# UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
## POSGRADO EN CIENCIAS BIOLÓGICAS
FACULTAD DE CIENCIAS
ECOLOGÍA

# INTERACCIONES ENTRE DOS ESPECIES DE MUÉRDAGO ENANO Y SU HOSPEDERO: IMPORTANCIA DE LAS ASOCIACIONES BIÓTICAS

## TESIS

QUE PARA OPTAR POR EL GRADO DE:

**DOCTORA EN CIENCIAS**

PRESENTA:

**MÓNICA ELISA QUEIJEIRO BOLAÑOS**

**TUTOR PRINCIPAL DE TESIS: DR. ZENÓN CANO SANTANA**
**FACULTAD DE CIENCIAS**
**COMITÉ TUTOR: DR. CARLOS MARTORELL DELGADO**
**FACULTAD DE CIENCIAS**
**DRA. MA. GRACIELA GARCÍA GUZMÁN**
**INSTITUTO DE ECOLOGÍA**

**MÉXICO, D.F., FEBRERO, 2015**

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POSGRADO EN CIENCIAS BIOLÓGICAS
FACULTAD DE CIENCIAS
DIVISIÓN DE ESTUDIOS DE POSGRADO

OFICIO FCIE/DEP/062/15

ASUNTO: Oficio de Jurado

**Dr. Isidro Ávila Martínez**
**Director General de Administración Escolar, UNAM**
**Presente**

Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día **22 de septiembre de 2014**, se aprobó el siguiente jurado para el examen de grado de **DOCTORA EN CIENCIAS** del (la) alumno (a) **QUEIJEIRO BOLAÑOS MÓNICA ELISA** con número de cuenta **300693669** con la tesis titulada: **"Interacciones entre dos especies de muérdago enano y su hospedero: importancia de las asociaciones bióticas"**, realizada bajo la dirección del (la) **DR. ZENÓN CANO SANTANA:**

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

**Atentamente**
"POR MI RAZA HABLARA EL ESPÍRITU"
Cd. Universitaria, D.F. a 27 de enero de 2015.

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DE POSGRADO

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# ÍNDICE

# Resumen

Las interacciones bióticas juegan un papel fundamental en los procesos demográficos de las plantas, pues afectan la obtención de recursos de forma positiva o negativa. La importancia de la competencia en la estructura de las poblaciones ha sido ampliamente estudiada, por ello, se reconoce el papel de los antagonismos como un factor determinante en la coexistencia de las especies. Sin embargo, el efecto de la competencia y de otras interacciones interespecíficas entre plantas parásitas ha sido poco abordado. Éstas son plantas con nutrición heterótrofa que dependen de una planta hospedera para obtener sus nutrientes. Esto genera la interrogante de si la dinámica poblacional y los procesos de infección de las plantas parásitas, como los muérdagos enanos (*Arceuthobium*), son afectados por las interacciones interespecíficas, y si se presentan los mismos mecanismos de coexistencia observados en las plantas autótrofas.

En los bosques templados del centro de México, *Arceuthobium globosum* y *A. vaginatum* se encuentran ampliamente distribuidos parasitando rodales de *Pinus hartwegii*, que es una especie de gran importancia forestal. Estas dos especies presentan coinfección dentro de un mismo hospedero, lo cual ha sido descrito como un fenómeno raro para el género. Por lo tanto, en esta tesis se explora el papel de las interacciones en la coexistencia de estas especies de muérdago enano, para lo cual se plantean las siguientes preguntas: i) ¿cómo afectan las interacciones interespecíficas la dinámica poblacional de los muérdagos enanos?, ii) ¿existen diferencias en los patrones de la infestación de las dos especies de muérdago enano que se encuentran en simpatría?, y iii) ¿qué efecto tiene la coexistencia de las dos especies de muérdago enano sobre el crecimiento de su hospedero? Las preguntas se abordan a lo largo de cuatro capítulos: en el primero se hace una revisión de literatura acerca de la competencia entre plantas parásitas, donde se encontró que, aunque se ha reportado la coinfección en distintas especies, no se ha abordado este tema. La literatura acerca de los organismos parásitos en general (en su mayoría parásitos de animales) indica que requieren una diferenciación de nichos para evitar competir por los mismos recursos, que se puede presentar como especialización en sus hábitos y/o segregación espacial dentro del hospedero. De acuerdo con lo anterior y con las similitudes y diferencias de las plantas parásitas con las plantas autótrofas, se hipotetizan los posibles resultados de la competencia entre plantas parásitas según el tipo de parasitismo y grado de dependencia que presentan hacia el hospedero.

En el capítulo dos se explora cómo las interacciones interespecíficas entre las dos especies afectan su dinámica poblacional, incluyendo el crecimiento poblacional y el potencial de colonización de nuevos hospederos. Para esto, se realizó un seguimiento de la infestación en un área de 1.1 ha dentro de la región de Zoquiapan (Parque Nacional Iztaccíhuatl Popocatépetl). Se encontró que la autorregulación es más fuerte que la competencia interespecífica; sin embargo, la intensidad y el signo de las interacciones entre las dos especies dependen fuertemente del tamaño de los hospederos y del proceso demográfico. Para el crecimiento poblacional en árboles previamente infestados se presenta competencia, excepto en árboles con un tamaño pequeño, donde *A. vaginatum* es facilitado por *A. globosum*. Para el proceso de colonización se presenta facilitación entre las dos especies; sin embargo, ésta pierde importancia en árboles de mayor porte. La importancia demográfica de las interacciones (el efecto sobre el tamaño poblacional) depende de la estructura del rodal (tamaño de los árboles, densidad y heterogeneidad en los tamaños), donde un rodal homogéneo favorece la facilitación, en tanto que el heterogéneo favorece la

competencia. También se determinó que las dos especies pueden llegar a la coexistencia, cumpliendo con el criterio de invasibilidad, pues si una de las especies está presente en un rodal es más probable que la segunda especie lo invada.

En el tercer capítulo se evaluaron los patrones de infestación de las dos especies de muérdago a partir de su incidencia (proporción de hospederos parasitados), severidad (número de parásitos por hospedero) y agregación dentro y entre sitios. Estas variables fueron evaluadas en 75 sitios de 3,300 $m^2$ distribuidos a lo largo de la región de Zoquiapan. Se encontró una clara dominancia de *A. vaginatum* en el área, ya que estuvo presente en la mayoría de los sitios. La incidencia de las dos especies está correlacionada negativamente y no se encontró un efecto significativo de otros factores, como la altitud y la pendiente. La incidencia y la severidad de cada especie tienen una relación lineal, lo que indica que hay un incremento uniforme de la severidad con la incidencia. Las dos especies se encuentran agregadas dentro de las parcelas (es decir, en los árboles), lo cual es un patrón común en los muérdagos enanos que tienen una dispersión limitada; sin embargo, sólo *A. globosum* muestra una agregación entre las parcelas, por lo que se puede pensar que existe una segregación espacial de esta especie.

En el cuarto capítulo se evaluó el efecto aislado y en conjunto de las dos especies de muérdago sobre el crecimiento, las relaciones alométricas y la susceptibilidad por tamaño de *P. hartwegii*. Para esto, se monitoreó el cambio en el dap y el tamaño de la copa de árboles de distinta talla durante tres años en el rodal de 1.1 ha. Se encontró que la tasa relativa de crecimiento está fuertemente influida por el tamaño inicial de los árboles, en tanto que la severidad de la infestación y la especie de muérdago presente no tuvieron un efecto significativo. Sin embargo, se presentaron diferencias en la relación dap-altura entre árboles no infestados e infestados: en general, los pinos parasitados alcanzan menos altura que los árboles no infestados que tienen el mismo dap. Por otro lado, *A. globosum* es más frecuente en pinos <2 m de extensión de la copa, pero tiene una mayor severidad en pinos mayores a dicha talla; mientras que, *A. vaginatum* no presenta un patrón claro en cuanto a la preferencia en el tamaño de los hospederos.

Las interacciones interespecíficas entre especies de muérdago es un tema poco explorado y, sin embargo, éstas tiene consecuencias importantes en la dinámica poblacional de estas plantas parásitas y posibles implicaciones un manejo forestal adecuado.

## Abstract

Biotic interactions play a fundamental role in plants demographic processes, because they affect resources uptake whether it is in a positive or negative way. The importance of competition on population structure has been widely studied, thus, the role of antagonisms as a determinant factor on species coexistence has been acknowledged. Effect of competition and other interspecific interactions between parasitic plants has not been fully addressed. These are plants with heterotrophic nutrition that depend on a host plant to obtain their nutrients. This raises the question of whether the population dynamics and the infection process of parasitic plants, such as dwarf mistletoes (*Arceuthobium*), are affected by interspecific interactions, and if it presents the same coexistence mechanisms observed for autotrophic plants.

In central Mexico temperate forests, *Arceuthobium globosum* and *A. vaginatum* are widely distributed parasitizing *P. hartwegii* stands, which is an important species for forestry. The two mistletoe species present co-infection within the same individual host, which has been described as an unusual phenomenon for the genus. Hence, in this thesis it is explored the role of interactions on these dwarf mistletoe species coexistence, for which the following questions arise: i) how interspecific interactions affect dwarf mistletoes population dynamics?, ii) are there any differences in infestation patterns of the two sympatric species?, and iii) what effect does mistletoe coexistence have on the growth of the host? These questions are addressed along four chapters: in the first one, a literature review about competition between parasitic plants is done, where it was found that, although co-infection has been reported in different species, the subject has not been studied. Literature on parasitic organisms in general (mostly animal parasites) indicates that niche differentiation is required for coexistence, which can be in form of habit specialization and/or spatial segregation within the host. According to the latter, and the similarities and differences of parasitic plants with autotrophic ones, it is hypothesized the possible outcomes of competition between parasitic plants according to the type of parasitism and dependence degree toward the host.

On chapter two it is explored how interespecific interactions between the two species affect population dynamics, including population growth and colonization potential of new hosts. For this, a follow up of infestation was done on an area of 1.1 ha on Zoquiapan region (Parque Nacional Iztaccíhuatl Popocatépetl). It was found that self-regulation is stronger than interspecific competition; however, intensity and sign of interactions between the two species depend strongly of host size and the demographic process. For population growth in previously infested trees competition is present, except for trees with a small size, where *A. vaginatum* is facilitated by *A. globosum*. For colonization process facilitation is depicted between the two species; nevertheless, this losses importance with larger trees. Demographic importance of interactions (the effect on population size) depends of the stand structure (tree size, density and size heterogeneity), where a homogeneous stand favors facilitation, whereas a heterogeneous one favor competition. It was also determined that the two species reach stable coexistence, fulfilling the invasibility criterion, hence if one species is already present in one stand, the probability of a second species invasion is greater.

On the third chapter, the infestation patterns of both mistletoes species are evaluated, including their incidence (proportion of parasitized hosts), severity (number of parasites for each host) and aggregation between and within stands. These variables were

evaluated in 75 stands of 3,300 $m^2$ distributed along the Zoquiapan region. It was found a clear dominance of *A. vaginatum* in the area, since it was present in most of the sites. Both species incidences were negatively correlated and it was not found a significant effect of other factors, such as elevation and slope. Incidence and severity of each species has a lineal relation, which indicates that there is a uniform increment of severity with incidence. Both species are aggregated within the plots (i.e., in the hosts), which is a consistent pattern in dwarf mistletoes that have a limited dispersal; however, only *A. globosum* shows an aggregated pattern between plots, so we may think that there is a spatial segregation of this species.

On the fourth chapter, the isolated and the joint effect of the two species of mistletoe on host growth were evaluated, as well as the allometric relationships and size susceptibility of *P. hartwegii*. For these, it was registered the change on dbh and crown spread on trees with different sizes during three years, on the 1.1 ha stand. It was found that the relative growth rate is strongly influenced by trees initial size, whereas infestation severity and infecting species were non-significant. However, differences occurred in the dbh-height relationship between infested and un-infested trees: generally, parasitized pines were shorter that non-parasitized trees with the same dbh. Furthermore, *A. globosum* is more frequent on pines <2 m of Crown spread, but has a greater severity in larger pines; meanwhile, *A. vaginatum* does not present a clear pattern in reference to host size preference.

Interspecific interactions between mistletoes species is a poorly explored subject and, nonetheless, this may have important consequences on the population dynamics of these parasitic plants and implications for forest management.

# INTRODUCCIÓN GENERAL

Los organismos no viven aislados en su medio, sino rodeados de diferentes elementos ambientales, tanto abióticos como bióticos. Dentro de los elementos bióticos, las interacciones constituyen las relaciones que se establecen entre uno o más individuos de la misma o de distinta especie (Del Val y Boege, 2012) que tienen consecuencias positivas o negativas en distintos niveles de los sistemas ecológicos (desde individuos hasta ecosistemas). Las interacciones interespecíficas (i.e., que ocurren entre individuos de especies distintas) suelen afectar los procesos demográficos de las poblaciones, ya que influyen en la supervivencia, el éxito reproductivo, el establecimiento y el desempeño de los organismos involucrados (Callaway y Walker, 1997).

Las interacciones bióticas juegan un papel importante en el mantenimiento de la diversidad de especies (Schemske *et al.*, 2009), ya que la estructura y la composición de una comunidad biológica es resultado de cuántas y cuáles especies pueden formar parte y llegar a una coexistencia estable (Chesson, 2000; Gaxiola y Armesto, 2012). La competencia es una interacción antagonista en la que las partes involucradas sufren efectos negativos sobre su adecuación, lo que resulta en tasas de crecimiento poblacional disminuidas (Gotelli, 1995). Esto sucede cuando dos individuos de la misma o distinta especie requieren de los mismos recursos para su desempeño, por lo tanto, afectan su disponibilidad para otros individuos. Debido a esto, se le ha dado un gran peso al estudio de la competencia como una de las relaciones más intensas entre las especies que determina la coexistencia entre éstas (Grace y Tilman, 1990).

El papel de las interacciones interespecíficas en la coexistencia de las especies, en particular la competencia, ha sido ampliamente estudiado en las plantas (Went, 1973; Austin, 1990; Bengtsson *et al.*, 1994; Chesson, 2000; Craine y Dybzinki, 2013). Si tomamos en cuenta que las plantas son organismos con movilidad limitada —es decir, que sólo pueden transportarse de un lugar a otro a través de sus propágulos, los mecanismos de explotación de recursos son básicos para su permanencia. Esto mismo ha llevado al surgimiento de adaptaciones que aparentemente están dirigidas a aumentar su habilidad competitiva para explotar recursos.

Una de las modificaciones morfológicas más interesantes se registra en las plantas que parasitan a otras plantas. Las plantas parásitas constituyen un grupo muy diverso: nueve órdenes, 18 familias, 270 géneros y 4500 especies, de distribución mundial (APG, 2003; Der y Nickrent, 2008). A pesar de que este hábito evolucionó independientemente en al menos 10 eventos distintos (Barkman *et al.*, 2007; Der y Nickrent, 2008), todas estas plantas tienen la característica común de que toman sus recursos del floema o del xilema de la planta hospedera a partir de raíces modificadas llamadas haustorios (Nickrent, 2002). Dentro de las plantas parásitas, los muérdagos pueden considerarse como un grupo clave debido a que el impacto que tienen dentro de la comunidad que habitan es desproporcionadamente grande en relación con su abundancia, ya que: i) son un factor de regulación poblacional importante (Mathiasen *et al.*, 2008), y ii) cuando tienen baja abundancia decrece la diversidad de organismos asociados al muérdago (Watson, 2001).

Los muérdagos son plantas hemiparásitas de tallos aéreos cuya característica distintiva es que presentan una cubierta de mucílago, la viscina, alrededor de su semilla que les permite adherirse a las ramas del hospedero (Aukema, 2003). Los muérdagos enanos (*Arceuthobium* spp; Viscaceae) son un grupo lleno de particularidades. Estas plantas son pequeños arbustos con hojas escuamiformes y flores poco conspicuas, generalmente del mismo color de sus tallos, y que dispersan sus semillas de forma balística (Mathiasen *et al.*, 2008); debido a la naturaleza de este hábito, estas plantas se encuentran sólo en el ámbito de distribución de su hospedero. Si, además de esto, sabemos que su dispersión balística no llega más allá de 14 m de distancia (Robinson y Geils, 2006) es fácil creer que la disponibilidad de hospederos es un recurso limitante, más aún si el muérdago tiene una alta especificidad por éste (Norton y Carpenter, 1998). Esto lleva a pensar en que existe competencia, tanto intra como interespecífica, entre los muérdagos por obtener los recursos que le provee el hospedero. Sin embargo, son pocos los casos reportados donde dos o más especies de muérdago enano parasiten al mismo hospedero (Hawksworth and Wiens, 1996). En la zona central de México se encuentra un área de simpatría entre dos especies de muérdago enano, *Arceuthobium globosum* y *A. vaginatum*, donde es común observar el parasitismo dual de estas dos especies (Fig. 1). Una gran cantidad de estudios se han realizado en la región de Zoquiapan dentro del Parque Nacional Iztaccíhuatl Popocatépetl, entre otras. En dicha zona se han registrado infestaciones de hasta 76% de los árboles parasitados por *A. globosum* (Hernández-Benítez *et al.*, 2005) y 47% por *A. vaginatum* (Queijeiro-Bolaños *et al.*, 2013). En esta y otras zonas cercanas, como en la cuenca del río Magdalena en el Distrito Federal, se han reportado algunos factores abióticos que pueden afectar su incidencia de manera significativa, como son la pendiente y la altitud (Hernández-Sánchez, 2012; Queijeiro-Bolaños *et al.*, 2013), así como el disturbio antropogénico, como incendios, la presencia de tocones y la distancia a brechas y caminos (Hernández-Sánchez, 2012; Queijeiro-Bolaños *et al.*, 2013). Entre los factores bióticos que afectan la incidencia se encuentran la comunidad biótica, la densidad de individuos hospederos y de individuos no hospederos (Hernández-Sánchez, 2012; Queijeiro-Bolaños *et al.*, 2013). Aunque la mayor parte de la literatura acerca de los muérdagos enanos se ha limitado a conocer su incidencia y efecto sobre el hospedero, y no comprende estudios sobre interacciones bióticas, se tiene evidencia de que existe una asociación negativa entre la incidencia de ambas especies y que tienen una distribución diferencial sobre el hospedero (Queijeiro-Bolaños *et al*., 2011, 2013).

Estas dos especies son las más extendidas en el territorio mexicano (Cibrián *et al.*, 2007), además de ser consideradas como uno de los agentes bióticos más dañinos para las actividades de aprovechamiento forestal (Madrigal *et al.*, 2007), ya que afectan miles de hectáreas arboladas en las cuales reducen el crecimiento de los árboles (hasta un 30% de reducción en altura con respecto a árboles no infectados) y alteran sustancialmente la anatomía de la madera del tronco (Cibrián *et al.*, 2007). A pesar de esto, no se tiene conocimiento acerca de su dinámica poblacional ni cómo influyen las interacciones interespecíficas en ésta, lo cual puede proveer una importante base científica para el manejo forestal.

En esta tesis se estudian las interacciones interespecíficas entre dos especies de muérdago enano que comparten el mismo recurso, *Arceuthobium globosum* y *A. vaginatum*. Específicamente, las preguntas planteadas son: i) ¿cómo afectan las interacciones interespecíficas la dinámica poblacional de los muérdagos enanos?, ii) ¿existen diferencias en los patrones de infestación de las especies de muérdago enano que se encuentran en simpatría?, y iii) ¿qué efecto tendrá la coexistencia de dos especies de muérdago enano sobre el crecimiento de su hospedero?

A manera de introducción, se incluye como **primer capítulo** una revisión del tema de la competencia entre plantas parásitas. En este capítulo se aborda primero la competencia entre plantas de manera generalizada, así como definiciones, mecanismos y métodos utilizados para estimar la importancia y la intensidad de la competencia. En segundo lugar, se explora la competencia entre organismos parásitos, así como cuáles son las similitudes y diferencias con los organismos de vida libre. Finalmente, se hace una evaluación acerca del conocimiento sobre competencia entre plantas parásitas y cuáles son las futuras direcciones de estudio.

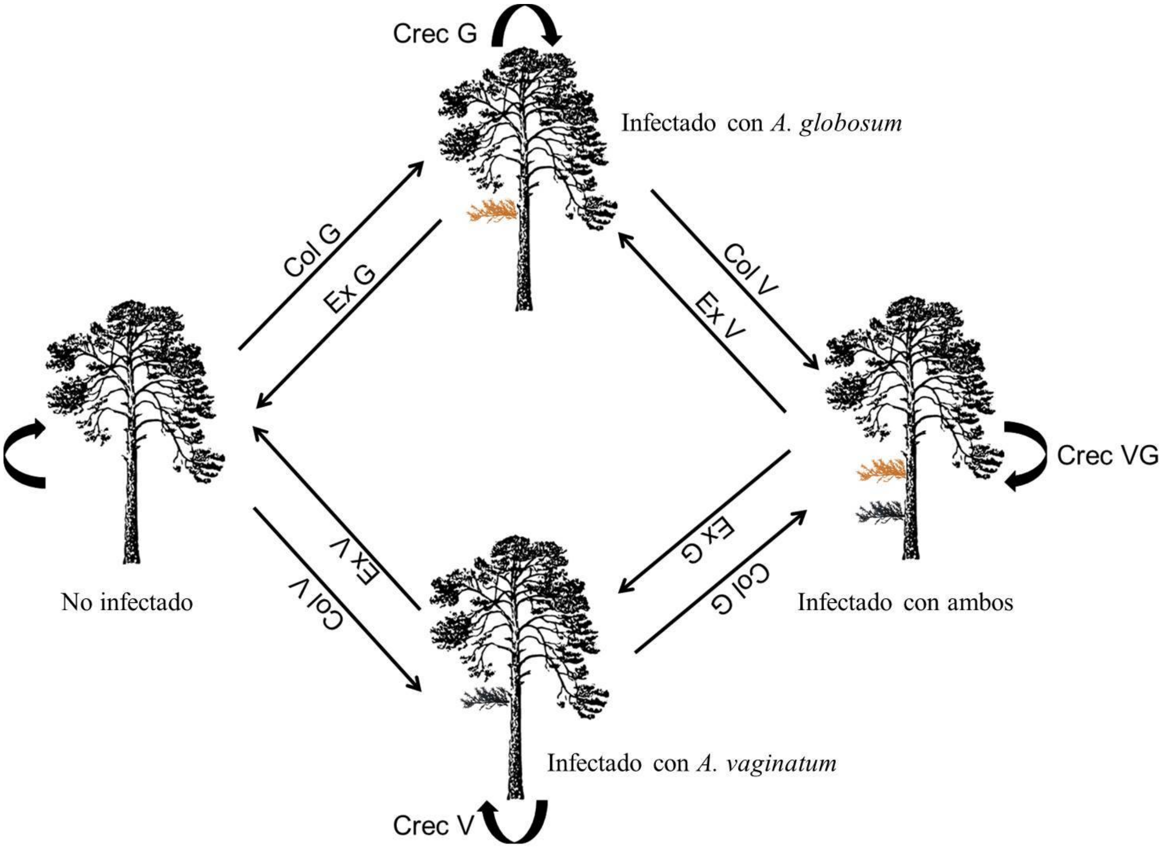
En el **segundo capítulo** se estudia el efecto de las interacciones interespecíficas en la dinámica poblacional de las dos especies de muérdago. El estudio se realizó en la zona aledaña al cerro El Papayo, en Zoquiapan (Parque Nacional Iztaccíhuatl Popocatépetl), Estado de México, en un rodal de 1.1 ha, que es el área donde se encuentra con mayor frecuencia y abundancia a las dos especies coexistiendo sobre *Pinus hartwegii*. Para conocer cómo las interacciones afectan la dinámica de estas especies se modelaron los procesos que incluyen el crecimiento de la población de muérdago en árboles ya infestados (o su desaparición -extinción local- en esos árboles) y la colonización de nuevos hospederos, tal como se ilustra en la Fig. 2. Asimismo, se probó si las dos especies podían llegar a la coexistencia estable de acuerdo con el criterio de invasibilidad (Turelli, 1977), el cual representaría la capacidad de una población de muérdago de infestar bosques previamente infestados por otra especie.

En el **tercer capítulo** se hace una evaluación de los muérdagos en una escala espacial mayor, donde se utilizan 75 parcelas de 0.33 ha dentro de la zona de Zoquiapan para describir la incidencia, la severidad y los patrones de agregación jerárquica de las dos especies. En este capítulo se busca saber si hay diferencias en los niveles de infestación, medidos mediante su incidencia (i.e., proporción de árboles infestados) y su severidad (o sea, la cantidad de muérdagos por hospedero), entre las dos especies, así como conocer si existe una relación negativa entre las incidencias de las especies. También se analiza la relación incidencia-severidad, ya que es una herramienta útil para diagnosticar fácilmente la infestación en los sitios. Adicionalmente, se busca evaluar si factores abióticos, como la altitud y la pendiente, que han sido reportados como determinantes en la presencia de muérdagos enanos, tienen algún efecto sobre la incidencia. Finalmente, se analizan los patrones de agregación de las dos especies, dentro y entre parcelas, esperando un patrón diferencial debido a la simpatría. Este capítulo corresponde a un artículo publicado en *European Journal of Forest Research* (2014, 133: 297-306).

En el **cuarto capítulo** se evalúa la coexistencia de las dos especies de muérdago a partir del efecto sobre el hospedero. Esto es, se compara la tasa relativa de crecimiento de *P. hartwegii* con condiciones distintas: no parasitados, parasitados por una sola especie (efecto aislado) y parasitado por ambas (efecto conjunto). Asimismo, se analiza si hay diferencias en las relaciones alométricas de los pinos (altura-diámetro) bajo estas mismas condiciones y si existen hospederos más susceptibles a la infestación debido a su tamaño. Este capítulo corresponde a un artículo aceptado en *Botanical Sciencies*.

Fig. 1. Coexistencia de *Arceuthobium globosum* y *A. vaginatum* en Zoquiapan, Edo. de México. Foto: M. Queijeiro-Bolaños.

Fig. 2 Procesos demográficos de *Arceuthobium globosum* (naranja) y *A. vaginatum* (negro). Col=colonización, Ex=extinción local, Crec=crecimiento, G=*A. globosum*, V=*A. vaginatum*.



# CAPÍTULO 1

# COMPETENCIA ENTRE PLANTAS PARÁSITAS

Artículo de revisión

## INTRODUCCIÓN

Todos los organismos que se encuentran coexistiendo en tiempo y en espacio interactúan entre sí de distintas formas -ya sea directa o indirectamente- y con distintas intensidades. Algunas interacciones son muy evidentes, tal como la depredación *sensu stricto*, mientras que otras, como la competencia, resultan menos conspicuas. Las interacciones competitivas han sido ampliamente reconocidas como una de las principales fuerzas ecológicas que moldean la dinámica de poblaciones (Connell, 1990; Wootton y Emmerson, 2005) y comunidades (Paine, 1980; Wootton, 1994; Morin, 2011), ya que es evidente que juega un papel importante en el ensamblaje de especies y que forma parte de los mecanismos de coexistencia de las mismas (Chesson, 2000), además de ser un importante agente de selección (Agrawal, 2001). Por esto, ha sido un tema de investigación recurrente en investigaciones de ecología vegetal, en los que se han discutido varios aspectos que van desde los mecanismos por los cuales opera la competencia hasta los métodos para cuantificar su importancia e intensidad (Freckleton y Watkinson 2001a; Wootton y Emmerson, 2005). El tema de competencia ha sido ampliamente estudiado en plantas autótrofas (que es el hábito más común en este grupo), en las cuales esta interacción depende sobre todo de la limitación por radiación solar, por nutrientes y por agua. Sin embargo, existe un relativamente pequeño grupo de plantas heterótrofas, las plantas parásitas, que pueden o no competir por el recurso lumínico, y por los recursos extraídos del sistema vascular del hospedero, siendo este último aparentemente el recurso más limitante. No obstante, no hay estudios formales sobre la competencia entre plantas parásitas.

Los organismos parásitos en general han sido muy estudiados desde los siguientes puntos de vista: distribución espacial (Aukema y Martínez del Río, 2002; Aukema, 2004; Solís y Suzán, 2014); virulencia y efectos negativos sobre el hospedero (Seem, 1984; Hatcher y Dunn, 2011); efecto indirecto sobre las interacciones de los hospederos con el resto de la comunidad biótica, principalmente con la fauna asociada (por ejemplo Watson, 2001); y competencia aparente entre especies hospederas (Hatcher y Dunn, 2011). Sin embargo, la competencia parásito-parásito - ya sea por luz o por el hospedero -, puede tener un efecto considerable en la estructura de sus poblaciones, así como derivar en una consecuencia evolutiva (Hatcher y Dunn, 2011).

Esta revisión se divide en dos secciones. En la primera se aborda el tema de la competencia entre plantas en general: definición, mecanismos y métodos apropiados para medir su efecto a nivel poblacional; en tanto que en la segunda se revisa el estudio de la competencia en organismos parásitos, con énfasis en las plantas parásitas, cómo se ha abordado su estudio y cuáles son las similitudes y diferencias con los organismos de vida libre. Con esta sección se busca responder si se ha estudiado la competencia parásito-parásito y, de ser así, cuáles han sido las aproximaciones de su estudio. Esto último tiene la finalidad de llegar a un diagnóstico de la competencia entre plantas parásitas y cuáles pueden ser las futuras direcciones de estudio.

## DEFINICIÓN DE COMPETENCIA Y MECANISMOS

La competencia puede ser definida como la reducción en la tasa de crecimiento poblacional debido a la disminución en la disponibilidad de recursos causada por los individuos dentro la comunidad (Freckleton y Watkinson, 2001a). El consumo y cambio en la disponibilidad de recursos por un individuo tiene como consecuencia que otro individuo crezca más lentamente, deje menos progenie o incluso muera (Connell, 1990). El consumo de los recursos puede llevarse a cabo por individuos de la misma especie dentro de la población, donde hablaríamos de competencia intraespecífica, o por individuos de distintas especies, donde se trata de competencia interespecífica. Es importante distinguir entre dos efectos substanciales pero independientes: la importancia demográfica y la intensidad de la competencia. La importancia demográfica se refiere al efecto de esta interacción en el crecimiento poblacional neto medido como el cambio en el número de individuos en un tiempo dado; en tanto que la intensidad es el efecto medido a nivel individual a través de un coeficiente *per capita* (Freckleton y Watkinson, 2001a; Martorell y Freckleton, 2014). En cuanto a los mecanismos, se definen principalmente dos, que son la interferencia y la explotación (Connell, 1990). El primero se refiere a una forma directa donde los organismos involucrados pueden tener una interacción física, mientras el segundo hace referencia a un mecanismo indirecto donde el consumo por parte de un organismo disminuye la disponibilidad de nutrientes para otros organismos (Grace y Tilman, 1990).

De lo anterior, podemos revisar brevemente cómo se ha abordado su estudio en las comunidades vegetales [ver Wootton y Emmerson (2005) para una revisión más detallada]. El estudio de las interacciones ha tenido distintos acercamientos, tanto teóricos, como observacionales y experimentales (Laska y Wootton, 1998; Wootton y Emmerson, 2005). Los métodos los podemos dividir arbitrariamente, según el concepto o índice usado, en los que miden la intensidad de la interacción y los que analizan la estrategia de estudio empleada (Laska y Wootton, 1998; Abrams, 2001; Wootton y Emmerson, 2005). De acuerdo con Wootton y Emmerson (2005), hay cuatro estrategias, estrechamente relacionadas con un diseño experimental particular, para estimar la intensidad de la interacción: los experimentos de campo, los de laboratorio, el trabajo observacional y el análisis de sistemas dinámicos.

En los experimentos de campo hay una manipulación de las variables en un contexto natural y, aunque probablemente sea la forma más acertada, generalmente se requiere el mismo número de tratamientos que de parámetros (aunque existen diseños experimentales que pueden ser utilizados para resolver este problema), hay muchas variables externas difíciles de controlar, puede haber un efecto indirecto de otras interacciones y puede existir error de muestreo en poblaciones pequeñas (Wootton y Emmerson, 2005). En este tipo de estudios se encuentran los experimentos de reemplazamiento, los de adición y los pareados simples, todos los cuales juegan con la densidad y la proporción de las especies involucradas en la interacción (Gibson *et al.*, 1999; Goldberg y Scheiner, 2001). Buenos ejemplos de este tipo de estrategia son los experimentos de Paine (1992) y Wootton (1994), en los que se removieron especies depredadoras o competidoras para posteriormente estimar el impacto sobre la comunidad.

