UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS

FACULTAD DE ESTUDIOS SUPERIORES IZTACALA

IMPACTO DE DOS ACTIVIDADES HUMANAS DE SUBSISTENCIA SOBRE LA ESTRUCTURA DE LAS BIOCOSTRAS Y SU EFECTO EN LA DINÁMICA DEL NITRÓGENO EN UN DESIERTO TROPICAL

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTORA EN CIENCIAS

PRESENTA:

JESSICA DE JESÚS SOSA QUINTERO

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CD. MX.   **ENERO 2020**

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COORDINACIÓN DEL POSGRADO EN CIENCIAS BIOLÓGICAS

FACULTAD DE ESTUDIOS SUPERIORES IZTACALA

OFICIO CPCB/1269/2019

ASUNTO: Oficio de Jurado

M. en C. Ivonne Ramírez Wence
Directora General de Administración Escolar, UNAM
P r e s e n t e

Me permito informar a usted que en la reunión ordinaria del Subcomité de Ecología y Manejo Integral de Ecosistemas y Biología Evolutiva y Sistemática del Posgrado en Ciencias Biológicas, celebrada el día **30 de septiembre de 2019** se aprobó el siguiente jurado para el examen de grado de **DOCTORA EN CIENCIAS** de la estudiante **SOSA QUINTERO JESSICA DE JESUS** con número de cuenta 408092753 con la tesis titulada **"Impacto de dos actividades humanas de subsistencia sobre la estructura de las biocostras y su efecto en la dinámica del nitrógeno en un desierto tropical."**, realizada bajo la dirección del **DR. HÉCTOR OCTAVIO GODÍNEZ ÁLVAREZ**, quedando integrado de la siguiente manera:

Presidente:	DR.	RAFAEL LIRA SAADE
Vocal:	DR.	NOÉ MANUEL MONTAÑO ARIAS
Secretario:	DRA.	SARA LUCÍA CAMARGO RICALDE
Suplente:	DRA.	MARÍA DE LOS ÁNGELES HERRERA CAMPOS
Suplente:	DR.	VÍCTOR MANUEL RIVERA AGUILAR

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

A T E N T A M E N T E
"POR MI RAZA HABLARA EL ESPÍRITU"
Ciudad Universitaria, Cd. Mx., a 21 de noviembre de 2019

COORDINADOR DEL PROGRAMA

DR. ADOLFO GERARDO NAVARRO SIGÜENZA

c. c. p. Expediente del alumno

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"La ciencia se compone de errores que, a su vez, son los pasos hacia la verdad"
Julio Verne

Índice

Resumen

Las biocostras o costras biológicas del suelo (CBS) son comunidades de cianobacterias, líquenes y briofitas que se distribuyen en zonas alpinas, polares y desérticas. En los desiertos pueden alcanzar hasta 70% de cobertura. Las biocostras son esenciales para el funcionamiento de los ecosistemas desérticos debido a que participan en la dinámica del nitrógeno (fijación, formas totales y disponibles, amonificación, nitrificación y mineralización). Sin embargo, su participación en esta dinámica es alterada por actividades humanas como la agricultura de riego y la ganadería. El impacto de estas actividades ha sido evaluado principalmente en desiertos templados, por lo que existen pocos datos para los desiertos tropicales. En los desiertos tropicales, las biocostras están ampliamente distribuidas y las principales actividades humanas son la agricultura de temporal y la extracción de leña. El objetivo de este trabajo fue evaluar el impacto de estas actividades en la riqueza específica y abundancia de las biocostras y su efecto en la dinámica del nitrógeno del suelo en el valle de Zapotitlán Salinas, un desierto tropical del centro de México. La agricultura de temporal consistió en un policultivo fertilizado con estiércol y la introducción de cabras después de la cosecha. Los campos de cultivo fueron abandonados hace 16 años. Estos campos tienen baja cobertura de vegetación y hojarasca, así como alta compactación del suelo, baja tasa de infiltración y bajo contenido de materia orgánica y nutrientes en el suelo. La extracción de leña consiste en cortar ramas de *Prosopis laevigata*. Esta actividad continúa en la actualidad y originó mezquitales con dosel abierto y dosel cerrado que difieren en la cantidad de leña extraída. En ambos mezquitales, la compactación del suelo fue baja y la tasa de infiltración, el contenido de materia orgánica y nutrientes fueron mayores que en los campos de cultivo. Las biocostras en los campos de

cultivo tuvieron 14-18 especies, 50-70% de cobertura y estuvieron dominadas por cianobacterias con heterocistos. En las biocostras de los sitios con extracción de leña se registraron 23-29 especies, 90% de cobertura y estuvieron dominadas por cianolíquenes y briofitas. En los sitios con agricultura de temporal, el suelo tuvo alta tasa de nitrificación y baja retención de nitrógeno en biomasa microbiana. El suelo en los sitios con extracción de leña presentó alto nitrógeno disponible, tasa de amonificación y retención de nitrógeno en biomasa microbiana. En conclusión, la agricultura de temporal tuvo efectos negativos sobre el suelo y la vegetación que favorecieron la cobertura de las cianobacterias, pero incrementaron la nitrificación. En contraste, la extracción de leña presentó menores efectos negativos sobre el suelo y la vegetación que favorecieron la cobertura de cianolíquenes y briofitas, e incrementaron las formas totales y disponibles de nitrógeno, así como la amonificación y la retención en biomasa microbiana en el suelo.

Abstract

Biocrusts or biological soil crusts (BSC) are communities of cyanobacteria, lichens, and bryophytes widely distributed in alpine, polar and desert zones. In deserts they can reach up to 70% cover. Biocrusts are essential for the functioning of desert ecosystems because participate in the N dynamics (fixation, total and available forms, ammonification, nitrification and mineralization). However, their participation in this dynamics is altered by human activities such as irrigation agriculture and livestock. The impact of these activities has been evaluated mainly in temperate deserts, however, little is known in tropical deserts. In tropical deserts, the biocrusts are widely distributed and the principal human activities are rainfed agriculture and firewood extraction. The objective of this thesis was to evaluate the impact of these human activities on the species richness and abundance of biocrusts and their effect on the soil N dynamics in the Zapotitlán Salinas valley, a tropical desert in central Mexico. The rainfed agriculture consisted of a polyculture fertilized with manure, where goats were introduced after harvesting. The croplands were abandoned 16 years ago. These croplands have low cover of vegetation and litter, as well as high soil compaction, low infiltration rate, and low content of organic matter and soil nutrients. The extraction of firewood consists of cutting branches of *Prosospis laevigata*. This activity continues today and originated mesquite shrublands with open- and closed-canopy that differ in the amount of firewood extracted. In both mesquite shrublands, soil compaction was low and the infiltration rate, the content of organic matter and nutrients were higher than in croplands. The biocrusts in croplands had 14-18 species, 50-70% cover, and were dominated by cyanobacteria with heterocysts. The biocrusts in sites with firewood extraction had 23-29 species, 90% cover, and were dominated by cyanolichens and bryophytes. In sites with

rainfed agriculture, the soils had high nitrification rate and low nitrogen retention in microbial biomass. The soil in sites with firewood extraction presented high available nitrogen, ammonification rate, and nitrogen in microbial biomass. In conclusion, rainfed agriculture had negative effects on the soil and vegetation that favored the cover of cyanobacteria, but increased nitrification. In contrast, the extraction of firewood had lower negative effects on the soil and vegetation that favored the cover of cyanolichens and bryophytes, and increased the total and available forms of nitrogen, as well as ammonification and retention in soil microbial biomass.

Capítulo 1

1.1 Introducción general

Las actividades productivas como la ganadería y la agricultura causan la degradación de los ecosistemas ya que alteran su estructura y funcionamiento (Reynolds et al., 2007). Dos componentes primordiales de los ecosistemas son la vegetación y el suelo, los cuales son afectados por la aplicación de agroquímicos, el uso de maquinaria, el sobrepastoreo y la remoción de la cobertura vegetal debido a que compactan el suelo, incrementan la erosión y alteran la disponibilidad de nutrientes. Además, modifican la estructura y actividad de los organismos del suelo como las biocostras (Asner et al., 2004; Belnap & Eldridge, 2003; Bashan & Bashan, 2010; Zhang et al., 2011).

Las biocostras son comunidades compuestas principalmente por cianobacterias, líquenes y briofitas que están asociadas con las partículas orgánicas e inorgánicas del suelo y crecen en los primeros centímetros de profundidad. Estas comunidades tienen características estructurales y funcionales que les permiten desarrollarse en zonas desérticas, donde se adaptan a condiciones extremas de temperatura, luz y largos periodos de sequía (Belnap, 2006). Los principales factores que influyen en su distribución son biogeográficos (límites de dispersión), climáticos (precipitación, temperatura y estacionalidad), edáficos (textura, pH y contenido de nutrientes), topográficos (características geomorfológicas) y bióticos (cobertura vegetal) (Bowker et al., 2016).

Las biocostras son fundamentales para el funcionamiento de los ecosistemas desérticos porque realizan diversas funciones que están relacionadas con la estabilidad del suelo, así como con la disponibilidad de agua y nutrientes. Las biocostras forman una capa compuesta por hifas de hongos, filamentos de cianobacterias, rizinas de líquenes y rizoides

de musgos, así como partículas y agregados del suelo, las cuales protegen la superficie del suelo de la acción erosiva de la lluvia y el viento (Mager & Thomas, 2011). Las biocostras también modulan la infiltración y escorrentía del agua en el suelo (Fischer et al., 2010; Kidron & Yair, 1997). Además, contribuyen a la acumulación y disponibilidad de nutrientes en el suelo como K, Ca, Mg, Mn y Zn y participan en la dinámica de nutrientes como el carbono y nitrógeno. Su participación en la dinámica del nitrógeno en los desiertos es especialmente importante debido a que este nutriente es limitante y susceptible al impacto de las actividades humanas (Jafari et al., 2004; Elbert et al., 2012; Delgado-Baquerizo et al., 2016).

En los últimos años se han realizado estudios detallados de la relación entre las biocostras y la dinámica del nitrógeno. Las biocostras pueden generar microambientes homogéneos en el suelo que modulan la actividad microbiana, la distribución de las formas totales y disponibles del N, así como los flujos del N en el suelo por la fijación, nitrificación, amonificación, desnitrificación, mineralización e inmovilización (Castillo-Monroy et al., 2010; Delgado-Baquerizo et al., 2013; 2014; Hu et al., 2015a; Hu et al., 2015b; Liu et al., 2016). La participación de las biocostras en la dinámica del N podría estar asociada con el grupo de organismos dominante, por ejemplo: las biocostras dominadas por cianobacterias y cianolíquenes favorecen la entrada de nitrógeno debido a que son organismos fijadores de N (Delgado-Baquerizo et al., 2013; Barger et al., 2016). Las biocostras son tapetes protectores que influyen en la comunidad y actividad de los organismos ligados a la dinámica del nitrógeno, ya que proveen condiciones de estabilidad en el suelo, contenido de humedad y protección contra la radiación solar (Delgado-Baquerizo et al., 2015; Liu et al., 2017).

Considerando lo anterior, las actividades productivas como la agricultura y la ganadería pueden causar cambios críticos en la estructura de las biocostras que podrían modificar su multifuncionalidad en el ecosistema. Por ejemplo, la agricultura de riego y la ganadería en los desiertos templados alteran las propiedades del suelo por el pisoteo del ganado, la aplicación de agroquímicos, la pérdida de la capa superficial del suelo y la remoción de la vegetación. Estas alteraciones pueden eliminar completamente a las biocostras o modificar su composición y cobertura, disminuyendo en 25-75% la entrada de N al suelo, así como sus formas totales y disponibles. Después de que la agricultura y la ganadería han dejado de ser practicadas, las biocostras pueden tardar en recuperarse entre 7 y 60 años. Sin embargo, la recuperación de sus funciones no ocurre de forma lineal o unidireccional, lo cual podría modificar su función en la dinámica del N (Huajie et al., 2009; Gómez et al., 2012; Zaady et al., 2013; Zhang et al., 2013).

Hasta ahora, los trabajos que han evaluado el impacto de la agricultura y la ganadería en la estructura de las biocostras y su efecto en la dinámica del nitrógeno se han enfocado en estimar cómo los cambios en la cobertura de los grupos taxonómicos de las cianobacterias, líquenes y briofitas afectan: (1) las formas totales y disponibles del N y (2) las tasas de transformación (amonificación y nitrificación) y retención del N (Evans & Belnap, 1999; Warren & Eldridge, 2003; Read et al., 2008; Huajie et al.,2009; Gómez et al., 2012; Zhao et al., 2010). Muy pocos trabajos han evaluado el cambio en la cobertura de los grupos funcionales de las biocostras y su efecto sobre la dinámica del N, a pesar de que los grupos funcionales son buenos indicadores y predictores de la función y el disturbio en los ecosistemas (Eldridge & Rosentreter 1999; Ponzetti & McCune, 2001; Lavorel & Garnier, 2002; Cornelissen et al., 2007). Algunos de estos trabajos fueron realizados en desiertos templados de USA y China, en donde los cambios en la entrada del N causados

por la ganadería estuvieron relacionados con la reducción de la cobertura de grupos fijadores de N (cianobacterias y cianolíquenes) y no fijadores (briofitas y clorolíquenes) (Evans & Belnap 1999; Huajie et al., 2009). Otro trabajo realizado en desiertos templados australianos mostró que la entrada y disponibilidad del N incrementaron en sitios con biocostras dominadas por grupos fijadores de N (cianobacterias con y sin heterocistos) (Williams & Eldridge, 2011).

El impacto de las actividades productivas en las biocostras y su efecto sobre la dinámica del nitrógeno en los últimos 20 años muestra que la mayoría de los trabajos: (1) solo han evaluado el efecto de la ganadería extensiva y la agricultura de riego, (2) el impacto de estas actividades en las biocostras solo ha considerado cambios en la composición taxonómica de las cianobacterias, líquenes y briofitas, (3) el efecto sobre la dinámica del nitrógeno solo ha considerado la entrada de N y las formas totales y disponibles, y (4) los trabajos han sido realizados principalmente en desiertos templados de EUA, España, China, Israel, Argentina y el sur de Australia (Roger & Lange, 1971; Anderson et al., 1982; Brotherson et al.,1983; Johansen y Clair; 1986; Marble y Harper 1989; Beymer y Klopatek, 1992; Hodgins y Rogers, 1997; Memmott et al., 1998; Kaltenecker et al.,1999; Ponzetti y Mc Cune, 2001; Muscha y Hild, 2006; Read et al., 2008; Read et al., 2011; Jiménez-Aguilar et al., 2009; Huajie et al., 2009; Zhao et al., 2010; Briggs y Morgan, 2012; Gómez et al., 2012; Dettweiler-Robinson et al., 2013; Zaady et al., 2013; Zhang et al., 2013; Concostrina-Zubiri et al., 2013).

Debido a esta situación, es necesario evaluar el impacto de las actividades productivas en los desiertos tropicales. En estos desiertos, a diferencia de los desiertos templados, la agricultura de temporal y la extracción de leña son las principales actividades humanas. Sin embargo, estas actividades son de subsistencia dados los escasos recursos

económicos de los grupos humanos que habitan estas regiones (Gerber et al., 2014). Además de lo anterior, es necesario evaluar el impacto de estas actividades no solo en la composición taxonómica, sino también en los grupos funcionales para entender la manera en que los cambios en la composición y estructura de las biocostras modifican el funcionamiento del ecosistema (Eldridge & Rosentreter 1999; Ponzetti & McCune, 2001; Lavorel & Garnier, 2002; Cornelissen et al., 2007). Finalmente, para entender el papel de las biocostras en la dinámica del N en el suelo en los desiertos tropicales es necesario evaluar no solo las formas totales y disponibles del N, sino también sus tasas de transformación y retención (Castillo-Monroy & Maestre, 2011).

En el desierto tropical del valle de Zapotitlán Salinas, Puebla, la agricultura de temporal y la extracción de leña son actividades de subsistencia que se realizan en las terrazas aluviales del río El Salado. Debido a estas actividades, en las terrazas aluviales existe un mosaico de sitios con diferentes tipos de cobertura vegetal como el campo de cultivo abandonado y el campo de cultivo abandonado con *Viguiera dentata*, los cuales son producto de la agricultura de temporal. Además existe el mezquital con dosel cerrado y el mezquital con dosel abierto, los cuales son producto de la extracción de leña. Sin embargo, no se ha evaluado el impacto de la agricultura de temporal y la extracción de leña en las propiedades del suelo y en la estructura de la vegetación. Además de lo anterior, las biocostras son un elemento dominante en el valle de Zapotitlán (Rivera-Aguilar et al., 2006; Rivera-Aguilar et al., 2009) que puede modificar el establecimiento de las plantas vasculares (Rivera-Aguilar et al., 2005, Godínez-Alvarez et al., 2011 y Sosa-Quintero, 2015) y la dinámica del carbono y nitrógeno en el suelo (Sandoval-Pérez et al., 2016). Sin embargo, no se ha evaluado el efecto de la agricultura de temporal y la extracción de leña

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sobre la estructura de las biocostras y su efecto sobre la dinámica del nitrógeno en las terrazas aluviales.

Considerando esta situación, en esta tesis doctoral realizada en un desierto tropical ubicado en el valle de Zapotitlan Salinas, Puebla, se plantearon las siguientes preguntas:

1) ¿Cuál es el manejo de la agricultura de temporal y la extracción de leña?

2) ¿Los campos de cultivo abandonados y los mezquitales tienen diferentes características de suelo y vegetación?

3) ¿Cuál es la estructura de las biocostras en los campos de cultivo abandonados y los mezquitales?

4) ¿Cómo es la dinámica del nitrógeno en el suelo asociado a las biocostras en los campos de cultivo y los mezquitales?

Para responder estas preguntas, los objetivos de este trabajo son:

1.2 Objetivo general

Determinar el efecto de la agricultura de temporal y la extracción de leña sobre la estructura de las biocostras y su efecto en la dinámica del nitrógeno.

1.3 Objetivos particulares

1) Evaluar el impacto de la agricultura de temporal y la extracción de leña sobre las características de la vegetación y las propiedades del suelo.

2) Evaluar el impacto de la agricultura de temporal y la extracción de leña sobre la composición y cobertura de las biocostras.

3) Analizar como los cambios en la composición y cobertura de las biocostras modifican la dinámica del nitrógeno.

1.4 Estructura de la tesis

Para cumplir los objetivos particulares, se realizaron tres trabajos de investigación que corresponden a los capítulos II-V de la presente tesis:

Capítulo II. Human activities in a tropical Mexican desert: Impact of rainfed agriculture and firewood extraction on vegetation and soil

En este trabajo se evaluó el impacto de la agricultura de temporal y la extracción de leña sobre la estructura de la vegetación y las propiedades del suelo. Para esto, se realizaron entrevistas a los dueños de los sitios de estudio para conocer la historia del manejo y se utilizaron indicadores ecológicos para examinar el posible impacto del manejo en la vegetación y el suelo.

Capítulo III. La agricultura de temporal y la extracción de leña modifican la riqueza de especies y abundancia de grupos taxonómicos y funcionales de las biocostras en un desierto tropical

En este trabajo se evaluó el impacto de la agricultura de temporal y la extracción de leña sobre la composición y estructura de las biocostras. Para esto se determinaron los organismos dominantes de las CBS y se calculó la riqueza específica. Además, se estimó la cobertura de la costra biológica, de los grupos taxonómicos (cianobacterias, líquenes y briofitas) y de los grupos funcionales (cianobacterias con heterocistos, cianobacterias sin heterocistos, cianolíquenes y clorolíquenes). Finalmente, se relacionó la presencia o ausencia de las especies y los grupos taxonómicos y funcionales con las características de suelo y vegetación de los campos de cultivo abandonados y los mezquitales.

Capítulo IV. Biocrusts modulate the impact of rainfed agriculture and firewood extraction on soil nitrogen dynamics in a tropical desert

En este trabajo se evaluó el impacto de la agricultura de temporal y la extracción de leña sobre las biocostras y su efecto en la dinámica del nitrógeno en el suelo. Para esto, se estimó la cobertura de las CBS, de los grupos taxonómicos (cianobacterias, líquenes y briofitas) y de los grupos funcionales relacionados con la dinámica del nitrógeno (cianobacterias con heterocistos, cianobacterias si heterocistos, cianolíquenes y clorolíquenes). Además, se cuantificaron las formas totales y disponibles de N, las tasas de transformación y el N en la biomasa microbiana. Por último, se relacionó la cobertura de las biocostras con los parámetros que definen la dinámica del N en el suelo.

