UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS
INSTITUTO DE GEOLOGÍA
MANEJO INTEGRAL DE ECOSISTEMAS

EFECTO DE LA CALIDAD Y CANTIDAD DE LA MATERIA ORGÁNICA DE TRES ESPECIES ARBÓREAS SOBRE LA DINÁMICA DEL CARBONO Y NUTRIENTES EN UN GRADIENTE ALTITUDINAL DE UN BOSQUE TEMPLADO DE ALTA MONTAÑA

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTORA EN CIENCIAS

PRESENTA:
ROSA ISELA JASSO FLORES

TUTOR PRINCIPAL DE TESIS:
DR. LEOPOLDO GALICIA SARMIENTO
INSTITUTO DE GEOGRAFÍA, UNAM

COMITÉ TUTOR:
DR. FELIPE FRANCISCO GARCÍA OLIVA
INSTITUTO DE INVESTIGACIONES EN ECOSISTEMAS Y SUSTENTABILIDAD, UNAM
DRA. ANGELINA MARTÍNEZ YRIZAR
INSTITUTO DE ECOLOGIA, CAMPUS HERMOSILLO, UNAM

CIUDAD UNIVERSITARIA, CD.MX ., SEPTIEMBRE, 2020.

UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS
INSTITUTO DE GEOLOGÍA
MANEJO INTEGRAL DE ECOSISTEMAS

EFECTO DE LA CALIDAD Y CANTIDAD DE LA MATERIA ORGÁNICA DE TRES ESPECIES ARBÓREAS SOBRE LA DINÁMICA DEL CARBONO Y NUTRIENTES EN UN GRADIENTE ALTITUDINAL DE UN BOSQUE TEMPLADO DE ALTA MONTAÑA

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTORA EN CIENCIAS

PRESENTA:
ROSA ISELA JASSO FLORES

TUTOR PRINCIPAL DE TESIS:
DR. LEOPOLDO GALICIA SARMIENTO
INSTITUTO DE GEOGRAFÍA, UNAM

COMITÉ TUTOR:
DR. FELIPE FRANCISCO GARCÍA OLIVA
INSTITUTO DE INVESTIGACIONES EN ECOSISTEMAS Y SUSTENTABILIDAD, UNAM
DRA. ANGELINA MARTÍNEZ YRIZAR
INSTITUTO DE ECOLOGIA, CAMPUS HERMOSILLO, UNAM

CIUDAD UNIVERSITARIA, CD.MX 2020

POSGRADO
CIENCIAS
BIOLÓGICAS

UNAM
POSGRADO

COORDINACIÓN DEL POSGRADO EN CIENCIAS BIOLÓGICAS
ENTIDAD INSTITUTO DE GEOLOGÍA
OFICIO CPCB/595/2020
ASUNTO: Oficio de Jurado

M. en C. Ivonne Ramírez Wence
Directora General de Administración Escolar, UNAM
Presente

Me permito informar a usted que en la reunión ordinaria del Subcomité de Biología Evolutiva, Ecología, Manejo Integral de Ecosistemas y Sistemática del Posgrado en Ciencias Biológicas, celebrada el día **24 de febrero de 2020** se aprobó el siguiente jurado para el examen de grado de **DOCTORA EN CIENCIAS** de la estudiante **JASSO FLORES ROSA ISELA** con número de cuenta **300267622** con la tesis titulada **"EFECTO DE LA CALIDAD Y CANTIDAD DE LA MATERIA ORGÁNICA DE TRES ESPECIES ARBÓREAS SOBRE LA DINÁMICA DEL CARBONO Y NUTRIENTES EN UN GRADIENTE ALTITUDINAL DE UN BOSQUE TEMPLADO DE ALTA MOÑTAÑA",** realizada bajo la dirección del DR. LEOPOLDO GALICIA SARMIENTO**,** quedando integrado de la siguiente manera:

Presidente:	DRA. YUNUEN TAPIA TORRES
Vocal:	DRA. SILKE CRAM HEYDRICH
Secretario:	DR. FELIPE FRANCISCO GARCÍA OLIVA
Suplente:	DRA. ROCIO JETZABEL ALCÁNTARA HERNÁNDEZ
Suplente:	DR. NOÉ MANUEL MONTAÑO ARIAS

Sin otro particular, me es grato enviarle un cordial saludo.

ATENTAMENTE
"POR MI RAZA HABLARÁ EL ESPÍRITU"
Cd. Universitaria, Cd. Mx., a 22 de septiembre de 2020

COORDINADOR DEL PROGRAMA

DR. ADOLFO GERARDO NAVARRO SIGÜENZA

COORDINACIÓN DEL POSGRADO EN CIENCIAS BIOLOGICAS
UNIDAD DE POSGRADO
Edificio D, 1° Piso. Circuito de Posgrados, Ciudad Universitaria
Alcaldía Coyoacán. C. P. 04510 CDMX
Tel. (+5255)5623 7002 http://pcbiol.posgrado.unam.mx/

Agradecimientos institucionales

Este trabajo es parte de la investigación doctoral de R. I. Jasso Flores, agradezco al Posgrado en Ciencias Biológicas de la Universidad Nacional Autónoma de México por su apoyo académico. Al Consejo Nacional de Ciencia y Tecnología (CONACYT) por el apoyo económico (Beca 50780-F) durante mis estudios y a la subvención PAPIIT-UNAM EN 104515 por los fondos que hicieron posible esta investigación.

A mi tutor principal el Dr. Leopoldo Galicia Sarmiento, gracias por tu tiempo, apoyo y dedicación invertidos en mi formación académica y personal. Gracias por incorporarme a tu equipo de trabajo, por tu disposición a innovar con esta investigación, siempre buscando opciones de cómo sí hacer posible este proyecto. Gracias por formar equipo conmigo.

A los miembros de mi Comité Académico, Dra. Angelina Martínez Yrízar, por estar al pendiente de mi persona y de mi proceso académico. Gracias por sus comentarios y acotaciones que enriquecieron este trabajo, las cuales exigieron mi crecimiento académico.

Al Dr. Felipe García Oliva, por su apoyo en momentos de crisis. Gracias por aceptarme en su laboratorio y mostrarme como hacer un trabajo de calidad y excelencia. Así como por sus comentarios, ideas y colaboraciones que hicieron que este trabajo sea maravilloso.

Gracias, los llevo en mi vida con gran estima.

Agradecimientos personales

Polo, gracias por tu tiempo y paciencia. Por darme un espacio en tu grupo y por estar conmigo en los momentos felices y críticos. Por el tiempo en carretera y esas aventuras en campo que se han vuelto leyenda. Por proyectar mis ideas y empoderarme para hacerlas crecer. Te estimo mucho, gracias por estar a mi lado durante ya casi 10 años.

Dr. Felipe, gracias por ser una gran inspiración para mi, lo admiro y respeto.

A los miembros del jurado, Dra. Yunuen Tapia Torres, Dra, Silke Cram Heydrich, Dra. Rocío Jetzabel Alcántara Hernández, Dr. Noé Manuel Montaño Arias por su paciencia, disposición y comentarios.

Dedicatoria

A mi padre Gilberto Jasso y a mis madres Rosa y Tita Flores, que fueron, son y serán mis árboles, mis pilares**,** gracias por amarme y darme la vida. Gracias por estar en cada parte de mi proceso. Por apoyarme y sostenerme no importa como y no importa que. Por cuidarme, darme felicidad y amor. Gracias por ser mi ejemplo de vida, familia, comprensión, tolerancia y disciplina, gracias por el valor y la fortaleza que muestran en cada día de su vida, los amo y los admiro.

A José Antonio Alcántara, amor mío gracias por regresarme a la vida y darme la libertad de descubrirme. Por tu apoyo incondicional y tu ser libre, amoroso y sincero. Gracias por el café y los conciertos matutinos, por las pláticas inagotables de música, películas, arte, política, ciencia y vida. Por disfrutar conmigo los placeres de la vida y enseñarme que siempre hay algo más que descubrir.

A Jorge Luis Hurtado, por ser mi carnal, por amarme, y ser uno de mis pilares. Gracias por este tiempo en el cual has sembrado una nueva perspectiva de lo que significa ser enfocado, comprometido y determinado, te amo mucho.

A Jorge Cortés, por ser mi acompañante cada una de las veces que te necesité y te necesito, gracias por estar para mi. Hemos generado tantas historias juntos que sería absurdo creer que algún día se olvidaran, somos el equipo perfecto. Por un verano increíble y las tardes de playa, por darme amor, abrazarme y quererme, te amo mucho guapo.

A mis amigos Laura A, Bruno, Itzi y Raiza. Laura, gracias por acompañarme, por compartir este espacio académico conmigo y darme amor y amistad. Por ser una amiga sincera y objetiva y limpiarme mis heridas cuándo lo necesitaba. Te quiero mucho.

Bruno, gracias por impulsarme y sostenerme, y en particular durante los primeros años de este proceso que fue uno de los momentos más críticos por los que pase, gracias por haber sido escucha y amistad. Gracias por todo.

Itzi, damita, gracias por escucharme, sostenerme y hacerme ver que el doctorado es solo una parte de la vida. Gracias por el café, risas y aguantar mi estrés inagotable.

Raiza, gracias por abrirme las puertas de tu hogar y de tu corazón. Gracias por las mañanas y las tardes de cocina y por compartir a Mijailchis. Te quiero conejo

Al Dr. Lorenzo Vázquéz Selem, gracias por enseñarme las maravillas de los bosques, por acompañarme a campo y por ser un compañero y amigo sincero.

A Enrique Pérez, ey, gracias por todo!!! Y en particular, por compartir el tiempo y espacio. “Porque al igual que tenéis ojos para ver la luz, oídos para oír los sonidos, tenéis un corazón para percibir, con él, el tiempo. Y todo el tiempo que no se percibe con el corazón está perdido” (Momo, Michael Ende, 1973).

A Héctor Medel Cobaxin, apestoso, solo escribiré… FIESTA, FIESTA, FIESTA!!! TRABAJO, TRABAJO, TRABAJO!!!!! Muak muak muak muak

A mis compañeros, Eliza S, Karla V, Karla S, Brenda, Iliana, Laura O, Balam, Lucas, Eloy, por todos los momentos divertidos, sus consejos y pláticas.

A Azucena Adame e IVM, por la energía y dirección que me dieron. Gracias

Índice

Capítulo uno

Are vegetation-soil systems drivers of ecosystem carbon contents along an elevational gradient in a highland temperate forest?

Capítulo dos

Soil organic matter dynamics and microbial metabolism along an altitudinal gradient in Highland tropical forests

Lista de figuras y cuadros

No.pag

Resumen general de la tesis

Capítulo uno

Are vegetation-soil systems drivers of ecosystem carbon contents along an elevational gradient in a highland temperate forest?

Capítulo dos

Soil organic matter dynamics and microbial metabolism along an altitudinal gradient in Highland tropical forests

Índice de abreviaturas

^{13}C CPMAS NMR	Espectroscopia de estado sólido del 13C NMR
A:OA	Proporción de alkyl:O-alkyl
Ai	índice aromático
Aj	*Alnus jorullensis*
alkyl C	Región del espectro 13C CP-MAS NMR (0-45 ppm)
AP	Fosfo-monoesterasa
Ar	*Abies religiosa*
aromatic C	Región del espectro 13C CP-MAS NMR (110-160 ppm)
BGL	β-1,4-glucosidase
C	Carbono (elemento)
carbonyl	Región del espectro 13C CP-MAS NMR (160-210 ppm)
C_{mic}	Carbono microbiano
CO^2	Dióxido de carbono
Ct	Carbono total
d.b.h	Diámetro a la altura del pecho
DES	Deshidrogenasa
COD/DOC	Carbono orgánico disuelto/dissolved organic carbon
NOD/DON	Nitrógeno orgánico disuelto/dissolved organic nitrogen
POD/DOP	Fósforo orgánico disuelto/dissolve organic phosphorous
DSC-TG	Calorimetría diferencial y termogravimetría
EE	Enzimas extracelulares
H´	Homeostasis
HB:HI	Proporción de hidrofobicidad
HPO_4^2	Ortofosfato
k0	Velocidad de descomposición
MAP	Precipitación media anual
MAT	Temperatura media anual
MRT	Tiempo medio de residencia
N	Nitrógeno (elemento)
NAG	β-1,4-N-acetylglucosaminidase
NH_4^+	Amonio
N_{mic}	Nitrógeno microbiano
NO_3^-	Nitrato
Nt	Nitrógeno total
O-alkyl C	Región del espectro 13C CP-MAS NMR (45-110 ppm)
OA:Ar	O-alkyl:aromatic ratio
OL	Capa orgánica, mantillo

OM	Materia orgánica
P	Fósforo (elemento)
Ph	*Pinus hartwegii*
P_{mic}	Fósforo microbiano
POX	Polyfenol oxidasa
Pt	Fósforo total
Q	Calor de combustión (J per gram)
Q1	Región del DSC que representa la materia orgánica lábil (<375 °C)
Q2	Región del DSC que representa la materia orgánica recalcitrante (375-475 °C)
Q3	Región del DSC que representa la materia orgánica extra-recalcitrante (475–550 °C)
COS/SOC	Carbono orgánico del suelo/soil organic carbon
MOS/SOM	Materia orgánica del suelo/soil organic matter
$T50_Q$	Temperatura a la que el 50% de la energía contenida en la materia orgánica se libera
TER	Proporción del elemento umbral/Treshold elemental ratio

Resumen general de la tesis

Los bosques templados de latitudes medias se establecen a lo largo de gradientes altitudinales donde la temperatura y la precipitación ejercen un efecto sobre la composición química de los residuos vegetales y la comunidad microbiana, modificando el proceso de descomposición de la materia orgánica y la dinámica del carbono y nutrientes del suelo. El objetivo general de esta investigación fue caracterizar cómo los cambios en la composición química de los residuos vegetales determinan la dinámica del carbono y nutrientes del suelo en un gradiente altitudinal de un bosque templado del centro de México. Los objetivos particulares fueron: 1) cuantificar los principales almacenes de carbono en tres diferentes sistemas de vegetación-suelo dominados por las especies arbóreas *Alnus jorullensis*, *Abies religiosa* y *Pinus hartwegii* distribuidos en un gradiente de elevación en el centro de México; y 2) analizar el efecto de la interacción de la cantidad y calidad de la materia orgánica derivada de las especies vegetales arbóreas dominantes y el metabolismo microbiano relacionado con la descomposición a lo largo de un gradiente altitudinal en un bosque templado de tierras altas en el centro de México.

En este trabajo se seleccionaron tres sistemas de vegetación-suelo templados a través de un gradiente altitudinal, en el que la temperatura disminuye conforme la elevación se incrementa y la especie arbórea dominante cambia con respecto con la altitud. En la parte baja se eligió *Alnus jorullensis* (3100 a 3200 msnm), en la parte media *Abies religiosa* (3500 a 3700 msnm) y en la parte alta *Pinus hartwegii* (3700 a 4000 m snm). En cada sistema vegetación-suelo se seleccionó un área de aproximadamente tres hectáreas de bosque y se establecieron cinco parcelas de 50 × 50 m al azar y separadas al menos 200 m entre ellas. Se colectaron muestras de hojarasca, mantillo, raíces finas y suelo para determinar la concentración y almacenes de carbono y nutrientes. Después se analizaron con resonancia

magnética nuclear de 13C en estado sólido con polarización cruzada y giro de ángulo mágico (^{13}C CPMAS NMR) y termografía para caracterizar la composición química y la proporción de compuestos lábiles y recalcitrantes de carbono. Por último, en el mantillo y suelo se determinó la concentración de carbono, nitrógeno y fósforo en su forma total (C_t, N_t y P_t), compuestos orgánicos disueltos (COD, NOD y POD), disponibles (NH_4^+, NO_3^- y HPO_4^{2}) y en biomasa microbiana (C_{mic}, N_{mic} y P_{mic}). Además, se caracterizó la respiración microbiana (CO_2) durante 14 días y la actividad enzimática relacionada con carbono (DES, BGL, POX), nitrógeno (NAG) y fósforo (AP).

En el primer capítulo se destaca el efecto de la especie sobre la diferencia de la magnitud de los almacenes de carbono aéreo, mantillo y suelo a través de un gradiente altitudinal (a partir de aquí tomamos a la vegetación y el suelo como una sola unidad, denominando a cada sistema con el nombre de la especie arbórea dominante *A. jorullensis*, *A. religiosa* y *Pinus hartwegii*). Los sistemas *A. religiosa* y *A. jorullensis* tuvieron el contenido total más alto y más bajo de carbono a nivel del ecosistema (301 y 228 Mg C ha^{-1}, respectivamente). El sistema vegetación-suelo de *A. religiosa* tuvo el mayor almacén de carbono de biomasa aérea (216 ± 31 Mg C ha^{-1}). El sistema vegetación-suelo *A. jorullensis* tuvo la mayor producción de biomasa de hojarasca (3.1 ± 0.08 Mg ha^{-1} año^{-1}); y el menor contenido de carbono en el mantillo (1.2 ± 0.32 Mg C ha^{-1}). Por lo tanto, el mantillo en el sistema de *A. jorullensis* tuvo marcadamente el tiempo de residencia más corto (8 años^{-1}), lo que sugiere tasas altas de descomposición del mantillo. Mientras que el almacén de carbono del suelo (a una profundidad de 1 m) fue mayor en *A. jorullensis* (189 Mg C ha^{-1}) y *P. hartwegii* (137 Mg C ha^{-1}) que en *A. religiosa* (68 Mg C ha^{-1}). Lo anterior sugirió que el efecto de la especie no se limita a la cantidad de producción de hojarasca o a la acumulación de carbono orgánico en el mantillo y suelo. Si no que trasciende hasta la composición química de los residuos vegetales. Y que además con los cambios en la temperatura derivados de la altitud modulan la tasa de descomposición en el bosque templado del centro de México.

En el capítulo dos se destaca la interacción entre la composición química de la materia orgánica y el metabolismo de la comunidad microbiana del mantillo y suelo a lo largo del gradiente altitudinal. La composición química de la hojarasca, raíces finas y mantillo del sistema de vegetación-suelo *A. jorullensis* tuvo una mayor proporción de compuestos Alkyl C (17 a 23%) y aromaticidad (11-53%), así como el mayor valor de $T50_Q$ (397-417 ºC) en el mantillo y suelo en comparación con *P. hartwegii*. Como consecuencia los valores de TER C:N y C:P del mantillo y suelo en el sistema *A. jorullensis* mostraron que la comunidad microbiana podría estar limitada por C. Lo que se relaciona con la alta concentración de Cmic en el mantillo y suelo (Cmic; 2.12 ± 0.36 y 2.68 ± 0.55 mg C g^{-1}), así como, con la actividad enzimática involucrada en despolimerizar C lábil (BGL; 2.25 ± 0.36 µmol pNP g^{-1} h^{-1},), N (NAG; 0.73 ± 0.15 - 0.07 ± 0.01µmol pNP g^{-1} h^{-1}) y la respiración microbiana (DES; 277 ± 118 - 3322 ± 180 µg TPF g^{-1} d^{-1}) en *A. jorullensis* con respecto a la comunidad microbiana en *P. hartwegii.* Por otro lado, el mantillo y suelo del sistema vegetación-suelo *P. hartwegii* dominaron los compuestos aromáticos asociados con la lignina (Alkyl C:Aryl C; 0.8 - 0.9). Además, los valores de TER C:N y TER C:P del mantillo de *Pinus* mostraron que la comunidad microbiana está co-limitada C:N y C:P, mientras que en el suelo está limitado por C. Lo que pudo haber estimulado la actividad de enzimática de POX (2.0 ± 0.5 µmol tyr g^{-1} h^{-1}) en *P. hartwegii*, debido a que esta enzima rompe los compuestos de N que están protegidos en las fibras de lignina y otros compuestos recalcitrantes.

La interacción y la magnitud de los tres principales factores modeladores de la descomposición (clima, calidad de la materia orgánica y la comunidad microbiana) cambió a lo largo del gradiente altitudinal en el bosque templado del Centro de México. Por un lado, el

clima se modifica con respecto al gradiente altitudinal, lo que ha provocado a lo largo del tiempo que las especies arbóreas hayan adaptado sus tejidos con compuestos extra recalcitrantes para resistir el estrés hídrico como los compuestos Alkyl y recalcitrantes que toleren las heladas como la lignina. De tal forma que la composición química y la temperatura definen el metabolismo microbiano y como consecuencia los almacenes y disponibilidad de nutrientes en el mantillo y suelo de los tres sistemas de vegetación-suelo.

Palabras clave. Actividad enzimática, bosques templados, carbono, gradiente altitudinal, nutrientes.

General abstract of the thesis

Temperate mid-latitude forests are established along altitudinal gradients where temperature and precipitation influence the chemical composition of plant residues and the microbial community, modifying the decomposition of organic matter process and the dynamics of soil carbon and nutrients. The general objective of this research was to characterize how changes in the chemical composition of plant residues determine the dynamics of soil carbon and nutrients in an altitude gradient of a temperate forest in central Mexico. The particular objectives were: 1) to quantify the main carbon stores in three different vegetation-soil systems dominated by the tree species *Alnus jorullensis*, *Abies religiosa*, and *Pinus hartwegii* distributed in an elevation gradient in central Mexico; and 2) analyze the effect of the interaction of the quantity and quality of the organic matter derived from the dominant arboreal plant species and the microbial metabolism related to decomposition along an altitudinal gradient in a temperate highland forest in the center from Mexico.

In this research, three temperate vegetation-soil systems were selected through an altitudinal gradient, in which the temperature decreases as the elevation increases and the dominant tree species changes with respect to altitude. In the lower altitude *Alnus jorulle*nsis (3100 to 3200 m asl) was chosen, in the middle altitude *Abies religiosa* (3500 to 3700 m asl) and in the upper altitude *Pinus hartwegii* (3700 to 4000 m asl). In each vegetation-soil system, an area of approximately three hectares of forest was selected, and five plots of 50 × 50 m were established at random and separated at least 200 m between them. Leaf litter, mulch, fine roots and soil samples were collected to determine the concentration and stores of carbon and nutrients. They were then analyzed with ¿cross-polarized, magic-angle twist?, solid-state 13C nuclear magnetic resonance imaging (13C

CPMAS NMR) and thermography to characterize the chemical composition and proportion of labile and recalcitrant carbon compounds. Finally, in litter and soil we analyzed total concentration of carbon, nitrogen and phosphorus (C_t, N_t and P_t), dissolved organic compounds (COD, NOD and POD), available (NH_4^+, $NO3^-$ and HPO_4^2) and microbial biomass (C_{mic}, N_{mic} and P_{mic}). In addition, microbial respiration (CO_2) for 14 days and the enzymatic activity related to carbon (DES, BGL, POX), nitrogen (NAG) and phosphorus (AP) were characterized.

The first chapter emphasizes the effect of the species on the difference in the magnitude of airborne carbon pools, litter and soil through an altitudinal gradient (from here we take vegetation and soil as a single unit, naming each system with the name of the dominant tree species *A. jorullensis, A. religiosa* and *Pinus hartwegii*). The *A. religiosa* and *A. jorullensis* systems had the highest and lowest total carbon content at the ecosystem level (301 and 228 Mg C ha^{-1}, respectively). The vegetation-soil system of *A. religiosa* had the largest above-ground biomass carbon store (216 ± 31 Mg C ha^{-1}). The vegetation-soil system *A. jorullensis* had the highest production of litterfall (3.1 ± 0.08 Mg ha^{-1} yr^{-1}); and the lowest carbon content in the litter (1.2 ± 0.32 Mg C ha^{-1}). Therefore, the litter in the *A. jorullensis* system had markedly the shortest residence time (8 $years^{-1}$), suggesting high rates of litter decomposition. While the soil carbon stock (at a depth of 1 m) was higher in *A. jorullensis* (189 Mg C ha^{-1}) and *P. hartwegii* (137 Mg C ha^{-1}) than in *A. religiosa* (68 Mg C ha^{-1}). The above suggested that; the effect of the species is not limited to the amount of litterfall or the accumulation of organic carbon in the litter and soil. If not, it transcends even the chemical composition of plant residues. And that also with changes in temperature derived from altitude modulate the rate of decomposition in the temperate forest of central Mexico.

Chapter two features the interaction between the chemical composition of organic matter and the metabolism of the microbial community of the litter and soil along the altitudinal gradient. The chemical composition of the litterfall, fine roots and litter of the vegetation-soil system *A. jorullensis* had a higher proportion of Alkyl C compounds (17 to 23%) and aromaticity (11-53%), as well as the highest value of $T50_Q$ (397-417 ºC) in the litter and soil compared to *P. hartwegii*. Therefore, the TER C: N and C: P values of the litter and soil in the *A. jorullensis* system showed that the microbial community could be limited by C. Which is related to the high concentration of C_{mic} in the litter and soil (C_{mic}; 2.12 ± 0.36 and 2.68 ± 0.55 mg C g^{-1}), as well as, with the enzymatic activity involved in depolymerizing labile C (BGL; 2.25 ± 0.36 µmol pNP g^{-1} h^{-1}), N (NAG; 0.73 ± 0.15 - 0.07 ± 0. 01µmol pNP g^{-1} h^{-1}) and microbial respiration (DES; 277 ± 118 - 3322 ± 180 µg TPF g^{-1} d^{-1}) in *A. jorullensis* with respect to the microbial community in *P hartwegii*. On the other hand, the litter and soil of the vegetation-soil system *P. hartwegii* dominated the aromatic compounds associated with lignin (Alkyl C: Aryl C; 0.8 - 0.9). In addition, the TER C: N and TER C: P values of Pinus litter showed that the microbial community is co-limited C: N and C: P, while in the soil it is limited by C. What could have stimulated the enzymatic activity of POX (2.0 ± 0.5 µmol tyr g^{-1} h^{-1}) in *P. hartwegii*, due to the fact that this enzyme breaks down the N compounds that are protected in lignin fibers and other recalcitrant compounds.

The interaction and magnitude of the three main modeling factors of decomposition (climate, quality of organic matter and microbial community) changed along the altitudinal gradient in the temperate forest of Central Mexico. On the one hand, the climate is modified with respect to the altitudinal gradient, which has caused over time that tree species have adapted their tissues with extra recalcitrant compounds to resist water stress such as Alkyl and recalcitrant compounds that tolerate frost like lignin. In such a way that the chemical

composition and temperature define the microbial metabolism and consequently the stores and availability of nutrients in the mulch and soil of the three vegetation-soil systems.

Keywords. Enzyme activity, temperate forests, carbon, altitudinal gradient, nutrients.

Introducción general de la tesis

Los bosques templados se caracterizan por establecerse sobre gradientes altitudinales, donde los cambios de temperatura y precipitación promueven que una sola especie arbórea se establezca en grandes extensiones geográficas dentro de un intervalo altitudinal (Körner 1999). Una de las principales incertidumbres sobre el ciclo del carbono (C) es entender cómo la interacción entre las especies vegetales y las diferencias de temperatura regulan los almacenes y flujos de C a través de los cambios en la elevación (Scowcroft et al. 2000; Becker et al. 2007; Körner 2007; De Deyn et al. 2008; Smith et al. 2009; Wang et al. 2018). Numerosos estudios han mostrado que los almacenes de carbono arbóreo aéreo disminuyen conforme incrementa la altitud (Liu et al. 2012). Debido a que las bajas temperaturas que se registran en las partes elevadas de los sistemas montañosos limitan los procesos fisiológicos responsables de la formación de tejido como la fotosíntesis, las tasas de respiración, la asignación de biomasa a las raíces y el crecimiento de los brotes (Körner 1989, 2015). Además, el periodo de crecimiento arbóreo es menor en comparación con la vegetación de zonas menos elevadas (Splechtna et al. 2000; Briffa et al. 2004; Liang et al. 2010; Takahashi et al. 2011).

Por otra parte, la cantidad y calidad de los residuos vegetales que las especies regresan al suelo está mediada por las adaptaciones fisiológicas de la vegetación al clima (Zhang et al. 2014) (Figura 1). Las diferencias en la fenología de la vegetación de los bosques templados previene el daño por congelación o deshidratación, ajustando el equilibrio entre la necesidad de escapar de los eventos de estrés y la necesidad de una estación de crecimiento suficientemente larga (Körner 2016). Por ejemplo, la vegetación perenne templada puede tener varias cohortes anuales de follaje como los pinos, mientras que la vegetación caduca, principalmente latifoliada, solo tiene una cohorte (Augusto et al. 2015). Asimismo, las adaptaciones foliares también se relacionan con la composición química del tejido, por ejemplo, la síntesis de compuestos para protección y/o tolerancia al clima como las ceras y la lignina; y compuestos de reserva o estructurales como el almidón y la celulosa tienden a incrementar en ambientes de mayor estrés, reduciendo así la calidad química de la materia orgánica que retornan al suelo (Tharayil et al. 2011; Berg y McClaugherty 2014; Cesarano et al. 2016). Otro mecanismo fisiológico que regula la calidad química de los residuos orgánicos es la reabsorción de nutrientes de las hojas senescentes a las hojas verdes, al minimizar la pérdida de nutrientes como N y P se reduce la calidad química de la materia orgánica (Liu et al. 2004; Vergutz et al. 2012; Berg y McClaugherty 2014). Todas estas adaptaciones se reflejan en la calidad de la materia orgánica, y junto con la temperatura y la humedad, así como con la capacidad metabólica de la comunidad microbiana, modulan el proceso de descomposición a lo largo de los gradientes altitudinales (Prescott et al. 2000; Scowcroft et al. 2000; Cornwell et al. 2008) (Figura 1).