Los experimentos de laboratorio, por su parte, tienen la gran ventaja de que se pueden aislar a las especies de las que nos interesa medir la interacción (Wootton, 1994; Wootton y Emmerson, 2005); sin embargo, no queda claro si la respuesta la podemos extrapolar a condiciones naturales y generalmente se expresan en una magnitud mayor que en condiciones de campo, lo que significa que tienen poco realismo aunque nos permite medir el efecto y la respuesta de una interacción (Wootton, 1994; Gibson *et al.*, 1999; Wootton y Emmerson, 2005). Al igual que los experimentos de campo, se pueden manipular las densidades de las especies. Bender *et al.* (1984) propusieron los experimentos de pulso y de presión. En los experimentos de pulso se mide la densidad y el crecimiento de las especies de una comunidad como respuesta a la perturbación (i.e., manipulación de la densidad) de una o un conjunto de especies y en los de presión se crean cambios sostenidos en la densidad de una o varias especies (i.e., se mantiene un número predeterminado, ya sea agregando o removiendo individuos) seguido por la medición de la densidad y crecimiento poblacional de las especies después de que la comunidad ha alcanzado el equilibrio (Bender *et al.*, 1984). Sin embargo, en este tipo de experimentos existe el problema de que no todas las poblaciones son manipulables y que generalmente no se obtiene una respuesta lineal (Wootton, 1994).

Por otro lado, los datos observacionales son útiles para medir la intensidad de una interacción sin necesidad de realizar manipulaciones (Freckleton y Watkinson 2001a; Ives *et al.*, 2003; Wootton y Emmerson, 2005; Martorell y Freckleton, 2014). Este método nos permite estimar la intensidad y la importancia de las interacciones a partir de datos obtenidos en censos poblacionales, en muestras grandes y a largo plazo, representado como una superficie de respuesta cómo cambia la densidad de una especie focal con distintas combinaciones de densidad de las especies asociadas (Law y Watkinson, 1987; Law *et al.*, 1997; Freckleton y Watkinson, 2001a; Daamgard y Fayolle, 2010).

Finalmente, los modelos dinámicos ajustan los cambios en abundancia o biomasa en el tiempo (Wootton y Emerson, 2005). Estos modelos funcionan bien en intervalos de tiempo largos y se incluye el error de medición en el modelo (Ives *et al.*, 2003), ya que en las series de tiempo puede haber correlación serial que puede llevar a una mala interpretación de los resultados y se puede presentar retroalimentación entre las variables (Wootton, 1994; Wootton y Emmerson, 2005). Se han propuesto análisis de regresión múltiple dinámicos y análisis de series de tiempo, en los cuales se miden cambios en densidad o biomasa en el tiempo (Pfister, 1995; Wootton, 1994).

En cuanto a los índices, hay cuatro que han sido los más frecuentemente usados: la matriz comunitaria, la matriz jacobiana, la matriz jacobiana inversa y la matriz de remoción (Laska y Wootton, 1998), según se expone a continuación. La matriz comunitaria nos da como resultado el efecto *per capita*, es decir, el efecto directo a corto plazo que tiene un individuo de una especie sobre un individuo de una segunda especie (Laska y Wootton, 1998; Wootton y Emmerson, 2005). Éste se basa en el coeficiente de competencia $\alpha$ de la ecuación de Lotka-Volterra donde se obtiene una matriz con cuatro elementos: el efecto de la $x$ en $y$, el efecto de $y$ en $x$, el efecto de $x$ en $x$ y el efecto de $y$ en $y$ (MacArthur 1972, Laska y Wootton 1998).

La matriz de elementos jacobianos, por su parte, representa el efecto directo de un individuo de una especie sobre la población completa de una segunda especie en (o cerca de) el equilibrio, y generalmente se usa cuando se aplican experimentos de pulsos (May, 1973; Laska y Wootton, 1998; Wootton y Emmerson, 2005), los cuales se refieren a una alteración rápida de la abundancia de una especie y, posteriormente, se registra la repuesta del resto de la comunidad (Bender *et al*., 1984). Por otro lado, la matriz jacobiana invertida se obtiene tomando la inversa de la matriz jacobiana y predice el cambio en las condiciones de equilibrio del sistema con la adición sustancial de individuos de una especie focal y nos permite, al contrario de los dos métodos anteriores, incorporar efectos indirectos (Yodzis, 1988; Laska y Wootton, 1998, Wootton y Emmerson, 2005).

Finalmente, la matriz de remoción nos muestra las diferencias en abundancia en una especie focal en presencia o ausencia de una o más de las especies con las que interactúa, como una manera de probar el efecto que tiene una interacción en su comunidad (Paine, 1992; Laska y Wootton, 1998; Wootton y Emmerson, 2005).

Existen otras medidas de la intensidad de la interacción obtenidas a partir de estudios empíricos, tal como puede ser la obtención de coeficientes de relaciones directas e indirectas por medio de un análisis de rutas (*path analysis*) y modelos de cadenas de Markov (Paine, 1992; Wootton, 1994; Mitchell, 2001; Wootton y Emmerson, 2005). Obviamente, las estrategias pueden usar distintos tipos de índices dependiendo del contexto y del sistema de estudio. Además, existen índices modificados o creados específicamente para cada tipo de interacción, como son el índice de diferencia cruda y el índice de Paine para una interacción depredador-presa (Berlow *et al.*, 1999) o los 24 índices para estimar la intensidad de la competencia analizados con detalle por Weigelt y Jolliffe (2003).

## PLANTAS PARÁSITAS, EXTRACCIÓN DE RECURSOS Y COMPETENCIA

Las plantas parásitas se caracterizan por obtener una parte o la totalidad de sus recursos a partir de otra planta, por lo que se les ha llegado a considerar como organismos heterótrofos (Musselman y Press, 1995; Heide-J∅rgensen, 2008). Están asociadas obligadamente a un hospedero para extraer agua y solutos inorgánicos a partir de su sistema vascular; sin embargo, pueden o no ser fotosintéticamente activas (Musselman y Press, 1995), en cuyo caso, el grado de dependencia hacia el hospedero varía (Tabla 1). Las plantas holoparásitas son 100% dependientes de los fotosintatos del hospedero, mientras que en las hemiparásitas, al ser fotosintéticamente activas, existe un gradiente de dependencia: mientras algunas especies extraen sólo nutrientes inorgánicos, otras, como los muérdagos enanos (*Arceuthobium* spp.), derivan más del 70% de los asimilados orgánicos a través del xilema (Stewart y Press, 1990; Press y Whittaker, 1993; Hawksworth y Wiens, 1996; Hibberd y Jeschke, 2001), como son amidas, aminoácidos, ácidos orgánicos y azúcares del hospedero (Govier *et al.*, 1967). Un rasgo esencial de las plantas parásitas es el haustorio, que es la estructura que liga al parásito y al hospedero, pues sirve para la absorción y almacenaje de nutrientes y es capaz de seleccionar los solutos que toma (Govier *et al.*, 1967; Musselman y Press, 1995).

Para extraer y seleccionar estos solutos la planta parásita debe tener una tasa de transpiración, potencial hídrico y concentración osmótica mayores que la del hospedero, modificando la arquitectura hidráulica de la planta parasitada (Stewart y Press, 1990; Hawksworth y Wiens, 1996; Meinzer *et al.*, 2004). En este caso, las plantas parásitas mantienen abiertos los estomas por un tiempo prolongado, incluso de noche, provocando una mayor tasa de transpiración en el hospedero y, por lo tanto, un mayor transporte de solutos, llevando al hospedero a un fuerte estrés hídrico (Graves, 1995; Press *et al.*, 1999). Asimismo, al tener las plantas parásitas una mayor conductancia en las hojas, tienen una menor resistencia a la difusión de $CO_2$, lo que, en combinación con las bajas tasas fotosintéticas y las altas tasas de transpiración, resultan en un bajo aprovechamiento de agua (Press *et al.*, 1999).

Las plantas parásitas tienen en el hospedero un recurso limitante al requerir la presencia de otra planta para establecerse exitosamente y desempeñarse adecuadamente. Por esto, es lógico predecir que las plantas parásitas deben presentar competencia cuando más de un individuo se encuentra extrayendo recursos del mismo sistema vascular. La competencia por recursos abióticos, como la radiación solar, pueden o no tenerla, dependiendo de si son hemiparásitas u holoparásitas. La toma de nutrientes y agua depende para los parásitos totalmente de la disponibilidad de estos recursos dentro del hospedero, por lo cual constituyen en este caso especial recursos bióticos, creando una relación compleja, pues la misma toma de los recursos modifica significativamente rasgos fisiológicos del hospedero, como son la asignación de los recursos y las tasas de transpiración (Press, 1995; Meinzer *et al.*, 2004; Press y Phoenix, 2005).

La tasa de crecimiento de una población de plantas parásitas, por lo tanto, debe estar limitada por la cantidad de recursos bióticos disponibles (i.e., los hospederos y su estado fisiológico) y cuántos individuos de la misma especie están coexistiendo en la zona y en el mismo hospedero (i.e., competencia intraespecífica). Por ejemplo, el modelo de crecimiento de *Rhinanthus alectoropholus* (planta hemiparásita de raíz) predice que el crecimiento y la biomasa acumulada de la planta parásita está correlacionada con el crecimiento del hospedero, pero, además, la parásita debe tener una virulencia intermedia y, por tanto, densidades intermedias (Hautier *et al.*, 2010). Con una virulencia alta, es decir múltiples individuos parasitando al mismo hospedero individual, los recursos son consumidos más rápidamente (Frank, 1996), afectando al hospedero y a los parásitos conespecíficos (Hautier *et al.*, 2010).

No existen reportes formales de dos o más especies de plantas parásitas compitiendo por los mismos recursos, pues generalmente se ha abarcado el tema de la competencia aparente o mediada por una planta parásita (Hatcher y Dunn, 2011), donde se afirma que las plantas parásitas tienen un efecto similar al de los parásitos animales en las comunidades (Press y Phoenix, 2005). Sin embargo, en algunos trabajos se registra la coexistencia de dos o más especies parasitando a la misma especie hospedera e incluso al mismo individuo, sin que se aborde directamente el tema de competencia (Tabla 2). Por lo tanto, no es posible hacer una revisión basada en estudios publicados de cómo es la competencia interespecífica entre plantas parásitas. No obstante, los estudios de otros organismos parásitos nos pueden brindar un marco de referencia sobre los posibles resultados de la competencia entre plantas parásitas.

La competencia entre organismos parásitos puede involucrar competencia directa por recursos (Dobson, 1985; Hochberg y Holt 1990; Holt y Dobson, 2006) o competencia mediada por la inmunidad de los hospederos (Pedersen y Fenton, 2007), en la que la coinfección puede cambiar la susceptibilidad hacia algunos parásitos, modificando, por lo tanto, el resultado de la interacción (Telfer *et al.*, 2008). A partir de estos trabajos se ha llegado a la conclusión de que la persistencia de dos especies parásitas compartiendo una especie de hospedero no ocurrirá a menos de que exista una diferenciación de nichos entre los organismos parásitos (Hatcher y Dunn, 2011), por lo que la coexistencia implica la existencia muy probable de un grado de especialización en sus hábitos.

Los trabajos sobre competencia intra e interespecífica entre especies parásitas están enfocados a parásitos invertebrados (por ejemplo, tremátodos y artrópodos) y microparásitos (bacterias, protistas y virus) de animales vertebrados (como ratones, peces, artrópodos y moluscos), donde la virulencia (grado de patogenicidad del parásito, indicado por la relación entre el número de parásitos y la pérdida de adecuación del hospedero; Nowak y May, 1994) afecta la interacción – un parásito con mayor virulencia podría tener la ventaja competitiva ya que puede excluir al competidor antes de que logre su transmisión (Frank, 1996) - y aumenta la dominancia de algunas especies en las comunidades de parásitos debido a una competencia asimétrica (Bordes y Morand, 2008). Algunos autores han analizado modelos poblacionales para estudiar los mecanismos de coexistencia entre organismos parásitos, donde coincidentemente llegan a la conclusión de que debe existir un grado de diferenciación de nichos para que las especies parásitas puedan coexistir (Dobson 1985, Hochberg y Holt 1990, Holt y Dobson 2006). Además, se da un evento de exclusión competitiva por parte de la especie que tenga mayor virulencia y pueda mantener su población a bajas densidades (Frank, 1996; de Roode *et al.*, 2005); de otro modo, la coinfección sólo es posible si hay algún grado de diferenciación de nichos, ya sea por la especialización en las estructuras o tejidos a parasitar, diferenciación en los estadios de desarrollo del hospedero susceptibles a ser infectados o por la agregación espacial dentro de éste (Hatcher y Dunn, 2011).

También se ha observado que la infección previa de una especie puede impedir la infección de una segunda especie, sirviendo como un tipo de protección hacia el hospedero o, incluso, para el primer parásito en llegar (Hatcher y Dunn, 2011). En infecciones duales (o coinfecciones), el parásito más virulento tendrá una ventaja competitiva si es que ha podido reproducirse y dispersarse antes de que muera el hospedero porque, de lo contrario, esto sería una desventaja (Frank, 1996). Generalmente los estudios realizados abarcan sólo competencia por explotación, aunque se ha registrado que también puede haber interferencia por exudados de toxinas (Massey *et al.*, 2004; Brown *et al.*, 2009). Por otro lado, han surgido distintos modelos de la dinámica poblacional de dos especies parásitas con coinfección. Dobson (1985), por ejemplo, revisa la dinámica de helmintos parásitos, y llega a la conclusión de que debe existir una segregación espacial dentro de las cavidades del hospedero para que dos especies de parásitos puedan coexistir.

Algunas de las observaciones anteriores pueden ser retomadas para las plantas parásitas; sin embargo, debe tomarse en cuenta que el grado de dependencia hacia el hospedero varía, por lo que el mecanismo y el resultado de la interacción deben ser distintos para cada caso (Tabla 3). En el caso particular de las plantas parásitas de raíz, la competencia puede asemejarse más a la experimentada por las plantas autótrofas, ya que parte de los nutrientes se obtienen de la raíz del hospedero y otra parte del suelo (Smith, 2000). Además, pueden parasitar las raíces de distintos individuos simultáneamente por lo que no dependen exclusivamente de un sólo individuo a lo largo de su vida. Por lo tanto, se puede presentar competencia intra o interespecífica por las raíces del hospedero; sin embargo, se espera que difiera el resultado de la competencia según su capacidad fotosintética. En el caso de las hemiparásitas, éstas pueden ser facultativas y sobrevivir un tiempo sin hospedero, aunque con un desempeño bajo (Smith, 2000; Heide-Jorgensen, 2008). Esto les confiere una ventaja ante la exclusión competitiva de la raíz de un hospedero, ya que puede estar infectando otro individuo o sobrevivir un tiempo hasta lograr encontrar las raíces de otro. También experimentan competencia por radiación solar, tanto con otras plantas parásitas o incluso con las especies hospederas (Hatcher y Dunn, 2011). En cambio, las holoparásitas, al no ser fotosintéticamente activas, no pueden sobrevivir sin estar adjuntas a un hospedero (Nickrent y Musselman, 2004; Heide-Jorgensen, 2008) y, a menos de que esté asociada con más de un individuo a la vez, su población será afectada en caso de ser excluidas de un individuo. Además, las plantas holoparásitas presentan una mayor dependencia y virulencia hacia el hospedero (Nickrent *et al.*, 1997), por lo que consumen una mayor cantidad de recursos y, por tanto, se esperaría una competencia más intensa.

En estas plantas, el patrón de distribución de nutrientes en el suelo va influir significativamente en su desempeño y en sus interacciones, tanto de parasitismo como de competencia (Hutchings *et al.*, 2003). Muchas especies vegetales de vida libre responden a la heterogeneidad del suelo con la proliferación de raíces en micrositios ricos en nutrientes (Casper *et al.*, 2000), lo que puede derivar en una fuerte competencia en las zonas del suelo concentración de éstos (Hutchings *et al.*, 2003). Para las plantas parásitas de raíz, esto implica que se concentrarán en las zonas donde exista una mayor acumulación de nutrientes y raíces, generando fuerte competencia intra e interespecífica.

La heterogeneidad en la distribución de recursos para las plantas parásitas de tallo estaría representada por la distribución del hospedero, ya que no dependen directamente de los nutrientes en el suelo. Se sabe que las parásitas de tallo, en particular los muérdagos (Loranthaceae y Viscaceae), muestran una autocorrelación espacial dentro del hospedero, entre hospederos y a nivel paisaje (Aukema, 2003; Queijeiro-Bolaños *et al.*, 2014). Entonces la disponibilidad y distribución espacial de los hospederos van a ser los factores centrales en la abundancia de parásitas de tallo, y éstas tenderán a agregarse en un mismo hospedero por lo que la competencia se esperaría que fuera intensa, aunque va a diferir según el grado de dependencia por fotosintatos (i.e., si son holo o hemiparásitas).

Existen pocos ejemplos de holoparásitas de tallo. Quizá el género más representativo es *Cuscuta* (Convolvulaceae), ya que es sumamente invasiva (Hatcher y Dunn, 2011). Dentro de este género se han descrito especies con mínima actividad fotosintética (como *C. reflexa*; Haberhausen *et al.*, 1992), pero en otras, como *C. europea*, la función fotosintética ha sido totalmente perdida (Machado y Zetsche, 1990). Las holoparásitas de tallo pueden extenderse a otros hospederos -como es el caso de *Cuscuta*- o permanecer sobre el mismo individuo; sin embargo, tienen la capacidad de ocupar prácticamente toda la copa del hospedero (Fig. 1), por lo que su alta dominancia y dependencia difícilmente permitirían la coexistencia con otras especies. En caso de coexistir, se esperaría que la competencia resulte asimétrica, donde la asimetría implica la repartición desigual de recursos como consecuencia de una ventaja competitiva por parte de los individuos más grandes (Freckleton y Watkinson, 2001b).

Las plantas hemiparásitas de tallo, por otro lado, tienen un menor grado de dependencia hacia el hospedero (Nickrent y Musselman, 2004; Heide-Jorgensen, 2008), lo que implica que la competencia debe ser menos intensa en comparación con las holoparásitas, y que pueden competir por el recurso lumínico. Sin embargo, existe un gradiente en la actividad fotosintética de estas plantas, tal como fue mencionado anteriormente, en el cual algunas obtienen el mayor porcentaje de sus fotosintatos a partir del hospedero (Press y Phoenix, 2005). No obstante, se sabe muy poco de la respuesta de las plantas parásitas a los factores abióticos que afectan su desempeño y, sobre todo, existen pocos estudios de la influencia de la radiación solar (Shaw y Weiss, 2000). Por ejemplo, de lo poco que se ha reportado, hay estudios que registran que hay una mayor penetración del haustorio cuando la semilla de la planta parásita es expuesta a la luz que cuando ésta no es expuesta, y que esta exposición favorece la producción de tallos y frutos, por lo que es un estímulo necesario para la reproducción (Scharpf, 1972; Shaw y Weiss, 2000). Cuando hay sombreo por parte del hospedero, se reduce el tamaño de los tallos de la parásita, pero el efecto del parasitismo hacia el hospedero se incrementa para compensar la falta de luz (Matthies, 1995).

También se ha visto que la infección por hemiparásitas es común en sitios de dosel abierto, comúnmente considerados como lugares de baja productividad (Press y Phoenix, 2005), y es muy frecuente en árboles altos, ya que en alturas bajas hay una menor asimilación de carbono por el efecto de sombreado del hospedero (Graves, 1995; Shaw y Weiss, 2000). Por lo tanto, hay una correlación positiva entre la abundancia de las hemiparásitas y la intensidad de radiación solar en la copa de los árboles (Bickford *et al.*, 2005). Se ha reportado que los aclareos forestales estimulan el crecimiento de plantas parásitas hasta en un 35%, pues hay una mayor entrada de radiación hacia las copas de los árboles y, a su vez, los hospederos sufren menos competencia por recursos con otros árboles (Bickford *et al.*, 2005). No obstante, hace falta información que revele claramente el papel de la radiación solar y otros recursos abióticos en el desempeño de las plantas parásitas.

Las hemiparásitas de tallo son menos invasivas que las holoparásitas y se pueden encontrar hasta tres especies distintas sobre un individuo (Arruda *et al.*, 2013). Esto puede deberse a que su infestación es localizada; es decir, que los tallos se desarrollan cerca del punto original de la infección (Hawksworth y Wiens, 1996), permitiendo la colonización de otros individuos en otras partes del hospedero. Sin embargo, en los muérdagos enanos (Viscaceae) la coexistencia es raramente registrada, pues sólo existen 13 reportes formales de dos especies sobre un mismo individuo (ver p. ej., Hawksworth y Wiens, 1996 y Queijeiro-Bolaños *et al.*, 2011; ver detalles en Tabla 2) y se alude a la hipótesis de la "exclusión competitiva del hospedero". Aunque no hay un mecanismo descrito, Hawksworth (1969) define en dicha hipótesis que si una especie de *Arceuthobium* está presente en una zona parasitando a su hospedero principal, una segunda especie de muérdago enano parasitará raramente a esta misma especie de hospedero. En algunas localidades específicas se puede ver el parasitismo dual entre muérdagos enanos, como es el caso de *A. globosum* y *A. vaginatum* coinfectando a *Pinus hartwegii* (Fig. 2a). En dicha zona se reportó una prevalencia de 35% de árboles parasitados, de los cuales 1% contenían a las dos especies (Queijeiro-Bolaños *et al.*, 2014). El desarrollo de los haustorios en los muérdagos enanos puede ser localizado o sistémico; la infección sistémica (o isofásica) es aquélla en la que el sistema endofítico del muérdago crece junto con el cambium de la rama infectada, por lo que el haustorio de un solo individuo puede invadir internamente gran parte del tejido del hospedero (Hawksworth y Wiens, 1996). De las especies en las que se ha registrado el parasitismo dual, sólo en un caso una de ellas crea infección sistémica (*A. americanum*), mientras que el resto son anisofásicos (Hawksworth y Wiens, 1996). Esta situación puede facilitar la coexistencia, al mantener los haustorios localizados en una zona; en cambio, un haustorio distribuido a lo largo de las ramas del hospedero pueden crear interferencia con otros individuos (Fig. 2b).

Vale la pena distinguir las diferencias entre plantas parásitas anuales y perennes. En general, las parásitas perennes tienen un aprovechamiento de recursos a partir del hospedero moderado, pues sí se conduce al hospedero hacia un mal estado de salud o a incrementar su mortalidad tiene como resultado una baja supervivencia de la misma parásita (Musselman y Press, 1995). Por ejemplo, las parásitas presentes en bosques templados (como los muérdagos) dependen de especies forestales de vida larga (Mathiasen *et al.*, 2008), por lo cual su tasa de consumo debe permitir niveles al menos basales de desempeño del hospedero. Los muérdagos enanos (*Arceuthobium* spp.) han sido considerados como uno de los agentes biológicos que ocasionan más pérdidas forestales en rodales comerciales (Geils y Hawksworth, 2002; Heide-Jorgensen, 2008); sin embargo, estas plantas, aunque incrementan la probabilidad de mortalidad de sus hospederos al facilitar la infección de otros patógenos (Hawksworth y Wiens, 1996), rara vez lo matan, a menos de que la infestación tenga un gran nivel (Shaw *et al.*, 2008). No hay estudios directos, pero se supone que un alto nivel de infestación incrementa la competencia intraespecífica, lo que a su vez altera la disponibilidad de recursos (esto es, los hospederos), razón por la cual se esperaría que la competencia entre estas plantas sea intensa, pero no importante a nivel poblacional.

A las plantas parásitas anuales no les afecta poblacionalmente acabar rápidamente con todos los recursos del hospedero, pues están buscando reproducirse a la brevedad (Nickrent y Musselman, 2004). Las parásitas que causan problemas agrícolas son, generalmente, de ciclos anuales y por lo tanto extraen recursos más agresivamente, incluso ocasionando la pérdida total en un cultivo local (Heide-Jorgensen, 2008), como es el caso de *Striga hermonthica* parasitando a *Zea mays* en distintos países africanos (Smith *et al.*, 1995). Otros ejemplos son plantas de los géneros *Cuscuta* (Convolvulaceae), *Cassytha* (Lauraceae) y *Orobanche* (Orobanchaceae) (Heide-Jorgensen, 2008). Bajo estas condiciones es difícil pensar en la coexistencia con otras parásitas, y es común que una sola especie sea la dominante en cultivos (Heide-Jorgensen, 2008). Estas plantas explotan rápidamente los recursos antes de que otras colonicen el mismo espacio, como respuesta evasiva a la competencia.

A partir de esta revisión, se pueden suponer los posibles resultados de la competencia según los distintos tipos de plantas parásitas (Tabla 3). En resumen, la coexistencia entre plantas parásitas dependerá de los siguientes factores: i) la disponibilidad de hospederos y su patrón de distribución; ii) el punto de conexión parásita-hospedero, i.e., si es por debajo o encima del suelo; iii) la actividad fotosintética de la parásita; y iv) si el ciclo de vida de las parásitas es anual o perenne.

Las plantas parásitas representan un gran reto en cuanto a su estudio, ya que en la mayoría de éstas resulta difícil realizar experimentos manipulativos debido a su naturaleza. En general, las semillas de estas plantas son capaces de germinar en condiciones experimentales (Hawksworth y Wiens, 1996; Whigham *et al.*, 2008); sin embargo, éstas mueren al poco tiempo si no realizan una conexión temprana con el hospedero (Whigham *et al.*, 2008). Los experimentos de perturbación que involucran la remoción de individuos también resultan complicados, ya que del haustorio remanente pueden brotar nuevos tallos (Hawksworth y Wiens, 1996), por lo que no se elimina el efecto del parasitismo ya que éste sigue extrayendo nutrientes (Press y Phoenix, 2005). Sin embargo, se ha demostrado que con especies hemiparásitas de raíz de vida anual es posible realizar experimentación, donde en un tiempo relativamente corto pueden infectar a un hospedero y crecer, como *Rhinantus alectorolophus* (Hautier *et al.*, 2010). Esto no es posible con las especies perennes que tardan un tiempo considerable en establecerse, tal como es el caso de los muérdagos enanos que, en ocasiones, producen tallos cuatro años después de haber germinado y penetrado al hospedero (Hawksworth y Wiens, 1996).

Finalmente, podemos preguntarnos ¿cómo pueden evaluarse las interacciones competitivas entre dos o más especies de plantas parásitas? Es decir, cómo pueden estimarse la intensidad y la importancia demográfica en especies que coexistan sobre un mismo hospedero, así como cuál es la consecuencia medible de esta interacción. Para esto deben tomarse en cuenta las restricciones antes descritas en cuanto a su manipulación. Ha sido probado que es posible la experimentación con plantas anuales parásitas de raíz (Hautier *et al.*, 2010), mientras que, para parásitas de tallo, como los muérdagos, se ha experimentado sólo para conocer la viabilidad y germinación de las semillas, así como la inoculación en hospederos potenciales (Scharpf, 1970; Deeks *et al.*, 2001; Brandt *et al.*, 2005). Las especies de ciclo anual presentarían ventajas de uso en este caso, ya que queda claro que en las anuales los experimentos de perturbación (i.e., modificación de las densidades) son viables, mientras que en las perennes esto representa un reto debido a su lento crecimiento. Para estas últimas se requieren hacer estudios a largo plazo donde se pueda monitorear su respuesta ante las interacciones con otras especies. En este sentido, se podrían realizar experimentos de perturbación, cuya respuesta sería en un tiempo considerablemente largo, o censos de los cambios en su abundancia para posteriormente ajustar modelos dinámicos. Ya que la emergencia de tallos puede tomar años, resulta más conveniente la segunda opción y obtener superficies de respuesta a partir de observaciones en campo, donde no es necesario realizar algún tratamiento manipulativo (Freckleton y

Watkinson, 2001a). Sin duda esto conlleva desventajas como no poder aislar los efectos ambientales o los que tengan que ver con el desarrollo y desempeño del hospedero, pero con un conjunto de datos grandes a largo plazo es posible tener una buena aproximación.

Por otro lado, al ser el hospedero su recurso limitado, pueden existir restricciones para realizar experimentos en condiciones controladas. No obstante, es posible tener hospederos de la misma edad o tamaño, que tengan las mismas condiciones ambientales (temperatura y humedad, entre otros), así como cuidar aspectos como la distribución de nutrientes, distancia mínima entre hospederos y densidad, entre otros. Por ejemplo, una plantación forestal de árboles coetáneos representa un buen sistema de estudio.

¿Cuál es la consecuencia medible de esta interacción? En distintos estudios se ha evaluado el efecto de las interacciones a través de comparar distintas variables de grupos de plantas expuestos a la interacción y grupos control, tales como son la tasa de consumo de recursos, el tamaño o biomasa, la abundancia, la mortalidad, la fecundidad, la reproducción recurso-dependiente y la tasa de crecimiento poblacional. Es importante evaluar si la interacción negativa deriva en un decremento en la tasa de crecimiento poblacional, con respecto a una condición de no coexistencia, o si sólo afecta el crecimiento, desarrollo y supervivencia de los individuos pero no la fecundidad. La interacción también puede tener influencia sobre los patrones de distribución, ya sea en el plano horizontal o en el vertical (sobre el hospedero), la cual puede ser una respuesta a la interacción competitiva o a la distribución de los recursos (hospedero).

En conclusión, a pesar de que no hay reportes donde se estudie explícitamente la competencia entre plantas parásitas, se puede decir que las recomendaciones son: i) buscar sistemas sencillos, donde sea posible realizar experimentación y manipulación, como en las parásitas anuales; ii) realizar estudios donde se puedan obtener censos a largo plazo, especialmente cuando se trata de plantas perennes; y, iii) ajustar modelos dinámicos teniendo un número grande de réplicas.

## DIRECCIONES FUTURAS

Tal como se ha expuesto a lo largo de la revisión, no hay estudios concretos sobre interacciones antagonistas entre dos o más especies de plantas parásitas y, aunque algunos estudios vislumbran la existencia de este tipo de interacción (Queijeiro-Bolaños *et al.*, 2014), no explican los mecanismos o las consecuencias poblacionales o a nivel de comunidad de estas interacciones. Por lo tanto, surgen preguntas y futuras direcciones de investigación al respecto, entre las que se encuentran las siguientes.

1. Los antagonismos pueden verse reflejados a distintos niveles de organización; el efecto directo se observa generalmente a nivel poblacional a través de un cambio en el tamaño poblacional o la exclusión de una población. Refiriéndonos a la competencia entre plantas parásitas: ¿cuál será su efecto a nivel de la comunidad biológica, incluyendo todos los componentes? Se ha mencionado que algunas plantas parásitas, como los muérdagos, pueden ser especies clave dentro de la comunidad ya que a pesar de su baja abundancia relativa tienen un impacto fuerte sobre otros componentes de la comunidad, por lo tanto alterando la composición y la diversidad (Watson, 2001). Sin embargo, no se ha contestado ¿cómo contribuye la competencia entre plantas parásitas a la matriz de interacciones? Y ¿alterará este factor la diversidad y composición de las comunidades vegetales?
2. ¿Se presentará una competencia simétrica o asimétrica? La asimetría generalmente se presenta cuando una de las especies competidoras tiene una mayor talla y por lo tanto un mayor consumo de recursos, lo que puede derivar en la exclusión competitiva de la segunda especie (Freckleton y Watkinson, 2001b) o, de la primera, ya que, de acuerdo a

Tilman (1990), sobrevive la especie que tenga menos requerimientos de recursos. Otra opción es la coexistencia con densidades más bajas y con un mal desempeño.

3. ¿Qué mecanismo actúa? Típicamente se espera que exista explotación en plantas compartiendo el mismo sustrato. En el caso de las plantas parásitas un haustorio penetrando ya sean raíces o tallos está prevaciando ese recurso. Sin embargo, el apresorio (estructura de penetración previa a la formación del haustorio) genera señalización bioquímica con el hospedero para poder establecerse (Whigham *et al.*, 2008). No ha sido evaluado si está vía bioquímica puede inhibir el establecimiento de otros individuos. Con esto surge otra pregunta, ¿en qué casos una especie ya establecida impedirá el establecimiento de una segunda especie como respuesta (o evasión) a la competencia, y en qué casos no?
4. ¿Cómo será la competencia en los distintos tipos de plantas parásitas? Es decir, ¿habrá diferencias entre plantas anuales y perennes? ¿Holoparásitas y hemiparásitas? ¿Parásitas de raíz y tallo? Es de esperarse que tanto en plantas anuales como las holoparásitas la competencia sea más intensa, ya que éstos van a tener una tendencia a consumir una mayor cantidad y más rápido los recursos. En el caso de las anuales, al tener un ciclo de vida corto, su desempeño no depende de la supervivencia del hospedero; mientras que, las holoparásitas extraen una mayor cantidad de recursos que las hemiparásitas, aunque son menos agresivas que las anuales.
5. ¿Cómo será la competencia en parásitas estructurales? Este tipo de parasitismo implica el daño físico, reducción en el crecimiento o menor producción de estructuras reproductivas ocasionado por plantas epífitas, como *Tillandsia recurvata* (Montaña *et al.*, 2007), o por plantas trepadoras leñosas, como lianas (Stevens, 1987; Pérez-Salicrup y Meijere, 2005) o algunas especies de *Ficus* (Laman, 1995). Estas plantas pueden

presentar competencia por luz y espacio, tanto con sus conespecíficos como con otras plantas parásitas y su hospedero. ¿Seguirán los mismos patrones que las plantas parásitas *sensu stricto*, o se asemejarán más a las plantas autótrofas?

