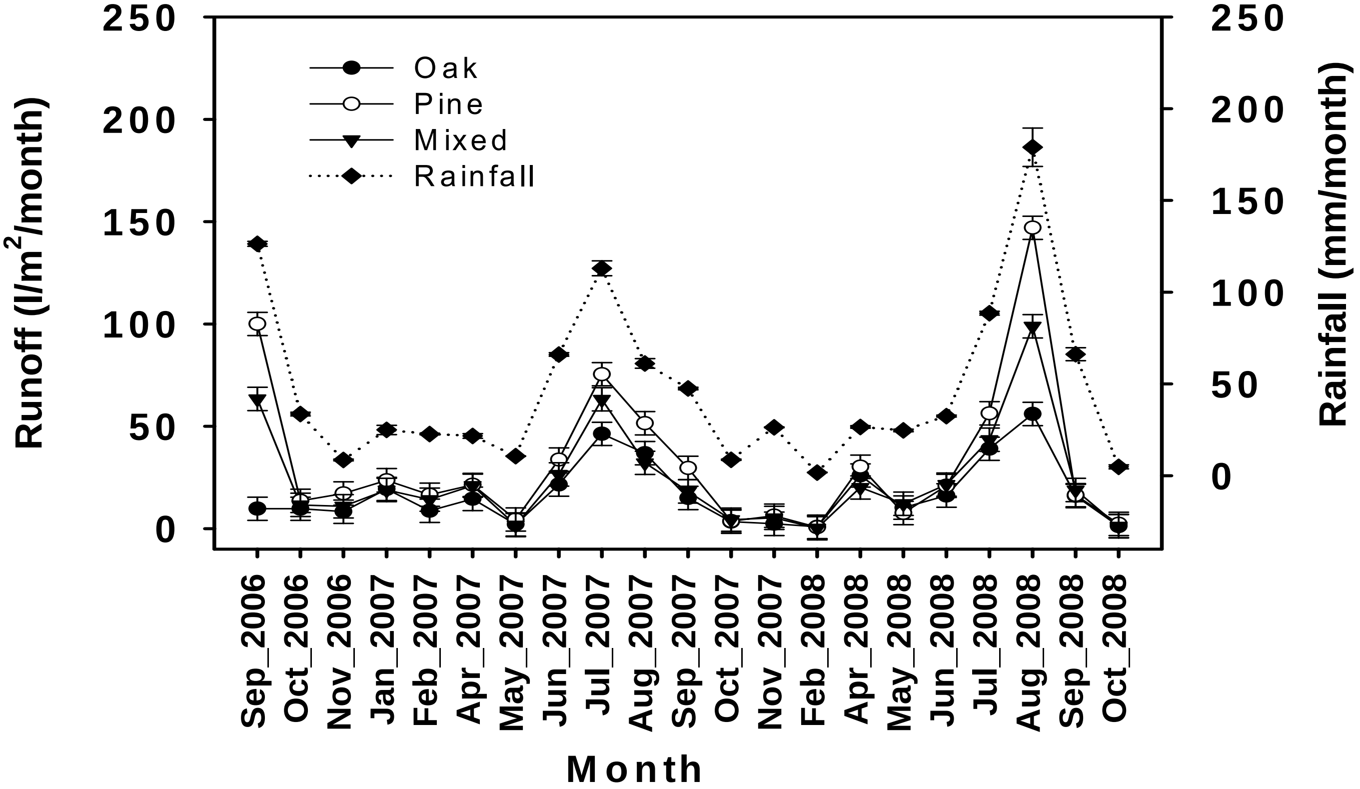


**Figure 1.2** Variation in runoff (l/m$^2$/month; left axis), and monthly precipitation (mm/month; right axis) between September 2006 and October 2008. Data represent monthly means for each stand type.

Overall, rainfall size at each event was positively correlated with throughfall (*P* = 0.0001; Fig. 1.1a; Annex 1-8), stemflow (Fig. 1.1b; Annex 1-9), and runoff (Fig. 1.2; Annex 1-10). The most remarkable increases in the three hydrological fractions were observed at the peak of the wet season. Runoff was greater in monospecific stands of *P. cembroides* than in mixed stands and in monospecific stands of *Q. potosin,* yet only at the peak of the wet season in the three years of monitoring.

## 1.4 Discussion

This research showed that tree species and stand characteristics play an important role controlling hydrological processes at the ecosystem level in semiarid forests in Central Mexico. Results from this study provide evidence that rainfall water gets differently distributed once it reaches the tree canopy depending on tree species and stand characteristics. Results from this study suggest that throughfall and runoff are controlled by canopy and litter characteristics. For instance the higher throughfall in *Q. potosina* stands compared to *P. cembroides* and mixed stands, likely resulted from a leaky canopy (highest light transmittance as a surrogate of canopy openness). Throughfall in monospecific stands of *Q. potosina* and *P. cembroides* was negatively correlated with light transmittance, while it was positively correlated in mixed stands suggesting that mixed stands had a structural arrangement of branches that most likely facilitated the collection and channeling (like a funnel effect) of more water regardless of the gaps in the canopy. *Pinus cembroides* showed a more stable canopy structure due to its evergreeness that includes leaf-lifespans of 3-5 years. In contrast, *Q. potosina* with deciduous leaves contributes to a greater canopy dynamics, as it sheds most of its leaves in spring (March-April) during the driest period of the year. At the time of greatest leaf loss, new leaves start emerging so that the leaf-less period of *Q. potosina* is very short. Conifers and broadleaved trees differ in structure and architecture; the arrangement of needles around twigs and branches confers a clumped structure of the canopy. Also, branches in tree crowns usually exhibit denser groupings than in broadleaved trees (Smolander, 2006). Since leaf area in the canopy is negatively correlated with light transmittance and light interception (Vose *et al.,* 1990; Pypker *et al.,* 2005), the canopy resembles a biological watershed. Typically, coniferous species exhibit higher rainfall interception than broadleaved trees when grown under similar environmental conditions (Moreno *et al.,* 1993; Cantú-Silva and González-Rodríguez, 2001). Close correlation between throughfall (Fig. 4a) and light transmittance in this study suggest that canopy structure was the principal control of the size of throughfall. In a similar study, Cantú-Silva and González-Rodríguez (2001) showed that rain interception was higher in mixed *P. ponderosa*-

*Quercus* spp. (23%) stands than in monospecific stands of *P. ponderosa* (19.2%) and *Quercus* spp. (13.2%); they did no present data on throughfall. One would have expected throughfall to be highest in *Quercus* spp. where interception was lowest.

In monospecific *P. cembroides* stands, runoff showed a positive relationship with transmittance, i.e. more runoff water was recorded in open canopies (high transmittance). This mechanism was not observed in *Q. potosina,* even though these stands showed greater light transmittance (canopy openness). The different patterns could be a result of the effect of litter water absorption and retention, which was higher for *Q. potosina* litter than for *P. cembroides* litter influencing runoff and infiltration. Thus, although *Q. potosina* canopies enhanced throughfall, litter packing and texture reduced runoff, contrary to canopy and litter characteristics of *P. cembroides* stands. In mixed stands, the redistribution and size of fluxes was different from that of monospecific stands. According to Yu *et al.* (2008), at semiarid sites vegetation growth may depend not only on the amount of vertical rainfall but also on the amount of water redistribution by surface runoff, which in turn depends greatly on vegetation features and patterns.

Runoff, in addition was controlled to a large extent by litter water absorption and retention. In this study, litter water content was used as an indicator of litter water storage capacity (Table 1). The lower runoff in monospecific stands of *Q. potosina* seemed to have been associated in part with a 25% greater capacity of oak litter to store water compared to litter of monospecific *P. cembroides* stands. Additionally, *Q. potosina* produced more litterfall (Table 1) than *P. cembroides,* which contributes to a greater water storage potential of oak litter compared to pine litter (Pérez-Suárez *et al.,* 2009). These findings show that in this semiarid forest ecosystem, litter cover is an important hydrological component in controlling both water and energy transfer between the sub-canopy atmosphere and the soil.

Stem diameter greatly influenced the size of stemflow in the different stand types, especially in *Q. potosina* trees. For *P. cembroides*, no significant relationship was apparent. It is important to consider also factors such as bark roughness, as it may greatly influence water storage capacity of stems, besides the position of structural elements that influence stemflow (Návar, 1993; Návar *et al.,* 1999). At rainfall events less than 4.6 mm, no stemflow was recorded for both species. A study by Cantú-Silva and González-Rodríguez (2001) in northeastern Mexico showed that in a temperate forest, stemflow of *P. pseudostrobus* and *Quercus spp.* trees did not occur at rainfall events smaller than 4mm.

The variability in rainfall events during the study period had an important influence on throughfall, stemflow and runoff fluxes (Fig. 1); so rainfall events smaller than 1.4 mm did no trigger throughfall in any of the stand types. According to Owens *et al.* (2006), this response is not surprising, since a large portion of small rainfall events is intercepted by the canopy and never reaches the ground surface. Rainfall events triggering runoff were larger than 3 mm. Therefore, several meteorological factors may affect water fluxes in a forest stand that include rainfall intensity, rainfall amount, rainfall duration, and direction of storm movement.

## 1.5 Conclusions

This research showed that tree species and stand characteristics play an important role in controlling hydrological processes at the ecosystem level in semiarid forests in Central Mexico. Results from this study provide evidence that rainfall is unevenly distributed once it reaches the tree canopy and forest floor depending on the functional matrix of species presents in a stand. Thus, form, stem diameter, spatial arrangement of leaves and branches, life form and spatiotemporal changes in the canopy cover and litter cover contribute to a functional matrix of traits that influence the redistribution of rainfall by throughfall, stemflow and runoff. Each species could be enhancing different hydrological processes when co-occurring with other species. Therefore, ecohydrological studies are important for our understanding of the effect of specific-species characteristics on the water cycle within forest ecosystems, mainly in water limiting ecosystems.

### 1.6 References

Cantú-Silva, I., and González-Rodríguez, H. (2001). Interception loss, throughfall and stemflow chemistry in pine and oak forests in northeastern Mexico. *Tree Physiol.* **21**, 1009-1013.

Cardona, B.A. (2007). Hidrogeoquímica de sistemas de flujo, regional, intermedio y local resultado del marco geológico en la mesa central: reacciones, procesos y contaminación. Tesis doctorado, UNAM, Instituto de Geofísica, México, DF, 238p.

Carlyle-Moses, D.E., Flores, J.S., and Price, A.G. (2004). Throughfall and throughfall spatial variability in Madrean oak forest communities of northeastern Mexico. *J. Hydrol.* **297,** 124-135.

Deguchi, A., Hattori, S., and Park, H-T. (2005). The influence of seasonal changes in canopy structure on interception loss: Application of the revised Gash model. *J. Hydrol.* **318**, 1-4.

García, E. (1988). Modificaciones al sistema de clasificación climática de Köppen para adaptarlo a las condiciones de la República Mexicana. Instituto de Geografía, UNAM, México.

INEGI. (2002). Síntesis de Información Geográfica del Estado de San Luis Potosí. Instituto Nacional de Estadística, Geografía e Informática, México.

Krämer, I. and Hölscher, D. (2009). Rainfall partitioning along a tree diversity gradient in a deciduous old-growth forest in Central Germany. *Echohydrol.* **2**, 102-114.

Lanner, R.M. 1981. The piñon pine. A natural and cultural history. Ronald M. Lanner. University of Nevada Press. United States of America.

Levia, Jr, D.F. and Frost, E.E. (2003). A review and evaluation of stemflow literature in the hydrologic and biogeochemical cycles of forested and agricultural ecosystems. *J. Hydrol.* **274,** 1-29.

Littell, R.C., Henry, P.R., and Ammerman, C.B. (1998). Statistical Analysis of Repeated Measures Data Using SAS Procedures. *J. Anim. Sci.* **76,** 1216-1231.

Loik, M.E., Breshears, D.D., Lauenroth, W.K., Belnap, J. (2004). A multiscale perspective of water pulses in dryland ecosystems: climatology and ecohydrology of the western USA. *Oecologia.* **141**, 254–268.

Mbano, D., Chinseu, J., Ngongondo, C., Sambo, E., Mul, M. (2009). Impacts of rainfall and forest cover change on runoff in small catchments: a case study of Mulunguzi and Namadzi catchment areas in southern Malawi. *Malawi J. Sci. & Technol.* **9,** 11-17.

Mingzhong, Z., Hongye, Z., Jie, J., Liangtao, S., and Yucang, S. (2009). Grass litter decomposition rate and water-holding capacity in dry-hot Valley of Jinshajiang River. *J. Nat. Sci.* **14**, 92-96.

Moreno, G., Gallardo, J.F. and Ingelmo, F. (1993). Effects on rainfall gradient on tree water consumption and soil fertility on *Quercus pyrenaica* forest in the Sierra de Gata (Spain*). Acta Geol. Hisp*. **29**, 119-129.

Návar, J. (1993). The causes of stemflow variation in three semi-arid growing species of northeastern Mexico. *J. Hydrol.* **145,** 175-190.

Návar, J., Charles, F., Jurado, E. 1999. Spatial variations of interception loss components by Tamaulipan thornscrub in northeastern Mexico. *For. Ecol. Manage.,* **124**, 231-239.

Owens, M.K., Lyons, R.K., and Alejandro, C.J. (2006). Rainfall portioning within semiarid juniper communities: effects of event size and canopy cover. *Hydrol. Proc.*. **20**, 3179-3189.

Pérez-Suárez, M., Arredondo, M.T., Huber-Sannwald, E., and Vargas-Hernández, J.J. (2009). Production and quality of senesced and green litterfall in a pine–oak forest in central-northwest Mexico. *Forest. Ecol. Manage. In press*

Pierce, L.L., and Running, S.W. (1988). Rapid estimation of coniferous forest leaf areas index using a portable integrating radiometer. *Ecology* **69**, 1762-1767.

Pypker, T.G., Bond, B.J., Link, T.E., Marks, D., and Unsworth, M.H. (2005). The importance of canopy structure in controlling the interception loss of rainfall: examples from a young and an old-growth Douglas-fir forest. *Agric. For. Meteor.* **130**, 113-129.

Robert, M.F. (1977). Notas sobre el estudio ecológico y fitogeográfico de los bosques de *Pinus cembroides*, Zucc., en México. *Ciencia Forestal* **10**, 49-58.

Rzedowski, J. (1978). Vegetación de México. Limusa. México.

SAS Institute Inc., 2002-2003. SAS user's guide, Version 9.1.3. SAS Institute, Inc., Cary, NC., USA.

Smolander, S. (2006). Radiative transfer, interception and scattering in coniferous forests: models and applications for production ecology and remote sensing University of Helsinki Academic dissertation The Finnish Society of Forest Science Unioninkatu, Helsinki, Finland.

Spies, T.A. (1998). Forest structure: a key to the ecosystem. *Nor. Sci*. **72**, 34-39.

Toba, T., and Ohta, T. (2005). An observational study of the factors that influence interception loss in boreal and temperate forests. *J. Hydrol.* **313**, 208-220.

Vose, J.M. and W.T. Swank. (1990). Assessing seasonal leaf area dynamics and vertical leaf area distribution in eastern white pine (Pinus strobus L.) with a portable light meter. *Tree Physiol.* **7**, 125-134.

Yu, M., Gao, Q., Epstein, H.E., and Zhang, X. 2008. An ecohydrological analysis for optimal use of redistribution water among vegetation parches. *Ecol. Appl.* **18**, 1679-1688.

Zhuowen, Z., Yusheng, C., Zhiyong, Z., Hongxia, C., Yunfei, L, Dongyun, W., Juanjuan, S.. (2006). Water-holding characteristics of litter in different forest at the Lianxiahe. *Front. For. China*. **4**, 413-418.

# CHAPTER 2

## Production and quality of senesced and green litterfall in a pine-oak forest in central-northern Mexico

### Summary

Litterfall is an important ecological process in forest ecosystems, influencing the transfer of organic matter and nutrients from vegetation to the soil. The production of different litterfall fractions as well as nutrient content and nutrient inputs by senesced and green leaf-litter were examined in a semiarid forest from central-northern Mexico. One year monthly litter sampling was carried out in monospecific and mixed stands of *Quercus potosina* and *Pinus cembroides*. Litterfall displayed a marked bimodal pattern with the largest annual amount (5,993 ± 655 kg/ha/yr) recorded in mixed stands, followed by *Q. potosina* (4,869 ± 510 kg/ha/yr), and *P. cembroides* (3,023 ± 337 kg/ha/yr). Leaves constituted the largest fraction of total litterfall reaching almost 60%, while small branches contributed with 20-30%. Overall, N content in leaf-litter was higher while lignin content was significantly lower for *Q. potosina* than for *P. cembroides*. Thus, greater litter quality together with higher litter production caused the largest C, N and P inputs to forest soils to occur in monospecific *Q. potosina* stands. Green leaf fall displayed significantly lower lignin:N and C:N ratios in *Q. potosina* than *P. cembroides* suggesting faster decomposition and nutrient return rates by the former. Although only two green leaf fall events were recorded, they accounted for 18% and 11% of the total N and P input, respectively, from leaf-litter during the study period. Apart from the large spatio-temporal heterogeneity introduced by differences in litter quantity and quality of evergreen, deciduous and mixed stands, green litterfall appears to represent a much more important mechanism of nutrient input to semiarid forest ecosystems than previously considered.

**Key words:** semiarid forest, green leaf-litter, spatial heterogeneity, litter production, *Pinus cembroides*, *Quercus potosina*

## 2.1 Introduction

Litterfall links biomass production and decomposition and therefore is a fundamental process in nutrient cycling in forest ecosystems (Meentemeyer *et al.,* 1982). Litterfall consists of leaves, twigs, flowers, inflorescences, fruits and other plant structures; with leaves making up most of the annual litter production and nutrient input on forest floors (Meentemeyer *et al.,* 1982; Pausas, 1997; Arunachalam *et al.,* 1998). Factors contributing to differences in litter productivity and quality include annual precipitation, annual minimum and maximum temperature (Berg and Meentemeyer, 2001; Liu *et al*., 2004; Caritat *et al.,* 2006), soil moisture (Vitousek, 1984; Roig *et al.,* 2005), soil fertility (Sariyildiz and Anderson, 2005), altitude (Röderstein *et al.,* 2005), and tree species composition (Pausas, 1997).

At regional scales, it has been established that mean annual precipitation received by tropical, subtropical and temperate forest ecosystems has a tighter control on litterfall of broadleaf than of coniferous species, although the opposite was reported for boreal forest ecosystems (Liu *et al.,* 2004). At short temporal scales (e.g. months), the influence of precipitation on litter production is not clear, however it seems to be seasonal and to interact closely with soil moisture differences associated with topography. For instance, in water-limited ecosystems litterfall may exhibit pronounced lag effects with intense leaf shedding after the rainy season or with the initiation of soil drying (Martínez-Yrízar and Sarukhán, 1990; Pavón *et al.,* 2005). Additionally, natural disturbances such as pests extreme droughts, heavy winds, hail and intense rainfall events may cause green leaf fall and/or enhance the rate of litterfall of senescent leaves (Meentemeyer *et al.,* 1982; Caritat *et al.,* 2006). Green leaf fall has been shown to contain up to 1.5 times more N and up to three times more P than senesced leaves (Lodge *et al.,* 1991; Lin *et al.,* 2003; Sariyildiz and Anderson, 2005). Since green leaves have significantly lower C:N and lignin:N ratios than senesced leaves (Fonte and Showalter, 2004), green leaf-fall is expected to decompose more rapidly and thereby considerably enhance nutrient cycling in forest ecosystems (Melillo *et al.,* 1982; Lodge *et al.,* 1991; Ostertag *et al.,* 2003; Sariyildiz and Anderson, 2005).

Extreme wind and/or hail events and associated green leaf fall occur frequently in semiarid regions (Holmgren *et al.,* 2006), probably playing an important, yet rarely documented role in nutrient cycling of semiarid forest ecosystems.

*Pinus cembroides* Zucc. (Mexican pinyon) and *Quercus potosina* Trel. (San Luis Potosi oak) are the two dominant tree species in the semiarid pine-oak forest ecosystem in central-northern Mexico (Ramamoorthy *et al.,* 1993). *Quercus potosina* and *P. cembroides* occur either in patches of pure stands or in mixtures; *Q. potosina* grows generally on more fertile sites than *P. cembroides* (Rzedowski, 1978). *Quercus potosina* has deciduous leaves, which are shed in a major shedding event, while *P. cembroides* has 3-4-year old leaves, whose oldest cohorts are usually shed in episodic shedding events (Zavala and García, 1991). Considering differences in leaf lifespan between deciduous and evergreen species and the temporal shedding of leaves of the two tree life forms, one expects a higher nutrient input through litterfall by *Q. potosina* than by *P. cembroides*. Particularly for the semiarid forests from central-northern Mexico, little is known about the spatial and temporal dynamics of nutrient return through leaf-litter and the degree to which heavy rainfall, hail or extreme wind events may contribute to green leaf-litter and nutrient input.