El proceso de descomposición determina la dinámica de carbono y nutrientes del suelo (Prescott et al. 2000; Cornwell et al. 2008). Sin embargo, la magnitud del efecto de cada uno de los factores sobre el proceso de descomposición cambia con respecto a su disponibilidad (Cleveland et al. 2014). Esto es particularmente interesante en los bosques templados, donde a lo largo de gradientes altitudinales la disponibilidad de recursos cambia (Aerts 1997; Prescott 2010; Augusto et al. 2015). Por ejemplo, la dominancia de una especie arbórea en intervalos altitudinales determina la composición química y/o calidad del mantillo y con esto se modifica la labilidad y disponibilidad de nutrientes, así como el flujo de energía para la comunidad microbiana (Prescott 2010; Heuck y Spohn 2016). La calidad química derivada de las especies vegetales se ha descrito como la resistencia de los compuestos orgánicos a ser despolimerizados por los microorganismos (Kleber 2010). Es decir, los componentes lábiles de la materia orgánica son los primeros recursos en ser utilizados por los microorganismos (proteínas, aminoácidos, glucosa, almidón, celulosa y hemicelulosa), mientras que la lignina, los compuestos alifáticos y lípidos se conservan selectivamente (Almendros et al. 2000; von Lützow et al. 2008).

Técnicas analíticas como la calorimetría diferencial de barrido (DSC), describen la estabilidad térmica de los compuestos orgánicos, o su resistencia a ser combustionados (Barros et al. 2011). Como resultado, a través de un gradiente de temperatura se distribuye la proporción de compuestos lábiles y recalcitrantes de la materia orgánica (Barros et al. 2007 y 2011). Esta técnica destacó en investigaciones como las de Duguy y Rovira (2010) donde se caracterizó el efecto de incendios forestales sobre la composición química de la materia orgánica del suelo (MOS), así como en Rovira et al. (2008) donde se analizó el cambio de la calidad química en la materia orgánica con diferentes tiempos de descomposición. Por otro lado, la espectroscopia de resonancia magnética nuclear (RMN) de estado sólido ^{13}C con polarización cruzada y giro del ángulo magnético (CPMAS), nos da la oportunidad de obtener información estructural puntual sobre la materia orgánica (Kögel-Knabner 1997). Bonanomi et al. (2017) destacan que las regiones C-alkyl, C-methoxyl, O-alkyl y di-O-alkyl C (compuestos alifáticos y carbohidratos) del espectro son cruciales para entender los efectos de la materia orgánica sobre la dinámica de la comunidad microbiana. Por ejemplo, en las primeras etapas de la descomposción se relacionaron los compuestos de la región O-alkyl con la comunidad bacteriana y fúngica, mientras que en etapas avanzadas compuestos de las regiones recalcitrantes como C-alkyl y aromatic presentaron influencia sobre la proliferación de raíces en especies vegetales (Bonanomi et al. 2017).

Lo anterior es interesante debido a que la comunidad microbiana modifica la disponibilidad de nutrientes C:N:P a través de sintetizar enzimas extracelulares (EE), las cuales despolimerizan los compuestos orgánicos y vuelven disponibles los nutrientes para la vegetación y los propios microorganismos (Sinsabaugh et al. 2002) (Figura 1). La síntesis de enzimas requiere la inversión de nutrientes por parte de la comunidad microbiana hasta en una proporción 1:1:1 (C:N:P), lo que puede llegar a representar hasta el 2% del carbono asimilado en su biomasa (Sinsabaugh et al. 2008). Estudios diversos han observado que la comunidad microbiana puede invertir una mayor cantidad de recursos en la síntesis de EE que en su crecimiento, lo que significa una reducción del metabolismo microbiano (Sinsabaugh y Follsand 2011; Schimel y Weintraub 2003). Con respecto a esto, estudios como Tapia-Torres et al. (2015), Zhang et al. (2019) y Sinsabaugh y Follstad (2011), han utilizado el concepto de TER (relación del elemento umbral), el cual es la intersección de la teoría metabólica ecológica que describe la organización ecológica en términos termodinámicos, y la teoría estequiométrica ecológica que describe la organización ecológica en términos de disponibilidad de recursos elementales (Sterner y Elser 2002) (Figura 1). El TER define la razón de elementos en la que el crecimiento microbiano cambia entre la limitación de nutrientes (C:N o C:P) o la energía (representada por C) (Tapia-Torres et al. 2015; Sterner y Elser, 2002). Esto es relevante en los sistemas templados, debido a que el clima, la vegetación (calidad y cantidad de la materia orgánica) y las propiedades del suelo varían drásticamente en distancias cortas y a lo largo de gradientes altitudinales (Körner 1999). Lo que podría generar limitaciones en la disponibilidad de nutrientes para los microorganismos a los largo del gradiente altitudinal, y modificar el proceso de descomposición (Figura 1). Una mejor comprensión de la adquisición de nutrientes y las características metabólicas de la comunidad microbiana a lo largo de un gradiente ambiental ayudaría a dilucidar los mecanismos del ciclo del C, así como de otros nutrientes en los ecosistemas templados bajo situación de cambio climático.

Se espera que el calentamiento del clima lleve a un aumento en las tasas de descomposición, y como consecuencia, a un mayor flujo de dióxido de carbono a la atmósfera (Aerts 2006). Es probable que estos efectos se manifiesten más en los biomas fríos (sitios de alta latitud y gran altitud) porque ahí se ha predicho que el calentamiento será mayor, debido a que la descomposición en estas regiones está fuertemente limitada a la temperatura (Aerts 2006). Los bosques templados de México se encuentran comúnmente dentro de los cinturones montañosos y son el segundo ecosistema con mayor distribución a nivel nacional (17% del territorio nacional) (Challenger, 1998). Además, se ha reportado que los bosques templados de México son los ecosistemas más vulnerables al cambio climático debido a su restringida distribución geográfica en zonas altitudinales elevadas (Villers-Ruíz y Trejo-Vázquez 1998). Y para finales del siglo actual los climas adecuados para el establecimiento de los bosques templados, en particular los de coníferas situados en la Franja Volcánica Transversal Mexicana, se pueden reducir en un 92% para el 2090 (Sáenz-Romero et al. 2012).

En particular, la región del Izta-Popo las temperaturas mínimas han aumentado durante los últimos 50 años en zonas del Nevado de Toluca y región Izta-Popo (Islas 2011). Mientras que la precipitación en las regiones montañosas está decreciendo en un uno por ciento, como consecuencia el contraste estacional en los ecosistemas templados disminuye y los glaciares de la zona se retraen comprometiendo los recursos hídricos (Islas 2011). Lo anterior sugiere que la composición de las poblaciones arbóreas de la región puede verse afectada por la disponibilidad de agua como consecuencia de las variaciones de temperatura. Y que la vulnerabilidad de la vegetación dependerá de la plasticidad fenotípica, de las estrategias y la capacidad de la vegetación para adaptarse a los nuevos regímenes climáticos (Esperón-Rodríguez y Barradas 2014). Podemos resumir dos estrategias de las especies, por un lado, pueden tolerar la sequía como el caso de *Alnus sp.* o migrar hacia sitios de establecimiento más elevados como se ha pronosticado para *Abies* y

Pinus (Sáenz-Romero et al. 2012; Estrada-Contreras et al. 2015). Esperón-Rodríguez y Barradas (2014) mencionan que los individuos de altitudes bajas serán más vulnerables a los cambios de temperatura en comparación con los árboles que se establecen en las partes medias y altas del gradiente altitudinal. En un modelo sobre vulnerabilidad de especies para Veracruz, Esperón-Rodríguez y Barradas (2014) mencionan que la especie latifoliada *Alnus sp* puede tolerar un incremento de 2ºC; sin embargo la especie presentaría estrés hídrico y sería vulnerable a los cambios ambientales (Esperón-Rodríguez y Barradas 2014). Asimismo, Allen et al. (2015) mencionan que la respuesta más probable ante el cambio climático de los bosques de la Franja Volcánica Transversal Mexicana es la muerte o la migración de las especies a zonas más elevadas. Una migración de 300-400m es necesitaría para compensar las predicciones climáticas para el año 2030 bajo el escenario A2 del IPCC; sin embargo, la tasa de migración es de cuatro metros cada diez años volviendo poco probable el avance altitudinal de las especies de altitudes medias como *Abies religiosa* (Sáenz-Romero et al. 2012; Sánchez-Salas et al. 2011). *Pinus hartwegii* se caracteriza por tener una mayor vulnerabilidad a la cavitación en comparación con especies de otras familias de coníferas debido a la altitud y la temperatura de establecimiento (Sáenz-Romero et al. 2013). A pesar de estas adaptaciones, la especie ha registrado una reducción de 10.6 % en su crecimiento relativo consecuencia del aumento de la temperatura en los últimos 100 años establecimiento (Sáenz-Romero et al. 2013). Asimismo, debido al deshielo de los glaciares del volcán Iztaccíhuatl *Pinus hartwegii* incrementó en 200m su límite arbóreo superior en las últimas décadas, brindándole nuevas áreas para colonizar (Villers-Ruiz y Castañeda-Aguado 2013).

Cada vez hay más interés sobre la importancia del legado de la vegetación en la modulación de los procesos ecosistémicos, sobre todo ante la posibilidad de una migración de especies como consecuencia de las variaciones climáticas (Carrillo et al. 2012). Y las diferencias ambientales que se producen en cortas distancias en las regiones montañosas vuelven a los sistemas templados modelos de estudio ideales para evaluar los efectos del calentamiento global sobre los ciclos biogeoquímicos. La realización de experimentos en entornos naturales es una opción prometedora para realizar evaluaciones más realistas de cómo responderán los procesos biogeoquímicos al cambio climático y revelar efectos que no se pueden detectar fácilmente con experimentos en entornos controlados o artificiales (Tito et al. 2020; Ma y Chang 2019). Existe un número creciente de estudios que aprovechan los gradientes ambientales naturales, incluidos los latitudinales (Yang et al. 2019) y elevacionales (Nottingham et al. 2019) en estudios de cambio climático y biogeoquímica. No obstante que en el país se ha prestado atención al efecto del calentamiento global sobre el ciclo de carbono, las posibles modificaciones en la interacción planta-microorganismos-clima ha sido poco explorada.

Por lo anterior, la pregunta principal de esta investigación fue ¿Cuál es el efecto de la composición química de la materia orgánica de tres sistemas de vegetación-suelo contrastantes sobre el proceso de descomposición a través de un gradiente altitudinal en un bosque templado del centro de México?. Los objetivos particulares fueron: 1) cuantificar los principales almacenes de carbono en tres diferentes sistemas de vegetación-suelo dominados por las especies arbóreas *Alnus jorullensis*, *Abies religiosa* y *Pinus hartwegii* distribuidos en un gradiente de elevación en el centro de México; y 2) analizar el efecto de la interacción de la cantidad y calidad de la materia orgánica derivada de las especies vegetales arbóreas dominantes y el metabolismo microbiano relacionado con la descomposición a lo largo de un gradiente altitudinal en un bosque templado de tierras altas en el centro de México.

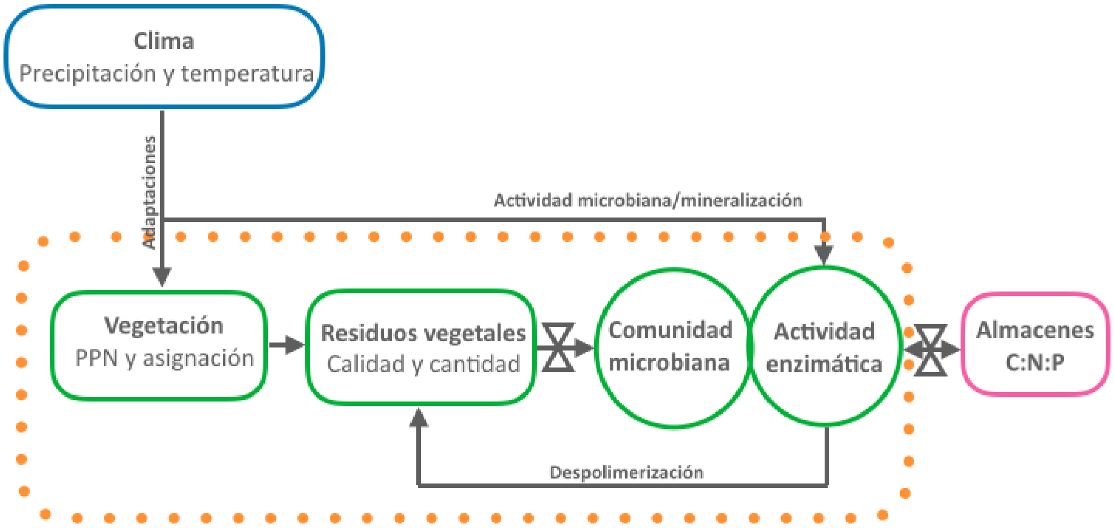

Figura 1. Diagrama conceptual que ilustra los principales factores moduladores del proceso de descomposición de la materia orgánica. La interacción del clima y la vegetación se da a varias escalas temporales, a corto plazo la interacción de la temperatura, la vegetación (calidad y cantidad de materia orgánica) y la comunidad microbiana son el principal factor modulador de la descomposición (Aerts 2006). A mediano y largo plazo, la temperatura modula la composición química de los residuos vegetales, así como la composición de la vegetación (Aerts 2006). Lo anterior en conjunto determina la dinámica del carbono y nutrientes en un ecosistema (Modificado de You et al. (2014).

Referencias

Aerts, R. 1997. Climate, Leaf Litter Chemistry and Leaf Litter Decomposition in Terrestrial Ecosystems: A Triangular Relationship. Oikos 79(3): 439. doi:10.2307/3546886.

Aerts, R. 2006. The freezer defrosting: global warming and litter decomposition rates in cold biomes. J. Ecol. 94(4): 713–724. doi:10.1111/j.1365-2745.2006.01142.x.

Allen, C.D., Breshears, D.D., y McDowell, N.G. 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere 6(8): 1–55. doi:10.1890/ES15-00203.1.

Ali, R.S., Poll, C., y Kandeler, E. 2018. Dynamics of soil respiration and microbial communities: Interactive controls of temperature and substrate quality. Soil Biol. Biochem. 127: 60–70. doi:10.1016/j.soilbio.2018.09.010.

Almendros, G., Dorado, J., González-Vila, F.J., Blanco, M.J., y Lankes, U. 2000. 13C NMR assessment of decomposition patterns during composting of forest and shrub biomass. Soil Biol. Biochem. 32(6): 793–804. doi:10.1016/S0038-0717(99)00202-3.

Augusto, L., De Schrijver, A., Vesterdal, L., Smolander, A., Prescott, C., y Ranger, J. 2015. Influences of evergreen gymnosperm and deciduous angiosperm tree species on the functioning of temperate and boreal forests: Spermatophytes and forest functioning. Biol. Rev. 90(2): 444–466. doi:10.1111/brv.12119.

Babst, F., Bouriaud, O., Papale, D., Gielen, B., Janssens, I.A., Nikinmaa, E., Ibrom, A., Wu, J., Bernhofer, C., Köstner, B., Grünwald, T., Seufert, G., Ciais, P., y Frank, D. 2014. Above-ground woody carbon sequestration measured from tree rings is coherent with net ecosystem productivity at five eddy-covariance sites. New Phytol. 201(4): 1289–1303. doi:10.1111/nph.12589.

Baldock, J.A., Oades, J.M., Waters, A.G., Peng, X., Vassallo, A.M., y Wilson, M.A. 1992. Aspects of the chemical structure of soil organic materials as revealed by solid-state<Superscript>13</Superscript>C NMR spectroscopy. Biogeochemistry 16(1): 1–42. doi:10.1007/BF00024251.

Barros, N., Salgado, J., y Feijóo, S. 2007. Calorimetry and soil. Thermochim. Acta 458(1–2): 11–17. doi:10.1016/j.tca.2007.01.010.

Barros, N., Salgado, J., Villanueva, M., Rodriquez-Añón, J., Proupin, J., Feijóo, S., y Martín-Pastor, M. 2011. Application of DSC–TG and NMR to study the soil organic matter. J. Therm. Anal. Calorim 104(1): 53–60. doi:10.1007/s10973-010-1163-4.

Becker, A., Körner, C., Brun, J.-J., Guisan, A., y Tappeiner, U. 2007. Ecological and Land Use Studies Along Elevational Gradients. Mt. Res. Dev. 27(1): 58–65. doi:10.1659/0276-4741(2007)27[58:EALUSA]2.0.CO;2.

Berg, B., y McClaugherty, C. 2014. Plant Litter. Springer Berlin Heidelberg, Berlin, Heidelberg. Available from http://link.springer.com/10.1007/978-3-642-38821-7 [accessed 3 September 2015].

Bonanomi, G., Cesarano, G., Lombardi, N., Motti, R., Scala, F., Mazzoleni, S., y Incerti, G. 2017. Litter chemistry explains contrasting feeding preferences of bacteria, fungi, and higher plants. Sci Rep 7. doi:10.1038/s41598-017-09145-w.

Briffa, K.R., Osborn, T.J., y Schweingruber, F.H. 2004. Large-scale temperature inferences from tree rings: a review. Glob. Planet. Change 40(1–2): 11–26. doi:10.1016/S0921-8181(03)00095-X.

Burns, R.G., DeForest, J.L., Marxsen, J., Sinsabaugh, R.L., Stromberger, M.E., Wallenstein, M.D., Weintraub, M.N., y Zoppini, A. 2013. Soil enzymes in a changing environment: Current knowledge and future directions. Soil Biol. Biochem. 58: 216–234. doi:10.1016/j.soilbio.2012.11.009.

Carrillo, Y., Ball, B.A., Strickland, M.S., y Bradford, M.A. 2012. Legacies of plant litter on carbon and nitrogen dynamics and the role of the soil community. Pedobiologia 55(4): 185–192. doi:10.1016/j.pedobi.2012.02.002.

Cesarano, G., Incerti, G., y Bonanomi, G. 2016. The Influence of Plant Litter on Soil Water Repellency: Insight from 13C NMR Spectroscopy. PLOS ONE 11(3): e0152565. doi:10.1371/journal.pone.0152565.

Cleveland, C.C., Reed, S.C., Keller, A.B., Nemergut, D.R., O'Neill, S.P., Ostertag, R., y Vitousek, P.M. 2014. Litter quality versus soil microbial community controls over decomposition: a quantitative analysis. Oecologia 174(1): 283–294. doi:10.1007/s00442-013-2758-9.

Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O., Hobbie, S.E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., Quested, H.M., Santiago, L.S., Wardle, D.A., Wright, I.J., Aerts, R., Allison, S.D., van Bodegom, P., Brovkin, V., Chatain, A., Callaghan, T.V., Díaz, S., Garnier, E., Gurvich, D.E., Kazakou, E., Klein, J.A., Read, J., Reich, P.B., Soudzilovskaia, N.A., Vaieretti, M.V., y Westoby, M. 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecol. Lett. 11(10): 1065–1071. doi:10.1111/j.1461-0248.2008.01219.x.

Cui, Y., Bing, H., Fang, L., Jiang, M., Shen, G., Yu, J., Wang, X., Zhu, H., Wu, Y., y Zhang, X. 2019. Extracellular enzyme stoichiometry reveals the carbon and phosphorus limitations of microbial metabolisms in the rhizosphere and bulk soils in alpine ecosystems. Plant Soil. doi:10.1007/s11104-019-04159-x.

De Deyn, G.B., Cornelissen, J.H.C., y Bardgett, R.D. 2008. Plant functional traits and soil carbon sequestration in contrasting biomes. Ecol. Lett. 11(5): 516–531. doi:10.1111/j.1461-0248.2008.01164.x.

Duguy, B., y Rovira, P. 2010. Differential thermogravimetry and differential scanning calorimetry of soil organic matter in mineral horizons: Effect of wildfires and land use. Org. Geochem. 41(8): 742–752. doi:10.1016/j.orggeochem.2010.05.015.

Esperón-Rodríguez, M., y Barradas, V. 2014. Potential vulnerability to climate change of four tree species from the central mountain region of Veracruz, Mexico. Clim. Res. 60(2): 163–174. doi:10.3354/cr01231.

Estrada-Contreras, I., Zamora, M.E., Castillo-Campos, G., y Soto, O.R. 2015. Climate change and effects on vegetation in Veracruz, Mexico: an approach using ecological niche modelling. Acta Bot. Mex. (112): 73–93.

Glaser, B., Turrión, M.-B., Solomon, D., Ni, A., y Zech, W. 2000. Soil organic matter quantity and quality in mountain soils of the Alay Range, Kyrgyzia, affected by land use change. Biol. Fertil. Soils 31(5): 407–413. doi:10.1007/s003749900187.

Heuck, C., y Spohn, M. 2016. Carbon, nitrogen and phosphorus net mineralization in organic horizons of temperate forests: stoichiometry and relations to organic matter quality. Biogeochemistry 131(1–2): 229–242. doi:10.1007/s10533-016-0276-7.

Islas, H. 2011. "ANÁLISIS DE LA TENDENCIA DE NEVADAS EN LA SIERRA NEVADA, MÉXICO." Tesis de Licenciatura en Geografía. Universidad Nacional Autónoma de México, Ciudad de Mexico.

Keiser, A.D., y Bradford, M.A. 2017. Climate masks decomposer influence in a cross-site litter decomposition study. Soil Biol. Biochem. 107: 180–187. doi:10.1016/j.soilbio.2016.12.022.

Kleber, M. 2010. What is recalcitrant soil organic matter? Environ. Chem. 7(4): 320. doi:10.1071/EN10006.

Kögel-Knabner, I. 1997. 13C y 15N NMR spectroscopy as a tool in soil organic matter studies. Geoderma 80(3–4): 243–270.

Kögel-Knabner, I. 2002. The macromolecular organic composition of plant and microbial residues as inputs to soil organic matter. Soil Biol. Biochem. 34(2): 139–162. doi:10.1016/S0038-0717(01)00158-4.

Kögel-Knabner, I. 2017. The macromolecular organic composition of plant and microbial residues as inputs to soil organic matter: Fourteen years on. Soil Biol. Biochem. 105: A3–A8. doi:10.1016/j.soilbio.2016.08.011.

Körner, C. 1989. The nutritional status of plants from high altitudes. Oecologia 81(3): 379–391.

Körner, C. 1999. Alpine Plant Life. Springer Berlin Heidelberg, Berlin, Heidelberg. Available from http://link.springer.com/10.1007/978-3-642-98018-3 [accessed 13 June 2016].

Körner, C. 2007. The use of 'altitude' in ecological research. Trends Ecol. Evol. 22(11): 569–574. doi:10.1016/j.tree.2007.09.006.

Körner, C. 2015. Paradigm shift in plant growth control. Curr. Opin. Plant Biol. 25: 107–114. doi:10.1016/j.pbi.2015.05.003.

Körner, C. 2016. Plant adaptation to cold climates. F1000Research 5. doi:10.12688/f1000research.9107.1.

Liang, E., Wang, Y., Xu, Y., Liu, B., y Shao, X. 2010. Growth variation in Abies georgei var. smithii along altitudinal gradients in the Sygera Mountains, southeastern Tibetan Plateau. Trees 24(2): 363–373. doi:10.1007/s00468-009-0406-0.

Liu, C., Westman, C.J., Berg, B., Kutsch, W., Wang, G.Z., Man, R., y Ilvesniemi, H. 2004. Variation in litterfall-climate relationships between coniferous and broadleaf forests in Eurasia. Glob. Ecol. Biogeogr. 13(2): 105–114. doi:10.1111/j.1466-882X.2004.00072.x.

Liu, Y., He, N., Wen, X., Xu, L., Sun, X., Yu, G., Liang, L., y Schipper, L.A. 2018. The optimum temperature of soil microbial respiration: Patterns and controls. Soil Biol. Biochem. 121: 35–42. doi:10.1016/j.soilbio.2018.02.019.

Liu, Y., Zhang, Y., y Liu, S. 2012. Aboveground carbon stock evaluation with different restoration approaches using tree ring chronosequences in Southwest China. For. Ecol. Manag. 263: 39–46. doi:10.1016/j.foreco.2011.09.008.

Ma, M., y Chang, R. 2019. Temperature drive the altitudinal change in soil carbon and nitrogen of montane forests: Implication for global warming. CATENA 182: 104126. doi:10.1016/j.catena.2019.104126.

Nottingham, A.T., Bååth, E., Reischke, S., Salinas, N., y Meir, P. 2019. Adaptation of soil microbial growth to temperature: Using a tropical elevation gradient to predict future changes. Glob. Change Biol. 25(3): 827–838. doi:10.1111/gcb.14502.

von Lützow, M., Kögel-Knabner, I., Ludwig, B., Matzner, E., Flessa, H., Ekschmitt, K., Guggenberger, G., Marschner, B., y Kalbitz, K. 2008. Stabilization mechanisms of organic matter in four temperate soils: Development and application of a conceptual model. J. Plant Nutr. Soil Sci. 171(1): 111–124. doi:10.1002/jpln.200700047.

Parque Nacional Izta-Popo Zoquiapan. 2018. Parque Nacional Izta-Popo Zoquiapan. Available from http://iztapopo.conanp.gob.mx/listado_de_especies.php [accessed 21 March 2018].

Prescott, C.E. 2010. Litter decomposition: what controls it and how can we alter it to sequester more carbon in forest soils? Biogeochemistry 101(1–3): 133–149. doi:10.1007/s10533-010-9439-0.

Prescott, C.E., Zabek, L.M., Staley, C.L., y 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(11): 1742–1750.

Razavi, B.S., Liu, S., y Kuzyakov, Y. 2017. Hot experience for cold-adapted microorganisms: Temperature sensitivity of soil enzymes. Soil Biol. Biochem. 105: 236–243. doi:10.1016/j.soilbio.2016.11.026.

Rovira, P., Kurz-Besson, C., Coûteaux, M.-M., y Ramón Vallejo, V. 2008. Changes in litter properties during decomposition: A study by differential thermogravimetry and scanning calorimetry. Soil Biol. Biochem. 40(1): 172–185. doi:10.1016/j.soilbio.2007.07.021.

Sáenz-Romero, C., Lamy, J.-B., Loya-Rebollar, E., Plaza-Aguilar, A., Burlett, R., Lobit, P., y Delzon, S. 2013. Genetic variation of drought-induced cavitation resistance among Pinus hartwegii populations from an altitudinal gradient. Acta Physiol. Plant. 35(10): 2905–2913. doi:10.1007/s11738-013-1321-y.

Sáenz-Romero, C., Rehfeldt, G.E., Duval, P., y Lindig-Cisneros, R.A. 2012. Abies religiosa habitat prediction in climatic change scenarios and implications for monarch butterfly conservation in Mexico. Forest Ecol. Manag. 275: 98–106. doi:10.1016/j.foreco.2012.03.004.

Sánchez-Salas, J., Guerra, V.M.M., Domínguez, R.P., Arredondo, F.M.S., Hernández, E.S.O., y Jurado, E. 2011. Cambio climático:?` precursor de migración de especies vegetales en la montaña más alta del norte de México? CIENCIA-UANL 14(2): 137–143.

Schimel, J., y Schaeffer, S.M. 2012. Microbial control over carbon cycling in soil. Front. Microbiol. 3. doi:10.3389/fmicb.2012.00348.

Schimel, J., y Weintraub, M. 2003. The implications of exoenzyme activity on microbial carbon and nitrogen limitation in soil: a theoretical model. Soil Biol. Biochem. 35(4): 549–563. doi:10.1016/S0038-0717(03)00015-4.

Scowcroft, Paul.G., Turner, D.R., y Vitousek, P.M. 2000. Decomposition of Metrosideros polymorpha leaf litter along elevational gradients in Hawaii. Glob. Change Biol. 6(1): 73–85. doi:10.1046/j.1365-2486.2000.00282.x.

Sinsabaugh, R.L., Carreiro, M.M., y Repert, D.A. 2002. Allocation of extracellular enzymatic activity in relation to litter composition, N deposition, and mass loss. Biogeochemistry 60(1): 1–24. doi:10.1023/A:1016541114786.

Sinsabaugh, R.L., y Follstad, J.J. 2011. Ecoenzymatic stoichiometry of recalcitrant organic matter decomposition: the growth rate hypothesis in reverse. Biogeochemistry 102(1–3): 31–43. doi:10.1007/s10533-010-9482-x.

Sinsabaugh, R.L., Lauber, C.L., Weintraub, M.N., Ahmed, B., Allison, S.D., Crenshaw, C., Contosta, A.R., Cusack, D., Frey, S., Gallo, M.E., Gartner, T.B., Hobbie, S.E., Holland, K., Keeler, B.L., Powers, J.S., Stursova, M., Takacs-Vesbach, C., Waldrop, M.P., Wallenstein, M.D., Zak, D.R., y Zeglin, L.H. 2008. Stoichiometry of soil enzyme activity at global scale. Ecol. Lett. 11(11): 1252–1264. doi:10.1111/j.1461-0248.2008.01245.x.

Smith, W.K., Germino, M.J., Johnson, D.M., y Reinhardt, K. 2009. The Altitude of Alpine Treeline: A Bellwether of Climate Change Effects. Bot. Rev. 75(2): 163–190. doi:10.1007/s12229-009-9030-3.

Splechtna, B.E., Dobrys, J., y Klinka, K. 2000. Tree-ring characteristics of subalpine fir (Abies lasiocarpa (Hook.) Nutt.) in relation to elevation and climatic fluctuations. Ann. For. Sci. 57(2): 89–100.

Tapia-Torres, Y., Elser, J.J., Souza, V., y García-Oliva, F. 2015. Ecoenzymatic stoichiometry at the extremes: How microbes cope in an ultra-oligotrophic desert soil. Soil Biol. Biochem. 87: 34–42. doi:10.1016/j.soilbio.2015.04.007.

Takahashi, K., Okuhara, I., Tokumitsu, Y., y Yasue, K. 2011. Responses to climate by tree-ring widths and maximum latewood densities of two Abies species at upper and lower altitudinal distribution limits in central Japan. Trees 25(4): 745–753. doi:10.1007/s00468-011-0552-z.

Tharayil, N., Suseela, V., Triebwasser, D.J., Preston, C.M., Gerard, P.D., y Dukes, J.S. 2011. Changes in the structural composition and reactivity of Acer rubrum leaf litter tannins exposed to warming and altered precipitation: climatic stress-induced tannins are more reactive. New Phytol. 191(1): 132–145. doi:10.1111/j.1469-8137.2011.03667.x.

Tito, R., Vasconcelos, H.L., y Feeley, K.J. 2020. Mountain Ecosystems as Natural Laboratories for Climate Change Experiments. Front. For. Glob. Change 3. Frontiers. doi:10.3389/ffgc.2020.00038.