Sin duda quedan muchos aspectos por estudiar de las plantas parásitas, ya que al tener un hábito parásito presentan particularidades interesantes que pueden moldear sus respuestas ante las interacciones antagonistas, las cuales valen la pena ser exploradas.

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Tabla 1. Tipos de plantas parásitas de acuerdo a la estructura que parasitan y la capacidad fotosintética que poseen. Se mencionan algunas familias representativas de cada tipo. Basado en Musselman y Press (1995), Heide-Jorgensen (2008) y Nickrent (2013).

| | | Capacidad fotosintética | |
|---|---|---|---|
| | | Activa | Perdida |
| Estructura parasitada | Raíz | Hemiparásita de raíz.<br>Olacaceae, Convolvulaceae, Orobanchaceae, Lauraceae | Holoparásita de raíz.<br>Rafflesiaceae, Hydnoraceae, Balanophoraceae, Orobanchaceae |
| | Tallo | Hemiparásita de tallos.<br>Loranthaceae, Viscaceae, Misodendraceae, Eremolepidaceae | Holoparásita de tallos.<br>Convolvulaceae, Apodanthaceae |

Tabla 2. Literatura donde se reportan dos o más especies de plantas parásitas en coexistencia. Basado en artículos científicos publicados; no se tomaron en cuenta tesis ni reportes técnicos. Búsqueda realizada en Scopus.

| Especies involucradas | Hospedero | Tipo de parasitismo | Localidad | Descripción | Referencia |
|---|---|---|---|---|---|
| *Arceuthobium globosum*<br>*A. vaginatum* | *Pinus hartwegii* | Hemiparásitas de tallo | Zoquiapan, Edo. de México, México | Dos especies de muérdago enano que parasitan al mismo hospedero; presentan una asociación negativa de sus incidencias y distribución diferencial sobre el tronco del hospedero. Se sugiere una interacción antagónica. | Queijeiro-Bolaños *et al.*, 2011; 2013 |
| *Dendrophtora* sp.<br>*Phoradendron* sp.<br>*Orycanthus* sp.<br>*Passovia* sp.<br>*Psittacanthus* sp.<br>*Struthanthus* sp.<br>*Tripodanthus* sp. | *Tapirira obtusa*<br>*Aspidosperma spp.*<br>*Mimosa calodendron*<br>*Senegalia polyphylla*<br>*Anadenanthera sp.*<br>Malpighiaceae *sp. 1*<br>*Guazuma ulmifolia*<br>*Miconia ferruginata*<br>*Myrcia tomentosa*<br>*Citrus* sp.<br>*Vochysia pyramidalis* | Hemiparásitas de tallo | Salto Magessi, Mato Grosso, Brasil | Registro de la presencia de éstos muérdagos en la zona del Cerrado, Brasil; se pueden encontrar hasta tres especies de muérdago en un mismo hospedero. | Arruda *et al.*,2013 |
| *Pedicularis tricolor*<br>*P. rex* | *Hordeum vulgare*<br>*Medicago truncatula,*<br>*Trifolium subterraneum*<br>*Solanum lycopersicum* | Hemiparásitas de raíz | Shangri-la, Provincia de Yunnan, China | Relación parásito-hospedero; se evaluó la preferencia de hospedero para las dos especies, además del efecto que tienen los distintos hospederos sobre el | Li *et al.*, 2012 |

| | | | | | |
|---|---|---|---|---|---|
| | | | | crecimiento y la asignación de biomasa en los tallos de los muérdagos. | |
| *Psittacanthus biternatus*<br>*P. eucalyptofolius*<br>*P. plagiophyllus* | *B. coccolobifolia*<br>*B. crassifolia*<br>*P. ramiflora*<br>*V. macrocarpa*<br>*A. occidentale* | Hemiparásitas de tallo | Santarém, Pará, Brasil | Efecto del fuego y la abundancia de los hospederos sobre la distribución de tres especies de muérdago congenéricas y simpatricas en la savana amazónica. | Fadini y Lima, 2012 |
| *Hydnora africana*<br>*H. visseri* | *Euphorbia gregaria*<br>*E. gummifera*<br>*E. mauritanica*<br>*E. dregeana*<br>*E. caput-medusae*<br>*Euphorbia triangularis* | Holoparásita de raíz | Región de Karas, Namibia, y Provincia del Cabo Norte, Sudáfrica | Descripción de una nueva especie (*Hydnora visseri*); se discuten las diferencias fenológicas y de preferencia de hospederos de *H. visseri* con su congénero simpátrico *H. africana.* | Bolini *et al.*, 2011 |
| *Phoradendron sp.*<br>*P. cordata*<br>*P. calyculaus*<br>*Pthriusa abdita* | Se registraron 50 especies de hospederos | Hemiparásitas de tallo | Fazenda Rio Negro, Nhecolândia, Brasil | Estructura de las redes de interacciones (anidamiento y modularidad) entre los muérdagos y sus hospederos; se muestra la intensidad de la interacción entre los muérdagos y sus hospederos. | Genini *et al.*, 2011 |
| *Cordylanthus mollis*<br>*C. maritimus subsp. palustris* | *Distichlis spicata* | Hemiparásitas de raíz | Tomales Bay Estuary y San Francisco Estuary, California, Estados Unidos | Efecto de las plantas parásitas sobre la salinidad, aireación y composición de la comunidad vegetal del suelo en las marismas de California. La relación parásito hospedero aminora el | Grewell, 2008 |

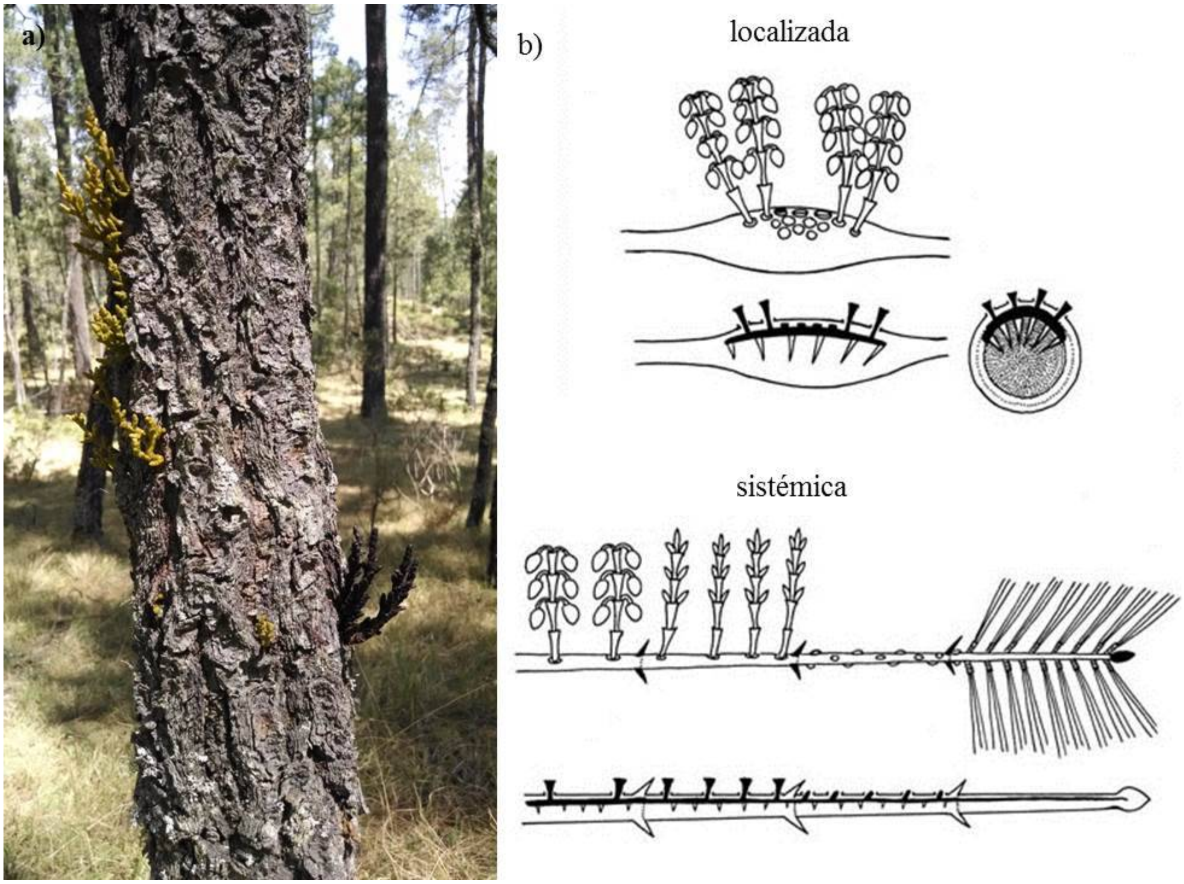
| | | | | | |
|---|---|---|---|---|---|
| | | | | estrés físico, incrementando la riqueza específica de plantas. | |
| *Santalum lanceolatum*<br>*Amyema* spp. | *Acacia tetragonophylla* | Hemiparásita de raíz/ Hemiparásita de tallo | Parque Nacional Sturt, Nueva Gales del Sur, Australia | Patrón de distribución espacial de *S. lanceolatum* y su hospedero. Sólo se menciona la presencia en la zona de dos especies de *Amyema*. | Watson *et al.*, 2007 |
| *Arceuthobium* spp. | *Pinus* spp.<br>*Abies* spp. | Hemiparásitas de tallo | Canadá, Estados Unidos y México | Los autores mencionan 12 casos de infección simultánea de dos especies de muérdago enano | Hawksworth y Wiens (1996) |

Tabla 3. Resultado esperado de la competencia interespecífica entre plantas parásitas según el tipo de parasitismo presentado. *Forma del parasitismo* hace referencia al número de hospederos que puede parasitar un sólo individuo y al espacio (cobertura) que ocupan sobre éste.

| Tipo de parasitismo | | Forma del parasitismo | Resultado esperado de la coexistencia |
|---|---|---|---|
| Holoparásita | Tallo | Uno o múltiples hospederos simultáneos, muy invasivas de las ramas y copas. | Al ser muy invasivas y ocupar prácticamente toda la superficie del hospedero, es difícil que se pueda establecer otra especie parásita sobre el mismo individuo. La competencia se esperaría que fuera asimétrica. Coexistencia difícil por el grado de dependencia al hospedero, por lo que consumen una mayor cantidad de recursos, intensificando la competencia. Sin embargo, en las plantas que parasitan más de un hospedero simultáneo, pueden ser excluidas de un individuo y permanecer en otro. |
| | Raíz | Múltiples hospederos simultáneos, además de poder tomar algunos nutrientes del suelo. Su distribución no está estrictamente ligada a la de un hospedero individual en particular. | La coexistencia dentro de una misma zona puede ser viable, ya que si hay exclusión competitiva de la raíz de un individuo, puede permanecer en las raíces de otro. Puede haber diferenciación de nichos por medio de una preferencia hacia algún hospedero, ocasionando agregación. |
| Hemiparásita | Tallo | Un solo hospedero, la infección generalmente es muy localizada en las ramas. | A diferencia de las holoparásitas, un individuo no es tan invasivo; sin embargo, al ocupar el sistema vascular se puede esperar competencia por explotación o interferencia. Puede haber exclusión competitiva o diferenciación en las estructuras del hospedero a parasitar. Se espera que gane el que pueda sobrevivir con una menor cantidad de recursos, que tal vez sea la especie más generalista. |
| | Raíz | Múltiples hospederos simultáneos. Pueden ser facultativas y sobrevivir por un tiempo sin hospedero, aunque su desempeño se ve afectado. | Igual que la holoparásita de raíz, aunque también hay competencia por radiación solar y, por lo tanto, por espacio horizontal. Sin embargo, al ser facultativas permiten la coexistencia. |

Figura 1. *Cuscuta tinctoria* sobre un parche de vegetación en el estado de Michoacán. Tomada de Costea (2013).

Figura 2. a) *Arceuthobium globosum* (color amarillo) y *A. vaginatum* (color negro) coparasitando a un individuo de *Pinus hartwegii* (Foto de M. Queijeiro-Bolaños). b) Tipos de parasitismo en muérdagos enanos: localizado y sistémico (tomado de Nickrent, 2013).



# CAPÍTULO 2

# EFFECTS OF INTERESPECIFIC INTERACTIONS BETWEEN TWO DWARF MISTLETOE SPECIES (*Arceuthobium* SPP.) ON THEIR POPULATION DYNAMICS

Queijeiro-Bolaños, M., C. Martorell y Z. Cano-Santana. Effects of interespecific interactions between two dwarf mistletoe species (*Arceuthobium* spp.) on their population dynamics.

## Abstract

Interspecific interactions have a fundamental role in plant population dynamics, as they may set the conditions for species coexistence. Stable coexistence is achieved by stabilizing mechanisms in which populations are self-limited, avoiding competitive exclusion. Parasitic plants, like dwarf mistletoes, offer the opportunity to study competition for resources that are different from those consumed by most plants, allowing for a better understanding of the interaction. Two species of dwarf mistletoes, *Arceuthobium globosum* and *A. vaginatum*, co-infected *Pinus hartwegii* in Central Mexico. We explored how interspecific interactions between these two species affect their population dynamics at two different stages of population development (colonization of new hosts and subsequent growth), and if heterogeneity in resource availability (host density and size structure) affects these interactions. To estimate interactions, we fitted demographic models to a 3 yr time series of dwarf mistletoe infection on 266 *P. hartwegii* trees. We found that self-regulation was stronger than interspecific competition. The intensity and sign of interspecific interactions changed depending on host size and demographic process: population growth in already infested trees was reduced by competition, except for smaller hosts where *A. vaginatum* was facilitated by *A. globosum*. Colonization of new hosts was enhanced by the previous infection by the other species, showing intraguild facilitation. Demographic importance of interactions (effect on population size) depended of stand structure: in homogeneous forests, facilitation predominates, increasing the population sizes of both species, whereas the opposite occurs in heterogeneous forests. Both species achieved stable coexistence, fulfilling the invasibility criterion. Our results agree with what theory states for non-parasitic plants, where stabilizing mechanisms allow dwarf mistletoe coexistence. Knowing the role of interactions may contribute to the understanding of mistletoes' dynamics, as well as bring interesting implications for forest management.

**Key words:** dwarf mistletoe, population dynamics, interspecific interactions, interaction shift, competition, facilitation, invasibility criterion, coexistence.

## Introduction

Intra- and interspecific interactions are key factors shaping the structure and dynamics of plant populations (Connell, 1990; Wootton and Emmerson, 2005). Interactions affect different demographic processes, such as population growth (Freckleton and Watkinson, 2001; Rees *et al*, 1996; Silander and Pacala, 1990) and colonization of new spaces (Bertness, 1991; Callaway, 1995; Martorell and Freckleton, 2014; Michalet *et al.*, 2006). Competitive interactions among coexisting species have long puzzled ecologists, as they may set limits to coexistence (Gause, 1934; Hardin, 1960). Depending on competition type and strength, stable or unstable coexistence may occur. Stable coexistence is based on equalizing mechanisms that minimize the magnitude of fitness differences, delaying local extinction but not preventing it. In contrast, stabilizing mechanisms occur when intraspecific competition is larger than the interspecific competition (making the latter negligible), in turn indefinitely precluding the extinction of competing species (Adler *et al.*, 2007; Chesson, 2000).

Under stable coexistence, population sizes are strongly bounded (Chesson, 2000). If competition is mainly intraspecific, and species become rare due to external factors such as disturbances, competition is reduced and populations grow back to its previous numbers (Chesson, 2000; Turelli, 1978). This is better explained by the invasibility criterion: if competing species are able to invade (i.e., increase from low density) in the presence of the rest of the community, stable coexistence occurs (Chesson, 2000; Gotelli, 1995; Ives, 1988; Turelli, 1978). Stabilization mechanisms may arise in different ways, such as differences in the ecological requirements of the coexisting species (i.e., coexisting species do not have a complete niche overlap) or from specialist natural enemies (Abrams and Rueffler, 2009; Burns and Strauss, 2011; Chesson, 1991, 2000; Leibold, 1995). In such cases, species are strongly self-limited, keeping them from depleting resources and driving their competitors to extinction.

Taking space into account is important when analyzing competition. Species segregation in space can act as a stabilizing mechanism too, because it ameliorates interspecific competition (Potthoff *et al.*, 2006; Stoll and Prati, 2001). Plants must exploit resources rapidly before other plants colonize the same space, or else must tolerate competition once other plants arrive (Bolker and Pacala, 1999). Nevertheless, heterogeneity in resource distribution may enhance intra and interspecific competition if the resources – and the competitors– are concentrated in specific areas, creating hot spots of interactions in nutrient-rich patches (Casper *et al.*, 2000; Hutchings *et al.*, 2003; Potthoff *et al.*, 2006; Snyder and Chesson, 2004; Stoll and Prati, 2001; Turnbull *et al.*, 2007). At the same time, fluctuations on resource supply and spatial heterogeneity can promote coexistence by enhancing the invasibility capacity (Chakraborty and Li, 2010). Since most of resources are heterogeneously distributed in nature, this can have a significant ecological implications, even altering the outcome of interactions between species (Wijesinghe *et al.*, 2005).

Facilitative interactions can also promote species coexistence. Moreover, competitive and facilitative mechanisms can operate simultaneously within the same species mixture (Callaway and Walker, 1997), and interactions shifts can occur depending on factors like life stage, plant density, indirect interactions and abiotic environment (Brooker and Callaghan, 1998; Callaway and Walker, 1997; Martorell and Freckleton, 2014). Facilitation has a strong effect on species composition and diversity, where one species can modify the local environment, thus benefiting neighboring species directly or indirectly with their presence (Bruno *et al.*, 2003; Callaway and Walker, 1997).

The attempts to understand plant-plant interactions and their mechanisms of coexistence are numerous. Parasitic plants may provide new insights into these interactions because the resources they depend on are very different from those used by other plants, being even considered as plants with heterotrophic nutrition. At the same time, parasitic plants share some basic attributes with autotrophic plants such as lack of mobility and modular growth. But differ to the latter because they take their nutrients from the vascular system of other plants (the host) through a specialized structure called haustorium (Musselman and Press, 1995; Nickrent, 2002). Although intuitively it is believed that two parasites taping the same vascular system must be experiencing exploitative competition for the host’s resources (Press and Phoenix, 2005), the subject has not been explored formally. Few studies have analyzed parasite-parasite interactions (whether intra- or interspecific) from a population dynamics viewpoint (Scharpf and Parmeter, 1982; Donohue, 1995) and these studies are restricted to invertebrate parasites of animals (Hatcher and Dunn, 2011). As it happens with non-parasitic organisms, studies with parasites have shown evidence for stabilizing mechanisms: the coexistence or co-infection requires some degree of niche differentiation among competitors (Holt and Dobson, 2006a), or else one species will competitively exclude the others. The niche differentiation can come in form of spatial segregation within and among hosts (Dobson, 1985b).

Parasitic plants such as dwarf mistletoes, offer the opportunity to test the effect of interspecific interactions on population dynamics and the mechanisms of coexistence of sympatric plants with heterotrophic nutrition. Because dwarf mistletoes take most of their photosynthates from the vascular system of the host (over 70%; Press 1995, Mathiasen *et al.*, 2008) we can assume that competition is mainly for host resources (i.e., photosynthates, water and mineral nutrients) rather than for light. Dwarf mistletoes are common components of temperate forests, and they are widespread on commercially valuable conifers (Mathiasen *et al.*, 2008). For this reason, dwarf mistletoes have been a frequent subject of research, with emphasis on their parasitic effects on the host (e.g., decreased growth and fecundity; Mathiasen *et al.* 2008), changes on water use efficiency (Sala *et al.*, 2001), and decreased photosynthetic capacity (Meinzer *et al.*, 2004), but the effects of one mistletoe species on others have been overlooked. Due to their host-dependency, stand structure (host spatial distribution, density, age and size) might be an important factor influencing vertical and horizontal spread and intensity of the mistletoe infection because of limited seed dispersal (Robinson and Geils, 2006). In general, mistletoe infection is clumped on a few trees while the rest have little infection (Aukema, 2003; Donohue, 1995; Shaw *et al.*, 2005); that is, a high host density is associated with a low proportion of infected trees, but not necessarily with the number of parasites per host (Donohue, 1995). Trees with larger crowns represent a better seed source, as it improves the dispersion height and also the light incidence on mistletoe shoots; thus, maintaining larger mistletoe populations (Arriaga *et al.*, 1988; Shaw *et al.*, 2005). Different dwarf-mistletoe species may parasitize the same trees; thus, competition for resources in the vascular stream (similar to soil resources competition; Tilman, 1990) and for space is expected, thus influencing significantly mistletoes population dynamics.

In this study we explore interspecific interactions between two dwarf mistletoe species, *Arceuthobium globosum* and *A. vaginatum,* co-infecting the same host species (*Pinus hartwegii*), and their respective population dynamics. We analyze whether such population dynamics depend on the population growth within infested trees and colonization potential of new hosts, and test whether stable coexistence is expected based on the invasibility criterion, i.e., the capability of mistletoe populations to recover when their density is low and the other species is at its equilibrium (Turelli, 1978). The invasibility criterion is especially relevant for management, as it allows us to assess whether parasites can invade a forest that is already infested by other mistletoe species. Additionally, we analyze how spatial heterogeneity in resource availability (i.e., host density and size structure) correlates with the interactions among parasites.

## Methods

### *Study area and species*

The study site is the Papayo and Zoquiapan subregion within the Iztaccíhuatl Popocatépetl National Park (19°18’08.4’’ N, 98°42’10.7’’ W), Central Mexico, which is a 4-ha open *Pinus hartwegii* forest. The climate is temperate sub-humid with rains concentrated from June to September; the average annual rainfall is 941 mm, and the mean annual temperature is 9.7 °C (Arriaga *et al.*, 2002). The site is at 3420 m a.s.l., in average, with negligible slope. Other tree species, such as *Alnus jorullensis* and *Abies religiosa,* also occur in low frequency.

In this area, two dwarf mistletoe species coexist parasitizing *P. hartwegii*: *Arceuthobium globosum* Hawksworth and Wiens subsp. *grandicaule* Hawksworth and Wiens and *Arceuthobium vaginatum* (Willdenow) Presl subsp. *vaginatum*. The two species closely resemble each other in that both have scale-like leaves, with flowers, fruits and leaves the same color as the shoots. *A. globosum* is yellow-green shrub of 18-70 cm height, whereas *A. vaginatum* is dark brown or blackish shrub of 20-55 cm height. Both are widely distributed on Mexico and are considered to cause important damage on pine forests (Hawksworth and Wiens, 1996). In Mexico they have been reported to parasitize 13 and 14 pine species, respectively, seven of which they share. At our study site they parasitize *Pinus hartwegii*, even sharing the same individual tree. Mistletoes belonging to this genus are perennial plants that live longer than 10 years, and they can survive as cryptic infections without aerial shoots (Robinson and Geils, 2006); that is, the hypertrophy on the host branch caused by the endophytic system of the mistletoe makes the infection perceivable. They have a ballistic mechanism of dispersion, in which their seeds are explosively discharged, reaching a maximum distance of 14 m (Robinson and Geils, 2006). Colonization of new hosts is favored by large tree-crowns with larger seed-catching areas (Arriaga *et al.*, 1988). Unlike other dwarf mistletoes, these two species develop over the whole host, including the tree trunk (Queijeiro-Bolaños *et al.*, 2011).

### *Field survey*

Interactions and their effects on populations can be estimated from repeat-survey data of abundances if we have a long observational period and large amount of individuals (Freckleton and Watkinson, 2001; Ives *et al.*, 2003). To produce such data, in November 2008 we marked all the *Pinus hartwegii* individuals taller than 1.5 m, in an area of 11 000 $m^2$ within the Papayo sub-region. These pines were either not infected, infected with *A. globosum*, with *A. vaginatum*, or both species. We assessed the dwarf mistletoe infection on each tree every six months for three years using a Modified Dwarf Mistletoe Rating system

(MDMR) based on Hawksworth (1977; Table 1). The conventional DMR is not recommended for small trees or for trees with irregular branching and long poles (Hawksworth, 1977). Moreover, it does not consider stem infection, which is very common on our study species, and it does not distinguish light from severe infections. Because we required a more precise measure of the infection to be able to detect changes trough time, in our rating system the tree was divided into thirds, and each third was qualitatively rated. We used the following values for each third of the tree: 0, no infection; 1, a sprout or branch hypertrophy; 2, less than 20% of branches infected; 3, 21-30% of branches infected; 4, 31-50% of branches infected; 5, 51-70% of branches infected; and 6, more than 71% of branches infected (Table 1). Afterwards, the thirds ratings were added, giving an index ranging from zero to 18. Additionally, we measured for each pine tree the stem diameter at breast height (dbh) and the distance between all trees.

### *Population dynamics and interaction modeling*

To measure interactions between mistletoe species we set a discrete-time model for population dynamics (Freckleton and Watkinson, 2001; Ives *et al.*, 2003; Martorell and Freckleton, 2014). This allowed us to estimate the intensity of the interactions and to project their effects to the whole population. Dwarf mistletoes form clumps making it very difficult to discern between individuals, so we used the MDMR ratings as a measure of abundance in a host. With these data we modeled separately two processes for each species: growth, i.e., changes in MDMR in individual trees (which may result in the extinction from a host if MDMR drops to zero), and colonization of un-infected trees.

To account for interactions we included the MDMRs of both species in the growth model: if species interact, the growth (change in MDMR) of a focal species (the species on which the effect of the interaction is measured) would depend both on its own MDMR and on that of the associated species. These effects correspond to intra and interspecific interactions, respectively. Tree size was also considered in the model because it affects MDMR (Arriaga *et al.*, 1988; Godfree *et al.*, 2003). Because seeds from neighboring trees may reach an infected tree and affect its MDMR, we also incorporated in the model a dispersion term proportional to

$$M_{i,t} = \sum_{j \neq i}^{n} N_{j,t} D_j / d_{ij} \qquad (1)$$

where $M_{i,t}$ is a measure of the potential influx of seeds into the $i^{\text{th}}$ tree at time $t$+1 from neighboring hosts, $N_{j,t}$ and $D_j$ are the MDMR and size (dbh) of the $j^{\text{th}}$ tree at time $t$, and $d_{ij}$ is the distance between the $i^{\text{th}}$ and $j^{\text{th}}$ trees. This equation was chosen because more seeds are expected to be produced in heavily infested trees, and because MDMR is relative to tree size, so more seeds would be produced in large hosts than in smaller ones having the same MDMR. However, mistletoe seeds travel relatively small distances (Robinson and Geils, 2006), so we expected that seed arrival in the $i^{\text{th}}$ tree would diminish with distance to seed donors.

To model the change in MDMR in a host, we tested different functions commonly used to describe population growth, and selected the one with the lowest Akaike information criterion (AIC; Bolker, 2007). The best model was the Gompertz growth equation with a binomially distributed error (Table A1; Appendix). Thus, we developed the following general equation for each focal mistletoe species:

$$N_{i,t+1} \sim \mathrm{B}\left(p = N_{i,t} e^{(r(D_i) + \left(f_g(D_i) - 1\right) \ln N_{i,t} + a_g(D_i) \ln S_{i,t}} + \gamma M_{i,t}, n = 18\right) \qquad (2)$$

where $n$ and $p$ are the parameters of the binomial distribution, $S_{i,t}$ is the MDMR of the associate species in the $i^{\text{th}}$ tree at time $t$, $\gamma$ is a proportionality coefficient, $r(D_i)$ is the intrinsic rate of increase in MDMR of the focal species, and $f_g(D_i)$ and $a_g(D_i)$ represent the intraspecific and interspecific interaction coefficients, respectively. The latter three parameters may depend on the dbh of the host, and we assumed that they did linearly so (for instance, $r(D_i) = a_r + b_rD_i$, where $a_r$ and $b_r$ are constants, see Appendix, Table A2). Using the general eqn (2), we tested five different models. In all of them, the MDMR after one semester was assumed to depend on the MDMR of the focal species at the beginning of the period and

1. the rate of increase and intraspecific competition,
2. both the previous parameters and interspecific competition,
3. as 1, but the rate of increase depends on the tree's dbh (this can be expected because the amount of resources available to the parasite's growth are expected to depend on the host's size),
4. as 3, but with the rate of increase and intraspecific competition changing with dbh (a result that may be expected because the growth rate and competition parameter are frequently correlated in these kind of models, C.M., pers. obs., and because competition may be affected by resource availability),
5. as 4, but allowing interspecific competition to change with dbh as well, and
6. only the rate if increase and interspecific competition changing with dbh.

(see Table 2 for the respective equations). All these models were compared using AIC. After the best model was chosen, we tested whether including the dispersion term $\gamma M_{i,t}$ was justified using the same criterion (Appendix, Table A3). The models' parameters were estimated through maximum likelihood using the observed changes in MDMR in infected trees every semester as input data (Freckleton and Watkinson, 2001; Ives *et al.*, 2003). We used the package bbmle (Bolker and R Development Core Team, 2012) for R (R Development Core Team, 2012) for maximum likelihood estimation.

For colonization potential we used only data of trees with no infection ($N_{i,t}=0$) at time $t$, and modeled the change in their MDMR at time $t+1$. Again we tested a number of alternative formulations for this model using AIC (Appendix, Table A4). In the best one, the infection of a previously un-colonized tree depends entirely on the propagules provided by the neighboring hosts; hence, the colonization potential of the $i^{\text{th}}$ tree, $c_{p,i}$, due dispersion from its vicinity was calculated as:

$$c_{p,i} = \kappa M_{i,t}^{\alpha} \tag{3}$$

where $\kappa$ and $\alpha$ are constants. The colonization potential may be restricted by the size of the host and the pre-existing infection of the associated species. The restriction may range from nonexistent (in which case 100 % of the colonization potential is achieved) to complete (i.e., the MDMR of the focal species may remain as zero despite seed arrival). Hence, the restriction ($h_i$) was modeled as a logistic function, which is bounded between zero and one:

$$h_{i,t} = \frac{e^{\beta+\delta D_i + a_c(D_i)S_{i,t}}}{1+e^{\beta+\delta D_i + a_c(D_i)S_{i,t}}} \tag{4}$$

where $\delta$ is the effect of host size and $a_c(D_i)$ is the interspecific interaction intensity during colonization, which again was assumed to be a linear function of dbh (intraspecific competition is zero in non-colonized trees). The MDMR of colonists was found to follow a Poisson distribution (Appendix, Table A4), so the MDMR of the focal species on a previously un-colonized host, was modeled as:

$$N_{i,t+1} \sim \mathrm{P}\left(\lambda = c_{p,i} h_{i,t}\right) \tag{5}$$

where $\lambda$ is the parameter of the Poisson distribution.

As before, we tested the effects of tree size and interactions on colonization using five models derived from eqn. (4):

7. there is no restriction to colonization ($h_{i,t} = 1$),
8. the restriction to colonization depends on dbh only,
9. the restriction depends on interactions only,
10. both dbh and interactions determine the level of restriction,
11. as 9, but the interaction intensity changes with dbh.

(See table 3 for the specific functions). The best model was chosen using AIC.

*Demographic importance of interactions*

To estimate the demographic importance of interactions, i.e., their effect on the population sizes of both mistletoe species (Martorell and Freckleton, 2014), we performed spatially-explicit simulations of the population dynamics of each species growing alone and in a mixture. In each simulation we started with a forest with 1000 hosts (see below), a random subset of which were infected. Using equations (2) and (5) and binomial and Poisson random-number generators, respectively, we proceeded to simulate the changes in MDMR in each host over time (See Appendix; Figure A1). The model was iterated 2500 times. The population size $N$ was estimated as the sum of the MDMR in all trees in the forest averaged over the last 2460 iterations. The first 40 were dropped as they reflected only transient dynamics. The demographic importance of the interactions was calculated as a log-response ratio (Goldberg and Scheiner, 2001):

$$I = \ln\left(N_c / N_a\right) \tag{6}$$

where $N_c$ is the population size of the focal species in coexistence with the second, and $N_a$ is the population size in the absence of the associated species. Positive $I$ values indicate that the population size increases in the presence of the associated species, i.e., that the net effect of the interaction is facilitative; in contrast, competition predominates if $I$ is negative.