Monthly production and quality of litterfall of senesced and green leaves were monitored in three distinctive stands of the semiarid forest ecosystem in central Mexico including mixed and pure stands of *Q. potosina* and *P. cembroides*. We hypothesized that (i) annual total litter production is higher in *Q. potosina* than *P. cembroides* stands and intermediate in mixed stands; (ii) monthly leaf-litter fall in *Q. potosina* and mixed stands exhibit a unimodal distribution compared to episodic patterns in *P. cembroides* stands, (iii) annual total leaf-litter N and P input is higher in *Q. potosina* than *P. cembroides* stands; (iv) green leaf fall adds significantly to total leaf-litter C, N and P inputs to forest soils; and (v) monthly litterfall does not correlate linearly with precipitation events but is mostly driven by changes in soil water content.

## 2.2 Materials and methods

### **2.2.1** Study site

The study was carried out in a sub-watershed close to the community “La Amapola” (101°08’-101°04’ W, 22°00’-22°04’ N) (INEGI, 2002) in the Sierra San Miguelito, an uplifted plate area in the southernmost part of the physiographic province Mesa Central in central Mexico (Cardona, 2007) with elevations ranging between 2,100 and 2,800 m above sea level The region is characterized by a temperate semiarid climate (García, 1988) with 8 months (from October to May) dry season and 4 months (from June to September) Average annual precipitation in this region reaches 530 mm whereas average monthly temperatures range between -3°C in winter (December-February) to almost 21°C in summer (June-August) (García, 1988; INEGI, 2002).

The landscape is characterized by abrupt and irregular topography dominated by slopes steeper than 30°. Parental material consists of igneous rhyolitic rocks with poorly developed soils classified as Leptosols according to FAO’s classification system (Cardona, 2007) and rock outcrops on the surface. The vegetation is characterized by semiarid pine-oak forests with *P. cembroides* Zucc., and *Q. potosina* Trel., as the most abundant species, with intermixed *Pinus johannis* Rob Pass., other *Quercus* spp., *Yucca* spp. and *Dasylirion* spp. (Rzedowski, 1978). The dominant tree species occur in similar-sized monospecific and mixed tree stands forming a heterogeneous mosaic of evergreen, deciduous and mixed tree-stand patches (>100m$^2$) within the watersheds. Average tree height of *P. cembroides* is 4.2 ± 0.2m with average diameter of 17.2 ± 0.56 cm. Relative canopy cover varies between 30% and 60% (Hernández-Reyna and García, 1985). Average tree height of *Q. potosina* is 2.5 ± 0.06 m, with average diameters of 16.0 ± 0.3cm and relative cover varies between 10% and 80%. These single-species and mixed forest stands form single-layered canopies. According to dendrochronological assessments (Cetina *et al.,* 1985), the current average tree age is 81± 8 year. Average tree density per stand type was 2,325 ± 193 individuals/ha in monospecific stands of *Q. potosina* 950 ± 185 plants/ha in monospecific stands of *P. cembroides* and 2,000 ± 492 plants/ha in mixed stands.

The forest understory includes species of the genera *Opuntia*, *Agave*, *Mammillaria* and *Euphorbia* (Robert, 1977; Rzedowski, 1978). The forest floor is characterized by surface accumulations of mor humus, including three shallow layers: fresh litter, partially decomposed but recognizable litter,, and relatively homogeneous humus. Overall, the depth of this organic layer is highly variable (0-20cm) at small spatial scales (<20cm) because of abundant rock outcrops and deep pockets of litter accumulation between them.

In the study area, no stem-boring insects or other herbivores were observed that may have interfered with forest productivity and/or litterfall.

### **2.2.2** Sampling design of litterfall

Three forest stand types, including monospecific *Q. potosina*, monospecific *P. cembroides* and mixed pine-oak stands, were selected along the upper half of a 2km long sub-watershed with average slope inclination of 20-25°. The lower part of the slope from this study was excluded, as it was much steeper, with highly irregular topography and often rugged inaccessible terrain, where other factors than soil moisture and or precipitation may play a more important role in litter production. For each stand type, four 10m x 10m plots were randomly selected along the 2km transect. In the three tree-stand types, litter traps were randomly located beneath monospecific and mixed tree canopies, where branch and leaf densities were more or less similar. Since the focus of this study was comparing litterfall among different tree species and stand types rather than in determining total forest litterfall, stand types with rather homogeneous canopy densities; were selected however within these stand types (with average extent of 500-700m$^2$) litter traps were randomly located beneath canopies. Within each plot, three litter traps (40cm x 40cm x 5cm wooden frames with 1 mm mesh nylon screen attached to the bottom of the frame; Image 2.1) (12traps/stand type) were horizontally positioned >10cm above the soil surface allowing the mesh to hang slightly to avoid litter loss.

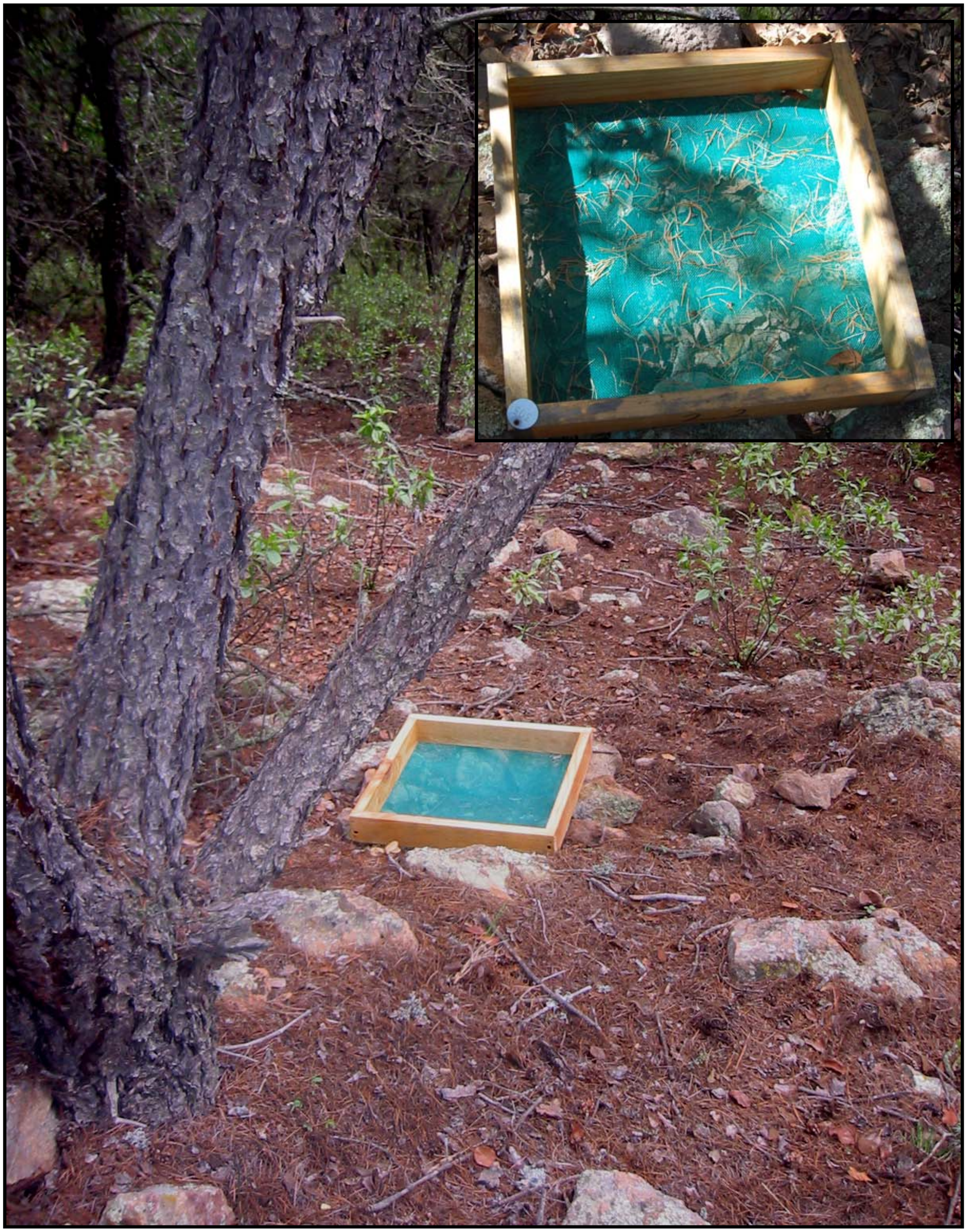


**Photo 2.1** Litter traps used to collect litterfall between September 2006 and August 2007

Between September 2006 and August 2007, each litter trap was emptied into separate paper bags at monthly intervals. In the laboratory of the Division of Environmental Sciences, IPICYT, San Luis Potosi, Mexico, litter trap material was separated into leaves, twigs (< 2cm in diameter), and miscellaneous fragments (i.e. fine plant residues, bark, pieces of insect bodies, feces, etc.). During the sampling period, two extreme precipitation events in June and August of 2007 caused green leaf fall. Following these events, which coincided with the monthly collection dates, all litter was collected from the traps and later separated into senesced and green litter. At these dates, green leaf-litter was collected additionally from one 1m x 1m quadrant in each plot to obtain sufficient material for chemical leaf analysis. Annual litter production of green litter was calculated from litter collected from the three traps per plot. For the chemical analysis of green leaf-litter, material from the three litter traps and the 1m$^2$ quadrant were pooled for each plot. To calculate annual nutrient input per unit area, the total area (1.16m$^2$) where green leaf-litter was collected was used as reference and converted to one hectare. For litter production, each litter fraction was dried to constant weight at 65 °C, and thereafter weighed. Monthly and annual total litter production was determined for pooled and individual litter fractions. Total litterfall (excluding green leaf-litter) and litter fractions are reported as monthly dry weight per unit area (kg/ha/month). Each precipitation event was recorded in the study area with four standard rain gauges to examine potential correlations between litterfall and precipitation events. At each plot, two soil psychrometers (PST-55, WESCOR) were inserted at 10cm depth to record soil water potential at biweekly intervals.

### **2.2.3** Chemical analysis

Chemical analyses were conducted for monthly litterfall of senesced and green leaves. Lignin content, total C, N and P concentration were determined for each sample of leaf-litter of *Q. potosina* and needle-litter of *P. cembroides*, from both monospecific and mixed stands. For lignin analysis, dried leaf-litter was ground with a Wiley Mill (1mm mesh screen*)* and a homogenized subsample was analyzed with a fiber analyzer (ANKOM) using the acid detergent fiber (ADF) method. In sequential extractions with $H_2SO_4$ and CTAB, the soluble components of lignin-cellulose were separated, followed by $H_2SO_4$ (72% by weight) digestion yielding lignin detergent acid as the remaining residue. Elemental N and C of litter material were determined with an elemental analyzer (COSTECH, ECS 4010) using the combustion method. Leaf-litter P concentration was determined with acid digestion and the phosphovanadomolybdate spectrophotometric method (Reuter *et al.,* 1986; Benton *et al.,* 1991) at the Soils Laboratory in Colegio de Postgraduados, Texcoco, Mexico. Since no litterfall occurred in November and December 2006, nutrient concentration data are reported for only 10 months. In case of lignin, data are reported for only eight months because leaf-litter samples of January and March did not contain sufficient material for lignin analysis. Leaf/needle-litter concentrations of C, N, and P, are reported in mg $g^{-1}$, and lignin content is reported in percentage. Leaf-litter C: N, lignin: N and N: P ratios were used as leaf-litter quality indices.

### **2.2.4** Statistical analysis

For the analyses of total litter production, individual litter fractions, and leaf-litter C, N, P, and lignin concentrations, and C: N, lignin: N and N: P ratios of senesced leaves repeated measures analysis of variance was applied using the GLM procedure in the SAS System (Littell *et al.,* 1998). For the analysis of total litterfall, two factors were considered including stand type (between subjects) and sampling date (within subjects). For the analysis considering senesced leaves, twigs, and miscellaneous litterfall, litter fraction nested within stand type was included as a third factor. Prior to analysis, data were tested for normality using Shapiro-Wilk's test; variables that did not meet normality criteria were log-transformed prior to analysis. For *post hoc* multiple mean comparisons, Tukey's test was applied with a minimum significance level of $P \leq 0.05$. For all variables, least square means and one standard error are reported; for monthly and annual total litter production back-transformed least square means and one standard error are reported (Sokal and Rohlf, 1994).

To compare total annual production and nutrient input between senesced and green leaf-litter (nutrient concentration multiplied by total leaf-litter biomass per unit area) by species in each stand type (monospecific *Q. potosina*, monospecific *P. cembroides*, mixed *Q. potosina* and mixed *P. cembroides)* a one-way ANOVA and for *post hoc* mean comparisons Tukey's test were applied (*P* <0.05).

For comparisons of litter production, nutrient input and litter quality indices between green and senesced leaves produced in the months of June and August, one-way ANOVAs were applied. Specifically, for litter production, the senesced and green leaves that accumulated in litter traps were used. For nutrient input the senesced litter from litter traps and the green litter of the trap and 1m x 1m quadrate were used. Subsequently, orthogonal contrasts were defined for the following predetermined comparisons between leaf-litter types for nutrient concentration and litter quality indices: (1) senesced *vs.* green leaves from *Q. potosina* in monospecific stands; (2) senesced *vs.* green leaves from *Q. potosina* in mixed stands; (3) green leaves from *Q. potosina* in monospecific *vs.* mixed stands; (4) senesced *vs.* green leaves from *P. cembroides* in monospecific stands; (5) senescent *vs*. green leaves from *P. cembroides* in mixed stands; and (6) green leaves from *P. cembroides* in monospecific *vs.* mixed stands. All statistical analyses were performed using SAS System v. 9.1.3 for Windows (SAS System, Cary, NC 2002-2003).

## 2.3 Results

### **2.3.1** Monthly and annual total litterfall

Litterfall (including all fractions) occurred throughout the year, except in November and December 2006 (Fig. 2.1a). Forest stand types (stand type main effect; $P \leq 0.0125$, Fig. 2.1a; Annex 2-1) exhibited greater litter production in monospecific *Q. potosina* and mixed stands than in monospecific *P. cembroides* stands. Overall, monthly litterfall showed high seasonal variation (time main effect; $P = 0.0001$) with a bimodal and significantly greater production in March/April and June (Fig. 2.1a) compared to all other months. There was no significant time by stand type interaction for annual total litter production ($P = 0.1672$). Mixed stands had the largest annual total litterfall (5,993 ± 655 kg/ha), followed by monospecific *Q. potosina* stands (4,869 ± 510 kg/ha) and *P. cembroides* stands (3,023 ± 337 kg/ha).

### **2.3.2.** Monthly and annual litterfall of different litter fractions

The three stand types differed significantly in the production of various litterfall fractions during the course of the study year (time by litterfall fraction nested within stand type interaction; $P = 0.0001$, Fig. 2.2; Annex 2-2). In months when litterfall occurred, always all litterfall fractions were present in the litter traps (Fig. 2.2). In monospecific *Q. potosina* and mixed stands, most leaf-litterfall occurred in March and April (Fig. 2.2a and c, respectively), and in monospecific *P. cembroides* stands in April (Fig. 2.2b). Leaf-litter quantity deposited in April did not differ among stand types. In April and June, more twig material was observed on forest floor in mixed rather than monospecific stands. It was in these two months when overall most non-leaf litterfall occurred. Trees in monospecific *Q. potosina* stands shed more of each litter fraction than trees in monospecific *P. cembroides* stands; leaf-litter was almost twice as high in monospecific *Q. potosina* stands than in monospecific *P. cembroides* stands (stand type main effect; $P = 0.0011$; Annex 2-2).

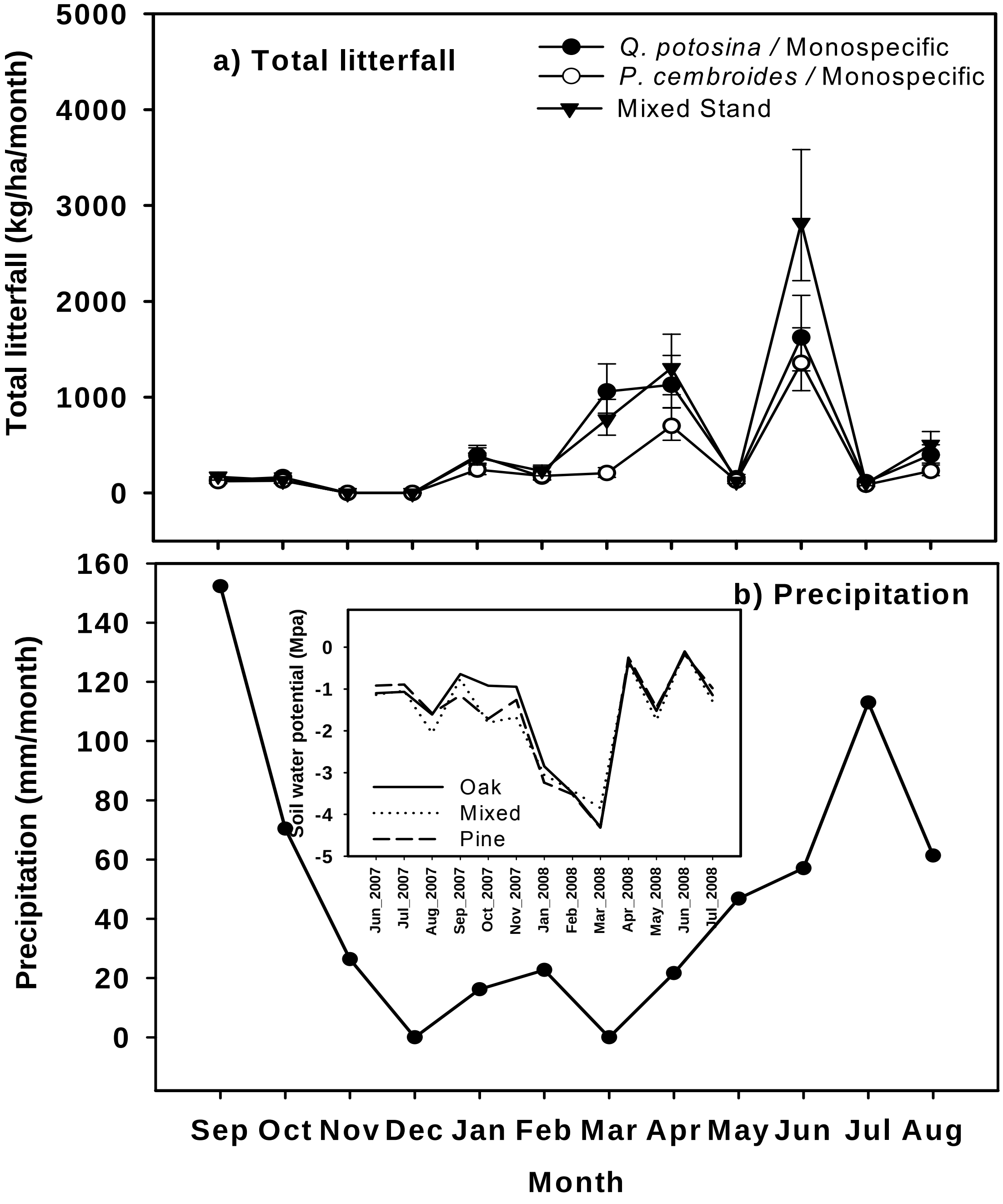


**Figure 2.1** (a) Monthly variation in total litterfall for different forest stand types between September 2006 and August 2007 (month by stand type interaction *P* = 0.1672). (b) Monthly precipitation in the study site between September 2006 and August 2007. Inset, soil water potential (MPa) recorded during the study at the experimental plots.