Vancampenhout, K., Wouters, K., De Vos, B., Buurman, P., Swennen, R., y Deckers, J. 2009. Differences in chemical composition of soil organic matter in natural ecosystems from different climatic regions – A pyrolysis–GC/MS study. Soil Biol. Biochem. 41(3): 568–579. doi:10.1016/j.soilbio.2008.12.023.

Van de Putten Wim H., Bardgett D., Bever D., Bezemer T. Martijn, Casper Brenda B., Fukami Tadashi, Kardol Paul, Klironomos John N., Kulmatiski Andrew, Schweitzer Jennifer A., Suding Katherine N., Voorde Tess F. J., Wardle A., y Hutchings Michael. 2013. Plant–soil feedbacks: the past, the present and future challenges. J. Ecol. 101(2): 265–276. doi:10.1111/1365-2745.12054.

Vergutz, L., Manzoni, S., Porporato, A., Novais, R.F., y Jackson, R.B. 2012. Global resorption efficiencies and concentrations of carbon and nutrients in leaves of terrestrial plants. Ecol. Monogr. 82(2): 205–220. doi:10.1890/11-0416.1.

Villers-Ruiz, L., y Castañeda-Aguado, D. 2013. Species and plant community reorganization in the Trans-Mexican Volcanic Belt under climate change conditions. J MT SCI-ENGL 10(6): 923–931. doi:10.1007/s11629-013-2719-0.

Villers-Ruíz, L., y Trejo-Vázquez, I. 1998. Climate change on Mexican forests and natural protected areas. Glob. Environ. Change 8(2): 141–157.

Wang, A., Wang, X., Tognetti, R., Lei, J.-P., Pan, H.-L., Liu, X.-L., Jiang, Y., Wang, X.-Y., He, P., Yu, F.-H., y Li, M.-H. 2018. Elevation alters carbon and nutrient concentrations and stoichiometry in *Quercus aquifolioides* in southwestern China. Sci. Total Environ. 622–623: 1463–1475. doi:10.1016/j.scitotenv.2017.12.070.

Waring, B.G., Weintraub, S.R., y Sinsabaugh, R.L. 2014. Ecoenzymatic stoichiometry of microbial nutrient acquisition in tropical soils. Biogeochemistry 117(1): 101–113. doi:10.1007/s10533-013-9849-x.

Xu, Y., Chen, Z., Fontaine, S., Wang, W., Luo, J., Fan, J., y Ding, W. 2017. Dominant effects of organic carbon chemistry on decomposition dynamics of crop residues in a Mollisol. Soil Biol. Biochem.115: 221–232. doi:10.1016/j.soilbio.2017.08.029.

Yang, S., Yao, F., Ye, J., Fang, S., Wang, Z., Wang, R., Zhang, Q., Ma, R., Wang, X., Jiang, Y., Dorodnikov, M., Li, H., y Zou, H. 2019. Latitudinal pattern of soil lignin/cellulose content and the activity of their degrading enzymes across a temperate forest ecosystem. Ecol. Indic. 102: 557–568. doi:10.1016/j.ecolind.2019.03.009.

You, Y., Wang, J., Huang, X., Tang, Z., Liu, S., y Sun, O.J. 2014. Relating microbial community structure to functioning in forest soil organic carbon transformation and turnover. Ecol. Evol. 4(5): 633–647. doi:10.1002/ece3.969.

Zhang, J., Ai, Z., Liang, C., Wang, G., Liu, G., y Xue, S. 2019. How microbes cope with short-term N addition in a Pinus tabuliformis forest-ecological stoichiometry. Geoderma 337: 630–640. doi:10.1016/j.geoderma.2018.10.017.

Zhang, H., Yuan, W., Dong, W., y Liu, S. 2014. Seasonal patterns of litterfall in forest ecosystem worldwide. Ecol. Complex. 20: 240–247. doi:10.1016/j.ecocom.2014.01.003.

Chapter one

Are vegetation-soil systems drivers of ecosystem carbon contents along an elevation gradient in a highland temperate forest?

Isela Jasso-Flores[1,2], Leopoldo Galicia[1], Felipe García-Oliva[3] and Angelina Martínez-Yrizar[4]

1 Departamento de Geografía Física, Instituto de Geografía, Circuito exterior, S/N, Universidad Nacional Autónoma de México, México, DF, 04510, México.

2 Posgrado en Ciencias Biológicas, Unidad de Posgrado, Edificio D, 1º piso, Circuito de Posgrados, Ciudad Universitaria, Coyoacán, CDMX, 04510, México

3 Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México. AP 27-3, Santa María de Guido, Morelia, 58090, Michoacán, México.

4 Instituto de Ecología, Universidad Nacional Autónoma de México. Colosio y Sahuaripa s/n, Los Arcos, Hermosillo, C. 83250, Sonora, México.

Corresponding Author

lgalicia@igg.unam.mx

Published on Canadian Journal of Forest Research DOI 10.1139/cjfr-2018-0245

Abstract

Vegetation-soil systems differentially influence the ecosystem processes related to the carbon cycle, particularly when one tree species is dominant over wide geographic regions that are undergoing climate change. The objective of this study was to quantify the stocks of ecosystem carbon in three vegetation-soil systems along a highland altitudinal gradient in central Mexico. The vegetation-soil systems, from lower to higher elevation, were dominated by *Alnus jorullensis*, *Abies religiosa* and *Pinus hartwegii*, respectively. Above and belowground tree biomass was determined in each system, along with the litter, coarse woody debris, roots and litterfall. The *A. religiosa* system had the greatest stock of aboveground biomass carbon (216 ± 31 Mg C ha^{-1}). The *A. jorullensis* system had the greatest production of litterfall (3.1 ± 0.08 Mg ha^{-1} yr^{-1}); however, the carbon content of this litter layer (1.2 ± 0.32 Mg C ha^{-1}) was lower than of *P. hartwegii* (10.1 ± 0.28 Mg C ha^{-1}). Thus, the litter layer in the *A. jorullensis* system had markedly the shortest residence time (8 yr^{-1}), suggesting high rates of litter decomposition. The soil carbon stock (at soil depth 1 m^{2}) was greater in *A. jorullensis* (189 Mg C ha^{-1}) and *P. hartwegii* (137 Mg C ha^{-1}) than in *A. religiosa* (68 Mg C ha^{-1}). The *A. religiosa* and *A. jorullensis* systems had the highest and lowest total ecosystem C content (301 and 228 Mg C ha^{-1}, respectively). However, upward migration of the *A. religiosa* system in response to global climate change could cause losses by 2030 of 187 Mg C ha^{-1} associated with aboveground biomass.

Key words: biomass and carbon stocks, altitudinal gradient, vegetation-soil systems, temperate forest.

1. Introduction

The effect of plant species on ecosystem processes depends on their physiology, ecology and their interaction with climate and soil (Binkley 1995; Chapin FS et al. 2011; Augusto et al. 2015). Vegetation-soil systems represent the interactions between vegetation development and composition, soil properties and primary productivity that must be responsible for the shifts in litter quality and decomposability in forest ecosystems (Pernilla Brinkman et al. 2010; Augusto et al. 2015). In temperate highland vegetation-soil systems, altitudinal differences generate different types of forests, soils, climatological and meteorological conditions that regulate biogeochemical processes (Zhou et al. 2015). In several studies, the climate factors are considered as the main factor of ecosystems processes (Scowcroft et al. 2000; Cornwell et al. 2008; Berg et al. 2010), but other studies reported that vegetation characteristics are the main factor of litter decomposition (Zhang et al. 2008). For example, it has been suggested that 30% of the variation in litter decomposition rates is explained by temperature and precipitation, while about 70% of the variation in decomposition rates and nutrient dynamics is due to variables related to vegetation characteristics (Zhang et al. 2008). These modulate the processes that determine the structure and functioning of terrestrial ecosystems such as decomposition and nutrient dynamics (Vitousek 1982; Binkley 1995; Chapin FS et al. 2011; Vesterdal et al. 2013). In the temperate and boreal forests of Canada and USA functional differences in terms of the carbon cycle among species of evergreen gymnosperms (*Abies*, *Pseudotsuga*, *Tsuga*, *Picea* and *Pinus*) and deciduous angiosperms (*Betula*, *Fagus* and *Quercus*) have been widely studied (Vesterdal et al. 2013, Augusto et al. 2015). For example, it has been determined that the stock of carbon in the aboveground in the evergreen vegetation-soil systems (≈255.46 Mg C ha^{-1}) is greater than the broadleaf systems in temperate ecosystems of medium latitudes (≈110.55 Mg C ha^{-1}) (Galicia et al. 2018). Zhang et al. (2014) reported that broadleaved deciduous soil-vegetation systems produced more litterfall than evergreen systems (600 and 470 g m^{-2} a^{-1}, respectively). However, the magnitude of the stock is given by the balance between the carbon inputs by means of the plant residues and their output through the decomposition (Cornwell et al. 2008).

On the other hand, Laganière et al. (2010), propose that in broadleaf systems the largest inflow of soil organic carbon (SOC) in the soil is derived from aboveground litter and its decomposition. In contrast, the SOC of the soils in the evergreen coniferous systems can be determined by the quantity and turnover of belowground litter, for example, the root biomass because the decomposition of the aboveground litter is very limited. This shows the strong role of plant species on the composition/balance/amount of organic material in the soil, and that the importance of soil's C stabilization mechanisms may differ among systems (Sollins et al. 1996). The quantity and quality of the plant residues from the vegetation to the soil varies among systems. The litterfall of evergreen coniferous systems has a greater proportion of lignified tissue than that of the deciduous broadleaf systems (Kögel-Knabner 2002; Vergutz et al. 2012). The quantity and quality of the plant residues determine the decomposition rate of the organic material, while they also restrict or promote the accumulation of carbon in the litter layer of the system (Berg and McClaugherty 2014). However, as altitude increases the climate shifts toward more stressful conditions as lower mean temperatures, lower precipitation and higher solar radiation, thus, a shorter growing season influence negatively plant growth and organic matter decomposition (Körner 1999; Zhu et al. 2010). Therefore, the predictions of global climate change make it imperative to determine the functional role of plant species in terms of their contribution to carbon stocks within forest ecosystems (De Deyn et al. 2008).

This is particularly important for the highland forests of the tropical regions, which are highly vulnerable to climate change since their geographic distribution is restricted to altitudinal zones with specific ranges of temperature and rainfall (Solomon et al. 2007; Galicia et al. 2015). Indeed, it has been estimated that the area of temperate forests in Mexico could have diminished 92% by the year 2090 because of increased temperatures and soil water deficit conditions (Körner 1999; Allen et al. 2010; Sáenz-Romero et al. 2012; Esperón-Rodríguez and Barradas 2014). Modeling for central Mexico suggests that by 2030 the vegetation-soil systems of evergreen coniferous forests will need to migrate by approximately 300-400 m above their current elevational range to ensure survival (Sánchez-Salas et al. 2011). In the central region of Mexico, the increase in temperature over recent decades has allowed *Pinus hartwegii* to become established 200 m higher than its previous upper limit (Torres 2013; Villers-Ruiz and Castañeda-Aguado 2013). Such changes in the distribution and mortality of temperate vegetation-soil systems could modify inputs of material and energy, thus altering ecosystem function, especially the carbon cycle; and ecosystem services such as climate regulation and carbon stock. There are few studies examining how the carbon cycle is influenced by temperate forests at elevations of >3000 m in tropical regions where the tree line can reach 4200 m a.s.l. (Chávez-Vergara et al. 2016, 2018). The objective of the present study was therefore to quantify the carbon in the main ecosystem stocks of three different vegetation-soil systems dominated by *Alnus jorullensis*, *Abies religiosa* and *Pinus hartwegii* and distributed along an elevational gradient in central Mexico. It is expected that the two evergreens coniferous vegetation-soil systems will have a greater stock of C than will the deciduous broadleaf system, mainly within the biomass. It is also expected that the broadleaf system will have higher litterfall production with higher rates of litter decomposition.

2 Material and methods

2.1. Study site

The present study was conducted along an elevational gradient from 3100 to 4000 m a.s.l. in the Iztaccíhuatl-Popocatépetl National Park, which is situated on the Trans-Mexican Volcanic belt (Lauer 1978). As a consequence of the biogeography and geology of the study system, it is impossible to find all three species on the same altitudinal floor (2000 to 4000 m a.s.l.). The Izta-Popo National Park is part of the Mexican Transverse Volcanic Belt, is a zone of transition and contact of Nearctic and Neotropical components and is considered one of the most diverse regions of the country due to the geological and ecological processes (Morrone 2010). The genera of the different biogeographic regions were the result of speciation processes in situ, adapted to the new micro-environments formed at higher and lower mountains positions. The formation of microclimates selected and influenced the distribution of functional traits of the species or communities in several altitudinal levels, for example, at higher elevation the Nearctic vegetation was established and in the lowlands the Neotropical vegetation types are well distributed (Challenger and Caballero 1998). The altitudinal distribution of dominant species in forests can be an ideal model to analyze the impacts of global warming on the distribution of species and changes in the carbon cycle. Three different vegetation-soil systems distributed along this elevation gradient were selected for study (Table 1): a) *Alnus jorullensis* (3100 to 3200 m a.s.l.), b) *Abies religiosa* (3500 to 3700 m a.s.l.) and c) *Pinus hartwegii* (3700 to 4000 m a.s.l). Species of the lower strata for the *Alnus* system are, *Acaena elongate, Salix sp., Baccharts conferta, Eupatorium pazcuarense*. In *Abies* they dominate *Baccharis conferta, Salix paradoxa, Ribes ciliatum, Symphoricarpos microphyllus, Senecio angulifolius, Alchemilla procumbens* y *Acaena elongata* are the dominant species. And for *Pinus hartwegii, Muhlenbergia quadridentata* is the dominant species (Rzedowski et al. 2001; Villaseñor 2004; Sánchez-González et al. 2005; Rzedowski 2006; Parque Nacional Izta-Popo Zoquiapan 2013). Mean annual temperature decreases with elevation, with a difference of 5 °C between the *Alnus* and *Pinus* systems. The *Abies* and *Pinus* systems have the highest and lowest mean annual precipitation, respectively, with a marked difference of 400 mm yr^{-1} between them. However, the rainfall has a seasonal pattern in all three systems, with 53% concentrated in the summer months (May-October) (Heil et al. 2003). The Lang index is lower in the *Alnus* system than in the others, suggesting a higher drought stress in the *Alnus* system (Villers-Ruiz and Castañeda-Aguado 2013). The thickness of the litter layer increases with altitude, and there may be a difference of up to 8 cm between the vegetation-soil system *Alnus jorullensis* and *Pinus hartwegii*. The soils in all three systems are Andosols, but soil diagnostic properties (World reference base for soil resources 2006) and pH differ (Table 1). Basal area and tree height are greater for *Abies* than for *Alnus* and *Pinus* systems (Table 1).

2.2 Experimental design

In each of the three vegetation-soil systems, five 50 x 50 m plots were randomly established at distances of at least 200 m.

2.2.1 Sampling of biomass and above- and belowground plant carbon

Estimation of live aboveground tree biomass used allometric equations for each tree species reported in previous studies conducted in the forests of central Mexico (Table 2). For this, the diameter breast height (dbh) and height of all of the live standing individuals > 2.5 cm diameter and > 1.3 m in height were measured in each plot (Mendoza-Ponce and Galicia 2010) (Table 2). To determine the carbon concentration (mg g^{-1}) in the stem, five trees were selected per plot that were healthy and without apparent damage, and two samples were obtained from each individual with a Pressler drill (44 mm / 16 '') to make a sample composed of a plot. Also, in these individual samples of live leaves (20 per arboreal individual) were collected, exposed to the sun, healthy and without apparent damage to make a sample composed of a plot.

The biomass of the coarse woody debris (CWD) was estimated in two sub-plots of 5 x 5 m established in each of the plots, and the diameter and length of all the CWD > 2.5 cm in diameter and > 50 cm were measured of length to obtain the volume of each woody piece through the formula of the cylinder (Hansen et al. 2009). To determine the carbon concentration (mg g^{-1}) in the CWD, a composite sample was made of all the residues collected per plot.

$$V = [\pi h\ (R_1^2 + R_1R_2 + R_2^2)]/3$$

where h is length and R_1 and R_2 are the diameters at the extremes of the cylindrical piece

The estimation of the belowground biomass was made by two sampling methods. The first, characterizes the variation of the radical biomass with respect to the depth. In one of the five plots of each vegetation-soil system, a $1m^3$ pit was made, an area with the highest tree density and among adult trees selected. All the roots contained in three depths (0 to 20 cm, 20 to 50 cm and 50 to 100 cm) were collected. The second sampling was to characterize the spatial variance of the root biomass in three vegetation-soil systems. We established three 50 m long transects randomly distributed in each of the five sampling plots, a soil sample of the first 30 cm depth was collected with a nucleator of 82 mm diameter every 10 m to obtain the radical biomass (n = 15 samples per system). In both sampling the roots were manually separated in thick (<2 mm) from the thick (> 2 mm) with 60 and 120 mesh sieves, dried at 60 ° C for 72 hours, weighed and reported as Mg ha^{-1}. The contents of C were calculated by multiplying the mass by the concentration of C of each of the samples.

The mass of the litter layer was determined by collecting the layer down to the first mineral soil horizon in three sub-plots of 25 x 25 cm distributed at random within each sampling plot (*n* = 15 per vegetation-soil system), making a distinction between the layer of recent deposition and the fermentation layer. The determination of the type of the aboveground litter was done according to Siebe et al. (1996). The samples were stored in paper bags inside black plastic bags for transport to the laboratory, where they were dried at 60 °C for 72 hours and then weighed and ground in the Laboratory of Experimental Edaphology (IGg-UNAM). To determine ash-free dry weight, an aliquot of 2 g was taken from each 25 X 25 cm subsample and incinerated at 600 °C for 4 h in a muffle furnace. The ashes were then weighed and the percentage in the aliquot weight was used to determine ash-free dry weight of litter layer samples.

2.3 Determination of soil organic carbon

In each vegetation-soil system, total organic carbon content was determined from the soil profiles 1 m deep. From each soil horizon, three undisturbed soil samples were taken with an 82 mm core. These were placed in plastic bags and taken to the laboratory for determination of bulk density, texture and C concentration (Siebe et al. 1996). These samples were dried at 60 °C for 72 h and were ground prior to analysis. The mean C concentration of the three samples for each soil horizon was used to calculate the total soil C stock. This value of C concentration was multiplied by the thickness of the horizon and the bulk density (Siebe et al. 1996; Peña-Ramírez et al. 2009). Furthermore, in each plot of each vegetation-soil system, five 50 m transects were established and a soil sample was taken every 10 m from the first 30 cm of soil depth with an 82 mm diameter core in order to form a compound sample per transect (n = 5 per vegetation-soil system type). The samples were placed in black plastic bags and treated and analyzed in the same manner as the samples collected per horizon.

2.4 Litterfall, decomposition constants and mean residence time of the aboveground litter

Fourteen healthy and apparently undamaged adult trees of the target species were chosen in each vegetation-soil system. Litterfall traps of mesh size 0.50 cm were placed beneath the canopy of these trees, positioned at 1.30 m above ground level and at 1.5 m from each tree trunk. The litterfall deposited in the litter traps was collected monthly from January 2015 to January 2016. The litterfall samples were stored in paper bags until they were processed in the laboratory. The material was dried at 60 °C for 72 h and then weighed, with the mass expressed as Mg ha^{-1}.

The decomposition constant (k0) of the litter was determined from the mass balance equation of Olsen (1963):

$$k0 = A/F$$

where A represents the annual litterfall production (Mg ha^{-1}) and F is the biomass of the litter layer (Mg ha^{-1}). The mean residence time (t_R, years) was obtained from the inverse value of k0:

$$t_R = F/A$$

2.5 Chemical and physical analysis

All C concentrations of leaf, litterfall, litter, roots and soils were conducted in a total carbon analyzer (UIC model CM5012, Chicago, USA). Total C was determined by combustion and coulometric detection (Huffman 1977). This value was assumed to represent the concentration of total organic carbon since these soils did not contain carbonates. Soil texture was determined by the standard pipette method and bulk density by the cylinder method (Flores Delgadillo and Alcalá Martínez 2010).

2.6 Statistical analysis

The total carbon content of the litterfall was analyzed by one-way analysis of variance that compared the three vegetation-soil systems (*Alnus*, *Abies* and *Pinus*). The C content of the plants and the plant residues were analyzed with a two-factors ANOVA: plant stocks (stems, branches, foliage, litter, coarse woody debris and roots) and the vegetation-soil systems (*Alnus*, *Abies* and *Pinus*). When the results of the analyses were significant, means were compared with a Tukey HSD test ($p \leq 0.05$). In addition, for each vegetation-soil system, a

Spearman correlation analysis was conducted among the C concentrations of the litter layer, coarse woody debris, roots and soil (30 cm depth) from the samples obtained from the transects in each site and the concentration of soil carbon (30 cm depth) and soil texture (30 cm depth).

3. Results

3.1 Biomass, decomposition rate and mean residence time of the plant residues

Total biomass of *A. religiosa* was 2.5 times higher than *P. hartwegii* and five times higher than *A. jorullensis* (F = 3.7, $p < 0.02$; Figure 1). The biomass of the litter represented between 2% and 8.8% of the total biomass and differed significantly among the systems, with the highest values in the *Pinus* system and the lowest in the *Alnus* system (F = 57.9, $p < 0.001$; Table 4). Fine root biomass made the lowest contribution to the total biomass (between 1.4% and 2.6%) but was higher in the *Abies* and *Pinus* systems (7.2 ± 1.4 and 5.8 ± 0.6 Mg ha^{-1}, respectively) than in that of *Alnus* (2.4 ± 0.4 Mg ha^{-1}; F = 6.85, $p < 0.002$). The aboveground:belowground biomass ratio was higher in *Abies* (47 ± 8.5) than in *Alnus* and *Pinus* systems (14 ± 2 and 20 ± 2; F = 16, $p < 0.001$), while the aboveground:dead biomass ratio (coarse woody debris and litter layer) was lower in *Alnus* (1.4 ± 0.6) than in *Abies* and *Pinus* systems (8 ± 1.3 and 3 ± 0.4, respectively; F = 19, $p < 0.001$).Annual litterfall was 1.5 times greater in the system with the deciduous species (*Alnus*) than in the two systems with evergreen conifers (*Pinus* and *Abies*; F = 57.9, $p < 0.001$; Table 3). The decomposition rate of the litter layer was one order of magnitude greater in the *Alnus* system than in the other two systems (Table 3). The mean residence time of the litter layer was therefore lower in the *Alnus* system (8 yr) than in the two systems dominated by conifer species (93 and 105 yr for *Pinus* and *Abies*, respectively; F = 5.80; $p < 0.01$; Table 3).

3.2 Carbon stocks in the vegetation-soil systems

The concentration of C in foliage, branches and litter layer was significantly greater in the *Pinus* system than for *Abies* or *Alnus* (F = 997, $p < 0.001$; F = 464.7, $p < 0.001$ and F = 21.12, $p < 0.001$, respectively), whereas the concentration of C in the coarse woody debris was significantly higher in the *Alnus* system (F = 9.06, $p < 0.001$; Table 4).

Carbon stocks were significantly affected by the interaction of the vegetation-soil system with the plant component (F = 133, $p < 0.0001$, Table 4). The carbon stocks of the stems differed significantly among the three vegetation-soil systems, being highest in *Abies*, followed by *Pinus* and, finally, *Alnus* (F = 133, $p < 0.0001$). Within systems, C stocks of the stems and litter layer in *Alnus* were significantly higher than that of the roots (F = 133, $p < 0.0001$). In the *Abies* system, the C stock of the stems was significantly greater than the other components (F = 133, $p < 0.0001$, Figure 3). In the *Pinus* system, the stem C stock was significantly greater than in the roots (F = 133, $p < 0.0001$, Table 4).

The SOC content at 30 cm depth was greater in the *Pinus* system than in the other two (F = 88.1, $p < 0.0001$, Table 5). In the *Alnus* system, the SOC in the top 30 cm of soil correlated positively with the biomass of total woody coarse debris residues ($r^2 = 0.49$; $p = 0.03$) and with the percentage of silt ($r^2 = 0.82$; $p = 0.03$). In contrast, in the *Abies* system the SOC stock correlated positively with the biomass ($r^2 = 0.68$; $p = 00.04$) and carbon concentration of the fine roots ($r^2 = 0.47$, $p = 0.04$).

The SOC stock at 1 m soil depth were greater in the *Alnus* and *Pinus* systems (189 and 137 Mg C ha^{-1}, respectively) than in that of *Abies* (68 Mg C ha^{-1}). In the *Alnus* and *Pinus* systems, the SOC stock decreased abruptly from the first horizon to the deeper horizons, whereas the SOC was distributed relatively evenly among horizons in the *Abies* system (Table 7). Silt dominated the top 30 cm of soil in the *Alnus* system, while sands dominated these horizons of the *Abies* and *Pinus* systems (Table 5).

The *Abies* system had ≈30% more total ecosystem C content (301 ± 24 Mg C ha^{-1}) than the *Alnus* system (228 ± 26 Mg C ha^{-1}), with values in the *Pinus* system being intermediate (244 ± 18 Mg C ha^{-1}). The proportions of carbon in the aboveground, forest floor, belowground and soil components differed among the three systems (Figure 2). In the *Abies* system, 72% of the ecosystem C was contained in the aboveground biomass, whereas in the *Alnus* and *Pinus* systems the SOC content contributed the most (83% and 56%, respectively; Figure 2).

4 Discussions

4.1 Carbon stocks in above- and belowground biomass

In this study, the two-evergreen coniferous vegetation-soil systems (*Abies* and *Pinus*) had higher stocks of above and belowground biomass carbon than did the broadleaf vegetation-soil system (*Alnus*), as reported for temperate and boreal forests of Canada and USA (Vogt 1991; Augusto et al. 2015). Because the ages of the *Abies* and *Pinus* systems are relatively similar (125 and 160 years respectively), their higher aboveground biomass is attributed to higher growth rate (Jasso-Flores 2014; Augusto et al. 2015). For example, *A. religiosa* has wider growth rings (3.41 ± 0.24 mm) and high dbh (34 cm) than *P. hartwegii* (1.63 ± 0.15

mm; 23 cm, respectively); which suggests that *A*. *religiosa* has a high growth rate (Jasso-Flores 2014). The two-evergreen coniferous vegetation-soil systems (*A*. *religiosa* and *P*. *hartwegii*) reported the highest above-ground and below-ground biomass stocks compared to the broadleaf vegetation-soil systems (*A*. *jorullensis*). Similarly, Liang et al. (2010) reported growth rings of 4.2 mm wide (at 3600 m a.sl) and 3 mm (at 3800 m a.sl) in *A*. *georgei* var. smithii. In contrast, the slower growth of *P*. *hartwegii* can be attributed to low temperatures, which favor a greater allocation of resources for the maintenance of metabolic function than for growth and tissue production (Hoch and Körner 2003). This pattern of narrower growth rings in *P. hartwegii* is consistent among the main mountains of Mexico and is related to the local low temperatures (Gómez-Guerrero et al. 2013). Unfortunately, we have no data regarding growth ring width for *A. jorullensis* in our study site, but its phenology suggests that this species is growing under greater drought stress than the two-coniferous vegetation-soil systems. In Nepal and Iran, *Alnus* sp. systems represent a reservoir of forest carbon, with arboreal carbon stocks similar to those reported in this study (21 – 30 Mg C ha^{-1}) (Dahal et al. 2013; Haghdoost et al. 2013). In addition to their probable lower growth rate, species of this genus store resources in the form of non-structural carbon in order to tolerate biotic and abiotic stress factors after the leaves are fallen, and to generate new foliar tissue without favoring accumulation of carbon in the stems (Fajardo et al. 2012). In the present study site, an altitudinal advance of two arboreal species has been registered; García García (2000) and Torres (2013) have reported the progress of *A. religiosa* and *P. hartwegii*. Likewise, it has been observed that the altitudinal limits of *Quercus robur, Ulmus glabra, Acer platanoides, Alnus glutinosa and Betula pendula*, have had an advance of 500 - 800 m above their historical establishment limit (Kullman 2008; Grabherr et al. 2010). Finally, the resistance to drought stress shown by *A. jorullensis* in the present study could favor its spread above its current elevation range in response to global climate change.

4.2 Input and permanence of forest floor carbon stocks

Litterfall production and decomposition are key processes that determine the carbon cycle in forest ecosystems. The litterfall production values of the *Alnus* system in the present study (3.1 Mg ha^{-1} yr^{-1}) are similar to those of other species of *Alnus* and of deciduous systems of *Quercus*. However, in northwestern Mexico litterfall production in the evergreen coniferous systems is only one-half (1.3 Mg ha^{-1} yr^{-1}) of that of the deciduous systems (Pérez-Suárez et al. 2009) and one-half of those of the *Abies* and *Pinus* systems examined in this study (1.4 and 1.9 Mg ha^{-1} yr^{-1}, respectively). The phenology of the dominant plant species determines the amount and chemical composition of the plant residues of this flow among evergreen coniferous and deciduous broadleaf species (Augusto et al. 2015). Zavitkovski and Newton (1971) report that the production of litterfall of *Alnus rubra* is 2 Mg ha^{-1} yr^{-1}, this being within the ranges reported for *Quercus potosina* (3 Mg ha^{-1} yr^{-1}) in a northwestern region of Mexico (Pérez-Suárez et al. 2009). This supports the contention that deciduous broadleaf soil-vegetation systems produce more litterfall than evergreen coniferous systems (Zhang et al. 2014). However, the input of plant residues does not explain the accumulation of carbon in the litter layer of the systems. In our research, evergreen coniferous soil-vegetation systems had the largest aboveground litter mass and C stock of the aboveground litter layer than in the deciduous broadleaf system. This pattern is consistent with that reported by Gao et al. (2014) for a temperate forest northwest of China. As well as by Vogt et al. (1986) at a global level, report that the evergreen coniferous systems can maintain up to 70% more carbon in the aboveground litter than the broadleaf systems. Accumulation of carbon on the forest floor depends on the decomposition rate and the mean residence time of the plant residues (Berg and McClaugherty 2014). In the present study site, the TMR of the carbon storage in the aboveground litter of the evergreen coniferous systems is higher than in the broadleaf systems, suggesting a low decomposition rate of the pine species. Zhang et al. (2008) has reported that the decomposition rate of perennial systems is slower (3.9 yr^{-1}) than the broadleaf deciduous systems (7.9 yr^{-1}).