The demographic importance of the interaction may depend on the attributes of the forest such as density and size structure (Fichtner *et al.*, 2012). Thus, we performed simulations changing the stand density, the mean dbh of hosts, and the heterogeneity of dbh-values in the stand. We used the densities 0.01, 0.02, 0.05, 0.1, and 0.2 ind $m^{-2}$ (the observed density was 0.02). A dbh value was assigned to each tree in the artificial forest using a log-normal distribution with means 0.1, 0.14, 0.19, 0.27, 0.38, and 0.53 m (which are within the observed dbh range in the study site) and standard deviations 0 (homogeneous forest), 0.25, 0.5, and 1 (high heterogeneity forest; see Appendix for further details).

To assess if coexistence is stable through the invasibility criterion, i.e., if the presence of one mistletoe species does not preclude infestation by the other, we performed a second set of simulations. We generated an artificial forest with 1000 trees, setting the density and dbh of the hosts to the values observed in our forest (See Appendix, Table A7). We infected some trees with one of the mistletoe species, and iterated the model until it attained its equilibrium population size. We then introduced the other species by infecting different numbers (range 1-300) of randomly selected trees with an initial MDMR of one. The model was then iterated 100 times, and we recorded whether the new species was still present. If so, it was considered that the invasion was successful. This procedure was repeated 50 times. To assess if the infestation success is affected by an already established mistletoe species, invasion was also simulated for forests that had none of the species present.

## Results

Models 5 and 6 were the best models for *A. globosum* and *A. vaginatum* population growth, respectively, based on AIC differences (Table 2). This means that the population dynamics of dwarf mistletoes in an infected tree is better explained by both intra and interspecific interactions, and that the intensity of intra and interspecific competition, as well as the rate of increase, is better explained by the host's dbh (except for intraspecific competition for *A. vaginatum*). Both species, regardless of tree size, displayed a strong intraspecific competition in the growth model, shown as a decrease in growth rate as its own abundance increased (Fig. 1). Intraspecific competition was remarkably stronger than interspecific interactions, as shown by the steeper slope (decrease in growth rate per MDMR unit) over the conspecific-density axis compared with the heterospecific axis. Intraspecific competition became more intense with host size for *A. globosum* (Fig. 1a-f), but not for *A. vaginatum* (Fig. 1g-i). The growth rate of *A. globosum* was larger in trees with several large, heavily infested trees in its vicinity, i.e., with high dispersal rates (comparison of the models with and without dispersion term; $\Delta$AIC = 4.14; Fig. 1a-f). In contrast, there was no distinguishable effect of dispersal rate on *A. vaginatum* ($\Delta$AIC = 2.00).

The intensity and type of interspecific interactions between the two species in the growth model depended largely on the host size. For *A. globosum*, the growth rate diminished as the MDMR of *A. vaginatum* increased, indicating interspecific competition, which strengthened with tree size (Fig. 1a-f). In contrast, *A. vaginatum* presented an interaction shift depending on host size: in small trees (dbh=0.03 m, Fig. 1g) the growth rate of *A. vaginatum* increased with *A. globosum* abundance, indicating a greater susceptibility to infection by *A. vaginatum* under these conditions. On the contrary, in large trees (dbh=0.6 m, Fig. 1i) the interaction became competitive. The transition towards competition occurred near a dbh = 0.35 m (Fig. 1h). See Appendix for coefficients values (Table A5).

For both species, the mean number of colonists increased with $M_{i,t}$ (Fig. 2), indicating that greater densities of heavily-infested, large hosts in the vicinity resulted in greater chances that a healthy host became infected. However, colonization was affected by the presence of the associated species and the host' mean dbh (Table 3; see Table A6 on Appendix for coefficients). In small trees where the interacting species was absent, the MDMR of recently-colonized trees was drastically smaller compared with large trees (Fig. 2). In the presence of the second species, the mean number of colonists increased, even matching the colonization potential without restriction in trees that were already heavily infested by the second species (Fig. 2a, d). Hence, facilitation took place during colonization of small trees. In medium-sized (dbh=0.26 m; Fig. 2b, e) and large hosts (dbh=0.51 m; Fig. 2c, f), facilitation became less important.

For the simulations of population dynamics of *A. globosum* on whole forests we used models 5 and 10. In this species, evidence was insufficient to discern between models 10 and 11, so we chose the simplest one. In *A. vaginatum* we used models 6 and 10. Here, models 8 and 9 were also supported by the data (Table 3), but because both include dbh and interaction, we used model 10 which includes both variables.

The sign and magnitude of the demographic importance of interactions depended on host's dbh, density and stand heterogeneity. This was striking for *A. globosum* (fig. 3), where positive interactions were of great importance on homogeneous stands (fig. 3a), especially in sparse forests composed of small trees. The rest of dbh and density combinations show competition (Fig. 3a). With increasing forest heterogeneity, the effect of facilitation vanished (Fig. 3c and d). The changes in demographic importance with forest structure were less drastic for *A. vaginatum*; in fact, the four types of forests showed almost the same pattern (fig. 4). Almost all combinations of dbh and density revealed positive interactions, with competition occurring only on large-tree forests and low densities. The peak in facilitation observed was again observed for small-tree forests at low densities, and (in contrast with *A. globosum*) got sharper with heterogeneity.

Infestation probability increased very rapidly with the number of trees initially infected: when as few as 0.1% (10 individuals) of the trees in the forest became infected, the persistence of the invading species was almost certain. The presence of one mistletoe species increased the probability of stand infestation by the second species (Fig. 5). However, when the number of initial infected trees was large (>10), this facilitative process lost its importance (Fig. 5).

## Discussion

Numerous studies have tested the role of intra and interspecific interactions on plant population dynamics; nevertheless, very few of these have focused on parasitic plants (see Hautier *et al.*, 2010 for an example including density-dependence on *Rhinanthus alectorolophus*). When two species with similar ecological requirements coexist in the same space, competitive exclusion should be expected. In this study, two dwarf mistletoe species are sharing the same host tree and, therefore, resources, leading them to possibly compete; nevertheless, they experience stable coexistence. Dwarf mistletoe population dynamics shared some characteristics with non-parasitic plants, such as: i) population dynamics is driven by interactions, both intra and interspecific (Chesson, 2000; Connell, 1990), ii) resource availability and heterogeneity have an important influence on strength and sign of the interactions (Casper *et al.*, 2000; Hutchings *et al.*, 2003; Turnbull *et al.*, 2007), iii) coexistence is promoted by stabilizing mechanisms (Chesson, 1991, 2000), and iv) interaction shifts occur depending on the demographic process (Brooker and Callaghan, 1998; Martorell and Freckleton, 2014). However, it is important to highlight the particularities that this parasitic system provides.

### *Intra and interspecific effects*

We found compelling evidence for intraguild mutualism among mistletoes. Intra-guild mutualism takes place among species that consume the same resource (Crowley and Cox, 2011) and thus compete, as it happens in our system, buy yet may have positive effects on each other, such as an improve resource location or inhibition of a third competitor (Crowley and Cox, 2011), which eventually can be translated as population growth. Recent evidence shows that intraguild mutualism may be much more common in nature than previously though (Crowley and Cox, 2011). The mechanisms for the competitive effect that mistletoes have on each other, i.e., resource consumption, are straightforward to envisage, but it is less clear why facilitation occurs. In parasitic species, a species may facilitate a second species by weakening the host and reducing its resistance (Nebeker *et al.*, 1995; Tkacz and Schmitz, 1986). This would be a case of by-product facilitation occurring between parasites because consumption by one predator modifies preys conditions, benefiting the second predator (Crawley *et al.*, 2013). Second, it is known that photosynthates produced by mistletoes may provide some resources to their host (Hawksworth and Wiens, 1996); needlesless pines survive longer when they are infected than the uninfected pines as a result of possible traslocation of photosynthates from mistletoe to the host(Weir, 1916). Also, it has been found radioactive photosynthates from *A. americanum* on *Pinus contorta* (Rediske and Shea, 1961; Okonkwo, 1966). There is evidence too of RNA exchange between parasitic plants and their host, as a probable mechanism of coordinate development (Westwood *et al.*, 2009). Thus, the availability of nutrients may be changed by the presence of one parasitic plant. The latter may benefit nutrient uptake by a second species, and favor coexistence via facilitation of nutrients uptake; however, physiological relationships within this context need further research.

As expected from coexistence theory, stabilizing mechanisms seem to be involved in the coexistence of our mistletoe species. It was evident that intraspecific competition was more intense than the interspecific one for both species, thus, self-limiting population growth and precluding competitive exclusion (Chesson, 2000). Niche differences, which can be manifested in morphological differences, resources uptake and specialized interactions (Levine and HilleRisLambers, 2009), cause species to limit their own population more than they limit their competitors, resulting in a negative frequency-dependent growth (Levine *et al.*, 2008). The latter was found for both mistletoe species (Fig. 1), suggesting that niche differences exist (Chesson, 2000; Levine and HilleRisLambers, 2009). There is evidence that dwarf mistletoes have a differential distribution over the host stem (Queijeiro-Bolaños *et al.*, 2011), and, from recent data, it seems to be some sort of differential preference of host size, where large trees seem to be a more suitable host for *A. vaginatum* , whereas *A. globosum* has no preference (pers. obs.). It is not possible from our data to detect if equalizing mechanisms are acting. If we recall that such mechanisms are important only if differences in fitness between species are small (Chesson, 2000), they are likely to be weak as suggested by the fact that *A globosum* had greater growth rates than *A. vaginatum* (Fig 1c, f, i).

Although stabilizing mechanisms have been discussed in different studies dealing with "ordinary" competition (see for example Chesson, 2003, Adler *et al.*, 2007, Levine *et al.*, 2008, Levine and HilleRisLambers, 2009), our results show that positive interactions may enhance stability when intra-guild facilitation occurs. At high densities, we would expect competition to predominate as the resource becomes depleted, as Fig. 1 shows, so the positive components of the interaction are likely to become more important at low densities. This may prevent either species from becoming extinct when it is at low density, fulfilling the invasibility criterion (Turelli, 1978). The fact that the probability of invasion at very low densities of the focal mistletoe species was always increased when the associated species was present (even if the associated species may have a negative effect on the population size of the focal one when both are at equilibrium densities) illustrates how a stabilizing effect may arise from intraguild facilitation.

In other studies dealing with plant-plant interactions it has been found that facilitation is more intense during colonization stage and competition on growth stage of established populations (e.g. Miriti, 2006, Martorell and Freckleton, 2014). This seems to occur because the  presence of one species ameliorates harsh or stressful conditions that strongly affect seedlings; meanwhile, once established, individuals tolerate stress and compete for mutual resources (Brooker and Callaghan, 1998; Brooker *et al.*, 2008). The mechanism for the interaction shift with ontogeny in mistletoes seems to be different. We do not yet fully understand how pines may fight mistletoe infection, and if these mechanisms can be abated in infected trees. However, if this is the case, and if mistletoe seedlings are especially sensitive to the defenses of the tree, facilitation is expected to play an important role during the early stages of the life cycle and thus during colonization, as we observed.

Small trees represent nutrient poor patches, and as such the intensity of positive interactions may be expected to be greater than that of competition (Casper *et al.*, 2000; Hutchings *et al.*, 2003). Smaller individuals are in a faster growth rate, which could be convenient for the mistletoes. In line with this idea, *Arceuthobium vaginatum*, once established, showed a shift from facilitation to competition with host size. Alternatively, the resources provided by the mistletoe to the tree may make a greater relative contribution to the photosynthate balance of small pines that have relatively few leaves compared to large trees.

### *Demographic importance*

Resource availability and spatial arrangement, in this case represented by host size, density and stand heterogeneity, have been recognized as important factors influencing the outcome of interactions on population dynamics of two or more competing species (Casper *et al.*, 2000; Hutchings *et al.*, 2003; Wijesinghe *et al.*, 2005). Our results suggest that this is also the case in mistletoes. The importance and sign of interactions depended of stand structure. Under some conditions, the negative component of the intraguild mutualism interaction predominated, while facilitation prevailed in others.

Heterogeneous environments where the availability in resource quality and availability is variable – in this case uneven sized stands-, may enhance interspecific competition and intraspecific aggregation (Casper *et al.*, 2000; Ives, 1995). Dwarf mistletoes have short distance dispersal mechanisms, which allows them to disperse seeds up to a distance of 14 m (Robinson and Geils, 2006), and in many cases to the same source tree, thus, causing intraspecific aggregation and thus augmenting intraspecific competition; also, large trees represent nutrient rich patches that concentrate a greater quantity of competing individuals (Casper *et al.*, 2000; Hutchings *et al.*, 2003). It has been reported that in uneven-aged forest, dwarf mistletoes clump on larger trees, creating interactions "hot spots" (Smith, 1977; Shaw *et al.*, 2005). This would seem to explain why competition increased with heterogeneity in *A. globosum*. However, we did some data exploration using Morisita's index of dispersion (Krebs, 1999) for all forest types (homogeneous and heterogeneous with the different densities and dbh combinations), and we found no significant relationship between stand heterogeneity and aggregation, casting some doubts on this explanation.

Facilitation, present in homogeneous and low heterogeneity forests, has a great importance, especially with smaller trees and low densities. It is known that low density, open stands favor mistletoe spread, as light incidence improves fruiting and seeding (Shaw *et al.*, 2008); the latter, coupled with facilitative effects that we observed in small pines, promotes mistletoes thriving.

### *Implications for Management*

The key role of mistletoes on biological communities has been poorly acknowledged (Watson, 2001). These taxa have long been seen as harmful parasites, especially for forestry productive activities, so control methods have emerged constantly in literature (Hawksworth and Wiens, 1996; Conklin, 2000; Geils and Hawksworth, 2002; Shaw *et al.* 2009), including biological, chemical and genetic resistance methods. The most common one is the silvicultural control: usual management prescribes stand modifications, such as spacing trees, removal of infected overstory, density reduction, and even-age composition (Hawksworth and Wiens, 1996; Shaw *et al.*, 2009). This kind of management seems to work fine for stands where only one mistletoe species is found, as is the case of most of US and Canada coniferous forests in which coexistence is rare between mistletoe species (Hawksworth and Wiens, 1996). In the present study we showed that when two species are coexisting and parasitizing the same individual host and stand, interspecific interactions matter and in consequence control strategies should be different.

Considering facilitation between mistletoes is of special importance for designing control strategies. Stands that were already infested by one mistletoe species not only could be invaded by the second species, but the invasion was facilitated by the resident species, increasing the infestation probability of the stand.

If we consider management through stand structure modification, we can promote facilitation processes between mistletoes species. For instance, *A. globosum* experienced facilitation by *A. vaginatum* with low densities of small trees, and even-sized stands. This result highlights that homogenizing the size structure of the stand may actually accelerate the geographic-range rate of expansion of this mistletoe and increase the infestation. *A. vaginatum* was facilitated at several density and size combinations, so the modification of the stand structure would have little impact on this species if *A. globosum* is already present. Facilitative effects between both species also imply that the control of one of them is unlikely to succeed unless the other species is also contained.

As it may be expected in intraguild facilitation, we also found evidence for competition. Under certain conditions, competition between predators may reduce the effects that have on prey compared to the case where only one predator is present (Sih *et al.*, 1998), although the opposite may also happen. In the former scenario, the fact that infestation probabilities increase once one mistletoe has colonized a stand may actually have positive effects on the hosts. However, competition between mistletoes probably arises because they deplete resources (tree sap), which would have a negative impact on the host that also depends on them.

In conclusion, interactions between dwarf mistletoes present an overlooked and underestimated research opportunity, where negative interactions resemble below-ground competition of non-parasitic plants, involving resources such as water, mineral nutrients and space (Casper *et al.*, 2000), but where competition for light is negligible. These species also display facilitation, as it happens in many other plants. It is interesting to note that, despite the peculiarities of the mistletoe resource-acquisition strategies, our results coincide with what theory states for non-parasitic plants as it refers to population dynamics. It remains interesting how these processes function with coexisting parasitic species, where, from our results, interactions shifts and invasibility are perceived as emerging research subjects on parasitic plants, as it suggest that parasites enhance invasion by other competing parasitic species.

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Table 1. Modified Dwarf Mistletoe Rating system (MDMR) used in this study. The MDMR class is assigned to each third of the tree; then the thirds score are summed to get the overall tree rating. Its equivalence to Hawksworths' (1977) DMR scale is also shown.

| MDMR class | Percentage of infected branches | Hawksworths' (1977) DMR class |
|---|---|---|
| 0 | Non infected | 0 |
| 1 | Sprout | 1 |
| 2 | <20% | 1 |
| 3 | 21-30% | 1 |
| 4 | 31-50% | 1 |
| 5 | 51-70% | 2 |
| 6 | >70% | 2 |

Table 2. Growth models tested, accounting for change in MDMR due to intraspecific competition, interspecific competition and host size. See text for a detailed explanation on each model. ∆AIC refers to the difference between the lowest AIC and the rest of the models.

| Model | Equation | ∆AIC | |
|---|---|---|---|
| | | *A. globosum* | *A. vaginatum* |
| 1 | $N_{i,t+1} = N_{i,t} \exp\left(r + (f_g - 1)\ln N_{i,t}\right)$ | 186.7 | 2.9 |
| 2 | $N_{i,t+1} = N_{i,t} \exp\left(r + (f_g - 1)\ln N_{i,t} + a_g \ln S_{i,t}\right)$ | 187 | 1.4 |
| 3 | $N_{i,t+1} = N_{i,t} \exp\left([a_r + b_r D_i] + (f_g - 1)\ln N_{i,t}\right)$ | 8.0 | 3.0 |
| 4 | $N_{i,t+1} = N_{i,t} \exp\left([a_r + b_r D_i] + ([a_f + b_f D_i] - 1)\ln N_{i,t}\right)$ | 8.2 | 6.8 |
| 5 | $N_{i,t+1} = N_{i,t} \exp\left([a_r + b_r D_i] + ([a_f + b_f D_i] - 1)\ln N_{i,t} + [a_a + b_a D_i]\ln S_{i,t}\right)$ | **0.0** | 2.0 |
| 6 | $N_{i,t+1} = N_{i,t} \exp\left([a_r + b_r D_i] + (f_g - 1)\ln N_{i,t} + [a_a + b_a D_i]\ln S_{i,t}\right)$ | 1.6 | **0.0** |

Table 3. Colonization potential model tested with different values for the restriction term, ranging from no restriction to restriction with interspecific interaction and host's dbh effect. $\Delta$AIC refers to the difference between the lowest AIC and the rest of the models.

| | | $\Delta$AIC | |
|---|---|---|---|
| Model | Equation | *A. globosum* | *A. vaginatum* |
| 7 | $h_{i,t} = 1$ | 18.3 | 5.2 |
| 8 | $h_{i,t} = \frac{e^{\beta+\delta D_i}}{1+e^{\beta+\delta D_i}}$ | 8.7 | 0.9 |
| 9 | $h_{i,t} = \frac{e^{\beta+a_c S_{i,t}}}{1+e^{\beta+a_c S_{i,t}}}$ | 2.4 | 0.8 |
| 10 | $h_{i,t} = \frac{e^{\beta+\delta D_i+a_c S_{i,t}}}{1+e^{\beta+\delta D_i+a_c S_{i,t}}}$ | **0** | **0** |
| 11 | $h_{i,t} = \frac{e^{\beta+\delta D_i+[a_c+b_c D_i]S_{i,t}}}{1+e^{\beta+\delta D_i+[a_c+b_c D_i]S_{i,t}}}$ | 0.3 | 2 |

Fig. 1 Finite growth rate of the two dwarf mistletoes species in function of their own abundance, the abundance of the second species, host dbh and migration (*M*). For *Arceuthobium globosum:* a) dbh=0.03, *M*=1; b) dbh=0.3, *M*=1; c) dbh=0.6, *M*=1; d) dbh=0.03, *M*=12; e) dbh=0.3, *M*=12; and f) dbh=0.6, *M*=12; for *A. vaginatum*: g) dbh=0.03; h) dbh=0.3, and i) dbh=0.6.

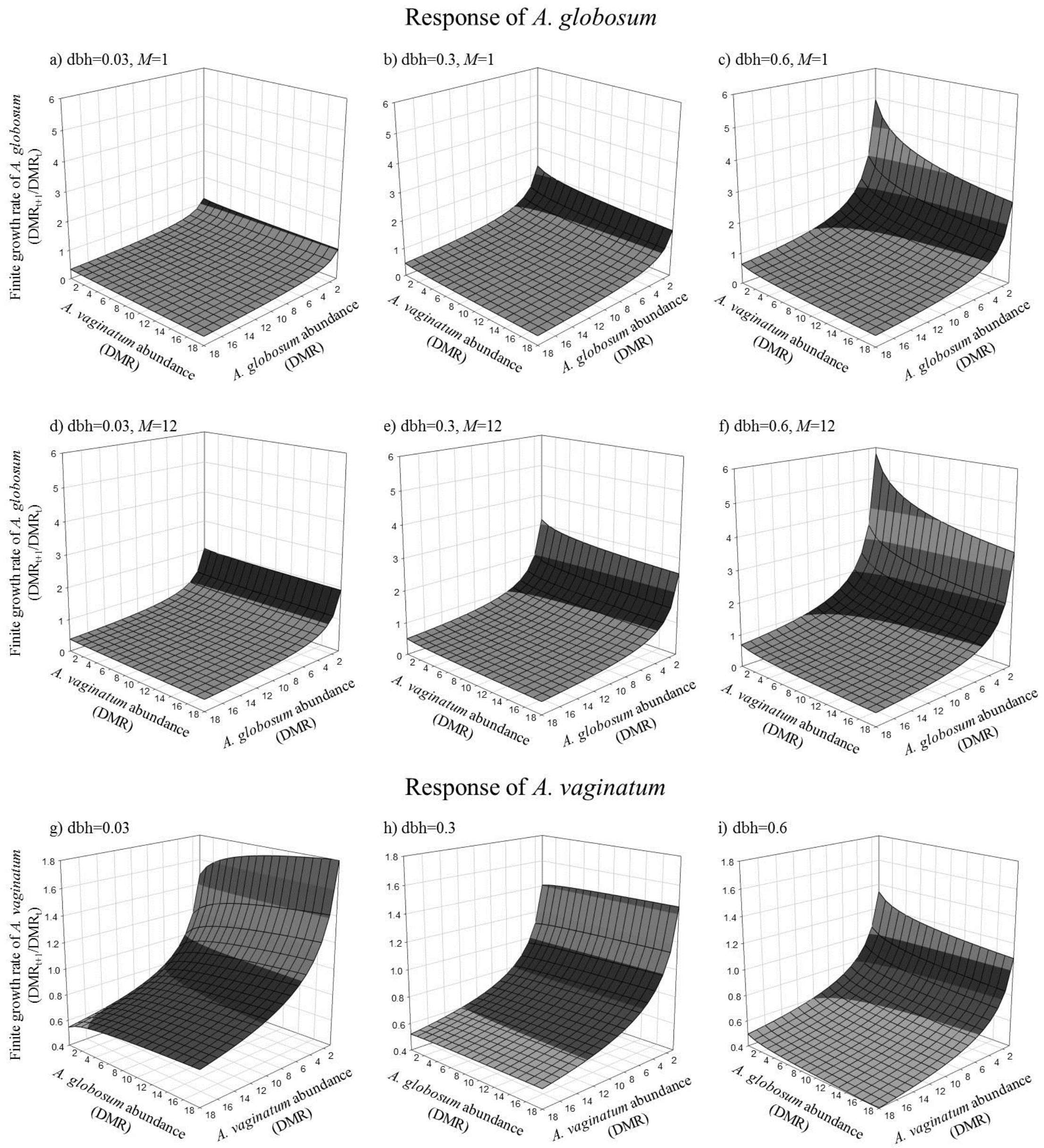


Fig. 2 Colonization potential for *Arceuthobium globosum* (a, b and c) and *A. vaginatum* (d, e and f) in function of the migration (x-axis) and the dbh. The lines within each plot represent differences on the restriction term: no restriction, size restriction (where $S_t$=0), and size restriction plus presence of the other species ($S_t \neq 0$). $S_t$ refers to second species DMR.

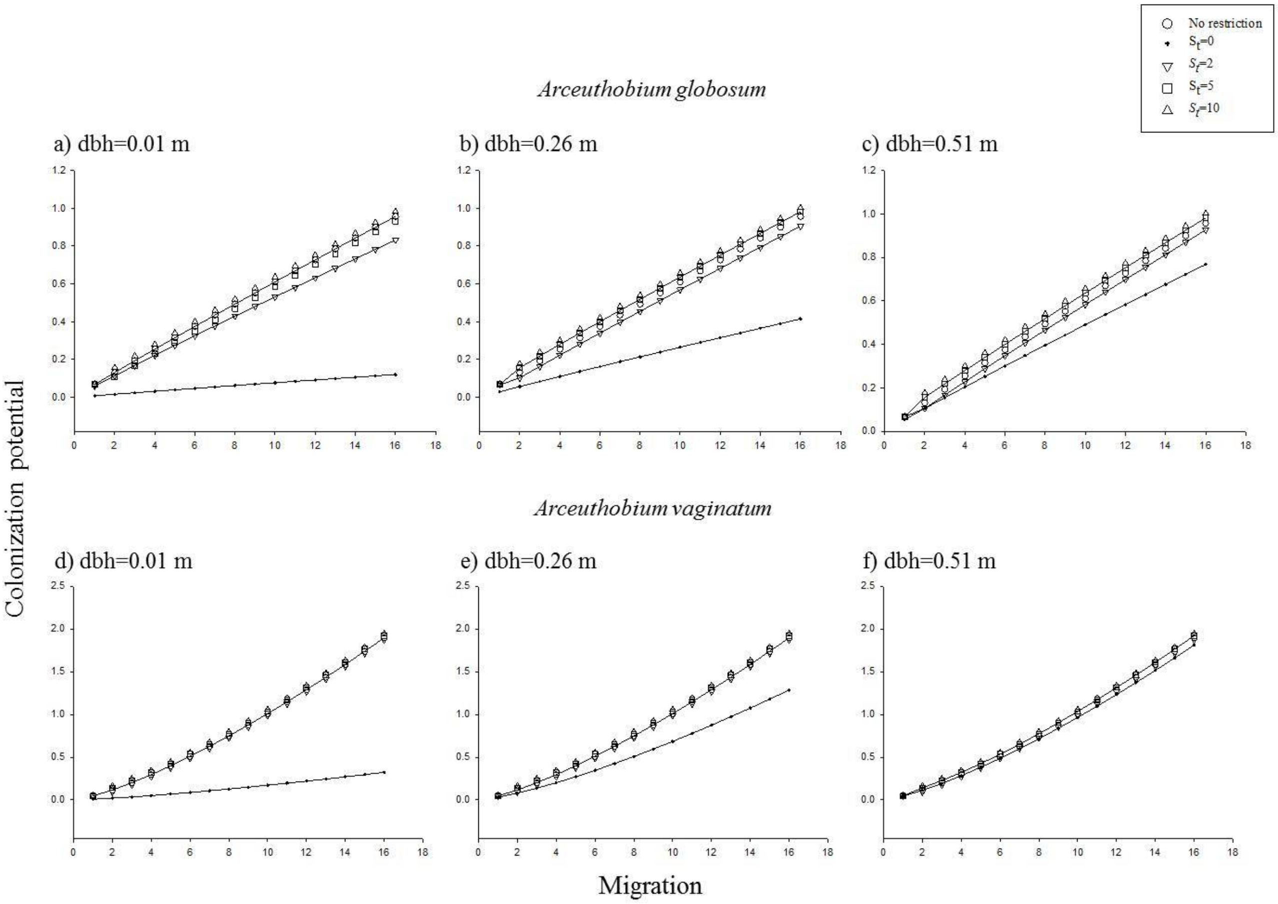


Fig. 3 Demographic importance of interspecific interactions for *Arceuthobium globosum*, in function of the host mean dbh, stand density and heterogeneity. a) sd=0, b) sd=0.25, c) sd= 0.5 and d) sd=1.

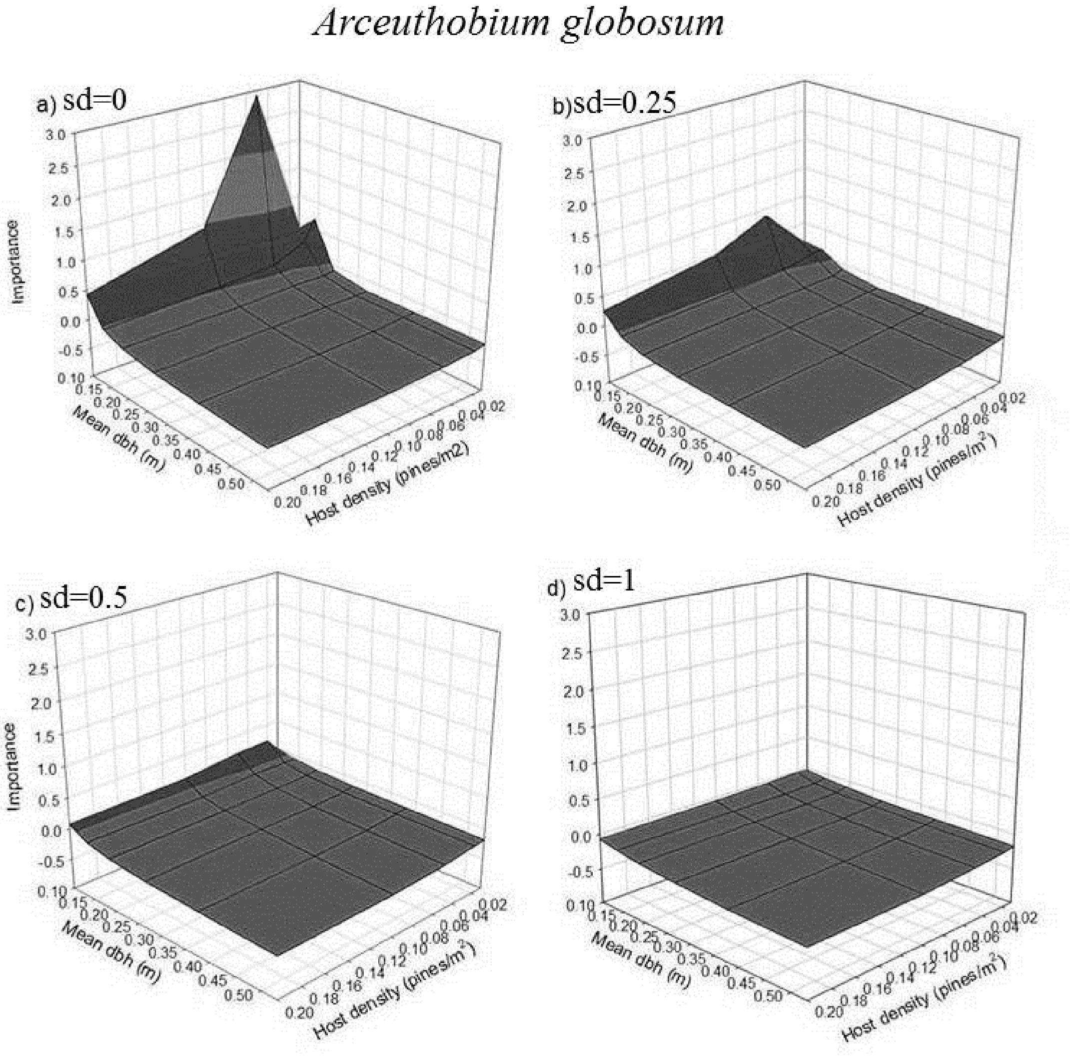


Fig. 4 Demographic importance of interspecific interactions for *Arceuthobium vaginatum*, in function of the host mean dbh, stand density and heterogeneity. a) sd=0, b) sd=0.25, c) sd= 0.5 and d) sd=1.