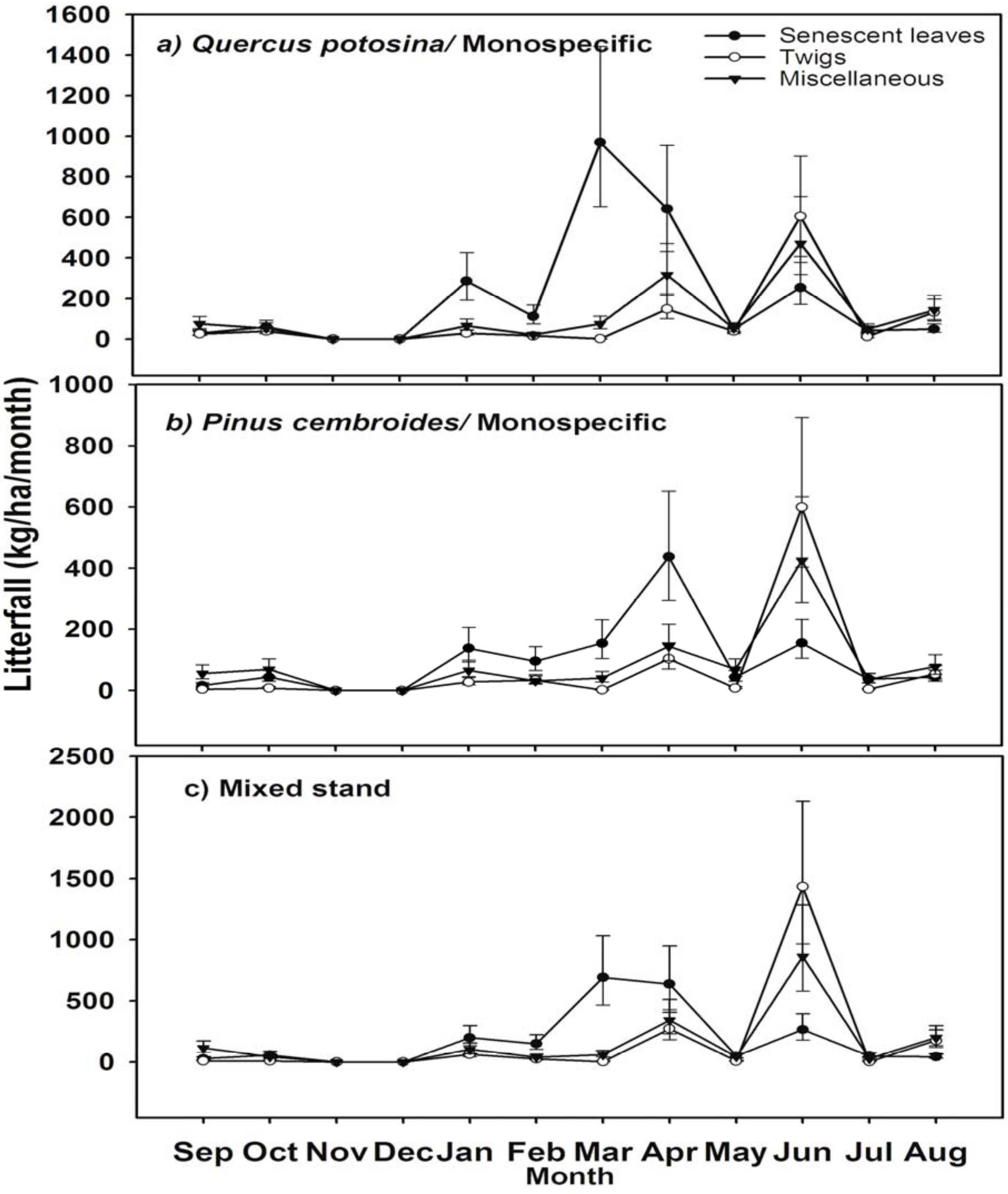


**Figure 2.2** Monthly variation in litterfall fractions between September 2006 and August 2007 for (a) monospecific *Quercus potosina*, (b) monospecific *Pinus cembroides,* and (c) mixed stands (month by litter fraction nested within stand type interaction*;* *P* = 0.0001).

The relative contribution of green leaf-litter to annual total leaf-litter was 10.5% and 13.3% for *Q. potosina* and *P. cembroides* in monospecific stands, and 12.0% and 10.2% for *Q. potosina* and *P. cembroides* in mixed stands, respectively (Table 2.1a, b). *Quercus potosina* in monospecific stands produced 70% more green leaf-litter than *P. cembroides* in mixed stands and 40% more than *P. cembroides* in monospecific stands and *Q. potosina* in mixed stands (Table 2.1b).

**Table 2.1** Annual total leaf-litter production and nutrient input (back-transformed data; dry mass, kg/ha/yr ± 1SE) of (a) senesced leaf-litter and (b) green leaf-litter of *Q. potosina* and *P. cembroides* in monospecific (mo) and mixed (mx) stands.

| **Species** | **Leaf-litter dry mass** | **C** | **N** | **P** |
|---|---|---|---|---|
| **(a) Senesced leaf-litter** | | | | |
| *Q. potosina* / mo | $2820 \pm 307^{a}$ | $1421 \pm 709^{a}$ | $31 \pm 13^{a}$ | $2.0 \pm 0.87^{a}$ |
| *P. cembroides* / mo | $1360 \pm 128^{b}$ | $599 \pm 48^{ab}$ | $20 \pm 4^{ab}$ | $1.8 \pm 0.22^{a}$ |
| *Q. potosina* / mx | $1497 \pm 161^{b}$ | $709 \pm 74^{ab}$ | $14 \pm 2^{b}$ | $1.2 \pm 0.44^{ab}$ |
| *P. cembroides* / mx | $930 \pm 87^{c}$ | $498 \pm 148^{b}$ | $6.5 \pm 1.6^{b}$ | $0.7 \pm 0.08^{b}$ |
| **(b) Green leaf-litter** | | | | |
| *Q. potosina* / mo | $332 \pm 61^{a}$ | $183 \pm 33^{a}$ | $4.1 \pm 0.9^{a}$ | $0.25 \pm 0.06^{a}$ |
| *P. cembroides* / mo | $197 \pm 16^{ab}$ | $101 \pm 9^{ab}$ | $2.6 \pm 0.3^{ab}$ | $0.13 \pm 0.02^{ab}$ |
| *Q. potosina* / mx | $209 \pm 19^{ab}$ | $111 \pm 18^{ab}$ | $2.0 \pm 0.3^{b}$ | $0.13 \pm 0.02^{ab}$ |
| *P. cembroides* / mx | $106 \pm 19^{b}$ | $57 \pm 9^{b}$ | $1.2 \pm 0.16^{b}$ | $0.08 \pm 0.00^{b}$ |

Different letters in columns indicate significant differences among species and stand types at a $P \leq 0.05$

### 2.3.3 Nutrient concentration and annual total nutrient input through leaf-litter

Overall, C and P concentrations of leaf-litter changed over time in all stand types (time main effect; $P = 0.0001$; Fig. 2.3a and c, respectively; Annex 2-3 and 2-5, respectively). Carbon and P concentrations of leaf-litter were significantly higher in September and October 2006 than during the rest of the study year. Nitrogen concentration of leaf-litter changed over time and differed among forest stands (interaction stand type x time; $P = 0.0001$; Fig. 2.3b; Annex 2-4). In September 2006, N concentration of leaf-litter for *Q. potosina* was up to 100% higher than that of *P. cembroides* both in monospecific and mixed stands. Still, N concentration of leaf-litter of *Q. potosina* in monospecific and mixed stands dropped gradually from 17-18.5mg/g to 7-8mg/g between September 2006 and April 2007. Nitrogen concentration remained higher in *Q. potosina* than in *P. cembroides* throughout the year with some overlap between April and July 2007. When comparing *P. cembroides* from monospecific and mixed stands, little variation in monthly N concentration of leaf-litter occurred except for a significant drop in April (from 8mg/g to 4.5mg/g) in mixed stands.

Annual total C input from leaf-litter in monospecific *Q. potosina* stands was almost three times higher than that in mixed *P. cembroides* stands (Table 2.1), with intermediate C inputs for monospecific *P. cembroides* and mixed *Q. potosina* stands. Annual total N input from leaf-litter of monospecific *Q. potosina* stands was two to three times higher than that of mixed *Q. potosina* and mixed *P. cembroides* stands, while intermediate N in monospecific *P. cembroides* stands (Table 2.1a). Annual P input from leaf-litter of *P. cembroides* trees was significantly higher in monospecific than in mixed stands, while for *Q. potosina* no differences were observed with respect to stand type (Table 2.1a).

Carbon and P input from green leaf-litter was three and four times higher, respectively, in monospecific *Q. potosina* stands than in mixed *P. cembroides* stands (Table 2.1b, $P < 0.05$). Nitrogen input from green leaf-litter was at least double in monospecific *Q. potosina* than in mixed *Q. potosina* and *P. cembroides* stands (Table 2.1b, $P < 0.05$). The relative contribution of C, N, and P by green leaves to the annual total input was 10.8% for C, 12.6% for N and 9.4% for P.

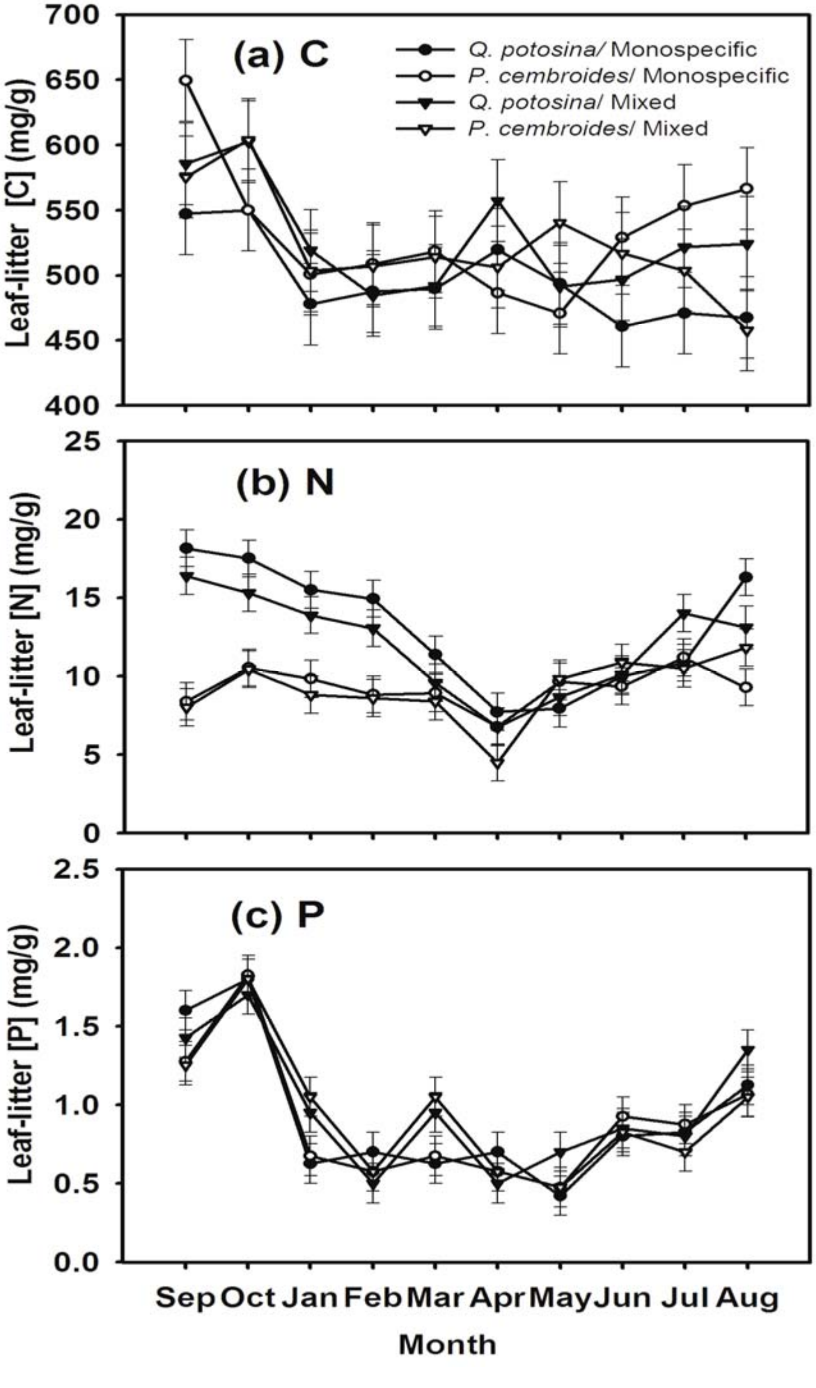


**Figure 2.3** Monthly variation in nutrient concentration of (a) carbon (C), (b) nitrogen (N), and (c) phosphorus (P) of leaf-litter between September 2006 and August 2007 for leaf litter in monospecific *Quercus potosina* and *Pinus cembroides* and mixed stands. Vertical bars are standard errors. Species by month interaction*;* (a) *P* = 0.7274, (b) *P* = 0.0001 and, (c) *P* = 0.2885.

**Table 2.2** Contrasts of predetermined mean comparisons between senesced and green leaf C, N, P concentration, lignin content and litter quality indices considering monospecific and mixed stands of *Q. potosina* and *P. cembroides.*

| | **Contrast** | **C (mg/g)** | **N (mg/g)** | **P (mg/g)** | **Lignin (%)** | **C:N** | **Lignin:N** | **N:P** |
|---|---|---|---|---|---|---|---|---|
| **1** | **MQ-S *vs.* MQ-G** | NS | NS | NS | 25.9 *vs.* 19.8* | NS | 22.5 *vs.* 14.1* | NS |
| **2** | **XQ-S *vs.* XQ-G** | NS | NS | NS | 24.6 *vs.* 21.2* | NS | NS | NS |
| **3** | **MQ-G *vs.* XQ-G** | NS | NS | NS | NS | NS | NS | NS |
| **4** | **MP-S *vs.* MP-G** | NS | NS | 1.04 *vs.* 0.08* | NS | 59.7 *vs.* 45.9* | NS | 9.6 *vs.* 15.3* |
| **5** | **XP-S *vs.* XP-G** | NS | NS | NS | NS | NS | NS | NS |
| **6** | **MP-G *vs.* XP-G** | NS | NS | NS | NS | NS | NS | NS |

Abbreviations refer to monospecific stands (M), mixed stands (X), senesced (S) and green leaves (G); *Quercus potosina* (Q), *Pinus cembroides* (P).

*Indicates a significant difference in mean comparisons at $P \leq 0.05$; *NS* indicates comparison is not significant at $P \leq 0.05$.

### **2.3.4** Leaf-litterfall quality

Lignin content of leaf-litter differed significantly between stand types and months (stand type x time interaction; *P* = 0.0001; Annex 2-3). Throughout the study year, lignin content of needle litterfall was 5-10% higher in *P. cembroides* than in *Q. potosina* both in monospecific and mixed stands (Fig. 2.4a). In both species, maximum lignin content was observed in October 2006 and July 2007 with values as high as 42% in *P. cembroides* and around 30% in *Q. potosina*. The lowest lignin content occurred between April and May 2007 with 32% and 22% for *P. cembroides* and *Q. potosina*, respectively.

For litter quality indices (C: N, N: P, and lignin: N ratios; Annex 2), significant differences were observed among stand type and months (both $P \leq 0.05$). The C: N and lignin: N ratios of leaf and needle litterfall showed an uni-modal pattern for all stand types with a pronounced peak in April but otherwise similarly low ratios throughout the rest of the monitoring year. The April peak of C:N and lignin:N ratios of leaf-litter for *P. cembroides* was higher in mixed than in monospecific stands, while these ratios were significantly lower leaf-litter in *Q. potosina* in monospecific and mixed stands. The N: P ratios of leaf and needle litterfall were lowest in September/October 2006 and April 2007. Overall, N: P ratios were higher in leaf-litter of *Q. potosina* than *P. cembroides* in both stand types.

### **2.3.5** Nutrient concentration and quality of senescent *vs*. green leaf-litter

In monospecific *Q. potosina* stands, N and P concentration and C: N and N: P ratios did not differ between senescent and green leaf-litterfall, however lignin content and the lignin:N ratio were significantly higher in senescent litter compared to green leaf fall (Table 2.2; contrast 1). For monospecific stands of *P. cembroides,* P, C: N ratio and N: P ratio differed significantly between senesced and green needle litter fall (Table 2.2; contrast 4) with less P but more N in green needle fall. For mixed stands in contrast, nutrient characteristics of litterfall types differed only in *Q. potosina*, with a significantly higher lignin concentration in senescent than green leaf-litter (Table 2.2; contrast 2).

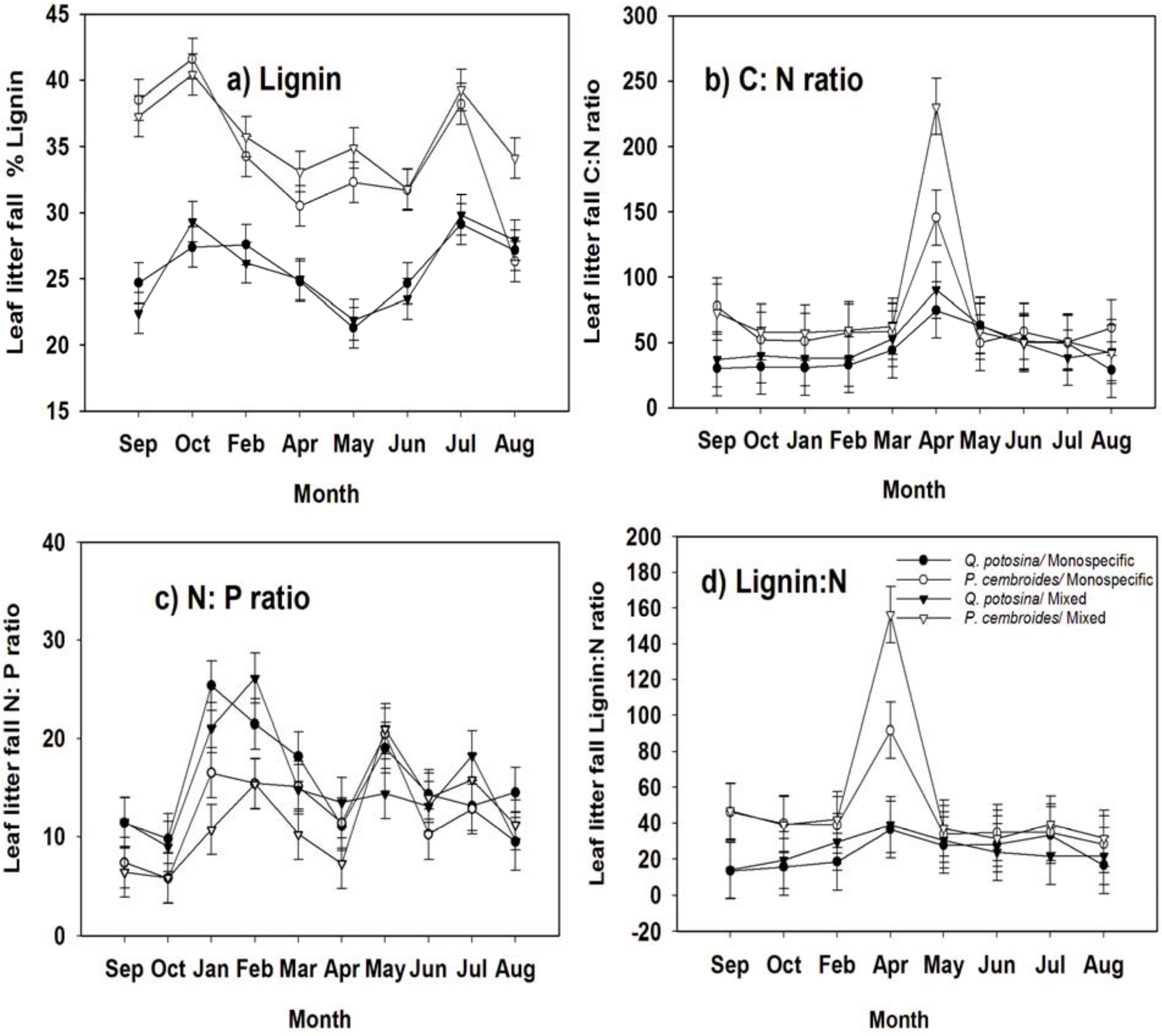


**Figure 2.4** Monthly variation in litter quality indices (a) lignin, (b) C: N ratio, (c) N: P ratio, and d) lignin: N ratio for pine and oak leaf-litter in monospecific *Quercus potosina*, monospecific *Pinus cembroides* and mixed stands between September 2006 and August 2007. Vertical bars are standard errors. Species by stand type by month interaction*; (*a) *P* =0.0001, (b) *P* =0.4204, (c) *P* =0.1368 and, (d) *P* =0.1923.

### **2.3.6** Correlation between precipitation and litterfall

Between July 2006 and June 2007, a total of 588mm of precipitation was recorded; 75% of the annual precipitation fell between June and October 2006 (Fig. 2.1b). Pearson correlation analysis between monthly litterfall and precipitation for monospecific *Q. potosina* and *P. cembroides* stands (r=-0.47, r=-0.44) and mixed *Q. potosina* and *P. cembroides* stands (r=-0.44, r=-0.32; n=12, *P* >0.05) did not show a significant correlation during the 12-months sampling period.

## 2.4 Discussion

In mixed evergreen-deciduous forest ecosystems, in addition to climatic controls nutrient cycling is influenced by both species-specific differences in chemical characteristics of leaf-litter (Hooper and Vitousek, 1997; Enright, 1999; Tang and Ohsawa, 2002) and differences in leaf life-span and associated leaf shedding patterns (Rentería *et al.,* 2005). All of these characteristics contribute to the spatial and temporal dynamics in nutrient input in semiarid forest ecosystems. Based on our study, the evergreen *P. cembroides* and deciduous *Q. potosina*, both slow-growing species, exhibited important differences in monthly leaf-litter production, litter quality and leaf life-span. These traits together with the patchy distribution of tree species in monospecific and mixed stands, contribute to a marked spatiotemporal pattern of nutrient input in semiarid forest ecosystems of central-northern Mexico.

Effects of insect herbivory on litter production were not detected at the study site, thus can be discarded as a potential interfering control of litter production. Overall, accuracy of litterfall estimates depends on the scheme of litter trap placement. In our study, placement of litter traps beneath mixed stands with overlapping canopies of pine and oak (mixed forest stand) may have introduced a certain bias regarding litter amount, however it was precisely one of our objectives to compare litter quantity and quality of overlapping mixed and single-layered monospecific tree stands.