As we expected, the evergreen coniferous vegetation-soil systems had higher total ecosystem C stock than the broadleaf system, mainly within biomass. The *Abies* system had the highest amount (301 Mg C ha^{-1}), concentrating 72% of the total within aboveground biomass, and the *Alnus* system had the lowest amount (228 Mg C ha-1) with 83% concentrated within the soil profile. These results suggest that the ecosystem C stock of the *Abies* system is more vulnerable to human disturbances (deforestation, fires, etc.) and the effects of global climate change than is the *Alnus* system, because the ecosystem C content is concentrated in the aboveground stocks biomass (García-Oliva et al. 2006). However, with evergreen systems, the organic matter is accumulated at the forest floor, due the degree of protection of C is less for the litter and hence vulnerable to loss by external disturbances (fire, erosion, etc.), compared to C incorporate directly in the mineral soil and in interaction with mineral surfaces or protected by aggregates (Sollins et al. 1996). For example, Sánchez-Salas et al. (2011) expected that the coniferous vegetation-soil systems would migrate by approximately 300 - 400 m above their current elevation range in Central Mexico by 2030. Therefore, the *Abies* system would be replaced by the *Alnus* system, losing 187 Mg C ha^{-1} associated with the aboveground biomass C content, representing a 62% reduction in the ecosystem C pool. In the long term, however, shifts in vegetation-soil systems distributions, particularly in terms of the predominant plant functional types or growth forms, may also result in overall shifts in litter quality and decomposability.

5. Conclusions

The greatest stock of aboveground biomass carbon was in the *Abies* system, owing to the higher growth rate as indicated by the widths of the growth rings. In the *Alnus* system, the magnitude of the input of plant residues was inversely related to the carbon stock on the forest floor due to the decomposition of the aboveground litter layer. The chemical composition of the plant residues in the systems determined the decomposition constant and the mean residence time of the litter layer. The highest proportion of soil organic carbon (SOC) was found in the first soil horizon in the systems of *Alnus* and *Pinus*. Changes in species distribution as a result of climatic change could modify the input of organic material as well as the mechanisms that determine concentrations of SOC. For this reason, understanding the effect of vegetation-soil systems on the carbon cycle along highland elevational gradients requires characterization of the processes that control the SOC (decomposition of the litter, microbial activity and soil fauna dynamics and composition).

6 Acknowledgments

This work is part of the doctoral research of the first author. R. I. Jasso Flores acknowledges Posgrado en Ciencias Biológicas of Universidad Nacional Autónoma de México for academic support during her studies, and CONACYT (Grant 50780-F) for doctoral scholarships. We thank Rodrigo Velázquez-Duran for his assistance during chemical analyses. Funds for this research were provided by PAPIIT-UNAM grant IN 104515.

7 References

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H. (Ted), Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A., and Cobb, N. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manag. 259(4): 660–684. doi:10.1016/j.foreco.2009.09.001.

Augusto, L., De Schrijver, A., Vesterdal, L., Smolander, A., Prescott, C., and Ranger, J. 2015. Influences of evergreen gymnosperm and deciduous angiosperm tree species on the functioning of temperate and boreal forests: Spermatophytes and forest functioning. Biol. Rev. 90(2): 444–466. doi:10.1111/brv.12119.

Avendaño, H., Ma, D., Acosta Mireles, M., Carrillo Anzures, F., Barra, E., and D, J. 2009. Estimación de biomasa y carbono en un bosque de Abies religiosa. Rev. Fitotec. Mex. 32(3): 233–238.

Berg, B., Davey, M.P., De Marco, A., Emmett, B., Faituri, M., Hobbie, S.E., Johansson, M.-B., Liu, C., McClaugherty, C., Norell, L., Rutigliano, F.A., Vesterdal, L., and Virzo De Santo, A. 2010. Factors influencing limit values for pine needle litter decomposition: a synthesis for boreal and temperate pine forest systems. Biogeochemistry 100(1–3): 57–73. doi:10.1007/s10533-009-9404-y.

Berg, B., and McClaugherty, C. 2014. Plant Litter. Springer Berlin Heidelberg, Berlin, Heidelberg. Available from http://link.springer.com/10.1007/978-3-642-38821-7 [accessed 4 September 2015].

Binkley, D. 1995. The Influence ofTree Species on Forest Soils: Processes and Patterns. *In* Proceedings of the trees and soil workshop. p. 994. Available from http://www.agronomysociety.org.nz/uploads/94803/files/SP10_1._KA_-_tree_spp_influence_on_forest_soils.pdf [accessed 27 November 2016].

Carrillo Anzúres, F., Acosta Mireles, M., Flores Ayala, E., Juárez Bravo, J.E., and Bonilla Padilla, E. 2014. Estimación de biomasa y carbono en dos especies arboreas en La

Sierra Nevada, México. Rev. Mex. Cienc. Agríc. 5(5): 779–793. doi:doi.org/10.29312/remexca.v5i5.901.

Challenger, A., and Caballero, J. 1998. Utilización y conservación de los ecosistemas terrestres de México: pasado, presente y futuro. *In* 1. ed. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad [u.a.], México, D.F.

Chapin FS, I., Matson, P.A., and Vitousek, P. 2011. Principles of Terrestrial Ecosystem Ecology. Springer Science & Business Media.

Chávez-Vergara, B., Merino, A., González-Rodríguez, A., Oyama, K., and García-Oliva, F. 2018. Direct and legacy effects of plant-traits control litter decomposition in a deciduous oak forest in Mexico. PeerJ 6: e5095. doi:10.7717/peerj.5095.

Chávez-Vergara, B., Rosales-Castillo, A., Merino, A., Vázquez-Marrufo, G., Oyama, K., and García-Oliva, F. 2016. Quercus species control nutrients dynamics by determining the composition and activity of the forest floor fungal community. Soil Biol. Biochem. 98: 186–195. doi:10.1016/j.soilbio.2016.04.015.

Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O., Hobbie, S.E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., Quested, H.M., Santiago, L.S., Wardle, D.A., Wright, I.J., Aerts, R., Allison, S.D., van Bodegom, P., Brovkin, V., Chatain, A., Callaghan, T.V., Díaz, S., Garnier, E., Gurvich, D.E., Kazakou, E., Klein, J.A., Read, J., Reich, P.B., Soudzilovskaia, N.A., Vaieretti, M.V., and Westoby, M. 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecol. Lett. 11(10): 1065–1071. doi:10.1111/j.1461-0248.2008.01219.x.

Dahal, K.N., Kafle, G., Dahal, K.N., and Kafle, G. 2013. Organic Carbon in Soil and Biomass of an *Alnus nepalensis* Forest in Kathmandu, Nepal. Int. J. Agric. For. 3(6): 240–243. doi:10.5923/j.ijaf.20130306.06.

De Deyn, G.B., Cornelissen, J.H.C., and Bardgett, R.D. 2008. Plant functional traits and soil carbon sequestration in contrasting biomes. Ecol. Lett. 11(5): 516–531. doi:10.1111/j.1461-0248.2008.01164.x.

Esperón-Rodríguez, M., and Barradas, V. 2014. Potential vulnerability to climate change of four tree species from the central mountain region of Veracruz, Mexico. Clim. Res. 60(2): 163–174. doi:10.3354/cr01231.

Fajardo, A., Piper, F.I., Pfund, L., Körner, C., and Hoch, G. 2012. Variation of mobile carbon reserves in trees at the alpine treeline ecotone is under environmental control. New Phytol. 195(4): 794–802. doi:10.1111/j.1469-8137.2012.04214.x.

Flores Delgadillo, L., and Alcalá Martínez, R. 2010. MANUAL DEL LABORATORIO DE FISICA DE SUELOS1.pdf. Available from http://www.geologia.unam.mx/igl/deptos/edafo/lfs/MANUAL%20DEL%20LABORATORIO%20DE%20FISICA%20DE%20SUELOS1.pdf [accessed 8 February 2017].

Galicia, L., Chávez-Vergara, B.M., Kolb, M., Jasso-Flores, R.I., Rodríguez-Bustos, L.A., Solís, L.E., Cruz, V.G. de la, Campuzano, E.P., and Villanueva, A. 2018. Perspectivas del enfoque socioecológico en la conservación, el aprovechamiento y pago de servicios ambientales de los bosques templados de México. Madera Bosques 24(2). doi:10.21829/myb.2018.2421443.

Galicia, L., Gómez-Mendoza, L., and Magaña, V. 2015. Climate change impacts and adaptation strategies in temperate forests in Central Mexico: a participatory approach. Mitig. Adapt. Strateg. Glob. Change 20(1): 21–42. doi:10.1007/s11027-013-9477-8.

Gao, Y., Cheng, J., Ma, Z., Zhao, Y., and Su, J. 2014. Carbon storage in biomass, litter, and soil of different plantations in a semiarid temperate region of northwest China. Ann. For. Sci. 71(4): 427–435. doi:10.1007/s13595-013-0355-z.

García García, R. 2000. Comportamiento de la dinámica sucesional de Abies religiosa (HBK) Schl. et. Cham., y Pinus hartwegii Lindl. en la estación forestal experimental Zoquiapan, Estado de México. Universidad Autónoma Chapingo, Mexico, Chapingo, Texcoco, Edo. de México.

García-Oliva, F., Hernández, G., and Gallardo Lancho, J.F. 2006. Comparison of ecosystem C pools in three forests in Spain and Latin America. Ann. For. Sci. 63(5): 519–523. doi:10.1051/forest:2006034.

Gómez-Guerrero, A., Silva, L.C.R., Barrera-Reyes, M., Kishchuk, B., Velázquez-Martínez, A., Martínez-Trinidad, T., Plascencia-Escalante, F.O., and Horwath, W.R. 2013. Growth decline and divergent tree ring isotopic composition (δ^{13}C and δ^{18}O) contradict predictions of CO_2 stimulation in high altitudinal forests. Glob. Change Biol. 19(6): 1748–1758. doi:10.1111/gcb.12170.

Grabherr, G., Gottfried, M., and Pauli, H. 2010. Climate Change Impacts in Alpine Environments. Geogr. Compass 4(8): 1133–1153. doi:10.1111/j.1749-8198.2010.00356.x.

Haghdoost, N., Akbarinia, M., and Hosseini, S.M. 2013. Land-use change and carbon stocks: A case study, Noor County, Iran. J. For. Res. 24(3): 461–469. doi:10.1007/s11676-013-0340-2.

Hansen, K., Vesterdal, L., Schmidt, I.K., Gundersen, P., Sevel, L., Bastrup-Birk, A., Pedersen, L.B., and Bille-Hansen, J. 2009. Litterfall and nutrient return in five tree species in a common garden experiment. For. Ecol. Manag. 257(10): 2133–2144. doi:10.1016/j.foreco.2009.02.021.

Heil, G.W., Bobbink, R., and Boix, N.T. 2003. Ecology and Man in Mexico's Central Volcanoes Area. Springer Science & Business Media.

Hoch, G., and Körner, C. 2003. The carbon charging of pines at the climatic treeline: a global comparison. Oecologia 135(1): 10–21. doi:10.1007/s00442-002-1154-7.

Huffman, E.W.D. 1977. Performance of a new automatic carbon dioxide coulometer. Microchem. J. 22(4): 567–573. doi:10.1016/0026-265X(77)90128-X.

Jasso-Flores, I. 2014. Crecimiento, biomasa y carbono arbóreo en un gradiente altitudinal en bosques templados. M.Sc. thesis, Department of Physical Geography. Universidad Nacional Autónoma de México, DF, México.

Kögel-Knabner, I. 2002. The macromolecular organic composition of plant and microbial residues as inputs to soil organic matter. Soil Biol. Biochem. 34(2): 139–162. doi:10.1016/S0038-0717(01)00158-4.

Körner, C. 1999. Alpine Plant Life. Springer Berlin Heidelberg, Berlin, Heidelberg. Available from http://link.springer.com/10.1007/978-3-642-98018-3 [accessed 13 June 2016].

Kullman, L. 2008. Thermophilic Tree Species Reinvade Subalpine Sweden—Early Responses to Anomalous Late Holocene Climate Warming. Arct. Antarct. Alp. Res. 40(1): 104–110. doi:10.1657/1523-0430(06-120)[KULLMAN]2.0.CO;2.

Laganière, J., Paré, D., and Bradley, R.L. 2010. How does a tree species influence litter decomposition? Separating the relative contribution of litter quality, litter mixing, and forest floor conditions. Can. J. For. Res. 40(3): 465–475. doi:10.1139/X09-208.

Lauer, W. 1978. Timberline Studies in Central Mexico. Arct. Alp. Res. 10(2): 383. doi:10.2307/1550769.

Liang, E., Wang, Y., Xu, Y., Liu, B., and Shao, X. 2010. Growth variation in Abies georgei var. smithii along altitudinal gradients in the Sygera Mountains, southeastern Tibetan Plateau. Trees 24(2): 363–373. doi:10.1007/s00468-009-0406-0.

Mendoza-Ponce, A., and Galicia, L. 2010. Aboveground and belowground biomass and carbon pools in highland temperate forest landscape in Central Mexico. Forestry 83(5): 497–506. doi:10.1093/forestry/cpq032.

Morrone, J.J. 2010. Fundamental biogeographic patterns across the Mexican Transition Zone: an evolutionary approach. Ecography 33(2): 355–361. doi:10.1111/j.1600-0587.2010.06266.x.

Parque Nacional Izta-Popo Zoquiapan. 2013. Parque Nacional Izta-Popo Zoquiapan. Available from http://iztapopo.conanp.gob.mx/listado_de_especies.php [accessed 21 March 2018].

Peña-Ramírez, V.M., Vázquez-Selem, L., and Siebe, C. 2009. Soil organic carbon stocks and forest productivity in volcanic ash soils of different age (1835–30,500 years B.P.) in Mexico. Geoderma 149(3–4): 224–234. doi:10.1016/j.geoderma.2008.11.038.

Pérez-Suárez, M., Arredondo-Moreno, J.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. For. Ecol. Manag. 258(7): 1307–1315.

doi:10.1016/j.foreco.2009.06.031.

Pernilla Brinkman, E., Van der Putten, W.H., Bakker, E.-J., and Verhoeven, K.J.F. 2010. Plant–soil feedback: experimental approaches, statistical analyses and ecological interpretations. J. Ecol. 98(5): 1063–1073. doi:10.1111/j.1365-2745.2010.01695.x.

Rojas-García, F., De Jong, B.H.J., Martínez-Zurimendí, P., and Paz-Pellat, F. 2015. Database of 478 allometric equations to estimate biomass for Mexican trees and forests. Ann. For. Sci. 72(6): 835–864. doi:10.1007/s13595-015-0456-y.

Rzedowski, J. 2006. Vegetación de México. 1a. Edición digital, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. México. 504pp.

Rzedowski, J., Rzedowski, G.C. de, Instituto de Ecología, Centro Regional del Bajío, México, and Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. 2001. Flora fanerogámica del Valle de México. Instituto de Ecología, Centro Regional del Bajío : Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Pátzcuaro, Michoaca.

Sáenz-Romero, C., Rehfeldt, G.E., Duval, P., and Lindig-Cisneros, R.A. 2012. Abies religiosa habitat prediction in climatic change scenarios and implications for monarch butterfly conservation in Mexico. For. Ecol. Manag. 275: 98–106. doi:10.1016/j.foreco.2012.03.004.

Sánchez-González, A., López-Mata, L., and Granados-Sánchez, D. 2005. Semejanza florística entre los bosques de Abies religiosa (H.B.K.) Cham. & Schltdl. de la Faja Volcánica Transmexicana. Investig. Geográficas (56): 62–76.

Sánchez-Salas, J., Guerra, V.M.M., Domínguez, R.P., Arredondo, F.M.S., Hernández, E.S.O., and Jurado, E. 2011. Cambio climático:?` precursor de migración de especies vegetales en la montaña más alta del norte de México? Cienc.-UANL 14(2): 137–143.

Scowcroft, P.G., Turner, D.R., and Vitousek, P.M. 2000. Decomposition of Metrosideros polymorpha leaf litter along elevational gradients in Hawaii. Glob. Change Biol. 6(1): 73–85. doi:10.1046/j.1365-2486.2000.00282.x.

Siebe, C., Jahn, R., and others. 1996. Manual para la descripción y evaluación ecológica de suelos en el campo. Available from http://www.sidalc.net/cgi-bin/wxis.exe/?IsisScript=UACHBC.xis&method=post&formato=2&cantidad=1&expresion=mfn=091256 [accessed 8 February 2017].

Sollins, P., Homann, P., and Caldwell, B.A. 1996. Stabilization and destabilization of soil organic matter: mechanisms and controls. Geoderma 74(1–2): 65–105. doi:10.1016/S0016-7061(96)00036-5.

Solomon, S., Intergovernmental Panel on Climate Change, and Intergovernmental Panel on Climate Change (*Editors*). 2007. Climate change 2007: the physical science basis: contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge ; New York.

Torres, C. 2013. Análisis de los cambios del límite superior del bosque en el volcán Iztaccíhuatl. Universidad Nacional Autónoma de México, México, D.F.

Vergutz, L., Manzoni, S., Porporato, A., Novais, R.F., and Jackson, R.B. 2012. Global resorption efficiencies and concentrations of carbon and nutrients in leaves of terrestrial plants. Ecol. Monogr. 82(2): 205–220. doi:10.1890/11-0416.1.

Vesterdal, L., Clarke, N., Sigurdsson, B.D., and Gundersen, P. 2013. Do tree species influence soil carbon stocks in temperate and boreal forests? For. Ecol. Manag. 309: 4–18. doi:10.1016/j.foreco.2013.01.017.

Villaseñor, J.L. 2004. Los géneros de plantas vasculares de la flora de México. Bol. Soc. Botánica México (75). Available from http://www.redalyc.org/resumen.oa?id=57707506 [accessed 20 March 2018].

Villers-Ruiz, L., and Castañeda-Aguado, D. 2013. Species and plant community reorganization in the Trans-Mexican Volcanic Belt under climate change conditions. J. Mt. Sci. 10(6): 923–931. doi:10.1007/s11629-013-2719-0.

Vitousek, P. 1982. Nutrient cycling and nutrient use efficiency. Am. Nat.: 553–572. doi:10.1086/283931.

Vogt, K. 1991. Carbon budgets of temperate forest ecosystems. Tree Physiol. 9(1–2): 69–86. doi:10.1093/treephys/9.1-2.69.

Vogt, K.A., Grier, C.C., and Vogt, D.J. 1986. Production, Turnover, and Nutrient Dynamics of Above- and Belowground Detritus of World Forests. *In* Advances in Ecological Research. *Edited by* A.M. and E.D. Ford. Academic Press. pp. 303–377. Available from http://www.sciencedirect.com/science/article/pii/S0065250408601221 [accessed 15 November 2016].

World reference base for soil resources. 2006 A framework for international classification, correlation, and communication. *In* 2006 ed. Food and Agriculture Organization of the United Nations, Rome.

Zavitkovski, J., and Newton, M. 1971. Litterfall and litter accumulation in red alder stands in western Oregon. Plant Soil 35(1–3): 257–268. doi:10.1007/BF01372656.

Zhang, D., Hui, D., Luo, Y., and Zhou, G. 2008. Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. J. Plant Ecol. 1(2): 85–93. doi:10.1093/jpe/rtn002.

Zhang, H., Yuan, W., Dong, W., and Liu, S. 2014. Seasonal patterns of litterfall in forest ecosystem worldwide. Ecol. Complex. 20: 240–247. doi:10.1016/j.ecocom.2014.01.003.

Zhou, Y., Clark, M., Su, J., and Xiao, C. 2015. Litter decomposition and soil microbial community composition in three Korean pine (Pinus koraiensis) forests along an altitudinal gradient. Plant Soil 386(1–2): 171–183. doi:10.1007/s11104-014-2254-y.

Zhu, B., Wang, X., Fang, J., Piao, S., Shen, H., Zhao, S., and Peng, C. 2010. Altitudinal changes in carbon storage of temperate forests on Mt Changbai, Northeast China. J. Plant Res. 123(4): 439–452. doi:10.1007/s10265-009-0301-1.

Figures and tables

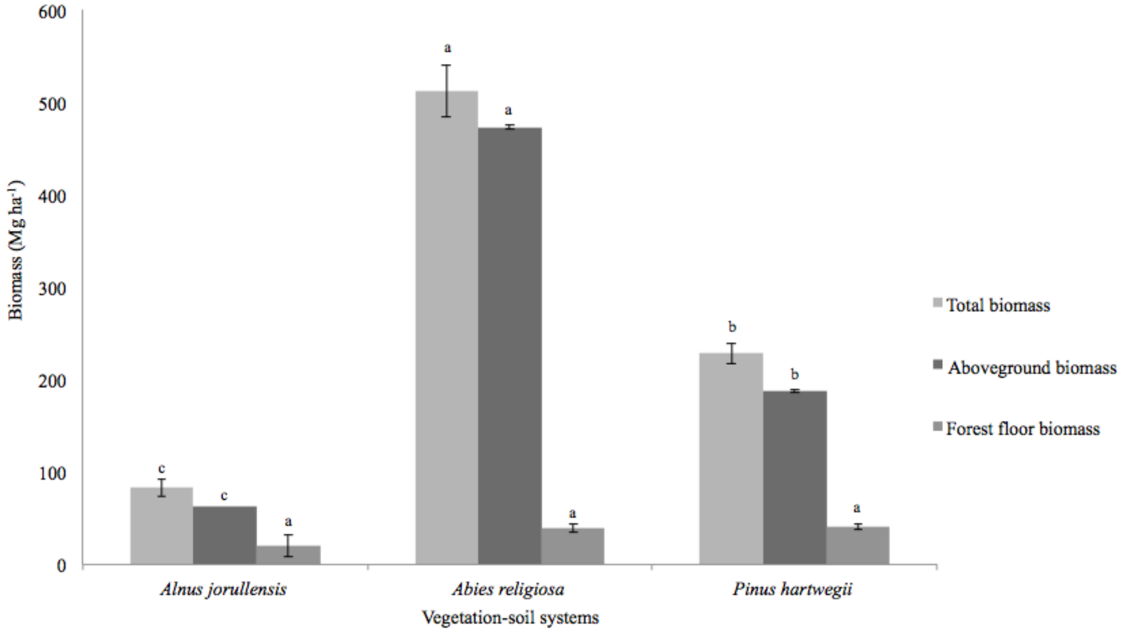

Figure 1. Biomass stocks of three vegetation-soil systems of temperate forest, Mexico. The forest floor stocks include litter and coarse woody residues. Different letters between vegetation-soil systems within each stock indicate significant differences (Tukey HDS test p≤ 0.05).

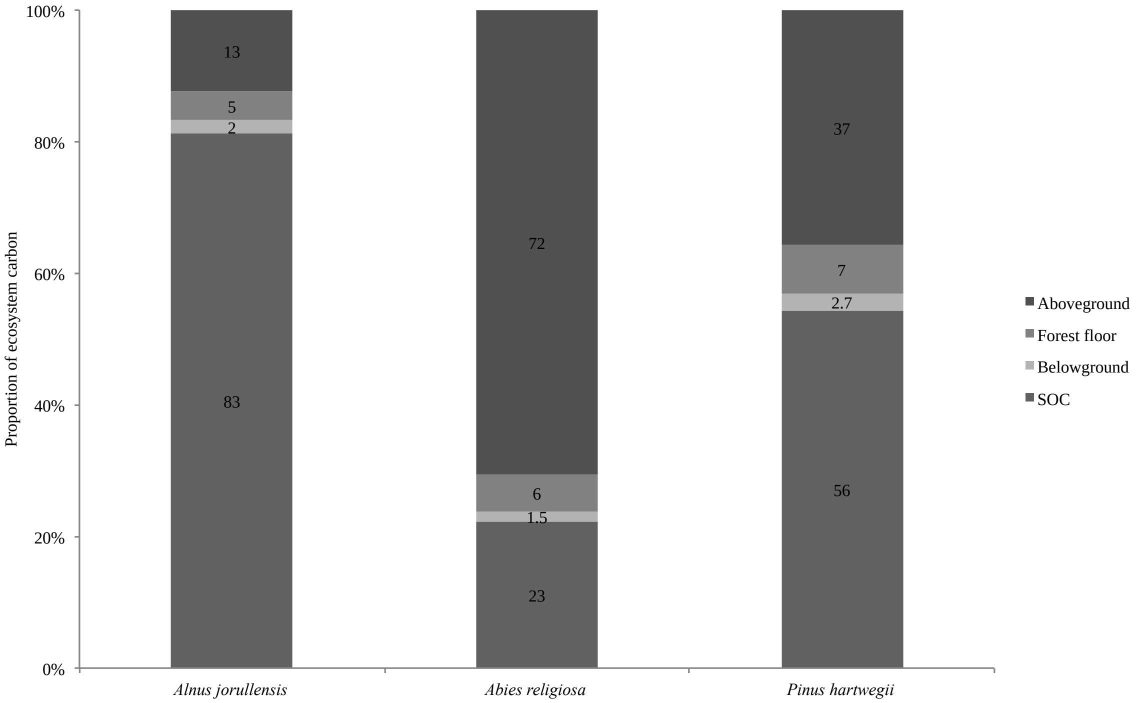

Figure 2. Relative contribution of parts of the vegetation-soil system to the total C content: above and belowground tree carbon, forest floor (litter and coarse woody residues) and soil organic carbon (1m^2). The numbers within the bars indicate the percentage of the total C within that vegetation-soil system.

Table 1. Environmental and vegetation characteristics of three vegetation-soil systems on an altitudinal gradient in a temperate forest in central Mexico. Lang Index calculated as MAP/MAT.

	Alnus jorullensis 3100 m a.s.l.	***Abies religiosa*** 3500 m a.s.l.	***Pinus hartwegii*** 3700 m a.s.l.
Climate			
MAT (ºC)	10	7.5	5
MAP (mm)	1100	1300	<900
Lang Index[1]	110	173	180
Litter layer characteristics			
Type	moder	moder	moder
Depth (cm)	2	5-7	5-10
Cover (%)	100	100	100
Soil characteristics (0-30 cm)			
Edaphic clasification (WRB 2006)	silandic Andosol	vitric Andosol	vilandic Andosol
Bulk density (g cm^3)	0.69	0.67	0.64
pH	6.07	6.20	4.33
Texture	Silty clay loam	Sandy loam	Sandy loam
Tree characteristics			
Phenology	Deciduous	Evergreen	Evergreen
Tree density (tree ha^{-1})	284.8 ± 51.4 a	245.6 ± 34 a	226.4 ± 19.2 a
Tree basal area (m^2 ha^{-1})	11.8 ± 0.80 a	30.9 ± 0.80 b	17.9 ± 2.5 a
d.b.h (cm)	20 ± 0.4 c	34 ± 1 a	23 ± 1 b
Height (m)	10.4 ± 0.74 a	23.1 ± 1.95 b	15 ± 0.9 a
Tree dominance (%)	90%	100%	100%

MAP, Mean annual precipitation; MAT, mean annual temperature, [1] Villers-Ruiz and Castañeda-Aguado (2013).

Table 2. Allometric equations to estimate aboveground tree biomass for the three vegetation-soil systems of highlands temperate forest, Mexico. Shown: Equations, diameter used to estimate tree biomass for the published equation, and locality at which the equations were developed.

Alnus jorullensis [1]	$Y = 0.0195\ (\mathrm{d.b.h})^{2.7519}$	d.b.h 11-30 cm	Texcoco
Abies religiosa [2]	$Y = 0.0713\ (\mathrm{d.b.h})^{2.5104}$	d.b.h 10-79 cm	Tlaxcala
Pinus hartwegii [3]	$Y = 0.0635\ (\mathrm{d.b.h})^{2.472}$	d.b.h 3-58 cm	Parque Nacional Izta-Popo, Zoquiapan y Anexo

Source: [1]Carrillo Anzúres et al. (2014); [2]Avendaño et al. (2009); [3]Rojas-García et al. (2015)

Table 3. Litter biomass, litterfall rate, decomposition litter rate (*k*) and mean residence time (MRT) of three vegetation-soil systems of highlands temperate forest, Mexico. Different letters indicate that means are significantly different among the systems (Tukey HDS test p≤ 0.05).

	Litter (Mg ha^{-1})	**Litterfall** (Mg ha^{-1} yr^{-1})	***k* litter** (yr^{-1})	**MRT** (Year)
Alnus jorullensis	2.5 ± 0.3^{c}	3.1 ± 0.08^{a}	0.12 ± 0.04^{a}	8 ± 10^{b}
Abies religiosa	13.1 ± 0.7^{b}	1.4 ± 0.03^{b}	0.01 ± 0^{b}	93 ± 17^{a}
Pinus hartwegii	20.1 ± 0.3^{a}	1.9 ± 0.02^{b}	0.01 ± 0^{b}	105 ± 46^{a}

Table 4. Carbon concentration and carbon contents in vegetation components in the three vegetation-soil systems of highlands temperate forest, Mexico. Different uppercase letters indicate significant differences among the systems; different lowercase letters indicate differences among the components within each vegetation-soil system (Tukey HDS test; p≤ 0.05).