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Capítulo 2

Human activities in a tropical Mexican desert: Impact of rainfed agriculture and

firewood extraction on vegetation and soil

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RESEARCH ARTICLE

WILEY

Human activities in a tropical Mexican desert: Impact of rainfed agriculture and firewood extraction on vegetation and soil

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Abstract

The impacts of human activities on temperate and subtropical deserts have been evaluated worldwide. However, data about tropical deserts are scarce. In this study, we evaluated the impacts of rainfed agriculture and firewood extraction on vegetation and soil of abandoned croplands (mesquite cropland and goldeneye cropland) and mesquite shrublands (open-canopy mesquite and closed-canopy mesquite) in a tropical Mexican desert. We interviewed peasants to understand their management practices and evaluated vegetation traits and soil properties of sites. We also examined the impacts of land management on vegetation and soil with structural equation modeling. Rainfed agriculture consisted of cultivating crops, fertilizing with manure, and introducing goats to croplands after harvest. Goldeneye cropland had higher canopy cover, vegetation structure, and litter cover than mesquite cropland. However, soil in both croplands was highly compacted with low infiltration rate, organic matter, and nutrient content. Firewood extraction only consisted of removing mesquite branches. Open-canopy mesquite had lower canopy and litter cover and higher biological soil crust cover than closed-canopy mesquite. The soil in both shrublands was less compacted with relatively high infiltration rate, organic matter, and nutrient content. Rainfed agriculture decreased soil nutrient content due to removal of native vegetation, plowing, and goat introduction to croplands. In contrast, firewood extraction maintained a relatively high soil nutrient content because branch removal enables the establishment of biological soil crusts, which increased the infiltration rate and nutrient availability. Thus, firewood extraction has a lower impact on the structure and function of fluvial terraces than rainfed agriculture in this tropical desert.

KEYWORDS
abandoned croplands, ecosystem structure and function, fluvial terraces, land management, mesquite shrubland, soil properties, vegetation traits

1 | INTRODUCTION

Human activities such as agriculture and firewood extraction negatively impact the structure and function of ecosystems (Chazdon, 2003; Chettri, Sharma, Deb, & Sundriyal, 2002; Vitousek, Mooney, Lubchenco, & Melillo, 1997). These activities decrease plant cover and therefore simplify vegetation structure (Bellemare, Motkzkin, & Foster, 2002; Hermy & Verheyen, 2007). Furthermore, they compact

soil and decrease the infiltration capacity of soil, thus increasing runoff. Such changes favor soil loss by erosion and decrease litter and nutrient contents of soil (Braimoh, 2006; Lesschen, Cammeraat, Kooijman, & van Wesemael, 2008; Ruecker, Schad, Alcubilla, & Ferrer, 1998; Zhou, Li, Chen, Zhang, & Li, 2011). The negative impacts of agriculture and firewood extraction on ecosystems can persist even after these activities are ceased, creating sites with particular vegetation and soil characteristics that differ from those

of the original ecosystems (Alvarez, Villagra, Villalba, Cony, & Alberto, 2011; Krause, Pugh, Bayer, Lindeskog, & Arneth, 2016; Suding, Gross, & Houseman, 2004).

The impact of agriculture on temperate deserts has been extensively evaluated in the United States and Australia (Cramer & Hobbs, 2007; Morris, Monaco, & Sheley, 2011; Standish, Cramer, Hobbs, & Kobryn, 2006). In these regions, agriculture reduces the richness and cover of plant species (Lesschen et al., 2008; Plieninger, Hui, Gaertner, & Huntsinger, 2014; Sato et al., 2016) as well as the humidity, organic matter content, and availability of nitrogen, carbon, and phosphorus in soil. However, studies on the impact of human activities such as rainfed agriculture and firewood extraction in tropical deserts are scarce because only five studies were found in the ecological literature of the last 28 years (Ayoub, 1998; Braimoh, 2006; Chidumayo, 2013; El Tahir, Ahmed, Ardö, Gaafar, & Salih, 2009; Mahiri & Howorth, 2001). Rainfed agriculture and firewood extraction include different management practices that can modify vegetation and soil characteristics and thus, alter the structure and function of tropical deserts. For example, rainfed agriculture includes the removal of native vegetation, which modifies plant species composition, decreases plant cover, and increases soil susceptibility to erosion. Moreover, it includes plowing and fertilizing that compact soil and modify the content and dynamics of soil nutrients (Compton & Boone, 2000; McLauchlan, 2006; Wani, Rockström, & Oweis, 2009; Zalidis, Stamatiadis, Takavakoglou, Eskridge, & Misopolinos, 2002). In addition, it includes a period in which croplands are not cultivated that intensifies soil erosion (Cramer & Hobbs, 2007; Plieninger et al., 2014). During this period, croplands can also be used to introduce small animals such as goats, which compact soil (Barbier, 2000; Wani et al., 2009). Firewood extraction includes the removal of secondary branches and understory, which decrease plant cover and increase soil susceptibility to erosion, causing the loss of soil fertility (Bensel, 2008; Rüger, Williams-Linera, Kissling, & Huth, 2008). Studies carried out in tropical African deserts have found that rainfed agriculture and firewood extraction alter vegetation and soil characteristics, increase soil loss, and reduce ecosystem productivity (Ayoub, 1998; Braimoh, 2006; Chidumayo, 2013; El Tahir et al., 2009; Mahiri & Howorth, 2001). Yet data on tropical American deserts are practically inexistent. The evaluation of the impact of human activities in these deserts is necessary because some deserts, including Mexican deserts, have high biological diversity and endemism (Trejo & Dirzo, 2002). In addition, these deserts are frequently inhabited by human groups with scarce economic resources that depend on rainfed agriculture and firewood extraction for their subsistence. Because of these circumstances and low rainfall levels, these ecosystems have low resilience to the impacts of human activities (Casas et al., 2001; Gerber, Nkonya, & von Braun, 2014; McAuliffe, Sundt, Valiente-Banuet, Casas, & Viveros, 2001). Therefore, evaluating the impacts of rainfed agriculture and firewood extraction in tropical American deserts will contribute to understanding how these activities modify the structure and function of these ecosystems.

The present study examines the Zapotitlán Salinas Valley, a tropical desert in central southern Mexico with high biological diversity and endemism (Dávila et al., 2002). In this desert, the peasants have practiced rainfed agriculture and firewood extraction in fluvial

terraces for many years. Rainfed agriculture is no longer currently practiced, but firewood extraction continues to the present date. These activities have apparently had negative effects on the vegetation and soil of fluvial terraces and have originated distinct types of vegetation cover. However, up until the present date, no relevant studies have been carried out in the region. The objective of the present study was to evaluate the impacts of rainfed agriculture and firewood extraction on the vegetation and soil of fluvial terraces. To fulfill this objective, we interviewed the peasants of different sites to understand their land management practices. In addition, we evaluated the vegetation traits and soil properties of sites with distinct plant cover. Finally, we examined the possible impacts of land management on vegetation traits and soil properties. We hypothesized that rainfed agriculture and firewood extraction would decrease the vegetation structure and would deteriorate the soil properties of fluvial terraces. Accordingly, we expected that the sites where these activities were practiced would have low plant and litter cover, wide basal and canopy gaps, and high bare soil cover. Furthermore, these sites would have compact soils with low infiltration capacity as well as low content of organic matter and nutrients.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was carried out in the Zapotitlán Salinas Valley located inside the Tehuacán-Cuicatlán Biosphere Reserve in Puebla, Mexico. The average annual temperature is 21 °C, and the annual average rainfall is 400 mm (López-Galindo et al., 2003). Field work was carried out in the fluvial terraces of the Salado River (18°19′N, 97°27′W; 1,300–1,400 m a. s. l.), which have soils of sandy loam, clay loam, and silty clay loam texture. The original plant community was mesquite (Prosopis laevigata) shrubland mixed with columnar cacti (Myrtillocactus geometrizans, Stenocereus stellatus, and Pachycereus hollianus; Valiente-Banuet et al., 2000). However, this community has been altered by rainfed agriculture and firewood extraction. Observations conducted in the region have shown that rainfed agriculture consists of removing the native vegetation for cultivation of traditional crops. It also includes complementary activities such as the introduction of goats to croplands when they are not cultivated. However, croplands are abandoned after several years because of their low productivity. Firewood extraction consists of removing the secondary branches of mesquite, although the understory can also be removed. Other activities such as charcoal production and collection of food and medicinal plants can also be carried out in the terraces. Rainfed agriculture and firewood extraction have originated four types of plant cover: (a) abandoned croplands containing P. laevigata (mesquite) and Parkinsonia praecox with a canopy cover of approximately 30% (mesquite cropland); (b) abandoned croplands containing Viguiera dentata (toothleaf goldeneye) with a cover of approximately 55% (goldeneye cropland); (c) open-canopy mesquite shrubland containing P. laevigata and M. geometrizans with a cover of approximately 30% (open-canopy mesquite); and (d) closed-canopy mesquite shrubland containing P. laevigata, M. geometrizans, P. hollianus, and Opuntia

decumbens with a cover of approximately 58% (closed-canopy mesquite). We selected three sites in each type of plant cover and determined the land management practices, vegetation traits, and soil properties. All sites were selected from the same fluvial terraces to control for geomorphological unit and soil origin and to therefore enable their comparison.

2.2 | Land management

To understand the land management practices in our sites, we performed 12 semistructured interviews with the peasants to obtain data on rainfed agriculture and firewood extraction. With respect to rainfed agriculture, data on cultivated plant species, type of crop and plowing, use of agrochemicals, and period of use were collected. Data on complementary activities conducted after harvest such as introduction of small animals to croplands were also collected. When this activity was performed by peasants, data collected were type of animals, number of animals, and length of time in the field. With respect to firewood extraction, the quantity of firewood extracted per visit and the number of visits per week were recorded. The interviews consisted of asking open-ended questions to the peasants to obtain data about the issues that interested us. The interviews lasted approximately 30–180 min and were conducted in the field or at peasant's home.

2.3 | Vegetation traits

To determine the vegetation traits of each site, we calculated indicators of vegetation structure and function based on (a) the line-point intercept method, (b) the vegetation structure method, and (c) the gap intercept method (Herrick, Van Zee, Havstad, Burkett, & Whitford, 2005a). In each site, we placed three 30-m-long measuring tapes over the ground surface. These tapes were each separated by 10 m and oriented toward the north. For the line-point intercept method, we placed a pole of 3 m in height at every meter along the tape to record the plant species, litter, biological soil crusts, rocks, and bare soil that intercepted the pole only once. With these data and the 30 sampling points per transect, we calculated the percentage of canopy cover, basal cover, litter cover, biological crust cover, rock cover, and bare soil cover. For the vegetation structure method, we placed a pole of 3 m in height divided into 30 segments of 10 cm at 5, 15, and 25 m along the tape to record the number of segments covered by vegetation. The segments were observed through a 140-cm sighting pole that was placed 5 m before and after the pole. With these data and the 30 segments per pole, we calculated the percentage of visual obstruction. Finally, for the gap intercept method, we recorded the beginning and end points of gaps between plant canopies and gaps between plant bases that were intersected by the tape. Gaps were classified in three categories depending on their length: 50–100, 100–200, and >200 cm. With the sum of the length per category and the total length of the transect, we calculated the percentage of gaps of 50–100, 100–200, and >200 cm between plant canopies and between plant bases (Herrick et al., 2005a).

2.4 | Soil properties

To determine the physical and chemical properties of the soil, we carried out field measurements and collected soil samples for laboratory analysis. In the field, temperature was measured with a 76-mm immersion Brannan thermometer. Infiltration was measured using a PVC pipe (11 cm in diameter, 15 cm in height) buried 3 cm in the ground to record the infiltration time of 250 ml of water (Herrick, Van Zee, Havstad, Burkett, & Whitford, 2005b). Compaction was measured with an impact penetrometer. Specifically, a mass of 2 kg was released at a height of 50 cm, and the number of blows necessary to introduce the penetrometer 5 cm in the soil were recorded (Herrick & Jones, 2002). We performed three measurements in open spaces and three under shrubs at each site.

Soil samples were collected from the first 10 cm of soil using a cylinder with a diameter of 7.5 cm. Samples were collected only from the first 10 cm because nutrient transformations occur at this depth (Crowther et al., 2016). We collected six samples in open spaces and six under shrubs at each site. The samples of each microenvironment were mixed to obtain a composite sample that was dried at 75 °C and sieved with 2-mm mesh. The samples were then analyzed in the Laboratorio de Fertilidad de Suelos, Colegio de Postgraduados, Montecillo, Mexico. The following soil properties were determined: texture (hydrometer method; Bouyoucos, 1962), bulk density (BD; cylinder method; USDA, 1999), humidity (gravimetric method), organic matter (OM; oxidation method; Walkley & Black, 1934), cation exchange capacity (CEC; $BaCl_2$ method), pH (1:2 relationship of soil: deionized H_2O), electric conductivity (EC; 1:5 relationship of soil: deionized H_2O), total carbon (TC; automated C-analyzer [SHIMADZU 5005AW]), total nitrogen (TN; acid digestion in H_2SO_4 concentrated using a Technicon Autoanalyzer IIW), potassium (K; atomic emission), phosphorus (P; Olsen method), and available nitrogen (NO_3^- and NH_4^+; 2 M KCl extraction; Robertson et al., 1999). We performed three replicates for each soil property.

2.5 | Statistical analysis

Vegetation traits were compared among sites using a one-way analysis of variance and multiple Tukey comparisons. The percentages were normalized by angular transformation. Soil properties were compared among sites with a nested analysis of variance in which microenvironments were nested within sites and paired Student t tests. The proportions were normalized by the Box-Cox transformation. The analyses were carried out in the JMP statistical software, version 10.

To evaluate whether a relationship existed between vegetation traits and soil properties, we performed Spearman correlations. In addition, we carried out a nonmetric multidimensional scaling (NMDS) ordination of management, vegetation traits, and soil properties. In this ordination, we used the Bray–Curtis dissimilarity index considering a matrix of 12 sites (i.e., three replicates of mesquite cropland, goldeneye cropland, open-canopy mesquite, and closed-canopy mesquite) by two management variables (i.e., rainfed agriculture and firewood extraction), seven vegetation variables (i.e., visual obstruction, canopy cover, bare soil cover, biological crust cover, litter cover,

gaps of 50–100 cm in the canopy, and basal gaps of 100–200 cm), and 10 soil variables (i.e., infiltration rate, pH, EC, BD, OM, TC, TN, C:N ratio, P, and NH_4^+). The NMDS was complemented with a similarity percentages (SIMPER) analysis to quantify differences among sites and variables that explained differences. The correlations were carried out in the JMP statistical software, version 10. The NMDS and SIMPER were performed in R 3.0.2.

To evaluate the possible impacts of land management on vegetation traits and soil properties, we used structural equation modeling. In general, these models consist of (a) model specification based on the preexisting knowledge, (b) parameter estimation through maximum likelihood procedures, and (c) model testing with statistical tests such as chi-square test and root mean square error of approximation (Grace, 2006). The models were fitted to the data in an exploratory way to evaluate whether management is related with negative effects on vegetation structure, and vegetation structure is related with negative effects on soil properties based on the ecological literature (Álvarez-Yépiz, Martínez-Yrízar, Búrquez, & Lindquist, 2008; Singh, Singh, & Ghoshal, 2017). The variables included in the models had the largest number of correlations such as canopy cover, bare soil, visual obstruction, OM, infiltration rate, C:N ratio, P, total C and N, and NH_4^+. We assumed that land management (i.e., rainfed agriculture and firewood extraction) is negatively related with canopy cover. Thus, canopy cover was used as a surrogate for land management, and it was included in the models as 1–canopy cover. Bare soil and visual obstruction were the variables used for vegetation structure whereas OM, infiltration rate, C:N ratio, P, total C and N, and NH_4^+ were the variables used for soil properties. All variables in percentage were normalized to improve the linearity in the relationships between the variables in the models. In addition to the models, we calculated the standardized total effects (i.e., direct effects plus indirect effects) of the variables included in the models. The structural equation models were calculated in the AMOS software, version 23.0 (IBM, SPSS, New York, USA).

3 | RESULTS

3.1 | Land management

Mesquite cropland and goldeneye cropland were cleared of vegetation 68 years ago for the annual cultivation of maize, beans, alfalfa, tomatoes, tomatillos, and chili peppers. Soils were only fertilized with manure, and no agrochemicals were used. Harvest was only destined for household subsistence and local sale. After harvest, around 200 goats were introduced to the croplands for approximately 2 months per year. However, these croplands were abandoned 13 years ago because of their low productivity (Table S1).

Open-canopy mesquite and closed-canopy mesquite were never cleared for agriculture or used for goats. However, open-canopy mesquite is used to extract 40 kg of firewood per week and to gather fruits from the cactus *Hylocereus undatus*. Closed-canopy mesquite is not used for any productive activity except in one site

where the peasants produce charcoal and extract 20 kg of firewood per week (Table S1).

3.2 | Vegetation traits

Visual obstruction, canopy cover, and litter cover in mesquite cropland and open-canopy mesquite were similar but lower than in goldeneye cropland and closed-canopy mesquite (Table 1). In addition, both mesquite cropland and open-canopy mesquite had a high proportion of gaps between plant canopies of 50–100 and >200 cm. Meanwhile, bare soil cover in mesquite cropland was higher than in the rest of the sites. Biological crust cover was highest in open-canopy mesquite followed by goldeneye cropland, mesquite cropland, and closed-canopy mesquite. The remaining vegetation traits did not significantly differ among sites (Table S2).

3.3 | Soil properties

Infiltration rate, EC, CEC, OM, total C and N, C:N ratio, P, and NH_4^+ were similar in mesquite cropland and goldeneye cropland but lower than in open-canopy mesquite and closed-canopy mesquite. The differences between the latter two sites were not significant (Table S3). Mesquite cropland and goldeneye cropland also had greater BD than open-canopy mesquite and closed-canopy mesquite. The pH was highest in mesquite cropland and decreased in goldeneye cropland, open-canopy mesquite, and closed-canopy mesquite (Table 2).

Soil properties in open spaces and under shrubs were similar in mesquite cropland and goldeneye cropland but differed in open-canopy mesquite and closed-canopy mesquite. In the latter sites, infiltration rate, OM, total C and N, and NH_4^+ were lower in open spaces than under shrubs. In contrast, BD, compaction, and NO_3^- were higher in open spaces than under shrubs. The percentages of sand, silt, and clay as well as soil temperature and humidity did not differ between open spaces and under shrubs (Table S3).

3.4 | Relationship between vegetation traits and soil properties

Canopy cover, visual obstruction, and litter cover were positively correlated with total C and N. In contrast, bare soil cover was negatively correlated with litter cover, CEC, total C and N, and P. Infiltration rate and OM were positively correlated with total C and N, P, C:N ratio, and NH_4^+, whereas BD was negatively correlated with these variables (Table S4).

The sites formed four groups according to land management, vegetation traits, and soil properties (Figure 1). The two croplands, mesquite cropland and goldeneye cropland, were 34% dissimilar and differed from both open-canopy mesquite (33–39%) and closed-canopy mesquite (68–71%). Open-canopy mesquite and closed-canopy mesquite were 57% dissimilar. Infiltration rate explained 29–89% of the differences among sites followed by visual obstruction (70–71%), percentages of gaps in the canopy >200 cm (45–68%) and litter cover (60%; Table S5).

TABLE 1 Vegetation traits (mean ± standard error) in sites with different vegetation cover

Vegetation traits	Sites			
	Mesquite cropland	Goldeneye cropland	Open-canopy mesquite	Closed-canopy mesquite
Visual obstruction (%)	25.58 ± 8.66 b	53.17 ± 5.02 ab	40.78 ± 11.48 b	83.70 ± 4.45 a
Canopy cover (%)	29.33 ± 5.74 b	54.88 ± 2.56 a	30.22 ± 7.77 b	58.22 ± 0.80 a
Bare soil cover (%)	14.88 ± 4.5 a	2.88 ± 1.55 ab	0.88 ± 0.44 b	0.22 ± 0.22 b
Basal cover (%)	1.77 ± 1.45	0.66 ± 0.38	1.55 ± 0.88	3.11 ± 0.58
Biological crust cover (%)	42.93 ± 12.53 ab	54.78 ± 11.40 ab	81.08 ± 5.59 a	24.04 ± 1.47 b
Rock cover (%)	2.93 ± 1.32	–	2.21 ± 2.21	–
Litter cover (%)	47.03 ± 9.82 b	87.03 ± 4.36 a	60.74 ± 9.16 b	93.33 ± 6.46 a
Canopy gaps (%)				
50–100 cm	3.38 ± 1.16 a	0.72 ± 0.44 ab	1.51 ± 0.33 ab	0.22 ± 0.22 b
100–200 cm	3.89 ± 2.36	2.09 ± 1.06	1.39 ± 0.80	0.46 ± 0.46
>200 cm	48.16 ± 15.22 a	6.03 ± 6.03 bc	47.20 ± 15.15 ab	–
Basal gaps (%)				
50–100 cm	3.17 ± 1.64	1.34 ± 0.36	1.47 ± 0.98	1.61 ± 0.77
100–200 cm	7.57 ± 2.56 a	–	1.58 ± 1.58 ab	3.87 ± 2.12 ab
>200 cm	87.05 ± 3.50	97.13 ± 1.09	84.02 ± 12.27	91.80 ± 3.32

Note. The traits with "–" have zero values. For each trait, letters indicate significant differences among sites ($P < 0.05$).