### **2.4.1** Total litter production by stand type

As predicted, monospecific deciduous *Q. potosina* stands produced overall more litterfall than monospecific coniferous *P. cembroides* stands*.* Average tree density in our study plots (2,325 *Q. potosina,* 950 *P. cembroides* and 2,000 in mixed stands) corroborates these differences but did not help explain a greater litter production in mixed compared to monospecific *Q. potosina* stands. Greater litter production in mixed stands might have resulted from differences in canopy structure, in that mixed stands have double-layered canopies while monospecific stands have single-layered canopies (Binkley *et al.,* 1992). Tree canopies of mixed stands may overall occupy more volume per tree species than tree canopies of monospecific stands. Other factors accounting for this pattern may include species-specific canopy architectures, tree size-related canopy layering, or changes in the foliage: branch ratio (Dearden *et al.,* 2006).

The range of total litterfall observed in our study coincides with ranges reported for other similar ecosystems. For instance, the woodland ecosystems forming part of the Tamaulipan thornscrub in northeastern Mexico (a water-limited ecosystem) produced litterfall in the range of 4,619 to 7,171kg/ha/yr (González-Rodríguez *et al.,* 2007), whereas the dry tropical forest varies from 3,950 to 6,580kg/ha/yr (Martínez-Yrízar and Sarukhán, 1990). Given the close similarity in total litter production among semiarid oak-pine forest, the Mexican Tamaulipan thorn scrub and the Mexican dry tropical forest, it appears that the significantly higher mean annual precipitation in these forest and woodlands (805 and 790mm, respectively) compared to semiarid oak-pine forests (520mm) is not the only environmental factor controlling litter production in these seasonally dry ecosystems. Other factors such as soil depth, soil fertility, etc. may play equally important roles. In semiarid woodlands for instance, Schuster and collaborators (2005) reported an overall >20% decline in litter production under limited soil water and soil nutrient conditions and under the effects of insect herbivores. Liu *et al.* (2004) presented a global analysis of litterfall controlling factors in coniferous and broadleaf forests in Eurasia and they concluded that annual mean temperature plays a more important role in litterfall patterns than precipitation. While freezing temperatures do occasionally occur in these semiarid oak-pine forests in Mexico, winters were relatively mild in recent years and particularly during the study year.

### **2.4.2** Spatiotemporal variation in litter production

Contrary to our hypothesis, monthly litterfall followed a bimodal pattern as a consequence of both phenological and disturbance effects which in this study were expressed by two intense storms. Talking a closer look at the temporal distribution of litterfall of different litter fractions, it becomes apparent that it was mostly *Q. potosina* that contributed to the bimodal pattern both in monospecific and mixed stands, while litter input of *P. cembroides* was rather uni-modal as it occurred mainly in June (Fig. 2.1a). The first flush of litterfall in *Q. potosina* occurred in March/ April coinciding with two aspects: the end of the dry season (Fig 2.1b) and the peak of soil water deficit (Fig 2.1b, inset). The second flush occurred in June at the beginning of the wet season soon after the site had received the first large (17mm) rainfall event. Breaking and thrashing effects of moistened branches on smaller twigs and leaves might explain the second peak of deposition of twigs and miscellaneous (Fig. 1b). For *P. cembroides,* needle litter (Fig. 2.2b) was more pronounced in dry (January-April, Fig. 2.1b) than wet months. Thus, for the evergreen species, major leaf-litterfall occurred also at the end of the dry season (April, Fig 2.2). The absence of litterfall in November and December was unexpected, as low temperature and drought are common environmental cues in these months and should have triggered senescence and leaf shedding. However, in this particular winter, the study site received a significant number of small rainfall events in November that may have saturated the soil and reduced litterfall (Fig. 2.1b) and also temperatures remained relatively mild. Hence, it was suggest that the environmental conditions did not cause sufficient stress to trigger leaf senescence and shedding.

The strong seasonality in leaf-litterfall recorded in other ecosystems with a variety of deciduous and evergreen species (West, 1985; Maya and Arriaga, 1996; Berg and Meentemeyer, 2001; Liu *et al.,* 2001; Pavón *et al.,* 2005) has been ascribed to interactive effects of weather patterns (e.g. drought), species phenology (Binkley *et al.,* 1992; Liu *et al.,* 2001; Berg and Meentemeyer, 2001), distribution of precipitation events (Knapp *et al.,* 2002; Liu *et al.,* 2004), and an overall 2-6 months lag response in litterfall after the rainy season (Martínez-Yrizar and Sarukhán 1990). Although a somewhat inverse relationship between monthly litterfall and monthly precipitation was observed during the study year, the data of this study did not show a significant negative correlation between stand type and monthly precipitation. Although our data base covers a short-period to allow identifying this type of relationship, our results suggest that weather conditions (the peak of the dry season) together with the peak of soil water deficit (Fig. 2.1b) were the main controls for leaf-litterfall.

### **2.4.3** Spatiotemporal variation in leaf-litter quality

Results from this study suggest spatiotemporal variation in nutrient input into these semiarid pine-oak forests that are principally driven by inherent species differences in leaf chemical composition, nutrient resorption efficiencies, species composition of tree stands and weather variability. Changes in chemical composition of litterfall of senesced leaves along the sampled year and comparisons with green leaf-litter reflect patterns of nutrient reallocation and/or re-absorption prior to abscission of leaves (Killingbeck, 1996; Rentería *et al.,* 2005). The lowest recorded N concentration coincided with the peak of leaf-litter and the highest soil water deficit observed in April (Fig. 2.1b). This suggests that *Q. potosina* is highly efficient in reabsorbing N prior to the main leaf-litterfall event. However, in June 2007 during the second pulse of litter shedding, relative N input per leaf-litter was higher than the one observed in April. At first glance, this response does not seem to reflect nutrient conservation, however, this litterfall event was triggered by a heavy storm, and hence nutrient resorption was likely incomplete and quality of litterfall improved. Contrasted to the dry tropical forests (Rentería *et al.,* 2005), leaf resorption efficiency seems to be controlled by low soil water availability. The N content observed at the first peak of litterfall in this study appeared to confirm this mechanism for semiarid pine-oak forest.

Chemical characteristics of *P. cembroides* needle litter did not vary as much throughout the year as did *Q. potosina* leaf-litter. However, in the evergreen species, N resorption efficiency at the end of the dry season was higher in mixed than in monospecific stands, suggesting that soil N availability may be limiting in the presence of *Q. potosina* trees (Vitousek, 1984). The deposited needles of the evergreen *P. cembroides* had a relatively high, slightly fluctuating lignin concentration throughout the year in both stand types; however the lignin:N ratio showed only one marked peak in April, which again was higher for the shed needles in the mixed stands than in monospecific stands. In several forest ecosystems, lignin concentration of litter depends on the proportion of sun and shade leaves due to their differences in structural characteristics (Sariyildiz and Anderson, 2003). The forest in this study area is structured by small statured trees (3-6 m high), with a low leaf area index located in a single canopy strata, so leaf stratification and presence of sun and shade leaves is improbable in this site. Our results revealed that a more efficient leaf N resorption mechanism (Fig. 2.3b) rather than an overall lower needle N concentration explained the relatively low litter quality in mixed *P. cembroides* stands. Evergreen species are less dependent on soil nutrient pools, because major leaf senescence usually coincides with new leaf growth and thus allows direct nutrient translocation from old to new tissue (Vitousek, 1984). Leaf-litter quality may also change due to soil characteristics affecting quality of green and senesced needles of evergreen species. Sariyildiz and Anderson (2006) reported that under different soil fertility conditions Scots pine showed significant variation in cell wall constituents (lignin, cellulose, etc.) and mineral elements (N, P, K, etc.) when comparing different needle age classes, suggesting soil fertility to have an important role in litter quality and decomposition rates. In this study, the decrease in leaf-litter N concentration observed in April may have been related to newly forming, strong resource sinks associated with emerging bud meristems and shoot elongation, which has been reported to occur in these forest ecosystems between March and April (Zavala and García, 1991). Phosphorous concentration in all stand types also dropped dramatically between the end of summer and January, however, there was not a clear control associated with this pattern.

Considering C: N and lignin: N ratios, both species shed litter of lower quality during the peak of litterfall (March-April) while litter of higher quality was shed in early summer (June-August), which may contribute to a temporal increase in soil nutrient availability (Vitousek, 1984; Austin and Sala, 2002; Anu and Sabu, 2007). The observed data confirm our prediction that leaf-litter of *Q. potosina* had higher quality (lower C: N and lignin: N ratios) in both green and senesced litterfall than that of *P. cembroides.* Myers *et al.* (1994) considers litter with C: N ratios ≤25 of high quality and consequently favors decomposition. Lignin: N ratios ≥29 are reported to correlate negatively with decomposition (Melillo *et al.,* 1982). In species with high leaf lignin content the best predictor of litter decomposition is the lignin: N ratio (Melillo *et al.*, 1982; Taylor *et al.,* 1989). Thus, only *Q. potosina* showed lignin:N ratios within a range suggesting high litter quality (Fig. 2.4).

### **2.4.4** Nutrient input by green leaf-litter

Similar to other studies contrasting the quality of green and senesced leaves (Fonte and Schowalter, 2004; Anu and Sabu, 2007), this study showed differences in chemical composition and quality of litterfall types for both *Q. potosina* and *P. cembroides*. Green leaf-litter of *Q. potosina* exhibited lower lignin concentration than litterfall of senesced leaves in both monospecific and mixed stands. However, in contrast to our prediction C, N, and P concentration did not differ between senesced and green leaves in both tree species; this was attributed to nutrient leaching of green leaf-litter during rain events (Chapin and Molainen, 1991; Aerts and Chapin, 2000; Pérez-Suárez *et al.,* 2008). This however, seems unlikely as litter material shortly was collected after the extreme precipitation events. Contrary to the expectations, P concentration was higher in senesced needles than in green-needle fall. Studies reporting high P concentration in senesced leaves suggest that this could be related to stress effects. Chapin and Molainen (1991) argued that a high P concentration in senesced leaves of Alaskan birch leaves might have derived from an accumulation of amino acids and inorganic phosphates in response to osmotic stress. The experimental set-up of this study does not allow us to isolate the underlying mechanisms of the high P concentration. Since litter quality indices determine decomposition and N mineralization rates (Melillo *et al.*, 1982; Berg and McClaugherty, 2008), the lower lignin: N and C: N ratios of green leaf-litter of *Q. potosina* in monospecific stands and of *P. cembroides* in monospecific stands, respectively, suggest that green leaf-litter may decompose and mineralize faster in these semiarid forest ecosystems. Still, green leaf-litter may also contain recalcitrant chemical compounds like tannins and phenolic compounds that could slow down litter decomposition (Berg and McClaugherty, 2008). While nutrient concentrations did not differ between senesced and green leaf-litter, it was rather the high relative contribution to the year-total nutrient input that was remarkable in this study. Two single extreme weather events may account for up to 18% of year-total nutrient input to semiarid ecosystems, thereby significantly contributing to the spatiotemporal patterning of nutrient input, nutrient cycling and ultimately forest productivity. This is one of the first studies to quantify the importance of green leaf-litter in semiarid forest ecosystems.

## 2.5 Conclusions

Land use change is the main disturbing factor contributing to change tree species composition in semiarid forest ecosystems. This transformation carries out changes in canopy structure and subsequently in soil surface cover by different litter types, altering several ecosystems processes. The findings of this study, regarding litterfall production, quality of leaf-litter and nutrient inputs from each species suggest that species-specific leaf-litter traits of single-species or mixed species tree stands may contribute to differential spatial and temporal dynamics of nutrient inputs and potentially influence several ecosystem processes including regulation of the soil organic matter pool, nutrient dynamics and release of nutrients for plant growth. Apart from this green litterfall appears to represent a much more important mechanism of nutrient input to semiarid forest ecosystems than previously considered.

## 2.6 References

Aerts, R., and Chapin, F.S. III. (2000). The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Adv. Ecol. Res.* **30**, 1-67.

Anu, A., and Sabu, T.K. (2007). Seasonal variation in the litter chemical quality of a wet evergreen forest in the Western Ghats. *Curr Sci.* **93**, 391-394.

Arunachalam, A., Arunachalam, K.M., Pandey, H.N., and Tripathi, R.S. (1998). Fine litterfall and nutrient dynamics during forest regrowth in the humid subtropics of north-eastern India. *For. Ecol. Manage.* **110**, 209-219.

Austin, A.T., and Sala, O.E. (2002). Carbon and nitrogen dynamics across a natural precipitation gradient in Patagonia, Argentina. *J. Vegetation Sci*. **13**, 351-360.

Benton, J.J., Wolf, B., and Mills, H.A. (1991). Plant Analysis Handbook. A practical Sampling, Preparation, Analysis and Interpretation Guide. Micro-Macro Publishing Inc., Athens Georgia, USA.

Berg, B., and McClaugherty, C. (2008). Plant Litter. Decomposition, Humus Formation, Carbon Sequestration, 2nd ed. Springer, Berlin-Heidelberg, Germany.

Berg, B., and Meentemeyer, V. (2001). Litter fall in some European coniferous forests as dependent on climate: a synthesis. *Can. J. For. Rese*. **31**, 292-301.

Binkley, D., Dunkin, K.A., Debell, D., and Ryan, M.G. (1992). Production and nutrient cycling in mixed plantation of *Eucalyptus* and *Albizia* in Hawaii. *For. Sci*. **38**, 393-408.

Caritat, A., García-Berthou, E., Lapeña, R., and Vilar, L. (2006). Litter production in a *Q. potosina suber* forest of Montseny (NE Spain) and its relationship to meteorological conditions. *Ann. For. Sci.* **63**, 791-800.

Cardona, B.A. (2007). Hidrogeoquímica de sistemas de flujo, regional, intermedio y local resultado del marco geológico en la mesa central: reacciones, procesos y contaminación. Tesis doctorado, UNAM, Instituto de Geofísica, México, DF, pp. 238.

Cetina-Alcalá, V.M., García-Moya, E., and Keyes, M.R. (1985). Análisis estructural de un bosque de *Pinus cembroides* Zucc., en La Amapola, S.LP. *In*: Flores

J.E. (Ed.), Primer Simposium Nacional sobre Pinos Piñoneros. Facultad de silvicultura y Manejo de Recursos Renovables. Universidad Autónoma de Nuevo León. Reporte científico (especial 2), 100-109.

Chapin, F.S.III, and Moilanen, L. (1991). Nutritional controls over nitrogen and phosphorus resoption from Alaskan birch leaves. *Ecology* **72**, 709-715.

Dearden, F.M., Dehlin, H., Wardle, D.A., and Nilsson, M.C. (2006). Changes in the ratio of twig to foliage in litter fall with species composition and consequences for decomposition across a long term chronosequence. *Oikos* **115**, 453-462.

Enright, N.J. (1999). Litterfall dynamics in a mixed conifer-angiosperm forest in northern New Zealand. *J. Biog*. **26**, 149-157.

Fonte, S.J., and Schowalter, T.D. (2004). Decomposition of greenfall *vs*. senescent foliage in a tropical forest ecosystem in Puerto Rico. *Biotropica* **36**, 474-482.

García, E. (1988). Modificaciones al sistema de clasificación climática de Köppen para adaptarlo a las condiciones de la República Mexicana. Instituto de Geografía, UNAM, México.

González-Rodríguez, H., Cantú-Silva, I., Ramírez-Lozano, R.G., and Gómez-Meza, M.V. (2007). Litter fall deposition in subtropical woodlands, Northeastern Mexico. Conference on International Agricultural Research for Development. University of Gottingen, Germany.

Hernández-Reyna, A., and García, M.E. (1985). Análisis estructural de los piñonares del altiplano potosino. *Agrociencia* **62**, 7-20.

Holmgren, M., Stapp, P., Dickman, C.R., García, C., Graham, S., Gutiérrez, J.R., Hice, C., Jaksic, F., Kelt, D.A., Letnic, M., Lima, M., López, B.C., Meserve, P.L., Milstead, W.B., Polis, G.A., Previtali, M.A., Richter, M., Sabaté, S., and Squeo, F.A. (2006). Extrem climatic events shape arid and semiarid ecosystems. *Front. Ecol. Environ*. **4**, 87-95.

Hooper, D.U., and Vitousek, P.M. (1997). The effects of plant composition and diversity on ecosystem processes. *Science* **277**, 1302-1305.

INEGI. (2002). Síntesis de Información Geográfica del Estado de San Luis Potosí. Instituto Nacional de Estadística, Geografía e Informática, México.

Killingbeck, K.T. (1996). Nutrients in senescing leaves: keys to the search for potential resorption and resorption proficiency. *Ecology* **77**, 1716–1727.

Knapp, A.K., Fay, P.A., Blair, J.M., Collins, S.L., Smith, M.D., Carlisle, J.D., Harper, C.W., Danner, B.T., Lett, M.S., and McCarron, J.K. (2002). Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *Science* **298**, 2202-2205.

Lin, K.C., Hamburg, S.P., Tang, S.I., Hsia, Y.J., and Lin, T.C. (2003). Typhoon effects on litter fall in a subtropical forest. *Can. J. For. Rese*. **33**, 2184-2192.

Littell, R.C., Henry, P.R., Ammerman, C.B. (1998). Statistical analysis of repeated measures data using SAS procedures. *J. Ani. Sci.* 76, 1216-1231.

Liu, C.J., Wetsman, C.J., and Ilvesniemi, H. (2001). Matter and nutrient dynamic of pine (*P. cembroides tabulaeformis*) and oak (*Q. potosina variabilis*) litter in North China. *Silva Fennica* **35**, 3-13.

Liu, C., Wetsman, C.J., Berg, B., Kutsch, W., Wang, G.Z., Man, R., and Ilvesniemi, H. (2004). Variation in litterfall-climate relationships between coniferous and broadleaf forest in Eurasia. *Global Ecol. Biogeog*. **13**, 105-114.

Lodge, D.J., Scatena, F.N., Asbury, C.E., and Sanchez, M.J. (1991). Fine litter fall and related nutrient inputs resulting from hurricane Hugo in subtropical wet and lower montane rain forests of Puerto Rico. *Biotropica* **23**, 336-342.

Maya, Y., and Arriaga, L. (1996). Litterfall and phenological patterns of the dominant overstorey species of a desert scrub community in northwestern Mexico. *J. Arid Environ*. **34**, 23-35.

Martínez-Yrízar, A., and Sarúkhan, J. **1990**. Litterfall patterns in a tropical deciduous forest in Mexico over a five-year period. *J. Trop. Ecol*. **6**, 433-444.

Myers, R.J.K, Palm C.A., Guevas, E., Gunatilleke, I.U.N., and Brossard, M. (1994). The synchronization of nutrient mineralization and plant nutrient demand. *In*: The biological Management of Tropical Soil Fertility (eds. Woomer, P.L., and Swift, M.J.) pp. 81-116.

Meentemeyer, V., Box, E.O., and Thompson, R. (1982). World patterns and amounts of terrestrial plant little production. *BioScience* **32**, 125-128.

Melillo, J.M., Aber, J.D., and Muratore, J.F. (1982). Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* **63**, 621-626.

Myers, R.J.K, Palm C.A., Guevas, E., Gunatilleke, I.U.N., and Brossard, M. (1994). The synchronization of nutrient mineralization and plant nutrient demand. *In*: The biological Management of Tropical Soil Fertility (eds. Woomer, P.L., and Swift, M.J.) pp. 81-116.

Ostertag, R., Scatena, F.N., and Silver, W.L. (2003). Forest floor decomposition following hurricane litter inputs in several Puerto Rican Forests. *Ecosystems* **6**, 261-273.

Pausas, J.G. (1997). Litter fall and litter decomposition in *Pinus sylvestris* forests of the Eastern Pyrenees. *J. Vegetation Sci*. **8**, 643-650.

Pavón, N.P., Briones, O., and Flores, R.J. (2005). Litter production and nitrogen content in an intertropical semi-arid Mexican scrub. *J. Arid Environ.* **60**, 1-13.

Pérez-Suárez, M., Fenn, M.E., Cetina-Alcalá, V.M., Aldrete, A. (2008). The effects of canopy cover on throughfall and soil chemistry in two forest sites in the Mexico City air basin. *Atmosfera* **21**, 83-100.

Ramamoorthy, T.P., Bye, R., Lot, A., and Fa, J. (1993). Biological Diversity of Mexico: Origins 2nd Distribution, Oxford University Press, USA.

Rentería, L.Y., Jaramillo, V.J., Martínez-Yrízar, A., and Pérez-Jiménez, A. (2005). Nitrogen and phosphorus resorption in trees of a Mexican tropical dry forest. *Trees* **19**, 431-441.

Reuter, D.J., Robinson, J.B., Peverill, K.I., and Proce, G.H. (1986). Guidelines for collecting, handling and analyzing plant materials. *In*: Reuter, D.J., Robinson, J.B. (eds.), Plant Analysis; An Interpretation Manual. Inkata Press, Sidney-Melbournes, Australia, pp. 20-33.

Robert, M.F. (1977). Notas sobre el estudio ecológico y fitogeográfico de los bosques de *Pinus cembroides*, Zucc., en México. *Ciencia Forestal* **10**, 49-58.

Röderstein, M., Hertel, D., and Leuschner, C. (2005). Above- and below-ground litter production in three tropical mountain forests in southern Ecuador. *J. Trop. Ecol*. **21**, 483-492.

Roig, S., del Río, M., Cañellas, I., and Montero, G. (2005). Litterf all in mediterranean *P. cembroides pinaster* Ait. stands under different thinning regimes. *For. Ecol. Manage.* **206**, 179-190.