	Carbon concentration (mg g^{-1})			**Carbon contents** (Mg C ha^{-1})		
	Alnus jorullensis	***Abies religiosa***	***Pinus hartwegii***	***Alnus jorullensis***	***Abies religiosa***	***Pinus hartwegii***
Shoot	463.4 ± 1.27^{A}	465.3 ± 6.51^{A}	485.3 ± 7.41^{A}	18.6 ± 0.003^{Ca}	181 ± 0.025^{Aa}	57.4 ± 0.011^{Ba}
Stem	460 ± 1^{B}	455.5 ± 5.54^{C}	490 ± 6.73^{A}	6.1 ± 0.001^{Aab}	15.4 ± 0.002^{Ab}	20.9 ± 0.004^{Abc}
Foliage	406.9 ± 1.1^{B}	401.9 ± 3.95^{B}	469.7 ± 1.11^{A}	2.9 ± 0^{Aab}	16.6 ± 0.002^{Ab}	9.3 ± 0.002^{Ac}
Coarse woody debris	511.4 ± 3.51^{A}	481.1 ± 7.53^{B}	501.9 ± 5.01^{AB}	8.9 ± 8^{Abc}	12.5 ± 2.7^{Ab}	10.5 ± 4.4^{Ac}
Litter	418.8 ± 8.70^{B}	378.6 ± 8.63^{C}	452 ± 6.22^{A}	1.6 ± 0.13^{Ca}	5 ± 0.26^{Bb}	7.6 ± 0.10^{Ac}
Root	406.6 ± 3.01^{A}	385.5 ± 12.5^{A}	378.9 ± 20.9^{A}	1 ± 0.14^{Ac}	2.9 ± 0.58^{Ab}	2.2 ± 0.22^{Adc}

Table 5. Soil characteristics of the top 30 cm in the in the three vegetation-soil systems of highlands temperate forest, Mexico. Different letters indicate that means are significantly different among the systems (Tukey HDS test p≤ 0.05).

	Texture (%)			**C** (mg g^{-1}) (1 m)	**SOC** (Mg C ha^{-1}) (30 cm)
	Sand	Silt	Clay		
Alnus jorullensis	22 ± 0.2	55 ± 0.3	24 ± 0.1	69.7 ± 1.63 b	82.08 ± 1.92^{b}
Abies religiosa	64 ± 0.4	32 ± 0.3	4 ± 0.2	79.9 ± 9.18 ab	91.6 ± 10.53^{b}
Pinus hartwegii	64 ± 0.1	30 ± 0.3	6 ± 0.1	94.1 ± 1.8 a	101.7 ± 1.96^{a}

Table 6. Soil characteristics for the horizons in the three vegetation-soil systems of highlands temperate forest, Mexico.

	Horizon (WRB, 2006)	**Depth** (cm)	**Bulk density** (g cm^3)	**Carbon concentration** (mg g^{-1})	**Soil organic C content** (Mg C ha^{-1})	**%SOC***
Alnus jorullensis	Ah	0-17	0.69 ± 0.01	98.4 ± 3.9	115.41 ± 2.17	61 ± 2
	AB	17-23	0.99 ± 0.01	20.2 ± 0.9	11.89 ± 0.18	6 ± 0.2
	Bw1	23-47	0.87 ± 0.04	10.7 ± 0.2	22.44 ± 1.03	11 ± 1
	Bw2	47-60	0.85 ± 0.02	10 ± 0.2	11.09 ± 0.36	6 ± 0.3
	BC	60-100	0.87 ± 0.02	8.3 ± 0	28.83 ± 0.98	15 ± 1
Abies religiosa	Ah1	0-9	0.67 ± 0.04	42.2 ± 8.6	25.52 ± 1.78	32 ± 2
	Ah2	9-32	1 ± 0.04	9.1 ± 0.3	21.82 ± 0.89	27 ± 0.9
	2Cw1	32-58	1 ± 0.1	4.1 ± 0.1	11.37 ± 0.15	14 ± 0.1
	Cw2	58-100	1 ± 0.04	4.8 ± 0.3	20.61 ± 0.92	26 ± 0.4
Pinus hartwegii	Ah	0-10	0.64 ± 0.07	90.5 ± 4	57.42 ± 6.80	37 ± 7
	C	10-17	0.95 ± 0.03	6.2 ± 1.1	4.09 ± 0.14	2 ± 0.13
	1AC	17-39	1.08 ± 0.02	10.1 ± 0.7	24.24 ± 0.51	15 ± 0.5
	2AC	39-73	1.06 ± 0.01	9.6 ± 0	34.99 ± 0.45	23 ±0.4
	3Ah	73-100	0.93 ± 0.01	12.7 ± 2.1	31.98 ± 0.39	21 ± 0.2

* Relative contribution of soil organic carbon (SOC) to 1 m depth in the soil profile in the vegetation-soil systems

Chapter two

Soil organic matter dynamics and microbial metabolism along an altitudinal gradient in Highland tropical forests

Isela Jasso-Flores[1,2], Leopoldo Galicia[1], Bruno Chávez-Vergara[4,5], Agustín Merino[6], Yunuen Tapia-Torres[7] and Felipe García-Oliva[3*]

[1] Departamento de Geografía Física, Instituto de Geografía, Circuito exterior, S/N, Universidad Nacional Autónoma de México, Coyoacán, CDMX, 04510, México. Email: isela.jasso.flores@gmail.com; lgalicia@igg.unam.mx.

[2] Posgrado en Ciencias Biológicas, Unidad de Posgrado, Edificio D, 1º piso, Circuito de Posgrados, Ciudad Universitaria, Coyoacán, CDMX, 04510, México

[3] Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México. AP 27-3, Santa María de Guido, Morelia, 58090, Michoacán, México. fgarcia@cieco.unam.mx.

[4] Departamento de Ciencias Ambientales y del Suelo, Instituto de Geología, Circuito exterior, S/N, Universidad Nacional Autónoma de México, México, CDMX, 04510, México. chavezvb@geologia.unam.mx

[5] Laboratorio Nacional de Geoquímica y Mineralogía. Circuito de la Investigación Científica S/N C.P. 04510 CDMX

[6] Department of Soil Science and Agricultural Chemistry University of Santiago de Compostela. E-27002 Lugo, Spain. agustin.merino@usc.es

[7] Escuela Nacional de Estudios Superiores Unidad Morelia, Universidad Nacional Autónoma de México, Morelia, Michoacán, México. ytapia@enesmorelia.unam.mx

Corresponding Author

fgarcia@cieco.unam.mx

Published on Science of the Total Environment DOI 10.1016/j.scitotenv.2020.140143

Abstract

The highland forests of tropical regions are highly vulnerable to climate change because of increased soil water deficit conditions through rising temperatures. Several authors have reported that labile molecules dominate soil organic matter (SOM) at higher elevations, and it is therefore more vulnerable to the rising temperatures associated with climate change. The objective of the present study was to analyze the effect of interaction between the chemical composition of organic matter derived from the dominant plant species and the metabolism of the forest floor (organic layer and mineral soil) microbial community along an elevational gradient in a highland forest in Central Mexico. The study compared three vegetation-soil systems that represent three different elevational levels: *Alnus*-system (3100 m.a.s.l.), *Abies*-system (3500 m.a.s.l.) and *Pinus*-system (3700 m.a.s.l.). The SOM produced in the lowest site is more recalcitrant (i.e., higher Alkyl:O-Alkyl ratio) as a result of the lower water availability than in the highest site. The results of Threshold Elemental Ratio$_{C:N}$ (TER$_{C:N}$) and TER$_{C:P}$ for the organic layer were lower than their C:N and C:P ratios in the organic layer, supporting that the microbial community of the organic layer in the site of lowest elevation must be limited by the carbon source, rather than by N and P. However, these results were not found in the mineral soil, suggesting that the drivers of organic matter decomposition differ between the organic layer and the mineral soil. As a conclusion, our results suggest that the chemical recalcitrance of organic matter (at the lowest site) and temperature (at the highest site) reduce the microbial metabolic activity in the forest floor. Integrated study of plant-derived organic material and the microbial metabolism of the forest floor is therefore required to achieve a full understanding of the vulnerability of tropical mountain ecosystems to climate change.

Key words: chemical composition of organic matter, microbial metabolism, Threshold Elemental Ratio, temperature rise, Mexico.

1. Introduction

Several authors have reported the high vulnerability of highland forests of the tropical regions to climate change, due to increased soil water deficit conditions as a result of rising temperatures, among other factors (Solomon et al., 2007; Allen et al., 2010; Sáenz-Romero et al., 2012). Soil organic matter decomposition can be accelerated by climate warming, since it has been assumed that temperature is the main factor that controls decomposition rate (Davidson and Janssens, 2006). For example, for a Tibetan alpine ecosystem, Cui et al. (2019) reported that microbial metabolism is most constrained at higher elevations (<3200 m) with low temperatures than at lower elevations (2800 m) with warmer temperatures, and SOM decomposition therefore decreases with elevation. Together with the metabolism of soil microbial communities, which controls enzyme-catalyzed processes (Davidson and Janssens, 2006; Blagodatskaya et al., 2016; Cui et al., 2019), some authors have recently proposed that SOM decomposition is also affected by other factors controlled by plant community composition, such as the quantity and chemical characteristics of the organic matter (Kögel-Knabner, 2002; Bonanomi et al., 2013). These two factors can be coupled in combination with temperature and can modify the decomposition of organic matter along elevational gradients in highland forests of tropical regions (Nottingham et al., 2015; Zhou et al., 2015; He et al., 2016). For example, plant species produce a higher proportion of waxes and lipids in order to cope with water stress in sites at lower elevations with warmer conditions (Dodd and Poveda, 2003). Similarly, fine roots and the forest floor were found to have a higher proportion of recalcitrant molecules, such as alkyl compounds (i.e. lipids, cutin and suberin), in a semi-arid site than in a subhumid site in a tropical dry forest in Mexico (Campo and Merino, 2016), and other molecules such as tannins and other polyphenols can be increased in warmer and drier conditions (Tharayil et al., 2011). These compounds have been reported in drought-adapted plants (Boom et al., 2005) and play a limiting role in the decomposition process (Tharayil et al., 2011). Therefore, plants in sites with higher water-stress conditions promote the accumulation of complex molecules within their tissues in order to improve their drought tolerance (Campo and Merino, 2016). This increase in the proportion of complex molecules has also been reported along elevational gradients in sites with warmer temperatures (lower elevation) compared to those with colder temperatures (higher elevation). For example, Zimmermann et al. (2012) reported that the proportion of alkyl compounds decreased with elevation along a 3000 m tropical forest transect.

The quantity and chemical characteristics of the organic matter control it's decomposition, but the metabolism of the soil microbial community also plays a key role in the process, since the SOM represents the main source of energy, carbon and nutrients for heterotrophic microorganisms (Davidson and Janssens, 2006; Nottingham et al., 2015; Blagodatskaya et al., 2016; Nottingham et al., 2016). Synthesis of extracellular enzymes by the microbial community responds to nutrient shortages for the microbial community of the organic layer (Rillig et al., 2007; Sinsabaugh et al., 2009). For example, in conditions of low nutrient availability, the microbial community invests less energy in biomass growth and more in the production of extracellular enzymes with which to acquire the scarce nutrients (Schimel et al., 2007). In order to measure this condition, Sterner and Elser (2002) proposed the *threshold elemental ratio* (TER) as a tool for evaluating the limiting factors for the microbial community. The TER defines the element ratio at which microbial growth shifts from energy limitation (represented by C) to nutrient limitation (represented by N and P). Where the C:N or C:P ratios of organic sources for the microbial community exceed the respective TER, this suggests that the microbial community is co-limited by either C-N or C-P (Sterner & Elser, 2002; Tapia-Torres et al., 2015; Ostertag and DiManno, 2016; Augusto et al., 2017). A microbial community that invests more energy in nutrient acquisition than in population growth, in order to maintain its C:N:P ratio, is considered homeostatic (Sterner and Elser, 2002).

Despite the importance of enzymatic catalysis, it has been observed that the activities of extracellular enzymes are affected by different factors that alter their structural integrity and activation energy needed for an efficient catalytic activity, as pH and temperature, respectively

(Baldrian, 2009). Particularly related to temperature effect, different authors have reported that the activity of extracellular enzymes is restricted at low temperatures (e.g., at high elevations), decreasing the incidence of depolymerization and, thus, reducing the release of monomers (Blagodatskaya et al., 2016; Nottingham et al., 2016; Siles et al., 2017; Cui et al., 2019). In contrast, warmer sites (e.g., at low elevations) promote such extracellular activity (Blagodatskaya et al., 2016). However, the interaction of the chemical characteristics of plant-derived material and extracellular enzyme-catalyzed processes plays an important role in SOM decomposition by increasing the availability of both energy and substrates. For example, the microbial community must invest more energy in extracellular enzyme production in order to cleave recalcitrant organic compounds (Allison et al., 2014; Chávez-Vergara et al., 2018) than is produced by the plant species under water stress conditions (low elevation; Dodd and Poveda, 2003). In this latter condition, the soil microbial community can be C limited, rather than N or P limited (Tapia-Torres et al., 2015; Montiel-González et al., 2017).

Factors that control the decomposition processes along a highland forest elevational gradient include the interactions among organic matter quality, microbial metabolisms and climatic variables (Djukic et al., 2010; Nottingham et al., 2015). Study of the relative importance of these factors along the elevational gradient is critical for the construction of scenarios regarding the organic matter decomposition and energy flow of these ecosystems, considering the projected effects of climate change. In this context, some studies have analyzed the effect of temperature on microbial growth and extracellular enzyme activity (Nottingham et al., 2015; Blagodatskaya et al., 2016; Nottingham et al., 2016; Cui et al., 2019; Nottingham et al., 2019), and the effect of temperature on soil organic matter decomposition (Giardina et al., 2014; Zimmermann et al., 2012) along an elevational gradient. However, to date, there has never been an integral analysis of the effects of temperature on the chemical characteristics of organic matter, microbial metabolisms (enzymatic activities), and their interaction, along a forest elevational gradient.

The objective of the present study was therefore to analyze the effect of the interaction between the chemical composition of organic matter derived from the dominant plant species and the metabolism of the microbial community of the forest floor (organic layer and mineral soil), along an elevational gradient in a highland forest of central Mexico. The study was conducted in the Iztaccíhuatl-Popocatépetl National Park, comparing three vegetation-soil systems that represented three elevational levels: *Alnus jorullensis* (3100 m.a.s.l.), *Abies religiosa* (3500 m.a.s.l.) and *Pinus hartwegii* (3700 m.a.s.l.). Although the differences in elevation among these sites are relatively narrow, mean air temperature decreased by 5°C from the lowest to the highest site, and the lowest site presents lower water availability than the highest site (Jasso-Flores et al., 2019). We hypothesized that: a) the organic matter (litterfall and roots) produced by the plant community in the lowest site will be more recalcitrant because the plant species have to cope with water stress, and b) consequently, the forest floor microbial community in the lowest site will be limited by energy, rather than by N and P, because it must invest more energy in the depolymerization of these recalcitrant molecules.

2. Methods

2.1. Study site

The study was conducted in the Iztaccíhuatl-Popocatépetl National Park in the Trans-Mexican Volcanic Belt in central Mexico. Three vegetation-soil systems were selected along an elevational gradient (Jasso-Flores et al., 2019). The lowest site (3100 m.a.s.l.) is dominated by *Alnus jorullensis* Kunth (*Alnus*-system), while the middle site (3500 m.a.s.l.) presents *Abies religiosa* (Kunth) Schltdl. & Cham. as the dominant tree species (*Abies*-system) and the *Pinus*-systems of the highest site (3700 m.a.s.l.) are dominated by *Pinus hartwegii* Lindl. Mean average annual temperature decreases with elevation (10 °C and 5 °C for the lowest and highest sites, respectively; Jasso-Flores et al., 2019), while the Lang aridity index increases (110 and 180 for the lower and higher sites, respectively; Jasso-Flores et al., 2019), meaning that the lowest site is drier than the highest site. Moreover, the soils in the three sites belong to the group of Andosols, but each with different physical and chemical properties (Jasso-Flores et al., 2019). Accumulation of plant residues in the soil organic layer and soil organic carbon both increase at higher elevations, because the resident time of organic layer increases considerably with elevation (Jasso-Flores et al., 2019).

2.2. Sampling design

In an area of approximately three hectares of forest, five sampling plots of 50 x 50 m were randomly established at a distance of at least 200 m apart, in each of the three studied vegetation-soil systems (Jasso-Flores et al., 2019). In total, fourteen circular litterfall traps of 0.5 cm in diameter were placed under adult trees for monthly collection over a period of 12 months (January 2015 to January 2016). The mass of the organic layer was determined by collecting all organic material overlying the mineral soil from three sub-plots of 25 x 25 cm distributed at random within each sampling plot, from which one compound sample was produced per sampling plot (n = 5 per vegetation-soil system). The fresh samples were stored in black plastic bags at 4 °C until subsequent laboratory analysis. Furthermore, five 50 m transects were established in each vegetation-soil system site and a soil sample taken every 10 m from the first 30 cm of soil depth with a 8.25 cm diameter core and mixed to form one compound sample per transect in each vegetation-soil system (n = 5 per vegetation-soil system type). These samples were also kept in black plastic bags at 4°C until subsequent laboratory analysis. In the same transects, soil samples were taken for root biomass sampling (15 samples per vegetation-soil system). Thin (<2 mm) and thick (<2 mm) roots were obtained using 60 and 120 mesh sieves, respectively. All vegetal samples (litterfall, organic layer and roots) were dried at 60 °C for 72 h and ground prior to laboratory analysis.

2.3. Laboratory Analysis

Chemical characterization of organic compounds by solid-state ^{13}C CP-MAS NMR.

Litterfall, fine roots, organic layer and soil samples were analyzed by solid-state ^{13}C NMR spectroscopy (in an Agilent Varian VNMRS-500-WB spectrometer, operated at a proton resonance frequency of 500 MHz and using a zirconia rotor of volume 160 µL). Carbon chemical shifts were referenced to the carbon methylene signal of solid adamantane at 28.92 ppm. Cross Polarization Magic Angle Spinning (1D CPMAS) analysis of the samples was performed under the following conditions: contact time 1 min, inter-scan delay 1 s (a proton T1 experiment was performed to check the suitability of this time interval) and MAS rate 12 kHz. The number of scans was *ca*. 10000 - 35000 and the cross-polarization time was set at 1 m. Mineral soil samples were demineralized five times beforehand with 10% (w-to-w) hydrofluoric acid (HF) for 2 h each time (Merino et al., 2018). This procedure serves to eliminate paramagnetic interferences.

For integration, the spectra were divided into four regions representing different chemical environments of a ^{13}C nucleus: alkyl C (0–45 ppm), O-alkyl C (45–110 ppm), aromatic C (110–160 ppm) and carbonyl C (160–210 ppm). For a more detailed examination of the organic matter (OM) composition in the samples, the chemical shift regions were further divided (Knicker and Lüdemann, 1995), as follows: i) 10-45 ppm alkyl C: terminal methyl groups, methylene groups in aliphatic rings and chains. ii) 45-110 ppm O-alkyl C: methoxyl groups and C6 of some polysaccharides (45-60 ppm); C2-C5 in hexoses, C of some amino acids, higher alcohols and the aliphatic part of lignin structure (60-90 ppm); anomeric C of carbohydrates, C2-C6 of the syringyl unit of lignin (90-110 ppm); iii) 110-160 ppm aromatic C: C-H and C-C carbons and guaiacyl C2, C6 in lignin (110-140 ppm, aromatic C); aromatic COR or CNR groups (140-160 ppm, phenolic C); iv) 160-220 ppm carboxyl C: carboxyl C, carbonyl C and amide C. The contributions of the various C groups to total C were determined using MestreNova software, version 11 (Mestrelab Research Inc., Santiago de Compostela, Spain). The integral regions were corrected for the areas of spinning side bands (SSB), when these appeared in the spectra. Each SSB area was subtracted from that of the region in which it appeared, according to Knicker et al. (2005).

We examined specific integrated regions to calculate indexes associated with decomposability: alkyl:O-alkyl ratio (A:OA), O-alkyl:aromatic ratio (OA:Ar), aromaticity index (Ai) (Almendros et al., 2000; Bonanomi et al., 2013) and hydrophobicity ratio (HB:HI) (Spaccini et al., 2006), as follows:

$$HB/HI = [(0\text{-}45) + (110\text{-}160)] / [(45\text{-}110) + (160\text{-}200)] \qquad \text{Equation (1)}$$

Thermal characterization of organic compounds by differential scanning calorimetry and thermogravimetry (DSC-TG)

Litterfall, fine roots, organic layer and soil samples were analyzed by differential scanning calorimetry and thermogravimetry (DSC-TG) in order to determine the thermal resistance of the organic matter, (Mettler-Toledo Intl. Inc). The samples (4 mg) were placed in aluminum pans under dry air (O_2 flux; flow rate of 50 mL^{-1} min^{-1}) and scanned at rate of 10 °C min^{-1}. The temperature ranged between 50 and 600 °C. Samples of indium (melting point: 156.6 °C) were used to calibrate the instrument.

Heat of combustion (Q, in J per gram) was determined by integrating the DSC curves (in Wg^{-1}) over the exothermic region (150– 600 °C). Data recorded at <150 °C were disregarded in order to exclude weight losses and energy changes associated with moisture loss (Fernández et al., 2011). The temperatures at which 50% of the energy is released (DSC) under the given conditions ($T50_Q$ DSC) were also determined. The SOM content was determined from the difference in weight of the material burned at 150 and 600 °C.

The area under the DSC curves was analyzed and divided into three partial heat release groups, representing different degrees of resistance to thermal oxidation: labile organic matter, (200-375 °C); recalcitrant organic matter (375-475 °C); and Extra- recalcitrant organic matter (475-600 °C). The resulting partial heats of combustion were designated Q_1, Q_2 and Q_3 for DSC.

Nutrient content analysis

Total nutrients. Samples were dried at a constant temperature of 105 ° C for 72 hours, sieved through a 2 mm mesh and ground in an agate mortar in order to allow measurement of total C, N and P concentrations. All forms of carbon were determined with a UIC total carbon analyzer model CM5012 (Chicago, USA), while the N and P forms were colorimetrically analyzed using a Bran-Luebbe Auto Analyzer 3 (Norderstedt, Germany). Total C was determined by combustion and coulometric determination (Huffman, 1977), while total N (Nt) and total P (Pt) were determined from the acid digestion of concentrated H_2SO_4 with K_2SO_4 plus $CuSO_4$ as a catalyzer. Nt was determined by the micro-Kjeldahl method (Bremmer, 1996) and Pt by the colorimetric method with molybdate after the reduction of ascorbic acid (Murphy & Riley, 1962).

Available nutrients. Ammonium (NH_4^+) and nitrate (NO_3^-) were extracted from 10 g of soil and 2 g of soil organic layer with 2M KCl, filtered through Whatman #1 paper (Robertson et al., 1999) and determined according to the procedures of the Bran-Luebbe autoanalyzer. Inorganic and organic P were extracted with 0.5 M $NaHCO_3$ and determined as orthophosphates in the autoanalyzer.

Dissolved nutrients. For determination of dissolved C, N and P, 2 g of soil organic layer and 20 g of fresh soil were shaken for 1 h with deionized water and filtered through Whatman #42 paper and a 0.45 μm nitrocellulose membrane (Jones and Willet, 2006). Dissolved organic C (COD) was determined by combustion and coulometric determination (Huffman, 1977). Dissolved organic N

(NOD) and dissolved organic P (POD) were determined following acid digestion. The NOD was determined from the difference between the digested N and NH_4^+ from extractions in water. The POD was determined from the difference between the digested P and orthophosphates (Jones and Willett, 2006).

Nutrients in microbial biomass. Microbial C and N were determined by the direct fumigation-extraction method with chloroform in fresh samples (Vance et al., 1987). After spraying chloroform 20 g of soil and 2 g of soil organic layer in a vacuum chamber for 24 h at 26°C, the samples were extracted with K_2SO_4 0.5 N, through Whatman #42 paper (Brookes et al., 1985). C_{mic} and N_{mic} were calculated as the difference of concentration between the fumigated and non-fumigated samples. The correction factors used were k_{EC} (extractable part of microbial biomass C) of 0.45 and k_{EN} (extractable part of microbial biomass N) of 0.54 (Brookes et al., 1985; Joergensen, 1996; Joergensen & Mueller 1996). For microbial P, the same method described above was used in 5 g soil and 2 g soil organic layer, and the samples extracted with $NaHCO_3$ and filtered through Whatman # 42 paper (Cole et al., 1977). Microbial P was calculated as the difference of P concentration between fumigated and non-fumigated samples, the correction factor used was k_{EP} =0.45 (Brookes et al., 1982).

Enzymatic activity. We determined the enzymatic activity of five enzymes associated with C, N and P acquisition. The potential activities of β-1,4-glucosidase (BGL), phosphomonoesterases (AP), dehydrogenase (DES), polyphenol oxidase (POX) and β-1,4-N-acetylglucosaminidase (NAG) were measured using 2 g of soil and 0.5 g of organic layer and 30 ml of 1X MUB (Modified Universal Buffer) adjusted to the pH of the site samples. The activity of BGL, NAG and AP was characterized using a method based on the colorimetric determination of p-nitrophenol (p-NP) released after incubation of the sample with the substrate linked to p-NP for 2 h at 25 °C and spectrophotometric quantification at 410 nm (Tabatabai and Bremner, 1969; Verchot and Borelli, 2005). The absolute activity of BGL, NAG and AP was expressed as the p-NP produced hr^{-1} g^{-1} of dry soil (Chávez-Vergara et al., 2014). POX activity was measured after adding 2,2'-azino-bis (3-ethylbenzthiazoline-6-sulfuric acid) (ABTS) and incubating the samples for 2 h at 25 °C. Determination was made spectrophotometrically at 460 nm (Verchot and Borelli, 2005) and expressed as tyrosine produced hr^{-1} g^{-1} of dry soil. DES activity was determined through the reduction of triphenyl tetrazolium chloride (TTC) to triphenyltriazolium formazan (TPF) (Alef, 1995) for 24 h at 25 °C. Following spectrophotometric quantification at 546 nm, the total reaction was expressed as TPF day^{-1} g^{-1} of dry soil.

2.4. Data analysis

Statistical analyses

The total, dissolved, microbial and enzymatic data of C, N and P in the soil organic layer and soil of the three vegetation-soil systems were analyzed separately through one-way analyses of variance (ANOVA). Where differences were found to be significant ($P \leq 0.05$), a Tukey post hoc test was performed. In addition, a Pearson correlation was conducted between the dissolved nutrients, microbial and enzymatic activity of the three vegetation-soil systems.

Stoichiometric, homeostasis and threshold element ratio

To determine the degree of homeostasis of C:N and C:P in the microbial community, equation 2 was used:

$$H' = {}^{1}\!/_{m} \qquad \text{Equation (2)}$$

Where m is the slope of $\log_e$ C:N_R (resource) versus $\log_e$ C:N_B (microbial biomass), or the slope of $\log_e$ C:P_R versus $\log_e$ C:P_B, respectively. $H' > 1$ denotes that the microbial community is homeostatic, while $H' \approx 1$ indicates the absence of homeostasis (Sterner and Elser, 2002; Tapia-Torres et al., 2015).

To determine the enzymatic stoichiometry, the enzymatic activity data were normalized with the concentration of dissolved organic carbon (DOC) of each sample (Tapia-Torres et al., 2015). The data was then transformed to $\log_e$ in order to normalize the variance and the following relationships evaluated through a type II regression using SMATR (SMATR, R Development Core Team, 2007): BGL vs NAG and BGL vs AP (Tapia-Torres et al., 2015). Using the intercepts in SMA regressions for $\log_e$ (BGL) vs $\log_e$ (NAG) and for $\log_e$ (BGL) vs $\log_e$ (AP) (n_0 and $p_{0,}$ respectively) and the elementary ratios in the microbial biomass, the threshold value of the elementary relationship was determined ($TER_{C:N}$ and $TER_{C:P}$) using equations 3 and 4, as described by Sinsabaugh et al. (2009):

$$TER_{C:N} = \left(\left({}^{BGL}\!/_{NAG}\right) B_{C:N}\right) \Big/ n_0 \qquad \text{Equation (3)}$$

$$TER_{C:P} = \left(\left({}^{BGL}\!/_{AP}\right) B_{C:P}\right) \Big/ p_0 \qquad \text{Equation (4)}$$

Where:

$TER_{C:N}$ and $TER_{C:P}$ are the threshold ratios (dimensionless), *BGL/NAG* is the enzymatic activity ratio of β-1,4-glucosidase and β-1,4-N-acetylglucosaminidase, and *BGL/AP* is the enzymatic activity ratio of β-1,4-glucosidase and phosphomonoesterase. $B_{C:N}$ and $B_{C:P}$ are the C:N and C:P ratios of the microbial biomass, and n_0 and p_0 are the intersections of the regressions of the enzymatic stoichiometry (SMA regressions).

3. Results

3.1. Organic matter characterization

3.1.1. Molecular composition by solid-state ^{13}C NMR spectrometry

The spectra (Figure 1) and relative contents of the major C-molecule types (Table 1) for the different components studied (litterfall, fine roots, mineral soil) were calculated by integrating the chemical shift ranges.

Litterfall. The spectra of the litterfall were dominated by *O*-alkyl C associated with carbohydrates (56-65% of total intensity and alkyl C (14-20% of the total intensity) compounds. Prominent signals at 73 and 104 ppm, attributed to cellulose and hemicelluloses, were observed. A shoulder at 59 ppm revealed the presence of methoxyl signals. The alkyl region was dominated by peaks at *ca*. 30 and 20 ppm, which were mainly attributed to long- and short-chain aliphatic molecules, respectively, in cuticular structures. The aromatic and phenolic C compounds in the chemical-shift regions of 110–160 ppm (González-Pérez et al., 2004) made up 17-19% of the total intensity. Peaks in this region indicated the presence of lignin and tannins, at 145 and 153 ppm (Preston et al., 1997). The content of carboxyl structures (organic acids and amide contribution, at 170 ppm: Skjemstad et al., 1996) was around 5%. The most important differences between species-systems were the higher contribution of alkyl C in the *Alnus*-system (3100 m.a.s.l.) and, related to this, higher alkyl C:*O*-alkyl C (Table 1) and also the higher presentation of aromatic (Aryl) compounds related to well-defined peaks at *ca*. 116 (C3 and/or C5 in p-hydroxyphenil subunits of lignin (H) and *ca*. 129 ppm (C2 and/or C6 in H and other highly condensed aromatics C), *ca*. 145 and 154 ppm (syringil/hydrolysable tannins and guaiacyl/condensed tannins, respectively; Almendros et al., 2000; Kögel-Knabner, 2002).