3.5 | Impact of land management on vegetation traits and soil properties

Land management, defined as 1–canopy cover, was negatively related with visual obstruction, which is both directly and indirectly related with bare soil cover. Visual obstruction was positively related with OM, and OM was positively related with infiltration rate (χ^2 = 8.51, df = 5, P = 0.13; root mean square error of approximation [RMSEA] = 0.25, P = 0.14, 90% CI [0.00, 0.53]), total C (χ^2 = 9.77, df = 5, P = 0.08; RMSEA = 0.29, P = 0.09, 90% CI [0.00, 0.57]), total N (χ^2 = 5.51, df = 3, P = 0.13; RMSEA = 0.28, P = 0.15, 90% CI [0.00, 0.64]), P (χ^2 = 6.96, df = 5, P = 0.22; RMSEA = 0.19, P = 0.24, 90% CI [0.00, 0.49]), C:N ratio (χ^2 = 5.62, df = 5, P = 3.44; RMSEA = 0.11, P = 0.36, 90% CI [0.00, 0.44]), and NH_4^+ (χ^2 = 5.14, df = 4, P = 0.23; RMSEA = 0.16, P = 0.29, 90% CI [0.00, 0.51]). However, land management was only directly related with visual obstruction in total N. Management was also directly and positively related with NH_4^+ (Figure 2). Land management had a negative total effect on infiltration rate (−0.508), total C (−0.612), total N (−0.595), P (−0.572), and C:N ratio (−0.559) and a positive total effect on NH_4^+ (0.042). Visual obstruction and OM had positive effects on all variables (>0.500; Figure 3).

4 | DISCUSSION

Rainfed agriculture and firewood extraction decreased the vegetation structure and deteriorated the soil properties of fluvial terraces in agreement with our hypothesis. These changes originated sites with particular vegetation and soil characteristics. Rainfed agriculture in the studied fluvial terraces consisted of removing the native vegetation to establish croplands, plowing with yoke or tractor, cultivating different types of crops, fertilizing with manure, and introducing goats to croplands for 2 months, after harvest. These management practices had contrasting effects on vegetation traits and negative effects on

soil properties. Goldeneye cropland had higher canopy cover, visual obstruction, and litter cover as well as lower bare soil cover and proportions of gaps between plant canopies than mesquite cropland. These differences may be due to *V. dentata* increased the vegetation structure of goldeneye cropland. *V. dentata* is a native, ruderal species capable of colonizing disturbed sites because its seeds are dispersed by wind and form seed banks in the soil. Furthermore, it grows in bare areas with high solar radiation and temperature (Justo, 2015; Sarquis, Coria, & González-Rodríguez, 2010; Schilling, 2006; Scott & Morgan, 2012; Vibrans, 2009). In contrast to vegetation traits, goldeneye cropland and mesquite cropland had highly compacted soils with low infiltration rates and low content of OM and nutrients. These soil properties were similar in open spaces and under shrubs. The similarities between soil properties in goldeneye cropland and mesquite cropland suggest that *V. dentata* does not modify compaction, infiltration, and nutrient content in goldeneye cropland. Other studies carried out in tropical deserts have also found that rainfed agriculture decreased vegetation cover as well as infiltration, OM content, and nutrients in soil (Ayoub, 1998; Chidumayo, 2013; El Tahir et al., 2009; Ogle, Breidt, & Paustian, 2005).

Firewood extraction in the studied fluvial terraces consisted of removing the secondary branches of mesquite, one to two times per week. This management practice had contrasting effects on vegetation traits and positive effects on soil properties. Open-canopy mesquite had lower canopy cover, visual obstruction, and litter cover as well as higher proportions of gaps between plant canopies and biological crust cover than closed-canopy mesquite. These differences may be due to the greater extraction of firewood in open-canopy mesquite than in closed-canopy mesquite. In open-canopy mesquite, peasants extract around 40 kg of firewood per week; in closed-canopy mesquite, peasants only extract 20 kg per week. The higher firewood extraction in open-canopy mesquite produce wide gaps between plant canopies and create areas without vegetation that are occupied by biological soil crusts. In fact, the cover of biological soil crust was

TABLE 2 Soil's physical and chemical properties (mean ± standard error) in open space and under shrubs in sites with different vegetation covers

Soil properties	Mesquite cropland Open space	Under shrubs	Goldeneye cropland Open space	Under shrubs	Open-canopy mesquite Open space	Under shrubs	Closed-canopy mesquite Open space	Under shrubs
Sand (%)	33.76 ± 2.50	34.21 ± 3.15	40.88 ± 4.37	46.21 ± 5.74	40.21 ± 7.31	37.99 ± 7.22	37.99 ± 3.96	35.54 ± 4.61
Silt (%)	47.45 ± 1.92	46.34 ± 2.96	46.22 ± 1.97	41.33 ± 1.92	42.00 ± 3.67	43.33 ± 1.33	46.88 ± 1.73	44.22 ± 3.08
Clay (%)	18.77 ± 4.42	19.44 ± 5.96	12.89 ± 2.70	12.45 ± 4.00	17.78 ± 10.00	18.67 ± 8.00	15.12 ± 3.15	20.23 ± 3.85
BD (kg/m^3)	1.37 ± 0.06	1.29 ± 0.08	1.26 ± 0.01	1.25 ± 0.03	1.25 ± 0.67	0.95 ± 0.07	1.11 ± 0.41	0.66 ± 0.07
Compaction (Jcm^{-1})	13.98 ± 0.69	10.84 ± 0.84	10.64 ± 3.03	13.17 ± 2.88	13.39 ± 3.26	7.90 ± 0.28	11.95 ± 1.90	5.88 ± 0.98
Soil moisture (%)	6.43 ± 0.53	12.98 ± 3.76	9.12 ± 1.81	13.01 ± 2.37	10.48 ± 1.43	12.07 ± 1.43	9.58 ± 1.87	18.02 ± 3.97
Infiltration rate (mm/hr)	57.95 ± 12.21	123.21 ± 75.69	30.22 ± 1.41	47.61 ± 10.5	22.09 ± 5.32	358 ± 108.65	89.93 ± 23.94	2,059.85 ± 845.60
Temperature (°C)	31.94 ± 4.47	26.88 ± 4.14	32.66 ± 4.81	29.11 ± 3.60	33.55 ± 3.05	26.94 ± 1.20	32.33 ± 5.85	24.72 ± 1.81
OM (%)	2.01 ± 0.34	2.63 ± 0.57	2.26 ± 0.29	2.36 ± 0.09	2.38 ± 0.65	5.19 ± 0.81	7.15 ± 1.32	11.16 ± 0.90
CEC (meq/100 g)	13.30 ± 1.17	13.68 ± 1.46	15.23 ± 0.70	20.12 ± 1.54	16.54 ± 3.54	18.80 ± 3.44	20.27 ± 2.73	25.49 ± 1.69
pH	8.32 ± 0.04	8.21 ± 0.04	8.17 ± 0.07	8.40 ± 0.05	8.42 ± 0.11	8.26 ± 0.05	8.01 ± 0.02	7.92 ± 0.14
EC (Ds/m)	0.42 ± 0.08	0.36 ± 0.06	0.54 ± 0.11	0.33 ± 0.01	0.35 ± 0.15	0.34 ± 0.04	1.00 ± 0.35	0.68 ± 0.24
Total C (mg/g)	7.42 ± 1.51	9.70 ± 2.00	10.21 ± 1.09	11.14 ± 1.09	9.72 ± 3.23	25.99 ± 5.12	36.24 ± 7.05	62.95 ± 7.44
Total N (mg/g)	1.10 ± 0.14	1.33 ± 0.24	1.50 ± 0.13	1.86 ± 0.53	1.31 ± 0.28	2.63 ± 0.33	2.81 ± 0.47	5.76 ± 0.53
C:N	6.55 ± 0.21	7.22 ± 0.35	6.77 ± 0.12	6.53 ± 1.04	6.97 ± 1.77	9.69 ± 0.65	13.36 ± 3.32	10.86 ± 0.67
K (cmol/kg)	0.89 ± 0.12	1.33 ± 0.31	1.41 ± 0.10	1.54 ± 0.25	1.12 ± 0.32	1.45 ± 0.29	1.20 ± 0.21	1.80 ± 0.19
P (mg/g)	0.01 ± 0.00	0.009 ± 0.00	0.01 ± 0.00	0.007 ± 0.00	0.01 ± 0.00	0.024 ± 0.00	0.027 ± 0.00	0.073 ± 0.02
NH$_4^+$ (mg/g)	0.01 ± 0.00	0.01 ± 0.00	0.01 ± 0.00	0.01 ± 0.00	0.01 ± 0.00	0.021 ± 0.00	0.015 ± 0.00	0.022 ± 0.00
NO$_3^-$ (mg/g)	0.046 ± 0.00	0.026 ± 0.00	0.10 ± 0.05	0.01 ± 0.00	0.03 ± 0.01	0.017 ± 0.00	0.073 ± 0.02	0.026 ± 0.00

Note. BD: bulk density; OM: organic matter; CEC: cation exchange capacity; EC: electrical conductivity.
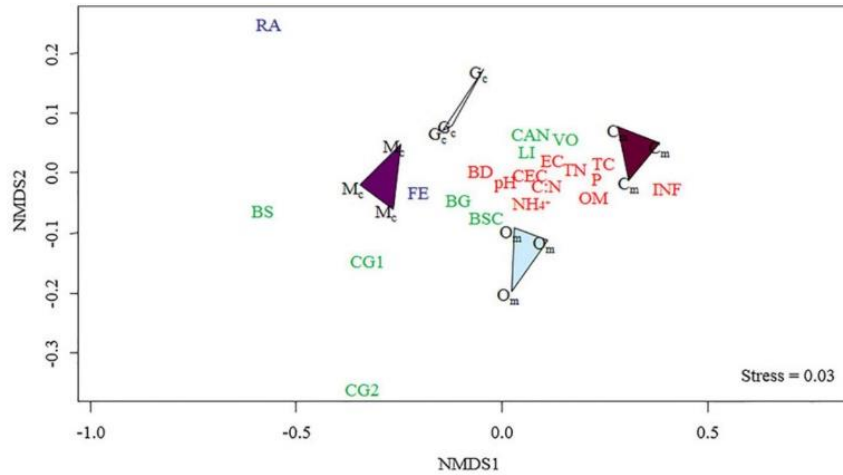
FIGURE 1 Nonmetrical multidimensional scaling (NMDS) ordination of land management (blue letters), vegetation traits (green letters), and soil properties (red letters). BG: basal gaps 100–200 cm; BS: bare soil cover; BSC: biological soil crust cover; BD: bulk density; CAN: canopy cover; CEC: cation exchange capacity; CG1: canopy gaps 50–100 cm; CG2: canopy gaps >200 cm; C_m: closed-canopy mesquite; EC: electrical conductivity; FE: firewood extraction; G_c: goldeneye cropland; INF: infiltration rate; LI: litter cover; M_c: mesquite cropland; O_m: open-canopy mesquite; OM: organic matter; P: phosphorus; RA: rainfed agriculture; TC: total C; TN: total N; VO: visual obstruction [Colour figure can be viewed at wileyonlinelibrary. com]
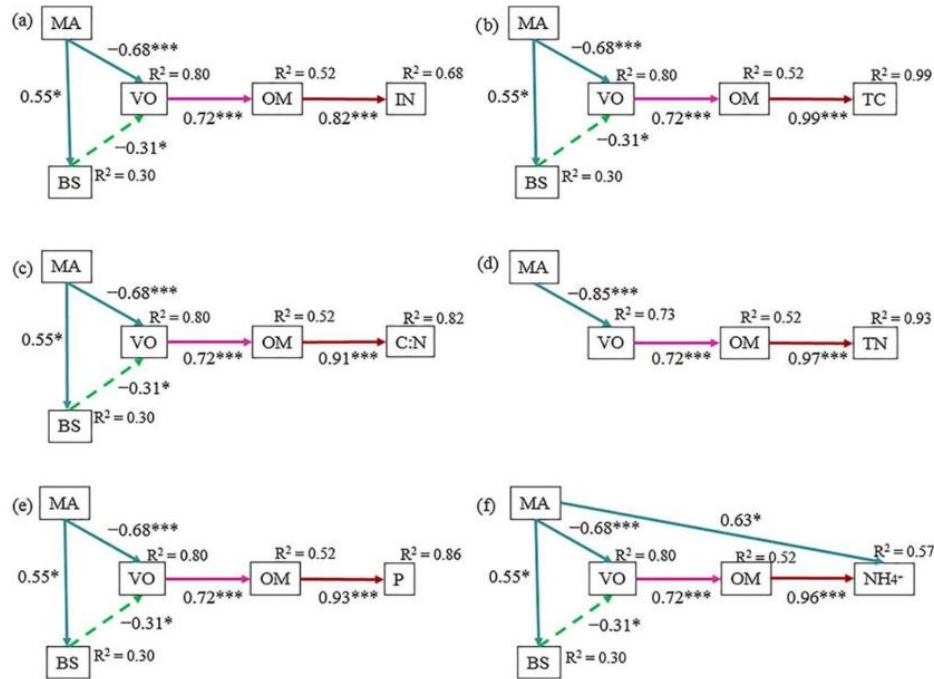

FIGURE 2 Effects of land management (MA; blue arrows), visual obstruction (VO; purple arrows), bare soil (BS; green arrows), and organic matter (OM; red arrows) on (a) infiltration rate (IN), (b) total carbon (TC), (c) C:N, (d) total nitrogen (TN), (e) phosphorus (P), and (f) NH_4^+. The continuous and discontinuous arrows indicate positive and negative relationships, respectively. *$P < 0.05$, **$P < 0.01$, and ***$P < 0.001$ [Colour figure can be viewed at wileyonlinelibrary.com]

significantly higher in open-canopy mesquite than in any other site. In contrast to vegetation traits, open-canopy mesquite and closed-canopy mesquite had slightly compacted soils with relatively high infiltration rates and relatively high content of OM and nutrients. These soil properties were better under shrubs than in open spaces. The similarities between soil properties in open-canopy mesquite and closed-canopy mesquite suggest that biological soil crusts improve the infiltration rate and nutrient content of soil in open-canopy mesquite. Biological soil crusts are fundamental for the function of deserts because they can increase the infiltration rate and favor the retention and availability of soil nutrients (Belnap & Lange, 2001). Our results were similar to those reported for tropical African

deserts where firewood extraction reduce vegetation cover and OM content and nutrients in soil (Ayoub, 1998; Braimoh, 2006).

The contrasting impacts of rainfed agriculture and firewood extraction on the vegetation structure and soil properties drive different effects on soil nutrient concentration. Thus, rainfed agriculture removes the native vegetation, which decreases vegetation structure and increases bare soil cover. These changes in vegetation decrease the litter cover and infiltration rate of soil. The infiltration rate of soil is also decreased by the soil compaction caused by plowing and goat introduction to croplands. The low litter cover and infiltration rate in turn may decrease the OM flux to the soil and limit the OM transformations, leading to decreases in the content of total nitrogen, total
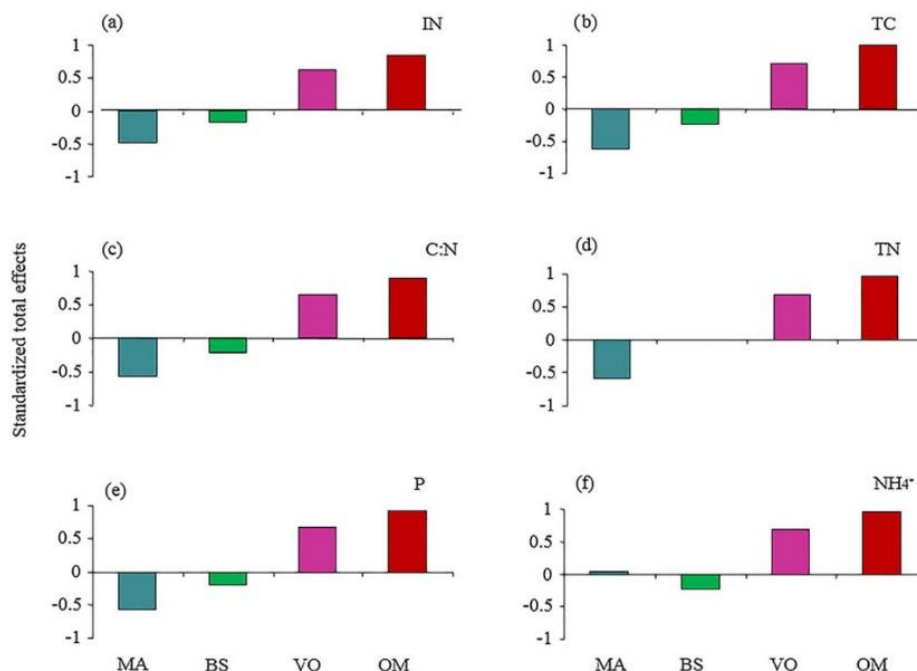
FIGURE 3 Standardized total effects (direct plus indirect effects) of land management (MA), visual obstruction (VO), bare soil (BS), and organic matter (OM) on (a) infiltration rate (IN), (b) total carbon (TC), (c) C:N, (d) total nitrogen (TN), (e) phosphorus (P), and (f) NH_4^+ [Colour figure can be viewed at wileyonlinelibrary.com]

carbon, C:N ratio, and phosphorus in soil. Although the NH_4^+ content of soil may increase due to the fertilization with manure. The low carbon and nitrogen content may decrease the microbial activity and mineralization (Griffin, He, & Honeycutt, 2005). The negative effects on soil nutrient concentration because of rainfed agriculture occur in both open spaces and under shrubs. In contrast to rainfed agriculture, firewood extraction only removes the secondary branches of one dominant plant species. This branch removal decreases vegetation structure and increases bare soil cover, thus negatively affecting soil nutrient concentration as previously described for rainfed agriculture. However, the increase in bare soil cover enables the establishment and development of biological soil crusts that ameliorate these negative effects on soil nutrients. In our study site, biological soil crusts increased the content of organic and labile C, total nitrogen, NH_4^+, NO_3^- in soil, the microbial biomass, and N mineralization (Sandoval Pérez et al., 2016). The amelioration of negative effects on soil nutrient concentration by biological soil crusts is greater in terraces with high firewood extraction than in terraces with low firewood extraction as well as in open spaces than under shrubs. The soil nutrient concentration, microbial activity, and mineralization in terraces with rainfed agriculture and firewood extraction differ from those in terraces without human activities. In these last terraces, plants form fertility islands in which soil has higher concentrations of organic matter, C and N as well as higher microbial activity and N mineralization than soil outside them (Perroni-Ventura, Montaña, & García-Oliva, 2006, 2010).

5 | CONCLUSIONS

Rainfed agriculture and firewood extraction decreased vegetation structure and deteriorated soil properties, originating sites with particular vegetation and soil characteristics. However, rainfed agriculture decreased the soil nutrient content due to management practices such as removal of the native vegetation, plowing, and goat introduction to croplands. In contrast, firewood extraction maintained a relatively high soil nutrient content because removal of secondary branches enables the establishment of biological soil crusts, which increased the infiltration rate and nutrient availability. Thus, firewood extraction has a lower impact on the structure and function of fluvial terraces than rainfed agriculture in the Zapotitlán Salinas valley.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Capítulo 3

La agricultura de temporal y la extracción de leña modifican la riqueza de especies y abundancia de grupos taxonómicos y funcionales de las biocostras en un desierto tropical

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La agricultura de temporal y la extracción de leña modifican riqueza de especies y abundancia de grupos taxonómicos y funcionales de las biocostras en un desierto tropical

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Resumen

Las biocostras son comunidades de briofitas, líquenes y cianobacterias distribuidas en zonas alpinas, polares, áridas y semiáridas. En las zonas áridas templadas, la agricultura de riego y la ganadería modifican la estructura de las biocostras. Sin embargo, el impacto de este tipo de actividades en las biocostras de las zonas áridas tropicales no ha sido evaluado. El valle de Zapotitlan Salinas es un desierto tropical con alta abundancia de biocostras, en donde las principales actividades son la agricultura de temporal y la extracción de leña. En este trabajo se evaluó la riqueza y cobertura de las biocostras en campos de cultivo abandonados y sitios de extracción de leña. Se colectaron 720 muestras de biocostras para determinar la riqueza específica y la cobertura de biocostras, grupos taxonómicos (briofitas, líquenes y cianobacterias) y grupos funcionales (cianobacterias con y sin heterocito, clorolíquenes y cianolíquenes). Las biocostras en los campos de cultivo tuvieron 14-18 especies, 50-70% de cobertura y estuvieron dominadas por cianobacterias con heterocistos. Las biocostras en los sitios con extracción de leña tuvieron 23-29 especies, 90% de cobertura y estuvieron dominadas por cianolíquenes. En conclusión, la agricultura de temporal y la extracción de leña modifican diferencialmente la cobertura de las biocostras, la agricultura de temporal redujo la cobertura total de biocostras a diferencia de la extracción de leña que favoreció la cobertura total de biocostras.