Rzedowski, J. (1978). Vegetación de México. Limusa. México.

Schuster T.D., Cobb N.S., Whitham T.G. and Hart S.C. (2005). Relative importance of environmental stress and herbivory in reducing litter fall in a semiarid woodland. *Ecosystems* **8**, 62-72.

Sariyildiz, T., and Anderson, J.M. (2003). Decomposition of sun and shade leaves from three deciduous tree species as affected by their chemical composition*. Biol. Fertil. Soils* **37**, 137-146.

Sariyildiz, T., and Anderson, J.M. (2005). Variation in the chemical composition of green leaves and leaf litters from three deciduous tree species growing on different soil types. *For. Ecol. Manage*. **210**, 303–319.

Sariyildiz, T. and Anderson, J.M. (2006). Intra-specific variation in cell wall constituents of needle age classes of Pinus sylvestris in relation to soil fertility status in Southwest England. *Silva Fennica* **40**, 15-26.

SAS Institute Inc., 2002-2003. SAS user's guide, Version 9.1.3. SAS Institute, Inc., Cary, NC., USA.

Sokal, R.R., and Rohlf, F.J. (1994). Biometry: the principles and practices of statistics in biological research. 3rd. WH Freeman, New York, USA.

Schuster, T.D., Cobb, N.S., Whitham, T.G. and Hart, S.C. (2005). Relative importance of environmental stress and herbivory in reducing litter fall in a semiarid woodland. *Ecosystems* **8**, 62-72.

Tang, C.Q., and Ohsawa, M. (2002). Coexistence mechanisms of evergreen, deciduous and coniferous trees in a mid-montane mixed forest on Mt. Emei, Sichuan, China. *Plant Ecology* **161**, 215-230.

Taylor, B.R., Parkinson, D., and Parsons, W.F.J. (1989). Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. *Ecology* **70**, 97-104.

Vitousek, P.M. (1984). Litter fall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology* **65**, 285-298.

West, N.E. (1985). Aboveground litter production of three temperate semidesert shrubs. *Am. Mid. Nat.* **113**, 158-169.

Zavala, C.F., and García, M.E. (1991). Fenología y crecimiento del brote anual de *P. cembroides* Zucc. de San Luis Potosí, México. *BIOTAM* **3**, 5-14.

# CHAPTER 3

## Rainfall effect on early-stage mixed leaf-litter decomposition in a semiarid pine-oak forest in central-northwest Mexico: testing Ostrofsky's hypotheses

### Summary

The interaction of litter types from different tree species is important to explore to understand the underlying mechanisms of litter decomposition in water-limited ecosystems. The role of rainfall and soil humidity on early-stage leaf litter decomposition of *Quercus potosina* and *Pinus cembroides* was examined based on Ostrofsky's hypotheses (2007). 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 0.25, 0.50, 0.75, and 1.0 year fraction after incubation. Overall, leaf-litter from *Q. potosina* had higher quality with a higher concentration of soluble compounds, K, Ca, Mn and low lignin concentration than litter from *P. cembroides*. After one year, 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 ($k_L$) and a later phase with a lower rate of mass loss of the recalcitrant litter fraction ($k_R$). The labile fraction was lost during the first three months of the study; this coincided with the months of highest rainfall and thus triggered a rapid release of soluble compounds from litter. Higher soil humidity in microsites of mixed compared to monospecific tree stands seemed to have enhanced the differences in the rate of litter mass loss of the two tree species when incubated as mixed and pure litter. Overall, decomposition of litter from *Q. potosina* and *P. cembroides* was mostly controlled by physico-chemical litter characteristics and by the diverse litter microenvironments generated by forest tree species composition. Hence, decomposition of a leaf-litter mixture is a response to multiple factors in semiarid forests ecosystems of Central-Northern Mexico.

**Key words:** litter mixtures, litter quality, microsite, *Pinus cembroides*, *Quercus potosina.*

## 3.1 Introduction

Decay of litterfall through physical (e.g. leaching) and biological (microbial activity) processes are an important source of inorganic ions for tree growth (Melillo *et al.,* 1982, Berg and McClaugherty, 2008). Most of our understanding of decomposition derives from mass loss studies using single species leaf litterbags (Coûteaux *et al*., 1995; Aerts, 1997; Gartner and Cardon, 2004). In naturally mixed forests, however, forest floors receive litter from a mixture of co-occurring tree species. Species vary in leaf-litter quantity and quality and thus in their potential decomposition rates (Gallardo and Merino 1993; Berg and Laskowski 2006, Pérez-Harguindeguy, 2008; Ball *et al.,* 2008; Vivanco and Austin, 2008). Since species-specific decomposition rates are also influenced by the immediate physico-chemical and biotic environment of decaying material, the process of decomposition of mixed species litter may be directly influenced by the interaction of different decomposing leaf material (Wieder and Lang, 1982; Gartner and Cardon, 2004; Ostrofsky, 2007).

The interaction of several leaf litter types can potentially enhance or inhibit decomposition compared to single-species decomposition (Garner and Cardon, 2004; Ganjegunte *et al.,* 2005; Pérez-Harguindeguy *et al.,* 2008). Decomposition effects may be (i) additive, when the decomposition rate of multiple species-mixtures can be predicted from single-species decomposition rates (Ball et al., 2008; Vivanco and Austin, 2008), or (ii) non-additive, when litter decomposes at different rates in pure versus mixed litter conditions (Taylor *et al.,* 1989; Ganjegunte *et al*., 2005; Ball *et al*., 2008). The rate of mass loss of mixed species litter depends on (i) species-specific litter properties (Moore and Fairweather, 2006; Vivanco and Austin, 2008), (ii) species-specific enhancing or inhibiting effects on belowground processes (Vivanco and Austin, 2008), and (iii) on soil faunal controls and species litter diversity (Hättenschwiler and Gasser, 2005).

Four principal hypotheses on prevailing decomposition mechanisms of mixed leaf litterbags have been synthesized by Ostrofsky (2007). Hypothesis one suggests that in litter mixtures of initially contrasting leaves, mass loss rate of slowly processed recalcitrant leaves might be accelerated when co-occurring with rapidly decomposing leaves of species with a higher concentration of labile material. The underlying mechanism may be related to a higher litter nutrient concentration attracting a more rapid colonization of decomposing micro-flora and -fauna. Hypothesis two proposes that rapidly decomposing leaves might reduce their decaying rates when co-occurring with slowly processed leaves, as a consequence of higher concentration of water-soluble defense or inhibitory compounds (e.g. tannins and other phenolics) of the slow-growing species. Hypothesis three proposes that the structural stability of mixed-species leaf litterbags generated by slowly decomposing leaves might provide a more persistent habitat for decomposing organisms, thereby accelerating overall decomposition rates, or protect rapidly processed material from abrasion and leaching, thereby slowing down overall decomposition rates. Finally, since none of these effects are mutually exclusive, both facilitative and/or inhibitory mechanisms could occur simultaneously, so that observed mass rate changes in mixed-litterbags may represent the net effect of multiple processes.

While litter quality largely prevails as the principal endogenous control of litter decomposition under favorable conditions (Coûteaux *et al*., 1995), climate is the dominant external control in areas of water limitation (Berg *et al*., 1993; Coûteaux *et al.,* 1995; Murphy, 1998). Previous work has identified two phases of decomposition: an early phase of decomposition of labile fractions and a later phase of decomposition of recalcitrant litter fractions (Coûteaux *et al*., 1998; Berg and Laskowski, 2006). The early phase of litter decomposition is principally affected by rainfall and its influence on resource lixiviation principally in water limited forest ecosystem (De Santo *et al.,* 1993; Gallardo and Merino, 1993; Coûteoux *et al*., 1995; Murphy *et al.,* 1998). According to De Santo *et al.* (1993) water explained 49 to 81% of mass loss during early decomposition of needle-litter in different coniferous forests. As rainfall triggers weathering, leaching and transportation of nutrients and chemical compounds, it may also stimulate the interaction of different litter types in litter mixtures. Thus, a facilitation and/or inhibition mechanism mediated by rain would support Ostrofsky's first hypothesis in the early decomposition phase.

In the semiarid forests of central-northern Mexico, *Pinus cembroides* Zucc., (Mexican pinyon) and *Quercus potosina* Trel. (San Luis Potosi oak) are the dominant tree species (Rzedowski, 1978) that form patches/cluster of single and mixed-species stands. *Quercus potosina* has deciduous leaves, which are shed at the end of the dry season in a major shedding event (Pérez-Suárez *et al.,* 2009). *Pinus cembroides* in contrast is a coniferous species with 3-4 yr old leaves, whose oldest cohorts are usually shed in episodic events (Zavala and García, 1991; Pérez-Suárez *et al.,* 2009). *Quercus potosina* displays higher leaf-litter quality (lower lignin: N ratio and lower lignin content) than *P. cembroides*. Difference in leaf morphology (needles *vs.* broadleaves) also might create different litter microenvironments as a consequence of differential litter packing that may affect litter decomposition. Water retention in litter layer of *Q. potosina* stands is higher than in *P. cembroides* stands (Pérez-Suárez *et al.,* 2009), which may also influence litter decomposition (Pataki *et al.,* 1998; Yan *et al.,* 2004).

This study was designed to test Ostrofsky's (2007) hypotheses and the underlying mechanisms of early-phase decomposition rates of leaf litter mixtures with different litter quality and leaf-litter packing. Decomposition bags with pure or mixed leaf-litter of *P. cembroides* and *Q. potosina* were used to test the following hypotheses: (i) the rate of mass loss of *P. cembroides* leaf litter (slowly decomposing litter of lower quality) will increase, when decomposing in the presence of *Q. potosina* with higher litter quality (more rapidly decomposing) (Ostrofsky's first hypothesis); (ii) higher quality leaf litter of *Q. potosina* will decrease its rate of mass loss when decomposing in the presence of leaf litter of *P. cembroides* (Ostrofsky second hypothesis); (iii) a mixed litter-pack will provide greater structural stability favoring faster leaf litter decomposition rates (Ostrofsky's third hypothesis), and (iv) mass loss changes of mixed leaf litter represents the net effect of multiple processes.

## 3.2 Materials and methods

### **3.2.1** 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 masl. The region is characterized by a temperate semiarid climate (García, 1988) with 8 months (from October to May) of dry season and 4 months of wet season (from June to September). Average annual precipitation in this region reaches 530 mm, whereas average monthly temperatures range between -3°C in winter (December-February) and almost 21°C in summer (June-August). Parent material is igneous rhyolite rock with poorly developed Leptosol soils (FAO’s classification system) (Cardona, 2007). The landscape is characterized by abrupt and irregular topography, with a large proportion of rock outcrops, and the majority of slopes steeper than 30°. The forest floor is highly heterogeneous with a litter layer covering the soil surface between rock outcrops. The litter layer is approximately 0 cm to 10 cm deep and is composed of moor humus with three thin layers: the top layer of fresh litter, the intermediate partially decomposed litter layer and at the base transformed material consisting of relatively homogeneous humus.

The vegetation is characterized by *Pinus cembroides* Zucc., and *Quercus potosina* Trel., with intermingled *Pinus johannis* Rob Pass., other *Quercus* spp., *Yucca* spp. and *Dasylirion* spp. (Rzedowski, 1978). The understory is composed of species belonging to the genera *Opuntia*, *Agave*, *Mammillaria* and *Euphorbia* (Robert, 1977; Rzedowski, 1978).

### **3.2.2** Litterbag preparation

Between March and April 2007, recently abscised leaves were collected using several 1 $m^2$ elastic nets spread below tree canopies of *Q. potosina* and *P. cembroides*. Collected litter was cleaned from any foreign material and thoroughly mixed to ensure the purity and homogeneity of the samples. Litterbags (20 cm x 20 cm; Photo 3.1) were assembled using a polyethylene mesh (mesh size: 1.0 mm x 1.5 mm). For single *Q. potosina* and *P. cembroides* litterbags, ten grams of air-dried leaf-litter were evenly spread in the bags. For mixed leaf-litterbags an equivalent amount (5g : 5g) of abscised leaves of the two species was evenly spread in the bags. Litterbags were sealed with a heat sealer and labeled with aluminum tags before they were arranged and anchored into the soil with non-corrosive nails. Additionally, empty litterbags were installed as blanks. Five samples (30 g each) of *Q. potosina* and *P. cembroides* leaf-litter were analyzed to determine initial litter quality.

**Photo 3.1** Arrangement of leaf litterbags used for *in situ* incubation in the Sierra San Miguelito, San Luis Potosi.

### **3.2.3** Experimental set-up

Three microsite types were selected within the forest matrix considering monospecific stands of *Q. potosina* and *P. cembroides* and mixed pine-oak stands. Four replicates of each microsite type were chosen yielding a total of 12 plots. The plots were distributed within 4 ha (2000 m x 20 m) study area. All microsites were selected considering similar topographic features, landscape position, exposure and altitude to minimize potential confounding effects. Beneath the canopy of each forest stand type an area of approximately 2 m x 2 m was selected to place the litterbags. Within each plot, litterbags were placed in seven to nine columns (depending of available space) running parallel to the slope and in three to four lines maintaining a minimum distance of 30 cm between litterbags. Litterbags and blanks were intermingled in the plots. A total of 112 (28 per plot; 16 litterbags and 12 blanks) bags were placed in each microsite; altogether, 336 litterbags were placed in the study area for this experiment. The study was initiated on May 30, 2007. At each of four sampling dates (August and November, 2007; February and May, 2008) seven bags per plot were collected (4 litterbags subsamples and 3 blanks).

To examine the effect of rain on the rate of litter decomposition and litter nutrient dynamics, four standard rain gauges were placed along the 12 plots in the study site (along a 2 km transect), and each rain event was recorded during the time of the experiment. Additionally, two soil psychrometers (PST-55, WESCOR) were inserted in each plot into the litter layer at 10 cm depth, where soil water potential was recorded every two weeks from June 2007 to July 2008. To evaluate the water content in each litter type (pure *P. cembroides*, pure *Q. potosina*, mixed), two litter samples from a 20 cm x 20 cm area were collected from the top litter layer in each plot. Water content was determined with the gravimetric method.

### **3.2.4** Determination of litter mass loss

At each sampling date (0.25, 0.5, 0.75 and 1.0 year after incubation), a total of 48 leaf litterbags and 36 blanks were collected and kept in separate plastic bags that were put in ice chests during transportation. In 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 hours 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: *Q. potosina* pure leaf-litter, *P. cembroides* pure leaf-litter, *Q. potosina* mixed leaf-litter and *P. cembroides* mixed leaf-litter. For the blank bags, the content was dried and weighed and used to correct for potential incorporation of material during the incubation period. Also, 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 four hours to determine the remaining ash-free dry matter content (% AFDM), which was then used to correct leaf litter dry mass according to:

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

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

### **3.2.5** Standard cotton strip decomposition test

In order to separate the effects of microclimate from litter quality type on decomposition rate, a cellulose degradation test was implemented using a standard unbleached 100% cotton fabric (96% pure cellulose; Belnap *et al.,* 2005). Cotton strips (6 cm-wide and 15 cm-long) were wrapped up in aluminum foil in sets of five, autoclaved at 121 °C for 30 minutes to avoid contaminating the litter layer by potential introduced microorganisms. Sterilized strips remained in aluminum foil packets and sealed plastic bags until inserted into the litter. A set of cotton strips were buried and incubated for 30 days during the dry season (February) and another set for the same period during the rainy season (June). A total of 20 cotton strips were buried per microsite (mixed, oak and pine) and month. In 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. At the end of each incubation period, cotton strips were placed between sheets of blotting paper, wrapped in foil packets and stored in a cooler for their transportation to the laboratory. In the laboratory soil and roots were carefully removed from the cotton strips. When strips were moist, they were first dried at room temperature. Afterwards, strips were wrapped in aluminum foil in packs of 5, sealed tightly with tape and autoclaved (121°C, 30 minutes). For each cotton strip, tensile strength was determined at the College of Textile Engineering at Instituto Politecnico Nacional, Mexico City. Tensile strength measures indirectly cloth decomposition by cellulolytic activity in the litter layer (Image 3.2) and is expressed in units of force (Newton) (Belnap *et al.,* 2005).

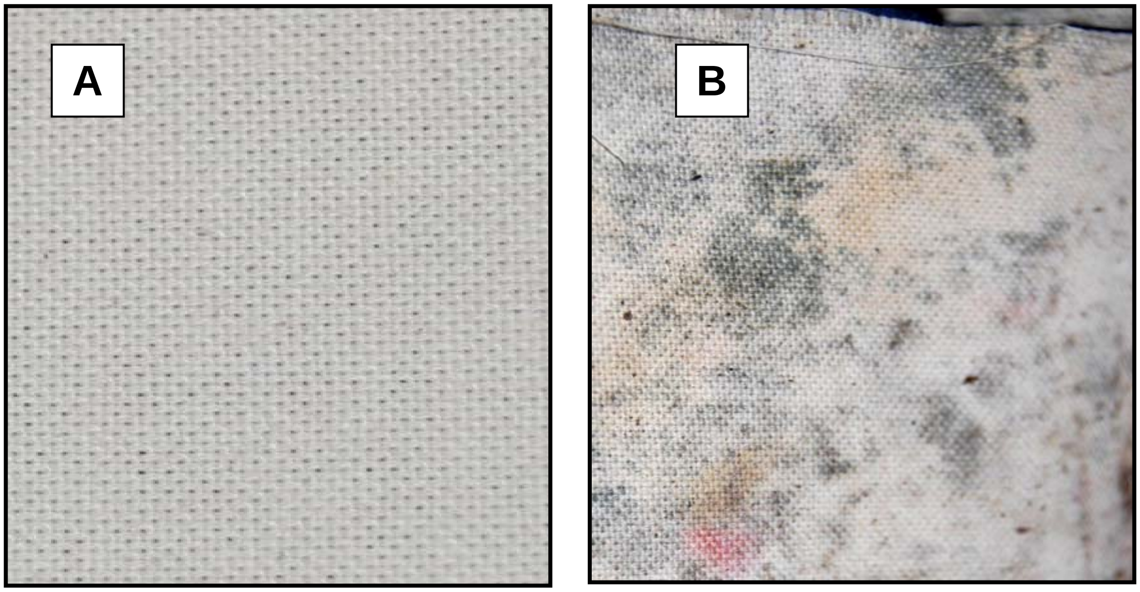


**Photo 3.2** Cotton strip before (A) and after (B) *in situ* incubation of 30 days

### **3.2.6** Chemical analysis of initial leaf litter quality

Five sub-samples (30g each) of the original leaf-litter of *Q. potosina* and *P. cembroides* were ground with a Wiley$^{TM}$ mill to pass a No. 20 stainless steel mesh (1 mm mesh size). The ground material was analyzed to determine initial litter quality. The ground material was processed further with an ANKOM$^{200}$ 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 the difference in filter bag weights under sequential extractions of NDF, ADF and ADL. The NDF procedure removes soluble cell components from leaf-litter such as simple sugars and amino acids, thus %NDF corresponds to the remaining non-soluble fraction. The soluble cell material (referred to as soluble compounds) was calculated by subtracting %NDF from 100. Acid Detergent Fiber removes cellulose leaving a residue of lignin and “lignin-like” compounds such as cutin, acid detergent insoluble nitrogen, and acid insoluble ash. Finally, ADL is the lignin content after digestion with sulfuric acid. Percent cellulose content is calculated as the difference between %ADF and %ADL. Sub-samples of leaves from each species were analyzed for dry mass (105 °C for 48 hours), moisture content, and ash mass (500 °C for five hours).

Phosphorous (P), Potassium (K), Sodium (Na), Calcium (Ca), and Magnesium (Mg) concentration of litter were determined at the Soil Fertility Laboratory of the Colegio de Postgraduados, Texcoco, Mexico using Atomic Absorption (Ca, Mg), Atomic Emission (Na, K) and the phosphovanadomolybdate spectrophotometer method (P). Total carbon (C) and nitrogen (N) were analyzed of pulverized samples with an Elemental Analyzer (Costech ECS 4010). To estimate litter quality C:N, lignin:N and N:P ratios were calculated with the initial concentrations of individual components. For litter samples collected during the consecutive sampling times, only C, N, lignin, C:N, lignin:N ratios, soluble compounds and cellulose were determined and/or calculated.

**3.2.7** Statistical analysis

For initial litter quality a one-way ANOVA was used to test differences in chemistry (moisture content, ash, N, C, P, K, Ca, Mg, Na, Mn, soluble compounds, cellulose, lignin, and C:N, lignin:N and N:P ratios) between pine and oak litter. Differences in mass loss among four leaf litter types (pure and mixed litter of *Q. potosina*, pure and mixed litter of *P. cembroides*) considering four consecutive sampling dates were examined with a two-way ANOVA including leaf litter type and time of incubation as main factors. To describe the dynamics of temporal mass loss, the decomposition constants, *k* of the four litter types were obtained for each microsite (four plots x four leaf litter types) by fitting the temporal decay of remaining mass to the double exponential decay model (Wieder and Lang, 1982; Ostrofsky, 2007):

$$M_t = M_L\, e_L^{-k\mathrm{L}t} + M_R\, e_R^{-k\mathrm{R}t}$$

*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 estimate model parameters, the double exponential decay model was fitted with SigmaPlot v.7.0.