Soil Organic layer. The organic layer was dominated by O-alkyl C. This region occupied 57-61% of the total spectra of all species. The *Pinus*-system (3700 m.a.s.l.) had higher alkyl C (23%) and Aryl C (20%) than the other species (Table 1), while peaks in the alkyl region at 29 ppm (associated to aliphatic C), the aromatic region at 55 ppm (methoxyl C), 115 (H-lignin), 129 ppm (condensed aromatics) and the carboxyl region at 171 ppm (carboxyl) were most prominent in the *Alnus*-system (Figure 1). The ratios of ^{13}C NMR regions showed that the *Pinus*-system had higher aromaticity (25%) while the *Alnus*-system and *Abies*-system (3500 m.a.s.l.) presented higher Alkyl C:Aryl ratios (Table 1).

Fine roots. The spectra of fine roots were dominated by *O*-alkyl compounds (72-80% of total intensity), the alkyl and aromatic regions showed similar signals and made up 9-17% of the C compounds. The carboxyl region presented a very low signal (1%). The most notable differences between species-systems were the higher signals in the alkyl region (*ca*. 21 and 28 ppm) in the *Alnus*-system and in the O-alkyl region in the *Pinus*-system. In the Aryl region, the *Pinus*-system showed apparent peaks at 150 and 140 ppm, related to lignin subunits. The peak at 172 ppm was most prominent in the *Alnus*-system fine roots. In general, the *Alnus*-system condition was most enriched by aliphatic compounds, while the *Abies*-system presented more aromaticity (Table 1).

Mineral soil. The spectra of mineral soil contrasted among the species, mainly due to the presence of a very prominent and broad peak at 129 ppm in the *Alnus*-system and *Abies*-system. The high intensity of this signal can be related to the high presence and accumulation of condensed aromatics (e.g. charcoal), derived from recurrent fire events. Other peaks had similar intensities but with less dominance of aromatics in the *Pinus*-system. This latter species presented lower aromaticity and hydrophobicity than the others (Table 1).

3.1.2. Oxidation resistance by thermal analysis

The DSC curves of the litterfall, soil organic layer, fine roots and mineral soil are shown in figure 2 and the parameters of the thermal analysis (T50 and partial heats of combustion) are shown in table 2.

Litterfall. The DSC curves of litterfall were bimodal with two prominent peaks, the first in the thermolabile region (*ca.* 350 °C) and the second in the recalcitrant region (*ca*. 450 °C), and a smoothed shoulder in Q3 (> 475°) only visible in the *Abies*-system. In the tree species, the order of the thermal fractions was recalcitrant organic matter Q2, (375-475 °C) > thermolabile fraction Q1 (<375 °C) > > extra-recalcitrant organic matter Q3 (475–550 °C). The distribution in percentages of these fractions was rather similar to that of the three vegetation-soil systems. The T50 value (loss of 50% of energy) was also quite similar for all three species (391-397 °C; Table 2).

Soil Organic layer. Contrasting shapes were visible among species-systems, but the signal in the Q1 region was very similar among all three species. Specifically, in the *Pinus*-system (3700 m.a.s.l.), a peak appeared in the Q2 region of similar intensity to that of the Q1 region while, in other conditions, the Q2 peaks were more prominent than the peak in the labile region (Q1). Only the *Abies*-system (3500 m.a.s.l.) presented a well-defined peak at *ca.* 500 °C, and this did not appear in other species (Figure 2). This peak is related to the formation of humus-like compounds (Rovira et al., 2008). The T50 value presented the order *Alnus*->*Abies*->*Pinus*-system (Table 2).

Fine roots. The most variability in the shape and position of peaks was observed in the fine root thermograms. In all species, the labile peak was lower than the recalcitrant peak. The labile peak intensity was similar between *Alnus* and *Pinus*, but the former appeared at a lower temperature than the latter (*ca*. 300°C and 330°C, respectively), Pinus did not present any other well-defined peak. A second prominent peak of similar intensity was observed in the recalcitrant region in both *Abies* and *Alnus* but with differences in the temperature at which it evolved in these two species

(400 and 450 °C, respectively). In relation to this, *Alnus* presented the higher recalcitrant fraction (50%) and higher T50 values. In contrast, in the DSC curve of the *Pinus*-system, the recalcitrant peak is considerably smaller and presented a lower T50 value (Table 2).

Mineral soil. All species thermograms were bimodal but with visible differences in the under-curve area. The lower shape and lower total heat flow (Q) of the *Abies*-system thermogram is related to lower SOM concentration in the mineral soil (fig. 2D). The DSC thermograms in the *Alnus*-system showed an accumulation of energy released at higher temperature that caused their distribution to be skewed to the right. This is consistent with the charcoal detected in the soil NMR spectra. In accordance, the SOM under the *Alnus*-system was more thermally stable (higher T50 values). The most recalcitrant compound concentration reflected in the Q2 region was related to higher abundance of a highly (probably pyrogenic) condensed and aliphatic accumulation.

3.2. Nutrient concentration and enzymatic activity in the soil organic layer

Tables 3 and 4 show the nutrient concentrations, enzymatic activity and elemental ratios of the organic layer in the three vegetation-soil systems. The organic layer in the *Pinus*-system (3700 m.a.s.l.) and *Abies*-system (3500 m.a.s.l.) had the highest and the lowest C concentrations, respectively (F = 343, p<0.001; Table 3), while the *Alnus*-system (3100 m.a.s.l.) had the highest N concentration (F = 359, p<0.001; Table 3). Moreover, the organic layer in the *Pinus*-system had the highest Ct:Pt ratio, while the organic layer in the *Alnus*-system had the lowest ratio value (F = 446, p<0.001; F = 22.12, p<0.001, respectively; Table 4). Moreover, the *Pinus*-system had the highest Nt:Pt ratio (F = 30.39, p<0.001; Table 4).

The concentrations of DOC and DOP in the organic layer did not differ among the three vegetation-soil systems, but the organic layer in *Abies*-system had lower dissolved organic nitrogen (DON) concentrations than in the other two vegetation-soil systems (F = 4.471, p=0.03; Table 3). The dissolved organic nutrient ratios did not differ among the three vegetation-soil systems (Table 4). The *Alnus*-system and *Abies*-system had the highest and lowest concentrations of C_{mic}, respectively (F = 4.737, p=0.03; Table 3), while the concentrations of N_{mic} and P_{mic}, and the C_{mic}:N_{mic}, C_{mic}:P_{mic} and N_{mic}:P_{mic} ratios did not differ among the three vegetation-soil systems (Table 3 and 4). The organic layer in the *Alnus*-system had higher activities of three enzymes (DES, BGL and NAG) than were found in the other two vegetation-soil systems (F = 7.969, p=0.006; F = 8.352, p=0.005, respectively; Table 3). However, the AP and POX activity did not differ among the three vegetation-soil systems (Table 3). Similarly, the enzyme activity ratios did not differ among the three vegetation-soil systems, but the NAG:AP ratio was higher in the organic layer in the *Alnus*-system than in the *Abies*-system (F = 5.88, p = 0.01; Table 4).

To test the strength of the stoichiometric homeostasis (the ability of a microorganism to maintain relatively constant ratios of elements within its biomass, under variable environmental conditions; Sterner and Elser 2002) of the microbial community in the organic layer, we calculated the microbial biomass elemental ratios and the elemental ratios in the organic layer (soil microbial resources). The slope between elemental ratios within microbial biomass and those of the organic layer (between $\log_e$ C:N_R and $\log_e$ C:N_B and between $\log_e$ C:P_R and $\log_e$ C:P_B) were not significant, suggesting that the microbial community was subjected to an elementary homeostasis in the organic layer in all three vegetation-soil systems (Table S2).

In addition, using the parameters from the enzymatic data and the microbial stoichiometric values (C:N:P), the organic layer in the *Alnus*-system and the *Abies*-system presented the highest and lowest values of estimated $TER_{C:N}$, respectively (F = 447, p<0.001; Fig. 3A). Furthermore, the value of $\log_e TER_{C:N}$ was higher than the value of the $\log_e$ C:N ratio of the organic layer in the *Alnus*-system ($\log_e$ C:N= 3.0), while the $\log_e TER_{C:N}$ values of the other two vegetation-soil systems were significantly lower than their C:N ratios in the organic layer ($\log_e$ C:N= 3.8 and 4.1 for the *Abies*-

system and the *Pinus*-system, respectively). Likewise, the $\log_e$ $TER_{C:P}$ in the organic layer of the *Alnus*-system was higher than that in the other two systems (F= 397, $p<0.001$; Fig. 3B) and the $\log_e$ $TER_{C:P}$ values were lower than the $\log_e$ C:P ratios of the organic layer in *Abies*-system and *Pinus*-system (6.9 and 6.6, respectively), while $\log_e$ $TER_{C:P}$ did not differ from the $\log_e$ C:P ratio of the organic layer (6.1) in the *Alnus*-system. These results suggest that the microbial community in the *Abies*- and *Pinus*-systems are co-limited by C-N and C-P, respectively, while the *Alnus*-system is limited by C.

3.3. Nutrient concentrations and enzymatic activity in the mineral soil.

Total soil N and P concentrations were higher in the *Alnus*-system (3100 m.a.s.l.) than in the other two vegetation-soil systems (F = 358.8, $p<0.0001$; F = 11.91, $p<0.001$, respectively; Table 5). In this context, the *Alnus*-system soil had the lowest values of C:N, C:P and N:P ratios (F = 446.1, p= 0.02; F = 22.12, p = 0.004; F = 13.42, $p<0.001$, respectively; Table 6). Similarly, the *Alnus*-system soil had higher concentrations of available NH_4^+ and HPO_4^{-2} than that of the other two vegetation-soil systems (F = 3.7, p= 0.05; F = 134, $p<0.001$, respectively; Table 5). The dissolved organic nutrients and nutrients within microbial biomass did not differ among the soils of three vegetation-soil systems (Table 5).

The *Alnus*-system soil had lower values of BGL activity than that of the other two vegetation-soil systems (F = 5.2, p= 0.02, Table 5; F=4.5, p = 0.03, respectively; Table 6), while the NAG, AP, POX and DES did not differ among the three vegetation-systems. Consequently, the *Alnus*-system soil had the lowest BGL:AP ratio values (F = 3.3, p=0.003; Table 6).

As in the organic layer, the regressions between C_{mic}:N_{mic} and C_{mic}:P_{mic} ratios and the respective elemental ratios of mineral soil (between $\log_e$ $C:N_R$ and $\log_e$ $C:N_B$ and between $\log_e$ $C:P_R$ and $\log_e$

$C:P_B$) did not differ from zero, with the exception of the C:N regression of the *Pinus*-system soil (3700 m.a.s.l. Table S2). These results suggest an elemental homeostasis of the soil microbial community in the three vegetation-soil systems, with the exception of the soil microbial community in the *Pinus*-system in relation to N (Table S2).

The *Alnus*-system and *Abies*-system (3500 m.a.s.l.) soils had the highest and lowest values of $\log_e$ $TER_{C:N}$ and $\log_e$ $TER_{C:P}$ (F = 447, p<0.001, and F= 398, p<0.001; respectively, Fig. 3). The values of $\log_e$ $TER_{C:N}$ were higher than the soil values of $\log_e$ C:N ratio ($\log_e$ C:N= 2.8, 4.1 and 3.1 for the *Alnus*-, *Abies*- and *Pinus*-systems, respectively), while the $\log_e$ $TER_{C:P}$ values were also higher than the soil $\log_e$ C:P ratio in the three vegetation-soil systems ($\log_e$ C:P = 3.8, 5.7 and 6.0 for the *Alnus*-, *Abies*- and *Pinus*-systems, respectively). In contrast to the situation in the organic layer microbial community, these results suggest that the soil microbial community is limited by C.

4. Discussion

According to Djukic and others (2010), SOM turnover along a highland forest elevational gradient is controlled by the chemical composition of the organic matter, the metabolism of the forest floor microbial community and climatic variables, as well as interactions among these factors. However, our results suggest that the main drivers of SOM turnover differed for the organic layer and mineral soil. In the following two sections, we discuss our results of chemical composition produced by the main plant species and microbial metabolism, while in the third section we integrate both of these factors along the elevational gradient.

4.1. Chemical and thermal characteristics of organic matter as a plant species adaptation to water availability along an elevational gradient.

The difference in average annual temperature between the lowest and highest site was only 5 °C, but the Lang Index (calculated as the ratio of mean annual precipitation: mean annual temperature) showed an increase with elevation (110, 173 and 180 for the *Alnus* (3100 m.a.s.l.)- *Abies* (3500 m.a.s.l.)-, and *Pinus*-systems (3700 m.a.s.l.), respectively; Jasso-Flores et al., 2019), suggesting higher water availability with increased elevation, with the greatest water deficit in the *Alnus*-system.

The chemical composition of vegetal residues could maintain the plant physiological metabolic adjustments in order to cope with the ecological and/or environmental conditions, known as after-life traits (Whitham et al., 2012; Genung et al., 2013). It is therefore expected that the chemical composition of organic matter is a consequence of how the dominant plant species cope with the environmental stress through physiological processes (Kögel-Knabner, 2002; Bonanomi et al., 2013). The organic matter chemical composition partially regulates the intrinsic vulnerability of organic molecules to decomposition, while the microbial community metabolism controls the extrinsic capacity for decomposition, and the interaction between these factors is regulated by climatic conditions. The interaction of both factors with the climatic conditions defines the SOM turnover observed along a highland forest elevational gradient (Djukic et al., 2010). Our results suggests that the water availability condition (associated in our case with elevation) regulates the chemical composition of organic matter in the litterfall and fine roots produced by the dominant plant species and some chemical characteristics are maintain in residues throughout the decomposition process in the organic layer and finally in the organic matter of mineral soil, supporting our first hypothesis that the soil organic matter produced in the lowest site is more recalcitrant, since it is derived from plant to cope with the lower water availability (the *Alnus*-system). The plant water deficit can drive the synthesis of most hydrophobic cuticles, characterized by enrichment of long-chain alkanes, as we observed in the most intense signal presented at *ca*. 30

ppm and the higher alkyl:O-alkyl and HB:HI ratios of litterfall, fine roots and organic layer in the *Alnus*-system (site of lowest elevation). Several authors have reported a higher proportion of aromatic (such as polyphenols and tannins) and aliphatic (such as cuticular waxes) compounds in plant tissues under drought conditions (Boom et al., 2005; De Deyn et al., 2008; Tharayil et al., 2011; Vishwanath et al., 2015; Campo and Merino, 2016). For example, Dodd and Poveda (2003) reported that *Juniperus communis* produced a higher proportion of wax and lipids in order to cope with water stress in a site of low elevation and warm conditions, compared to trees of the same species at higher, colder sites. The vegetal tissues in the *Alnus*-system*,* most visible in the organic layer and fine roots, consistently presented higher T_{50} values than those of other species, suggesting that these tissues require greater energy investment for biological degradation (Chávez-Vergara et al., 2018). However, the organic compounds of litterfall and root samples in the *Alnus*-system showed a peak in the labile region of lower temperature in the thermogram and higher concentration of carboxyl C in the ^{13}C NMR spectra than those shown by the organic compounds in the *Pinus*-system. This apparent discrepancy in the T_{50} values could be explained by the fact that most labile organic matter compounds are embedded in a complex structural matrix in the *Alnus*-system. Kögel-Knabner (2002) reported that, following decomposition of the leaf cuticle and root tissues, other organic compounds rich in soluble nutrients are released from the intratissular space.

Moreover, the chemical and thermal characteristics can be used as an indicator of the sensitivity of the organic matter in the mineral soil to biological oxidation (Barros et al., 2011; Merino et al., 2014). The differences in chemical composition between the organic layer and organic matter in mineral soil decreased with increasing elevation. For example, the proportion of aromatic compounds increased 15% from organic layer to soil organic matter in the *Alnus*-system, suggesting that the soil organic matter in the site of highest elevation (*Pinus*-system) is chemically less stable and with a higher thermal sensitivity to mineralization (lower T50) than in the lower sites, as was reported by Zimmerman et al. (2012) along a tropical forest gradient. Higher thermal sensitivity has been associated with a lower concentration of carboxyl C in the mineral soil by Erhagen et al. (2013); however, other factors must be considered, such as the physical protection of organic compounds, because this impedes rate of decomposition (Lavallee et al., 2000; Lützow et al., 2006; Cao et al., 2016). The soil physical protection is improved by the clay fraction and the carboxyl C in mineral soil, through soil aggregation (Lützow et al., 2006; Sarker et al., 2018). The site of highest elevation presents a soil texture with lower percentage of clay-size particles (Jasso-Flores et al., 2019) and with a lower carboxyl concentration than the lowest site, suggesting that the SOM would be more susceptible to decomposition once the microbial communities are not restricted by the colder environmental conditions prevalent in the highest site.

4.2. Microbial metabolism along the elevational gradient.

Our second hypothesis that the forest floor microbial community in the lowest site must be limited by energy source rather than by N and P, because this microbial community must invest more energy in the depolymerization of recalcitrant molecules, was supported by the results of $TER_{C:N}$ and $TER_{C:P}$ for the organic layer (Figure 3). In contrast, this hypothesis was not supported by the results for the mineral soil (Figure 4), suggesting that the drivers of organic matter decomposition can differ between the organic layer and the mineral soil.

In the organic layer, our results showed that the Log_e $TER_{C:N}$ and Log_e $TER_{C:P}$ were lower than the elemental stoichiometry of the resources (Ln C:N and Ln C:P) from the *Abies*- and *Pinus*-systems, suggesting that the microbial community of these systems is limited by N and P (Sterner and Elser, 2002). In contrast, our results suggest that the microbial community of the organic layer in the *Alnus*-system is limited by C. This C limitation is derived from the higher concentration of total N and P and the lower C:N and C:P ratios observed in the organic layer of the *Alnus*-system. Several authors have suggested that the metabolic microbial activity is limited by an unbalanced elemental stoichiometry of the nutrient resource, favoring the microbial community to be homeostatic (Sinsabaugh et al., 2009; Cleveland and Liptzin, 2017; Cui et al. 2019;). The $TER_{C:N}$ strongly correlated with the C:N and N:P ratios of the organic layer (R^2: -0.88 and 0.90, respectively) and the $TER_{C:P}$ also strongly correlated with the C:N, C:P and N:P ratios of the organic layer (R^2: -0.94, -0.82 and 0.55, respectively), showing that the microbial community has a strong elemental homeostasis in all three vegetation-soil systems. However, in spite of these findings, the absolute enzymatic activities in the nutrient-limited sites (*Abies*- and *Pinus*-systems) are lower than in the carbon-limited site (*Alnus*-system), as reported in previous studies of enzymatic activity in soils along elevational gradients (Nottingham et al., 2016; Cui et al., 2019). Two possible processes could explain our results from the organic layer. Firstly, the microbial community in the organic layer of the *Alnus*-system must produce a higher amount of C- and N-associated enzymes (BGL and NAG) to maintain a higher microbial growth (microbial C), since the organic layer of the *Alnus*-system has a higher proportion of recalcitrant organic molecules than the other two soil-vegetation systems (see above). Moreover, the organic layer of the *Alnus*-system has higher BGL:DOC ratio than that of either the *Abies*- or *Pinus*-systems (3.96, 3.57 and 1.76 nmol PNP μg DOC^{-1} h^{-1}, respectively), suggesting that the microbial community of the *Alnus*-system must produce a higher quantity of enzyme (BGL) per unit of available C (Tapia-Torres et al., 2015). Secondly, the lower temperatures in the sites of higher elevation (*Abies*- and *Pinus*-systems) could limit enzyme activity, as reported in previous studies (Nottingham et al., 2015; Xu et al., 2015; Zhou et al., 2015; Blagodatskaya et al., 2016; Cui et al., 2019). In this sense, Augusto et al. (2017) proposed that the main driver of N limitation is the severe climate condition (cold and dry) that acts to reduce N mineralization by microbial activity (Arnold et al., 2009; Wolf et al., 2011; Nottingham et al., 2015). This is also suggested by our data from the *Pinus*-system. Our results from the organic layer represent the first report of such data collected along an elevational gradient.

With respect to mineral soil, our results show that Log$_e$ TER$_{C:N}$ and Log$_e$ TER$_{C:P}$ were higher than the elemental stoichiometry of the resources (Ln C:N and Ln C:P) in the soil of the three soil-vegetation-systems, suggesting that the soil microbial community is limited by C availability rather than nutrient availability (Sterner and Elser, 2002). However, the availability of NH_4 and HPO_4 is higher in the soil of the *Alnus*-system, although this increase is not reflected in the concentration of C$_{mic}$, N$_{mic}$ and P$_{mic}$. The alkyl:O-alkyl of soil organic matter was clearly higher than in the organic layer of the *Alnus*-, *Abies*- and *Pinus*-systems. These results suggest that the labile C for microbial activity is more constrained in the soil than in the organic layer, particularly in the two lowest sites (*Alnus*- and *Abies*- *systems*). Soil C availability could therefore be the driving factor behind microbial activity in the mineral soil. Additionally, the BGL activity was higher in the *Pinus*-system than in the *Alnus*-system. Similarly, the *Pinus*-system has a higher BGL:DOC ratio than the *Alnus*- and *Abies*-systems (1.34 vs. 0.33 and 0.58 nmol PNP μg_{DOC}^{-1} h^{-1}, respectively), suggesting that the soil microbial community of the *Pinus*-system must produce a higher amount of enzyme per unit of available C (Tapia-Torres et al., 2015). Nottingham et al. (2016) reported that BGL activity increased at lower temperatures along an elevational gradient, and suggested two main mechanisms to explain the temperature acclimation of BGL: a) the presence of iso-enzymes adapted to colder temperatures, and b) higher substrate availability at higher elevations. In relation to the first mechanism, several studies have reported the thermal adaptation of iso-enzymes (Koch et al., 2007; Trasar-Cepeda et al., 2007; German et al., 2012; Nottingham et al., 2016), and we have no reason to reject this for our study site. For the second mechanism, Blagodatskaya et al. (2016) proposed that the low quantity and quality of organic substrate act to decrease the hydrolytic enzymes independently of temperature, which would explain the thermal adaptation of enzymes at higher elevations. In our study site, the higher alkyl:O-alkyl ratio of soil organic compounds in the soil of the *Alnus*-system compared to that of the *Pinus*-system (see above) could reduce the BGL activity by lowering the lability of the organic molecules. Our findings support the broad utility of the multidisciplinary approach used in this study to illustrate how the microbial community acquires limiting resources by regulating the decomposition of organic matter in the organic layer and mineral soil.

4.3. Responses of parameters associated with organic matter turnover along an elevational gradient of three vegetation-soil systems of the highlands of central Mexico.

According to our results, we have illustrated (Figure 5) the indicators that best support our conclusions related to the main drivers of the parameters associated with the turnover of organic matter (OM) characteristics (Figure 5a) and microbial metabolic activity (Figure 5b). The proportion of chemical recalcitrance of the plant-derived organic compounds of the studied components (litterfall, roots and organic layer) increased with reduction of the aridity index (Lang index) values. These results suggest that water availability is the main driver of the chemical composition of organic matter produced by the dominant plant species. The chemical recalcitrance of OM reduces the microbial metabolic activity in the lower water availability condition (site of lower elevation), but the lower environmental temperatures at higher elevations could limit soil microbial activity, as suggested by the lower dehydrogenase activity at higher sites. Therefore, the OM turnover could increase with rising temperatures, as predicted by the climate change model.

However, the effect of global climate change on soil organic matter decomposition is controversial in forest ecosystems along elevational gradients. Some authors have suggested that temperature increase has little effect on the most stable organic C fraction in mineral soil (Giardina et al., 2014), while the soil labile C organic compounds are more sensitive to temperature increases (Fissore et al., 2013). The vulnerability of these labile organic compounds is explained by the sensitivity of enzymes to temperatures, higher labile substrate availability (Wallenstein et al., 2011; Nottingham et al., 2016) and increased microbial activity under a warming condition in colder ecosystems

(Nottingham et al., 2019). In contrast, some authors have reported no changes in enzyme activity with increased temperatures in the coldest ecosystems (Blagodatskaya et al., 2016; Cui et al., 2019).

5. Conclusion

Our results suggest that water availability is the main driver of the chemical composition of organic matter produced by the dominant plant species. Therefore, the relative higher chemical recalcitrance of the OM reduces the microbial metabolic activity in the lower water availability condition (site of lower elevation), but the lower environmental temperatures at higher elevations could limit soil microbial activity, although the organic matter has higher chemical lability. Integrated study of plant-derived organic material and microbial metabolism in the forest floor is therefore required in order to fully understand the vulnerability of tropical mountain ecosystems to climate change.

Acknowledgments

We are grateful to Rodrigo Velázquez Durán and Ofelia Beltrán-Paz for assistance in the laboratory and to Alberto Valencia for assisting with the data analysis. The authors also thank the RIAIDT-University of Santiago de Compostela for the use of analytical facilities, and Montse Gómez and Carlos Roca for carrying out the DSC-TG and NMR spectroscopy analysis. R. I. Jasso Flores acknowledges the Posgrado en Ciencias Biológicas of the Universidad Nacional Autónoma de México for academic support during her studies and is grateful to CONACYT (Grant 50780-F) for doctoral scholarships. This work was financed by the Universidad Nacional Autónoma de México (PAPIIT DGAPA-UNAM grant: “El papel de la disponibilidad del carbono sobre la dinámica del Nitrógeno y Fósforo edáfico en ecosistemas contrastantes de México”, IN201718).

References

Alef, K., 1995. Dehydrogenase activity. In: Methods in applied soil microbiology and biochemistry, eds. K. Alef and P. Nannipieri, 228-231, San Diego, Academic Press.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manage. 259(4), 660. doi:10.1016/j.foreco.2009.09.001.

Allison, S.D., Chacon, S.S., German, D.P., 2014. Substrate concentration constraints on microbial decomposition. Soil Biol. Biochem. 79, 43–49. doi:10.1016/j.soilbio.2014.08.021.

Almendros, G., Dorado, J., González-Vila, F. J., Blanco, M.J., Lankes, U., 2000. 13C NMR assessment of decomposition patterns during composting of forest and shrub biomass. Soil Biol. Biochem. 32(6), 793–804. doi:10.1016/S0038-0717(99)00202-3.

Augusto, L., Achat, D.L., Jonard, M., Vidal, D., Ringeval, B., 2017. Soil parent materiall.L., Jonard, M., Vidal, D., and Ringeval, B. 2017. Soil parent materms. Glob. Change Biol. 23(9), 3808. doi:10.1111/gcb.13691.

Arnold, J., Corre, M.D., Veldkamp, E., 2009. Soil N cycling in old growth forests across an Andosol toposequence in Ecuador. For. Ecol. Manage. 257, 2079–2087. doi: 10.1016/j.foreco.2009.02.014

Baldrian, P., 2009. Microbial enzyme-catalyzed processes in soils and their analysis. Plant Soil Environ. 55, 370-378. doi:10.17221/134/2009-PSE

Barros, N., Salgado, J., Villanueva, M., Rodriquez-Añon, J., Proupin, J., Feijóo, S., Martín-Pastor, M., 2011. Application of DSC–TG and NMR to study the soil organic matter. J. Therm. Anal. Calorim. 104, 53-60. doi: 10.1007/s10973-010-1163-4

Blagodatskaya, E., Blagodatsky, S., Khomyakov, N., Myachina, O., Kuzyakov, Y., 2016. Temperature sensitivity and enzymatic mechanisms of soil organic matter decomposition along an altitudinal gradient on Mount Kilimanjaro. Sci. Report, 6, 22240. doi:10.1038/srep22240.

Bonanomi, G., Incerti, G., Giannino, F., Mingo, A., Lanzotti, V., Mazzoleni, S., 2013. Litter quality assessed by solid state ^{13}C NMR spectroscopy predicts decay rate better than C/N and Lignin/N ratios. Soil Biol. Biochem. 56, 40–48. doi:10.1016/j.soilbio.2012.03.003.

Boom, A., Sinninge Damsté, J.S., de Leeuw, J.W., 2005. Cutan, a common aliphatic biopolymer in cuticles of drought-adapted plants. Org. Geochem. 36(4), 595–601. doi:10.1016/j.orggeochem.2004.10.017.

Bremmer J.M., 1996. Nitrogen-total. In: Methods of soil analyses part 3: chemical analyses, eds., D. Spark, A. Page, M. Summer, M. Tabatabai, P. Helmke, 1085-1121, Soil Science Society of America, Madison, USA.

Brookes, P.C., Powlson D.S., Jenkinson D. S., 1982. Phosphorus in the soil microbial biomass. Soil Biol. Biochem. 16, 169-175. DOI 10.1016/0038-0717(84)90108-1.

Brookes, P., Landman, A., Pruden, G., Jenkinson, D., 1985. Chloroform fumigation and the release of soil nitrogen: a rapid direct method to measure microbial biomass nitrogen in soil. *S*oil Biol. Biochem. 17, 837-842.

Campo, J., Merino, A., 2016. Variations in soil carbon sequestration and their determinants along a precipitation gradient in seasonally dry tropical forest ecosystems. Glob. Change Biol. 22(5), 1942–1956. doi:10.1111/gcb.13244.

Cao, Z., Wang, Y., Li, J., Zhang, J., He, N., 2016. Soil organic carbon contents, aggregate stability, and humic acid composition in different alpine grasslands in Qinghai-Tibet Plateau. J. Mt. Sci. 13, 2015-2027. DOI: 10.1007/s11629-015-3744-y

Chávez-Vergara, B., Merino, A., González-Rodríguez, A., Oyama, K., García-Oliva, F., 2018. Direct and legacy effects of plant-traits control litter decomposition in a deciduous oak forest in Mexico. PeerJ 6, e5095. doi:10.7717/peerj.5095.