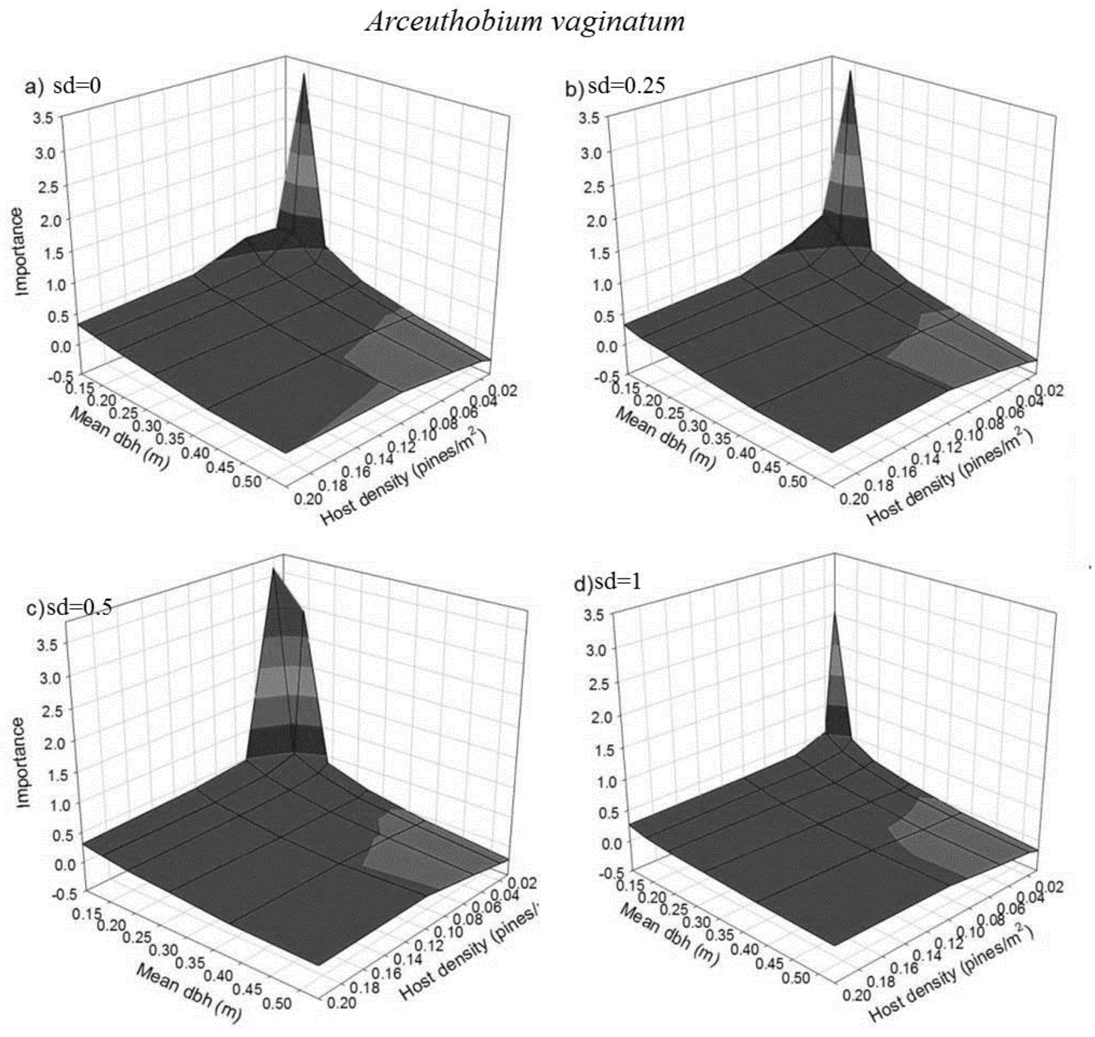
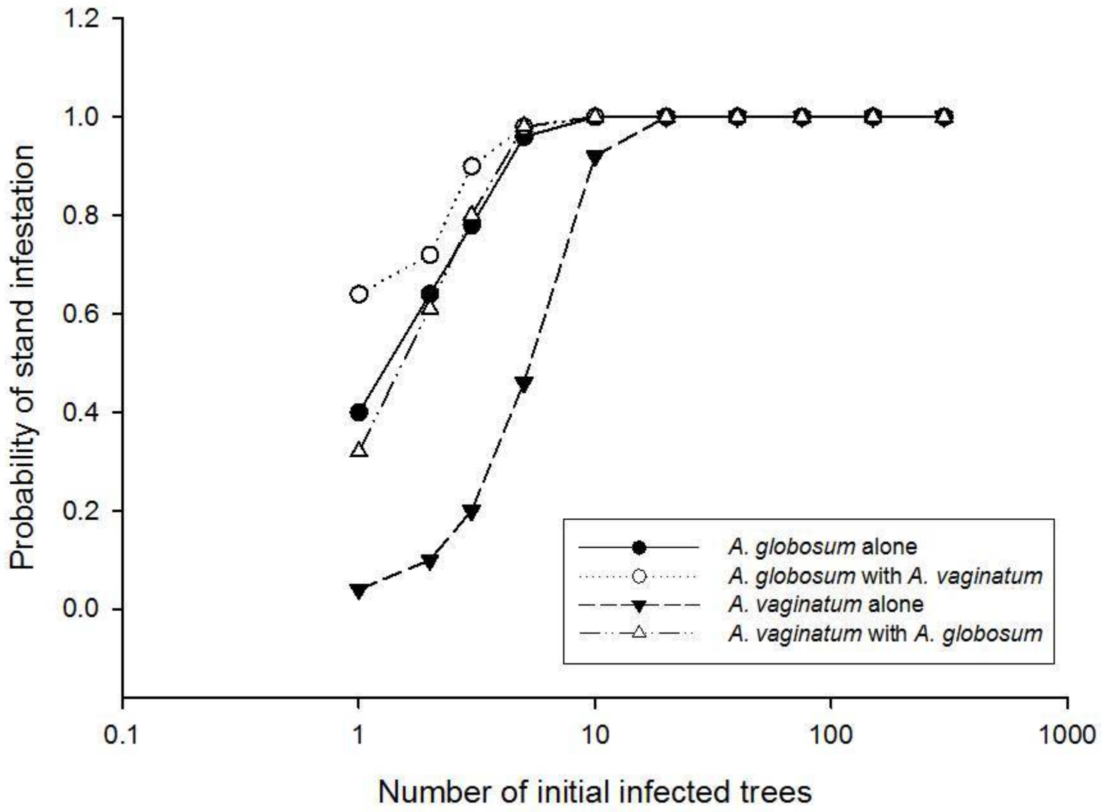


Fig. 5 Probability of stand infestation (y-axis) depending on the initial trees infected (x-axis) with a DMR=1. The lines within the plot correspond to the two species with two different conditions: no previous mistletoe infection or previously infected by the second species.



## Appendix

*Models selection and parameters estimations.*

To account for the effect of intra- and interspecific interactions on the growth dynamics of *A. globosum* and *A. vaginatum*, we needed to fit first a discrete-time growth model that estimated $N_{t+1}$ of the focal species, with finite and discrete error distribution. There were four single-species growth models that we could use for that purpose: Hassell, Ricker, Gompertz and Theta-Ricker models (B. Bolker, 2007; Kot, 2001). We tested the previously mentioned models with four different error distributions: Binomial, Poisson, Negative binomial and Hypergeometric. For this process we took into account only trees with $N_t \neq 0$, that on time *t+1* could remain the same, increase, decrease or become locally extinct.

Parameters were estimated using maximum likelihood with the function *mle2* (Bolker and *R* Development Core Team, 2011) in the statistical program *R* (*R* Development Core Team, 2012). We used the Akaike information criterion (AIC) to compare between models. Gompertz growth model with binomial distribution showed the smallest AIC for both species; hence we selected this one for posterior modeling.

*Table A1.* Population growth models tested for each species. Each model was fitted with four different error distributions. $N_t$=MDMR of focal species; $N_{t+1}$=MDMR of focal species in time *t+1*.

| | AIC | AIC |
|---|---|---|
| Hassell $N_{t+1}=\lambda N_t/(1+\alpha N_t)$ | *A. globosum* | *A. vaginatum* |
| Binomial | 2793.74 | 1321.2 |
| Poisson | 2843.76 | 1334.86 |
| Negative binomial | 2858.84 | 1339.48 |
| Hypergeometric | 2832.38 | 1319.2 |
| Ricker $N_{t+1}=N_t e^{(r(1-Nt/k))}$ | | |
| Binomial | 2795.24 | 1327.7 |
| Poisson | 2845.12 | 1340.62 |
| Negative binomial | 2850.6 | 1344.52 |
| Hypergeometric | 2902.16 | 1367.66 |
| Gompertz $N_{t+1}=N_t e^{(a+(b-1)\log(Nt))}$ | | |
| Binomial | **2788.94** | **1311.58** |
| Poisson | 2839.46 | 1327.18 |
| Negative binomial | 2837.12 | 1324.64 |
| Hypergeometric | 3360.32 | 1749.18 |
| Theta-Ricker $N_{t+1}= N_t e^{(r(1-(Nt/k)\theta))}$ | | |
| Binomial | 2791.04 | 1313.8 |
| Poisson | 2840.96 | 1324.56 |
| Negative binomial | 2850 | 1333.44 |
| Hypergeometric | 2916.16 | 1431.94 |

Once the Gompertz model was selected, we proceeded to test the effect of the associated species MDMR ($S_t$) and host size (dbh) (See Table 2 on text). Selected equation (eqn 2 on text) includes intra- and interspecific interactions and the effect of dbh, which affects directly the intrinsic rate of increase in MDMR, and the interactions coefficients.

*Table A2.* Linear functions of hosts' dbh with the intrinsic rate of increase ($r$), and the intraspecific ($f_g$) and interspecific ($a_g$) competition coefficients of the Gompertz population growth model (eqn 2) for the dwarf mistletoe species.

| Parameter | Linear function |
|---|---|
| $r(D_i)$ | $a_r + b_r D_i$ |
| $f_g(D_i)$ | $a_{fg} + b_{fg} D_i$ |
| $a_g(D_i)$ | $a_{ag} + b_{ag} D_i$ |

$a_r$, $b_r$, $a_{fg}$, $b_{fg}$, $a_{ag}$ and $b_{ag}$ are constants

Afterwards, we tested if including the dispersion term $\gamma M_{i,t}$ was justified. Again, the parameters were estimated with the function *mle2* and we used the AIC criterion for model selection. With this, we could justify the dispersion term only for *A. globosum*.

*Table A3.* Comparison of the growth model with and without the term of dispersion ($M$).

| | AIC | |
|---|---|---|
| Model | *A.globosum* | *A.vaginatum* |
| $N_{i,t+1}=N_{i,t}e^{(r(Di)+(fg(Di)-1)\ln Ni,t+ag(Di)\ln Si,t)}$ | 4219.84 | **1630.7** |
| $N_{i,t+1}=N_{i,t}e^{(r(Di)+(fg(Di)-1)\ln Ni,t+ag(Di)\ln Si,t)}+\gamma M$ | **4215.7** | 1632.7 |

To model colonization potential we needed to develop equations that could estimate the change in MDMR of a previously uninfected tree ($N_t$=0). The models depended on the host' dbh ($D_i$), because host size is directly related to colonization probability (Robinson and Geils, 2006), and the dispersion term ($M_{i,t}$), since the arrival of propagules would depend on the contribution of infected neighbors; we included as well the effect the MDMR of the associated species ($S_{i,t}$) to test the effect of interactions during this process. We tried the following models:

1) An equation that could estimate the change of $N_t$=0 to $N_t$=1; i.e. that colonization success could only be expressed with a MDMR of 1. For that we used only data of trees with initial 0 that became 1 in time *t+1*, and fitted a linear model with binomial error distribution.
2) Model of the change of $N_t$=0 to $N_t \neq 0$; i.e. that colonization success could be expressed with a MDMR different to 0 (1, 2, 3 and so on). For that model we used data of trees with initial 0 that became infected, with any MDRM value, in time *t+1*, and fitted a linear model with Poisson error distribution.
3) Model of the change of $N_t$=0 to $N_t \neq 0$ or remain 0; i.e. that colonization could have been or not successful. For that model we used data of trees with initial 0 and their following transition, whether they became infected or not in time *t+1*, and fitted a linear model with Poisson error distribution.

Each model was tested with the effect of the associated species ($S_t$), host size ($D_i$), dispersion ($M_i$), and their interactions. Parameters were estimated with standard *glm* procedure in *R* software, and then compared with AIC values.

4) The three models described previously showed an increasing colonization probability with no constrains. Therefore we tested a model where colonization potential depended entirely of propagules from neighboring trees, i.e. dispersion term, defined as:

$$c_{p,i} = \kappa M_{i,t}^{\alpha}$$

where $M_{i,t}$ is the dispersion term of *i*th tree in time *t* and $\kappa$ and $\alpha$ are constants. The latter function estimates how many colonists can get established in optimal conditions, it is without any kind of restrictions. Number of successfully established colonists may be constrained by the size (dbh) of the host (a larger tree is capable to support new colonist) and the previous infection of the associated species, in which case indicates the effect of the interaction. For that ,we modeled a logistic function that restricted the probability of colonization between 0 and 1.

With this function we tested the effect of associated species, host size and their interactions. We used the function *mle2* of R software for parameter estimation and models comparison was done with AIC.

*Table A4.* Colonization models tested for each species. Each model was fitted with different data, as specified in the table.

| | | AIC | | |
|---|---|---|---|---|
| | Error distribution | *A. globosum* | *A. vaginatum* | Data |
| **Model 1** | | | | |
| $N_{t+1} = \beta + a_c S_{i,t} + \delta D_i + kM$ | Binomial | 443.68 | 400.76 | Trees with initial zeros, that became infected on the next transition with a DMR=1 |
| $N_{t+1} = \beta + a_c S_{i,t} + \delta D_i + kM + \theta S_{i,t} D_i$ | Binomial | 441.2 | 402.34 | |
| $N_{t+1} = \beta + a_c S_{i,t} + kM + \varphi D_i M$ | Binomial | 445.35 | 402.03 | |
| $N_{t+1} = \beta + a_c S_{i,t} + \delta D_i + kM + \omega S_{i,t} M$ | Binomial | 445.52 | 402.74 | |
| $N_{t+1} = \beta + a_c S_{i,t} + \delta D_i + \theta S_{i,t} D_i + \varphi D_i M$ | Binomial | 443.52 | 403.87 | |
| $N_{t+1} = \beta + a_c S_{i,t} + \delta D_i + \theta S_{i,t} D_i$ | Binomial | 439.58 | 398.91 | |
| **Model 2** | | | | |
| $N_{t+1} = \beta + a_c S_{i,t} + \delta D_i + kM$ | Poisson | 452.28 | 671.72 | Trees with initial zeros, that became infected on the |
| $N_{t+1} = \beta + a_c S_{i,t} + \delta D_i + kM + \theta S_{i,t} D_i$ | Poisson | 450.34 | 671.49 | |
| $N_{t+1} = \beta + a_c S_{i,t} + \delta D_i + kM + \varphi D_i M$ | Poisson | 454.01 | 665.18 | |

| | | | | |
|---|---|---|---|---|
| $N_{t+1} = \beta + a_c S_{i,t} + \delta D_i + kM + \omega S_{i,t} M$ | Poisson | 454.13 | 673.6 | next transition with any DMR≠0 |
| $N_{t+1} = \beta + a_c S_{i,t} + \delta D_i + \theta S_{i,t} D_i + \varphi D_i M \cdot$ | Poisson | 452.62 | 668.4 | |
| **Model 3** | | | | |
| $N_{t+1} = \beta + a_c S_{i,t} + \delta D_i + kM$ | Poisson | 384.21 | 356.38 | Trees with initial zeros, and their next transition whether they became infected or not |
| $N_{t+1} = \beta + a_c S_{i,t} + \delta D_i + kM + \theta S_{i,t} D_i$ | Poisson | 380.05 | 355.68 | |
| $N_{t+1} = \beta + a_c S_{i,t} + \delta D_i + kM + \varphi D_i M$ | Poisson | 385.88 | 357.29 | |
| $N_{t+1} = \beta + a_c S_{i,t} + \delta D_i + kM + \omega S_{i,t} M$ | Poisson | 383.36 | 358.37 | |
| $N_{t+1} = \beta + a_c S_{i,t} + \delta D_i + \theta S_{i,t} D_i + \varphi D_i M \cdot$ | Poisson | 374.76 | 358.1 | |
| $N_{t+1} = \beta + a_c S_{i,t} + \delta D_i + kM + \theta S_{i,t} D_i + \epsilon$ | Poisson | 381.68 | 356.19 | |
| $N_{t+1} = \beta + a_c S_{i,t} + \delta D_i + \theta S_{i,t} D_i + \omega S_{i,t} M$ | Poisson | 381.31 | 356.31 | |
| **Model 4** | | | | |
| $\kappa M^{\alpha}(e^{\beta+acSt}/(1-e^{\beta+acSt}))$ | Poisson | 380 | 343.72 | Trees with initial zeros, and their next transition whether they became infected or not |
| $\kappa M^{\alpha}(e^{\beta+acSt+\delta D}/(1-e^{\beta+acSt+\delta D}))$ | Poisson | **373.66** | **342.94** | |
| $\kappa M^{\alpha}(e^{\beta+acSt+\delta D+\theta StD}/(1-e^{\beta+acSt+\delta D+\theta StD}))$ | Poisson | 374 | 344.94 | |

*Simulations on demographic importance*

To estimate the demographic importance of interactions, we used the growth (eqn 2) and colonization (eqn 5) models to simulate changes in MDMR trough time. The model was iterated 2500 times, and, as shown by the next figure, the first 40 iterations were discarded since it reflected transient dynamics.

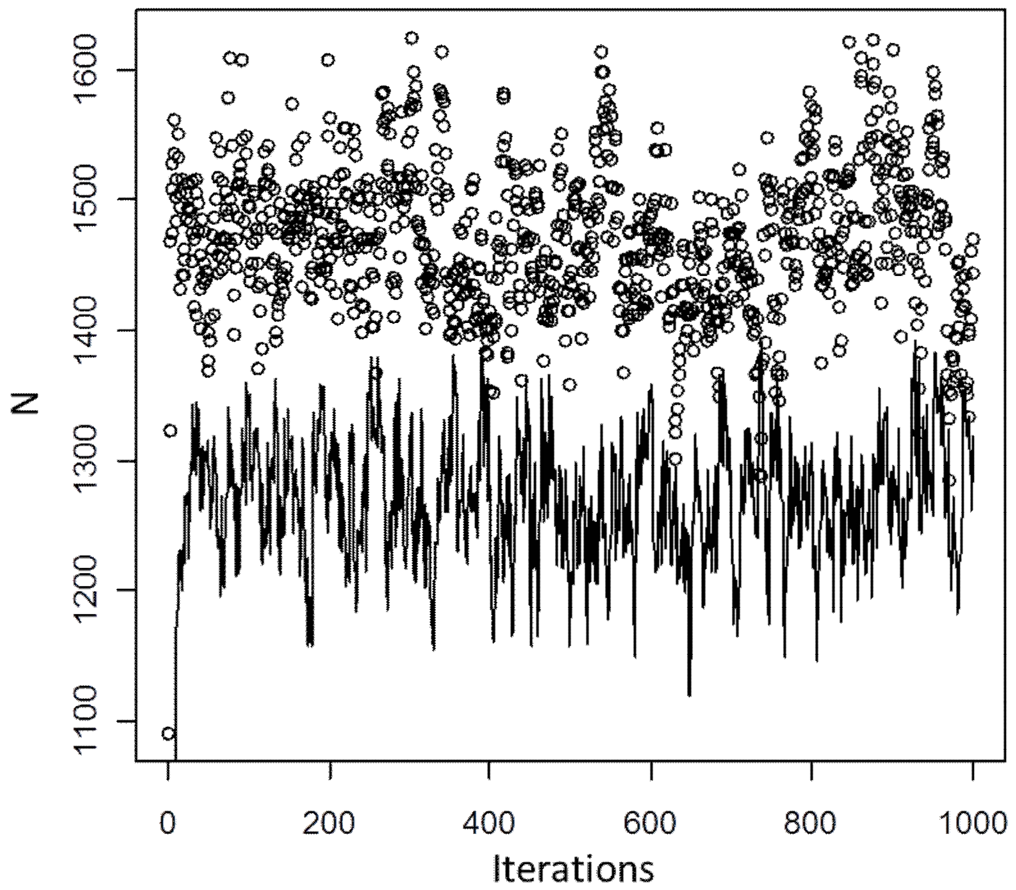


*Figure A1*. Example of model iteration. Dots represent *A. globosum*; solid line represents *A. vaginatum*.

To acknowledge for demographic importance of the interaction, we ran both models for growth and colonization on an artificial forest testing differences in stand structure. Density and host size structure influence demographic processes of dwarf mistletoes populations (Shaw *et al.*, 2005; Agne, 2013); thus we simulated stands with different stand densities, hosts dbh and heterogeneity in size. The observed density of the stand was 0.02 ind $m^{-2}$; however, in the study area, *Pinus hartwegii* forests can range from 0.01 to 0.2 ind $m^{-2}$ (Musalem y Solís, 2000), so we decided to following density interval: 0.01, 0.02, 0.05, 0.1 and 0.2 ind $m^{-2}$.

We assigned a dbh value to each pine, based in the observed values, which ranged from 0.03 to 0.58 m with a mean of 0.15 (sd=0.09). We choose six values so that the stands were represented by different means, ranging from the smallest trees to the larger ones. Because the higher frequencies were on trees smaller than 0.3 m, we took a narrower interval in values under 0.3 and the interval was wider for values above that.

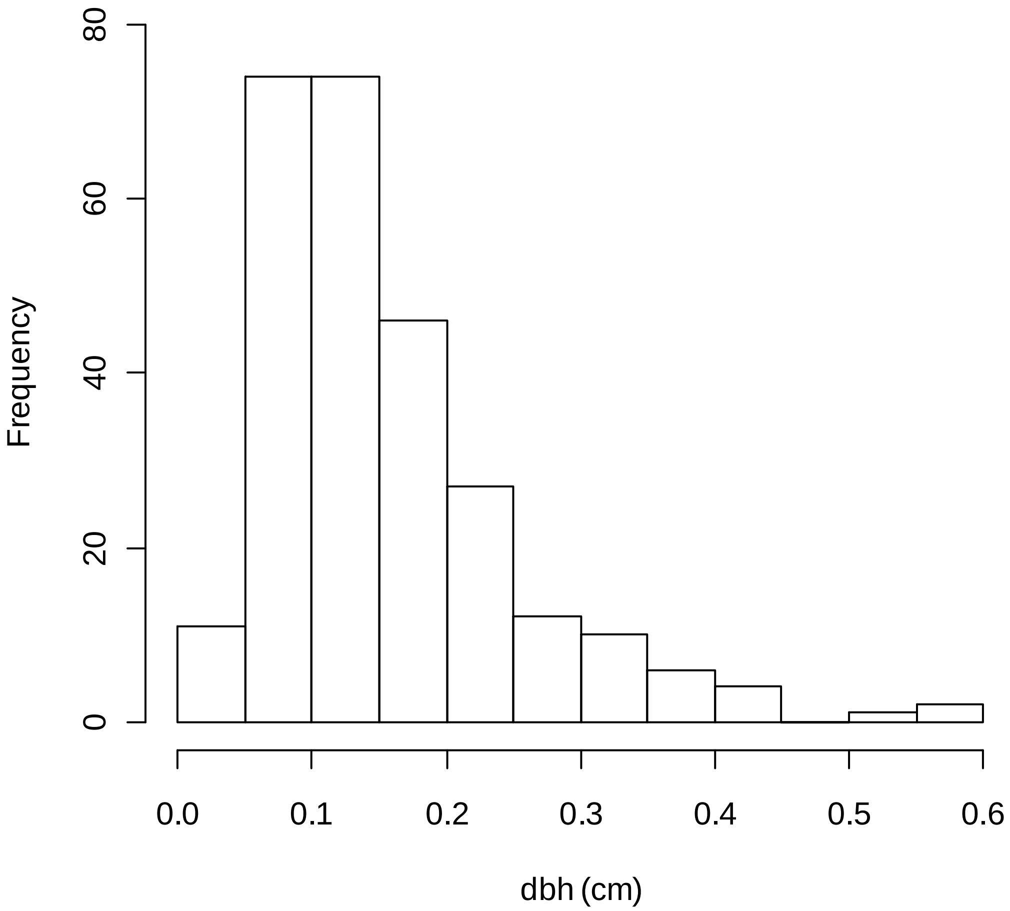


*Figure A2.* Histogram of observed dbh (m) values of *Pinus hartwegii* in the study site.

The dbhs were randomly assigned among the pines using a log-normal distribution with the aforementioned mean values and standard deviations of 0, 0.25, 0.5, and 1. The sd was chosen to test the role of even or uneven sized forests. A standard deviation equal to 0 means that all trees were the same size (an even size stand) and an sd equal to 1 represented a highly heterogeneous stand.

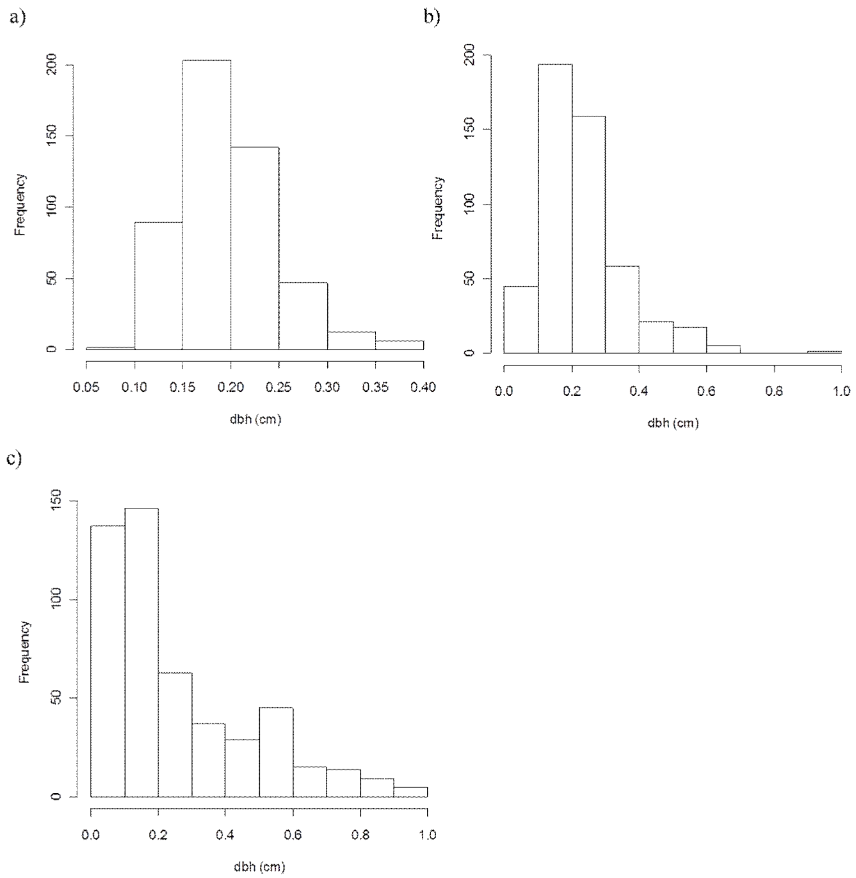


*Figure A3.* Histograms of random assigned dbh with log-normal distribution with a density of 0.05 ind $m^{-2}$, mean dbh of 0.19 m and standard deviations of a) 0.25, b) 0.5 and c) 1. Standard deviation of 0 was not ploted since all trees were the same size.

To assess the invasibility criterion, we created an artificially generated forest with the following initial conditions: 1000 trees, density=0.02 ind/$m^2$, dbh values taken randomly from observed data. Some trees were randomly infected and the model was iterated; afterwards, we infected trees at random with an initial MDMR of 1 and iterated 100 times. In the following table, is the detail of how many trees were infected and what were the probabilities of colonization when the stand was infested or not by the associated species.

*Table A7.* Probability of stand infestation. Infected refers to a stand that was already infested by the associated species.

| | *A. globosum* | | *A. vaginatum* | |
|---|---|---|---|---|
| Infected trees | Non-infected | Infected | Non-infected | Infected |
| 1 | 0.4 | 0.64 | 0.04 | 0.32 |
| 2 | 0.64 | 0.72 | 0.1 | 0.61 |
| 3 | 0.78 | 0.9 | 0.2 | 0.8 |
| 5 | 0.96 | 0.98 | 0.46 | 0.98 |
| 10 | 1 | 1 | 0.92 | 1 |

| | | | | |
|---|---|---|---|---|
| 20 | 1 | 1 | 1 | 1 |
| 40 | 1 | 1 | 1 | 1 |
| 75 | 1 | 1 | 1 | 1 |
| 150 | 1 | 1 | 1 | 1 |
| 300 | 1 | 1 | 1 | 1 |

*Coefficients*

The estimated coefficients for growth and colonization models are shown next.

*Table A5*. Parameter estimates for the growth model (eq. 2) for *Arceuthobium globosum* and *A. vaginatum*.

| Parameter | *A. globosum* | *A. vaginatum* |
|---|---|---|
| $a_r$ | 1.005 | 1.392 |
| $a_{fg}$ | 0.596 | 0.660 |
| $a_{ag}$ | 0.034 | -0.085 |
| $b_\mathrm{r}$ | 2.620 | -0.170 |
| $b_{fg}$ | -0.500 | - |
| $b_{ag}$ | 0.220 | 0.250 |
| $\gamma$ | 0.080 | - |

*Table A6.* Parameter estimates for the colonization model for *Arceuthobium globosum* and *A. vaginatum* (eq. 5).

| Parameter | *A. globosum* | *A. vaginatum* |
|---|---|---|
| $\kappa$ | 0.068 | 0.046 |
| $\alpha$ | -0.047 | 0.293 |
| $\beta$ | -2.001 | -1.677 |
| $a_c$ | 1.917 | 8.364 |
| $\delta$ | 6.672 | 9.310 |

# CAPÍTULO 3

# INCIDENCE, SEVERITY, AND AGGREGATION PATTERNS OF TWO SYMPATRIC DWARF MISTLETOES SPECIES (*Arceuthobium* spp.) IN CENTRAL MEXICO.

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ORIGINAL PAPER

# Incidence, severity, and aggregation patterns of two sympatric dwarf mistletoe species (*Arceuthobium* spp.) in Central Mexico

**Mónica Queijeiro-Bolaños · Zenón Cano-Santana · Graciela García-Guzmán**

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**Abstract** Dwarf mistletoes are widely studied because of their significant impact on host populations; however, few studies have focused on sympatric species. The understanding of their coexistence is important because it can provide useful knowledge for future management plans. We investigated the incidence, severity, and aggregation patterns of *Arceuthobium vaginatum* and *A. globosum* coexisting in Central Mexico. We estimated the correlation between both species incidences ($N = 75$ plots), the incidence–severity correlation ($N = 47$ plots) for each species, and the effect of biotic (host and non-host species abundance) and abiotic (altitude and slope) factors on the mistletoe incidence. In addition, we compared the hierarchical aggregation among and within plots of the two mistletoe species with a $\chi^2$ test. There is a clear dominance of *A. vaginatum* in the area, and both species incidences are negatively correlated with each other ($r_s = -0.54, P < 0.05$) and host abundance ($r = -0.26$, $P < 0.05$). The remaining factors were non-significant. Both species have a linear relationship between incidence and severity, i.e., they show a uniform increase in severity with incidence, which could help diagnose the degree of tree infection from incidence measurements. The species are aggregated within plots, but only *A. globosum* shows an aggregation among plots ($\chi^2 = 82.25$, $P < 0.001$); aggregation has not been shown previously for two sympatric dwarf mistletoe species. Our results can improve the scientific basis for forest management planning to control dwarf mistletoe and maintain biodiversity.

**Keywords** *Arceuthobium* spp. · *Pinus hartwegii* · Parasitism · Biotic factors · Abiotic factors · Parasitic interactions · Central Mexico

## Introduction

Dwarf mistletoes (*Arceuthobium* spp., Viscaceae) are the most important parasitic plants in the coniferous forests of North America because their infection causes a reduction in growth (both in height and in basal area) and fitness in host trees (Madrigal et al. 2007; Geils and Vásquez 2002; Cibrián et al. 2007; Shaw et al. 2008). Branch and stem deformations are common symptoms for some host species in addition to the reduction in water use efficiency and higher water stress (Hawksworth and Wiens 1996; Meinzer et al. 2004). However, dwarf mistletoes add vertical complexity to the community because the clumps and deformations offer refuge and nesting sites and nourishment to different animals (Watson 2001).