To test for differences in nutrient concentration a two-way ANOVA model was applied for leaf litter type and time as the main factors. For *post hoc* (mass loss and nutrient concentration) multiple mean comparisons, Tukey's test was applied with a minimum significance level of $P \leq 0.05$. To examine if accumulated rainfall and mass loss were correlated Pearson's correlation analysis was applied. To examine differences between the fitted decay functions the overlap of confidence intervals was examined. Tensile strength of cotton strips was compared with a two-way ANOVA with season (dry and rain) and microsite (monospecific *Q. potosina,* monospecific *P. cembroides* and mixed stands) as main factors. Water content of each litter type (oak, pine and mixed) was compared with a one-way ANOVA. Prior to analysis, data were tested for normality using Shapiro-Wilk's test, but based on the test any variable was 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).

## 3.3 Results

### **3.3.1** Initial leaf-litter quality

Freshly fallen *Q. potosina* leaf litter had significantly (litter type main effect; *P* ≤ 0.05; Annex 3-1) higher concentrations of soluble carbohydrates (11.87%), K (0.11%), Ca (0.45% times), Mn (956.2ppm) and N:P ratios (5.3 times) than *P. cembroides* needle litter (Table 3.1). In contrast, *P. cembroides* needle tissue had significantly (*P* ≤ 0.05; Annex 3-1) more lignin (6.96%), greater water content (0.26%) and more cellulose (1.91%) than *Q. potosina* leaves. Carbon and N concentration did not significantly differ between leaf litter types (Table 3.1).

**Table 3.1** Initial chemistry (means ± 1 SE; n=5) of *Q. potosina* and *P. cembroides* leaf-litter.

| **Component** | ***Q. potosina*** | ***P. cembroides*** |
|---|---|---|
| Moisture content (%) | 4.60 (± 0.07)$^a$ | 4.86 (± 0.05)$^b$ |
| Ash (%) | 6.38 (± 0.36)$^a$ | 1.97 (± 0.09)$^b$ |
| Soluble compounds (%) | 51.89 (± 0.27)$^a$ | 40.02 (± 0.34)$^b$ |
| Cellulose (%) | 22.84 (± 0.47)$^a$ | 24.75 (± 0.40)$^b$ |
| Lignin (%) | 27.69 (± 0.89)$^a$ | 34.65 (± 0.61)$^b$ |
| C (%) | 54.76 (± 1.82)$^a$ | 55.88 (± 1.78)$^a$ |
| N (%) | 0.93 (± 0.02)$^a$ | 0.94 (± 0.04)$^a$ |
| P (%) | 0.04 (± 0.002)$^a$ | 0.05 (± 0.004)$^b$ |
| K (%) | 0.30 (± 0.03)$^a$ | 0.21 (± 0.01)$^b$ |
| Ca (%) | 0.81 (± 0.02)$^a$ | 0.46 (± 0.03)$^b$ |
| Mg (%) | 0.10 (± 0.002)$^a$ | 0.10 (± 0.01)$^a$ |
| Na (%) | 0.01 (± 0.002)$^a$ | 0.00 (± 0.002)$^a$ |
| Mn (ppm) | 1139.20 (± 80.67)$^a$ | 183.00 (± 5.26)$^b$ |
| C:N ratio | 58.99 (± 3.25)$^a$ | 60.47 (± 4.25)$^a$ |
| Lignin:N ratio | 29.71 (± 0.91)$^a$ | 37.45 (± 2.26)$^b$ |
| N:P ratio | 20.07 (± 0.84)$^a$ | 14.94 (± 1.21)$^b$ |

Different letters in columns indicate significant differences between litter types at *P* ≤ 0.05

### 3.3.2 Mass loss

After one year of *in situ* leaf litter incubation, mass loss differed significantly among leaf litter types (leaf litter type main effect; *P* = 0.0001; Annex 3-2) with greater mass loss in *Q. potosina* (pure and mixed; Fig. 3.1a) than in *P. cembroides* (pure and mixed). Mass loss showed high seasonal variation (time main effect interaction; *P* = 0.0001) and between leaf litter types and months (time x leaf litter type main effect; *P* = 0.0212). Overall, leaf-litter decomposition (reported as remaining mass) exhibited a decay pattern (Fig. 3.1b) in leaf-litter types incubated in monospecific and mixed stands, with a close fit to the double exponential decay model ($R^2 > 0.97$; Table 3.2). Decomposition rate, *k,* of the labile litter fraction was significantly higher than that of the recalcitrant litter fraction for the two leaf-litters types in pure and mixed conditions (Table 3.2). There was no difference in *k* values of the labile and recalcitrant fraction when comparing pure and mixed litter incubation conditions.

**Table 3.2** Double exponential decay constants (*k*) and fits ($R^2$) for the early labile litter fraction ($k_{L;}$ ±1SE; *P* = 0.05) and the later recalcitrant litter fraction ($k_{R;}$ ±1SE; *P* = 0.05) of two litter types (*Quercus potosina*, *Pinus cembroides*) and two incubation conditions (pure and mixed litter).

| **Leaf-litter type** | **Condition** | **Labile ($k_L$)** | **Recalcitrant ($k_R$)** | **$R^2$** |
|---|---|---|---|---|
| *Q. potosina* | Pure | 11.10 (± 2.94)$^{a}$ | 0.0690 (± 0.01)$^{a}$ | 0.998 |
| *Q. potosina* | Mixed | 6.90 (± 3.73)$^{ab}$ | 0.0000 (± 0.07)$^{a}$ | 0.977 |
| *P. cembroides* | Pure | 5.29 (± 2.44)$^{b}$ | 0.0000 (± 0.06)$^{a}$ | 0.985 |
| *P. cembroides* | Mixed | 6.25 (± 3.76)$^{b}$ | 0.0000 (± 0.06)$^{a}$ | 0.972 |

Different letters in rows indicate significant differences among litter condition and litter type at $P \leq 0.05$.

Initial (0.25years) mass loss of *Q. potosina* leaf litter (15.0 ± 0.40%; Fig. 3.1b; $P \leq 0.05$) was significantly higher than that of *P. cembroides* needle litter (11.8 ± 0.0.41%; Fig. 3.1b). After 0.50 years, mixed-leaf litter of *Q. potosina* showed greater mass loss than pure leaf-litter of *Q. potosina* (19.1 ± 0.37% *vs.* 17.1 ± 0.55%: $P \leq 0.05$) (Fig. 3.1b).

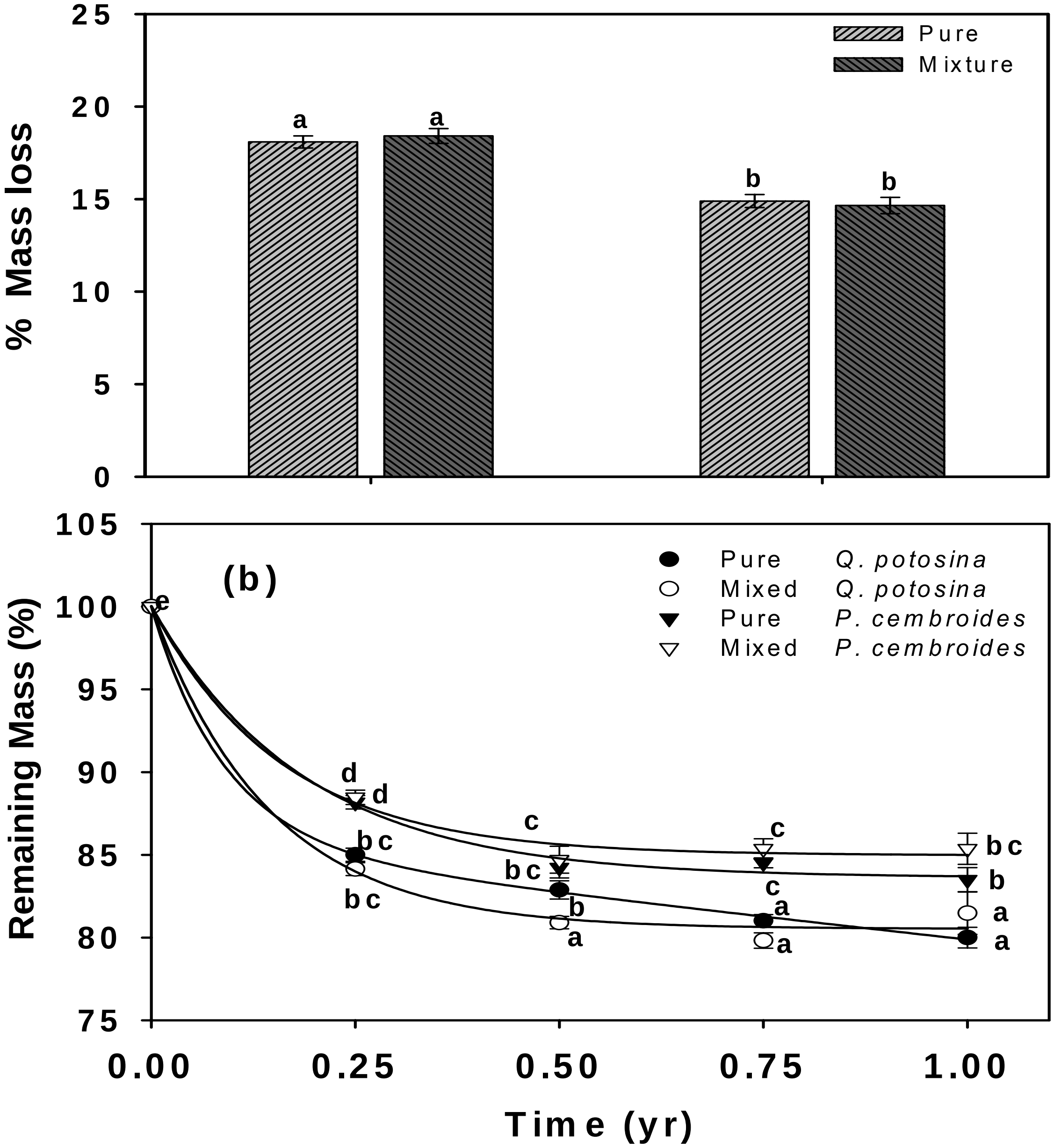
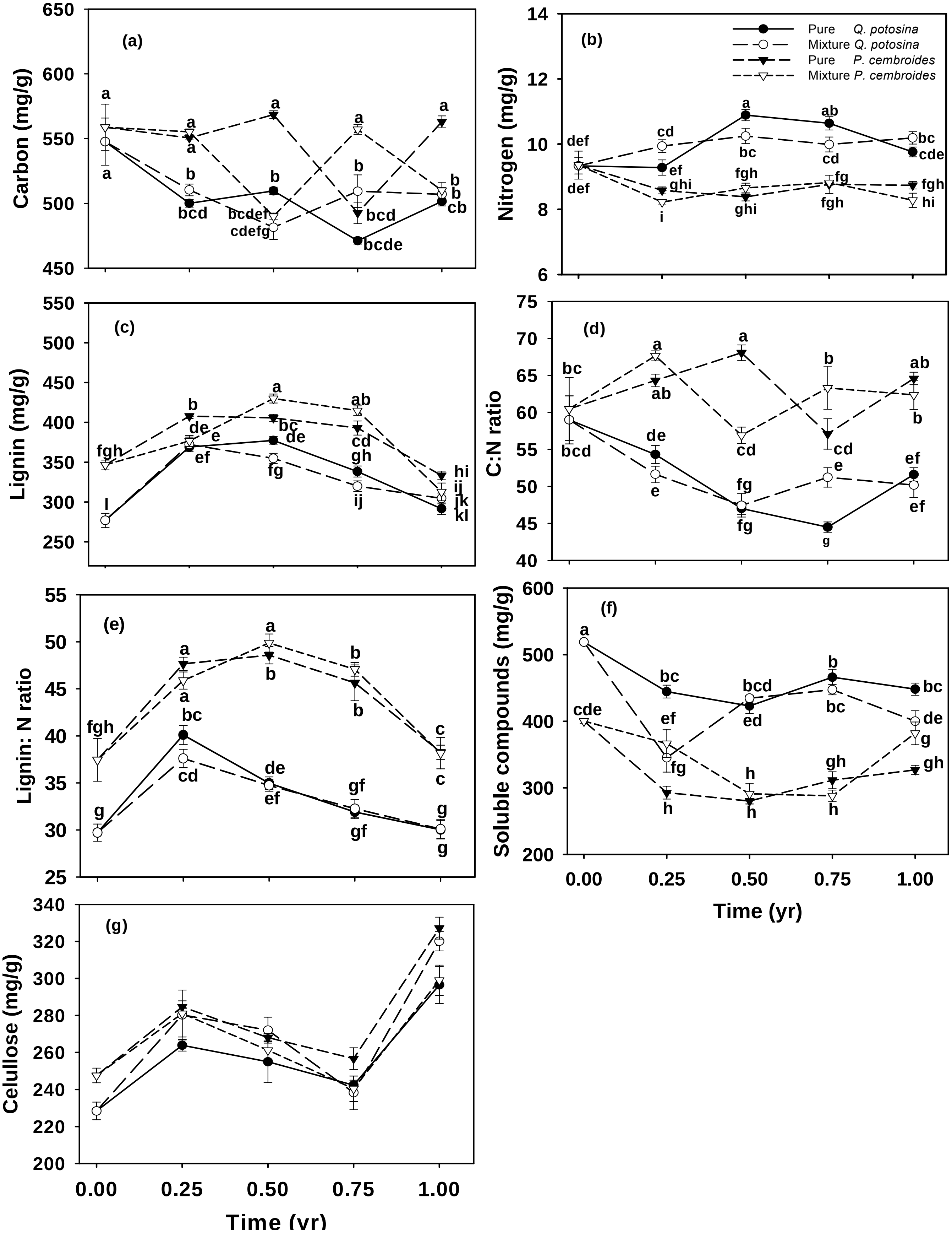


**Figure 3.1** Annual average percentages (%) of (a) mass loss of *Quercus potosina* and *Pinus cembroides* leaf litter incubated under pure and mixed species conditions. Leaf litter type ($P$ = 0.0001), time ($P$ = 0.0001) and species by time interaction ($P$ = 0.0212) were significant; (b) curve-fit of double decay function of percentage of ash-free dry mass (AFDM) remaining considering pure and mixed *Q. potosina* and *P. cembroides* leaf-litter during one year of *in situ* litter incubation. Vertical bars are one standard error ($P \leq 0.05$). Different letters indicate significant differences ($P \leq 0.05$).

Mass loss of *P cembroides* leaf litter did not differ between pure and mixed incubation conditions (Fig. 3.1b). Differences in mass loss between *Q. potosina* and *P. cembroides* leaf litter were maintained throughout the incubation year showing a rise at 1.0 year of incubation (Fig. 3.1b).

### **3.3.3** Leaf litter quality

Leaf litter types differed significantly in C and N concentration, and C:N ratio at the different sampling dates (leaf litter type x time interaction; $P \leq 0.0001$; Annex 3-3 and 3-4, respectively); but the leaf litter types did not differ in cellulose concentration at different sampling dates (leaf litter type x time interaction; $P = 0.7130$; Fig. 3.2g; Annex 3-9). Carbon concentration of *Q. potosina* litter was lower than that of *P. cembroides* litter at 0.25 yr of incubation, while N concentration of *Q. potosina* litter was higher than *P. cembroides* litter throughout the incubation period (Fig. 3.2a and b, respectively). When comparing litter quality of mixed and pure stands, litter C concentration of *P. cembroides* litter started differing at 0.5 years until 1.0 yrs of incubation, while for *Q. potosina* mixed and pure litter there were no differences among dates (Fig. 3.2a). Litter N concentration in *Q. potosina* litter differed between pure and mixed stands at 0.25, 0.5 and 0.75 years, while it was similar in both stand types for *P. cembroides* litter (Fig. 3.2b). C:N ratios (Fig. 3.2d) had a similar temporal dynamics as litter C concentration for both pure and mixed litter of *P. cembroides* and *Q. potosina*. The lignin, lignin:N ratio and soluble compounds (SC) concentration significantly differed among leaf litter types and incubation periods (leaf litter type x time, $P \leq 0.0001$; Annex 3-8), except for cellulose, which only differed with time (time main effect; $P = 0.0001$). Lignin percentage of *P. cembroides* leaf litter (pure and mixed) was higher at 0.5 and 0.75 years than that of *Q. potosina* litter (Fig. 3.2c). For *P. cembroides,* pure and mixed litter bags had different lignin percentages at 0.25, 0.5, and 0.75 years; whereas for *Q. potosina* pure and mixed litter differed only at 0.5 and 0.75 years. Litter lignin:N ratios were higher for *P. cembroides* than for *Q. potosina* leaf litter throughout the incubation period both in pure and mixed litter samples (Fig. 3.2e). Lignin:N ratios of pure and mixed *P. cembroides* litter differed only at 0.5 years of incubation.



(a)
Carbon (mg/g)
650
600
550
500
450
a
a
b
bcd
a
a
b
bcdef
cdefg
a
b
bcd
bcde
a
b
b
cb
(b)
Nitrogen (mg/g)
14
12
10
8
6
Pure Q. potosina
Mixture Q. potosina
Pure P. cembroides
Mixture P. cembroides
def
def
cd
ef
ghi
i
a
bc
fgh
ghi
ab
cd
fg
fgh
bc
cde
fgh
hi
(c)
Lignin (mg/g)
550
500
450
400
350
300
250
fgh
l
b
de
e
ef
a
bc
de
fg
ab
cd
gh
ij
hi
ij
jk
kl
(d)
C:N ratio
75
70
65
60
55
50
45
40
bc
bcd
a
ab
de
e
a
cd
fg
fg
b
cd
e
g
ab
b
ef
ef
(e)
Lignin: N ratio
55
50
45
40
35
30
25
fgh
g
a
a
bc
cd
a
b
de
ef
b
b
gf
gf
c
c
g
g
(f)
Soluble compounds (mg/g)
600
500
400
300
200
a
cde
bc
ef
fg
h
bcd
ed
h
h
b
bc
gh
h
bc
de
g
gh
0.00
0.25
0.50
0.75
1.00
Time (yr)
(g)
Celullose (mg/g)
340
320
300
280
260
240
220
200
0.00
0.25
0.50
0.75
1.00
Time (yr)

Overall, soluble carbohydrate (SC) concentration was higher in *Q. potosina* litter than in *P. cembroides* litter (litter type main effect; *P* = 0.0001). Soluble carbohydrate concentration showed a significant litter type by time interaction (*P* = 0.0001), SC in *Q. potosina* litter declined after 0.25 yr of incubation both in pure and mixed litter types, however the decline was greater in mixed than in pure litter. In contrast, in *P. cembroides* litter the drop in SC was greater in pure than in mixed litter samples. After one year, SC concentration was higher in pure than in mixed *Q. potosina* litter, while it did not differ between *P. cembroides* litter types (Fig. 3.2f).

### **3.3.4** Effects of rainfall and microsite on leaf litter decomposition

The total amount of rainfall that fell during the year of incubation was 337 mm, with the largest proportion (71%) falling in the first quarter of the study. Accumulated rainfall explained 97% of mass loss for *P. cembroides* leaf litter in pure and mixed incubation conditions (pure and mixed; $P < 0.05$; Fig. 3.3 c and d, respectively). In contrast, accumulated rainfall explained only 58% of mass loss of *Q. potosina* mixed-leaf litter ($R^2 = 0.58$; Fig. 3.3d). There was no significant difference in rainfall related mass loss between *P. cembroides* (pure and mixed) and *Q. potosina* (pure and mixed) litter.

Following a 30-day incubation period, tensile strength of cotton strips differed significantly between litter microsites (microsite main effect; P = 0.0082; Fig. 3.4) and season (season main effect; P < 0.0001); there was no significant microsite by season interaction (season x microsite main effect; P = 0.9029; Fig. 3.4). Cotton strips incubated in mixed litter microsites showed significantly lower tensile strength than those in pure *P. cembroides* litter microsites both during the dry and wet season. Tensile strength was lower in the wet season than in the dry season (Fig. 3.4).