Palabras clave: Briofitas, líquenes, cianobacterias, actividades humanas de subsistencia

Introducción

Las biocostras son comunidades compuestas principalmente por cianobacterias, líquenes y briofitas que se desarrollan sobre la superficie o en los primeros centímetros de profundidad del suelo. En las zonas áridas y semiáridas, estas comunidades ocupan los espacios entre la vegetación, en donde alcanzan hasta 70% de cobertura (Belnap & Lange, 2003). Aunque también pueden ocupar los especios debajo de los arbustos (Maestre et al., 2001; Gutiérrez Gutiérrez et al., 2017). Las biocostras en estas regiones participan en diversas funciones ecosistémicas como la estabilidad del suelo, la infiltración, la retención y disponibilidad de nutrientes, así como la modulación de la dinámica de nutrientes como el nitrógeno (Jafari et al., 2004; Barger et al., 2006; Belnap, 2006; Mager & Thomas, 2011; Fischer et al., 2010; Kidron et al., 2012; Sancho et al., 2016).

En las zonas áridas y semiáridas templadas, la participación de las biocostras en las funciones ecosistémicas puede ser alterada por actividades productivas como la ganadería y la agricultura de riego, debido a que modifican la composición de los grupos taxonómicos y funcionales. Así, por ejemplo, las modificaciones del suelo y la vegetación causadas por la ganadería reducen la cobertura de las algas, líquenes y musgos, aunque no afectan la riqueza específica (Roger & Lange, 1971; Anderson et al., 1982; Brotherson et al., 1983; Johansen & St Clair, 1986; Eldridge, 1998; Memmott et al., 1998; Zhang et al., 2013; Beymer & Klopatek, 1992; Hodgins & Rogers, 1997; Jiménez Aguilar et al., 2009; Concostrina Zubiri et al., 2014). Estas modificaciones también reducen la cobertura de los líquenes fijadores de nitrógeno (Ponzetti & Mc Cune, 2001; Huajie et al., 2009). Por su parte, las modificaciones del suelo y la vegetación causadas por la agricultura de riego eliminan completamente las biocostras (Zaady et al., 2016). Las biocostras solo pueden establecerse en los campos de cultivo después de 10-60 años de abandono (Zhao et al., 2010; Brigss y Morgan, 2012). Las cianobacterias son el primer

grupo en establecerse seguido por las briofitas y los líquenes (Brigss & Morgan, 2012). Las

biocostras pueden recuperar la composición de sus grupos taxonómicos; sin embargo, es posible

que la composición de los grupos funcionales no se recupere completamente (Read et al., 2011;

Gómez et al., 2012; Dettweiler-Robinson et al., 2013).

Las evaluaciones del impacto de la ganadería y la agricultura de riego en las biocostras

han considerado principalmente los cambios en la riqueza y abundancia de los grupos

taxonómicos y han sido realizadas en zonas áridas y semiáridas templadas. Debido a la

parcialidad de estos trabajos, es necesario realizar evaluaciones que consideren el impacto de las

actividades humanas sobre los grupos funcionales de las biocostras para entender su relevancia en

el funcionamiento de los ecosistemas áridos. Además, es necesario realizar evaluaciones en las

zonas áridas y semiáridas tropicales debido a que las biocostras y las actividades humanas en

estas zonas difieren de las zonas áridas templadas (Castillo-Monroy & Maestre, 2011; Gerber et

al., 2014; Rivera-Aguilar et al., 2009; Castillo Monroy et al., 2016).

El valle de Zapotitlan Salinas es una zona semiárida tropical en el centro de México, en

donde las biocostras tienen alta cobertura superficial y su composición taxonómica difiere de las

biocostras de las zonas áridas templadas de EUA (Rivera-Aguilar et al., 2006). Las biocostras

modifican el establecimiento de las plantas vasculares (Rivera-Aguilar et al., 2005; Godínez-

Alvarez et al., 2011; Sosa-Quintero, 2015), la infiltración del agua en el suelo (Barrera-Zubiaga

& Godínez-Alvarez, 2018) y la dinámica del nitrógeno y carbono (Sandoval Pérez et al., 2016).

Por otra parte, las principales actividades humanas en este valle son la agricultura de temporal y

la extracción de leña. Debido a estas actividades, actualmente existe un mosaico de sitios con

diferentes tipos de cobertura vegetal entre ellos campos de cultivo abandonados y mezquitales.

Los campos de cultivo tienen pobres condiciones de vegetación y suelo en comparación con los

mezquitales (Sosa-Quintero y Godínez-Alvarez, 2019). Sin embargo, se desconoce si las

diferencias en las condiciones de vegetación y suelo entre los sitios tienen algún efecto en las biocostras.

El propósito de este estudio fue evaluar el impacto de la agricultura de temporal y la extracción de leña en las biocostras, los grupos taxonómicos y los grupos funcionales. Para esto, las especies que conforman las biocostras fueron determinadas para estimar la riqueza específica, la cobertura total de la biocostra, la cobertura de los grupos taxonómicos y la cobertura de los grupos funcionales. Además, las especies, la cobertura de las biocostras y la cobertura de ambos grupos fueron relacionadas con el suelo y la vegetación de la agricultura y la extracción de leña. Debido a que los campos de cultivo abandonados tienen pobres condiciones de vegetación y suelo en comparación con los mezquitales, esperamos que las biocostras de los campos de cultivo tengan menor riqueza específica, cobertura total, cobertura de grupos taxonómicos y cobertura de grupos funcionales que las biocostras de los mezquitales. Los resultados de este estudio incrementarán el conocimiento de la estructura y funcionamiento de las biocostras en las zonas áridas y semiáridas tropicales.

Materiales y métodos

Área de estudio

El estudio fue realizado en las terrazas aluviales del valle de Zapotitlán Salinas (18° 19´ N, 97° 27´ W, 1300-1400 m s. n. m.), Puebla, que está ubicado dentro de la Reserva de la Biósfera del Valle de Tehuacán-Cuicatlán en el centro de México. La temperatura media anual es de 21°C y la precipitación media anual es de 400 mm (López-Galindo et al., 2003)**.** Específicamente, el estudio fue realizado en las terrazas aluviales del río El Salado. La vegetación original es el mezquital (*Prosopis laevigata* (Humb. et Bonpl. ex Willd) M.C. Johnston) mezclado con cactáceas columnares (*Myrtillocactus* geometrizans (Mart. ex Pfeiff.)

Console, *Stenocereus stellatus* (Pfeiff.) Riccob. y *Pachycereus hollianus* (F.A.C Weber) Buxb.;

Valiente-Banuet et al., 2000). Sin embargo, esta vegetación ha sido transformada a distintos tipos

de cobertura vegetal debido a la agricultura de temporal y la extracción de leña. La agricultura de

temporal consiste en un policultivo fertilizado con estiércol y la introducción de 200 cabezas de

ganado caprino durante 2 meses por año. Este manejo fue practicado por 60 años, pero

actualmente tiene 15 años de abandono. La agricultura de temporal originó dos tipos de cobertura

vegetal: (1) campos de cultivo abandonados y (2) campos de cultivo abandonados con *Viguiera*

dentata (Cav.) Spreng. La extracción de leña solamente consiste en la remoción de las ramas

secundarias de *Prosospis laevigata* y las plantas del sotobosque. Este manejo ha sido practicado

por más de 75 años y continúa en la actualidad. Los dueños de los sitios extraen 20-40 kg de leña

por mes (Tabla 1; Sosa-Quintero & Godínez Alvarez, 2019). Las diferencias en la extracción de

leña han originado otros dos tipos de cobertura vegetal: (3) mezquital con dosel abierto y (4)

mezquital con dosel cerrado. Ambas actividades, la agricultura de temporal y la extracción de

leña, han impactado negativamente las características de la vegetación y las propiedades del suelo

(Sosa-Quintero & Godínez-Alvarez, 2019). Los campos de cultivo abandonados tienen

vegetación con baja cobertura y el suelo tiene bajo contenido de materia orgánica, infiltración y

contenido de nutrientes en comparación con la vegetación y el suelo de los mezquitales. Además,

los suelos de los campos de cultivo abandonados tienen alta densidad aparente y pH en

comparación con los mezquitales (Tabla 1; Sosa-Quintero & Godínez-Alvarez, 2019).

Para cada uno de los cuatro tipos de cobertura vegetal, seleccionamos tres sitios en la

misma terraza aluvial para controlar el efecto del tipo de suelo (limo-arcillosos) y la unidad

geomorfológica, para un total de 12 sitios.

Riqueza específica

Para determinar la riqueza específica, se colectaron 30 muestras de biocostras en espacios abiertos (15) y debajo de arbustos (15) por sitio. Las muestras fueron colectadas en cajas de Petri de 7.5 cm de diámetro y transportadas al laboratorio para su identificación. El muestreo fue realizado en la temporada de secas y lluvia de 2016, para un total de 720 muestras. En el laboratorio, realizamos observaciones anatómicas y morfológicas de las cianobacterias, líquenes y briofitas con un microscopio estereoscópico Zeiss SteREO Discovery V8. Las cianobacterias fueron identificadas con las claves de Komarek (2003) y Komarek y Anagnostidis (2005) en el Laboratorio de Ficología, Facultad de Ciencias, Universidad Nacional Autónoma de México (UNAM). Los líquenes fueron identificados con las claves de Nash et al. (2002), McCune & Rosentreter (2007), y Brodo et al. (2001) en el Laboratorio de Líquenes del Instituto de Biología, UNAM. Las briofitas fueron identificadas con las claves de Delgadillo & Cárdenas (1990) y Sharp et al. (1994) en el Laboratorio de Briofitas del Instituto de Biología, UNAM.

Cobertura de biocostras, grupos taxonómicos y funcionales

Las especies de las biocostras fueron clasificadas en grupos taxonómicos y grupos funcionales. Los grupos taxonómicos fueron definidos con base en los tres tipos principales de organismos que conforman las biocostras: cianobacterias, líquenes y briofitas. Los grupos funcionales fueron definidos con base en la presencia de heterocistos y fotobionte: cianobacterias con heterocistos, cianobacterias sin heterocistos, cianolíquenes y clorolíquenes.

Para estimar la cobertura se utilizó una cuadrícula de 5×5 cm, dividida en 100 cuadros de 0.5 x 0.5 cm (Maestre et al., 2005), para contar el número de cuadros ocupados por las biocostras en cada caja de Petri. Con el número de cuadros ocupados por la biocostra, se calculó la cobertura total de las biocostras como el número de cuadros ocupados por todas las especies de la biocostra,

la cobertura de los grupos taxonómicos como el número de cuadros ocupados por cianobacterias, líquenes y briofitas, y la cobertura de los grupos funcionales como el número de cuadros ocupados por cianobacterias con heterocistos, cianobacterias sin heterocistos, cianolíquenes y clorolíquenes.

Relación entre suelo, vegetación y cobertura de biocostras

Para relacionar la vegetación y el suelo de los campos de cultivo abandonados y los mezquitales con la cobertura de las biocostras y la cobertura de los grupos taxonómicos y funcionales se usaron los datos reportados por Sosa-Quintero & Godínez-Alvarez (2019). Estos autores evaluaron el impacto de la agricultura de temporal y la extracción de leña en la vegetación y el suelo de los mismos sitios usados en este estudio, para lo que midieron 13 indicadores de la estructura y funcionamiento de la vegetación y 19 propiedades del suelo en campos de cultivo abandonados y mezquitales. De estos indicadores y propiedades, se consideraron aquellos que mostraron diferencias significativas entre los campos de cultivo abandonados y los mezquitales para analizar la relación entre la vegetación y el suelo, y la cobertura de las biocostras (Tabla 1).

Análisis estadísticos

La riqueza específica de las biocostras (número acumulado de especies por sitio) fue comparada entre los sitios con curvas de rarefacción usando el programa estadístico EstimateS. La cobertura de las biocostras, la cobertura de los grupos taxonómicos y funcionales (porcentaje) fueron comparadas entre los sitios con un ANOVA de una vía y pruebas de comparación de medias de Tukey usando el programa estadístico JMP versión 10. La cobertura fue normalizada con una transformación angular. La relación entre la vegetación y el suelo, y la cobertura de las

biocostras fue analizada con escalamiento multidimensional sin métrica (NMDS) en el programa

vegan en R versión 3.5.1. Para el escalamiento multidimensional construimos cuatro matrices: (1)

matriz de vegetación-suelo, la cual consistió en 24 muestras (4 tipos de cobertura vegetal $\times$ 3

sitios $\times$ 2 temporadas) y 16 variables de vegetación (obstrucción visual, cobertura de dosel,

cobertura de suelo desnudo, cobertura de hojarasca, claros en el dosel de 50-100 cm y >200 cm)

y suelo (tasa de infiltración, pH, densidad aparente, materia orgánica, C total, N total, fósforo,

C:N, NH^+_4 y NO^-_3), (2) matriz de especies, 24 muestras y 27 abundancias relativas (número de

muestras en donde cada especie fue encontrada dividido por el número total de muestras) de las

especies que conforman las biocostras, (3) matriz de grupos taxonómicos, 24 muestras y 3

abundancias relativas (suma de las abundancias relativas de las especies pertenecientes a cada

grupo taxonómico) de cianobacterias, líquenes y briofitas, y (4) matriz de grupos funcionales

consistente en 24 muestras y 4 abundancias relativas (suma de las abundancias relativas de las

especies pertenecientes a cada grupo funcional) de cianobacterias con heterocistos, cianobacterias

sin heterocistos, cianolíquenes y clorolíquenes. La matriz 1 fue relacionada con cada una de las

matrices 2-4 y el escalamiento fue realizado con el índice de disimilitud de Bray-Curtis. Además

del escalamiento multidimensional, se hizo un análisis de porcentajes de similitud (SIMPER)

para identificar las especies, los grupos taxonómicos y funcionales que explican las diferencias

entre los sitios. Este análisis fue hecho con el programa vegan en R 3.5.1.

Resultados

Riqueza específica

      Las biocostras de los campos de cultivo abandonados y los mezquitales estuvieron

conformadas por un total de 37 especies (Tabla 2). El campo de cultivo abandonado (14 spp.)

tuvo el menor número de especies, seguido por el campo de cultivo abandonado con *Viguiera*

dentata (18), el mezquital con dosel abierto (23) y el mezquital con dosel cerrado (29). Sin

embargo, estas diferencias no fueron significativas (Fig. 1). Con respecto a los grupos

taxonómicos, las cianobacterias tuvieron un número de especies similar en los dos campos de

cultivo abandonados y los dos mezquitales (8-9). Los líquenes tuvieron menor número de

especies en ambos campos de cultivo abandonados (4-6) que en los mezquitales abierto y cerrado

(9-11). Las briofitas también tuvieron menor número de especies en los campos de cultivo

abandonados (2-4) que en los mezquitales abierto y cerrado (5-8). Con respecto a los grupos

funcionales, las cianobacterias sin heterocistos y las cianobacterias con heterocistos tuvieron un

número similar de especies en los dos campos de cultivo abandonados (2-6) y los dos

mezquitales (2-7). Los cianolíquenes y clorolíquenes tuvieron menor número de especies en

ambos campos de cultivo abandonados (2-4) que en los mezquitales (3-8).

Cobertura de biocostras, grupos taxonómicos y funcionales

La cobertura de las biocostras (F = 12.0, g. l. = 3, 20, p < 0.000) fue menor en los campos

de cultivo abandonados (50-70%) que en los mezquitales (80-90%; Fig. 2a). Con respecto a los

grupos taxonómicos, la cobertura de las cianobacterias (F = 4.1, g. l. = 3, 20, p = 0.02) fue mayor

en los dos campos de cultivo abandonados (35-37%) que en el mezquital con dosel abierto (24-

32%). La cobertura en el mezquital con dosel cerrado no difirió de los campos de cultivo y el

mezquital con dosel abierto (Fig. 2b). La cobertura de líquenes (F = 11.5, g. l. = 3, 20 p < 0.000)

fue alta en el mezquital con dosel abierto (50%), intermedia en el mezquital con dosel cerrado

(35%) y el campo de cultivo con *Viguiera dentata* (23%), y baja en el campo de cultivo (21%;

Fig. 2c). La cobertura de briofitas (F = 34.2, g. l. =3, 20, p < 0.000) fue menor en los dos tipos de

campos de cultivo abandonado (0–6%) que en los dos mezquitales (24-28%; Fig. 2d). Con

respecto a la cobertura de los grupos funcionales, la cobertura de cianobacterias con heterocistos

(F = 3.8, g. l. = 3, 20, p = 0.03) fue mayor en ambos campos de cultivo abandonados (27-42%) que en el mezquital con dosel abierto (20%). La cobertura en el mezquital con dosel cerrado (43%) no difirió de los otros sitios (Fig. 2e). La cobertura de los cianolíquenes (F = 28.2, g. l. = 3, 20, p < 0.000) fue menor en los dos campos de cultivo abandonados (0-8%) que en los dos mezquitales (7-35%; Fig. 2g). Las coberturas de cianobacterias sin heterocistos (F = 0.6, g. l. = 3, 20, p = 0.61) (Fig. 2f) y clorolíquenes (F = 1.9, g. l. = 3, 20, p = 0.16) (Fig. 2h) fueron similares en todos los sitios.

Relación entre suelo, vegetación y cobertura de biocostras

Las especies de las biocostras, los grupos taxonómicos y los grupos funcionales formaron cuatro grupos que corresponden a campo de cultivo abandonado, campo de cultivo abandonado con *Viguiera dentata*, mezquital con dosel abierto y mezquital con dosel cerrado. Los dos campos de cultivo abandonado estuvieron relacionados con el pH y la densidad aparente del suelo, así como con la cobertura de suelo desnudo. Los dos mezquitales estuvieron relacionados con la tasa de infiltración, el porcentaje de materia orgánica, el nitrógeno total, carbono total, fósforo, C:N y NH_4^+ (Fig. 3a-c).

El análisis de similitud de las especies mostró que los campos de cultivo abandonados tuvieron 32% de disimilitud y fueron diferentes del mezquital con dosel abierto (44-50%) y del mezquital con dosel cerrado (43-50%). Los mezquitales difirieron 26% (Tabla 3). Las diferencias entre los campos de cultivo y los mezquitales fueron explicadas por la cianobacteria sin heterocistos *Placynthiella* sp. (11%), los cianolíquenes *Enchylium coccophorum* (10%) y *Polychidium dendriscum* (10%), el clorolíquen *Placidium lacinatum* (10%) y la briofita *Pseudocrossidium replicatum* (11%). El análisis de similitud de los grupos taxonómicos mostró que los campos de cultivo abandonados tuvieron 14% de disimilitud y fueron diferentes del

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mezquital con dosel abierto (28-32%) y del mezquital con dosel cerrado (29-35%). Los

mezquitales difirieron 13%. Las diferencias entre los campos de cultivo y los mezquitales fueron

explicadas por los líquenes (30-58%) y las briofitas (33-44%). Finalmente, el análisis de similitud

de los grupos funcionales mostró que los campos de cultivo abandonados tuvieron 17% de

disimilitud y fueron diferentes del mezquital con dosel abierto (22-25%) y del mezquital con

dosel cerrado (18-25%). Los mezquitales difirieron 15%. Las diferencias entre los campos de

cultivo y los mezquitales fueron explicadas por los cianolíquenes (36-52%) y las cianobacterias

con heterocistos (18-32%).

Discusión

La agricultura de temporal y la extracción de leña no modificaron la riqueza específica de

las biocostras, pero si modificaron la cobertura de las biocostras y la cobertura de los grupos

taxonómicos y funcionales. Estos resultados apoyan parcialmente la hipótesis de este estudio. De

manera similar, otros trabajos han reportado que la ganadería y la agricultura de riego solo

disminuyen la cobertura de las biocostras en desiertos templados (Zaady et al., 2016). Sin

embargo, algunos trabajos han reportado que la ganadería disminuye no solo la cobertura de los

grupos taxonómicos sino también la riqueza específica (Concostrina-Zubiri et al., 2014).

En la agricultura de temporal, las biocostras tuvieron 50-70% de cobertura y estuvieron

dominadas por cianobacterias, específicamente cianobacterias con heterocistos. Las especies de

cianobacterias fueron *Scytonema hialinum*, *Nostoc* sp., *Microseira* sp. y *Microcoleus vaginatus*.