Dwarf mistletoe population dynamics depend on spread and intensification events. Spread refers to the dispersion to new hosts (aloinfections), whereas intensification is the increase in severity within the tree (autoinfection) (Shaw et al. 2005). A distinctive feature of dwarf mistletoes is the

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M. Queijeiro-Bolaños (✉)
Posgrado en Ciencias Biológicas, Universidad Nacional Autónoma de México, Av. Universidad 3000, 04510 Mexico City, DF, Mexico
e-mail: mqueijeiro@ciencias.unam.mx

M. Queijeiro-Bolaños · Z. Cano-Santana
Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, Av. Universidad 3000, 04510 Mexico City, DF, Mexico

G. García-Guzmán
Departamento de Ecología Evolutiva, Instituto de Ecología, Universidad Nacional Autónoma de México, Av. Universidad 3000, 04510 Mexico City, DF, Mexico

**Table 1** Comparative description of the differential traits of study species

| Feature | *Arceuthobium vaginatum* | *Arceuthobium globosum* |
|---|---|---|
| Shoot height | 20–55 cm | 18–70 cm |
| Shoot color | Dark brown to black, rarely reddish | Yellow–green |
| Shoot type | Flabellate, pendulous | Flabellate, erect |
| Anthesis | March–April | January–May |
| Fruiting | August | July–November |
| Differential hosts | *Pinus arizonica*, *P. cooperi*, *P. engelmannii*, *P. herrerai*, *P. oaxacana* | *Pinus douglasiana*, *P. maximonoi*, *P. michoacana*, *P. pringlei*, *P. teocote* |
| Rare hosts | *Pinus culminicola*, *P. teocote* | Possibly *Cupressus* sp. |
| Distribution | Northern to Central Mexico | Central Mexico to Guatemala |

Both species have the following traits in common: dioecious; they have sexual dimorphism: Staminate plants tend to be taller than pistillate ones; pollination by anemophily; dispersion by explosive seed dehiscence mechanism; common hosts: *Pinus hartwegii*, *P. durangensis*, *P. lawsoni*, *P. montezumae*, *P. patula*, *P. pseudostrobus*, and *P. rudis*; their infection type is localized not systemic. Based on Hawksworth and Wiens (1996), Hawksworth et al. (2002) and Cibrián et al. (2007)

explosive discharge of their seeds, which restricts the dispersal to short distances, usually not more than 14 or 15 m (Escudero and Cibrián 1985; Robinson and Geils 2006; Mathiasen et al. 2008). This pattern of dispersion, combined with host availability, may confer an aggregated distribution of mistletoes (Robinson and Geils 2006). Environmental factors that influence mistletoe spread and survival include elevation, latitude, slope, and climate conditions (Weir 1918; Graham and Leaphart 1961; Queijeiro-Bolaños et al. 2013). Host architecture is an important factor in mistletoe establishment, affecting the likelihood that seeds arrive at secure sites with enough light availability (Shaw and Weiss 2000; Godfree et al. 2003; Shaw et al. 2005).

Dwarf mistletoes are considered important species in Mexican forests. Because 22 of the 47 known species of *Arceuthobium* are distributed in Mexico, this region is considered the largest diversity center of the genus (Hawksworth and Wiens 1996); moreover, dwarf mistletoes are observed in 30 of the 32 states, primarily in the largest mountain chains (Cibrián et al. 2007). There are two species of special consideration in Mexico. *Arceuthobium vaginatum* subsp. *vaginatum* (Willd.) is the most damaging species for forestry and is widely distributed from Northern to Central Mexico. It has the broadest known host range in the genus (13 species of Mexican pines; Hawksworth and Wiens 1996). *Arceuthobium globosum* subsp. *grandicaule* (Hawks. and Wiens) is the most abundant species in Central Mexico; it is also distributed in Central America. It has the second broadest host range (12 species of Mexican pines; Hawksworth et al. 2002). These two species are extremely similar, except some phenotypic and phenological differences (Table 1). The distribution of the two species converges on the Trans-Mexican Volcanic Belt, Central Mexico, where they are the only mistletoe species parasitizing *Pinus hartwegii* (Hawksworth and Wiens 1996). According to their distribution, the two species can coexist in other areas where other suitable host species are present (Hawksworth and Wiens 1996), but there are no records of a sympatric parasitism. These species occur not only in the same stands but also on the same individual trees, where they show a differential distribution over the tree stem (Queijeiro-Bolaños et al. 2011). Infection process is extremely similar for both species; they depend almost entirely on balistocoric dispersal of the seeds, where these may travel no more than 15 m (depending on slope and wind), and most of these (91 %) do not travel farther than 8.7 m (Escudero and Cibrián 1985). Although it is unknown for these two species, it has been registered for other dwarf mistletoes that some animals, such as squirrels and birds, may be long-distance vectors by passively taking some of the seeds on their fur and feathers (Hawksworth and Wiens 1996). These species form localized infections and produce aerial shoots throughout the year (Hawksworth et al. 2002).

A great deal of research has been conducted on dwarf mistletoes, particularly on the impacts of disease on timber production; however, few studies have looked at sympatry. Even when the sympatry of two dwarf mistletoes has been observed (Hawksworth and Wiens 1996), there are no scientific reports on the incidence, severity, and aggregation patterns of two coexisting dwarf mistletoe species. The aim of this study was to investigate the intensity (i.e., incidence and severity) and aggregation patterns of *A. vaginatum* and *A. globosum* in a Natural Protected Area in Central Mexico. Our specific objectives were to (1) assess the incidence of both species and the correlation between them, (2) investigate the relationship between incidence and severity rates, (3) determine the effect of abiotic factors (altitude and slope) over the mistletoe incidence, and (4) determine the hierarchical aggregation pattern of the two species. This study is a preliminary step in the research of the dwarf mistletoe associations.

## Materials and methods

### Study site

The study site is located in the Zoquiapan National Park (ZNP; 19°15–29´N, 98°37–45´W), in Central Mexico. ZNP has an area of 19,400 ha and is part of the Popocatépetl–

**Table 2** Range of the measured parameters on the plots *(N = 75)*

| Variable | Range |
|---|---|
| Number of trees per plot | 30–420 |
| Number of pines[a] per plot | 16–420 |
| *A. globosum*[b] (%) | 1–61.72 |
| *A. vaginatum*[b] (%) | 1–87.7 |
| Altitude (m) | 3,021–3,650 |
| Slope (%) | 0–36 |

[a] *Pinus hartwegii*

[b] Infected plots only

Iztaccíhuatl biological corridor (Arriaga et al. 2000). This region is important because it comprises a significant gradient of ecosystems due to the wide altitude range observed in the area (2,850–4,150 m; Vargas 1997; Arriaga et al. 2000). The climate is classified as temperate subhumid with the rainy season from June to September (Arriaga et al. 2000). The mean annual temperature is 9.7 °C, and the average annual rainfall is 941.3 mm (SMN 2010). The vegetation of the area is classified as "temperate forests" and is dominated by *P. hartwegii*, but other abundantly represented genera include *Pinus*, *Cupressus*, *Quercus*, *Alnus*, and *Abies*. The forest understory is primarily represented by tillering grasses such as *Muhlenbergia macroura* and *Festuca tolucencis* (Obieta and Sarukhán 1981; Arriaga et al. 2000). This area can be considered as an infection center because it accumulates the large infection rates of *A. vaginatum* and *A. globosum* (Hawksworth and Wiens 1996; Queijeiro-Bolaños et al. 2013).

## Data collection

In July 2009, we selected 75 plots, each 0.33 ha in size, based on map of the area; the selected plots should accomplish the following criteria: clear dominance of *P. hartwegii*, minimum area to fit a plot, accessibility, and non-fragmented by roads or logged areas. The plots were at least 100 m apart, centerline to centerline. The plots varied in altitude from 3,021 to 3,650 m and slope from relatively flat areas to high steepness (Table 2). For each plot, we counted the total number of pines and the number of trees parasitized by *A. globosum* and/or *A. vaginatum*. Mistletoe incidence was calculated as the percentage of pines infected by each species.

In addition, we obtained the dwarf mistletoe rating (DMR) for a subset of 47 of the 75 previously selected plots. DMR system is a qualitative measurement of the degree of infection per tree (Hawksworth 1977), and it is suitable as a measure of severity, which is the quantity of disease affecting entities within a sample unit (Seem 1984). The DMR system rates a tree by dividing the tree into thirds; each third is visually classified from 0 to 2, where 0 represents the absence of infection, 1 represents <50 % of the main branches infected, and 2 represents more than 50 % of main branches infected. The DMR for each tree is calculated as the sum of the score of the thirds. The mean DMR for each plot was calculated as the average of the DMRs of all trees, including infected and uninfected ones (Hawksworth et al. 2002).

## Statistical analysis

Field data were analyzed to evaluate the following:

### *Incidence and severity relationships*

A $\chi^2$ test was completed to determine whether the frequencies (number of observed infected trees) differed between mistletoe species. To evaluate the relationship between the incidence of one species and the incidence of the second one (incidence–incidence relationship), a Spearman's rank correlation was computed for the plots where both species coexisted. To know the relationship between the incidence (percentage of infected trees) and severity of the infection (mean DMR), we performed a linear regression for each species. This relationship is useful to diagnose the disease because it can predict the rate of increase in severity with increasing incidence. Furthermore, incidence is a measure that can be taken in an easier and precise manner, and it would permit the estimation of severity for disease assessment (Seem 1984). These analyses were carried out with Statistica 8.0 (StatSoft Inc. 2007) software.

### *Factors affecting dwarf mistletoe incidence*

We constructed one structural equation model (SEM) for each mistletoe species that estimated the causal relationships between the mistletoes incidence and other variables. From a previous work (Queijeiro-Bolaños 2007), we anticipated what causal paths may be important. For all models, we considered plot altitude and slope to be abiotic factors. The biotic factors we examined were abundance of non-host species, host tree abundance, and mistletoe incidence.

Parameters of the models were estimated using maximum likelihood, and goodness of fit was analyzed with a $\chi^2$ test. The fitted models were compared with the Akaike information criterion (AIC). The models were performed with the lavaan package for R (Rosseel 2011).

### *Aggregation*

To evaluate the aggregation at two different scales, we used the statistical method developed by Boulinier et al.

(1996) and adopted by Rist et al. (2011) for parasitic plants. This method allows us to distinguish the aggregation at two hierarchical levels: among plots and among trees within the plots, testing whether the mistletoes are distributed in a random fashion on both within- and among-plot scales (Boulinier et al. 1996). This method was applied for the DMR values obtained for 47 plots, for each mistletoe species.

If mistletoes are distributed among plots in a random fashion, according to a Poisson distribution, then

$$\sum_{j-1}^{N} \left(X_j - X_m\right)^2 \Big/ X_m$$

where $N$ is the total number of plots, $X_j$ is the mean DMR of plot $j$, and $X_m$ is the mean DMR pooling all plots. The degrees of freedom are calculated as $N - 1$. If mistletoes were distributed within plots in a random fashion, according to a binomial distribution, then

$$\sum_{j-1}^{N_p} \sum_{i-1}^{n_j} \left(x_{ij} - x_j\right)^2 \Big/ \left(x_j\left(1 - 1/n_j\right)\right)$$

where $N_p$ is the number of plots with at least two pines and one infected pine, $n_j$ is the number of pines in plot $j$, and $x_{ij}$ is the DMR of the pine $i$ of the plot $j$. The degrees of freedom are calculated as $n_p - N_p$, where $n_p$ denotes the number of pines in $N_p$.

To define the strength of the aggregation among and within plots, we used the measure $J$, which gives the global measure of aggregation (Boulinier et al. 1996). It is the sum of the aggregation among plots, $J_k$, and within plots, $J_j$. Each of these measures, $J_k$ and $J_j$, gives us the contribution to global aggregation; therefore, $J_k/J$ equals the proportion of aggregation due to among-plot patterns and $J_j/J$ the proportion due to aggregation within-plot patterns (Boulinier et al. 1996).

$$J_k = 1/n \sum_{j-1}^{N} n_j \left\{ X_j \left( X_j - 1 + \left(n_j - 1/n_j\right)^2 \right) \right\} \Big/ \{X_m(X_m - 1/n)\} - 1$$

$$J_j = 1/n \sum_{j-1}^{N} \left\{ J_j n_j X_j \left( X_j - 1 + \left(\left(n_j - 1\right)/n_j\right)^2 \right) \right\} \Big/ \{X_m(X_m - 1/n)\}$$

## Results

### Incidence–severity relationships

*Arceuthobium vaginatum* was detected in 67 plots, and *A. globosum* occurred in only 19 of the 75 plots (Fig. 1). Only four plots were free of infestation, and the two species coexisted in 15 plots. The incidences among plots were highly variable. The maximum incidence of *A. vaginatum* was 88 % of the trees infected and the minimum 1 %. In contrast, the maximum incidence of *A. globosum* was 62 % of the trees infected and the minimum 1 % (Table 2). The prevalence, i.e., the incidence of all plots pooled, was 35.46 % ($N = 11{,}100$ trees); it was determined that 27.6 % of the trees were infected by *A. vaginatum*, 6.7 % by *A. globosum*, and 1.15 % by both species.

Few non-infested plots occurred, and the trees infected by *A. vaginatum* were significantly more frequent than those affected by *A. globosum* ($\chi^2 = 26.8$, $df = 1$, $P < 0.001$). In addition, in plots where both mistletoe species were present, they had a significant negative correlation ($r_s = -0.54$, $p < 0.05$, $N = 15$; Fig. 2).

For the 47 plots where DMR was measured, we observed that the most common classes of infection are the lightest ones (1 and 2) for both species (Fig. 3). It is also clear that *A. vaginatum* is considerably more abundant than *A. globosum*. Mean DMR was highly variable among plots, with *A. globosum* ranging from 0.002 to 1.18 and *A. vaginatum* from 0.08 to 2.05.

The two species have a clearly linear relationship between incidence and mean DMR of the plots (Fig. 4). The regression equation for *A. globosum* is DMR $= -0.0014 + 0.0063$ (incidence) ($r = 0.99$, $r^2 = 0.97$, $P < 0.001$), where the slope coefficient indicates the rate of increment of DMR with the increment of incidence. The regression equation for *A. vaginatum* is DMR $= -0.0403 + 0.0073$ (incidence) ($r = 0.93$, $r^2 = 0.87$, $P < 0.001$).

### Factors affecting dwarf mistletoe incidence

The SEM proposed for the two species had a good fit [Table 3; model (a) for *A. globosum* and model (b) for *A. vaginatum*]. Figure 5 shows the partial correlation coefficients for each path. The abundance of both mistletoe species was negatively correlated with each other and with the abundance of host trees. These models explained 21 and 29 percent of the variation in the incidence of *A. globosum* and *A. vaginatum*, respectively.

Abundance of non-host species showed a negative, but marginally significant, relationship with *A. vaginatum* incidence. The abiotic factors, i.e., altitude and slope, were not significantly correlated with the incidence of the two mistletoe species. A full detail of path coefficients is presented in “Appendix.”

### Dwarf mistletoe aggregation

*Arceuthobium vaginatum* exhibited an aggregated pattern within plots ($\chi^2 = 354{,}903$, $df = 5{,}938$, $P < 0.0001$), yet

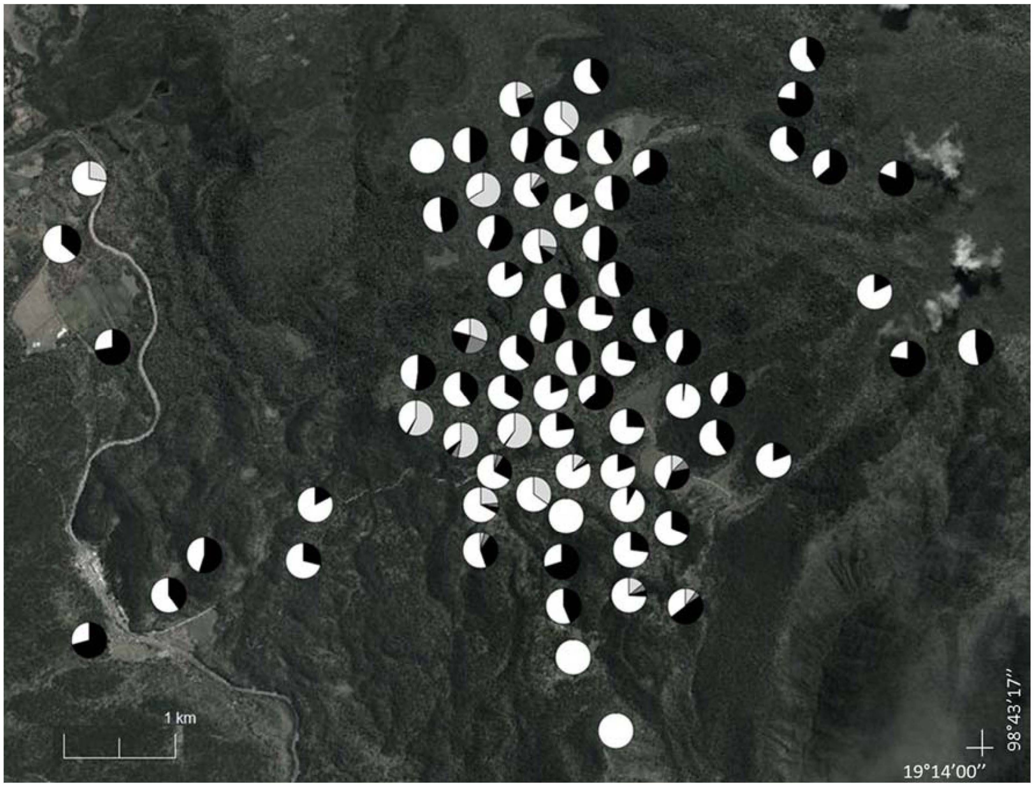

**Fig. 1** Location and incidence of the plots ($N = 75$) in ZNP. On each pie chart, *white* = percentage of non-infested trees, *black* = percentage of *Arceuthobium vaginatum*, *light gray* = percentage of *A. globosum*, and *dark gray* = percentage of trees infected with both species. Note that the size of the charts does not represent the size of the plot

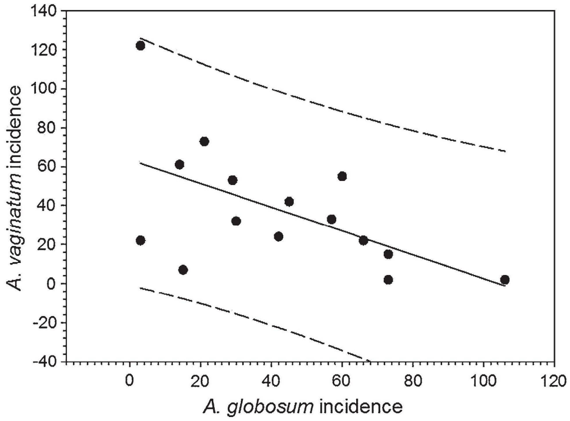

**Fig. 2** Spearman's rank correlation between *Arceuthobium globosum* and *A. vaginatum* incidences in the plots where they coexisted ($N = 15$). It is reported to have a negative and significant correlation ($r_s = -0.54$, $p < 0.05$)

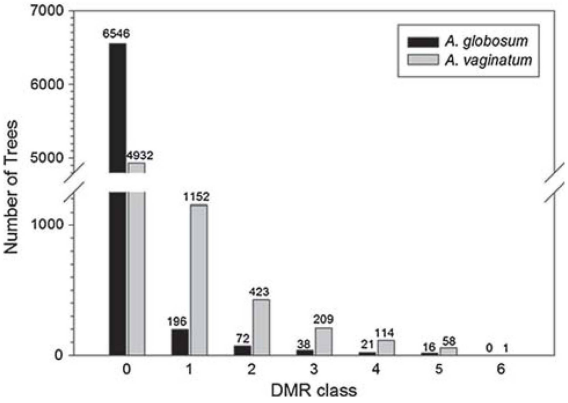

**Fig. 3** Frequency of pines (*Pinus hartwegii*) on each DMR class. *Numbers on bars* indicate the number of trees

had a random distribution among plots ($\chi^2 = 17.67$, $df = 46$, $P > 0.05$); within-plot aggregation represented the 63 % of the total aggregation. In contrast, *A. globosum* had an aggregated pattern within ($\chi^2 = 7{,}324$, $df = 1{,}328$, $P < 0.0001$) and among plots ($\chi^2 = 82.25$, $df = 46$, $P < 0.001$); within-plot aggregation explained 55 % of the total aggregation. Only a small number of trees had a heavy infection (Fig. 3), which coincides with the aggregation

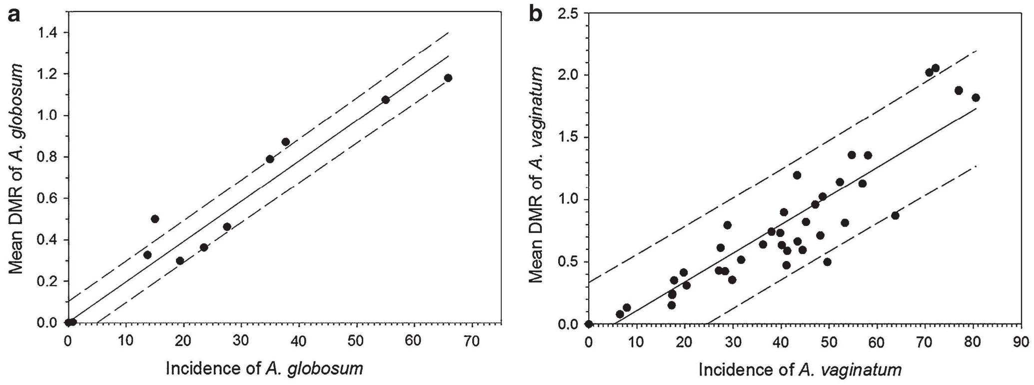

**Fig. 4** Incidence–mean DMR relationship of **a** *Arceuthobium globosum* and **b** *A. vaginatum*. The *solid lines* represent the linear regression, and the *dashed lines* represent the 95 % confidence interval

**Table 3** Model fit tested with a $\chi^2$ maximum likelihood ratio test and difference models

| Model | Model $\chi^2$ | *df* | *P* | AIC |
|---|---|---|---|---|
| *A. globosum* (a) | 1.31 | 1 | 0.31 | 2,844.9 |
| *A. vaginatum* (b) | 1.04 | 1 | 0.31 | 2,844.9 |

For all models, $N = 75$

**Table 4** Number of infected trees by *A. globosum* or *A. vaginatum*, with different DMR class of the other species

| DMR class | *A. globosum* | *A. vaginatum* |
|---|---|---|
| 0 | 1,882 | 268 |
| 1 | 50 | 43 |
| 2 | 9 | 16 |
| 3 | 10 | 7 |
| 4 | 1 | 6 |
| 5 | 5 | 3 |
| 6 | 0 | 0 |

pattern within trees. While only a few trees were infected with classes 1–5 of *A. globosum*, *A. vaginatum* infection was more prominent in these classes. When the two mistletoes species were infecting the same tree, the DMR of each species rarely reached a class above 3 (Table 4).

## Discussion

Our study indicates that *A. vaginatum* is more likely to be found in the Zoquiapan National Park than *A. globosum*, revealing its clear dominance in the surveyed zone. The overall prevalence of both species in the zone was 35 % of the trees, which is observed within the range reported in the literature for several mistletoe species. The prevalence values are highly variable not only among systems, places, and species but also within species in an area, for both Loranthaceae and Viscaceae families. In some cases, the incidence can range from 18.0 to 33.6 % in the same area (*A. oxycedri* on *Juniperus excelsa*; Sarangzai et al. 2010). Previous surveys have indicated that *Arceuthobium* spp. can infest 3–77 % *P. hartwegii* trees in ZNP (Andrade and Cibrián 1980; Hernández-Benítez et al. 2005), whereas in Nevado de Toluca (state of Mexico), they infest up to 94 % pines *P. montezumae* (Ramírez-Dávila and Porcayo-Camargo 2009). Likewise incidence, the mean DMR of both species is consistent with what has been found in studies performed in other areas, where it ranges between 1 and 3 (Andrade and Cibrián 1980; Trummer et al. 1998; Sarangzai et al. 2010; Maloney and Rizzo 2002).

Both species exhibited a linear relationship between incidence and mean DMR, showing a uniform increase in DMR with incidence. According to Seem (1984), this type of pattern can be explained by a greater predominance of autoinfection due to a short-range dispersal mechanism. These species do not form a systemic infection; nevertheless, they have an explosive dispersal of the seeds that allow them to spread to no more than 15 m apart. Therefore, this species should have a slow spread and a faster intensification. This relationship is useful to predict the DMR on a stand from taking only measurements of incidence, which simplifies the diagnosis. But these models are only applicable to this zone because of the high variability among areas and species.

According to our SEM models, there is a significant relationship between the incidences of both species. The incidence–incidence relationship between two different species of dwarf mistletoes is a non-explored subject, although the dual parasitism has been described in another 12 cases (Hawksworth and Wiens 1996). This kind of

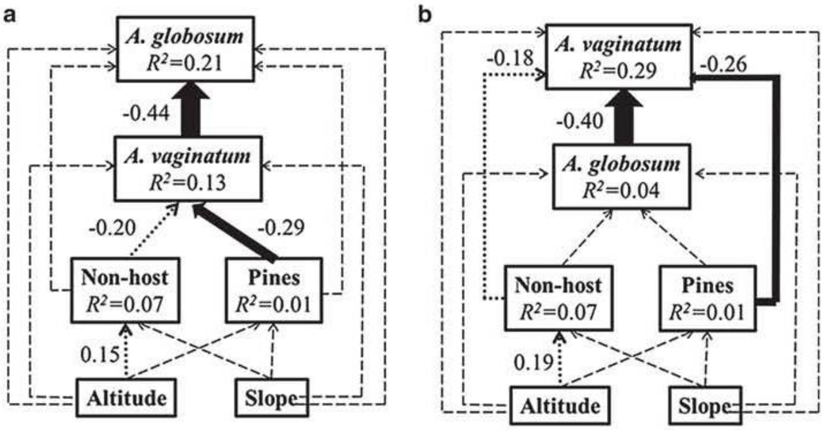

**Fig. 5** Fitted paths for models (**a**) and (**b**). *Solid paths* are statistically different from 0 ($P < 0.05$), whereas *dashed paths* are not. *Dotted paths* are marginally significant ($P < 0.08$). Path widths are proportional to the standardized regression coefficients. Only the coefficients for significant paths are shown. The $R^2$ of the endogenous variables are inside the variable boxes

association is infrequent for dwarf mistletoes, but is fairly common for other species such as *Phoradendron* and Loranthaceae members (see, for example, Genini et al. 2012). The sympatry of two *Arceuthobium* species is not unusual, but dual parasitism (two different species parasitizing a single host tree) is a rare event (Hawksworth and Wiens 1996). Hawksworth (1969) defined the term "competitive host exclusion" where if an *Arceuthobium* species is present in an area, other dwarf mistletoes species will rarely infest the same host. Nevertheless, the mechanism that controls this phenomenon has not been explained nor has been subjected to research, as stated by Hawksworth and Wiens (1996). In the case of *A. globosum* and *A. vaginatum*, they dual-parasitize *P. hartwegii*, a principal host for both species. But *A. globosum* was observed in a lower proportion than *A. vaginatum*, and the model shows that the two species have a negative relationship, possibly depicting some kind of host competitive exclusion process and a differential dispersal or recruitment patterns. All of these require further investigation. For example, when *A. americanum* and *A. vaginatum* subsp. *cryptopodum* are sympatric, the first one only parasitizes 13 % trees of *P. ponderosa* (secondary host) and the second one 64 % trees (principal host) (Hawksworth 1969).

The abundance of *P. hartwegii* was also a significant and negative variable, affecting the incidences of both mistletoe species, i.e., less hosts and more infection. Host availability and host demography are important factors determining the incidence of an obligate parasite (Donohue 1995). The negative correlation with host abundance has been observed for other mistletoe species, such as *Phoradendron pauciflorum* on *Abies concolor* (Maloney and Rizzo 2002). In low-density stands, the host trees have less competition for resources and have a better performance; thus, these stands are more appealing than the high-density stands (Bickford and Kolb 2005). In addition, the higher light incidence in less-dense stands favors the production of aerial shoots of the mistletoes (Shaw and Weiss 2000; Bickford and Kolb 2005; Robinson and Geils 2006).

Non-host species abundance is positively related to *A. vaginatum* incidence, although it was only marginally significant. This could be evidence that the non-host distribution also plays an important role in the creation of infection centers, similar to that reported in previous studies (Trummer et al. 1998; Maloney and Rizzo 2002), where the non-host forms a barrier, impeding the seed dispersal, and thus favoring the concentration of seeds among the same trees (Trummer et al. 1998).

Altitude and slope were not observed to be significant factors in determining the incidence of mistletoes and are, therefore, not informative in predicting where could we find each species or which areas are more susceptible for infestation. Ramírez-Dávila and Porcayo-Camargo (2009) reported that *Arceuthobium* spp. can be distributed equally within 2,850 and 3,150 masl and with any slope percentage. Even though the environmental variables are important determinants of the mistletoe species distribution on regional scales (Hawksworth 1969; Williams et al. 1972; Smith and Wass 1979), several microclimatic aspects should also be considered. These include the conditions that influence seedling establishment, such as optimal temperature, light exposure, and humidity, as shown for *A. tsugense* (Deeks et al. 2001) and *A. americanum* (Brandt et al. 2005).

Both species showed an aggregation pattern within trees, which coincides with the creation of infection centers. *A. vaginatum* did not show any aggregation at the plot level and presented a random distribution among areas. The patterns of aggregation that we observed are comparable with other reports on parasitic plants. These studies indicate that the majority of hosts are affected by a small amount of parasites, and only a few trees bear a large load of parasites (Norton et al. 1995; Aukema 2003; Ramírez-Dávila and Porcayo-Camargo 2009; Rist et al. 2011). The seed dispersal mechanisms have a strong influence on the spatial arrangement of parasitic plants. In case of dwarf mistletoes, the aggregation within the host is probably the result of the ballistic dispersal of the seeds, which promotes the short-distance spread or intensification within the same tree (Hawksworth and Wiens 1996). It has been reported for other species that 40 % of dispersed seeds are intercepted by trees (Hawksworth and Wiens 1996); from experimental data, we know that for *A. globosum*, the germination rate is of 55 %, and for *A. vaginatum*, it is 32 %, while the rest of these get desiccated. Furthermore, of these, only 2 % are successfully established on new trees (Queijeiro-Bolaños and Cano-Santana, unpublished data). The latter may confer an aggregated distribution within neighboring trees and the intensification on those already infected. In contrast, the aggregation among plots may have several causes, such as microhabitat preference, host defense mechanisms, habitat heterogeneity (including local disturbances), and biotic interactions (Medel et al. 2004). It could be a host exclusion mechanism, indicating a local process that reduces species overlap (Genini et al. 2012). We have evidence from 15 plots that when the two species do not coexist, they achieve a greater DMR rate. In contrast, when they share the same host, they did not accomplish a larger infection rate (Queijeiro-Bolaños, Cano-Santana, and García-Guzmán, unpublished data).

The local history of the site may have a great influence on dwarf mistletoe distribution and aggregation patterns. ZNP is an area that suffers from several types of disturbance such as natural and induced fires, legal and illegal unsustainable logging, landfill sites, and cattle grazing (Obieta and Sarukhán 1981; Arriaga et al. 2000). Disturbance can have an impact on mistletoe populations, and it is well known that fire has an influence on mistletoes occurrence and distribution patterns (Knight 1987; Kipfmueller and Baker 1998; Swanson et al. 2006). Although the present study is not addressed toward disturbance effects, we know from previous work that there is some evidence supporting the hypothesis that fire and logging may favor dwarf mistletoe incidence (Queijeiro-Bolaños 2007; Queijeiro-Bolaños et al. 2013). The plots on this work did not have evidence of logging (or this was minimum); however, we do not know the historical fire regime of the 75 plots. Nevertheless, fire in the past may have had an influence on the aggregation patterns of these two species, and this aspect needs further consideration.

Aggregation is a known pattern for parasitic plants, but it has never been shown for two sympatric dwarf mistletoe species, and this brings a new insight into dual parasitism. There are other significant ecological factors, playing an important role over the mistletoes incidence, such as the host and non-host species disposition; thus, we suggest that the study of the tree disposition (host and non-host) and seed dispersal may be relevant. Although some authors have modeled the ballistic and contagion of dwarf mistletoes (e.g., see Robinson and Geils 2006), their models did not include two sympatric and possibly competing species. Therefore, it is important to perform studies of distribution patterns, spread and intensification of dwarf mistletoe species in coexistence, and manipulative experiments that are focused on testing competitive interactions directly to give more insights into sympatric parasitism.

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## Appendix

See Table 5.