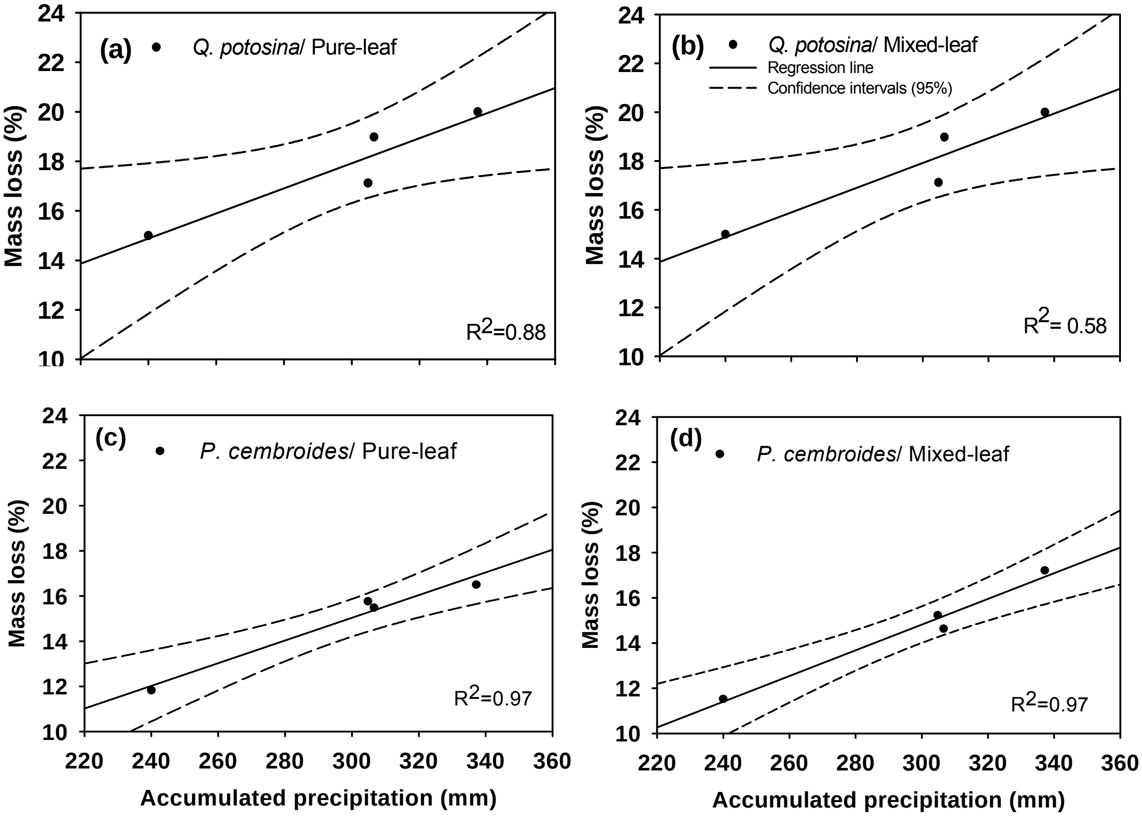


**Figure 3.3** Relationship between monthly accumulated precipitation and mass loss following a one-year incubation (four dates of sample collection) of leaf litter for *Quercus potosina* pure (a) and mixed (b), and *Pinus cembroides* pure (c) and mixed (d) conditions.

Soil water potential measured in the three stand microsites ranged between -0.01 MPa and -1.05 MPa in the months that received more than 40 mm of rain, while soil water potential dropped to -4.3MPa in the dry season (from January to March 2008; Fig. 3.5). Litter water content was significantly different among stand microsites. It was highest (*P* = 0.0001; Annex 3-11) for oak litter, lowest for pine litter and intermediate for mixed litter (Fig. 3.6).

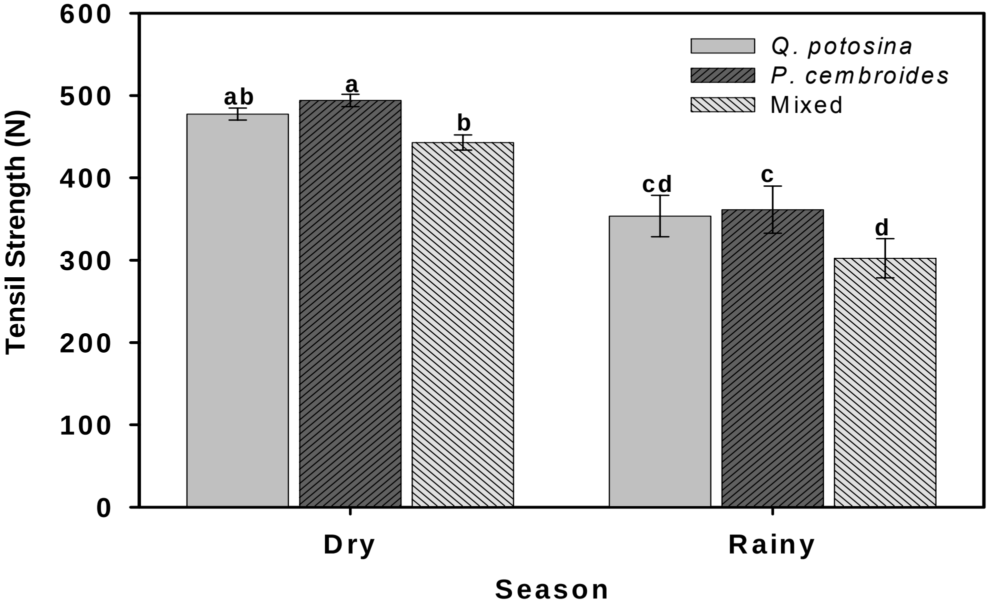


**Figure 3.4** Cotton strip tensile strength (Newton) incubated in *P. cembroides*, *Q. potosina* and mixed microsite litter. Microsite ($P$ = 0.0082) and season ($P$ = 0.0001) were significant, while microsite by season interaction was not significant ($P$ = 0.9029). Bars with different letters indicate significant differences ($P \leq 0.05$).

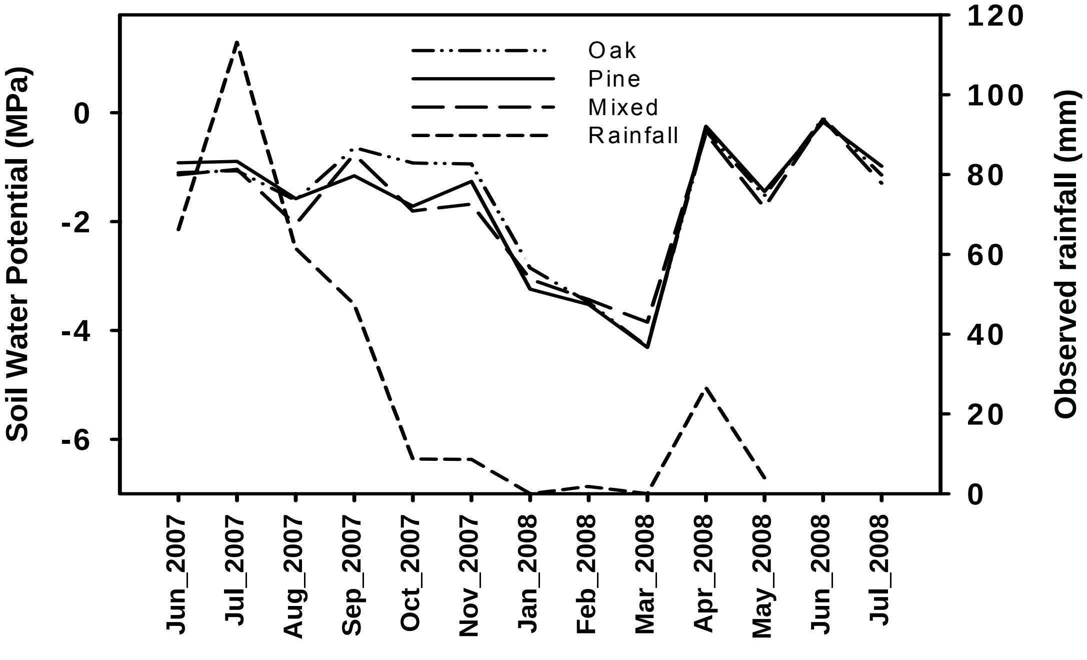


**Figure 3.5** Variation in soil water potential (MPa; left "y" axis) and monthly precipitation (mm; right "y" axis) at the study site in Sierra San Miguelito, San Luis Potosi, Mexico between June 2007 and July 2008.

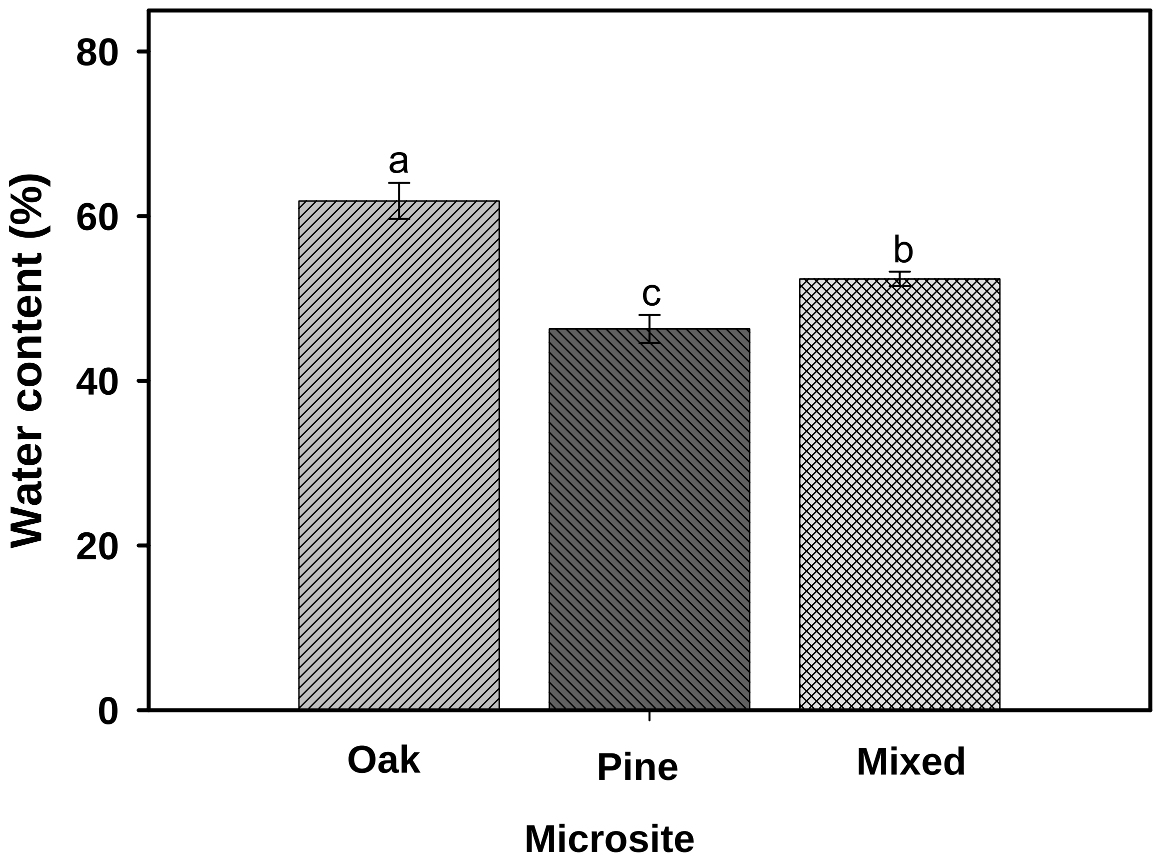


**Figure 3.6** Gravimetric water content of litter in the oak, pine and mixed microsite. Bars with different letters indicate significant differences (*P* = 0.0001).

### 3.5 Discussion

Interactions between plants, soil, decomposer organisms and hydrology regulate leaf-litter decomposition and nutrient cycling in forest ecosystems (Aerts, 1997; Berg and McClauherty, 2008), mainly when more than one leaf-litter type are decomposing on forest floors. In the present study, the hypotheses of Ostrofsky (2007) were tested by comparing decomposition rates of two contrasting leaf-litter types and the interacting effect of soil humidity. The study focused on the early phase of decomposition, when mass loss is largely controlled by precipitation. In the study, the effect on decomposition was evaluated considering inherent species-specific leaf litter quality, litter type mixtures, and soil moisture dynamics of two contrasting forest tree species with evergreen and deciduous life forms.

In pure tree stands, mass loss of *Q. potosina* leaf-litter occurred more rapidly than that of *P. cembroides,* confirming that broadleafed species decompose at a faster rate than coniferous species (Prescott *et al.,* 2000; Alvarez *et al*., 2008). For instance, broadleafed litter mass loss of mixed-wood forest types in British Columbia occurred at a faster rate than that of coniferous leaf litter but only during the first year of decomposition (Prescott *et al*., 2000). Since deciduous leaf litter usually has a higher concentration of labile compounds than coniferous species and since labile compounds are more easily leached out by rainfall facilitating decomposition by soil microflora and microfauna it is the decomposition of labile compounds that characterizes the early phase of litter decomposition (Gallardo and Merino, 1993; De Santo *et al.,* 1993). In this study, early-phase mass loss in both tree species occurred by decomposition of both labile and recalcitrant compounds, however with a much larger contribution of the labile fraction. Mass loss was most pronounced during the initial incubation period (0.25 years), coinciding with the largest annual rainfall input. Other studies have shown that moisture is an important control in litter decomposition in climates with water limitation (Cornejo *et al.,* 1994; Murphy *et al.,* 1998).

For the mixed stands, where litter on the forest floor is composed of a mixture of deciduous and coniferous leaves, it was proposed that slowly decomposing *P. cembroides* litter would decompose more rapidly when interacting with the faster decomposing litter of *Q. potosina* (hypothesis 1, Ostrofsky, 2007). Contrary to the prediction, in this one-year study, the presence of *Q. potosina* leaf litter did not enhance the decomposition rate of *P. cembroides* litter, when compared to decomposition rates of pure *P. cembroides* leaf-litter. These results suggest that *P. cembroides* leaf litter provides high structural stability attributable to highly lignified leaf tissue that likely has an overriding control on litter decomposition. Other studies have made similar observations, in that no distinctive species-specific litter effects were found in decomposition rates of mixed versus pure broadleafed and/or coniferous litter (Prescott *et al.,* 2000) or single and/or multi-species *Nothofagus* litter in Patagonian forests (Vivanco and Austin, 2008). Contrary to this study, Ganjegunte and collaborators (2005) reported that decomposition of *Pinus radiata* litter is delayed when incubated in the presence of understory species.

Mechanisms of mass loss at the early phase for *Q. potosina* leaf litter were contrary to expectations (second hypothesis; Ostrofsky, 2007). *Quercus potosina* mixed-leaf litter lost a larger amount of mass than pure-leaf litter (Fig. 3.1b). Most of this mass loss took place during the first 0.25 years of the study (Fig. 3.2b) probably due to a greater rate of SC leaching (>120 mg/g, Fig. 3.2f). The chemical mixture of oak (relatively high SC concentration) and pine litter (high cellulose and lignin concentration) may have triggered population growth of both bacteria and fungal species, respectively, which in turn may have enhanced the decomposition of SC and also the break down of lignified and cellulosic litter of the oak tissue whose concentrations were significantly lower in oak litter of mixed compared to pure incubations (cg. Fig. 3.2c, g; 0.5 years) coinciding with the significantly greater mass loss at 0.5 years (Fig. 3.1 b). This may be called a food chain-associated facilitative mechanism of decomposition of multiple-species litter mixtures. In contrast, litter mixtures may also exert inhibitory effects on litter decomposition of specific litter species, in that a greater abundance of water-soluble defensive and inhibitory compounds (tannins, phenolics, etc.) released by one litter species may reduce mass loss of another litter species. Results of this study demonstrate such potential inhibitory effects at 0.25 years, when high releases of *Q. potosina* SC seemed to have inhibited the release of *P. cembroides* SC (Fig. 3.2f) and also the breakdown of lignin (Fig. 3.2c). However, while the inhibitory effect on decomposition by high turn-over compounds (SC) seemed to have occurred almost instantly (compare curves of mixed oak and pine in Fig. 3.2f), it seemed to have a lag effect on halting decomposition of lignified material (compare mixed pine with pure pine curve at 0.25 and 0.5 years in Fig. 3.2c). In case of the inhibitory effect, these pronounced changes in the chemical litter environment were not reflected in differences in mass loss rates. Hence, our results suggest that interactive (facilitative and inhibitory) species litter mixtures can have quantitative and/or qualitative effects on litter decomposition. Soluble compounds include sugars, phenolics, hydrocarbons and glycerides (Berg and McClaugherty, 2008). In this study, an examination of changes in C and N litter tissue concentration (Fig. 3.2a, b) showed that most leached SC are probably made up of C-based compounds since no apparent leaching of N-based compounds was observed in *Q. potosina* mixed leaf litter.

Microenvironments derived from diverse litter mixtures may influence litter decomposition in two ways (Ostrofsky, 2007); first, by promoting a more persistent habitat for decomposing organisms and then accelerating decomposition of slow-decomposing species (such as *P. cembroides*), and/or second by the physical protection of rapid-decomposed species (such as *Q. potosina*) from the weakening effects of abrasion and leaching. In this study, standard cotton material was used to test potential micro-environmental effects of differential microbial activities as an underlying mechanism for differential leaf litter decomposition of pure and mixed-species litter. The results suggest that a mixture of litter of *P. cembroides* and *Q. potosina* appeared to favor microenvironmental conditions (e.g. soil humidity and aeration) probably also favoring differential microbial communities and higher microbial activity, together stimulating decomposition rates in litter mixtures compared to pure *P. cembroides* litter (Fig. 3.4). At the same time, mixed litter appeared to have protected *Q. potosina* leaf litter from abrasion and leaching, because, although *Q. potosina* mixed-leaf litter exhibited a higher mass loss rate than pure-leaf litter (Fig. 3.1b), the loss rate of the labile compounds of pure-leaf litter was greater than that of the recalcitrant compounds (Table 3.2). Overall, the pattern of mass loss rate was similar during both dry and wet seasons (Fig. 3.4). However, when taking a closer look at the water-content of *Q. potosina vs. P. cembroides* litter, it was found that the water content in soil under oak stands (Fig. 3.5) and in oak litter (Fig. 3.6) was greater than that associated with pine. This suggests that oak leaf litter had a greater capacity to retain water than pine leaf litter. Higher litter water content and most likely higher microbial activity, and a reduced effect of rainfall in mixed-leaf litter (55%) suggest that dissolution and leaching of compounds and nutrients was lower. Therefore, the activity of opportunistic microorganisms could have increased significantly the mass loss at 0.5 years in mixed-leaf litter from *Q. potosina*. Thus, the observed dynamics of soil water potential (Fig. 3.5) suggest that the water content of litter could be a factor that favors microenvironment conditions for microbial activity and thus for litter decomposition (Pataki *et al.,* 1998; Schimel *et al.,* 1999; Yan *et al.,* 2004; Berg and McClaugherthy, 2008).

In synthesis, this study demonstrates that decomposition of leaf litter depends on tree species-specific litter characteristics (quality), litter interaction types and microsite characteristics. Although tensile strength was lower (greater microbial activity) after the wet season than after the dry season, the overall pattern of tensile strength with respect to litter microenvironment remained constant (mixed > oak = pine). It is assumed that cotton decomposition was controlled mostly by the physic-chemical characteristics of the diverse litter microenvironments imposed by forest tree species composition, supporting hypothesis 3 of Ostrofsky (2007).

In accordance with previous studies (Gallardo and Merino, 1993; De Santo *et al.,* 1993), this study confirmed that rainfall leached a great amount of SC and became the main mechanism for mass loss at the early decomposition phase. Nevertheless, the effect of rainfall on mass loss also depended on leaf litter type. Accumulated rainfall explained 97% of mass loss of *P. cembroides* leaf litter incubated under pure and mixed conditions, while it explained only 88% and 55% of mass loss in *Q. potosina* pure- and mixed-leaf litter, respectively. The remainder of mass loss of *Q. potosina* leaf litter was a result of both interactive leaf-litter quality and/or microbial activity.

Thus, leaf litter mass loss observed in this study appeared to depend on the microenvironment created by the litter layer, accumulated rainfall and litter quality, so that mass loss changes in decomposing leaf litter represent the net effect of multiple processes such as were outlined by Ostrofsky (hypothesis 3). Where rainfall is markedly seasonal, moisture becomes an important regulator of decomposition and N mineralization (Cornejo *et al.,* 1994). Alternating wet and dry cycles may stimulate microbial activity through a change in microbial community composition by which fungi may prosper more in dry conditions compared to bacteria given their greater tolerance to water limitation (Berg and McClaugherthy, 2008).

## 3.6 Conclusions

The results of this study confirm that rainfall is an important factor in the rate of mass loss during the early phase of litter decomposition. It also suggests that rainfall controls interaction of litter material in mixed litter conditions during the early stage of decomposition as a consequence of leaching of soluble compounds from the litter. Nutrient leaching from litter depends on litter quality of each species and its associated litter microsite. Although the interactive effects of litter mixtures can be facilitative or inhibitory with respect to the chemical environment generated by litter interaction, species litter mixtures may have quantitative (affecting mass loss rate) and/or qualitative effects (differential chemical release without affecting mass loss rate) on tree litter decomposition. Mixed leaf-litter decomposition in a semiarid forest ecosystem of Central-Northern Mexico reflects a complex response matrix to multiple biophysical and chemical factors as has been proposed by Ostrofsky.

### 3.7 References

Aerts, R. (1997). Leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos* **79**, 439-439.

Alvarez, E., Fernández, M.L., Torrado, V., Fernández, M.J. (2008). Dynamics of macronutrients during the first stage of litter decomposition from forest species in a temperate area (Galicia, NW Spain). *Nutr. Cycl. Agroecosyst*. **80,** 243-256.

Belnap, J. Phillips S.L., Sherrod, S.K. and Moldenke, A. (2005). Soil biota can change after exotic plant invasion: does this effect ecosystem processes? *Ecology* **86,** 3007-3017.

Ball, B.A., Hunter M.D., Kominoski J.S., Swan C.M., and Bradford, M.A. (2008). Consequences of non-random species loss for decomposition dynamics: experimental evidence for additive and non-additive effects. *J. Ecology* **96**, 303-313.