Las cianobacterias son dominantes en los campos de cultivo abandonado porque son capaces de

establecerse en las condiciones de vegetación y suelo de estos sitios, mientras que los líquenes y

briofitas no pueden hacerlo. Las cianobacterias toleran altas temperaturas y baja humedad

(Belnap, 2006), por lo que pueden establecerse en los campos de cultivo abandonado con alta cobertura de suelo desnudo. La presencia de las cianobacterias sugiere que los campos de cultivo abandonados están en las etapas tempranas de la sucesión. Esta idea es apoyada por la presencia de *Nostoc* sp. y *Scytonema hialinum.* Estas cianobacterias ocurren en etapas tempranas de la sucesión (Yeager et al., 2007, 2012), debido a que pueden habitar suelos pobres en nitrógeno (Dodds et al., 1995; Belnap & Eldridge, 2003). Por otra parte, la presencia de la cianobacteria *Microcoleus vaginatus* sugiere que los campos de cultivo abandonados han comenzado a recuperarse debido a que esta especie es un indicador de la recuperación de los sitios impactados por actividades humanas (Belnap & Eldridge, 2003; Büdel et al., 2009; Kuske et al., 2012). Estos resultados concuerdan con lo reportado para otros sitios con actividades intensivas como la agricultura y la ganadería en desiertos templados, en los que el establecimiento de las cianobacterias ocurre después de que las actividades han sido abandonadas (Mager & Thomas, 2011, Dojani et al., 2014). Por su parte, los líquenes y las briofitas tuvieron baja cobertura en los campos de cultivo abandonados a causa de que estos sitios tienen suelos con alta densidad aparente y pH, así como bajo contenido de materia orgánica y nutrientes. Bowker et al. (2005) y Rivera-Aguilar et al. (2009) sugieren que el establecimiento de los líquenes y musgos disminuye en suelos con poco espacio poroso y baja infiltración. Además, el pH del suelo también puede disminuir el establecimiento de algunos géneros de líquenes como *Psora* (Eldridge & Ferris, 1999). En nuestro estudio, los líquenes de este género estuvieron ausentes de los campos de cultivo abandonados que tuvieron suelos con pH 8. Con respecto a la materia orgánica y los nutrientes, el bajo contenido de algunos nutrientes como el nitrógeno, carbono y fósforo disminuye el establecimiento de los líquenes y las briofitas en desiertos templados de Norteamérica (Bowker et al., 2005; Bowker et al., 2006). En los sitios de estudio, los líquenes y las briofitas tuvieron la menor cobertura en los campos de cultivo abandonados que tenían bajo

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contenido de materia orgánica y nutrientes. Por otra parte, el establecimiento de vegetación diferente a la original reduce la cobertura de líquenes y briofitas en desiertos templados (Kaltenecker et al., 1999; Belnap,2006). En este sentido, el establecimiento de *Viguiera dentata* en los campos de cultivo abandonados podría reducir la cobertura de líquenes y briofitas. Por último, la alta cobertura de las cianobacterias, en particular de las cianobacterias con heterocistos, en comparación con los líquenes sugiere que este grupo de organismos realizan el principal aporte de nitrógeno al suelo de los campos de cultivo abandonados. Las cianobacterias con heterocistos en las etapas tempranas de la sucesión de las biocostras pueden fijar N (Pepe-Ranney et al., 2016). Es necesario medir la dinámica del nitrógeno del suelo en estos sitios para confirmar estas ideas.

En la extracción de leña, las biocostras tuvieron 80-90% de cobertura y estuvieron dominadas por líquenes, específicamente cianolíquenes, y briofitas. Las especies de líquenes fueron *Enchylium coccophorum, Heppia solorinoides, Peltulla patellata, P. euploca, P. richardsii, Polychidium dendriscum* y *Psora crenata*. Las especies de briofitas fueron *Aloina hamulus, Brachymenium exile, Bryocrythrophyllum* sp., *Bryum argenteum, Diacranaceae, Didymodon rigidulus* var. *gracilis, Pseudocrossidium replicatum* y *P. crinitum*. La alta cobertura de los líquenes y las briofitas en los mezquitales podría deberse a que estos sitios tuvieron alta tasa de infiltración, alto contenido de materia orgánica y nutrientes en el suelo. Otros autores han sugerido que las biocostras bien desarrolladas y dominadas por líquenes y briofitas están ampliamente distribuidas en sitios con mayor contenido de nutrientes y materia orgánica (Lange et al., 1997; García-Pausas et al., 2004; Belnap, 2006). Las condiciones favorables de infiltración, materias orgánicas y nutrientes son propicias para el establecimiento de cianolíquenes del género *Enchylium,* los cuales participan en el ciclo del N (Evans & Belnap., 1999; Belnap et al., 2006). En desiertos templados, estos cianolíquenes vierten los nitratos

derivados de su metabolismo al suelo, los cuales están disponibles para la comunidad vegetal, las biocostras y otros microorganismos asociados (Weber et al., 2016). Además de *Enchylium*, el líquen *Psora* crenata también estuvo presente en los sitios de extracción de leña, aunque solo en los mezquitales con dosel abierto. Los líquenes de este género han sido registrados comúnmente en sitios impactados por la ganadería en desiertos templados, en el mediterráneo y en campos de cultivo abandonados de Australia (Eldridge & Ferris et al., 1999; Concostrina-Zubiri et al., 2018). La presencia de *Psora crenata* en los mezquitales con dosel abierto sugiere que estos sitios están más alterados que los mezquitales cerrados. Además de las condiciones de infiltración, materia orgánica y nutrientes del suelo, la existencia de áreas desprovistas de vegetación, sobretodo en el mezquital abierto, también favoreció el establecimineto de los líquenes. Los líquenes y las briofitas están adaptados a condiciones extremas de radiación solar (Weber et al., 2016). Así por ejemplo, la presencia de algunas especies de *Peltula* en el mezquital abierto podría deberse a que tienen una capa epinecreal que refleja y absorbe la radiación (Belnap, 2002). Por último, la alta cobertura de los líquenes, en particular de los cianolíquenes, y las briofitas en comparación con las cianobacterias sugiere que estos grupos de organismos realizan el principal aporte de nitrógeno al suelo de los mezquitales. Sin embargo, es necesario medir la dinámica del nitrógeno en estos sitios para confirmar estas ideas.

En conclusión, los resultados de este estudio indican que la agricultura de temporal y la extracción de leña modifican diferencialmente la cobertura de las biocostras, grupos taxonómicos y grupos funcionales. En la agricultura de temporal, las costras tienen baja cobertura y están dominadas por cianobacterias con heterocistos. En la extracción de leña, las costras tienen alta cobertura total y están dominadas por cianolíquenes y briofitas. El estudio a nivel de grupos taxonómicos es una aproximación de su participación en el funcionamiento del ecosistema. Sin embargo fueron las especies clasificadas en grupos funcionales, las cuales podrían ser los

mejores indicadores y predictores del disturbio y los cambios en el funcionamiento del

ecosistema (Eldridge & Rosentreter 1999; Ponzetti & McCune, 2001; Lavorel & Garnier, 2002;

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Tabla 1. Características de manejo, vegetación y suelo (media ± error estándar) en los sitios con agricultura de temporal (MC = campo de cultivo abandonado con mesquite, Gc = campo de cultivo abandonado con *Viguiera dentata*) y extracción de leña (Om = mezquital con dosel abierto, Cm = mezquital con dosel cerrado) en las terrazas aluviales del río El Salado en el Valle de Zapotitlan Salinas, Puebla. C = producción de carbón, F = producción de frutos de cactáceas. Para cada característica, las letras indican diferencias significativas entre los sitios.

Características	Sitios			
	Mc	Gc	Om	Cm
Manejo				
Tipo de manejo	Agricultura de temporal	Agricultura de temporal	Extracción de leña	Extracción de leña
Tipo de arado	Tractor y yunta	Tractor y yunta	-	-
Animales/sitio	200	200	-	-
Extracción de leña/mes	-	-	40 kg	20 kg
Otras actividades	-	-	C, F	C
Vegetación				
Obstrucción visual (%)	25.58 ± 8.66 b	53.17 ± 5.02 ab	40.78 ± 11.48 b	83.70 ± 4.45 a
Cobertura foliar (%)	29.33 ± 5.74 b	54.88 ± 2.56 a	30.22 ± 7.77 b	58.22 ± 0.80 a
Cobertura suelo desnudo (%)	14.88 ± 4.5 a	2.88 ± 1.55 ab	0.88 ± 0.44 b	0.22 ± 0.22 b
Cobertura hojarasca (%)	47.03 ± 9.82 b	87.03 ± 4.36 a	60.74 ± 9.16 b	93.33 ± 6.46 a
Claros en dosel (%):				
50–100 cm	3.38 ± 1.16 a	0.72 ± 0.44 ab	1.51 ± 0.33 ab	0.22 ± 0.22 b
> 200 cm	48.16 ± 15.22 a	6.03 ± 6.03 bc	47.20 ± 15.15 ab	-
Suelo				
Densidad aparente (kg/m^3)	1.33 ± 0.05a	1.25 ± 0.01a	1.10 ± 0.08 ab	0.89 ± 0.10b
Tasa infiltración (mm/hr)	135.87 ± 55.89	58.38 ± 9.23	285. 07 ± 134.23	1599.30 ± 875.54
Materia orgánica (%)	2.32 ± 0.32b	2.31 ± 0.13b	3.79 ± 0.78b	9.16 ± 1.14a
pH	8.26 ± 0.003a	8.28 ± 0.06a	8.34 ± 0.06a	7.96 ± 0.07b
C total (mg/g)	8.57 ± 1.23b	10.68 ± 0.72b	17.85 ± 4.53b	49.59 ± 7.52a
N total (mg/g)	1.21 ± 0.13b	1.68 ± 0.25b	1.97 ± 0.35b	4.29 ± 0.73a
C:N	6.89 ± 0.31b	6.65 ± 0.47b	8.33 ± 0.81b	12.11 ± 1.60a
P Olsen (mg/g)	0.01 ± 0.00b	0.01 ± 0.00b	0.01 ± 0.00b	0.05 ± 0.01a
NH_4^+ (mg/g)	0.01 ± 0.00	0.01 ± 0.00	0.01 ± 0.00	0.01 ± 0.00
NO_3^- (mg/g)	0.03 ± 0.00	0.05 ± 0.03	0.02 ± 0.00	0.04 ± 0.01

Tabla 2. Listado de especies de cianobacterias, líquenes y briofitas en los sitios con agricultura de temporal (MC = campo de cultivo abandonado con mesquite, Gc = campo de cultivo abandonado con *Viguiera dentata*) y extracción de leña (Om = mezquital con dosel abierto, Cm = mezquital con dosel cerrado) en las terrazas aluviales del río El Salado en el Valle de Zapotitlan Salinas, Puebla. Para cada especie, los grupos funcionales son: cianobacterias con heterocistos (H), cianobacterias sin heterocistos (WH), cianolíquenes (C) y clorolíquenes (CL).

Especie	Sitio				Grupo funcional
	Mc	Gc	Om	Cm	
Cianobacterias					
Aphanocapsa sp.	X	X	X		WH
Aphanothece sp.		X			WH
Asterocapsa sp.	X	X	X	X	WH
Chrococcidiopsis sp.	X	X	X	X	WH
Chroococcus minutus (Kützing) Nageli				X	WH
Gleocapsa sp.	X				WH
Hormathonema sp.		X			WH
Lyngbya sp.					WH
Microcoleus vaginatus Gomont ex Gomont	X	X	X	X	WH
Microseira sp.	X		X		WH
Nostoc sp.	X	X	X	X	H
Phormidium sp.			X	X	WH
Schizothrix sp.			X	X	WH
Scytonema hialinum N.L.Gardner	X	X	X	X	H
Líquenes					
Enchylium coccophorum (Tuck.) Otálora, P. M. Jørg. & Wedin.	X	X	X	X	C
Endocarpon loscosii Mnll. Arg.	X	X	X	X	CL
Heppia solorinoides (Nyl.) Nyl			X	X	C
Peltula patellata (Bagl.) Swinscow & Krog			X	X	C
Peltula euploca (Ach.) Poelt				X	C
Peltula sp.		X	X	X	C
Peltula richardsii (Herre) Wetmore	X	X	X	X	C
Placidium lacinulatum (Ach.) Breuss			X	X	CL
Placynthiella cf *uliginosa* (Schrader) Coppins & P. James	X	X		X	CL
Polychidium dendiscrum (Nyl.) Henssen		X	X	X	C
Psora crenata (Taylor) Reinke			X		CL
Endocarpon pusillum Hedwig				X	CL
Briofitas					
Aloina hamulus (C. Muell.) Broth	X		X	X	-
Brachymenium exile (Dosz et Molk.) Bosch et Lac				X	-
Bryoerythrophyllum sp.				X	-

Bryum argenteum Hedw.		X	X	X	-
Diacranaceae		X			-
Didymodon rigidulus var.gracilis (Hook. Grev.) Zand		X		X	-
Fissidens geehebii				X	-
Fissidens sp.				X	-
Pseudocrossidium crinitum (Schultz) R. H. Zander	X		X	X	-
Pseudocrossidium replicatum (Tayl.) Zand		X	X	X	-
cf *Riccia* sp.			X	X	-

Tabla 3. Disimilitud (%) de las especies, grupos taxonómicos y grupos funcionales entre los sitios con agricultura de temporal (MC = campo de cultivo abandonado con mesquite, Gc = campo de cultivo abandonado con *Viguiera dentata*) y extracción de leña (Om = mezquital con dosel abierto, Cm = mezquital con dosel cerrado). H = cianobacterias con heterocistos, WH = cianobacterias sin heterocistos.

Contraste de sitios	Disimilitud		
	Grupo taxonómico	**Grupo funcional**	**Especie**
Mc *vs.* Gc	14	17	32
	Líquenes 45	Cianobacterias H 44	*Nostoc* sp. 13
	Cianobacterias 32	Cianolíquenes 24	*Enchylium coccophorum* 12
		Cianobacterias WH 17	*Microcoleus vaginatus* 12
			Placynthiella sp. 9
			Endocarpon loscosii 9
Mc *vs.* Om	28	22	44
	Líquenes 52	Cianolíquenes 43	*Placidium lacinatum* 10
	Briofitas 38	Cianobacterias H 24	*Polichydium dendriscum* 8
		Clorolíquenes 20	*Aloina hamulus* 8
			Peltulla patellata 6
			Peltula sp. 6
			Pseudocrossidim replicatum 7
			E. coccophorum 6
Mc *vs.* Cm	29	18	43
	Briofitas 44	Cianolíquenes 36	*P. replicatum* 11
	Líquenes 30	Cianobacterias WH 29	*E. coccophorum* 6
		Cianobacterias H 22	*M. vaginatus* 6
			A. hamulus 6
			Heppia solorinoides 6
			P. lacinatum 6
			Schizotrix sp. 5
			P. patellata 5
Gc *vs.* Om	32	25	50
	Líquenes 58	Cianolíquenes 52	*P. dendriscum* 10
	Briofitas 29	Cianobacterias H 18	*P. lacinatum* 8
			Peltula sp. 8
			E. coccophorum 8
			Peltula patellata 7
			A. hamulus 7
			Placynthiella sp. 11
Gc *vs.* Cm	35	25	50
	Líquenes 35	Cianolíquenes 40	*E. coccophorum* 10
	Briofitas 33	Cianobacterias H 32	*P. replicatum* 7
			Nostoc sp. 7
			Placynthyella sp. 7
			M. vaginatus 6

|			*Peltula* sp. 6
			H. solorinoides 5
			P. lacinatum 5
Om *vs.* Cm	13	15	26
	Cianobacterias 42	Cianobacterias H 39	*Nostoc* sp. 8
	Líquenes 34	Cianobacterias WH 24	*M. vaginatus* 8
		Clorolíquenes 19	*E. loscosii* 7
			P. dendriscum 6
			Schizotrix sp. 6
			P. lacinatum 6
			P. replicatum 6
			Peltula sp. 5

Pies de figura

Figura 1. Riqueza específica de cianobacterias, líquenes y briofitas (± 95% intervalos de confianza) en sitios con agricultura de temporal (MC = campo de cultivo abandonado con mesquite, Gc = campo de cultivo abandonado con *Viguiera dentata*) y extracción de leña (Om = mezquital con dosel abierto, Cm = mezquital con dosel cerrado) en las terrazas aluviales del río El Salado en el Valle de Zapotitlan Salinas, Puebla.

Figura 2. Cobertura (media ± error estándar) de biocostra (a), cianobacterias (b), líquenes (c), briofitas (d), cianobacterias con heterocistos (e), cianobacterias sin heterocistos (f), cianolíquenes (g) y clorolíquenes (h). Las letras indican diferencias significativas entre los sitios.

Figura 3. Análisis multidimensional no métrico (NMDS) de especies (a), grupos taxonómicos (b) y grupos funcionales (c), y su relación con características de la vegetación y propiedades del suelo. *Chrococcidiopsis* sp. (Ch.sp), *Microcoleus vaginatus* (Mi.va), *Microseira* sp. (Mi.sp), *Nostoc* sp. (No.sp), *Schizothrix sp*. (Sch.sp), *Scytonema hialinum* (Sc.hi), *Enchylium coccophorum* (En.co), *Endocarpon loscossi* (En.lo), *Heppia* solorinoides (He.so), *Peltulla patellata* (Pe.pa), *Peltulla euploca* (Pe.eu), *Peltula* sp. (Pe.sp), *Peltula richardsii* (Pe.ri), *Placidium lacinatum* (Pl.la), *Placynthiella* sp. (Pl.sp), *Polychidium dendriscum* (Po.de), *Psora crenata* (Pso.cr), *Endocarpon pusillum* (En.pu), *Aloina hamulus* (Al.ha), *Brachymenium exile* (Br.ex), *Bryocrythrophyllum sp*. (Br.sp), *Bryum argenteum* (Br.ar), D*idymodon rigidulus* var. *gracilis* (Di.ri), *Pseudocrossidium crinitum* (Pse.cr), densidad aparente (deap), suelo desnudo (sude), amonio (amo), C:N, carbono total (Ct), materia orgánica (MOS), nitrógeno total (Nt), fósforo (PO_4), infiltración (in).