Chávez-Vergara, B., Merino, A., Vázquez-Marrufo, G., García-Oliva, F., 2014. Organic matter dynamics and microbial activity during decomposition of forest floor under two native neotropical oak species in a temperate deciduous forest in Mexico. Geoderma 235-236 (1), 133-145. DOI:10.1016/j.geoderma.2014.07.005

Cleveland, C.C., Liptzin, D., 2007. C:N:P stoichiometry in soil: is there a "Redfield ratio" for the microbial biomass? Biogeochem. 85(3), 235–252. ttps://doi.org/10.1007/s10533-007-9132-0

Cole, C. V., Elliott, E. T., Hunt, H. W., Coleman, D. C., 1978. Trophic interactions in soils as they affect energy and nutrient dynamics. V. Phosphorus transformations. Microb. Ecol. 4, 381-387. doi: 10.1007/BF02013281

Cui, Y., Bing, H., Fang, L., Jiang, M., Shen, G., Yu, J., Wang, X., Zhu, H., Wu, Y., Zhang, X., 2019. Extracellular enzyme stoichiometry reveals the carbon and phosphorus limitations of microbial metabolisms in the rhizosphere and bulk soils in alpine ecosystems. Plant Soil Doi: 10.1007/s11104-019-04159-x.

Davidson, E. A., Janssens, I. A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440(7081), 165–173. doi:10.1038/nature04514.

De Deyn, G.B., Cornelissen, J.H.C., Bardgett, R.D., 2008. Plant functional traits and soil carbon sequestration in contrasting biomes. Ecol. Lett. 11(5), 516–531. doi:10.1111/j.1461-0248.2008.01164.x.

Djukic, I., Zehetner, F., Tatzber, M., Gerzabek, M. H., 2010. Soil organic-matter stocks and characteristics along an Alpine elevation gradient. J. Plant Nutr. Soil Sci. 173(1), 30–38. doi:10.1002/jpln.200900027.

Dodd, R. S., Poveda, M.M., 2003. Environmental gradients and population divergence contribute to variation in cuticular wax composition in *Juniperus communis*. Biochem. Syst. Ecol. 31(11), 1257–1270. doi:10.1016/S0305-1978(03)00031-0.

Erhagen, B., Öquist, M., Sparrman, T., Haei, M., Ilsted, U., Hedenström, M., Schleucher, J., Nilsson, M., 2013. Temperature response of litter and soil organic matter decomposition is determined by chemical composition of organic material. Glob. Change Biol. 19,3858-3871. DOI: 10.1111/gcb.12342

Fernández, J.M., Plante, A.F., Leifeld, J., Rasmussen, C., 2011. Methodological considerations for using thermal analysis in the characterization of soil organic matter. J. Therm. Anal. Calorim. 104, 389-398. doi: 10.1007/s10973-010-1145-6

Fissore, C., Giardina, C. Kolka, R., 2013. Reduced substrate supply limits the temperature response of soil organic carbon decomposition. Soil Biol. Biochem. 67, 306-311. doi: 10.1016/j.soilbio.2013.09.007

German, D. P, Marcelo, K.R B., Stone, M.M., Allison, S.D., 2012. The Michaelis-Menten kinetics of soil extracellular enzymes in response to temperature: a cross-latitudinal study. Glob. Change Biol. 18,1468–1479. doi: 10.1111/j.1365-2486.2011.02615.x

Genung, M.A., Bailey, J.K., Schweitzer, J.A., 2013. The afterlife of interspecific indirect genetic effects: genotype interactions alter litter quality with consequences for decomposition and nutrient dynamics. PLoS One 8, e53718. DOI:10.1371/journal.pone.005371

Giardina, C.P., Litton, C.M., Crow, S.E., Asner, G.P., 2014. Warming-related increases in soil CO2 efflux are explained by increased below-ground carbon flux. Nat. Clim. Chang. 4, 822-827. Doi: 10.1038/NCLIMATE2322

He, X., Hou, E., Liu, Y., & Wen, D., 2016. Altitudinal patterns and controls of plant and soil nutrient concentrations and stoichiometry in subtropical China. Sci. Report, 6, 24261. doi:10.1038/srep24261.

Huffman, E. N., 1977. Performance of a new automatic carbon dioxide coulometer. Microchem. J. 22, 567-573. doi: 10.1016/0026-265X(77)90128-X

Jasso-Flores, I., Galicia, L., García-Oliva, F., Martínez-Yrizar, A., 2019. Are vegetation–soil systems drivers of ecosystem carbon contents along an elevational gradient in a highland temperate forest?. Can. J. For. Res. 49, 296-304. doi:10.1139/cjfr2018-0245.

Joergensen, R. G., 1996. The fumigation-extraction method to estimate soil microbial biomass: calibration of the K_{EC} value. Soil Biol. Biochem. 28, 25-31. doi: 10.1016/0038-0717(95)00102-6

Joergensen, R. G., Muller, T., 1996. The fumigation-extraction method to estimate soil microbial biomass: calibration of the K_{EN} value. Soil Biol. Biochem. 28, 33-37. doi: 10.1016/0038-0717(95)00101-8

Jones, D.L., Willett, V. B., 2006. Experimental evaluation of methods to quantify dissolved organic nitrogen (DON) and dissolved organic carbon (DOC) in soil. Soil Biol. Biochem. 38, 991-999. doi: 10.1016/j.soilbio.2005.08.012

Knicker, H., González-Vila, F., Polvillo, O., Gonzalez, J., Almendros, G., 2005. Fire-induced transformation of C- and N- forms in different organic soil fractions from a Dystric Cambisol under a Mediterranean pine forest (*Pinus pinaster*). Soil Biol. Biochem. 37, 701-718. doi: 10.1016/j.soilbio.2004.09.008

Knicker, H., Lüdemann, H. D., 1995. N-15 and C-13 CPMAS and solution NMR studies of N-15 enriched plant material during 600 days of microbial degradation. Org. Geochem. 23, 329-341. doi: 10.1016/0146-6380(95)00007-2

Koch, O., Tscherko, D., Kandeler, E., 2007. Temperature sensitivity of microbial respiration, nitrogen mineralization, and potential soil enzyme activities in organic alpine soils. Global Biogeochem. Cycles, 21(4). doi:10.1029/2007gb002983

Kögel-Knabner, I., 2002. The macromolecular organic composition of plant and microbial residues as inputs to soil organic matter. Soil Biol. Biochem. 34(2), 139–162. doi:10.1016/S0038-0717(01)00158-4.

Lavallee, J. M., Soong, J. L., Cotrufo, M. F., 2020. Conceptualizing soil organic matter into particulate and mineral-associated forms to address global change in the 21st century. Glob. Change Biol. 26, 261-273. doi: 10.1111/gcb.14859

Lützow, M. V., Kogel-Knabner, I., Ekschmitt, K., Matzner, E., Guggenberger, G., Marschner, B., Flessa, H., 2006. Stabilization of organic matter in temperate soils: mechanisms and their relevance under different soil conditions - a review. Eur. J. Soil Sci. 57(4), 426–445. doi:10.1111/j.1365-2389.2006.00809.x.

Merino, A., Ferreiro, A., Salgado, J., Fontúrbel, M.T., Barros, N., Fernández, C., Vega, J.A., 2014. Use of thermal analysis and solid-state ^{13}C CP-MAS NMR spectroscopy to diagnose organic matter quality in relation to burn severity in Atlantic soils. Geoderma 226-227, 376-386. doi:10.1016/j.geoderma.2014.03.009

Merino, A., Fonturbel, M.T., Fernández, C., Chávez-Vergara, B., García-Oliva, F., Vega, J.A., 2018. Inferring changes in soil organic matter in post-wildfire soil burn severity levels in a temperate climate. Sci. Total Environ. 627, 622-632. doi: 10.1016/j.scitotenv.2018.01.189

Montiel-González, C., Tapia-Torres, Y., Souza, V., García-Oliva, F., 2017. The response of soil microbial communities to variation in annual precipitation depends on soil nutritional status in an oligotrophic desert. PeerJ 5 e4007. doi:10.7717/peerj.4007.

Murphy, J., Riley, J. P., 1962. A modified single solution method for the determination of phosphate in natural waters. Anal. Chim. Acta 27, 31-36. doi: 10.1016/S0003-2670(00)88444-5

Nottingham, A.T., Turner, B.L., Witaker, J., Ostle, N.J., McNamara, N.P., Bardgett, R.D., Salinas, N., Meir, P., 2015. Soil microbial nutrient constraints along a tropical forest elevation gradient: a belowground test of biogeochemical paradigm. Biogeosci. 12, 6071-6083. doi:10.5194/bg-12-6071-2015.

Nottingham, A.T., Turner, B.L., Witaker, J., Ostle, N.J., Barrdgett, R.D., McNamara, N.P., Salinas, N., Meir, P., 2016. Temperature sensitive of soil enzymes along an elevation gradient in the Peruvian Andes. Biogeochem. 127, 217-230. doi: 10.1007/s10533-015-0176-2

Nottingham, A.T., Baath, E., Reischke, S., Salinas, N., Mier, P., 2019. Adaptation of soil microbial growth to temperature: using a tropical elevation gradient to predict future changes. Glob. Change Biol. 25, 827-838. Doi: 10.1111/gcb.14502

Ostertag, R., DiManno, N. M., 2016. Detecting Terrestrial Nutrient Limitation: A Global Meta-Analysis of Foliar Nutrient Concentrations after Fertilization. Front. Earth Sci. 4, doi:10.3389/feart.2016.00023.

Rillig, M.C., Caldwell, B.A., Wösten, H.A.B., Sollins, P., 2007. Role of proteins in soil carbon and nitrogen storage: controls on persistence. Biogeochem. 85(1), 25–44. doi:10.1007/s10533-007-9102-6.

Robertson, P. ., Coleman, D.C., Bledsoe, C. S., Sollins, P., 1999. Standard soil methods for long-term ecological research. Oxford University Press, New York.

Rovira, P., Kurz-Besson, C., Coûteaux, M.-M., Ramón Vallejo, V., 2008. Changes in litter properties during decomposition: A study by differential thermogravimetry and scanning calorimetry. Soil Biol. Biochem. 40(1), 172–185. doi:10.1016/j.soilbio.2007.07.021.

Sáenz-Romero, C., Rehfeldt, G. E., Duval, P., Lindig-Cisneros, R. A., 2012. *Abies religiosa* habitat prediction in climatic change scenarios and implications for monarch butterfly conservation in Mexico. For. Ecol. Manage. 275, 98–106. doi:10.1016/j.foreco.2012.03.004.

Sarker, T., Incerti, G., Spaccini, R., Piccolo, A., Mazzoleni, S., Bonanomi, G., 2018. Linking organic matter chemistry with soil aggregate stability: Insight from ^{13}C NMR spectroscopy. Soil Biol. Biochem. 117, 175-184. DOI: 10.1016/j.soilbio.2017.11.011

Schimel, J., Balser, T.C., Wallenstein, M., 2007. Microbial Stress-Response Physiology and Its Implications for Ecosystem Function. Ecology 88(6), 1386–1394. doi:10.1890/06-0219.

Siles, J. A., Cajthaml, T., Filipová, A., Minerbi, S., Margesin, R., 2017. Altitudinal, seasonal and interannual shifts in microbial communities and chemical composition of soil organic matter in Alpine forest soils. Soil Biol. Biochem. 112**,** 1–13. doi:10.1016/j.soilbio.2017.04.014.

Sinsabaugh, R.L., Hill, B.H., Follstad Shah, J.J., 2009. Ecoenzymatic stoichiometry of microbial organic nutrient acquisition in soil and sediment. Nature 462(7274), 795–798. doi:10.1038/nature08632.

Solomon, S., 2007. Climate change 2007: the physical science basis: contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge ; New York.

Spaccini, R., Mbagwu, J.S.C., Conte, P., Piccolo, A., 2006. Changes of humic substances characteristics from forested to cultivated soils in Ethiopia. Geoderma 132, 9-19. doi: 10.1016/j.geoderma.2005.04.015

Sterner, R.W., Elser, J. J., 2002. Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere. Princeton University Press.

Tabatabai, M.A., Bremner, J.M., 1969. Use of p-nitrophenyl phosphate for assay of soil phosphatase activity. Soil Biol. Biochem. 1, 301-307. DOI 10.1016/0038-0717(69)90012-1.

Tapia-Torres, Y., Elser, J.J., Souza, V., García-Oliva, F., 2015. Ecoenzymatic stoichiometry at the extremes: How microbes cope in an ultra-oligotrophic desert soil. Soil Biol. Biochem. 87, 34–42. doi:10.1016/j.soilbio.2015.04.007.

Tharayil, N., Suseela, V., Triebwasser, D.J., Preston, C.M., Gerard, P. D., Dukes, J.S., 2011. Changes in the structural composition and reactivity of Acer rubrum leaf litter tannins exposed to warming and altered precipitation: climatic stress-induced tannins are more reactive. New Phytol. 191(1), 132–145. doi:10.1111/j.1469-8137.2011.03667.x.

Trasar-Cepeda, C., Gil-Sotres, F., Leiros, M. C., 2007. Thermodynamic parameters of enzymes in grassland soils from Galicia, NW Spain. Soil Biol. Biochem. 39, 311–319. doi: 10.1016/j.soilbio.2006.08.002

Vance, E.D., Brookes, A. C., Jenkinson, D.S., 1987. An extraction method for measuring soil microbial biomass C. Soil Biol. Biochem. 19, 703-707. doi: 10.1016/0038-0717(87)90052-6

Vishwanath, S.J., Delude, C., Domergue, F., Rowland, O., 2015. Suberin: biosynthesis, regulation, and polymer assembly of a protective extracellular barrier. Plant Cell Rep. 34(4), 573–586. doi:10.1007/s00299-014-1727-z.

Verchot, L. V., Borelli T., 2005. Application of para-nitrophenol (pNP) enzyme assays in degraded tropical soils. Soil Biol. Biochem. 37, 625-633. DOI 10.1016/j.soilbio.2004.09.005.

Wallenstein, M., Allison, S., Ernakovich, J., Steinweg, J. M., Sinsabaugh, R., 2011. Controls on the temperature sensitivity of soil enzymes: a key driver of in situ enzyme activity rates. In: Soil enzymology, soil biology, eds. G. Shukla, A. Varma, 245-258, , Springer, Berlin.

Whitham, T.G., Gehring, C.A., Lamit, L.J., Wojtowicz, T., Evans, L.M., Keith, A.R., Smith, D.S., 2012. Community specificity: life and afterlife effects of genes. Trends Plant Sci. 17, 271–281. DOI: 10.1016/j.tplants.2012.01.005

Wolf, K., Veldkamp, E., Homeier, J., Martinson, G.O., 2011. Nitrogen availability links forest productivity, soil nitrous oxide and nitric oxide fluxes of a tropical montane forest in southern Ecuador. Global Biogeochem. Cycles, 25, GB4009, doi:10.1029/2010gb003876.

Xu, G., Chen, J., Berninger, F., Pumpanen, J., Bai, J., Yu, L., Duan, B., 2015. Labile, recalcitrant, microbial carbon and nitrogen and the microbial community composition at two Abies faxoniana forest elevations under elevated temperatures. Soil Biol. Biochem. 91, 1–13. doi:10.1016/j.soilbio.2015.08.016.

Zimmermann, M., Leifeld, J., Conen, F., Bird, M.I., Mier, P., 2012. Can composition and physical protection of soil organic matter explain soil respiration temperature sensitivity? Biogeochem. 107, 423-436. Doi: 10.1007/s10533-010-9562-y

Zhou, Y., Clark, M., Su, J., Xiao, C., 2015. Litter decomposition and soil microbial community composition in three Korean pine (Pinus koraiensis) forests along an altitudinal gradient. Plant Soil 386(1–2), 171–183. doi:10.1007/s11104-014-2254-y.

Figures and tables

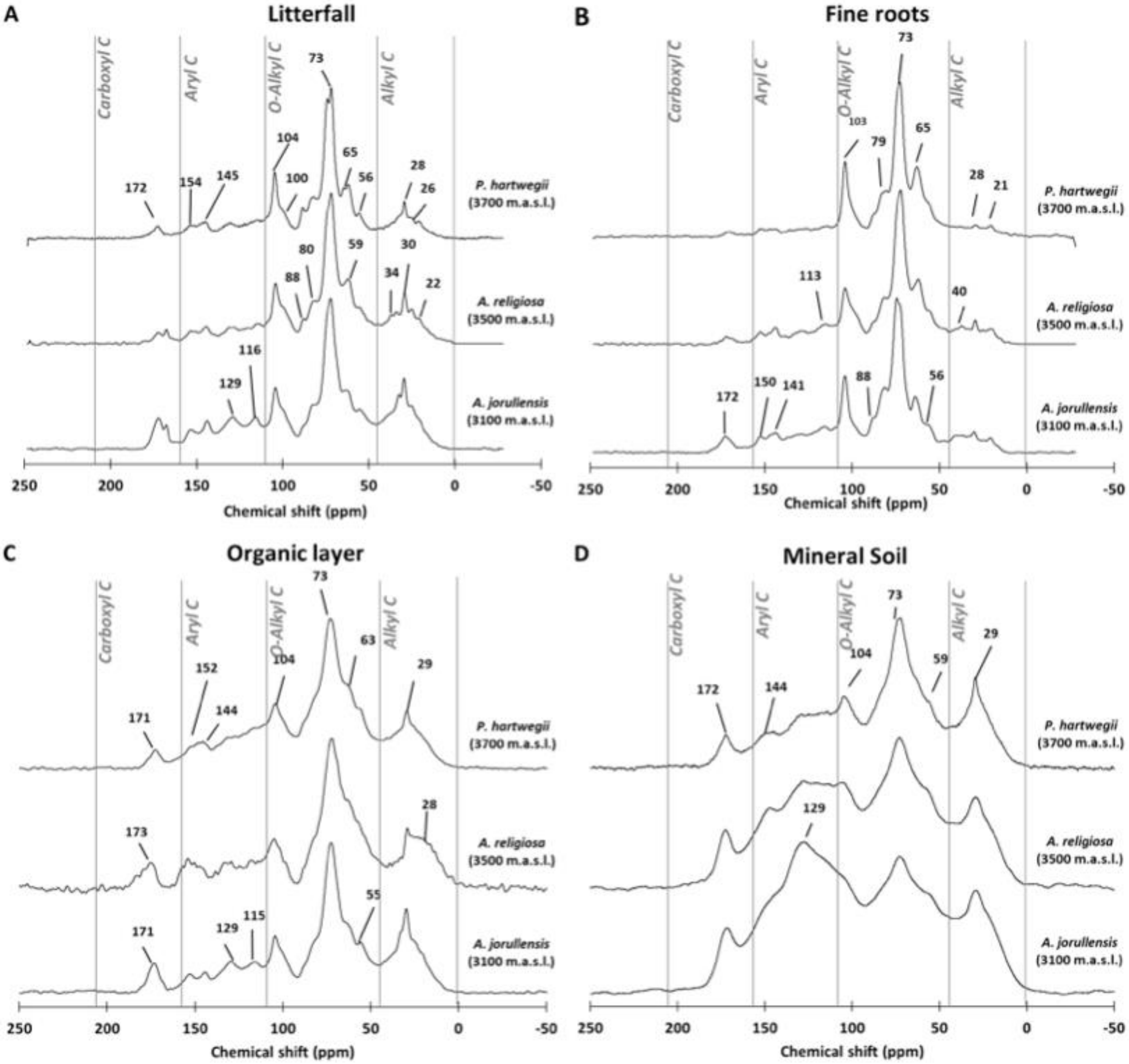

Figure 1. ^{13}C CPMAS NMR spectrograms of samples associated with vegetation-soil systems along an elevational gradient (*Alnus jorullensis* at 3100 m.a.s.l.; *Abies religiosa* at 3500 m.a.s.l. and *Pinus hartwegii* at 3700 m.a.s.l.): A) litterfall, B) fine roots, C) organic layer and D) Mineral soil (0-30 cm in depth)

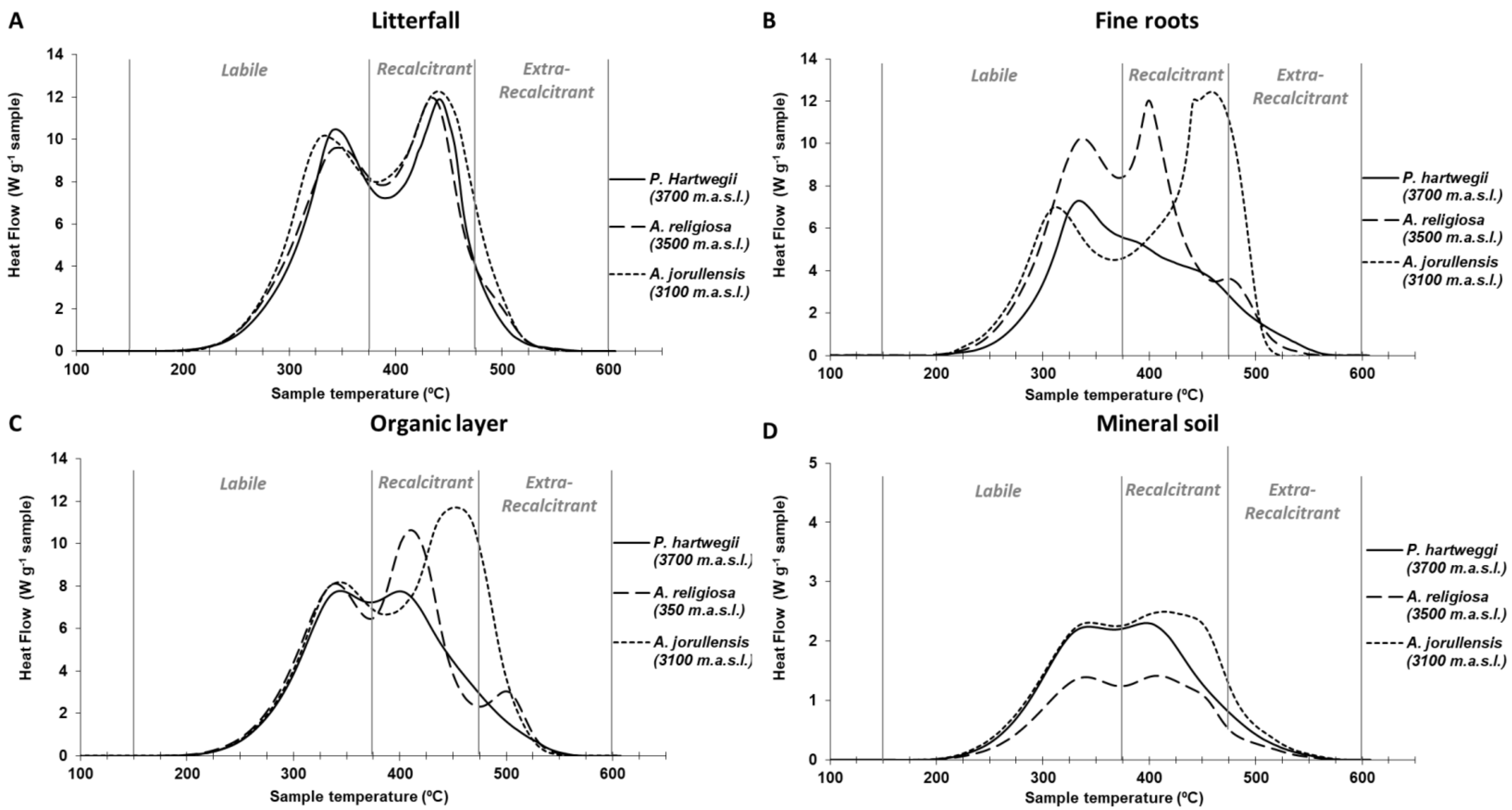

Figure 2. DSC Thermograms of samples associated with soil-vegetation systems along an elevational gradient (*Alnus jorullensis* at 3100 m.a.s.l.; *Abies religiosa* at 3500 m.a.s.l. and *Pinus hartwegii* at 3700 m.a.s.l.): A) litterfall, B) fine roots, C) organic layer and D) Mineral soil (0-30 cm in depth).

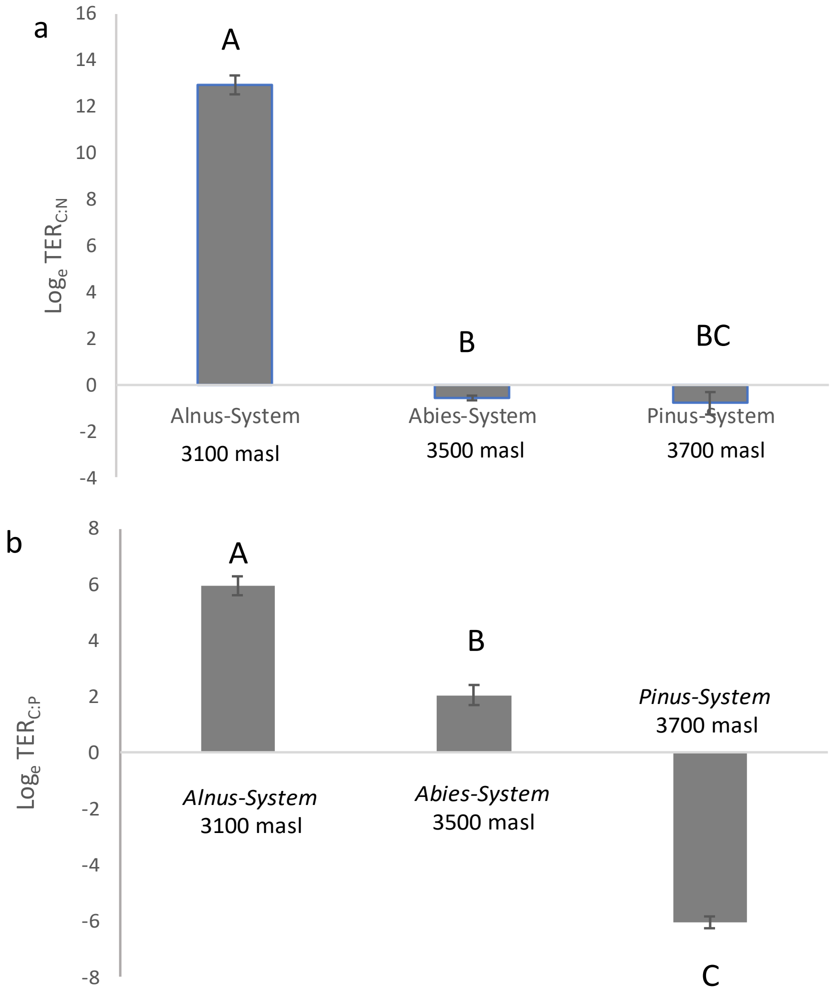

Figure 3. Threshold Elemental Ratio a) C:N (TER$_{C:N}$), and b) C:P (TER$_{C:P}$) of the microbial community in organic layer samples from three dominant temperate arboreal species from the highlands of central Mexico. Different uppercase letters indicate that the means differ significantly among species ($p \leq 0.05$).

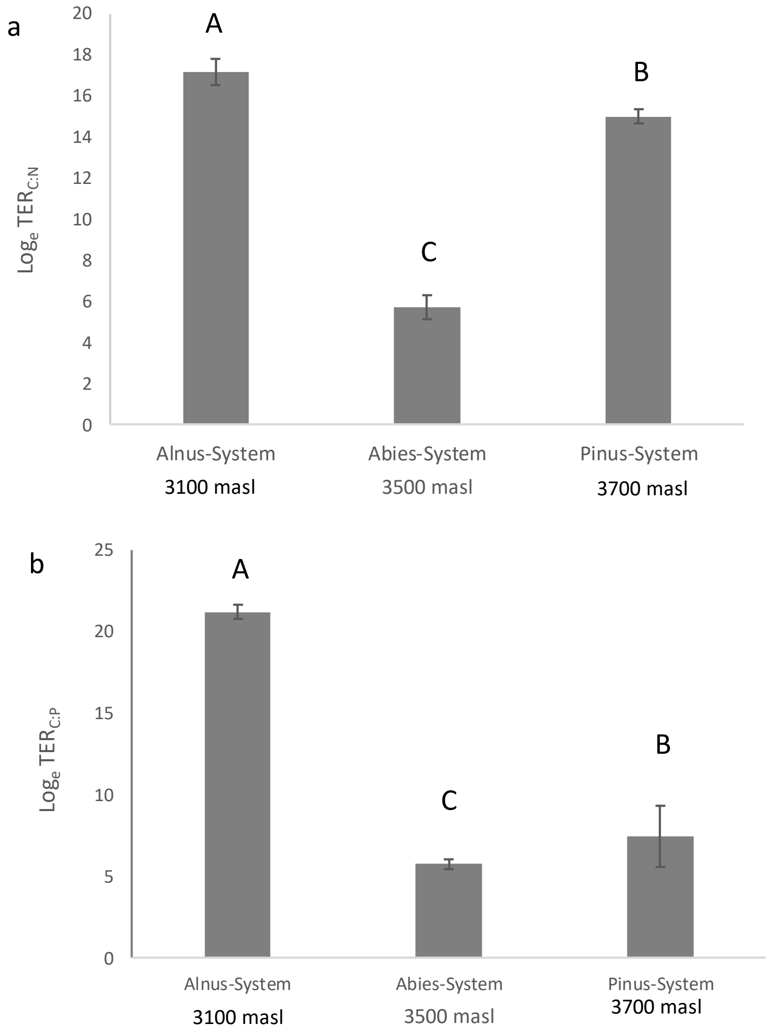

Figure 4. Threshold Elemental Ratio a) C:N (TER$_{C:N}$), and b) C:P (TER$_{C:P}$) of the microbial community in soil samples from three dominant temperate arboreal species from the highlands of central Mexico. Different uppercase letters indicate that the means differ significantly among species ($p \leq 0.05$).