Berg, B., Berg, M.P., Bottner, P., Box, E., Breymeyer, A.,de Anta, R.Ca.,Couteaux, M., Escudero, A., Gallardo, A., Kratz W., Madeira, M., Mälkönen, E. McClaugherty, C., Meentemeyer, V., Muñoz, F., Piussi P., Remacle, J., and de Santo, A.Vi. (1993). Litter mass loss rates in pine forests of Europe and Eastern United States: some relationships with climate and litter quality. *Biogeochemistry* **20**, 127-159.

Berg, B. and Laskowski, R. (2006). Litter Decomposition: A Guide to Carbon and Nutrient Turnover. Academic Press, United States of America.

Berg, B., and McClaugherty, C. (2008). Plant Litter: Decomposition, Humus Formation, Carbon Sequestration. 2nd edition, Springer. Germany. 338p.

Cardona, B.A. (2007). Hidrogeoquímica de sistemas de flujo, regional, intermedio y local resultado del marco geológico en la mesa central: reacciones, procesos y contaminación. Tesis doctorado, UNAM, Instituto de Geofísica, México, DF, 238p.

Cornejo, F.H., Varela, A., and Wright, J. (1994). Tropical forest litter decomposition under seasonal drought: nutrient release, fungi and bacteria. *Oikos* **70**, 83-190.

Coûteaux, M.M., Bottner P. and Berg, B. (1995). Litter decomposition, climate and litter quality. *Trends Ecol. Evol*. **10**, 63-66.

Coûteaux, M.M., McTiernan, K., Berg, B., Szuberla, D., and Dardennes, P. (1998). Chemical composition and carbon mineralisation potential of Scots pine needles at different stages of decomposition. *Soil Biol. Biochem***. 30,** 583–595.

De Santo, A.V., Berg B., Rutigliano, F.A., Alfani, A., and Fioretto, A. (1993). Factors regulating early-stage decomposition of needle litters in five different coniferous forests. *Soil Biol. Biochem*. **25**, 1423-1433.

Gallardo, A. and Merino, J. (1993). Leaf decomposition in two Mediterranean ecosystems of southwest Spain: influence of substrate quality. *Ecology* **74**, 152-161.

Ganjegunte, G.K., Condron, L.M., Clinton, P.W., and Davis, M.R. (2005). Effects of mixing radiata pine needles and understory litters on decomposition and nutrients release. *Biol. Fertil. Soils* **41,** 310-319.

García, E. (1988). Modificaciones al sistema de clasificación climática de Köppen para adaptarlo a las condiciones de la República Mexicana. Instituto de Geografía, UNAM, México, D.F. 246p.

Gartner, T.B. and Cardon, Z.G. (2004). Decomposition dynamics in mixed-species leaf litter. *Oikos* **104**, 230-246.

Harmon, M.E., Nadelhoffer, K.J. and Blair, J.M. (1999) Measuring decomposition, nutrient turnover, and stores in plant litter. *In:* Robertson, F.P., Coleman, D.C., Bledsoe, C.S., and Sollins, P. (Eds.). Standard Soil Methods for Long-Term Ecological Research. Oxford, USA. 202-240 p.

Hättenschwiler, S., and Gasser, P. (2005). Soil animals alter plant litter diversity effects on decomposition. *PNAS* **102,** 1519-1524.

INEGI. (2002). Síntesis de Información Geográfica del Estado de San Luis Potosí. Instituto Nacional de Estadística, Geografía e Informática, México.

Latter, P.M., and Walton, D.W.H. (1988). The cotton strip assay for cellulose decomposition studies in soil: history of the assay and development. In: Harrison AF, PM Latter, DWH Walton, (eds.) Cotton strip assay: an index of decomposition in soils. Grange-over-Sands, NERC/ITE, 7-10. (ITE Symposium, 24).

Melillo, J.M., Aber, J.D. and Muratore, J.F. (1982). Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* **63**, 621-626.

Moore, T.N., and Fairweather, P.G. (2006) Decay of multiple species of seagrass detritus is dominatd by species identity, with an important influence in mixing litters. *Oikos* **114**, 329-337.

Murphy, K.L., Klopatec J.M., Klopatec C.C. (1998). The effects of litter quality and climate on decomposition along an elevational gradient. *Ecol. Appl.* **8**, 1061-1071.

Ostrofsky M.L. (2007). A comment on the use of exponential decay models to test nonadditive processing hypotheses in multispecies mixtures of litter. *J. N. Am. Benthol. Soc.* **26**, 23-27.

Pataki, D.E., Oren R., Katul G., and Sigmon J. (1998). Canopy conductance of *Pinus taeda*, *Liquidambar styracifluan* and *Quercus phellos* under varying atmospheric and soil water condition. *Tree Physiol*. **18**, 307-315.

Pérez-Hanguindeguy N., Blundo, C.M. Gurvich, D.E, Díaz, S., Cuevas, E. (2008). More than the sum of its parts? Assessing litter heterogeneity effects on the decomposition of litter mixtures through leaf chemistry. *Plant Soil* **303**, 151-159.

Pérez-Suárez, M., Arredondo-Moreno J.T., Huber-Sannwald E., Vargas-Hernández J.J. (2009). Production and quality of senesced and green litter fall in a pine-oak forest in central-northwest Mexico. *For. Ecol. Manage*. (*in press*).

Prescott, C.E., Zabek, L.M., Staley C.L., Kabzems, R. (2000). Decomposition of broadleaf and needle litter in forests of British Columbia: influences of litter type, forest type, and litter mixtures. *Can. J. For. Res*. **30**, 1742-1750.

Robert, M.F. (1977). Notas sobre el estudio ecológico y fitogeográfico de los bosques de *Pinus cembroides*, Zucc., en México. *Ciencia Forestal* **10**, 49-58.

Rzedowski, J. (1978). Vegetación de México. Ed. Limusa. México, DF, 432p.

SAS Institute Inc., 2002-2003. SAS user's guide, Version 9.1.3. SAS Institute, Inc., Cary, NC., USA.

Schimel, J.P., Gulledge, J.M., Clein-Curley, J.S., Lindstrom, J.E., and Braddock J.F. (1999). Moisture effects on microbial activity and community structure in decomposing birch litter in the Alaskan taiga. *Soil Biol. Biochem*. **6**, 831-838.

Taylor, B.R., Parsons, W.F.J., and Parkinson, D. (1989). Decomposition of *Populus tremuloides* leaf litter accelerated by addition of *Alnus crispa* litter. *Can. J. For. Res.* **19**, 674–679.

Vivanco, L., and Austin, A.T. (2008). Tree species identity alters forest litter decomposition through long-term plant and soil interactions in Patagonia, Argentina. *J. Ecology* **96**, 727-736.

Wieder, R.K., and Lang, G.E. (1982). A critique of the analytical methods used in examining decomposition data obtained from litter bag. *Ecology* **63**, 1636-1664.

Yan, W., Qing-li, W., Li-min, D., Miao W., Li, Z., and Bao-qing, D. (2004). Effect of soil moisture gradient on structure of broad-leaven/Korean pine forest in Changbai Mountain. J*. For. Res*. **15,** 119-123.

Zavala, C.F., and García, M.E. (1991). Fenología y crecimiento del brote anual de *P. cembroides* Zucc. de San Luis Potosí, México. *BIOTA*M **3**, 5-14.

## General Conclusions

The present study evaluated how *Pinus cembroides* and *Quercus potosina,* two species with contrasting inherent life-history traits and growth characteristics, that influenced nutrient cycling and water redistribution in the semiarid forest ecosystem of central-northwest Mexico. The influence of these species on those important ecosystem processes was evaluated under monospecific and mixed conditions.

This study showed that *Q. potosina* and *P. cembroides* had contrasting structural traits that exerted differential effects on rainfall redistribution processes (throughfall, stemflow and runoff). Canopy gaps, stem diameter, litter water content and litter quantity were among the forest stand characteristics that controlled the different fluxes. Regarding rainfall characteristics, the results of this study show that the size of rainfall events played an important role in triggering some of these hydrological processes.

This study also characterized the contribution of different forest stand types to litter production and the potential nutrient inputs. In this case, clear differences in both litterfall production and nutrient inputs were observed for the composition of different stands. This study specifically highlighted the importance and contribution of green leaf fall and of extreme events contribution to nutrient cycling in semiarid forest ecosystems.

Finally, the study allowed testing of a theoretical framework regarding litter decomposition mechanisms at the early decomposition phase. Results from this experiment suggest that slow decomposing species from semiarid forest from central-northwest Mexico did not ascribe to expected mechanisms when incubated under mixed litter conditions. In contrast, mass loss from rapid decomposing species was favored under mixed litter conditions, which did not coincide with the framework used. Additionally, incubation of standard cotton material showed that improvement of the structural litter pack of mixed forest stands favored decomposition processes.

Leaf traits such as morphology, spatial arrangement, and leaf lifespan influenced rainfall interception, stemflow and throughfall. At the same time, on soil surface, some of these characteristics (e.g. litterfall production, quantity, morphology and chemical composition of litter) influenced runoff and litter decomposition and recycling of nutrients. This study points to the importance of using the approach of functional matrix as an integrative tool to evaluate the multiple effects of inherent characteristic of *Q. potosina* and *P. cembroides* on processes of cycling of nutrients and water in the forests ecosystem. It is also important to evaluate the effect of one species when it is found alone or mixed with others species in semiarid forests of central-northwest Mexico.

Based on the results of this study, we additionally suggest evaluating characteristics of stand types and species such as cover of canopies, roughness and repellency of stem bark of each species to evaluate their effect on the interception, retention and redistribution of rainwater. Moreover, we recommend evaluating directly the litter water content and its relationship with runoff, litter weathering and abundance of decomposing microorganisms in each stand type. Finally, in reference to decomposition, we suggest evaluating the temporal variation to long-term nutrients concentration and mass loss.

## Annex 1 Tables of ANOVA from statistical analysis of the Chapter I

| **Response Variables** | **ANOVA<br>Source of variation** | **df** | **F** | ***P*** |
|---|---|---|---|---|
| **1. Stem diameter (cm)** | Stand types | 3 | 2.04 | 0.1626 |
| **2. Transmittance** | Stand types | 2 | 19.32 | **<0.0001** |
| **3. Litter Quantity g/m$^2$** | Stand Type | 2 | 8.19 | **0.0024** |
| **4. Throughfall (liter per rainfall event)** | Transmittance (T) | 1 | 0.14 | 0.7217 |
| | Stand types (S) | 2 | 0.89 | 0.4572 |
| | Time (t) | 46 | 1.73 | **0.0044** |
| | S*t | 92 | 1.58 | **0.0028** |
| | T*S | 2 | 0.41 | 0.6821 |
| | T*t | 46 | 1.22 | 0.1732 |
| | T*S*t | 92 | 1.26 | 0.0797 |
| **5. Stemflow (liters per rainfall event)** | Diameter (D) | 1 | 41.49 | **0.0002** |
| | Stand types (S) | 3 | 18.42 | **0.0006** |
| | Time (t) | 57 | 0.59 | 0.9928 |
| | S*t | 170 | 1.09 | 0.2359 |
| | D*S | 3 | 22.48 | **0.0003** |
| | D*t | 57 | 1.74 | **0.0012** |
| | D*S*t | 170 | 1.21 | 0.0629 |
| **6. Runoff (liters per m$^2$ per rainfall event)** | Transmittance (T) | 1 | 0.28 | 0.6180 |
| | Stand types (C) | 2 | 0.71 | 0.5304 |
| | Time (t) | 20 | 7.80 | **<0.0001** |
| | S*t | 40 | 2.17 | **<0.0001** |
| | T*S | 2 | 6.17 | **0.0350** |
| | T*t | 20 | 3.34 | **<0.0001** |
| | T*S*t | 40 | 2.29 | **<0.0001** |
| **7. Reg procedure** | | | | |
| Dependent Variable | Runoff | | | |
| Independent Variable | Transmittance | | | |
| (a) *Q. potosina* | Model | 1 | 3.45 | 0.0643 |
| | Error | 282 | | |
| | Total | 283 | | |
| (b)*P. cembroides* | Model | 1 | 0.59 | 0.4425 |
| | Error | 282 | | |
| | Total | 283 | | |
| (c) Mixed | Model | 1 | 0.01 | 0.9335 |
| | Error | 282 | | |
| | Total | 283 | | |

## Annex 1 Tables of ANOVA from statistical analysis of the Chapter I (continuation)

| **Response Variables** | **ANOVA Source of variation** | **df** | **F** | ***P*** |
|---|---|---|---|---|
| **8. Reg procedure** | | | | |
| Dependent Variable | Throughfall | | | |
| Independent Variable | Rainfall size | | | |
| (a) *Q. potosina* | Model | 1 | 213.45 | **<0.0001** |
| | Error | 180 | | |
| | Total | 181 | | |
| (b)*P. cembroides* | Model | 1 | 564.0 | **<0.0001** |
| | Error | 179 | | |
| | Total | 180 | | |
| (c) Mixed | Model | 1 | 0.01 | **<0.0001** |
| | Error | 181 | | |
| | Total | 182 | | |
| **9. Reg procedure** | | | | |
| Dependent Variable | Stemflow | | | |
| Independent Variable | Rainfall size | | | |
| (a) *Q. potosina* | Model | | | **<0.0001** |
| | Error | | | |
| | Total | | | |
| (b)*P. cembroides* | Model | | | **<0.0001** |
| | Error | | | |
| | Total | | | |
| (c) Mixed | Model | | | **<0.0001** |
| | Error | | | |
| | Total | | | |
| **10. Reg procedure** | | | | |
| Dependent Variable | Runoff | | | |
| Independent Variable | Rainfall size | | | |
| (a) *Q. potosina/*Monospecific | Model | 1 | 268.19 | **<0.0001** |
| | Error | 225 | | |
| | Total | 226 | | |
| (b) *Q. potosina/*Mixed | Model | 1 | 315.28 | **<0.0001** |
| | Error | 226 | | |
| | Total | 227 | | |
| (c)*P. cembroides/*Monospecific | Model | 1 | 421.33 | **<0.0001** |
| | Error | 216 | | |
| | Total | 217 | | |
| (d) P. cembroides/ Mixed | Model | 1 | 442.93 | **<0.0001** |
| | Error | 224 | | |
| | Total | 225 | | |

## Annex 2 Tables of ANOVA from statistical analysis of the Chapter II

| Response Variables | ANOVA Source of variation | df | F | *P* |
|---|---|---|---|---|
| **1. Total Litterfall (kg/ha/year)** | Stand type (S) | 2 | 7.47 | **0.050** |
| | Time (t) | 11 | 280.96 | **<.0001** |
| | S*t | 22 | 1.34 | 0.1672 |
| **2. Litterfall (kg/ha/month)** | Stand type (S) | 2 | 6.49 | **0.0011** |
| | Fraction(S) | 6 | 18.47 | **<.0001** |
| | time (t) | 11 | 195.20 | **<.0001** |
| | S*t | 22 | 1.47 | 0.1017 |
| | t*Fraction(S) | 66 | 5.63 | **<.0001** |
| **3. Leaf-litterfall Carbon (mg/g)** | Stand type (S) | 3 | 2.50 | 0.1091 |
| | time (t) | 9 | 4.52 | **<.0001** |
| | S*t | 27 | 0.81 | 0.7274 |
| **4. Leaf-litterfall Nitrogen (mg/g)** | Stand type (S) | 3 | 27.34 | **<0.0001** |
| | time(t) | 9 | 12.86 | **<0.0001** |
| | S*t | 27 | 3.02 | **<0.0001** |
| **5. Leaf-litterfall Phosphorous (mg/g)** | Stand type (S) | 3 | 0.63 | 0.6094 |
| | t (t) | 9 | 39.52 | **<0.0001** |
| | S*t | 27 | 1.16 | 0.2885 |
| **6. Leaf-litterfall Lignin (%)** | Stand type (S) | 3 | 55.15 | **<0.0001** |
| | time (t) | 7 | 16.07 | **<0.0001** |
| | S*t | 21 | 3.09 | **<0.0001** |
| **7. Leaf-litterfall C:N ratio** | Stand type (S) | 3 | 4.55 | **0.0238** |
| | time (t) | 9 | 6.61 | **<0.0001** |
| | S*t | 27 | 1.04 | 0.4204 |
| **8. Leaf-litterfall N:P ratio** | Stand type (S) | 3 | 5.69 | **0.0117** |
| | time (t) | 9 | 10.74 | **<0.0001** |
| | S*t | 27 | 1.36 | 0.1368 |
| **9. Leaf-litterfall Lignin: N ratio** | Stand type (S) | 3 | 6.86 | **<0.0001** |
| | time (t) | 7 | 5.41 | **<0.0001** |
| | S*t | 21 | 1.3 | 0.1923 |
| **10. Green *vs.* Senescent litter** | | | | |
| N (mg/g) | Treatment | 7 | 1.76 | 0.1140 |
| C (mg/g) | Treatment | 7 | 1.25 | 0.2930 |
| Lignin (%) | Treatment | 7 | 14.56 | **<0.0001** |
| C:N ratio | Treatment | 7 | 1.46 | 0.2016 |
| P (mg/g) | Treatment | 7 | 0.57 | 0.7802 |
| Lingin:N ratio | Treatment | 7 | 6.45 | **<0.0001** |
| C:P ratio | Treatment | 7 | 0.57 | 0.7802 |
| P:N ratio | Treatment | 7 | 1.09 | 0.3799 |

# Annex 3 Tables of ANOVA from statistical analysis of the Chapter III

| **Response Variables** | **ANOVA Source of variation** | **df** | **F** | ***P*** |
|---|---|---|---|---|
| **1. Initial Litter Quality** | | | | |
| Moisture content (%) | Litter type | 1 | 10.61 | **0.0116** |
| Ash (%) | Litter type | 1 | 139.3 | **<0.0001** |
| Soluble Compounds (%) | Litter type | 1 | 740.25 | **<0.0001** |
| Cellulose (%) | Litter type | 1 | 9.59 | **0.0148** |
| Lignin (%) | Litter type | 1 | 41.69 | **0.0002** |
| C (%) | Litter type | 1 | 0.19 | 0.6739 |
| N (%) | Litter type | 1 | 0.00 | 0.9626 |
| P (%) | Litter type | 1 | 6.05 | **0.0337** |
| K (%) | Litter type | 1 | 9.63 | **0.0146** |
| Ca (%) | Litter type | 1 | 118.70 | **<0.0001** |
| Mg (%) | Litter type | 1 | 0 | 1.0000 |
| Na (%) | Litter type | 1 | 4.50 | 0.0667 |
| Mn (ppm) | Litter type | 1 | 139.91 | **<0.0001** |
| C: N ratio | Litter type | 1 | 0.08 | 0.7898 |
| Lignin: N ratio | Litter type | 1 | 10.05 | **0.0132** |
| N: P ratio | Litter type | 1 | 12.07 | **0.0084** |
| **2. Mass loss (%)** | Litter type (L) | 3 | 45.59 | **<0.0001** |
| | Time (t) | 3 | 44.45 | **<0.0001** |
| | L*t | 9 | 01.66 | **0.0212** |
| **3. Litter Carbon (mg/g)** | Litter type (L) | 3 | 30.68 | **<0.0001** |
| | Time (t) | 3 | 5.37 | **0.0013** |
| | L*t | 9 | 12.51 | **<0.0001** |
| **4. Litter Nitrogen (mg/g)** | Litter type (L) | 3 | 101.25 | **<0.0001** |
| | Time (t) | 3 | 8.39 | **<0.0001** |
| | L*t | 9 | 4.33 | **<0.0001** |
| **5. Litter lignin (mg/g)** | Litter type (L) | 3 | 60.90 | **<0.0001** |
| | Time (t) | 3 | 122.95 | **<0.0001** |
| | L*t | 9 | 8.94 | **<0.0001** |
| **6. Litter C: N** | Litter type (L) | 3 | 118.78 | **<0.0001** |
| | Time (t) | 3 | 11.88 | **<0.0001** |
| | L*t | 9 | 6.60 | **<0.0001** |
| **7. Litter lignin: N** | Litter type (L) | 3 | 158.78 | **<0.0001** |
| | Time (t) | 3 | 58.09 | **<0.0001** |
| | L*t | 9 | 4.77 | **<0.0001** |
| **8. Litter soluble compounds (mg/g)** | Litter type (L) | 3 | 116.80 | **<0.0001** |
| | Time (t) | 3 | 2.80 | **0.0407** |
| | L*t | 9 | 7.80 | **<0.0001** |

## Annex 3 Tables of ANOVA from statistical analysis of the Chapter III (continuation)

| Response Variables | ANOVA Source of variation | df | F | *P* |
|---|---|---|---|---|
| **9. Litter cellulose (mg/g)** | Litter type (L) | 3 | 4.66 | **0.0035** |
| | Time (t) | 3 | 57.07 | **<0.0001** |
| | L*t | 9 | 0.70 | 0.7130 |
| **10. Tensile strength (N)** | Stand type (S) | 2 | 5.02 | **0.0082** |
| | Time (t) | 1 | 75.67 | **<0.0001** |
| | S*t | 2 | 0.10 | 0.9029 |
| **11. Litter water content (%)** | Stand type (S) | 2 | 21.63 | **<0.0001** |