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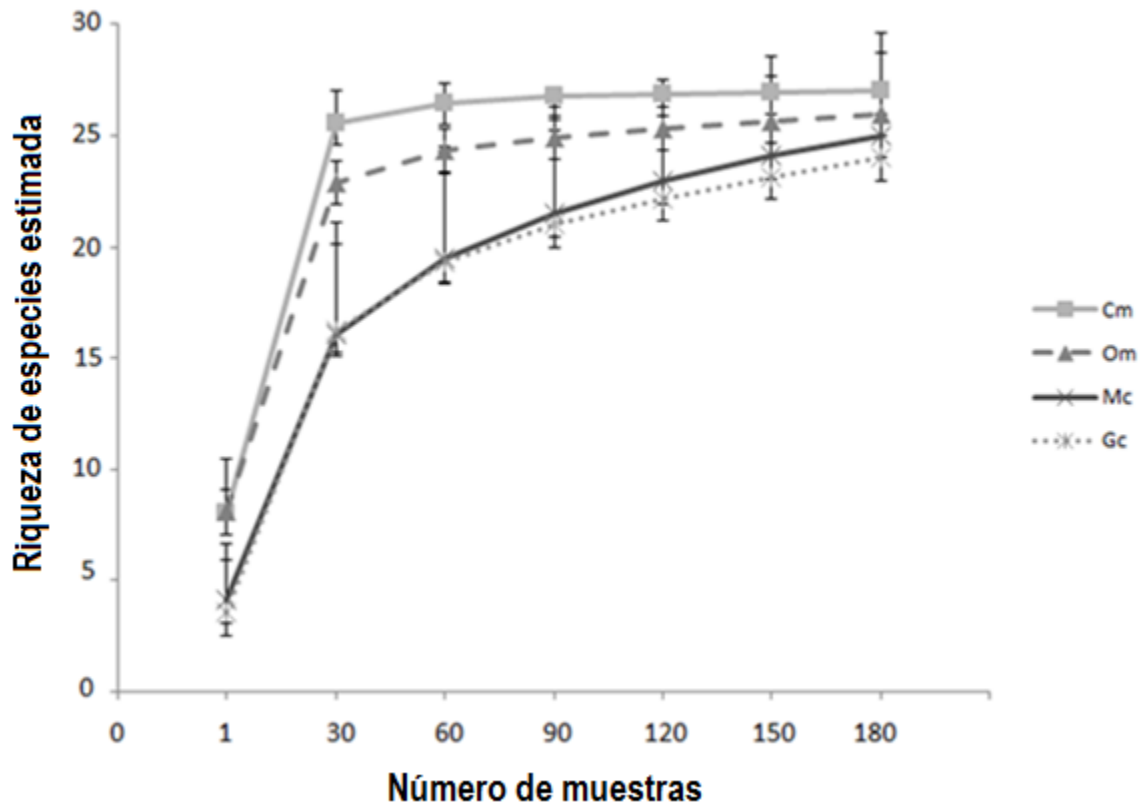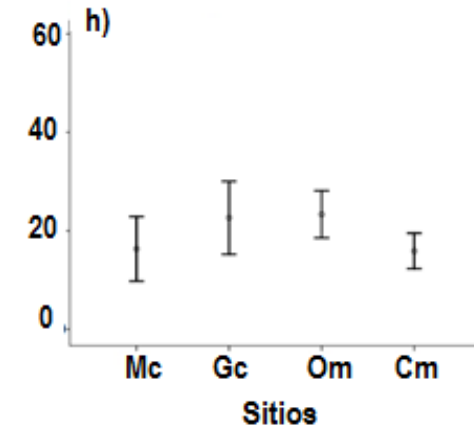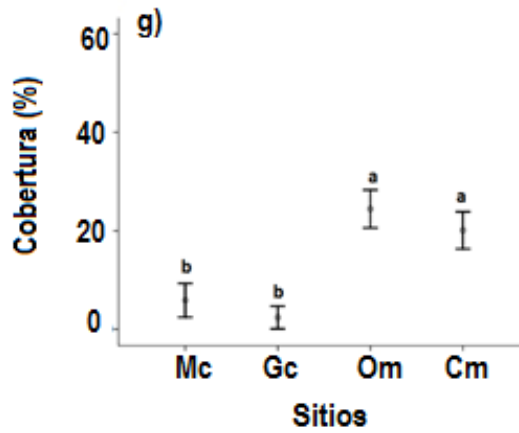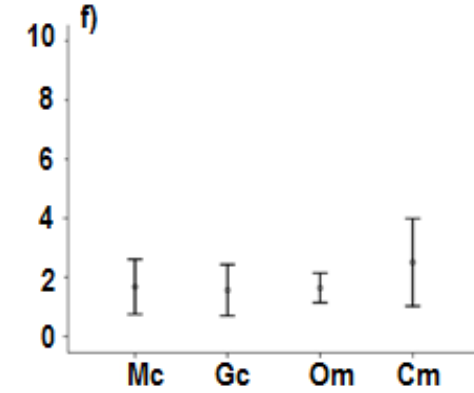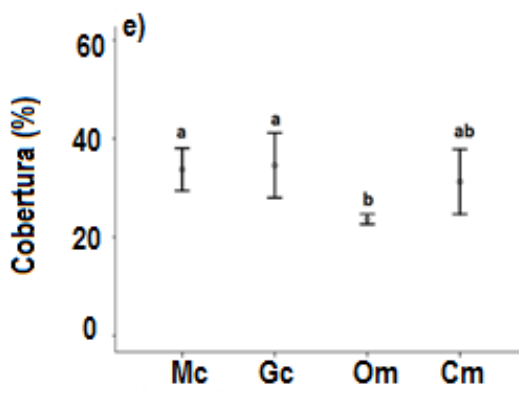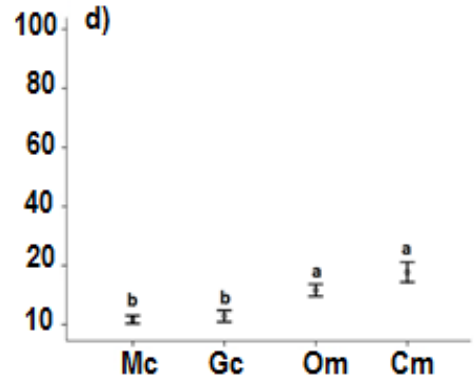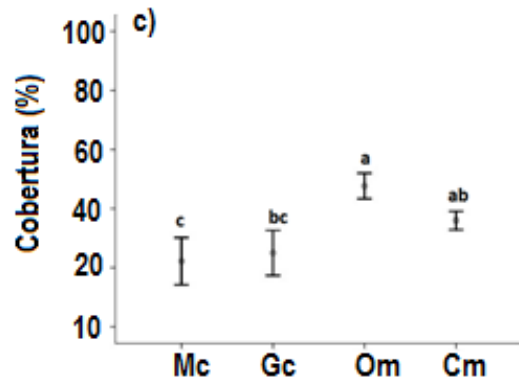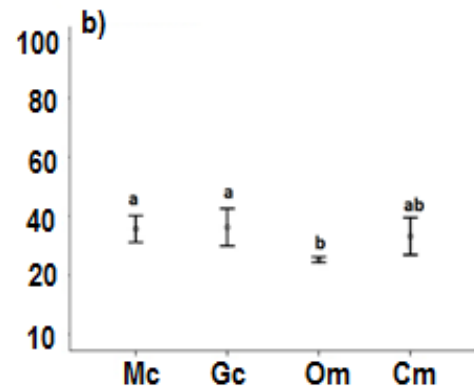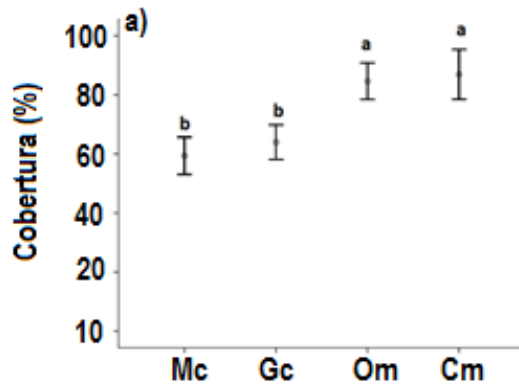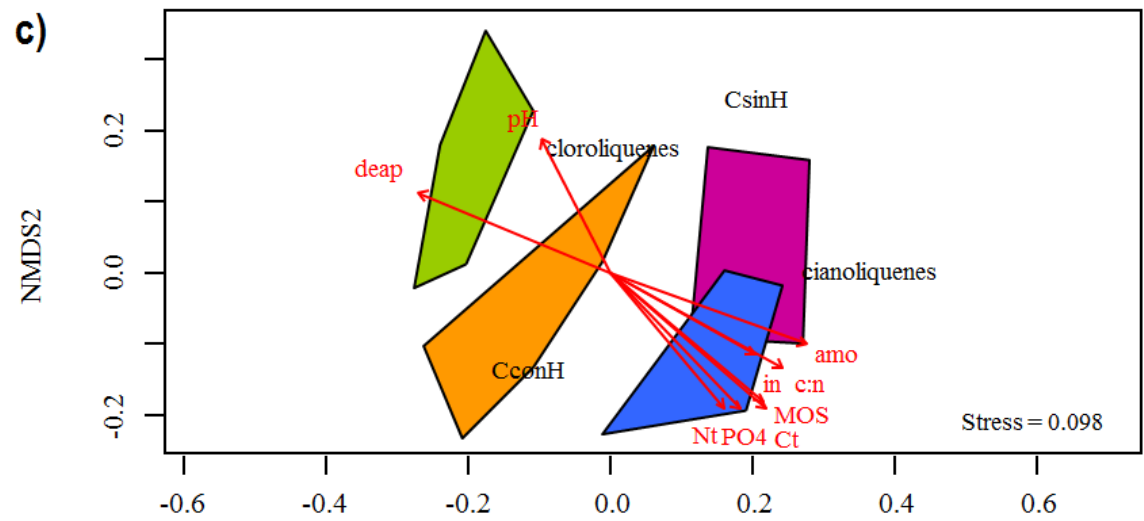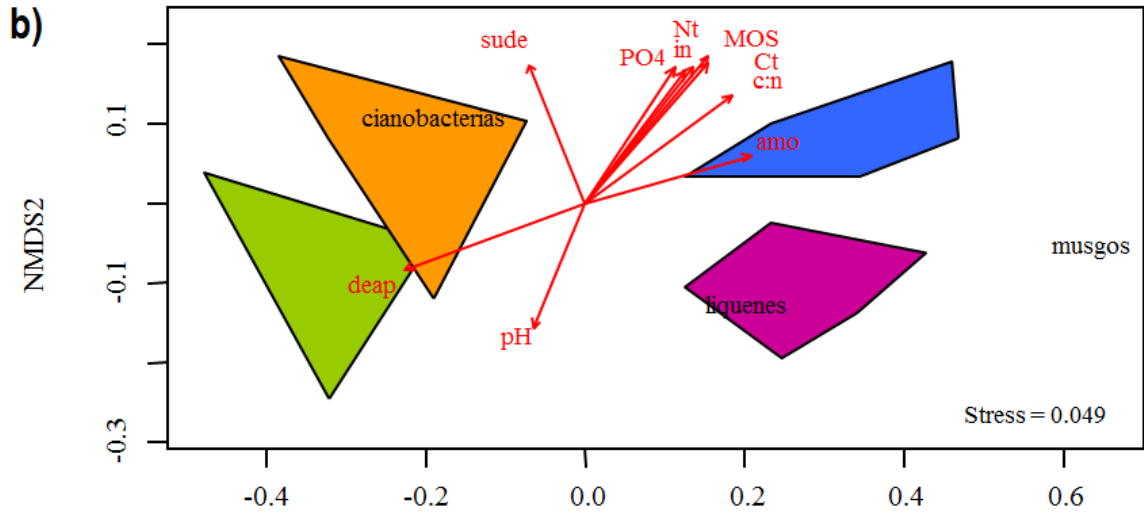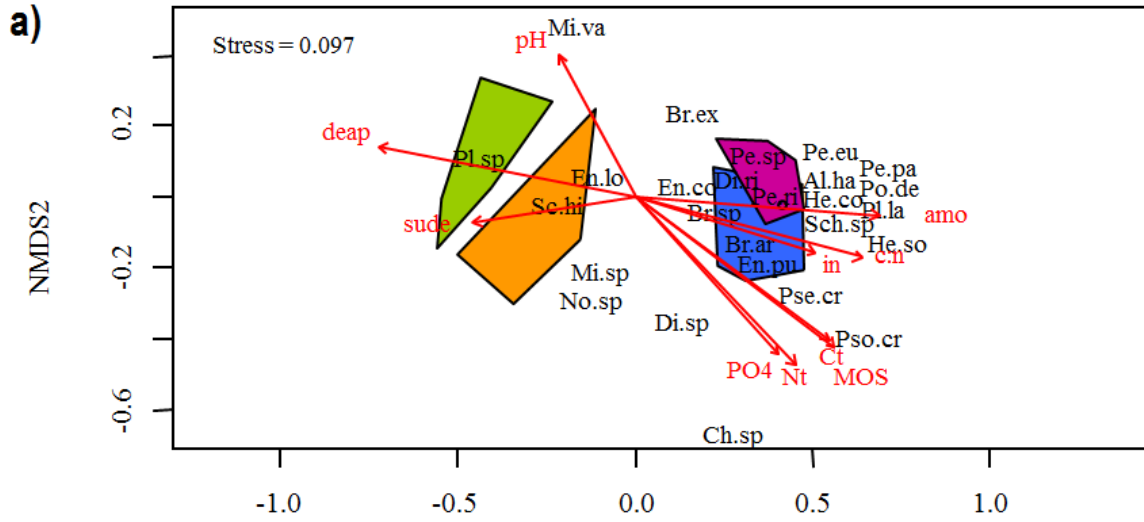
Capítulo 4

Biocrusts modulate the impact of rainfed agriculture and firewood extraction on soil nitrogen dynamics in a tropical desert

Sosa-Quintero Jessica, García-Oliva Felipe, Maestre Fernando T, Godínez-Alvarez Héctor

Biocrusts modulate the impact of rainfed agriculture and firewood extraction on soil nitrogen dynamics in a tropical desert

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Abstract

Biocrusts are communities composed of cyanobacteria, lichens, and bryophytes that create suitable microenvironments for the availability and transformation of nitrogen in desert soils. In temperate deserts, the intensive human activities such as livestock grazing and irrigated agriculture have negatively impacted the structure of biocrusts and their participation in the dynamics of nitrogen. However, in tropical deserts where subsistence activities are mainly practiced, their impact have not been evaluated on the structure of biocrusts and their effects on soil nitrogen dynamics. In a tropical desert in central Mexico, rainfed agriculture and firewood extraction modified the vegetation and soil properties originating abandoned croplands and mesquite shrublands, respectively. We evaluated the impact of these activities on biocrusts and N dynamics. The biocrusts in abandoned croplands had low cover and were dominated by cyanobacteria with heterocysts. The total and available N, ammonification rate, microbial activity, and microbial biomass N were low, whereas the nitrification was high. The biocrusts in mesquite shrublands had high cover and were dominated by cyanolichens and bryophytes. The total and available N, microbial activity, ammonification, and microbial biomass N were high. Our results suggest that cyanolichens and bryophytes may favor the retention of nitrogen in the system, thus modulating the impact of firewood extraction on soil N dynamics. On the other hand, cyanobacteria with heterocyst did not improve the availability and retention of nitrogen in the sites impacted by rainfed agriculture.

Keywords: Cyanolichens, cyanobacteria with heterocysts, bryophytes, functional groups, microbial biomass N

Introduction

Biocrusts are symbiotic micro-communities widely distributed in deserts between sparse

vegetation. These communities are a multifunctional component in these ecosystems (Bowker et

al., 2018) because they modulate hydrological processes, avoid erosion by wind and water,

increase soil fertility, and participate in nitrogen (N) and carbon (C) dynamics (Eldridge, 2001;

Barger et al., 2006; Bowker et al., 2010). With respect to N dynamics, biocrusts participate in

nitrogen transformations such as fixation, nitrification, ammonification, denitrification,

mineralization, and immobilization, and modulate the distribution of total and available nitrogen

(Castillo-Monroy et al., 2010; Delgado-Baquerizo et al., 2013a; Hu et al., 2014; Delgado-

Baquerizo et al., 2014; Hu et al., 2015; Liu et al., 2016; Sandoval et al., 2016). Therefore,

biocrusts are essential for nitrogen cycling in deserts, where the nitrogen is a limiting nutrient

(Vitousek et al., 1997; Elbert et al., 2012; Delgado-Baquerizo et al., 2016a).

The participation of biocrusts in N dynamics may be altered by the impact of productive

activities such as livestock grazing and irrigated agriculture. The livestock grazing modifies the

species composition and structure of biocrusts, thus reducing N fixation, total and available N,

and transformation rates such as ammonification (Evans & Belnap, 1999; Warren & Eldridge,

2003; Read et al., 2008; Zhang et al., 2013; Zhao et al., 2010; Huajie et al., 2009; Gómez et al.,

2012). The irrigated agriculture alters nitrogen transformations such as fixation depending on the

composition of biocrusts. The N fixation increases in biocrusts dominated by cyanobacteria in

contrast to moss-dominated biocrusts (Zhao et al., 2010).

The studies about the impact of livestock grazing and irrigated agriculture on biocrusts

and N dynamics have been performed mainly in temperate deserts of Australia, Mongolia, China,

Argentina, and USA (Evans & Belnap, 1999; Belnap & Eldridge 2001; Bowker et al., 2014;

Zaady et al., 2016). Therefore, data about the impact of human activities on biocrusts and N

dynamics in tropical deserts are practically unknown. These data are basic to understand the significance of biocrusts for the functioning of desert ecosystems because biocrusts are abundant in tropical deserts and their taxonomic composition differ from the composition of biocrusts in temperate deserts (Rivera-Aguilar et al., 2006). Furthermore, the human activities in tropical deserts are subsistence activities such as rainfed agriculture and firewood extraction which may differ in their impact on biocrusts from the productive activities in temperate desert.

This study evaluates the impact of rainfed agriculture and firewood extraction on biocrusts and soil N dynamics in the Zapotitlán Salinas Valley, a tropical desert in central southern Mexico. In this desert, the rainfed agriculture and firewood extraction have been practiced in fluvial terraces for the last 70 years. These activities have modified the vegetation and soil properties originating sites with distinct types of vegetation cover. The sites of rainfed agriculture have poorer conditions of vegetation and soil than the sites of firewood extraction (Sosa-Quintero & Godínez-Alvarez, 2019). The biocrusts in both sites have similar species richness, but differ in their abundance (Sosa-Quintero, unpublished data). However, it is unknown whether the differences in the abundance of biocrusts caused by the rainfed agriculture and firewood extraction modify the soil N dynamics. To fill this information gap, we evaluated (1) the cover of biocrusts and the cover of taxonomic and functional groups related to soil N dynamics in sites with distinct plant cover. Most studies on biocrusts and N dynamics have only evaluated changes in the total cover of biocrusts or in the cover of taxonomic groups. Therefore, we evaluated the cover of functional groups because it gives more information than the cover of biocrusts (Read et al., 2008) and is a sensitive indicator and predictor of function ecosystem and disturbance (Eldridge & Rosentreter 1999; Ponzetti & McCune, 2001; Lavorel & Garnier, 2002; Cornelissen et al., 2007). In addition to biocrust cover, we evaluated (2) the total and available N, the transformation rates, and the microbial biomass N into soil. Most studies on biocrusts and N

dynamics have only evaluated total and available N as well as transformation rates such as N fixation or ammonification. Therefore, we evaluated several aspects of the N dynamics to get a more complete overview of the impact of rainfed agriculture and firewood extraction. Finally, we evaluated (3) the possible relationship between the cover of the biocrusts and the N dynamics. We hypothesize that the poorer conditions of vegetation and soil in sites of rainfed agriculture than in sites of firewood extraction would have a higher impact on biocrust cover and N dynamics. Accordingly, we expected that biocrusts in sites of rainfed agriculture would have low cover of biocrusts as well as low cover of taxonomic and fuctional groups. Furthermore, sites of rainfed agriculture would have low total and available N forms, transformation rates, and microbial biomass N into soil.

Materials and methods

Study area

This study was carried out in the Zapotitlán Salinas valley located within the Tehuacán-Cuicatlán Biosphere Reserve in Puebla, Mexico. The fieldwork was carried out in the fluvial terraces of the Salado River (18° 19' N, 97° 27' W; 1300–1400 m a. s. l.). The average annual temperature is 21 °C and the annual average rainfall is 400 mm (López-Galindo et al., 2003). The soils are sandy loam, clay loam, and silty clay loam. The original plant community is mesquite (*Prosopis laevigata* (Humb. et Bonpl. ex Willd) M.C. Johnston) shrubland mixed with columnar cacti (*Myrtillocactus* geometrizans (Mart. ex Pfeiff.) Console, *Stenocereus stellatus* (Pfeiff.) Riccob. y *Pachycereus hollianus* (F.A.C Weber) Buxb.; Dávila et al., 2002).

Currently the mesquite shrubland has been transformed to four types of sites due to rainfed agriculture and firewood extraction. The rainfed agriculture consisted of removing the native vegetation to establish croplands, plowing with yoke or tractor, cultivating different types

of crops, fertilizing with manure, and introducing goats to croplands for 2 months, after harvest. This management was practiced for 60 years, but it has been abandoned 15 years ago. The rainfed agriculture created two sites: (1) mesquite cropland (Mc), which are abandoned croplands with *Prosopis laevigata* and *Parkinsonia praecox* (Ruiz & Pavon ex. Hook.) Harms. and (2) goldeneye croplands (Gc), which are abandoned croplands with *Viguiera dentata* (Cav.) Spreng. (toothleaf goldeneye). On the other hand, the firewood extraction consisted of removing the secondary branches of mesquite. This management is still practiced today at the study area. The firewood extraction has created two more sites: (3) open-canopy mesquite shrubland (Om), which is dominated by *P. laevigata* and *Myrtillocactus geometrizans*, and (4) closed-canopy mesquite shrubland (Cm), which is dominated by *P. laevigata*, *M. geometrizans*, *P. hollianus*, and *Opuntia decumbens* Salm-Dyck. Both management practices, rainfed agriculture and firewood extraction, have altered the vegetation traits and soil properties. Thus, the canopy cover, litter cover, infiltration rate, organic matter, and nutrient content are lower in sites of rainfed agriculture than sites of firewood extraction. Furthermore, the bare soil cover, gaps between plant canopies, and soil compaction are lower in sites of firewood extraction than sites of rainfed agriculture. The total biocrusts cover is higher in sites of firewood extraction, particularly in the Om, than in sites of rainfed agriculture (Sosa-Quintero & Godínez-Alvarez, 2019).

Sampling design

For each of the four sites, we selected three replicates to collect biocrust and soil samples. The replicates were located in the same fluvial terrace to control for geomorphological unit and soil origin (fluvial sediments). The biocrust and soil samples were taken at 30 points per site that were randomly placed in open spaces (15) and under shrubs (15). The biocrusts were collected in 7.5 cm Petri dishes. The soil was collected at 0-3 cm depth, after collecting the biocrust. The soil

samples from open spaces and under shrubs were mixed respectively to form a composite sample, stored in black plastic bags, and refrigerated at 4 °C for biogeochemical analysis. The sampling was performed in the dry (November) and wet (April) seasons in 2016.

Biocrust cover

To quantify the biocrust cover we used one 5×5 cm grid, divided in 100 squares of 0.5×0.5 cm, to count the number of squares occupied by the cyanobacteria, lichens, and bryophytes in each Petri dish. The counts were made with a stereoscopic microscope (Zeiss SteREO Discovery V.8). With the number of squares occupied by the biocrust, we calculated (1) the total cover of the biocrust as the number of squares occupied by all species of cyanobacteria, lichens, and bryophytes together, (2) the cover of the taxonomic groups as the number of squares occupied by all species of the biocrust grouped in cyanobacteria, lichens, and bryophytes, and (3) the cover of the functional groups as the number of squares occupied by all species of the biocrust grouped in cyanobacteria with heterocyst, cyanobacteria without heterocyst, cyanolichens, and chlorolichens. We used these functional groups because they emphasize the presence of heterocysts and photobionts, and thus they are related to N dynamics in soil (Solheim et al., 1996).