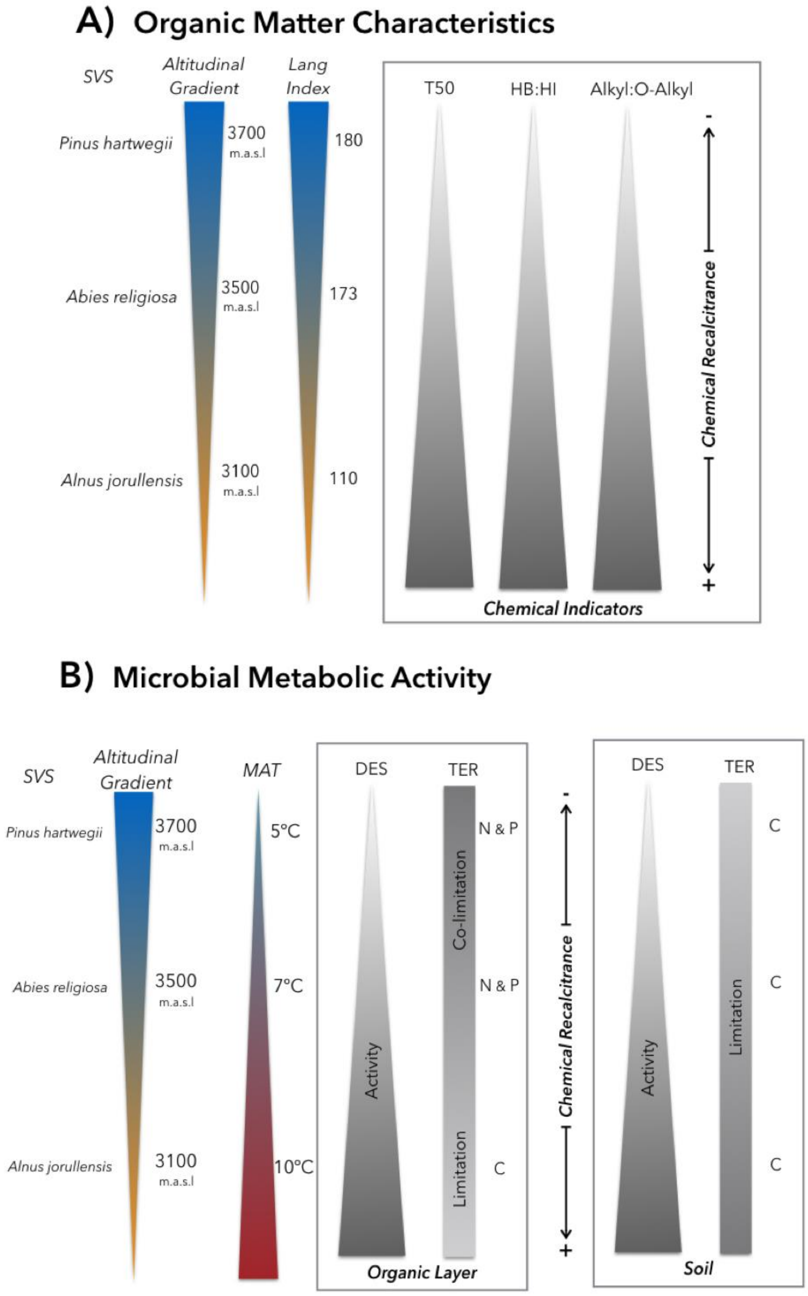

Figure 5. Main factors that determine the responses of parameters of A) organic matter characteristics and B) microbial metabolic activity in three dominant temperate arboreal species systems from the highlands of central Mexico**.** HB:HI is the hydrophobicity ratio, MAT is mean annual temperature, DES is activity of dehydrogenase and TER: threshold elemental ratio

Table 1. ^{13}C NMR parameters of samples associated with soil-vegetation systems (SVS) along an elevational gradient (*Alnus jorullensis* at 3100 m.a.s.l.; *Abies religiosa* at 3500 m.a.s.l. and *Pinus hartwegii* at 3700 m.a.s.l.). HB:HI is the hydrophobicity ratio.

Sample type	SVS	Alkyl	O-alkyl	Aromatic	Carboxyl	HB:HI	alkyl:O-alkyl	alkyl:arom	O-alkyl:arom	aromaticity
		%								%
Litterfall	*P. hartwegii*	13.9	64.8	16.8	4.47	0.44	0.21	0.83	3.86	20.2
	A. religiosa	14.5	63.5	17.5	4.50	0.47	0.23	0.83	3.63	21.4
	A. jorullensis	20.1	56.2	18.7	5.00	0.63	0.36	1.07	3.01	23.5
Fine roots	*P. hartwegii*	9.10	79.9	9.80	1.20	0.23	0.11	0.93	8.15	11.1
	A. religiosa	10.8	72.4	15.4	1.40	0.36	0.15	0.70	4.70	17.9
	A. jorullensis	16.9	71.9	9.80	1.40	0.36	0.24	1.72	7.34	11.1
Organic layer	*P. hartwegii*	16.4	61.3	17.2	5.10	0.51	0.27	0.95	3.56	20.2
	A. religiosa	22.0	57.9	16.1	4.00	0.62	0.38	1.37	3.60	19.0
	A. jorullensis	22.6	56.4	19.5	1.50	0.73	0.40	1.16	2.89	25.0
Mineral soil (0-30 cm in depth)	*P. hartwegii*	19.1	53.2	22.4	5.30	0.71	0.36	0.85	2.38	29.9
	A. religiosa	16.0	47.3	30.9	5.80	0.88	0.34	0.52	1.53	44.9
	A. jorullensis	16.5	41.9	34.9	6.70	1.06	0.39	0.47	1.20	53.0

Table 2. DSC-TG parameters of samples associated with soil-vegetation systems (SVS) along an elevational gradient (*Alnus jorullensis* at 3100 m.a.s.l.; *Abies religiosa* at 3500 m.a.s.l. and *Pinus hartwegii* at 3700 m.a.s.l.).

Sample type	SVS	OM loss	Q	Q'	Q50	$T50_Q$	Q1	Q2	Q3
		[%]	[J g^{-1}]	[J mg^{-1} OM]	[J g^{-1}]	[°C]	[%]	[%]	[%]
Litterfall	*P. hartwegii*	89.1	9931	11120	4965	391	42.9	52.4	4.70
	A. religiosa	84.3	10309	12240	5154	392	42.3	52.1	5.60
	A. jorullensis	85.0	11589	13631	5794	397	41.0	51.0	8.00
Fine roots	*P. hartwegii*	74.2	6421	8626	3211	377	49.2	41.3	9.50
	A. religiosa	78.1	9567	12327	4783	377	49.1	44.4	6.50
	A. jorullensis	81.9	9770	11902	4885	417	36.4	49.8	13.8
Organic Layer	*P. hartwegii*	67.0	7751	11589	3875	383	46.2	47.3	6.50
	A. religiosa	62.2	8659	14030	4330	390	43.0	48.2	8.80
	A. jorullensis	79.3	10573	13428	5286	414	35.4	50.6	14.0
Mineral Soil (0-30 cm in depth)	*P. hartwegii*	17.0	2361	13850	1181	378	48.0	45.3	6.70
	A. religiosa	10.4	1513	14969	756	382	45.9	46.9	7.20
	A. jorullensis	20.1	2775	13797	1388	389	43.4	48.9	7.70

Table 3. Average and standard error of nutrient concentrations and quantified ecoenzyme activities from the organic layer samples of three temperate dominate arboreal species from the highlands of central Mexico. Different uppercase letters indicate that the means differ significantly among species ($p \leq 0.05$). *: p=0.05; **: p=0.01; ***: p<0.001.

	***Alnus*-system 3100 m.a.s.l.**	***Abies*-system 3500 m.a.s.l.**	***Pinus*-system 3700 m.a.s.l.**
C total (mg g^{-1})***	419 ± 9 ^{B}	379 ± 9 ^{C}	452 ± 10 ^{A}
N total (mg g^{-1})***	20.5 ± 0.6 ^{A}	8.76 ± 0.1 ^{B}	7.30 ± 0.3 ^{C}
P total (mg g^{-1})***	0.97 ± 0.07 ^{A}	0.92 ± 0.05 ^{A}	0.60 ± 0.02 ^{B}
DOC (µg g^{-1})	568 ± 54	238 ± 27	470 ± 40
DON (µg g^{-1})	34 ± 8 ^{A}	6 ± 3 ^{B}	32 ± 9 ^{A}
DOP (µg g^{-1})	38 ± 5	34 ± 3	24 ± 9
Cmic (mg g^{-1})*	2.12 ± 0.36 ^{A}	0.87 ± 0.103 ^{B}	1.46 ± 0.33 ^{AB}
Nmic (mg g^{-1})	0.137 ± 0.04	0.13 ± 0.015	0.087 ± 0.022
Pmic (mg g^{-1})	0.033 ± 0.005	0.029 ± 0.03	0.028 ± 0.005
BGL (µmol pNP g^{-1} h^{-1})**	2.25 ± 0.36 ^{A}	0.85 ± 0.25 ^{B}	0.83 ± 0.29 ^{B}
NAG (µmol pNP g^{-1} h^{-1})**	0.73 ± 0.15 ^{A}	0.15 ± 0.02 ^{B}	0.38 ± 0.01 ^{AB}
AP (µmol pNP g^{-1} h^{-1})	2.5 ± 0.4	2.0 ± 0.3	1.7 ± 0.2
POX (µmol tyr g^{-1} h^{-1})	5.4 ± 1.8	2.1 ± 0.3	4.9 ± 0.8
DES (µg TPF g^{-1} d^{-1}) ***	3322 ± 180 ^{A}	2710 ± 395 ^{B}	787 ± 109 ^{C}

Dissolved organic C (DOC), N (DON), P (DOP), microbial C (C_{mic}), N (N_{mic}) and P (P_{mic}), β-1,4-glucosidase (BGL), β-N-acetyl-glucosaminidase (NAG), phosphomonoesterases (AP), polyphenol oxidase (POX) and deshydrogenase (DES).

Table 4. Average and standard error of nutrient ratios and ecoenzyme activity ratios from the organic layer samples of three dominant temperate arboreal species from the highlands of central Mexico. Different uppercase letters indicate that the means differ significantly among species (p ≤ 0.05). *: p=0.05; **: p=0.01; ***: p<0.001.

	***Alnus*-system** **3100 m.a.s.l.**	***Abies*-system** **3500 m.a.s.l.**	***Pinus*-system** **3700 m.a.s.l.**
Ct:Nt* **	20.4 ± 0.9 ^{C}	43.2 ± 1.5 ^{B}	62.3 ± 0.1 ^{A}
Ct:Pt* **	441 ± 33 ^{B}	417 ± 32 ^{B}	753 ± 33 ^{A}
Nt:Pt* **	21.8 ± 1.7 ^{A}	9.6 ± 0.6 ^{B}	12.1 ± 0.7 ^{B}
DOC:DON	36 ± 17	170 ± 80	23 ± 9
DOC:DOP	23 ± 6	7 ± 1	38 ± 28
DON:DOP	0.97 ± 0.29	0.16 ± 0.90	3.35 ± 2.49
Cmic:Nmic	25 ± 12	7 ± 1	24 ± 8
Cmic:Pmic	66 ± 10	31 ± 4	58 ± 17
Nmic:Pmic	4.2 ± 1.0	4.6 ± 0.7	2.7 ± 0.5
BGL:NAG	4.4 ± 1.6	5.8 ± 0.8	2.4 ± 0.6
BGL:AP	1.1 ± 0.3	0.47 ± 0.1	0.47 ± 0.1
NAG:AP **	0.31 ± 0.07 ^{A}	0.08 ± 0.01 ^{B}	0.21 ± 0.03 ^{AB}

Total carbon (Ct), N (Nt), P (Pt), dissolved organic C (DOC), N (DON), P (DOP), microbial C ($C_{\mathbf{mic}}$), N ($N_{\mathbf{mic}}$) and P ($P_{\mathbf{mic}}$), β-1,4-glucosidase (BGL), β-N-acetyl-glucosaminidase (NAG), phosphomonoesterases (AP), polyphenol oxidase (POX) and deshydrogenase (DES), specific enzymatic activity (SEA).

Table 5. Average and standard error of nutrient concentrations and quantified ecoenzyme activities from the mineral soil samples (0-30 cm in depth) of three dominant temperate arboreal species from the highlands of central Mexico. Different uppercase letters indicate that the means differ significantly among species ($p \leq 0.05$). *: p=0.05; **: p=0.01; ***: p<0.001.

	***Alnus*-system** **3100 m.a.s.l.**	***Abies*-system** **3500 m.a.s.l.**	***Pinus*-system** **3700 m.a.s.l.**
C total (mg g^{-1})	79 ± 5.0	83 ± 6.7	93 ± 1.2
N total (mg g^{-1})***	5.0 ± 0.1 ^{A}	1.6 ± 0.5 ^{C}	3.9 ± 0.2 ^{A}
P total (mg g^{-1})***	1.7 ± 0.16 ^{A}	0.3 ± 0.1 ^{B}	0.2 ± 0.1 ^{B}
DOC (µg g^{-1})	179 ± 27	276 ± 62	223 ± 16
DON (µg g^{-1})	14 ± 3	11 ± 2	10 ± 2
DOP (µg g^{-1})	29 ± 2	30 ± 1	19 ± 1
NH$_4^+$ (µg g^{-1})*	13 ± 5 ^{A}	6 ± 1 ^{AB}	2 ± 1 ^{B}
NO$_3^-$ (µg g^{-1})	0 ± 0	0.03 ± 0	0.14 ± 0
HPO$_4^2$ (µg g^{-1})***	19 ± 2 ^{A}	10 ± 1 ^{B}	10 ± 1 ^{B}
Cmic (mg g^{-1})	2.68 ± 0.55	2.34 ± 0.13	2.41 ± 0.52
Nmic (mg g^{-1})	0.089 ± 0.02	0.097 ± 11	0.106 ± 0.012
Pmic (mg g^{-1})	0.008 ± 0.002	0.012 ± 0.003	0.007 ± 0.002
BGL (µmol pNP g^{-1} h^{-1})*	0.06 ± 0.02 ^{B}	0.16 ± 0.08 ^{AB}	0.30 ± 0.03 ^{A}
NAG (µmol pNP g^{-1} h^{-1})	0.07 ± 0.01	0.07 ± 0.030	0.03 ± 0.01
AP (µmol pNP g^{-1} h^{-1})	0.24 ± 0.04	0.16 ± 0.05	0.17 ± 0.02
POX (µmol tyr g^{-1} h^{-1})	1.5 ± 0.5	1.1 ± 0.4	2.0 ± 0.5
DES (µg TPF g^{-1} d^{-1})	277 ± 118	217 ± 20	122 ± 6

Total C (Ct), N (Nt), P (Pt), dissolved organic C (DOC), N (DON), P (DOP), microbial C (C_{mic}), N (N_{mic}) and P (P_{mic}), β-1,4-glucosidase (BGL), β-N-acetyl-glucosaminidase (NAG), phosphomonoesterases (AP), polyphenol oxidase (POX) and deshydrogenase (DES).

Table 6. Average and standard error of nutrient ratios and ecoenzyme activities ratios from the mineral soil samples (0-30 cm in depth), nutrient ratio and ecoenzyme activity ratio in the soils of three dominant temperate arboreal species from the highlands of central Mexico. Different uppercase letters indicate that the means differ significantly among species ($p \leq 0.05$). *: p=0.05; **: p=0.01; ***: p<0.001.

	***Alnus*-system 3100 m.a.s.l.**	***Abies*-system 3500 m.a.s.l.**	***Pinus*-system 3700 m.a.s.l.**
Ct:Nt*	15.7 ± 0.7 ^{B}	72.2 ± 23 ^{A}	23.6 ± 1.1 ^{AB}
Ct:Pt**	47.5 ± 5.4 ^{B}	338.8 ± 83.8 ^{A}	450 ± 86.9 ^{A}
Nt:Pt***	3.0 ± 0.3 ^{B}	6.9 ± 2.4 ^{B}	18.7 ± 3.0 ^{A}
DOC:DON	15 ± 3	31 ± 11	29 ± 8
DOC:DOP	6 ± 1	11 ± 3	12 ± 1
DON:DOP	0.48 ± 0.07	0.50 ± 0.14	0.50 ± 0.11
Cmic:Nmic	46 ± 16	26 ± 4	23 ± 4
Cmic:Pmic	376 ± 60	228 ± 58	576 ± 236
Nmic:Pmic	12.3 ± 4.3	8.8 ± 1.4	26.1 ± 13
BGL:NAG	0.9 ± 0.2	4.9 ± 3.1	15.7 ± 6.4
BGL:AP**	0.24 ± 0.07 ^{B}	1.04 ± 0.29 ^{AB}	1.87 ± 0.34 ^{A}
NAG:AP	0.29 ± 0.05	1.03 ± 0.82	0.22 ± 0.08

Total C (Ct), N (Nt), P (Pt), dissolved organic C (DOC), N (DON), P (DOP), microbial C (C_{mic}), N (N_{mic}) and P (P_{mic}), β-1,4-glucosidase (BGL), β-N-acetyl-glucosaminidase (NAG), phosphomonoesterases (AP), polyphenol oxidase (POX) and deshydrogenase (DES), specific enzymatic activity (SEA).

Table S1. Regression between elemental ratios of microbial biomass and elemental ratios of resources (organic layer or soil) of three dominant temperate arboreal species from the highlands of central Mexico. Data in bold denote significant values ($p \leq 0.05$).

	$B_{C:N}$ vs TOC:TON			**$B_{C:P}$ vs COT:POT**		
	r	r2	p	r	r2	p
			Organic Layer			
Alnus jorullensis	-0.35	0.12	0.55	0.059	0.003	0.92
Abies religiosa	-0.18	0.032	0.77	-0.18	0.03	0.77
Pinus hartwegii	-0.79	0.62	0.11	-0.73	0.533	0.16
			Soil			
Alnus jorullensis	-0.064	0.004	0.91	-0.006	0.00004	0.99
Abies religiosa	0.83	0.69	0.08	-0.04	0.001	0.94
Pinus hartwegii	-0.93	0.88	**0.01**	-0.15	0.023	0.80

Discusión general y prospección futura de la tesis

En esta investigación el gradiente altitudinal sobre el que se establecen los bosques templados influyen directa e indirectamente sobre el ciclo de carbono. Modulan el incremento de carbono en la biomasa a través del crecimiento arbóreo y el almacén de carbono orgánico en el mantillo y suelo por medio del proceso de descomposición de la materia orgánica. Cada uno de estos procesos esta modulado por factores como el clima y el efecto de las especies (arbórea y/o microbiana), los cuales destacan en cada uno de los capítulos de la tesis (Cui et al. 2019, Berg y McClaugherty 2014, Körner, 2007, Blagodatskaya et al 2016). Por ejemplo, con respecto al crecimiento Liang et al. (2010), determinaron que las tasas de crecimiento arbóreo se restringieron con la elevación debido a que las bajas temperaturas en las cimas de las montañas, lo que limita los procesos fisiológicos responsables de la formación de tejidos, como la fotosíntesis y la asignación de C a diferentes partes del árbol. Además, Gómez-Guerreo et al. (2013) mencionan que el incremento del área basal incrementó en la década de 1980 con una disminución acentuada en los últimos años en especies como *Pinus hartwegii* y en *Abies* religiosa. Esto puede tener repercusiones en el manejo forestal, debido a que en las zonas altas se encuentran los árboles de mayor edad, y las reforestaciones en las partes bajas. También mencionan que la estimulación por CO_2 no ha sido suficiente para contrarrestar el estrés por sequía inducido por el cambio climático global del sistema (Gómez-Guerreo et al. 2013). Estudios futuros podrían indicar que la limitación por recursos como nutrientes podrían tener un papel importante en la modulación del proceso de crecimiento arbóreo. Es decir, explorar la idea de la fertilización *in situ* o la deposición de N podría mejorar la producción forestal de estas zonas, por ejemplo, Fenn et al. (2020) encontraron efectos significativos a la deposición de N sobre el incremento anual de C en un bosque de pino y oyamel en California.

Por otro lado, Wang et al. (2019), Xu et al. (2019) y Marek et al. (2020), mostraron el papel del clima sobre la descomposición de la materia orgánica del suelo. Entre las posibles explicaciones mencionan que un incremento en la temperatura acelera la actividad microbiana y una mayor disponibilidad de nutrientes, lo que resulta en una mayor tasa de descomposición (respiración heterotrófica, mayor emisión de CO_2 a la atmósfera). Contrario a este caso, en esta investigación se observó en el sistema de vegetación-suelo *Pinus hartwegii* que la poca disponibilidad de agua y las bajas temperaturas reducen la actividad microbiana, conservando los almacenes de carbono orgánico del mantillo y suelo. Sin embargo, se vuelve latente la vulnerabilidad de estos almacenes a su descomposición debido a los incrementos de temperaturas pronosticados por Sáenz-Romero et al. (2012) para las zonas templadas del centro de México.

Investigaciones como la de Cleveland et al. (2007) recalcan como el clima y la calidad de los compuestos orgánicos determinan el proceso de descomposición. En esta investigación, definimos que los cambios en la temperatura dados por el gradiente altitudinal determinó la velocidad y magnitud del proceso de descomposición. El cual influyó entre otras cosas sobre la actividad microbiana y en particular sobre la actividad enzimática y la disponibilidad de nutrientes. Además, apoyamos la investigación de Nottingham et al. (2016) donde se sugiere que el incremento en la actividad de BGL en los sistemas de bajas temperaturas, se debió a la presencia de iso-enzimas adaptadas a temperaturas frías, y a una mayor disponibilidad del sustrato a elevadas altitudes. Asimismo, y como ya hemos mencionado, la síntesis de enzimas requiere de una inversión de recursos, sacrificando en algunas ocasiones la asignación de recursos al incremento de biomasa de los microorganismos y entre más complejo o recalcitrante es el compuesto orgánico, más pasos enzimáticos requiere para ser asimilado por la comunidad microbiana (Bosatta y Agren 1999). Lo que sugiere como la interacción de la calidad de los compuestos orgánicos y el clima podrían alterar la respuesta de la comunidad microbiana con respecto a como utilizan el sustrato en escenarios de cambio climático. Por ejemplo, diferentes calidades de sustrato, derivado del recambio de especies, fertilización o diferente disponibilidad de sustratos y los cambios de temperatura previstos para los sistemas. Por ejemplo, Frey et al. (2013) encontraron una disminución en la eficiencia de uso del C con respecto al aumento de temperatura en sustratos recalcitrantes, asimismo, Ali et al (2018) encontraron el mismo efecto con la despolimeraización de la celobiosa en un sistema al este de Alemania.

Otra de las implicaciones de la interacción cambio climático (temperatura)-microorganismos-calidad de los compuestos orgánicos pueden llegar al punto de afectar la composición de la comunidad microbiana (Ali et al 2018). Por un lado, se ha demostrado que la disponibilidad de sustratos orgánicos recalcitrantes favorece el predominio de las comunidades de hongos que son capaces de despolimerizar compuestos como la lignina, lo que es relevante en sistemas templados donde se han reportado que los hongos juegan un papel importante en el proceso de descomposición de compuestos de especies de pinares (Zhang et al. 2008). Asimismo, cuando se combina un sustrato recalcitrante y el calentamiento del suelo se promueve la proliferación de hongos, mientras que la disponibilidad de sustrato lábil y el calentamiento del suelo incrementa la comunidad de bacterias (Castro et al. 2010). Sin embargo, esta relación entre la calidad de la materia orgánica, temperatura y la comunidad microbiana no es tan directa y requiere de análisis profundos sobre cómo podría modificarse el metabolismo de los microorganismos.

Conclusiones generales de la tesis

El mayor contenido de carbono arbóreo aéreo se determinó en el sistema de vegetación-suelo *Abies religiosa*, como consecuencia de una mayor tasa de crecimiento como lo indican los anchos de los anillos de crecimiento. La mayor proporción de carbono orgánico del suelo (COS) se encontró en el primer horizonte del suelo en los sistemas de Alnus y Pinus. En el sistema *Alnus jorullensis*, la magnitud de la entrada de residuos vegetales esta inversamente relacionada con el almacén de carbono en el mantillo, debido a la descomposición del almacén. La composición química de los residuos vegetales en los sistemas determinó la constante de descomposición y el tiempo medio de residencia de la capa de hojarasca. La disponibilidad de agua es el principal impulsor de la composición química de la materia orgánica producida por las especies vegetales dominantes. La recalcitrancia química relativamente más alta de la materia orgánica reduce la actividad metabólica microbiana en la condición de menor disponibilidad de agua (sitio de menor elevación). Las temperaturas ambientales más bajas en elevaciones más altas podrían limitar la actividad microbiana del suelo, a pesar de que la materia orgánica tiene una mayor labilidad química.

Los cambios en la distribución de especies como resultado del cambio climático podrían modificar la entrada de material orgánico, así como los mecanismos que determinan las concentraciones de C:N:P. Por esta razón, comprender el efecto de los sistemas vegetación-suelo sobre los ciclos biogeoquímicos a lo largo de los gradientes de elevación en los bosques templados de latitudes medias (México) implica caracterizar los procesos internos que controlan la descomposición de la materia orgánica (actividad microbiana y dinámica y composición de la microbiota edáfica). Por lo tanto, se requiere un estudio integrado del material orgánico derivado de plantas y el metabolismo microbiano en el suelo y mantillo del bosque para comprender plenamente la vulnerabilidad de los ecosistemas de montañas tropicales al cambio climático.

Referencias

Ali, R.S., Poll, C., and Kandeler, E. 2018. Dynamics of soil respiration and microbial communities: Interactive controls of temperature and substrate quality. Soil Biol. Biochem. 127: 60–70. doi:10.1016/j.soilbio.2018.09.010.

Blagodatskaya, E., Blagodatsky, S., Khomyakov, N., Myachina, O., and Kuzyakov, Y. 2016. Temperature sensitivity and enzymatic mechanisms of soil organic matter decomposition along an altitudinal gradient on Mount Kilimanjaro. Sci Rep 6(1): 22240. doi:10.1038/srep22240.

Bosatta, E., and Ågren, G.I. 1999. Soil organic matter quality interpreted thermodynamically. Soil Biol. Biochem. 31(13): 1889–1891. doi:10.1016/S0038-0717(99)00105-4.

Castro, H.F., Classen, A.T., Austin, E.E., Norby, R.J., and Schadt, C.W. 2010. Soil Microbial Community Responses to Multiple Experimental Climate Change Drivers. Appl. Environ. Microbiol. 76(4): 999–1007. ASM. doi:10.1128/AEM.02874-09.

Cleveland, C.C., Nemergut, D.R., Schmidt, S.K., and Townsend, A.R. 2007. Increases in soil respiration following labile carbon additions linked to rapid shifts in soil microbial community composition. Biogeochemistry 82(3): 229–240. doi:10.1007/s10533-006-9065-z.

Cui, Y., Bing, H., Fang, L., Jiang, M., Shen, G., Yu, J., Wang, X., Zhu, H., Wu, Y., and Zhang, X. 2019. Extracellular enzyme stoichiometry reveals the carbon and phosphorus limitations of microbial metabolisms in the rhizosphere and bulk soils in alpine ecosystems. Plant Soil. doi:10.1007/s11104-019-04159-x.

Fenn, M.E., Preisler, H.K., Fried, J.S., Bytnerowicz, A., Schilling, S.L., Jovan, S., and Kuegler, O. 2020. Evaluating the effects of nitrogen and sulfur deposition and ozone on tree growth and mortality in California using a spatially comprehensive forest inventory. Forest Ecol. Manag. 465: 118084. doi:10.1016/j.foreco.2020.118084.

Frey, S.D., Lee, J., Melillo, J.M., and Six, J. 2013. The temperature response of soil microbial efficiency and its feedback to climate. Nat. Clim. Change 3(4): 395–398. doi:10.1038/nclimate1796.

Gómez-Guerrero, A., Silva, L.C.R., Barrera-Reyes, M., Kishchuk, B., Velázquez-Martínez, A., Martínez-Trinidad, T., Plascencia-Escalante, F.O., and Horwath, W.R. 2013. Growth decline and divergent tree ring isotopic composition (δ^{13}C and δ^{18}O) contradict predictions of CO_2 stimulation in high altitudinal forests. Glob. Change Biol. 19(6): 1748–1758. doi:10.1111/gcb.12170.

Marek, M.V., Marková, I., Pavelka, M., Havránková, K., Macků, J., Rejšek, K., and Janouš, D. 2020. Chapter 2 - Potential changes in forest soil carbon stocks under different climate change scenarios. *In* Climate Change and Soil Interactions. *Edited by* M.N.V. Prasad and M. Pietrzykowski. Elsevier. pp. 21–36. doi:10.1016/B978-0-12-818032-7.00002-3.

Nottingham, A.T., Turner, B.L., Whitaker, J., Ostle, N., Bardgett, R.D., McNamara, N.P., Salinas, N., and Meir, P. 2016. Temperature sensitivity of soil enzymes along an elevation gradient in the Peruvian Andes. Biogeochemistry 127(2–3): 217–230. doi:10.1007/s10533-015-0176-2.

Sáenz-Romero, C., Rehfeldt, G.E., Duval, P., and Lindig-Cisneros, R.A. 2012. Abies religiosa habitat prediction in climatic change scenarios and implications for monarch butterfly conservation in Mexico. Forest Ecol. Manag. 275: 98–106. doi:10.1016/j.foreco.2012.03.004.

Villers-Ruíz, L., and Trejo-Vázquez, I. 1998. Climate change on Mexican forests and natural protected areas. Global Environ. Chang. 8(2): 141–157.

Wang, K., Peng, C., Zhu, Q., Wang, M., Wang, G., Zhou, X., Yang, Y., Ding, J., and Wei, H. 2019. Changes in soil organic carbon and microbial carbon storage projected during the 21st century using TRIPLEX-MICROBE. Ecol. Indic. 98: 80–87. doi:10.1016/j.ecolind.2018.10.045.

Xu, W., Yuan, W., Cui, L., Ma, M., and Zhang, F. 2019. Responses of soil organic carbon decomposition to warming depend on the natural warming gradient. Geoderma 343: 10–18. doi:10.1016/j.geoderma.2019.02.017.

Zhang, P., Tian, X., He, X., Song, F., Ren, L., and Jiang, P. 2008. Effect of litter quality on its decomposition in broadleaf and coniferous forest. Eur. J. Soil Biol. 44(4): 392–399. doi:10.1016/j.ejsobi.2008.04.005.