**Table 5** Coefficient values, standard errors, *Z* scores, and standardized path coefficients for the two fitted structural equation model

| Path | Estimate | SE | *Z* value | *P* | Standardized coefficients |
|---|---|---|---|---|---|
| a | | | | | |
| *A. vaginatum* → *A. globosum* | −0.394 | 0.097 | −4.080 | <0.001 | −0.449 |
| Altitude → *A. globosum* | 0.792 | 2.103 | 0.376 | 0.707 | 0.040 |
| Slope → *A. globosum* | −0.130 | 0.092 | −1.406 | 0.16 | −0.147 |
| Non-hosts → *A. globosum* | −0.169 | 0.688 | −0.245 | 0.806 | −0.027 |
| *P. hartwegii* → *A. globosum* | −0.232 | 0.445 | −0.521 | 0.603 | −0.056 |
| *P. hartwegii* → *A. vaginatum* | −1.361 | 0.508 | −2.680 | 0.007 | −0.289 |
| Non-hosts → *A. vaginatum* | −1.447 | 0.805 | −1.797 | 0.072 | −0.200 |

**Table 5** continued

| Path | Estimate | SE | *Z* value | *P* | Standardized coefficients |
|---|---|---|---|---|---|
| Slope → *A. vaginatum* | 0.046 | 0.11 | 0.414 | 0.679 | 0.045 |
| Altitude → *A. vaginatum* | 3.577 | 2.481 | 1.442 | 0.149 | 0.159 |
| Slope → *P. hartwegii* | −0.007 | 0.025 | −0.297 | 0.767 | −0.034 |
| Altitude → *P. hartwegii* | 0.356 | 0.552 | 0.645 | 0.519 | 0.075 |
| Altitude → Non-hosts | 0.598 | 0.348 | 1.720 | 0.085 | 0.193 |
| Pendiente → Non-hosts | 0.022 | 0.016 | 1.377 | 0.168 | 0.154 |
| b | | | | | |
| *A. globosum* → *A. vaginatum* | −0.461 | 0.113 | −4.080 | <0.001 | −0.404 |
| *P. hartwegii* → *A. vaginatum* | −1.221 | 0.461 | −2.649 | 0.008 | −0.259 |
| Non-hosts → *A. vaginatum* | −1.262 | 0.730 | −1.729 | 0.084 | −0.175 |
| Slope → *A. vaginatum* | −0.023 | 0.101 | −0.223 | 0.824 | −0.022 |
| Altitude → *A. vaginatum* | 3.292 | 2.245 | 1.466 | 0.143 | 0.147 |
| Altitude → *A. globosum* | −0.618 | 2.294 | −0.269 | 0.788 | −0.031 |
| Slope → *A. globosum* | −0.148 | 0.102 | −1.450 | 0.147 | −0.167 |
| Non-hosts → *A. globosum* | 0.402 | 0.745 | 0.539 | 0.590 | 0.063 |
| *P. hartwegii* → *A. globosum* | 0.305 | 0.470 | 0.649 | 0.516 | 0.074 |
| Slope → *P. hartwegii* | −0.007 | 0.025 | −0.297 | 0.767 | −0.034 |
| Altitude → *P. hartwegii* | 0.356 | 0.552 | 0.645 | 0.519 | 0.075 |
| Altitude → Non-hosts | 0.598 | 0.348 | 1.720 | 0.085 | 0.193 |
| Slope → Non-hosts | 0.022 | 0.016 | 1.377 | 0.168 | 0.154 |

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# CAPÍTULO 4

## GROWTH OF HARTWEG'S PINE (*Pinus hartwegii*) PARASITIZED BY TWO DWARF MISTLETOE SPECIES (*Arceuthobium* spp.)

Queijeiro-Bolaños, M. y Z. Cano-Santana. Growth of Hartweg's pine (*Pinus hartwegii*) parasitized by two dwarf mistletoes species (*Arceuthobium* spp.) Aceptado en *Botanical Sciences* (23/12/14).

## Abstract

Coniferous forests occupy a large extent (17%) of the Mexican territory. Within these forests, pines are a common and sometimes dominant component; however, several abiotic and biotic factors affect pines growth. Among the main biotic factors is the parasitic effect of dwarf mistletoes. In Zoquiapan (Iztaccíhuatl Popocatépetl National Park, Central Mexico) two dwarf mistletoe species coexist parasitizing *Pinus hartwegii*. The aim of this study was to know the effect of *Arceuthobium globosum* and *A. vaginatum,* either individually or as a pair, on *P. hartwegii* growth, allometric relations, and size susceptibility. We recorded diameter at breast height (dbh) and crown spread of *P. hartwegii* for 3 years on individuals infested by either one of the species, both, or none, as well as the infection severity. The relative growth rate (RGR) in diameter was strongly influenced by the pines initial dbh; whereas the infecting species or severity did not show a differential effect. The allometric relation of dbh and height was affected by parasitism, where the trees infected by both species were shorter than the uninfected and infected by *A. vaginatum* at the same dbh. The parasitic effect does not differ among these mistletoe species, and the host-size structure affects the presence and severity of infection; maintaining even-age stands provides a better scenario for a milder effect of parasitism, which should be considered for managing plans.

**Key words:** *Pinus hartwegii,* dwarf mistletoe, relative growth rate, allometry, parasitic plants

## Resumen

Los bosques de coníferas ocupan una gran extensión en el territorio mexicano (17%). Dentro de estos bosques, los pinos son componente comunes, y en ocasiones dominantes; sin embargo, diversos factores abióticos y bióticos afectan su crecimiento. Entre los principales factores bióticos se encuentra el efecto parasítico del muérdago enano. En Zoquiapan (Parque Nacional Iztaccíhuatl Popocatépetl, Centro de México) dos especies de muérdago enano coexisten y parasitan a *Pinus hartwegii*. El objetivo de este estudio es el de conocer el efecto de *Arceuthobium globosum* y *A. vaginatum*, solos o en conjunto, en el crecimiento de *P. hartwegii*, las relaciones alométricas y la susceptibilidad por tamaños. Registramos el diámetro a la altura del pecho (dap) y la dispersión de la copa de *P. hartwegii* por tres años en individuos infestados por alguna de las dos especies, ambas o ninguna, así como la severidad de la infestación. La tasa relativa de crecimiento (TRC) en diámetro estuvo fuertemente influida por el dap inicial de los pinos, mientras que la especie que infecta y la severidad no mostraron un efecto diferencial. La relación alométrica del dap y la altura fue afectada por el parasitismo, ya que, dentro de una misma categoría de dap, los árboles infectados por las dos especies fueron más bajos que los no infectados y los infectados por *A: vaginatum*. El efecto del parásito no difirió entre especies, y la estructura de tamaños del hospedero afecta la presencia y severidad de la infección: el mantenimiento de bosques de no coetáneos provee un mejor escenario para atenuar el efecto del parasitismo, observación que debe ser considerada en los planes de manejo.

**Palabras clave:** *Pinus hartwegii*, muérdago enano, tasa relativa de crecimiento, alometría, plantas parásitas

## Introduction

Coniferous forests represent 17% of the Mexican territory. About 90% of this area comprises *Pinus* or *Pinus-Quercus* species association (Rzedowski, 2006; INEGI, 2013). There are approximately 50 pine species described in Mexico, which represents more than 50% of all pine species around the world, many of these with distribution restricted to the country (Nieto de Pascual-Pola, 2009; GD, 2013). Moreover, pines can be distributed over a wide variety of climatic, topographic, and geologic conditions, ranging from cold to warm weathers, and from high mountains to the sea level (Rzedowski, 2006). Hartweg's pine (*Pinus hartwegii*) forests are of great ecological importance because they are the arboreal vegetation most tolerant to low temperatures and high altitudes, reaching the treeline limit at 4000–4200 m a.s.l. (Musalem and Solís, 2000; Rzedowski and Rzedowski, 2005; Rzedowski, 2006). Therefore, Hartweg's pines are distributed in almost all high mountain areas and peaks of Mexico, and they tend to form large monospecific stands (Musalem and Solís, 2000).

The main biotic agents that impact *Pinus hartwegii* growth are intraspecific and interspecific competition (Zepeda and Villarreal, 1987; Santillán, 1991; Geils and Hawksworth, 2002; Kunstler *et al.*, 2012), seed and cone predation by rodents (Musalem and Solís, 2002), and forest diseases (Musalem and Solís, 2002; Cibrián *et al.*, 2007). Among the principal forest diseases on *P. hartwegii* are enlisted insects, such as the Scotylid bark beetles, Torymidae wasps and Pyralidae moths, fungi (such as *Ganoderma* spp., *Poliporus* spp. and *Amillaria* spp.), and dwarf mistletoes (Musalem and Solís, 2002; Cibrián *et al.*, 2007).

Dwarf mistletoes (*Arceuthobium* spp., Viscaceae) are hemiparasitic plants and one of the most relevant disease causing agents in pines of the North American temperate forests (Shaw *et al.*, 2008; Mathiasen *et al.*, 2008). These parasitic plants are of ecological importance because they play a key role by providing resources, such as shelter and food, to different animal species enhancing community diversity (Watson and Herring, 2012; Chávez-Salcedo, 2013); moreover, they are of economic importance because their infection causes a reduction in growth and fitness in the host trees leading to a major forest product loss (Hawksworth and Wiens, 1996; Heide-Jorgensen, 2008). In Mexico, there is an annual loss of $2.0 \times 10^6$ $m^3$ of roundwood (Vázquez, 1993), whereas the loss in Western USA and Canada has been estimated as $11.3 \times 10^6$ $m^3$ and $3.8 \times 10^6$ $m^3$, respectively (Heide-Jorgensen, 2008).

The stand structure is strongly associated with dwarf mistletoe dynamics, where it has been shown that the crown volume and size of the dominant cohort decreases with infection intensity (Shaw *et al.*, 2005; Agne *et al.*, 2014).

These hemiparasitic plants form a complex root-like structure, called haustoriom, which is the organ of contact with the hosts' xylem and phloem (Hawksworth *et al.*, 2002). Through this connection, mistletoes take mineral nutrients, water and, although they have a photosynthetic capacity, most of their organic nutrients (Press, 1995). The latter have important effects on host performance, causing decreased growth, branch and stem deformations, reduced water use efficiency, decreased photosynthetic capacity, decreased fecundity and, with severe infection, death of the host (Geils and Hawksworth, 2002; Meinzer *et al.*, 2004; Mathiasen *et al.*, 2008). The impact can go from negligible to severe, depending on the level of the infection and the development status and vigor of the host (Musselman and Press, 1995). Some studies report that the effect on the hosts' growth is unnoticeable until the infection is severe (Hawksworth and Wiens, 1996; Geils and Hawksworth, 2002; Shaw *et al.*, 2008).

A decrease in the growth of the host has been recorded for different morphometric variables: diameter at breast height (dbh), tree height, volume, and basal area (Hawksworth and Wiens, 1996; Geils and Hawksworth, 2002; Shaw *et al.*, 2008). Andrade and Cibrián (1980) report a reduction of 19% and 29% in dbh and height, respectively, in *P. hartwegii* individuals parasitized by *Arceuthobium* spp. compared with healthy individuals. In other conifers, the reduction in parasitized individuals' dbh due to different dwarf mistletoe species ranges from 2% to 56%, where growth decrease is non-linearly related to infection class; that is, slight reduction is produced with light infection, but there is a threshold of severe infection after which reduction increases rapidly (Hawksworth and Wiens, 1996; Geils and Hawksworth, 2002). Similar results have been reported for the hosts' volume and basal area (Hawksworth and Wiens, 1996; Madrigal *et al.*, 2007; Shaw *et al.*, 2008).

Hartweg's pines are not only of ecological importance but also of an economic one (Eguiluz, 1978; Hernández, 1985; Musalem and Solís, 2002). Forest diseases, such as dwarf mistletoes, lessen their health for which it is important to investigate their effect in order to include this last aspect for management and reforestation plans. Although the effect of dwarf mistletoes on host performance has been widely studied, the joint effect of different species parasitizing the same host tree has not been investigated. In Zoquiapan (Central Mexico), two species of dwarf mistletoe, *A. globosum* and *A. vaginatum*, coexist parasitizing *P. hartwegii* on the same areas and even on the same individual host, showing an aggregated pattern within the host (Queijeiro-Bolaños *et al.*, 2014). Both mistletoe species have a complex interaction within each other, as they compete for host resources; however, under particular circumstances, they also facilitate each other's colonization (Queijeiro-Bolaños *et al.*, unpub. data). The latter makes us think that the effect of these species parasitism may be different when just one or two species are infecting the host.

The objectives of this study were to gain knowledge of the following aspects: a) the isolated and the joint effect of the infestation by *A. globosum* and *A. vaginatum* on *P. hartwegii* growth, b) how the allometric relationship of height and diameter at breast height is modified by the infestation, and c) which host size is more susceptible to infection by each species.

## Materials and methods

### *Study area*

The study was conducted in the Zoquiapan portion of the Iztaccíhuatl Popocatépetl National Park, State of México. It is located on the East Central part of the Trans-Mexican Volcanic Belt and comprises the main part of the Sierra Nevada (DOF, 2013). The study site was located at one side of the Southern slope of the Papayo Hill (19°18’ 08.4’’ N, 98° 42’ 10.7’’ W, 3420 m a.s.l.). The climate is temperate sub-humid with summer rains, mean annual temperature is 9.8°C (range: 1.3–18.3°C), and annual rainfall is 941 mm, with duration of the rainy season being June to September (SMN, 2013). Vegetation is classified as high mountain temperate forest, dominated by large extensions of *P. hartwegii* stands (Arriaga *et al*., 2002); other arboreal species present are *P. montezumae*, *P. ayacahuite*, *P. leiophylla*, *P. pseudostrobus*, *Abies religiosa*, *Cupressus lusitanica*, *Alnus jorullensis*, *Quercus crassipes*, *Q. rugosa*, and *Q. laurina*. Tussocky grasses, such as *Mulhenbergia macroura*, *M. quadridentata*, *Calamagrostis tolucensis*, and *Festuca tolucensis,* are the most frequent and conspicuous plant species on the understory (Obieta and Sarukhán, 1981; DOF, 2013).

*Study species.*

Hartwegs' pine or Mexican mountain pine, *Pinus hartwegii* (Lindl.), according to Rzedowski and Rzedowski (2005) and Musalem and Solís (2000), is typical of Mexican mountain ranges on altitudes from 2600 m to 4200 m, being most frequent on the Sierra Nevada region. It is a tree of 15–30 m in height and up to 75 cm dbh. The bark is thick, rough and scaly, and dark brown to gray in color. Branchlets are stiff, curving upwards with persistent leaf bases. Needles in fascicles are presented in groups of three, although sometimes five, of 6–18 cm length. Cones are grouped in two-six, and are obliquely ovoid, 7–14 cm, and reddish to almost black in color. The seeds are brown, 5–8 mm long, often having black spots, and wings of 12 × 20 mm. Generally, it can be distributed in monotypic stands, but in its lower altitudinal range it can be found coexisting with other trees, such as *Abies religiosa* and *Alnus jorullensis*.

In Zoquiapan, *P. hartwegii* is parasitized by *Arceuthobium globosum* subsp. *grandicaule* Hawks. and Wiens and *A. vaginatum* subsp. *vaginatum* (Mexican dwarf mistletoe), which is the zone where the three species converge (Hawksworth and Wiens, 1996; GD, 2013). The two mistletoe species have similar features: dioecious plants, with sexual dimorphism; anemophilous pollination and ballistochoric dispersal; and seven host species in common (*Pinus hartwegii*, *P. durangensis*, *P. lawsoni*, *P. montezumae*, *P. patula*, *P. pseudostrobus*, and *P. rudis*). *Arceuthobium globosum* is 18–70 cm tall with yellow-greenish shoots; it is distributed from Central Mexico to Guatemala. *Arceuthobium vaginatum* is 20–55 cm tall with brown-blackish shoots; tt is distributed from Northern to Southern Mexico (Hawksworth and Wiens, 1996; Cibrián *et al.*, 2007).

*Sampling and data analysis.*

In a 1.1 ha monotypic stand, we selected pine trees >2 m and 2.5 cm of diameter at breast height, because smaller trees are rarely infected by dwarf mistletoe (<2 %; Hernández-Benítez *et al.*, 2005). The stand has an average of 55.9% of trees infected by *A. globosum* and 22.9% by *A. vaginatum* (Queijeiro-Bolaños *et al.*, 2014). A total of 161 pines of different size and infection condition (i.e., pines infected by *A. globosum*, *A. vaginatum*, both species, or neither) were selected. From November 2008 to November 2011, we measured diameter at breast height (dbh), tree height, and average crown spread for each individual, every six months. The average crown spread was obtained by measuring the longest extent of the crown and the longest cross-extent, and then averaging the two measures (Blozan, 2004). The height was estimated by calculating the angle (α) with a clinometer from the observer to the tip of the tree, and then the distance (d) from the observer to the tree. The height was estimated by using the formula $h = d \times tan(\alpha)$.

We also measured the infection intensity with a modified dwarf mistletoe rating system (MDMR), based on Hawksworth's method (Hawksworth, 1977). In our system, the tree was vertically divided into thirds, and each third was rated into one of the following classes: 0, no infection; 1, sprout or hypertrophy; 2, less than 20% of branches infected; 3, 21 to 30%; 4, 31–50%; 5, 51–70%; and 6, more than 71%. The three thirds were summed for each individual, so the scale went from 0 to 18.

To evaluate the isolated and the joint effect of the dwarf mistletoe infection on *Pinus hartwegii* growth rate, we first tested with repeated measures ANOVA (Zar, 2010) whether there was a significant change in dbh, height, and crown spread over the three years. Because only dbh showed a significant change (Appendix), we computed the pines' annual relative growth rate (RGR) using dbh. We first analyzed separately, if there were significant differences between the infecting species (i.e., both species, *A. globosum*, *A. vaginatum*, or none) on dbh RGR and initial dbh by one way ANOVA and on MDMR by Kruskal–Wallis test. We then performed a linear model including, as main effects, the infection severity (MDMR) and mistletoe species (none, *A. globosum* alone, *A. vaginatum* alone, or both coexisting mistletoes), and pines' initial dbh as a covariate, as it was found to be related to RGR (See Results section). We used the records of MDMR and infecting species at the beginning of the study, because RGR for the three-year sampling must be a response of the previous conditions of parasitism, and three years is a short time to notice a significant change on MDMR or species present (linear analysis of RGR with final MDMR and species, and also with the average MDMR and species can be found in the Appendix).

To determine whether the relationship between height and dbh was modified by the infection, we fitted the Chapman-Richards model (Peng *et al.*, 2001) with non-linear least squares method (*nls*) for the following four types of infection: pines parasitized by *A. globosum*, *A. vaginatum*, and both, or neither. Chapman-Richards is a non-linear function that describes the changes in the relative dimensions of different parts of the pines, in this case height and dbh. The simplest form of the equation is as follows:

$$Y = \alpha(1 - e^{-\beta x})^{\gamma} \qquad (1)$$

where $Y$ refers to the tree height, $X$ is dbh, and $\alpha$, $\beta$, and $\gamma$ are the parameters of the asymptote, the rate and the form (Richards, 1959; Chapman, 1961). Peng *et al.* (2001) added dbh (1.3 m) to the function, to ensure that the total height equals 1.3 m when dbh is 0:

$$Y = 1.3 + \alpha(1 - e^{-\beta x})^{\gamma} \qquad (2)$$

The parameters of the four fitted curves were tested against a null model where the data sets of each condition (none, both species, *A. globosum*, or *A. vaginatum*) shared global parameters (i.e., a single curve for all the data), and tested with an extra sum of squares F test (Motulsky and Cristopoulos, 2003) with Prism 6 (GraphPad Software, 2014).

In order to know which host size is more susceptible to infection, either by one species or both, we prepared 7 × 4 contingency tables, with seven size categories based on crown spread (height and dbh were non-significant; hence it is not shown in the results) and four infection conditions (i.e., infecting species: no infection, *A. globosum*, *A. vaginatum*, or both species). Moreover, we prepared a 7 × 4 × 2 contingency table with the same seven size classes, four levels of infection [based on MDMR values: none, light (rates 1, 2, and 3), moderate (4, 5, and 6), and severe (7, 8, 9, and 10, because rates 11 to 18 were not found)], and two dwarf mistletoe species. For each contingency table, we performed a generalized linear model (glm) with Poisson error distribution and log link function (Crawley, 2007).

For tridimensional contingency tables, we first fitted the saturated model, where the main effects and the two and three-way interactions were present. Later, we compared it with models lacking the three and two-way interactions with a log-likelihood test (Crawley, 2007). Thereafter, we verified trough Pearson residuals whose categories were significant.

All analyses were performed using the *stats* package, except for Pearson residual analysis, which was performed using the *vcd* package (Meyer *et al.*, 2006, 2012; Zeileis *et al.*, 2007) both of the R software (R Development Core Team, 2012).

## Results

The relative growth rate (RGR) of *Pinus hartwegii* was strongly correlated with the pines initial dbh, where there was a clear tendency of a decrease in RGR as the trees become larger ($r^2 = 0.2$, $P < 0.001$; Figure 1). There were significant differences according to the parasitizing species (both, *A. globosum*, *A. vaginatum*, or none), on dbh RGR ($F_{(3,123)} = 2.3$, $P < 0.0001$; Figure 2A), MDRM ($\chi^2 = 32.46$, d.f. = 2, $P < 0.0001$; Figure 2B), and initial dbh ($F_{(3,126)} = 10.068$, $P < 0.0001$; Figure 2C). Trees infected by *A. vaginatum* showed larger RGR, followed by none-infected trees and trees with *A. globosum*, whereas trees with both mistletoes did not differ with those infected with *A. globossum* or uninfected trees (Figure 2A). On the other hand, trees infected by both species had a larger MDMR than each dwarf mistletoe alone (Figure 2B). In addition, the initial dbh of trees with both species was significantly larger than that of trees with *A. vaginatum* alone and the non-infested ones, but did not differ from trees with *A. globosum* alone (Figure 2C). Because we knew that the results of RGR could be misled by the influence of the initial size of the tree, we performed a linear model that included the effect of dbh as a covariate; only the initial dbh turned out to be significant (Table 1). That is, neither the slope nor the intercepts of RGR against initial dbh vary with the infecting species (Table 2, Figure 3). We observed that the RGR of uninfected trees or those infected by both or one species follow the same pattern of decrease with the size described before (Figure 1), suggesting no effect of the parasites.

The allometric relation between tree height and dbh was different for each type of infection (none, both species, *A. globosum*, or *A. vaginatum*; $F_{9,1291} = 2.072$, $P = 0.029$; Figure 4). After fitting the Chapman-Richards model (eq. 2) and plotting the predicted values and their confidence intervals (Figure 4), some patterns could be distinguished. For dbh < 30 cm, there are no clear differences between the infection conditions because the confidence intervals of the four curves overlap; however, on trees > 30 cm dbh, the curves start separating, although their intervals are still overlapped. On trees between 30 and 40 cm dbh, the curve of “both species” begins to look lower than the rest. Between 40 and 60 cm, it is noticeable that the curves of “none” and “*A. vaginatum”* completely overlap, showing no differences in height at those dbh sizes; however, the height of “both species” is considerably lower than the latter two, barely overlapping with those two intervals. *Arceuthobium globosum* showed a great variation; although the curve seems to be below the “none” and “*A. vaginatum*” and above both, the confidence interval is too wide to conclude any difference from the other curves.

We tested which crown spread classes were more frequently infected; dbh and height classes were non-significant, hence the results are not reported. In addition, crown spread is a better descriptor for mistletoe presence because it represents the seed “landing” area. There is a significant association between crown spread and infection type ($\chi2$ = 45.41, d.f. = 18, *P* = 0.0003), but only *A. globosum* showed a significant difference between the observed frequencies and that expected by chance in any crown spread size classes (Figure 5), where trees <2 m are more frequently infected than those expected by this species and trees of 2–3 m and 6.4 and 7.5 had a lower frequency. On the other hand, it is worth to mention that the MDMR increased its magnitude with crown spread size (i.e., the wider the crown, the more severe the infection would be; Figure 5).

The results of the three dimensional contingency table showed that the three-way interaction between crown spread classes, infection levels (none, light, moderate, and severe), and infecting mistletoe species (*A. globosum* and *A. vaginatum*) was non-significant (deviance = 1.19, d.f. = 3, *n.s.*); nevertheless, the following two–way interactions were significant: infection × crown spread class, species × infection, and species × dbh class (Table A6 on Appendix). According to Pearsons' standardized residuals, there are some differences between infection level and crown spread ($\chi^2$ = 58.355, d.f. = 18, $P < 0.0001$), where categories moderate or severe of *A. globosum* have, in general, higher observed frequency than expected by chance in trees greater than 1.96 m (Figure 6A), whereas *A. vaginatum* light severity is significantly larger only on trees 1.96–3 m, and underrepresented on trees smaller than 1.96 m (Figure 6B). *Arceuthobium vaginatum* had clearly a lower frequency on *P. hartwegii*, and, although non-significantly, has a greater severity on larger trees.

## Discussion

Our results showed that there is no significant effect of the dwarf mistletoe species, either alone or together, on *Pinus hartwegii* dbh RGR; nevertheless, there is evidence that dbh-height allometric relations are different depending on the infecting condition (either *Arceuthobium globosum*, *A: vaginatum*, both species, or none). In general, RGR for the four infecting categories follows the same decreasing pattern with dbh. This means that there is no difference between the infected trees (whether these have one or two species) and uninfected ones. The affection of dwarf mistletoes on the hosts' growth has been a common subject of research [see Geils and Hawksworth (2002) for a summary of works]. However, Geils and Hawksworth (2002) acknowledged that only few generalizations can be made for this parasitic genus, where the effect may depend on a mixture of the following factors: i) host-parasite species combination, where some mistletoe species are more harmful than others and some hosts show a higher resistance to infection (Tinnin, 1981; Hawksworth and Wiens, 1996); ii) severity of infection, because the effect can go from negligible with low intensity to lethal with a large load of parasites (Musselman and Press, 1995; Shaw *et al.*, 2008); iii) host vigor and developmental stage (Tinnin, 1981; Hawksworth and Wiens, 1996); and iv) density-dependent mechanisms and the activity of secondary parasites (Tinnin, 1981).

In the present case, contrary with what has been stated by other authors (Andrade and Cibrián, 1980 and Madrigal *et al.*, 2007), it seems that these species, and their combination, are not harmful to pines growth, because there is plenty of evidence that growth is arrested only by age (represented as initial dbh); RGR varies with the ontogenetic condition of the individuals, because there is a decrease in growth rates as the plants increase in biomass (Paine *et al.*, 2012), and this should be considered when modeling plant growth rates. The influence of the initial dbh on some growth measurement has been treated by other authors; for example, Shaw *et al.* (2008) found that the initial dbh of *Pseudotsuga menziesii*, infected with *A. tsugense*, explained a considerable amount of the variation in the basal area growth of infected trees.

It is worth mentioning that most studies reporting on the growth effect were conducted on even age (or even sized) stands, which provide a control of some variables, such as initial size, but are hardly extrapolated to natural conditions or uneven age stands. We are presenting evidence that patterns drawn for heterogeneous stands can be fairly different from homogeneous stands; moreover, we can argue that hosts growth on a stand with a heterogeneous size structure is not severely affected by dwarf mistletoes, indicating the convenience of maintaining forest heterogeneity.

Although no significant effect was shown on RGR, the allometric curves showed some interesting patterns. In general, trees infected with *A. globosum* and both species were shorter at dbhs >30 cm, compared with uninfected trees and those infected with *A.*

*vaginatum*. Although we cannot be certain about the history of the development of these trees and what factors could have affected their growth in the past, we can think of it as a consequence of the presence of mistletoe. Dwarf mistletoes can cause an abnormal biomass accumulation, provoking thicker boles due to hypertrophy or more voluminous crowns due to deformations such as witches' brooms (Hawksworth and Wiens, 1996). Moreover, the infection of dwarf mistletoes can modify stand structure, where the dominant and co-dominant cohort of pines tend to be shorter than uninfected ones (Agne *et al.*, 2014). In this pine species, infection is fairly common over the stem and could cause trees to still gain bole thickness as a response to infection but not height compared with non-infested trees. As expected, the lesser height was notorious for pines infected with both species and *A. globosum*; however, trees infected with *A. vaginatum* showed the same pattern than uninfected trees, demonstrating that the effect of this species could be null when it refers to allometric relationships. It is noteworthy that no differences can be depicted on trees <30 cm dbh, and this is probably because younger individuals have a greater increment in biomass (Paine *et al.*, 2012), and also because the infection is less severe on these individuals (Figure 5). A non-linear effect has been shown before, where the effect of dwarf mistletoes is not noticeable until the infection is severe (Geils and Hawksworth, 2002; Shaw *et al.*, 2008), and we had a bias toward smaller trees with light or moderate infection, but that is a reflection of the natural stand structure.

With respect to crown spread size susceptibility, some patterns agree with what was expected: most of the uninfected trees were the smallest ones and MDMR increased with tree size (Shaw *et al.*, 2005). Young trees are rarely parasitized because they cannot provide enough resources to the parasite and the consequences for them are mostly lethal (Press, 1995); however, a larger tree represents a better resource because it has a larger surface for seed reception (Arriaga *et al*., 1988; Hernández-Benítez *et al*., 2005) and can bear a larger load of parasites declining in health but not in mortality (Musselman and Press, 1995; Hawksworth and Wiens, 1996). From the results, it can be said that trees with a crown spread smaller than 1.96 m were more frequently infected by *A. globosum* (Figure 5), but this species is more severely on larger trees (Figure 6); whereas, the categories *A. vaginatum* or both species do not seem to be more or less frequent on any size category (Figure 5), but *A. vaginatum* showed lighter infections on smaller trees and greater infections on larger trees (although this last was not significant, Figure 6). However, infection of trees with *A. vaginatum* was a lot less frequent than that with *A. globosum*, suggesting that *A. vaginatum* might be less harmful. Forest canopy, here represented as crown spread, represents an important resource for mistletoes because it is not only the place for establishment but it also has the suitable conditions for these plants to perform adequately (Reid *et al*., 1995; Shaw, 2004). *Arceuthobium vaginatum* is a smaller plant with apparently lesser photosynthetic requirements than *A. globosum* (Calvin *et al*., 1984; Hawksworth and Wiens, 1996); thus, *A. globosum* could be gaining more benefit from larger trees, hence being more severe within these sizes.

Our results showed that these parasites are not significantly harmful for host growth, stating the importance of maintaining forest heterogeneity. This scenario where two dwarf mistletoes are coexisting is rare (Hawksworth and Wiens, 1996; Queijeiro-Bolaños *et al*., 2014); thus, it raises the question about how resources are used and shared among the two species. In addition, although these parasites may not be arresting pine growth in a noticeable way, we cannot state that these have no effect on forest industry activities, such as poor wood quality and lower roundwood production (Andrade and Cibrián, 1980; Madrigal *et al*., 2007; Logan *et al*., 2013).

## Conclusions

Our results suggest than *Arceuthobium globosum* and *A. vaginatum* do not have a joint effect on *Pinus hartwegii* dbh RGR. These lead us to think that the infection by these two parasites on this area is not detrimental for the host populations. Uneven-aged forests represent a more complex scenario where the severity of infection is commonly greater because there are more spaces to colonize (Shaw *et al.*, 2008). Nevertheless, the latter has been reported for single-species stands with the infection of only one mistletoe species; there are two species present in this area using the same host as a resource, and our results suggest that it may be helpful to maintain the complexity of an uneven-age forest to avoid the dominance of only one mistletoe species, which could be more harmful for the host.

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Table 1. Analysis of covariance of the effect of parasitizing species, MDMR, and initial dbh on pines RGR.

| | Df | SS | MS | *F* | *P* |
|---|---|---|---|---|---|
| MDMR | 1 | 0.029 | 0.029 | 2.628 | 0.108 |
| Initial dbh | 1 | 0.349 | 0.349 | 31.778 | **<0.0001** |
| Species | 3 | 0.049 | 0.016 | 1.487 | 0.222 |
| MDRM × dbh | 1 | 0.009 | 0.009 | 0.784 | 0.378 |
| MDMR × Species | 2 | 0.010 | 0.005 | 0.453 | 0.637 |
| Species × dbh | 3 | 0.053 | 0.018 | 1.600 | 0.193 |
| Species × dbh × MDMR | 2 | 0.016 | 0.008 | 0.740 | 0.479 |
| Residuals | 121 | 1.328 | 0.011 | | |

Table 2. Summary of the parameters of each level of the factor *Species* on RGR in the model $RGR = \beta_0 + \beta_1\text{dbh}$. No significant differences were found.

| | $\beta_0$ | $\beta_1$ |
|---|---|---|
| *A. globosum* | 0.2197 | −0.0483 |
| *A. vaginatum* | 0.2667 | −0.0445 |
| both | 0.5611 | −0.1545 |
| None | 0.3910 | −0.1073 |

Figure 1. Relation of RGR and initial dbh.