Total C, N, P, and available forms of N

The soil samples were dried at 75° C and ground in an agate mortar for the total N (TN), C (TC), and P (TP) analyses. The TC was determined with a Total Carbon Analyzer (UIC Mod. CM5012; Chicago, E.U.A). The TN was obtained with acid digestion (macro-Kjeldahl method; Bremmer, 1996). The TN and TP total forms were estimated by colorimetrical analyses (Bran- Luebbe Auto Analyzer III (Norderstedt, Germany). We used fresh samples to determine the available forms of nitrogen. The ammonium (NH_4^+) and nitrate (NO_3^-) were extracted using 2 M KCl, filtered

through Whatman No. 1 filters, and determined colorimetrically (phenol-hypochlorite method; Paul & Clark, 1989).

Transformation rates and microbial biomass N

The C and N mineralization as well as the ammonification and nitrification net rates were measured by incubation in aerobic conditions for 5 days. Soil fresh samples (80 g) were placed in PVC (polyvinyl-chloride) tube cores with a 0.250 mm mesh at the bottom. Each sample was wetted to field water holding capacity with deionized water and incubated in 1 L jars at 25 °C. Differences between pre- and post-incubation values of NH_4^+ and NO_3^- were used to calculate N mineralization, ammonification, and nitrification (Robertson et al., 1999, Binkley & Hart, 1989). Finally, the microbial biomass N was determined in fresh soil samples by the chloroform fumigation-extraction method (Vance et al., 1987). Fumigated and non-fumigated samples were incubated for 24 h at 17°C. The microbial biomass N was extracted from fumigated and non-fumigated samples with 0.5 M de K_2SO_4, and filtered through Whatman No. 1 paper. The filtrate was digested and determined by the macro-Kjeldahl method (Brookes et al., 1985). The microbial biomass N was calculated by subtracting the extracted N in non-fumigated samples from that in fumigated samples and dividing by 0.54, the KEN value (extractable part of microbial biomass N after fumigation; Joergensen and Mueller, 1996).

Statistical analysis

The biocrust cover (total cover of biocrust, cover of taxonomic groups, cover of functional groups), the TN, TC, and TP, the available forms of N (NH_4^+, NO_3^-) as well as the transformation rates (C and N mineralization, nitrification, ammonification) and microbial biomass N were analyzed with nested ANOVAs and paired Student t-tests to evaluate the effect of season, site,

season × site, and microhabitat nested within site. The angular and logarithmical transformations were applied to data to meet the normality assumption of the statistical test.

Linear regression analysis was performed to evaluate the relationship between the potential C mineralization rate and the total and available forms (TN, NH_4^+, NO_3^-), the transformation rates (ammonification, nitrification, N mineralization) and the microbial biomass N. Furthermore, we evaluated the relationship between the biocrust cover (total cover of biocrust, cover of taxonomic groups, and cover of functional groups) and the soil N dynamics (total and available N forms, the C and N transformation rates, and the microbial biomass N). All analyses were carried out in the JMP statistical software, version 10.

Results

Biocrust cover

The total cover of the biocrust was affected by the season, site, and their interaction as well as by the microhabitat nested within site (Table S1). The cover of the biocrust was higher in Om and Cm than in Mc and Gc during the dry season, and it was higher under shrubs than in open spaces (Table 1).

The cover of the taxonomic groups was affected by the site and microhabitat nested within site, but not by the season or season by site interaction (Table S1). The cover of cyanobacteria was similar in Mc and Gc, and it was higher than in Om and Cm. Furthermore, it was higher in open spaces than under shrubs. The cover of lichens and bryophytes, on the other hand, was similar in Om and Cm, and it was higher than in Mc and Gc. The cover of lichens was higher in open spaces than under shrubs whereas the cover of bryophytes was higher under shrubs than in open spaces (Table 1).

The cover of the functional groups was affected by the season or site, but not by the interaction season by site. Furthermore, it was affected by the microhabitat nested within site (Table S1). The cover of the cyanobacteria without heterocyst was lower in the dry season than in the wet season, and it was lower in the open spaces than under shrubs. The cover of the cyanobacteria with heterocyst was higher in Mc and Gc than in Om and Cm, and it was higher in open spaces than under shrubs. The cover of cyanolichens was lower in Mc and Gc than in Om and Cm, and it was higher in open space than under shrubs. The cover of chlorolichens was similar among the four sites during the dry and wet seasons as well as between open spaces and under shrubs (Table 1).

Total and available forms, transformation rates, and microbial biomass N

The total and available forms and the transformation rates of soil N showed a similar tendency in the dry and wet seasons. Thus, we only presented the results for the wet season. The total and available forms were affected by the site and microhabitat nested within site (Table S2). The TN, TC, TP, NH_4^+ and NO_3^- concentrations in the soil were low in Mc and Gc and tended to increase in Om and Cm. The concentration of both forms, total and available, was also higher under shrubs than in open spaces (Fig. 1).

The C mineralization, N mineralization, ammonification, nitrification, and microbial biomass N were affected by the site and microhabitat nested within site (Table S2). The C mineralization, ammonification, and microbial biomass N were low in Mc and Gc and tended to increase in Om and Cm. These variables were also higher under shrubs than in open spaces, except for the ammonification rate, which was higher in open spaces than under shrubs. In contrast, the N mineralization and nitrification were high in Mc and Gc and decreased towards

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Om and Cm. The N mineralization and nitrification were higher in open spaces than under shrubs in Mc and Gc (Fig. 2).

Relationships between potential C mineralization and the total and available forms of N, transformation rates, and microbial biomass N

The relationships between the potential C mineralization and the total and available forms of N, the transformation rates, and the microbial biomass N were analyzed only for the wet season. The C mineralization was positively related to TN ($r^2 = 0.54$ p = 0.006/ $r^2 = 0.80$ p = <0.0001), NH_4^+ ($r^2 = 0.46$ p = 0.01/ $r^2 = 0.31$ p = 0.05), ammonification ($r^2 = 0.27$ p = 0.07/ $r^2 = 0.25$ p = 0.09), and microbial biomass N ($r^2 = 0.48$ p = 0.01/ $r^2 = 0.61$ p = 0.002). These relationships were similar in open spaces and under shrubs. On the other hand, the C mineralization was negatively related to nitrification. This relationship was significant under shrubs but not in open spaces ($r^2 = 0.40$ p = 0.03).

Biocrust cover and soil N dynamics

Of all the relationships between the biocrust cover and soil N dynamics, the microbial biomass N was the only variable related to taxonomic and functional group. The relationship between the biocrust cover and the microbial biomass N varied depending on the type of cover and the microhabitat (Fig. 3). The total cover of the biocrust was not related to microbial biomass N either in open spaces or under shrubs. With respect to the cover of the taxonomic groups, the cover of the cyanobacteria was positively related to N only under shrubs whereas the cover of the bryophytes was positively related to N in open spaces and under shrubs. With respect to the cover of the functional groups, the cover of cyanobacteria with heterocyst was negatively related to N under shrubs. The cover of the cyanobacteria without heterocyst was positively related to N in

open spaces. The cover of the cyanolichens was positively related to N under shrubs (Fig. 3).

Finally, the cover of bryophytes was related to different process of N dynamics, although these

relationships were slightly significant. It was positively related to ammonification in open spaces

($r^2 = 0.27$ p = 0.08), negatively related to nitrification under shrubs ($r^2 = 0.32$ p = 0.06), and

positively related to C mineralization in open spaces ($r^2 = 0.29$ p = 0.06) and under shrubs ($r^2 =$

0.34 p = 0.05). In contrast, the microbial activity had negative relationships with cyanobacteria

with heterocysts ($r^2 = 0.31$ p = 0.07) and cyanobacteria cover ($r^2 = 0.27$ p = 0.09) under shrubs.

Discussion

In accordance to our hypothesis, the abandoned croplands had low cover of biocrusts dominated

by cyanobacteria with heterocysts. These sites also had low values of total and available N,

ammonification rate, and microbial biomass N, and high values of nitrification into soil. In

contrast, the mesquite shrublands had high cover of biocrusts dominated by cyanolichens and

bryophytes. In addition, these sites had high values of total and available N, ammonification rate

and microbial biomass N.

Impact of rainfed agriculture on biocrusts and soil N dynamics

The sites of rainfed agriculture had low cover of biocrusts as well as low cover of taxonomic and

functional groups. These biocrusts were dominated by cyanobacteria, particularly cyanobacteria

with heterocyst. However, the cover of lichens and bryophytes was low. The negative impact of

rainfed agriculture on the cover of biocrusts in the tropical desert of the Zapotitlán Salinas valley

is similar to the negative effect of livestock grazing or irrigated agriculture on biocrusts in

temperate deserts (Peterjohn & Schlesinger, 1990; Belnap & Eldridge, 2001; Colesie et al., 2016;

Zaady et al., 2013). The high cover of cyanobacteria in abandoned croplands may be due to these

organisms are adaptable and extremely resilient to the impact of human activities (Mager & Thomas, 2011). The agriculture completely removes biocrusts. However, once this activity is abandoned, the cyanobacteria can recover after 14-34 years or can reach 70% cover after 16 years in temperate deserts (Belnap & Eldridge, 2001; Zhao et al., 2010). During the biocrusts early formation, the cyanobacteria with heterocysts are the first colonizers which can contribute to the initial input of N. However, the changes in biocrust cover originated by rainfed agriculture decreased the total C and N, and available N in soils (Read et al., 2008; Huajie et al., 2009; Gómez et al., 2012; Zhang et al., 2013; Zaady et al., 2016). The decreases in these variables are significant because the activity of biocrusts dominated by cyanobacteria with heterocysts may be limited by the low C content, which is necessary for their activity. On the other hand, the low cover of lichens and bryophytes may be due to the modifications of soil properties and vegetation characteristics caused by the rainfed agriculture. This result is similar to the impact of livestock grazing in temperate deserts where it prevented the establishment of lichens and bryophytes (Warren & Eldridge, 2003).

In both abandoned croplands, mesquite cropland and goldeneye cropland, the C mineralization, which is a surrogate for microbial activity, the ammonification rates, and the biomass microbial N were low, whereas the nitrification and the mineralization N rates were high. The low carbon and nitrogen concentration in abandoned croplands may decrease the microbial activity (Griffin, He, & Honeycutt, 2005). In addition, the nitrification rate was negatively related to microbial activity. These results suggest that ammonium was not protected in microbial biomass due to low microbial activity. Furthermore, the nitrate could be lost from the system by leaching processes because of the high nitrification rate, as it occurs in disturbed sites (Zaady et al., 1996; Belnap, 1995).

The relationship between the cover of biocrusts and the microbial biomass N varied depending on the taxonomic and functional group as well as on the microhabitat. The cover of cyanobacteria and cyanobacteria with heterocyst was not related to microbial biomass N in open spaces. However, the cover of cyanobacteria without heterocyst was positively related to microbial biomass N. This last relationship may be due to the cover of cyanobacteria without heterocyst was higher in the mesquite shrublands, where microbial biomass N is high, than in the abandoned croplands. In contrast, the cover of cyanobacteria and cyanobacteria with heterocyst was negatively related to microbial biomass N under shrubs. This relationship may be due to the cover of cyanobacteria and cyanobacteria with heterocyst is higher in the abandoned croplands, where the microbial biomass N is low, than in the mesquite shrublands. The cover of the cyanobacteria without heterocyst was not related to microbial biomass N. These results suggest that the cyanobacteria with heterocysts are the main group of organism related to soil N dynamics in the sites of rainfed agriculture.

Impact of firewood extraction on biocrusts and N dynamics

The sites of firewood extraction had high cover of biocrusts as well as high cover of taxonomic and functional groups. The biocrusts were dominated by lichens, particularly cyanolichens, and bryophytes. However, the cover of cyanobacteria was low. These results are similar to those reported for sites with military training and sheep trampling, in which the vegetation cover is low with wide open spaces that are occupied by biocrusts dominated by the most resistant components such as lichens (Rogers & Lange, 1971; Johansen et al., 1998; Bowker, 2007). However, they differed from other results reported for other activities such as livestock grazing, fire and recreational traffic in temperate deserts. In these deserts, the impact of these activities decreases the cover of lichens and bryophytes (Warren & Eldridge, 2003; Ferrenberg et al.,

2015). The high cover of lichens and bryophytes in mesquite shrublands may be related to the management practices of firewood extraction, which consisted in the removal of the secondary branches of mesquite and understory. These practices increased the cover of open spaces, but at the same time, they maintained certain cover of vegetation. Lichens and bryophytes can grow in open spaces because they are tolerant to high radiation and extreme temperatures (Nash, 1996; Seppelt et al., 2016). However, lichens and bryophytes can also grow in the shaded areas under shrubs because they develop well in soils with high nutrient and water content (Eldridge & Rosentreter, 1999; Maestre et al., 2002; Belnap et al., 2006; Zhou et al., 2019).

The open- and closed-canopy mesquite shrublands had similar N dynamics despite the differences in the rate of firewood extraction. In both mesquite shrublands, the total C, N, and P as well as the available forms of N and the ammonification rate were high. Similarly, the microbial activity, inferred through C mineralization, and the microbial biomass N were also high. The similarity in soil N dynamics between open- and closed-canopy mesquite shrublands may be related to the high cover of lichens, particularly cyanolichens, in the open-canopy mesquite shrubland. This shrubland has a higher rate of firewood extraction than the closed-canopy mesquite shrubland and thus, it has a higher cover of open spaces occupied by cyanolichens. The cyanolichens may be contributing to the N input to the soil and, at the same time, they may be creating microenvironments with suitable conditions of soil temperature, organic matter content as well as nutrient and moisture availability for the activity of the microbial community associated to N dynamics (Maestre et al., 2008; Zhang et al 2009; Zhao et al., 2014; Delgado-Baquerizo et al., 2014; 2015; 2016b; Liu et al., 2016; Xiao et al., 2017; Bao et al., 2019). Further studies should evaluate the activity of the microbial community associated to biocrusts in the mesquite shrublands.

The relationship between the cover of lichens and bryophytes, and the microbial biomass N was similar for the taxonomic and functional groups in both microhabitats. The cover of bryophytes was positively related to microbial biomass N in open spaces and under shrubs. Likewise, the cover of cyanolichens was positively related to microbial biomass N under shrubs. These relationships may be due to the cover of bryophytes and cyanolichens were higher in both mesquite shrublands, where the N dynamics was better, than in the abandoned croplands.

Conclusions

This study highlights how the biocrusts modulate the impact of rainfed agriculture and firewood extraction on N dynamics in a tropical desert. The biocrusts in sites of rainfed agriculture had low cover and were dominated by cyanobacteria with heterocysts. The total and available N, microbial activity, transformation rates, and microbial biomass N were low into soil. This suggests that biocrusts did not improve the soil N dynamics in sites of rainfed agriculture. In contrast, the biocrusts in sites of firewood extraction had high cover and were dominated by cyanolichens and bryophytes. The total N, C and P, microbial activity as well as available N and ammonification rate were high. This suggest that biocrusts may be favoring the retention of N in microbial biomass in sites with firewood extraction.

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Table 1. Biocrust cover (%) (total, taxonomic group, and functional group) in open space and under shrubs for four sites (mesquite cropland, goldeneye cropland, open-canopy mesquite shrubland, and closed-canopy mesquite shrubland) during the dry and wet seasons in the fluvial terraces of the Zapotitlán Salinas valley, central México.
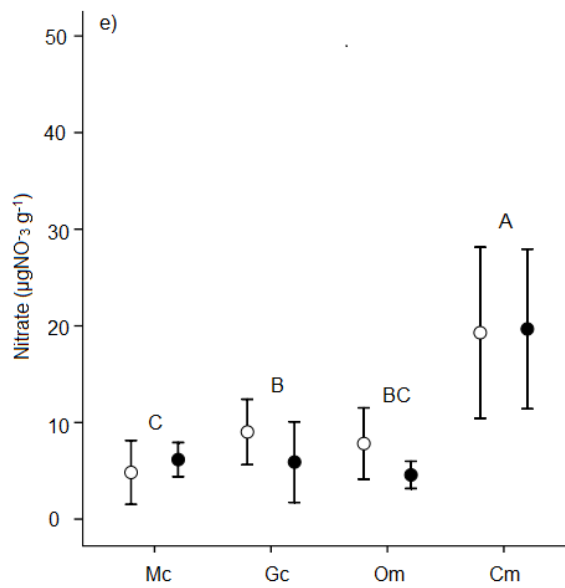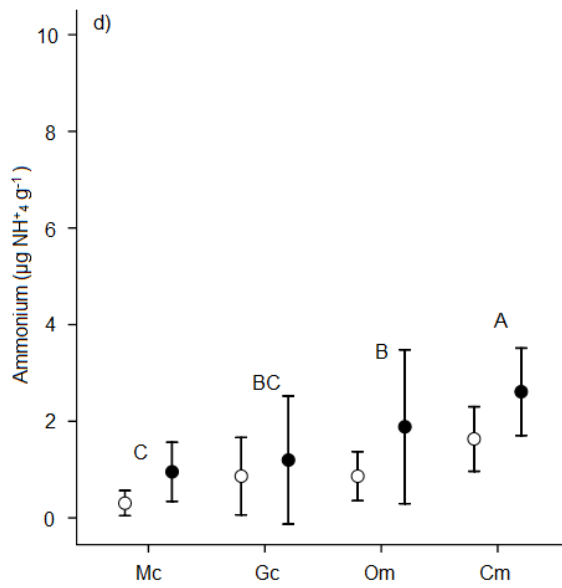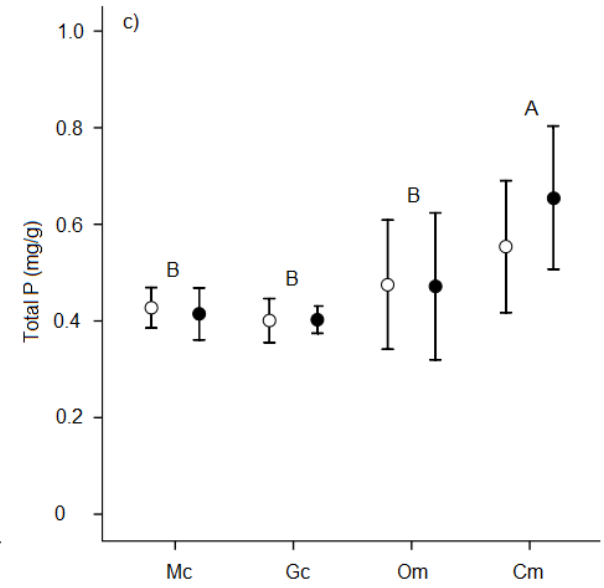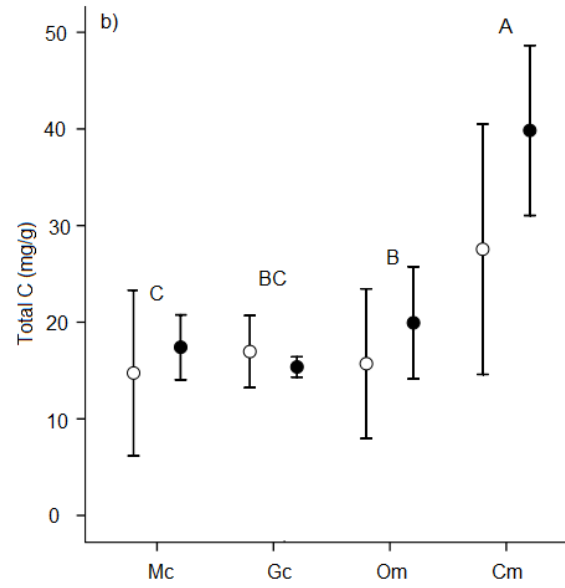
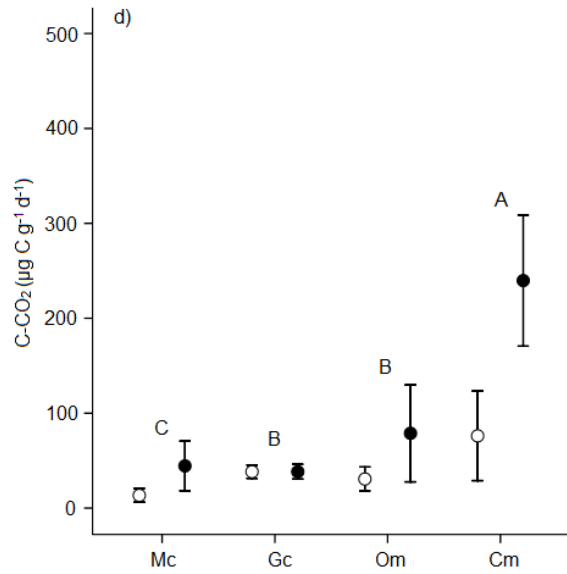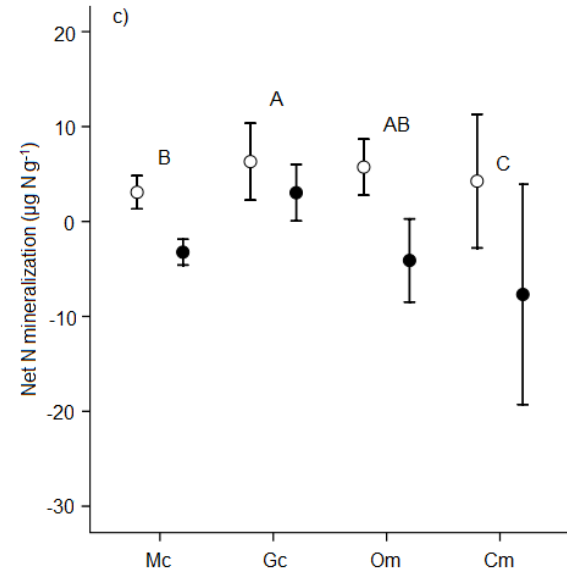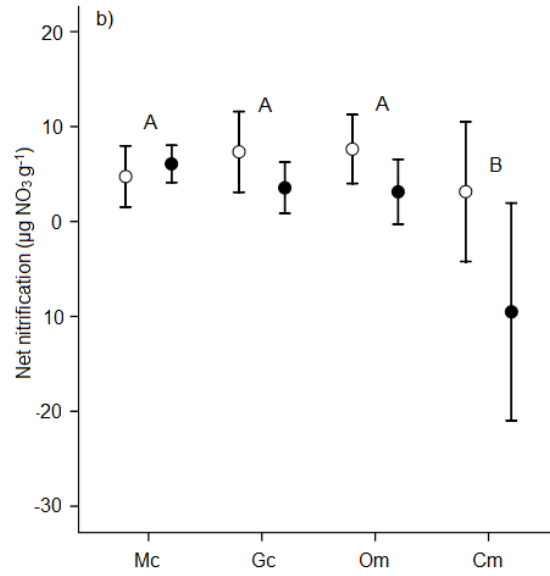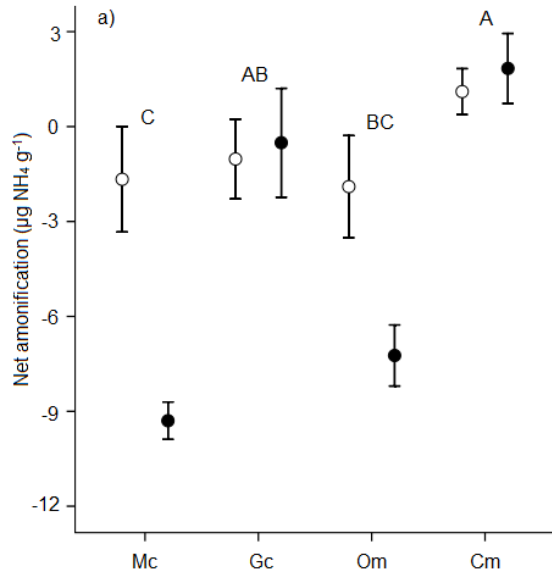| Type of cover (%)	Season	Mesquite cropland		Goldeneye cropland		Open-canopy mesquite shrubland		Closed-canopy mesquite shrubland	
		Open space	Under shrubs	Open space	Under shrubs	Open space	Under shrubs	Open space	Under shrubs
Total									
Biocrust	Dry	49.8 ± 10.8	70.7 ± 7.7	49.2 ± 2.3	76.9 ± 9.0	88.7 ± 1.2	85.9 ± 4.2	98.7 ± 1.3	90.3 ± 8.3
	Wet	52.2 ± 10.0	65.0 ± 4.2	59.1 ± 5.4	66.6 ± 4.6	83.6 ± 3.9	81.3 ± 9.7	81.5 ± 3.7	77.2 ± 2.2
Taxonomic group									
Cyanobacteria	Dry	35.1 ± 3.7	35.3 ± 4.7	28.1 ± 4.8	44.9 ± 6.0	23.7 ± 1.9	27.5 ± 1.8	33.3 ± 3.1	45.8 ± 0.4
	Wet	28.1 ±1.8	44.1 ± 6.5	30.1 ± 4.6	43.24 ± 7.5	26.4 ± 1.2	23.3 ± 0.8	28.1 ± 2.6	25.6 ± 3.0
Lichens	Dry	14.6 ± 7. 9	30.4 ± 10.2	21.2 ± 6.7	27.3 ± 10.1	63.7 ± 1.54	35.2 ± 4.1	55.0 ± 3.0	17.1 ± 1.9
	Wet	24.1 ± 9.3	19.8 ± 6.5	28.4 ± 2.9	17.5 ± 2. 6	56.4 ± 4.82	34.0 ± 4.8	48.4 ± 0.8	23.5 ± 5.4
Bryophytes	Dry	0.2 ± 0.0	5.0 ± 2.4	0.0 ± 0.0	4. 8 ± 2.9	1.3 ± 0.60	23.2 ± 3.1	10.4 ± 2.1	27.5 ± 6.7
	Wet	0.7 ± 0.7	1.1 ± 0.3	0.6 ± 0.6	5.9 ± 3.0	0.8 ± 0.44	24.0 ± 4.4	5.0 ± 1.2	28.1 ± 4.1
Functional group									
Cyanobacteria without heterocyst	Dry	0.1 ± 0.1	2.1 ± 0.9	0.0 ± 0.0	2.1 ± 0.9	0.2 ± 0.1	1.9 ± 0.6	1.0 ± 0.3	1.5 ± 0.4
	Wet	0.7 ± 0.1	3.7 ± 1.4	2.9 ± 0.9	1.3 ± 0.5	1.7 ± 0.2	2.5 ± 0.1	3.6 ± 1.0	4.0 ± 1.1
Cyanobacteria with heterocyst	Dry	35.0 ± 3.6	33.2 ± 3.8	28.1 ± 4.8	42.8 ± 5.1	23.4 ± 2.0	25.6 ±18.7	32.3 ±2.8	43.7 ± 0.9
	Wet	27.2 ± 1.4	39.7 ± 6.7	27.2 ± 4.9	42.0 ± 8.0	24.7 ± 1.2	20.8 ± 0.9	27.4 ± 4.3	21.6 ± 2.1
Cyanolichens	Dry	7.3 ± 3.3	5.4 ± 2.0	0.3 ± 0.2	2.1 ± 1.6	33.6 ± 3.9	16.9 ±2.8	35.7 ± 6.7	6.5 ± 0.9
	Wet	8.5 ± 4.2	2.6 ± 1.4	5.8 ± 4.4	1.2 ± 0.4	26.9 ± 1.2	14.5 ± 0.6	28.6 ± 2.4	9.6 ± 1.7
Chlorolichens	Dry	7.8 ± 5.0	25.0 ± 12.0	20.8 ± 6.5	25.2 ± 9.6	30.0 ± 2.7	18.3 ± 3.6	19.4 ± 5.7	10.5 ± 1.1
	Wet	16.1 ± 5.3	16.4 ± 4.8	22.5 ± 2.1	16.3 ± 2.9	29.6 ± 4.0	19.7 ± 4.7	19.8 ± 2.1	14.0 ± 5.3

Figure legends

Figure 1. Mean ± standard error of total carbon, total nitrogen, total phosphorus, ammonium (NH_4^+), nitrates (NO_3^-), and microbial biomass N in open spaces (white points) and under shrubs (black points) in mesquite cropland (Mc), goldeneye cropland (Gc), open-canopy mesquite (Om), and closed-canopy mesquite (Cm). Letters indicate significant differences between sites ($P \leq 0.05$).

Figure 2. C mineralization, ammonification, nitrification, N mineralization in open spaces (white points) and under shrubs (black points) in mesquite cropland (Mc), goldeneye cropland (Gc), open-canopy mesquite (Om), and closed-canopy mesquite (Cm). Letters indicate significant differences between sites ($P \leq 0.05$).
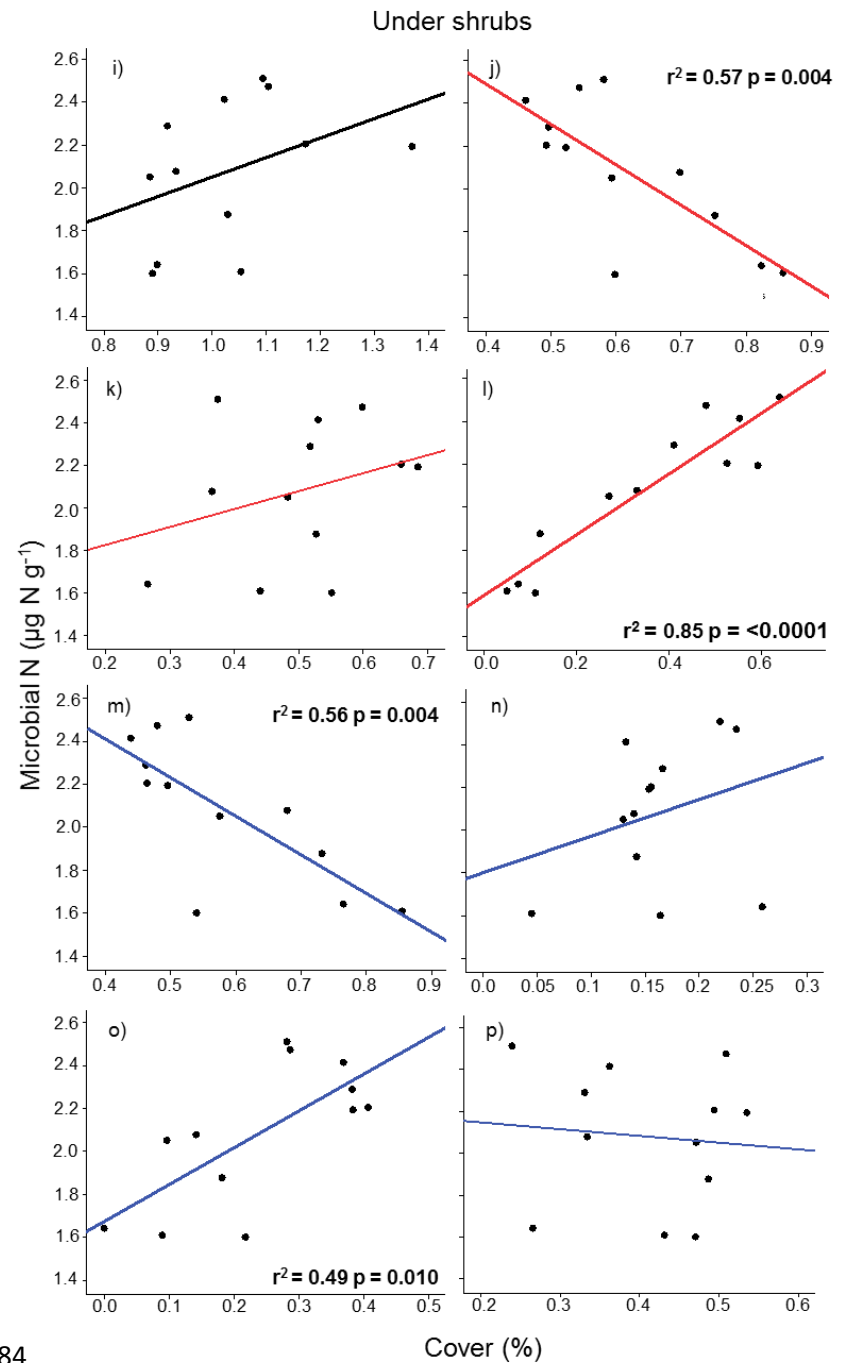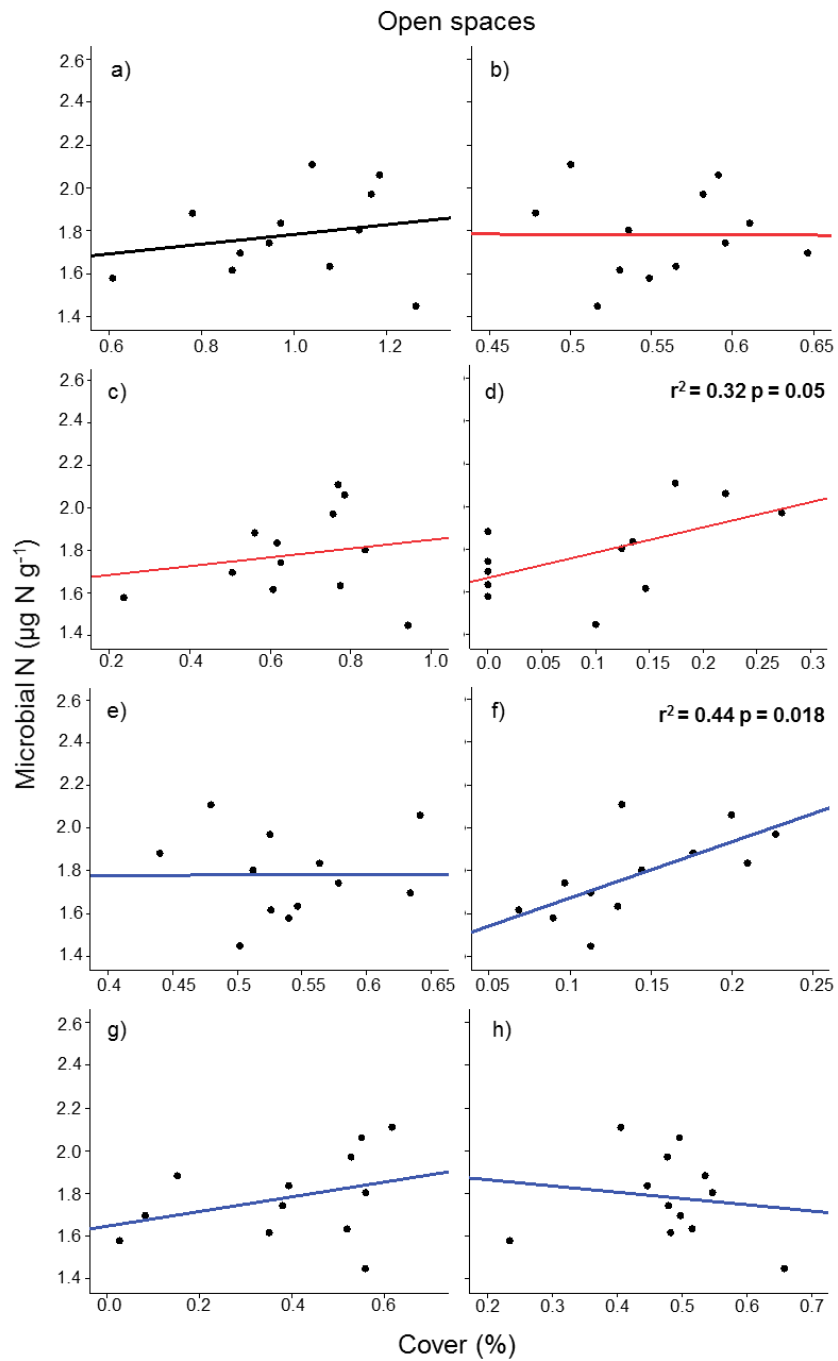
Figure 3. Relationships between the cover of biocrusts (black lines), the cover of taxonomic (red lines) and functional groups (blue lines), and microbial biomass N in open spaces (a-h) and under shrubs (i-p). Total cover of biocrust (a, i), cyanobacteria cover (b, j), lichen cover (c, k), bryophyte cover (d, l), cyanobacteria with heterocysts (e, m), cyanobacteria without heterocysts (f , n), cyanolichens (j, o), and chlorolichens (h, p). The r^2 and p values indicate the significant relationships.

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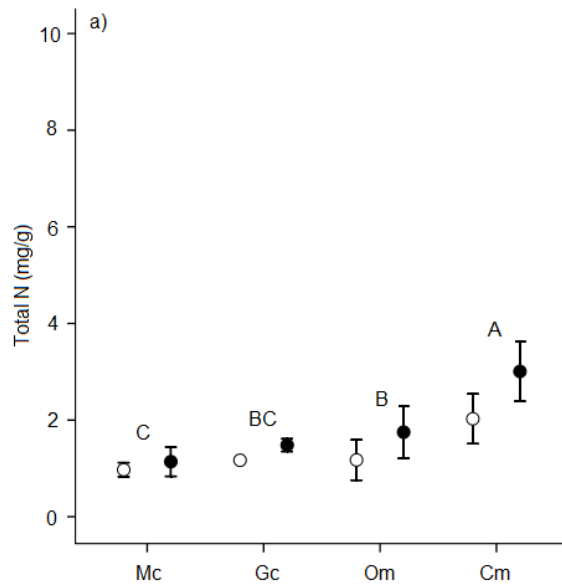
Open spaces — Under shrubs

a) b) c) d) e) f) g) h) i) j) k) l) m) n) o) p)

Microbial N (μg N g^{-1})

Cover (%)

d) $r^2 = 0.32$ p = 0.05
f) $r^2 = 0.44$ p = 0.018
j) $r^2 = 0.57$ p = 0.004
l) $r^2 = 0.85$ p = <0.0001
m) $r^2 = 0.56$ p = 0.004
o) $r^2 = 0.49$ p = 0.010

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Capítulo 5

Conclusiones generales y perspectivas

En los tres capítulos anteriores describimos el impacto de la agricultura de temporal y la extracción de leña en la riqueza específica y cobertura de las biocostras, y su efecto en la dinámica del N en el suelo (formas totales y disponibles, tasas de transformación y almacenamiento en biomasa microbiana) en las terrazas aluviales del Valle de Zapotitlán Salinas, Puebla. Ambas actividades de subsistencia tuvieron efectos negativos, pero la respuesta de las biocostras y la dinámica del nitrógeno fueron diferentes. Este trabajo es el primer esfuerzo en dilucidar la importancia de las biocostras en la dinámica del N en suelo de sitios impactados por actividades de subsistencia en un desierto tropical.

Con base en los resultados de cada capítulo lo siguiente:

1. La agricultura de temporal consistió en remover la vegetación original y los primeros centímetros del suelo para establecer campos de cultivo, en los cuales se introdujo ganado en la temporada de descanso y no se aplicó ningún agroquímico al suelo. Esta actividad fue realizada durante 60 años continuos, pero se dejó de practicar desde hace 15 años. Por el contrario, la extracción de leña solamente consistió en remover las ramas de *Prosopis laevigata*. Esta actividad ha sido realizada continuamente desde hace 75 años.

2. La agricultura de temporal disminuyó la cobertura de la vegetación y la hojarasca, así como el contenido de materia orgánica y nutrientes en el suelo. Además, incrementó la compactación del suelo. La extracción de leña, por el contrario, tuvo mayor cobertura de la vegetación y hojarasca, así como mayor contenido de materia orgánica y nutrientes en el

suelo. Los suelos tuvieron baja compactación y su tasa de infiltración fue relativamente alta.

3. Las biocostras en los sitios con agricultura de temporal tuvieron 14-18 especies, 50-70% de cobertura total y estuvieron dominadas por cianobacterias con heterocistos. Las biocostras en los sitios con extracción de leña tuvieron 23-29 especies, 90% de cobertura total y estuvieron dominadas por cianolíquenes y briofitas.

4. Los sitios con agricultura de temporal tuvieron menor N total y disponible, así como menor tasa de amonificación y N en biomasa microbiana, en comparación con los sitios de extracción de leña. Además, tuvieron mayor tasa de nitrificación.

5. En los sitios con agricultura de temporal, las cianobacterias con heterocistos estuvieron relacionadas con la biomasa microbiana, mientras que en los sitios con extracción de leña fueron los cianolíquenes y las briofitas.

Por último, el abandono de la agricultura de temporal favorece el establecimiento de biocostras dominadas por cianobacterias con heterocistos, las cuales podrían iniciar la recuperación de la dinámica del N en los sitios impactados por esta actividad. La extracción de leña ha favorecido el incremento en la cobertura de biocostras dominadas por cianolíquenes y briofitas, las cuales podrían mantener la disponibilidad, transformación y retención del N en el sistema.

Durante la realización de la tesis surgieron algunas preguntas que podrían abordarse en estudios futuros: ¿Cuál es el efecto de las actividades de subsistencia sobre la fenología de las biocostras? ¿Cómo es la recuperación de las biocostras en los sitios con agricultura de temporal? ¿Cuál es la comunidad microbiana asociada a las biocostras y su actividad?

¿Cómo es la fijación, desnitrificación y lixiviación del nitrógeno en las terrazas aluviales?

¿Cuál es el papel de las biocostras en la dinámica de otros nutrientes como el carbono y

fósforo en los sitios impactados por las actividades de subsistencia? ¿Qué características

funcionales de las biocostras podrían contribuir a la estabilidad del suelo y los procesos

hidrológicos? La respuesta a estas preguntas permitirá comprender el papel de las

biocostras en los desiertos tropicales.