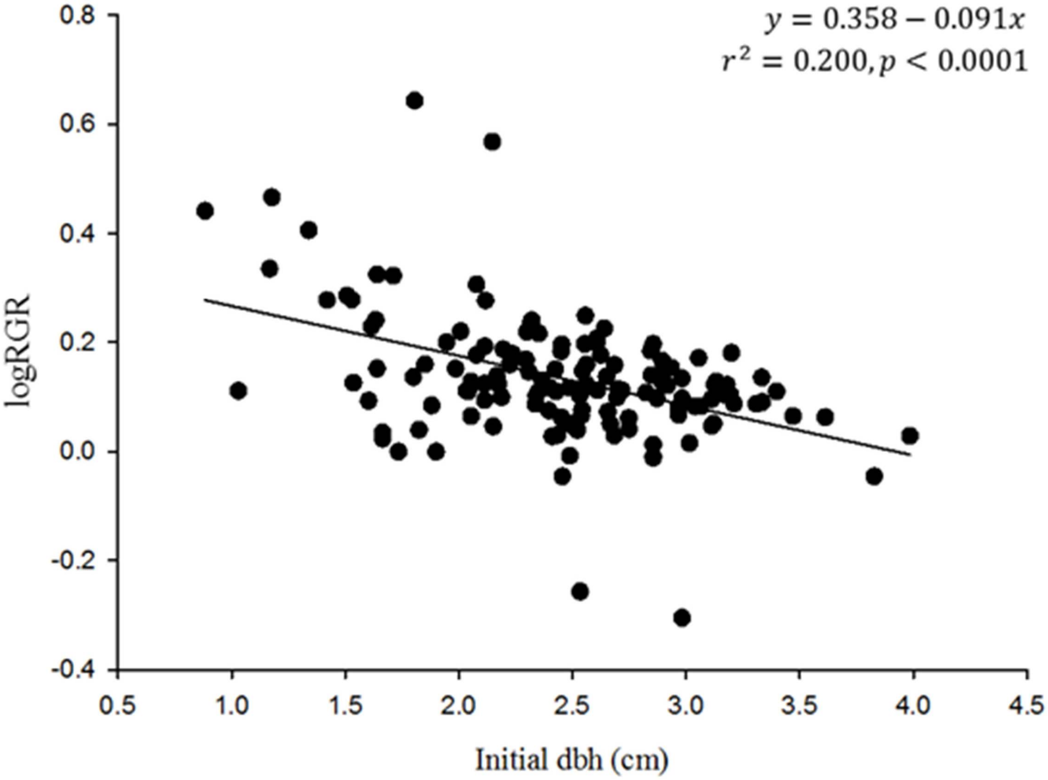


Figure 2. Separate effect of parasitizing species, *Arceuthobium globosum*, *A. vaginatum*, both species, or none, on the following aspects: A) RGR ($F_{3,\ 123} = 9.718$, $P < 0.0001$); B) mean MDRM ($F_{2,\ 87} = 26.305$, $P < 0.0001$), C) initial size ($F_{3,\ 126} = 13.649$, $P < 0.0001$). Letters above the boxes indicate significant differences according to Tukey’s HSD test.

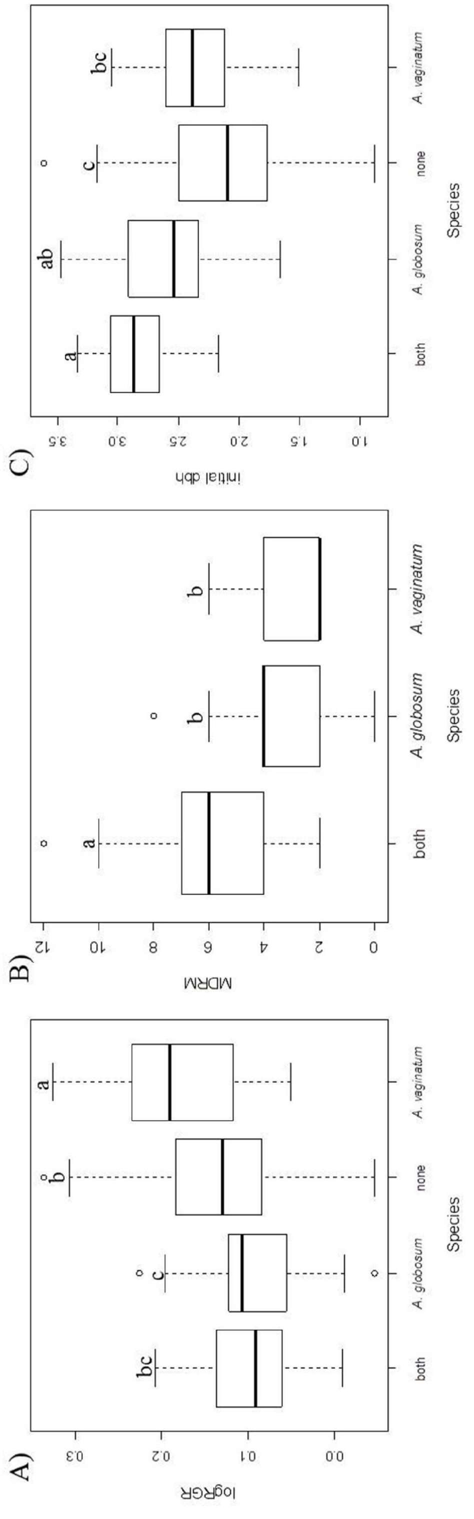


Figure 3. RGR with different initial dbh and different parasitizing species. *Arceuthobium globosum*: △ symbols and dashed line; *A. vaginatum*: × and dot-dash line; both species: ∘ and solid line; none: + and dotted line.

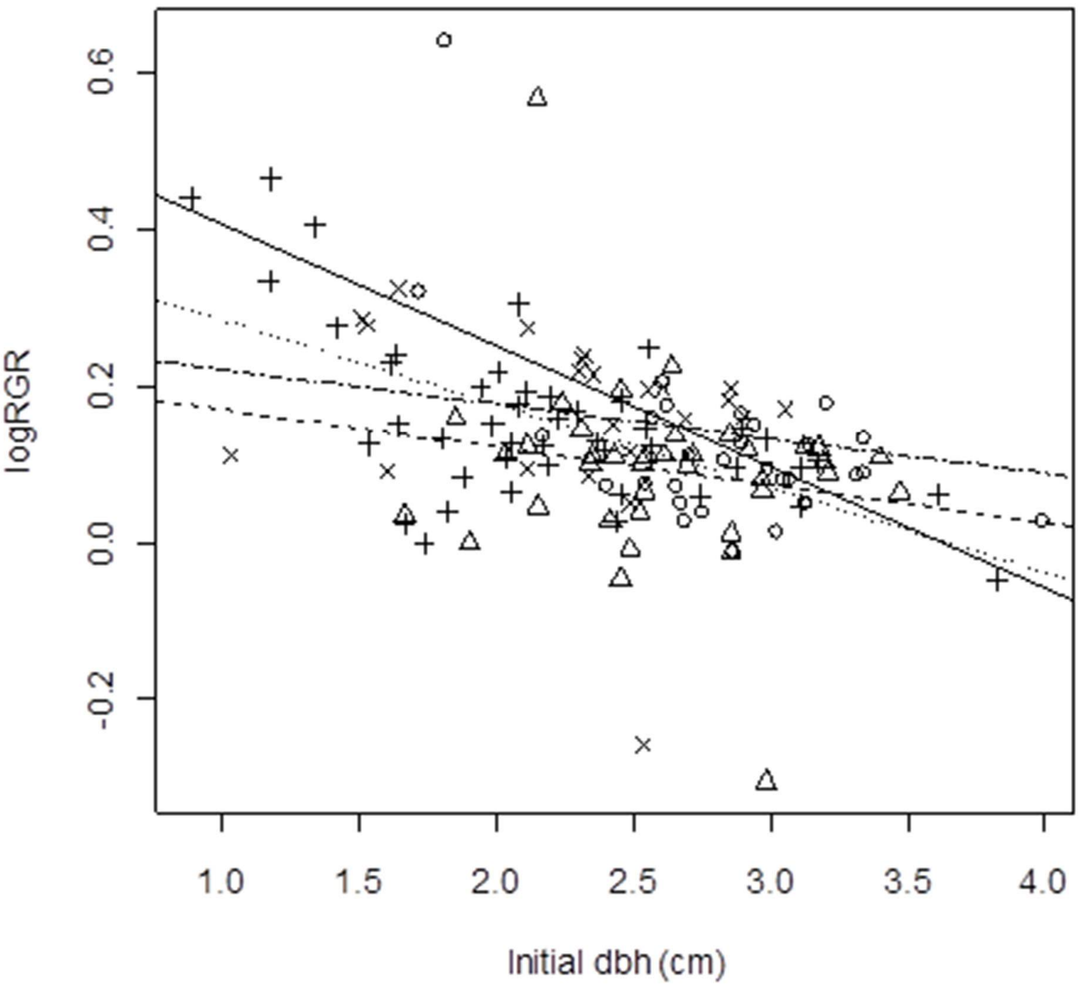


Figure 4. Allometric relation between *Pinus hartwegii* dbh and height. Dashed lines represent confidence intervals for each curve; *Arceuthobium globosum*: blue; *A. vaginatum*: orange; both species: red; none: green.

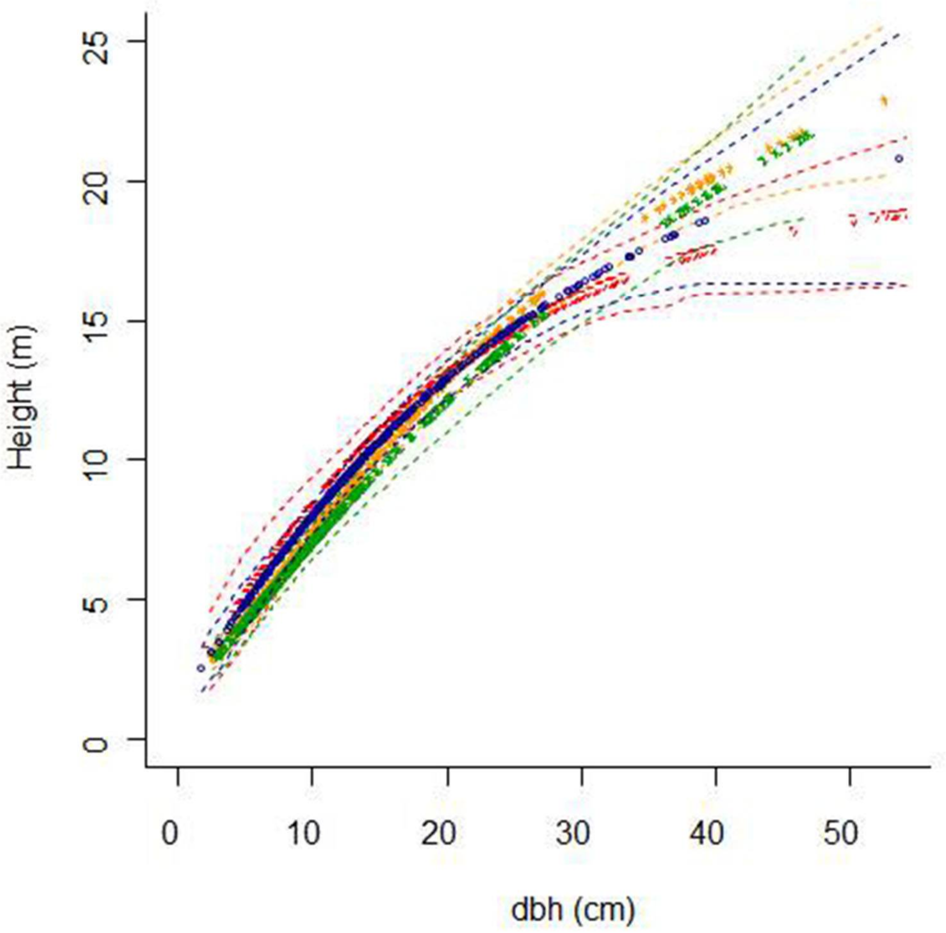


Figure 5. Number of pines on different crown classes ($\chi^2 = 45.421$, g.l. = 18, $P < 0.001$), parasitized by *Arceuthobium globosum*, *A. vaginatum*, both species, or none (left axis), and mean MDMR of *A. globosum* and *A. vaginatum* in this same classes (right axis). (+) symbol indicates a frequency higher than expected, whereas (−) indicates a frequency lower than expected.

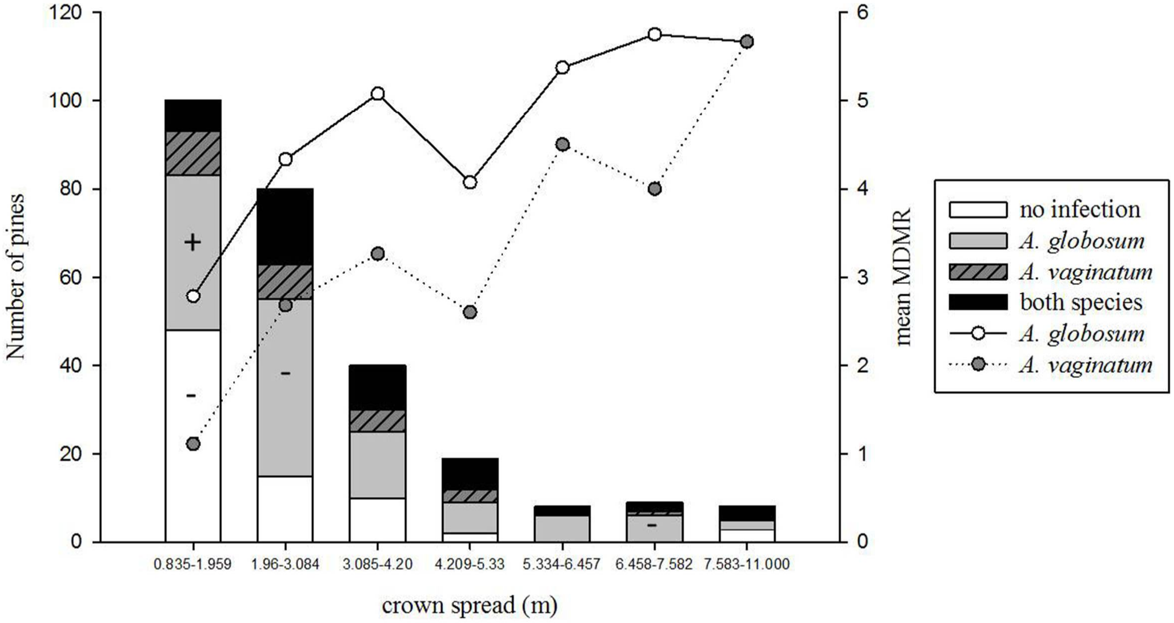
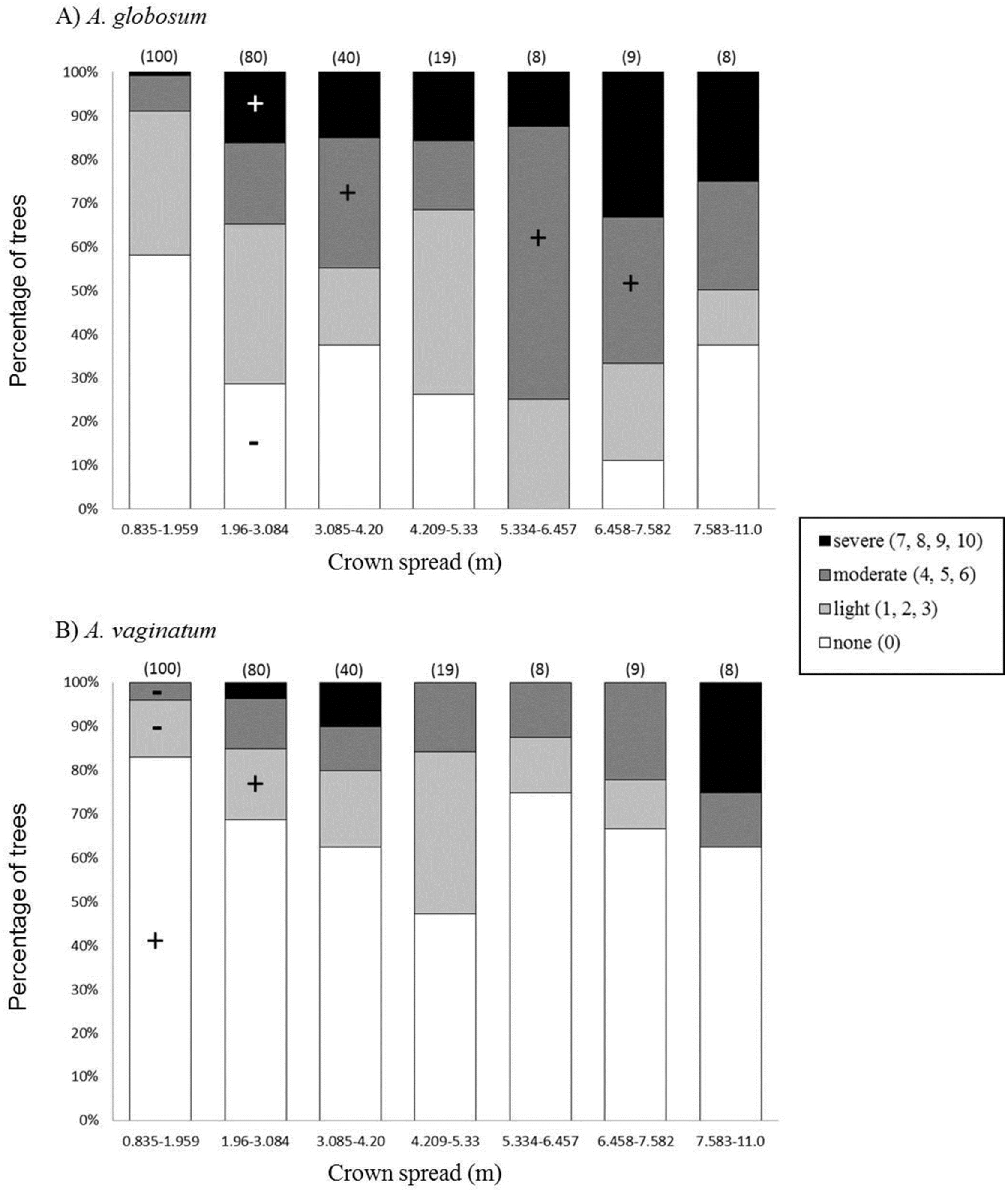


Figure 6. The percentage of *Pinus hartwegii* trees on different crown classes and their infection severity (none, light, moderate, or severe) of the following species: A) *Arceuthobium globosum* and B) *A. vaginatum*. (+) symbol indicates a frequency higher than expected, whereas (−) indicates a frequency lower than expected.



## Appendix

To test if there were any significant growth of pines dbh, height and crown spread, we tested the change in time of aforementioned variables with repeated measures ANOVA. Only dbh changed significantly with time; because of this result, we computed RGR only for dbh.

*Table A1. Repeated measures ANOVA of dbh (cm) in time.*

| | SS | Df | MS | *F* | *p* |
|---|---|---|---|---|---|
| Time (semesters) | 423.3 | 6 | 70.6 | 79.734 | **<0.001** |
| Error | 833.5 | 942 | 0.9 | | |

*Table A2. Repeated measures ANOVA of height (cm) in time.*

| | SS | df | MS | *F* | *p* |
|---|---|---|---|---|---|
| Time (semesters) | 51028 | 6 | 8504.6 | 1.924 | **0.074** |
| Error | 4242752 | 960 | 4419.5 | | |

*Table A3. Repeated measures ANOVA of crown spread (cm) in time.*

| | SS | df | MS | *F* | *P* |
|---|---|---|---|---|---|
| Time (semesters) | 1569.2 | 6 | 261.536 | 1.063 | **0.383** |
| Error | 171190.1 | 696 | 245.963 | | |

We considered that the three-year RGR is reflecting the results from the initial infection. Nevertheless, we also tested the effect of final infection (final records of MDMR and infecting species), as well as mean infection (mean MDMR and infecting species).The three analyses (initial MDRM, final MDMR and mean MDRM) showed that initial dbh is the main factor affecting RGR.

*Table A4. Summary of the effects of initial dbh and the different levels of final infecting species.*

| | Estimate | SE | *T* | *P* |
|---|---|---|---|---|
| Intercept | 0.399 | 0.046 | 8.574 | <0.0001 |
| Initial dbh | -0.097 | 0.016 | -6.106 | **<0.0001** |
| *A. globosum* | -0.048 | 0.023 | -2.046 | 0.043 |
| None | -0.042 | 0.027 | -1.559 | 0.121 |
| *A. vaginatum* | 0.017 | 0.030 | 0.573 | 0.568 |

*Table A5. Summary of the effects of initial dbh and the different levels of mean infecting species.*

| | Estimate | SE | *T* | *P* |
|---|---|---|---|---|
| Intercept | 0.205 | 0.025 | 8.189 | <0.0001 |

| | | | | |
|---|---|---|---|---|
| Initial dbh | -0.005 | 0.001 | -4.363 | **<0.0001** |
| *A. globosum* | -0.008 | 0.022 | -0.360 | 0.720 |
| None | -0.009 | 0.028 | -0.325 | 0.746 |
| *A. vaginatum* | 0.060 | 0.035 | 1.681 | 0.095 |

To test if two and three-way interaction on three dimensional contingency table were relevant to the model, we performed an ANOVA tests to compare the saturated model (with all possible interactions) against a model without the three-way interaction. Since these models didn't showed a significant difference, we kept with the simpler one, which we compared with different models without two-way interactions.

*Table A6. Models comparison for three dimensional contingency tables for crown spread.*

| Model 1 | Model 2 | Deviance | $p(>\|\chi^2\|)$ |
|---|---|---|---|
| Saturated (three and two-way interactions included) | Without three way-interaction | -0.94849 | 0.8137 |
| Withouth three-way interaction | Without infection×crown class | 39.502 | **<0.0001** |
| | Without species×infection | 58.54 | **<0.0001** |
| | Without species×crown class | 2.8898 | 0.08914 |

# DISCUSIÓN GENERAL

Existen numerosas evidencias del papel que juegan las interacciones bióticas, especialmente la competencia, en la coexistencia de las especies (Chesson, 2000) y su efecto sobre los distintos procesos demográficos de las poblaciones, como son el crecimiento y la colonización (algunos ejemplos recientes son los trabajos de Freckleton y Watkinson, 2001; Michalet *et al.*, 2006; y Martorell y Freckleton, 2014). Sin embargo, este tema no ha sido abordado para las plantas parásitas en general, ni en particular para los muérdagos. A pesar de que los muérdagos enanos son uno de los parásitos forestales más estudiados por el fuerte impacto que tienen en las actividades agroforestales (Mathiasen *et al.,* 2008), se han dejado de lado aspectos ecológicos importantes como las interacciones interespecíficas. Por lo tanto, el enfoque de este trabajo fue el de conocer cómo las interacciones interespecíficas afectan las poblaciones de dos especies de muérdago enano que comparten el mismo recurso limitante: el hospedero. Para esto, las interacciones fueron estudiadas desde tres perspectivas distintas: i) la dinámica poblacional de las dos especies en la escala de pinos parasitados dentro de un rodal (capítulo 2), ii) los patrones que presenta la infestación dentro de la zona de Zoquiapan (capítulo 3), y iii) el efecto que tienen las especies de muérdago enano, aisladas y en conjunto, sobre el crecimiento de su hospedero (capítulo 4). *Arceuthobium globosum* y *A. vaginatum* resultan un buen sistema de estudio para este propósito ya que, al contrario de la mayoría de las especies del género, presentan parasitismo dual (dos especies parásitas sobre un mismo individuo hospedero; Hawksworth y Wiens, 1996) en un sistema relativamente simple de una sola especie hospedera.

La dinámica poblacional de los muérdagos enanos está determinada por las interacciones interespecíficas y coincide con lo descrito para plantas autótrofas y algunos organismos parásitos invertebrados, ya que la coexistencia se logra por mecanismos estabilizadores y el signo (positivo o negativo) de la interacción depende de la etapa de desarrollo en las poblaciones (Holt y Dobson, 2006; Chesson, 2000; Martorell y Freckleton, 2014). Se presenta una fuerte autorregulación de las poblaciones, por lo que el efecto competitivo interespecífico resulta poco intenso. Además, se presenta facilitación intragremio entre las dos especies de muérdago enano, lo que contribuye a que se cumpla con el criterio de invasibilidad (Turelli, 1978). Lo último lleva a la conclusión de que los rodales previamente infestados por una especie serán fácilmente invadidos por una segunda especie. La importancia demográfica de la facilitación o de la competencia depende de la etapa de desarrollo de los muérdagos, pues la facilitación es importante para el proceso de colonización de nuevos individuos y la competencia influye en el crecimiento poblacional. Este cambio en el signo de las interacciones ha sido mostrado previamente en comunidades de plantas autótrofas, en las que resultan más importantes las interacciones positivas al mejorar las condiciones para el establecimiento de nuevos individuos (Miriti, 2006; Martorell y Freckleton, 2014). Esto puede implicar que al momento de colonizar nuevos árboles, los muérdagos tienen una mejor probabilidad de lograrlo cuando el hospedero ya ha sido parasitado por la otra especie. Sin embargo, es necesario mencionar que se desconoce el mecanismo por el cual actúa la facilitación.

Adicionalmente, la importancia demográfica de las interacciones depende de la estructura del rodal, donde en ambientes más heterogéneos la competencia es importante, mientras que en ambientes homogéneos lo es la facilitación. Esto coincide con otros estudios (Casper *et al.*, 2000; Hutchings *et al.*, 2003), en donde se encuentra que la heterogeneidad de los recursos (en este caso, representados por la densidad y distintos tamaños de hospederos) ocasiona que los individuos se agreguen en los puntos de alta disponibilidad de recursos y, por tanto, se intensifiquen las interacciones negativas.

A pesar de la complejidad en el cambio del signo de las interacciones mostrado en las poblaciones de muérdago enano, en un estudio realizado a una escala espacial más amplia donde se revisaron 75 parcelas de 3300 $m^2$ cada una, se pudo observar que las incidencias (porcentaje de árboles infestados) de las dos especies están asociadas de manera negativa (capítulo 3). A esta escala se puede ver la dominancia de *A. vaginatum*, lo cual a la escala de árbol no fue posible de detectar. En este contexto, queda claro que cuando las dos especies coexisten en los distintos sitios presentan una menor severidad que en los sitios donde no lo hacen, denotando un efecto negativo. Esto muestra que el resultado de las interacciones varía según la escala y el detalle con el que son estudiadas, ya que cuando se modelaron en la escala de árboles dentro de un solo rodal se pudo ver la complejidad de las interacciones positivas y negativas. En cambio, en una escala más amplia se observó que las interacciones negativas rigen los procesos de estas poblaciones. La habilidad competitiva que tiene cada especie, así como la probabilidad de colonizar nuevos espacios, puede cambiar según el sitio en el que los muérdagos se encuentren (Kneitel y Chase, 2003). De acuerdo con Danielson (1991), a nivel paisaje las interacciones se ven afectadas por las condiciones de los distintos parches, además de que hay efectos de selección de hábitat de las especies, que comprende la ubicación de sitios que puedan ser colonizados y la presencia de otras interacciones. Se ha visto que las especies dentro de las metacomunidades pueden hacer un uso diferencial de los recursos, tener diferente susceptibilidad a la depredación y tener una adecuación distinta según las condiciones bióticas y abióticas de los distintos sitios donde se encuentran (Tilman, 1982; Leibold, 1996; Kneitel y Chase, 2003).

Por otro lado, se encontró que en los rodales donde dominó *A. vaginatum* contenían en su mayoría árboles adultos, sin presentar la complejidad en la estructura de tamaños que se presentó en la zona del Papayo (que fue el rodal utilizado para la modelación de las interacciones).

Las dos especies de muérdago muestran patrones distintos de agregación, tal como es esperado para los muérdagos (Aukema, 2003). En el sistema estudiado, las dos especies se encuentran agregadas a nivel de árbol pero sólo *A. globosum* está agregada entre parcelas, restringiéndose entonces a pocos sitios, lo cual puede ser producto de la reducción del traslape de las áreas de coexistencia o simplemente del efecto del medio abiótico sobre su desempeño. La agregación intraespecífica puede deberse a la dispersión limitada (Stoll y Prati, 2001); sin embargo, esta agregación previene la frecuencia de superposición de áreas de ocupación, haciendo que sea más frecuente e intensa la competencia intraespecífica, por lo cual la agregación ha sido considerada como un mecanismo de coexistencia (Stoll y Prati, 2001). Los muérdagos enanos presentan comúnmente autoinfección dentro de un mismo árbol (Shaw *et al.*, 2005); además, la dispersión hacia otros árboles es lenta y la intensificación dentro de un mismo árbol rápida (Seem, 1984), lo cual concuerda con la evidencia de que la competencia intraespecífica es intensa, ya que hay una alta probabilidad de crecimiento en un mismo árbol

Por otro lado, desde la perspectiva del hospedero, no se encontró evidencia de que los muérdagos redujeran significativamente la TRC de los pinos (capitulo 4). El factor que influye principalmente en la reducción del crecimiento es el tamaño inicial de los árboles, ya que las plantas en general experimentan un decremento en las tasas de crecimiento con su desarrollo ontogénico (Paine *et al.*, 2012). Este resultado es interesante ya que contrasta con otros estudios que reportan que el muérdago enano tiene un efecto negativo fuerte sobre el crecimiento de sus hospederos (Hawksworth y Wiens, 1996); pero, en este caso al tratarse de un rodal heterogéneo sólo se refleja el efecto del dap sobre el crecimiento de los árboles. Idealmente los árboles tendrían que ser de la misma edad para distinguir el efecto, y podemos ver que en un rodal con una estructura de tamaños natural (poco manipulado), el muérdago aparentemente no causa un daño perceptible a sus hospederos. Se debe tomar en cuenta que los muérdagos son factores de regulación poblacional de los pinos (Musalem y Solís, 2000), y que en la mayor parte de los estudios donde se ha cuantificado la reducción en el crecimiento es en rodales coetáneos para aprovechamiento forestal. Sin embargo, los resultados muestran que el muérdago tiene aparentemente un efecto sobre la forma de los árboles. Se ha reportado que el cambio en la arquitectura del hospedero puede tener consecuencias a nivel fisiológico, como la eficiencia de uso de agua (Meinzer *et al.*, 2004), pero también puede afectar sus asociaciones bióticas, ya que se ha visto que algunos animales encuentran refugio en las estructuras modificadas por los muérdagos (Watson, 2001).

Cabe señalar que de acuerdo con los modelos de virulencia de parásitos (Frank, 1996), puede ocurrir exclusión competitiva por parte de la especie con mayor virulencia, afectando en gran medida al hospedero y a los individuos conespecíficos (Frank, 1996). En este caso el efecto de las dos especies, ya sea aislado o en conjunto, sobre la reducción del crecimiento del hospedero es imperceptible, indicando una baja “virulencia”, lo que puede estar permitiendo la coexistencia.

En conclusión, la dinámica poblacional de los muérdagos enanos tienen una fuerte influencia de las interacciones intra e interespecíficas, donde se llega a una coexistencia estable por mecanismos estabilizadores (Chesson, 2000). Es importante conocer la dinámica de las poblaciones de los organismos parásitos, en este caso de los muérdagos, ya que esto nos permite conocer más sobre la biología de estos organismos y cómo cambian sus poblaciones en el tiempo; esto último es relevante, ya que nos deja saber si estos organismos pueden colonizar nuevos espacios o incrementar su abundancia, lo cual puede ser incorporado a los planes de manejo. A partir de esto, se tienen interesantes perspectivas expuestas en cada uno de los capítulos, donde se resalta que es necesario continuar con los trabajos de investigación del papel de las interacciones interespecíficas sobre los muérdagos enanos, así como otras plantas parásitas, ya que el efecto que tengan va a depender del tipo de parasitismo. Más aun, se sugiere que es conveniente mantener la heterogeneidad del hábitat a través de rodales coetáneos, pues un ambiente heterogéneo favorece la coexistencia de las especies, ya que proporciona más micro ambientes y nichos disponibles (Tilman, 1982). Estos nichos espaciales y/o temporales son un requisito para mantener la coexistencia de las especies (Chesson, 2000), y en este caso, prevenir la facilitación e invasión de nuevos sitios.

El estudio de las interacciones entre plantas parásitas, como los muérdagos enanos, ha sido un tema no explorado previamente; a pesar de todas las particularidades que presentan este grupo de plantas, su estudio nos permite confirmar la teoría existente sobre el papel de las interacciones en la dinámica poblacional de las plantas y como son los patrones de coexistencia. Esto es relevante si se quiere comprender como se dispersa o intensifica la infestación de estas plantas sobre recursos forestales importantes. Más aun, el estudio de las interacciones y el comprender cómo es el desarrollo de los distintos procesos demográficos nos permite conocer si las poblaciones se mantienen estables o si se puede esperar una mayor probabilidad de invasión en rodales forestales.

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